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

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(Numbers given in the summary refer to certain key figures in the text which facilitate understanding.)

An account is given of the functional morphology, ecology, habits and feeding mechanisms, of a representative series of anomopod cladocerans of the family Chydoridae, embracing some 22 species belonging to 15 genera. Of these genera two are defined as new on the basis of this investigation.

Habits, which often depend on anatomical specializations of great complexity, are more diverse than has been supposed, and permit the exploitation of a diversity of ecological niches. The functional significance of many anatomical features is described. Carapace specializations, previously almost unstudied, are extremely important. Fundamental homologies not only within the Chydoridae but within the Anomopoda as a whole, can now be recognized and the feeding mechanism of all species can be related to one original type. By subtle modification of its various components, however, this basic mechanism has been adapted to very different ways of life and to different functions. The various species are described in a sequence which in part illustrates the progressive development of specialized ways of life rather than phylogeny, but light has been thrown on affinities, or lack of affinity, between certain species.

Alonopsis elongata (3) exhibits primitive behaviour. It swims over, and frequently settles on, surfaces, especially of stones. When it settles it rests on the ventral carapace margins (4), which show little elaboration. Under favourable conditions it can crawl forward by means of the first trunk limbs alone, though when necessary the antennae are used as props to maintain balance and

as levers to assist progression. They are also used for scrambling when required, and for this they are suitably armed. Food, whose nature is described, is collected from firm substrates by scrapers borne on trunk limbs 2 and 3. The trunk limbs and the complex feeding mechanism which they subserve are described (7). Entangling secretions are produced from trunk limbs 1 and 4.

In balancing ability, and associated structural features of the carapace margins, *Acroperus harpae* and *Camptocercus rectirostris* exhibit the same grade of organization as *Alonopsis*, and have a similar feeding mechanism, but show marked divergence in the carapace-headshield complex. Their close relationship is, however, confirmed. These genera exhibit progressive specialization of the trunk/post-abdomen joint, *Camptocercus* being most specialized.

Although no more adept at crawling than *Alonopsis*, *Alona affinis* has certain apparently trivial morphological features of great evolutionary potential, which have been exploited by more specialized crawlers. These and other anatomical features are described in relation to ecology, habits and the feeding mechanism. Comparison is made with three smaller species of *Alona*.

By widening the embayment, development of a marginal flange ventrally, elaboration of the carapace setae (37), and associated specializations, *Peracantha truncata* (34 to 36) has become an extremely efficient crawler over surfaces. Its efficiency is such that assistance from the antennae is no longer required, though they still serve as efficient oars for swimming. As projecting antennae are vulnerable to small predators and impede efficient crawling, especially in confined spaces, they are folded and their extremities tucked within the carapace. *Peracantha* frequents the leaves of plants from which, by means of fine-toothed scrapers of the second trunk limbs, it removes finely particulate food. Appendages involved in feeding are shown in figure 47, and the feeding mechanism is described. This employs the same elements as *Alonopsis*, but differs in ways related to habits, habitat preferences and the nature of the food. Only labral gland secretions (48) are employed. Two species of *Pleuroxus* are very similar to *Peracantha*.

Such specializations for crawling have been further exploited by *Alonella exigua* (50, 51) which has an even wider embayment, a broader ventral flange, and employs more marginal setae for balance. By virtue of its ability largely to seal the carapace chamber and vigorously to pump water from it, *A. exigua* is able to maintain a pressure difference between the water inside and outside the chamber which enables it to cling to and crawl over surfaces in any plane. Like a fly on a ceiling it can creep beneath leaves, such as floating leaves of *Potomageton*, and exploit a niche not available to its close relative *A. excisa*. It can even crawl inverted on smooth glass. Finely particulate food is collected by a feeding mechanism similar to that of *Peracantha* though different secretions are employed. Over short distances *A. exigua* is also a very efficient swimmer and attains, both relatively and absolutely, faster speeds than any chydorid yet tested.

A. excisa cannot perform the feats of which *A. exigua* is capable. Anatomical bases of the differences are revealed. *A. nana*, the smallest anomopod, has different habits from those of *A. exigua* and *A. excisa*. It is tolerant of a wide range of conditions, is less specialized either for crawling or swimming, and cannot protect its antennae in the same way. Some aspects of small size are discussed.

The animal known variously as *Alonella rostrata* and *Rhynchotalona rostrata* differs so markedly in its functional anatomy from the species of *Alonella* that it is assigned to a new genus, *Disparalona*. This species is specialized for scrambling among mud, usually in situations where a thin layer overlies a hard substratum, and to this end its antennae (56, 57) are specialized. Such a way of life also demands specializations of the carapace margins (58) very different from those of species which crawl over plants or stones. Most notable of its other anatomical features are specializations of trunk limb 3, whose gnathobase bears an enormously developed sweeping seta which in life is in almost incessant motion, sweeping along the food groove (60, 61). In this *Disparalona* is unique among the Chydoridae. Food is extracted from the mud in which the animal lives. Scraping is not involved. The feeding mechanism is described. Anatomical features of *Rhynchotalona falcata* show that its feeding mechanism cannot be the same as that of *Disparalona*.

The development of flat carapace margins has enabled the tropical *Dadaya* (62) to exploit the surface film of water, beneath which it creeps. The evolution of this habit can now be envisaged.

A. exigua has to work hard to remain attached by suction. If, however, inflow of water to the carapace chamber can be controlled by establishing a water-tight seal then, once the pressure is reduced, the only further effort required is that needed to expel such water as leaks in. This condition has been achieved by *Graptoleberis testudinaria* (63, 64 and 68) which has adopted habits akin to those of a gastropod mollusc. *Graptoleberis* settles on the ventral carapace margins and pulls itself along by its first trunk limbs whose slow, deliberate movements are to a large extent stereotyped for this function. The carapace has an enormous embayment, a very wide ventral flange, a specialized anterior flange, and setae of a highly specialized type (69–74), and is so shaped as to grant protection and allow other structures, such as the post-abdomen and antennae, to collaborate in the sealing of its chamber. The water-tight nature of the carapace chamber depends to a large extent on the employment of very fine setules which make up a labyrinth of minute channels through which water can flow only slowly. Leakage is countered by occasional use of an exopod pump. *Graptoleberis* rests and glides on a cushion of such fine setules (76).

The surfaces preferred for settlement are the leaves of aquatic plants, and here *Graptoleberis* occupies a very distinctive niche. Very fine particles are scraped by the second trunk limbs, with some assistance from the first. As there are no currents within the carapace chamber, food is moved entirely by direct movements of the limbs. The feeding mechanism (68, 82) is described and the functional evolution of gastropod-like habits discussed.

The animal hitherto known as *Chydorus globosus* (92, 93 and 95), is shown to have no place in the genus *Chydorus*, from which it is very different in structure and habits, and is assigned to a new genus, *Pseudochydorus*. Its specializations relate to its hitherto unknown habit of feeding on the dead bodies of other small crustaceans, and to defence. There is no ventral embayment so the carapace chamber can be completely closed, and the headshield fits closely against the carapace anteriorly so that a closed animal forms a defensive sphere. Furthermore the cuticle of the headshield and carapace is greatly thickened and sclerotized, being six or more times as thick as in most other chydorids (101, 102). The cephalic and thoracic appendages (103) are greatly modified for the collection and manipulation of food which is dragged into the median chamber and forked forward. The mandibles (104, 108 and 110) show marked skeletal specializations, and their musculature differs in several ways from that of all other investigated anomopods save *Anchistropus*, most noticeably in the complete absence of the 5c muscles. A large 'stomach' (111) is a further adaptation to the diet.

Anchistropus (112) is a parasite of *Hydra* on whose living tissues it feeds. Derivation of these habits from a detritus-scraping form is difficult to envisage. They could more easily have arisen from those of *Pseudochydorus*, to which *Anchistropus* shows many anatomical similarities, e.g. the arrangement of the mandibular muscular system (115) is shared by these genera alone. Their phyletic affinity is clear. *Anchistropus* feeds even on the nematocyst-bearing tentacles of *Hydra*. Its specializations include thickened and sclerotized carapace and headshield cuticle, thickening and sclerotization of the cuticle of the appendages and dorsal portion of the labrum, and an armour-plated food groove (116 to 119). The carapace secretes a layer of gelatinous material (112). The feeding mechanism is described, and the origin of parasitic habits discussed.

The genus *Chydorus*, like *Pseudochydorus*, has exploited the globular form, but the similarities are indicative of convergence and not of phyletic affinity. The habits and abilities of *Chydorus sphaericus* (120, 121) are described, and the important part played by the claws of the first trunk limbs (125) in clinging to surfaces is emphasized. Other anatomical features and the feeding mechanism are briefly mentioned. Comparison is made between this species, the similar *C. ovalis*, and *C. piger* which, although superficially similar, has specialized in other directions. Unlike *C. sphaericus* and *C. ovalis*, which employ the first trunk limbs for crawling over surfaces, *C. piger* is a bottom dweller and scrambles by means of its specialized antennae (134, 135). It is also specialized for defence. The ventral carapace margins of *C. piger* (130) and their armature (138) are very distinctive and are intimately related to habits. These and other differences (136 to 138), some of which are of taxonomic value, are described, and convergence between *C. piger* and *Pseudochydorus* is discussed.

Leydigia leydigii (139) is specialized for life in mud. This takes it into poorly oxygenated situations. A brisk respiratory current is therefore employed and haemoglobin is present in the blood. In mud, however, a respiratory current, if it passed through a typical chydorid-type filter would quickly clog the filters. In *Leydigia* it does not flow through the median sorting chamber and true filter feeding is not practised. Specializations for burrowing are shown by body form (139, 140), and by the antennae (143) and post-abdomen (139, 142) which provide the motive force for locomotion. The first trunk limbs are not employed. These are provided with long spines (144) which drag relatively large food masses towards the tips of the more posterior limbs where they are rotated (145) and

from which fragments are detached and passed to the sorting chamber. The anatomy of the limbs is described (146). The gnathobase of trunk limb 2 has a large setose spine and setules on its posterior face, both related to mud-frequenting habits. *Leydigia* and other anomopods can fill and empty their guts with great rapidity. This is important in quantitative studies on feeding.

From preserved specimens of *Monospilus dispar* it has been possible to recognize several structural features related to bottom-frequenting habits.

The relation of form to habits and habitat preferences among the Chydoridae is discussed. Although some are efficient swimmers, the most important correlations between structure and habits are usually associated with crawling or scrambling, over or through substrates. Swimming speeds of certain species are shown graphically (148). Changes in habits must sometimes have preceded structural changes in the Chydoridae, and habits have been important in determining evolutionary trends. The futility of looking for minute chemical differences in the environment, while ignoring fundamental differences in structure which are related to widely differing habits, is pointed out. Certain inter-generic relationships are indicated.

I. INTRODUCTION

This paper presents the major results of the first part of a general survey of the functional morphology, habits, feeding mechanisms and ecology of the Cladocera Anomopoda. The family Chydoridae is considered with the exception of *Eurycercus lamellatus* (O. F. Müller) of which a separate, detailed account has already been given (Fryer 1963). Of this family 22 species, belonging to 15 genera, have been studied in varying degrees of detail. Although not the most primitive family of the Anomopoda—evidence will be given later to show that this distinction belongs to the Macrothricidae—the Chydoridae exhibit a number of primitive attributes, and the disadvantages of dealing with this assemblage first are not great from the point of view of phylogeny. Several evolutionary trends and adaptive peaks have been recognized within the family and are described below, as are specialized organ systems. The evolutionary significance of many structural features, habits and abilities is also pointed out, but a detailed analysis of evolution within the context of the group now known as the Cladocera, and of the inevitable phylogenetic conclusions, is deferred until other families have been dealt with. This work is in progress.

A considerable amount of new information on the anatomy of the Anomopoda has been obtained, some of which has to be recorded in order to render functional aspects intelligible. Wherever possible descriptions of anatomical features are condensed by reference to illustrations.

For practical convenience the investigated genera are arranged without reference to the two recently erected subfamilies to which they belong (Frey 1967) and with whose delimitation I am in agreement. It is impossible to arrange the species in such a manner that all the primitive features are described first and their derivatives later. A given species may have specialized in one direction yet retain primitive features which are not directly related to this line of advance. Some of the specializations are mutually exclusive. Thus, while generalization on certain points is possible, differences are such that each species must be considered separately before matters concerning the group as a whole can be discussed. Here some of the needful information on the Chydoridae is presented.

II. Methods

In the examination of living animals each species has to be treated on its merits and the methods employed for the observation of, for example, *Graptoleberis* and *Leydigia*, are very different. When necessary, details are given under the species concerned. The methods employed for the examination of taxonomic characters are usually quite unsuited to the revelation of habits and abilities. No species yet studied performs on a clean, brightly illuminated slide (but two species have revealed much on suitably prepared slides) and information on supposed habits obtained from chydorids imprisoned in clean glass vessels is usually misleading. Suitable conditions, such as the provision of mud, detritus, or vegetation, according to the requirements of individual species are essential if habits and abilities are to be revealed. These can only be provided if something is known of the ecology of each species. Excessive illumination is to be avoided.

Living animals have often been examined after immersion in a non-toxic viscous medium ('cellulose nitrate') in which they can be turned for examination from any angle. This is most useful, but limb movements observed under such conditions have to be interpreted with care.

Except for the illustration of certain minute details, photography has severe limitations, but even technically bad photographs have proved useful in fixing either the orientation of the entire animal, or of certain structures, in life.

Dissections have usually been performed in polyvinyl lactophenol to which an appropriate stain has been added. Cast skins have also proved useful for the revelation of skeletal details.

Except for a few specimens obtained from various sources, all the large number of animals sectioned (more than 260 chydorids excluding *Eurycercus*) have been fixed in Zenker's fluid, which previously experience had shown to be the most satisfactory of the fixatives tried. Low viscosity nitrocellulose was used as the embedding medium and sections were cut at various thicknesses, but seldom less than 20 μm, according to requirements. Almost all were stained with Mallory's stain. Most of the animals studied are less than 1 mm in length and several are less than half this size so the handling of individual sections (necessitated by the L.V.N. technique) presents problems which are partly overcome by use of a one-solution Mallory stain. Any loss in the quality of staining was more than offset by the simplification of the technique and the reduced danger of fragmentation of fragile sections.

Swimming speeds were determined on individuals swimming in a channel excavated in a piece of Perspex and placed over a sheet of graph paper. The width of the channel (*ca.* 1 cm) was such as to allow ample freedom yet encourage movement in a straight line, but wavering was nevertheless a source of error. Whenever possible water in which the animals were living was used, and all measurements were made at room temperature. No attempt was made to make a long series of measurements or to compensate for temperature differences, the sole purpose being to obtain some idea of the sort of swimming speeds of which the various species are capable and to reveal differences.

III. STRUCTURE AND HABITS OF THE ANOMOPODA, WITH ESPECIAL REFERENCE TO THE CHYDORIDAE

Anomopods are generally capable of two kinds of locomotion. The primitive anomopod could both crawl and swim and a large proportion of extant species can still do likewise, though a few have lost the ability to swim and, at the opposite extreme, others are entirely pelagic. Members of the families Chydoridae and Macrothricidae are essentially benthic and littoral in habits and it is in these families that crawling is often as important as swimming, and in some cases is more important, particularly in the Chydoridae. Scrambling, which is different from crawling, is also employed by several species.

That the ability to crawl must have been an attribute of the primitive anomopod stock and that its loss in certain forms (Bosminidae, most, but not all, Daphniidae, and certain Macrothricidae) must be a derived condition, will be shown subsequently. The fact that all known species can use their antennae as oars by means of which they swim or (certain species of *Ilyocryptus*) row themselves over the bottom or among flocculent deposits, has obscured the importance of the first trunk limbs as locomotory organs, a function for which they must early have been differentiated. In fact some chydorids swim only infrequently and some are so specialized for crawling that they swim with reluctance and even with low efficiency. The use of the antennae for scrambling and burrowing, for which purpose, as here described for various species, they may in fact be highly specialized, seems also not to have been reported.

Crawling and feeding are often intimately related, so much so that in some species they are virtually part of the same mechanism. Although some species of the Chydoridae and Macrothricidae can extract suspended particles from a combined feeding/respiratory stream, the basic feeding mechanism of these families involves a mechanical scraping of attached or sedimented particles, or some modification of such a device.

The abandonment of scraping and allied devices is associated with the assumption of several different ways of life, the most successful of which have been those which have included complete emancipation from the need to collect settled material. (The phyletic assumptions implicit in this and other statements will be justified later.) The great exponents of this way of life, which need not be planktonic, are the Daphniidae and Bosminidae, and the anatomical and functional studies upon which this account is based seem to leave no reasonable doubt that, like the Chydoridae, both these families are derived from a macrothricid-like ancestor. Abundant evidence for this conclusion, which is opposed to the generally accepted view of the origin of the Daphniidae, will be presented later. Of these two families the Daphniidae is the more diverse, though concealed by the diversity of size and carapace form, which is associated with swimming or floating in different habitats, is a hidden similarity in limb structure and feeding mechanism. The Daphniidae, whose members are often regarded by those unfamiliar with their habits as being entirely planktonic, includes what are essentially littoral and to some extent even benthic forms as well as those which to varying degrees exhibit mastery of the pelagic way of life. Such a way of life, however, offers less scope for diversification of form and habits than does that of bottom-dwelling, crawling, and substrate-scraping and, considerable as it is, diversity within the Daphniidae is less than within the Chydoridae.

A derivation of the Anomopoda from the Ctenopoda cannot be justified. An attempt to reconstruct the ancestral anomopod will be made in a later publication, in which adaptive radiation will also be summarized, but here it is convenient to mention certain primitive features which place the necessary descriptive sections in an immediate evolutionary context. While the first trunk limbs of primitive anomopods were used for locomotion over substrates, the second scraped or stirred up particles and played an important part in passing food forwards to the mouth. The third pair assisted the second in food collection but fulfilled a more important role in the manipulation of the collected material. The fourth and fifth pairs helped to close the food-containing chamber laterally and posteriorly, to push food from it anteriorly along the food groove, and also to set up currents. In no extant species are the sixth limbs represented by much more than a simple flap which helps to seal the food-containing chamber posteriorly, and reduction of this limb must have taken place early in the evolution of the group. It is from such an arrangement of limbs that the present diversity has arisen.

Among the features which have been of particular importance in the evolution of the group three require mention here—perfection of different methods of locomotion, especially crawling, perfection of elaborate and highly specialized feeding mechanisms, and the utilization of the ventral carapace margins in connexion with both these activities and for other purposes. What are essentially similar trends in the elaboration of the ventral carapace margins have been pursued independently in two anomopod families and, in a modified manner, in a third. The margins have been utilized first as structures on which to balance during feeding and locomotion and, as a result of persistence in this habit by certain members of the Chydoridae, ultimately as essential and extremely specialized components of the apparatus used for attachment and locomotion. Here descriptions of the Chydoridae have been arranged in part to show the progressive evolution of this device as an adjunct to locomotion and feeding, though the various species do not constitute a phyletic series.

Chydorids are essentially vegetation-frequenting or bottom-dwelling animals which by various means creep over substrates or penetrate into bottom materials of various kinds. Although all can swim they are not planktonic. That ecologists have often failed to appreciate this stems in large measure from unfamiliarity with the living animals, and particularly with living animals which have the opportunity of behaving normally. Within the sort of habitats mentioned, they fill a variety of niches, and their habits and ways of life are more diverse than is generally appreciated. From an ecological point of view an expression such as 'weed-frequenting', while useful, tells us little of the precise habits of a particular species. Two species frequenting the same frond of a plant may behave in very different ways and exploit different niches. Both may exhibit marked specializations and these may be mutually exclusive.

Size and habits are mutually related and an appreciation of the size range of chydorids is important. The volume of the largest is several thousand times that of the smallest. Such differences demand different ways of life, and may allow two or more species to exploit the same environmental resource in different ways. Because they are small, chydorids can occur in enormous numbers. Smirnov (1963) records almost 1400000 *Chydorus sphaericus* on 1 m^2 of bottom and in the vegetation in the overlying cubic metre of water. For several other species he records densities of over 100000, often considerably more, and up to 950000 for *Peracantha truncata*, in a similar volume. The ecological importance of the family is thus readily apparent.

Anatomically, chydorids retain many attributes of the primitive anomopod stock, but also exhibit specializations associated with the exploitation of different substrates and with different methods of locomotion and feeding. In all species the carapace and headshield is stouter than in other families and is clearly an adaptation to benthic habits. A stout carapace has also permitted many specializations not attainable in other families which, contrariwise, have exploited ways of life from which chydorid carapace specializations debar them. Adaptive radiation in carapace form has played a great part in the evolutionary success of the Chydoridae.

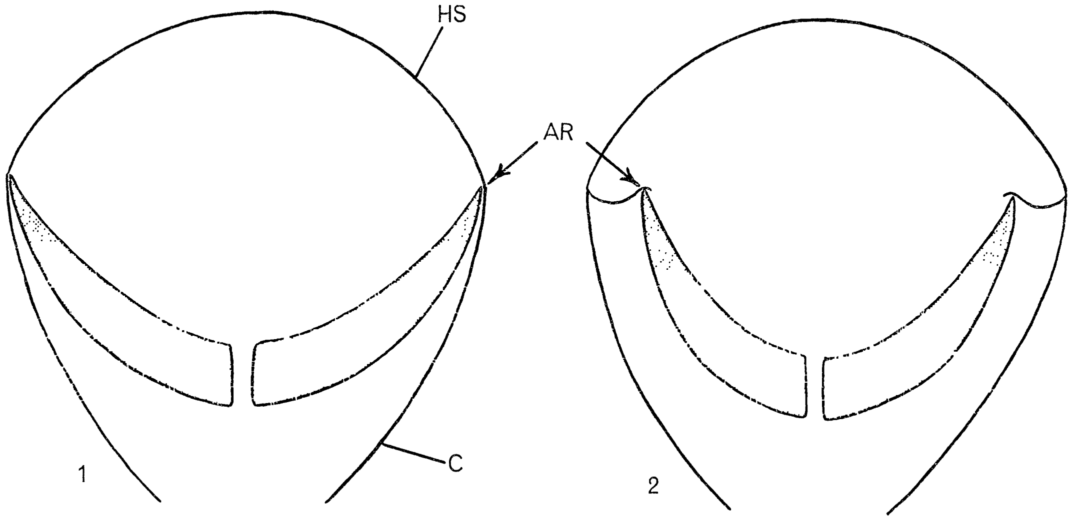
Except for those species which frequent unstable substrates, locomotion other than swimming is by means of the first trunk limbs. In some species progression over, and especially within, substrates is assisted by the antennae and post-abdomen. Food is usually collected largely by the second, manipulated by the third and fourth, and sometimes the fifth, trunk limbs. With three known exceptions a current of water is drawn almost continually between the carapace lobes by a pump constituted by the exopods of trunk limbs 4 or 5 or, in one case, trunk limb 5 alone. The principle of the pump is the same as that described for *Eurycercus* (Fryer 1963),

Food is passed to or drawn into a median chamber between the trunk limbs where, in many species, particles are filtered from the combined feeding/respiratory current by filter plates borne on the trunk limbs. In some species these are present on trunk limbs 2 to 5; in others one or more of these limbs may not be involved in filtration. In others filtration has been completely abandoned and food is handled by purely mechanical movements of the limbs. In all cases, whatever the nature of the food, it is passed dorsally to the median ventral food-groove along which it travels forward, in most cases against posteriorly flowing currents, to the mouthparts. Adaptive radiation of the Chydoridae consists in large measure of modifications of this complex apparatus, which are intimately related to modifications of the carapace and headshield, and which also frequently involve co-ordinated specializations of other structures such as the post-abdomen.

Most species feed on material which is scraped from the surfaces of plants, stones or sand grains, or is picked up from among bottom detritus or mud. Others have diverged very widely in feeding habits, sometimes in hitherto unsuspected ways: *Pseudochydorus globosus* is a scavenger and *Anchistropus emarginatus* a parasite which ingests the living tissues of *Hydra*.

Mandibular articulation and suspension, and the arrangement of the mandibular muscles, differ from species to species in a manner which in some cases permits phyletic deductions. Frey (1961) recognized that two of the major divisions of the Chydoridae as distinguished on the basis of head-pore arrangement differ also in mandibular articulation, and later provided details (Frey 1967). Within the Chydoridae there are two types of articulation, shown diagrammatically in figures 1 and 2. In type A, of which *Eurycercus* provides a described example (Fryer 1963) (see also photographs in Frey 1967), the mandibular articulation is located laterally at the point where headshield and carapace unite, i.e. at the fornix (figure 1). Articulation need not always involve the elaborate cup seen in *Eurycercus*, but the position where the mandible articulates is constant, and this is characteristic of all members of the Eurycercinae and Aloninae (Frey 1967). Articulation of type B, which characterizes the Chydorinae (Frey 1967), involves the development of a cuticular apodeme which carries the point of articulation away from the fornix (figure 2). Photographs of moulted exuviae which show the general nature of this type of articulation are given by Frey (1967), and detailed descriptions and illustrations of articulation in *Pseudochydorus globosus* and other species are given below.

In most species there are two suspensory ligaments on each side (figures 104, 115 and 126). The median (SUS) is generally the more robust. The lateral ligament (A SUS) does not bear direct vertical pull of the transverse mandibular tendon borne by the median, more or less vertical ligament, but it is directed to a large extent laterally. It also inclines forward so that, although attached to the endoskeletal complex of which the transverse mandibular tendon forms the central element, it passes anterior to the promotor roller muscles of the mandible. This ligament is readily seen in members of the Chydorinae (e.g. figures 104, 115 and 126) but is sometimes slender and often difficult to detect in members of the Aloninae, e.g. *Alonopsis* and *Camptocercus*, in which group it is so anterior that it serves perhaps as a brace rather than a suspensor. The situation in *Eurycercus* where only one wide suspensory ligament was described (Fryer 1963) is therefore not typical of the Chydoridae as a whole. Re-examination of *Eurycercus* in the light of findings in other genera has revealed a very fine lateral ligament, arising from the anterior portion of the endoskeletal complex and presumably the homologue of the lateral ligament in other genera but relatively more slender, and also other minute fibrils which need not be described here, but the arrangement in this genus is basically that of a single suspensor on each side.



Figures 1, 2. Diagrammatic transverse sections through the mandibular region to show the two types of articulation in the Chydoridae. 1, Type A; 2, Type B.
(*The key to the lettering of all figures is on pp.* 384–385.)

The load-spreading fibrils, so conspicuous in *Eurycercus* (Fryer 1963, text-fig. 18) are less well developed in most other species—presumably because the ratio of load to cuticle thickness is less, and the arrangement of the fibrils differs from species to species.

IV. THE STRUCTURE, HABITS AND FEEDING MECHANISM OF *ALONOPSIS ELONGATA* SARS

Although no one extant chydorid retains all the primitive features of the family, several such features are to be seen in *Alonopsis elongata*, which also exhibits behaviour of the kind which probably initiated a trend of great evolutionary importance.

(i) *Ecology and habits*

A. elongata (figure 3) is a littoral species characteristic of oligotrophic lakes, and occurs particularly on rocky or sandy shores, i.e. on firm bottoms, of both large and small lakes, but is sometimes to be found in sparse vegetation (Flössner 1964). In Britain it is common in such habitats in the northern part of the country and in North Wales, but has not been found in the south-east where suitable habitats are less common. In the English Lake District it is the characteristic species of the rocky margins of high-level, barren tarns (Smyly 1958) and occurs on suitable shores in other lakes and tarns.

An accomplished swimmer, *A. elongata* can sustain speeds somewhat in excess of 12 body lengths/s (about 9 mm/s) for at least 17 s, and a speed of about 13 body lengths/s has been recorded over a period of 13 s.

Alonopsis also crawls and scrambles. Its agility when scrambling is strikingly displayed by its ability to wend its way with great rapidity through tangled masses of filamentous algae. Movements are so rapid that they cannot be followed in detail, but are based essentially on use of the antennae. The post-abdomen, which can and does push on occasion, seems to be little used under such circumstances. The bilaterally compressed body facilitates passage through narrow gaps.

Crawling is intimately related to food collection. Although capable of filtering suspended material, *A. elongata* undoubtedly collects most, if not all, of its food from solid substrates. Indeed it often occurs in situations where suspended material is extremely sparse. Food collection entails settlement on some object from which material is removed. During settlement *A. elongata* utilizes the ventral margins of the embayment region of the carapace whose setae make contact with the substratum, and on which it balances (figure 4*B*). This habit, here seen in one of its least specialized forms, is widespread in the Chydoridae. Its exploitation, and elaboration of the structural features associated with it, have played an important part in the adaptive radiation of the Anomopoda.

On suitable surfaces *Alonopsis* balances easily on the setae of the carapace margins and grips with the first trunk limbs each of which is provided with grasping spines of which one is a definite hook (figure 7,*H*). During this process the antennae are laid alongside the outer surface of the carapace valves, and play no part in either attachment or locomotion. They remain still as the animal moves forward by the use of the first trunk limbs. Under less satisfactory conditions the antennae are used as both props and levers. They can be used independently, and one may be used while the other remains still. Provided the surface is suitable any orientation can be achieved and the animal can feed as readily with its ventral surface uppermost, when a definite load must be borne by the first trunk limbs, as it can when attachment is assisted by gravity. This achievement by such an elongate and bilaterally compressed species with relatively unmodified carapace margins foreshadows much more elaborate specializations in other species.

A. elongata has the habit, shared by a few other anomopods, of retaining one or more old carapaces after ecdysis. These embrace the carapace currently in use but can be cast very easily, and perhaps voluntarily. Shedding can often be induced by touching a specimen lying in a drop of water on a slide, and even contact with the surface film is sometimes a sufficient stimulus. A specimen can easily slip out of two carapaces in two successive operations. This is possibly a protective device, akin to the lizard's tail in function, by means of which *Alonopsis* can escape from predators such as cyclopoid copepods, some of which seize cladocerans with their grasping mouthparts.

The food cannot be described with precision as it includes fine particles, most of which are certainly already disintegrated before ingestion, and whose derivation is various, some probably being of terrestrial origin. Very few algae were seen in the guts examined—none in some. Inorganic particles are taken in, as are large dark lumps of organic matter which, while not always present, were frequently seen. The gut contents of specimens collected in several localities in the English Lake District are characteristically dark, almost black, and are often clearly composed of different material from that found in the gut of other species with or near which they may be living, even though the differences cannot be precisely defined.

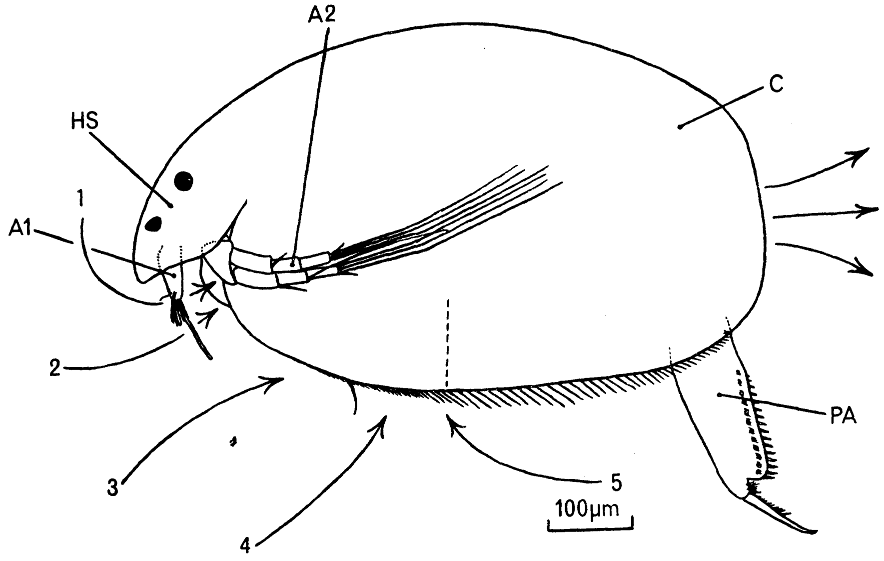
(ii) *Structure, other than of the appendages used in feeding*

This is an elongate, bilaterally compressed species (figure 3). Adult females attain a length of about 1 mm and a width of about 0·3 mm. Form and armature of the carapace margins are of great functional and phyletic significance in the Chydoridae but in most species have never been described, and certainly not adequately. The condition in *A. elongata* is both simple and primitive. Here the ventral margins are more or less straight in the lateral plane, though there is an angle, very obtuse and inconspicuous, but very important, anterior to the middle (figure 3). The carapace margins lie approximately parallel to each other posterior to the angle: anterior to it, in the vicinity of the trunk limbs, there is a distinct embayment on each side (figure 4, EM), as in *Eurycercus*. Posterior to the embayment they can be brought in contact with each other along most of their length by contraction of the carapace adductor muscle.

Anteriorly the carapace margins curve as shown in figures 3, 5 and 6 (ACM). The margin of each valve is thickened. Posteriorly the thickening is scarcely perceptible and along the ventral margin is slight and simple as far as the embayment. In the embayment region there is a distinct but narrow flange (shown diagrammatically in figure 4*A*). Anterior to this the flange virtually disappears and only a thickened rim is present, but there is a simple flange along the anterior margins (figures 5, 6, ACM). Internal to this cuticular elaboration there is, along the whole of the ventral margin, a row of short fine setules.

Anteriorly the margins of the valves approach each other. Their arrangement and relationship to the labrum are shown in figures 5 and 6. Because of the close contact between the anterior margins and the labrum this region is to a large extent sealed—a point of great functional and evolutionary significance.

The ventral, but not the anterior, margins are armed with setae whose length, spacing and orientation varies according to their location, though each is directed to a greater or lesser degree posteriorly and, usually, ventrally (figures 3, 4). About 68 setae are present



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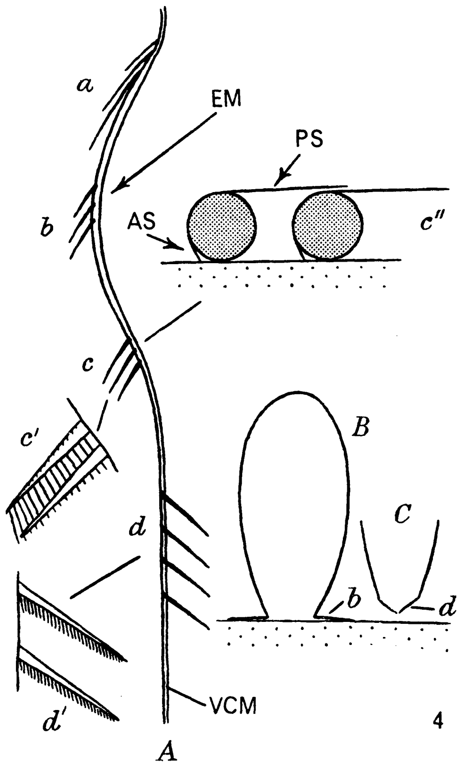

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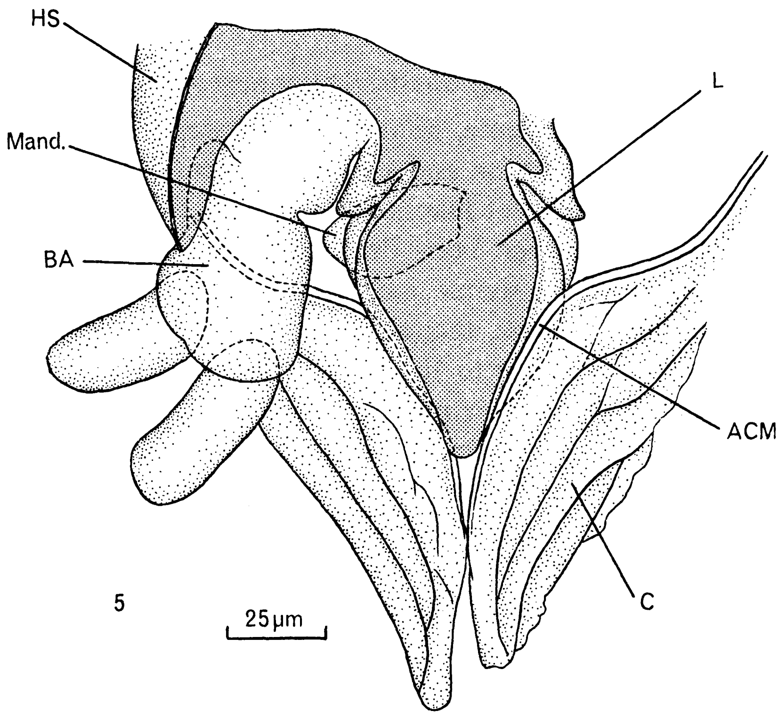

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FIGURES 3 to 5. *Alonopsis elongata.* (*For key to lettering see pp.* 384–385.)

FIGURE 3. Outline of adult female, lateral aspect, showing general form, and the direction of the currents which flow through the carapace chamber. The dotted vertical line shows the approximate position of trunk limb 4. The numbers refer to currents mentioned in the text.

FIGURE 4. Diagrammatic representation of the ventral carapace margin and its armature. *A* represents the right-hand carapace margin as seen from below with some of its setae, showing the arrangement at different levels. Inset *c′* shows the arrangement of the setae located at *c* and their setules, and inset *c″* shows the same setae in transverse section. Setae at *b* and *c* are of the same nature and orientation. *B* shows a transverse section of the body at the level of setae of the *b* region and reveals how these lie against the substratum in a crawling animal. *C* is a transverse section at the level of the *d* setae where the setae lie clear of the substratum.

FIGURE 5. Transverse section at the level of the anterior carapace margins which has sliced through the anterior tip of the labrum. From in front. The anterior carapace margin on the animal's left side is in the correct position: on its right it has been dislocated and pulled into the labrum.

but there is slight variation. Except for the first, the first nine are long (figure 4*A*, *a*), well spaced, and directed obliquely backward and somewhat outward and ventrally. Each has a posterior fringe of short and exceedingly fine setules. The next 22 or 23 are much shorter, and are directed outwards and sharply backwards (figure 4*A*, *b*, *c*, 4*B*, *b*). Each has a posterior fringe of fine setules, and a more elusive anterior row. The more posterior members of this series arise sufficiently close together for their posterior setules to reach back over the setae next behind. This it does to the outer (dorsal) side (figure 4*A*, *c*, *c*′, *c*″).

Behind the embayment the setae are at first longer than in the embayment region but diminish in length towards the posterior end of the carapace (figure 3). These are directed inwards and backwards and to some extent ventrally (figure 4*A*, *d*, *d*′, 4*C*, *d*). Each has a posterior fringe of setules (figure 4*A*, *d*′) and a barely detectable anterior fringe. The distance between adjacent setae is such that the posterior setules fail by a considerable distance to reach the seta next behind (figure 4*A*, *d*′) and are therefore incapable of fulfilling functions which they are called upon to perform in more specialized species.

Although simple, the carapace margins of *A. elongata* and their armature include all the basic elements which, exploited by certain species, have given rise to highly complex structures and extremely specialized habits and abilities.

The headshield is bluntly rounded in front. Beneath the anterior part of the headshield of *Eurycercus* is a zone of cork-like subepidermal connective tissue (Fryer 1963, text-fig. 6). No such zone is present in *A. elongata* which, unlike *Eurycercus*, does not to any extent use its less bluntly rounded headshield as a ram.

Similarly the demands made upon the post-abdomen (figure 3, PA) call for less strength than in *Eurycercus* and this structure is accordingly less powerful, being much less deep in the dorso-ventral plane and therefore longer in relation to its depth, and presumably a little lighter. Its armature of stout marginal denticles, which are longest towards the distal end, is related to the need to push from time to time on hard bottoms while the 'lateral squamae'—bundles of fine setules—may grant purchase if the post-abdomen pushes on a detritus covered stone. Although primitive in several respects *A. elongata* has a specialized trunk/post-abdomen articulation—this being an example of the mosaic nature of evolution in the Chydoridae. This specialization, not described here in detail, but which is of phyletic interest, involves thickening and sclerotization of the rim of the pivot on both the post-abdomen and the trunk, and the development of a conspicuous rod of sclerotized chitin on each side of the posterior extremity of the trunk.

The antennules (figure 3, A1), whose tips can be swung towards each other in the mid-line, project ventro-laterally. One terminal sensilla is much longer than the rest so that its tip lies adjacent to the substratum when the animal crawls. The subterminal sensilla is directed outwards so the simple antennule covers a relatively wide field.

The antennae are used not only for swimming, but also for scrambling. To facilitate the former they have long, distally located swimming setae: to assist in scrambling they have spines, here called scrambling spines, which are incorrectly illustrated even by Lilljeborg (1900). The endopod bears a stout spine at the distal extremity of the basal segment which is as long as or slightly longer than the second segment and is directed ventrally and backwards (figure 3). The segments can be flexed at the joints. When this happens the spine projects almost at right angles to the second segment and can be used as a claw. A spine is also present on the distal endopod segment. Both the basal and distal segments of the exopod bear stout spines distally which are directed backwards and outwards; that of the basal segment especially, which is the larger, being so directed. This spine in particular will be useful when *Alonopsis* passes through tangled masses of algae (section i) and for obtaining purchase on laterally located objects during scrambling.

The antennae arise just anterior to the anterior carapace margins and are directed ventrally and posteriorly when the animal is at rest. The basis of each (figure 5, BA) lies in very close proximity to the anterior carapace margin of its side. Although of no known functional significance in *Alonopsis* (unless it be to accelerate certain currents—see section iv) this close association is of great evolutionary interest as it is a relationship which has been exploited to fulfil an extremely important function in other species.

(iii) *The structure of the labrum and the limbs used in feeding*

The limbs are basically similar to those of *Eurycercus* but have numerous individual peculiarities.

The labrum is shown in figures 5 to 7. Although large gland cells (figures 6, ADGC and PDGC) and undoubted ducts (DG) are present, no secretion has ever been seen in any of the many sections prepared. Considering the success with which labral gland secretions can be demonstrated in several other chydorids and the frequent demonstration of other secretions in *A. elongata* (see below) it seems likely either that no secretions are produced by the labral glands or that they are produced in insignificant amounts. Functionally it appears that the labral gland secretions have been replaced by other secretions described below. Although perhaps not concerned with the entanglement of food particles the labrum nevertheless fulfills several other important functions.

The mandibles are similar in basic features to those of other anomopods (cf. *Eurycercus* (Fryer 1963) and *Chydorus sphaericus*, § XIX). The location of the molar region is indicated in figures 7 and 10. Articulation is of type A, of which it is a less specialized example than *Eurycercus*. The mandibles exhibit both skeletal and muscular asymmetry, the results of which are the same as in *Eurycercus*. An elaborate system of suspensory fibrils is used to spread the load imposed on the headshield cuticle by the major remotor muscles and the suspensory ligaments of the transverse mandibular tendon. (cf. *Eurycercus*, though there are differences in detail.) This fibril system is continuous posteriorly with a subepidermal fibril system from which the heart is suspended. The maxillules are typical in general form but bear only two spines (figure 7, Mxlle).

The first trunk limbs (figure 7, TL1) differ from those of *Eurycercus* in one very striking way. As in *Eurycercus* there are on each limb two distal lobes, the innermost of which bears three curved clasping hooks used for gripping the substratum. There are similar distal spines and the appendage is similarly armed with long setules. (Compare figure 7 and Fryer 1963, text-fig. 23.) An 'inner lobe' which bears three thick 'bottle-brush' setae is present in *Eurycercus*; in *A. elongata* its homologue is greatly reduced and represented only by a minute papilla bearing a single small soft seta, alongside which can sometimes be detected another minute seta (figures 7, 10, IL). Its reduction is possibly related to reduced importance of the labral gland secretions: in *Eurycercus* it is apparently concerned with the direction of secretions into the food groove. Ejector hooks (EH) are present. For other features see figure 7.

The outstanding difference between this limb and its counterpart in *Eurycercus* is that on its surface opens a duct from which entangling secretions are exuded. The orifice is located on the anterior face of the limb not far from its dorsal extremity (figures 6, 14, OR). From it extends backwards a duct which widens, at first gradually, then more rapidly so that while still within the confines of the first trunk limb it has a wide diameter and becomes part of a voluminous reservoir (figure 14, R1) which extends posteriorly and somewhat dorsally as far back as the level of trunk limb 3. In life the reservoir can be detected with suitable illumination as a shining vesicle. In sections of well-fixed, Mallory-

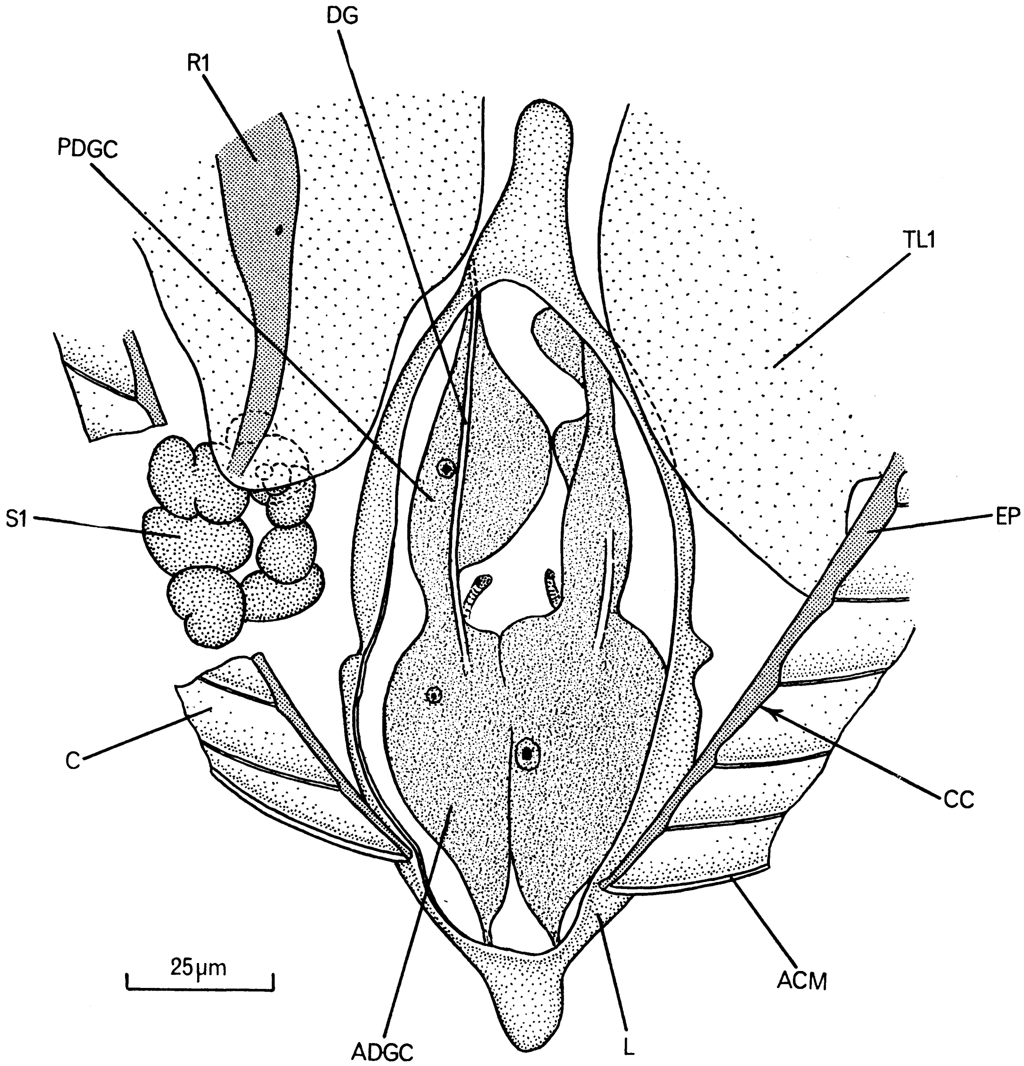


FIGURE 6. *Alonopsis elongata*. Horizontal slice through the region of the labrum and first trunk limbs showing the relationship of the carapace and labrum, the well-developed labral glands and ducts from which, however, no exuding secretions have been seen, and the copious production of entangling secretions from trunk limb 1. Only two of the dorso-ventral muscles of the labrum are shown. Note that the thickness of the carapace cuticle is such that it can be indicated only by a single line.

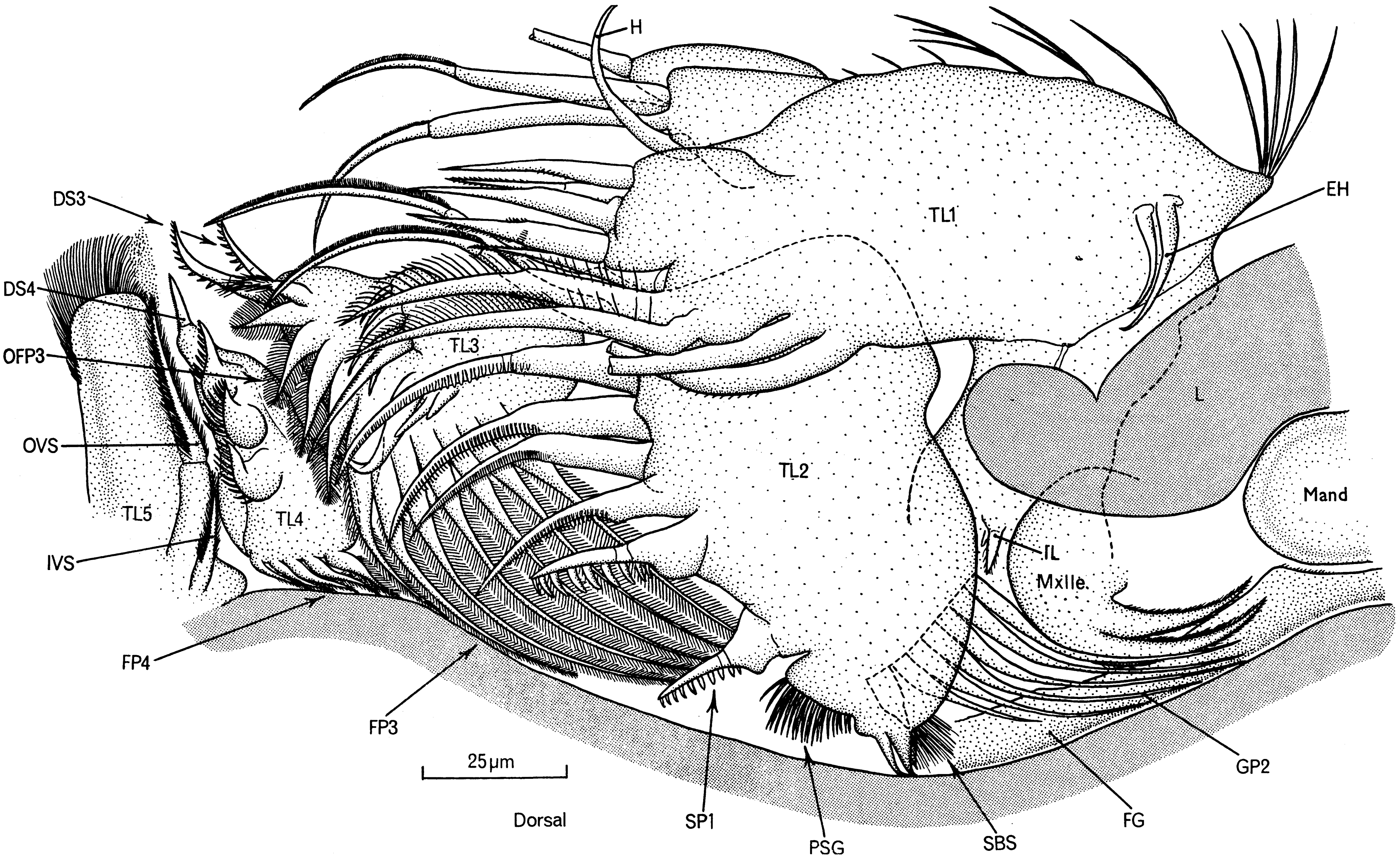


FIGURE 7. *Alonopsis elongata*. Median longitudinal slice through the trunk limbs to show the filter chamber. Note the rake-like nature of proximal spine no. 1 (SP1) of trunk limb 2.

stained material its contents stain bluish purple, while exuded material is always pale blue. There is thus no consistency in the staining reactions of the secretions of the labral glands of anomopod cladocerans (Cannon 1922; Fryer 1963), the secretions of the fourth trunk limbs of *Eurycercus* (Fryer 1963), and of *Alonopsis* (see below), and of the present reservoirs; but in all cases observed by the writer the secretion stains blue with Mallory's stain after coming in contact with water.

Fixation presumably causes copious exudation and coagulation of the secretion, which is often found in considerable amounts near the orifice of the duct. Often the material is in coils, much like tooth-paste squeezed from a tube (figure 6, S1). (cf. the labral gland secretion of *Eurycercus* (Fryer 1962, fig. 1; 1963, text-fig. 12).)

The second trunk limbs, (figure 7, TL2), while basically similar to those of *Eurycercus*, differ in the nature and orientation of their armature. In *Eurycercus* the gnathobase is armed with a row of filter setae which form a filter plate (Fryer 1963, text-figs. 25, 45). In *Alonopsis* the gnathobase bears a row of slender spines or setae (figure 7, GP2). These are not filter setae, nor is their orientation the same as the filter setae of *Eurycercus* which are directed more or less dorsally (i.e. towards the food groove) and curve only slightly so that their tips are directed somewhat anteriorly (Fryer 1963, text-figs. 25, 45). Functionally they and the gnathobasic filter plates of the limbs behind form a single filtering surface and their orientation is such that the limb can be swung through a considerable angle without disrupting this arrangement. In *Alonopsis* they are much more anteriorly directed (figures 7, GP2, 9, GS2, and 10, AGS). Because of this they are not functionally continuous with the wall of filter setae comprised by the gnathobasic filter plates of the more posterior appendages, but are separated from it by the corm of the appendage (figure 7).

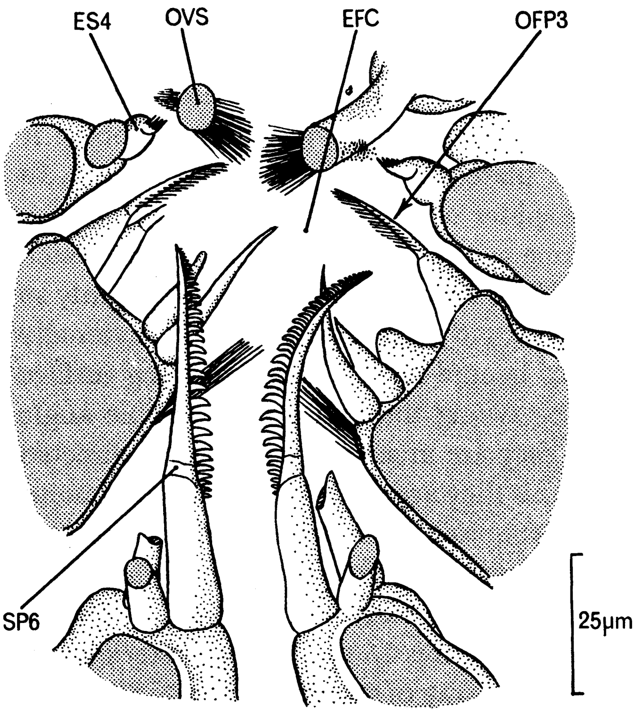
The gnathobasic setae are armed with setules which are extremely difficult to discern even with an oil-immersion lens. Details are shown in figures 15 to 17. The posteriormost gnathobasic seta is short and stout and has a brush-like array of setules (figures 7, SBS, 18). It is here called a 'shaving brush seta'.

The armature of the corm (figure 7) is similar to that of *Eurycercus*. Well-developed scrapers are present. Figure 7 shows how some of these are finely, others very coarsely toothed, and also how the most proximal scraper which, like the second, is functionally a rake, can reach the food groove when the limb swings forward. Trunk limb 2 fulfils the heaviest duties of any limb. Because of this its cuticle is thicker than that of the other limbs and more heavily sclerotized, especially distally and in the region from which the scrapers arise. Posteriorly there is a specialization in the form of a rib of folded, thickened, and sclerotized cuticle which runs obliquely across the face of the limb and whose pointed end lies dorsally (figures 19 to 21, PR). This strengthens the posterior face and provides a firm point of insertion (figures 19, 21, PM) for some of the muscles which move the limb.

The third trunk limbs (figure 7, TL3) are similar in many ways to those of *Eurycercus* but differ in one striking respect. The gnathobasic filter plate (figure 7, FP3) is composed of true filter setae and is functionally continuous with an outer 'filter plate' (OFP3) of which, however only the innermost component is a true filter seta. The setules of the rest are reguarly arranged as in a filter seta but are longer and, at least at their tips, less rigid. In fixed and mounted specimens their tips appear flaccid and brush-like.

At the distal extremity of the limb are two strong scrapers (figure 7, DS 3) which take part in the collection of food. Other features are shown in figures 7 to 9 and 12.

The fourth trunk limbs (figure 7, TL 4) resemble those of *Eurycercus*, but exhibit marked reduction of certain elements. The gnathobase of each bears a filter plate (figure 7, FP 4) made up of five true filter setae (cf. 8 or 9 in *Eurycercus*). There is no outer filter plate. The armature of the corm consists of four specialized spines arranged one above the other as in *Eurycercus* but very different in form. Of these the three proximal have a similar and characteristic form (figures 7 and 8, ES 4) though they differ in their denticulation, the most distal being the coarsest. The distalmost spine (figures 7 and 12, DS 4) is markedly different from the rest; being scraper-like in form.



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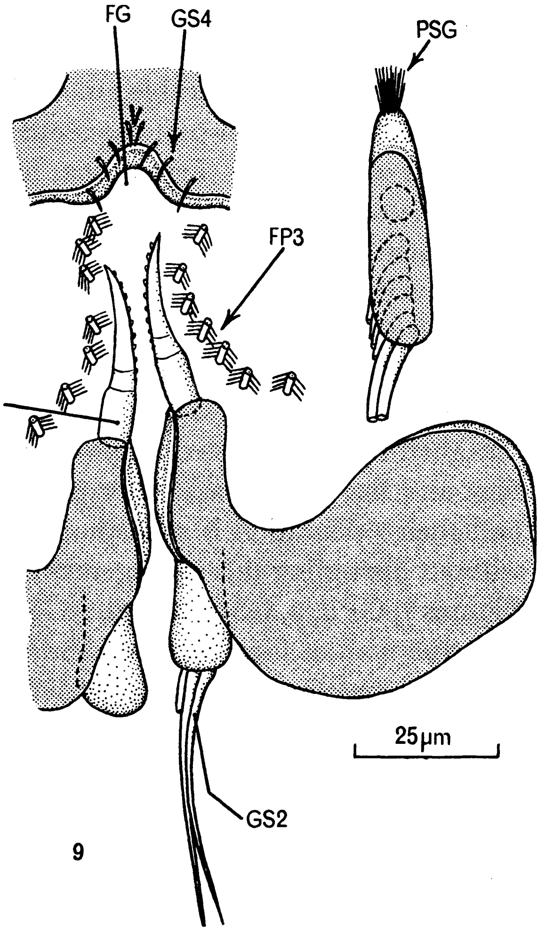

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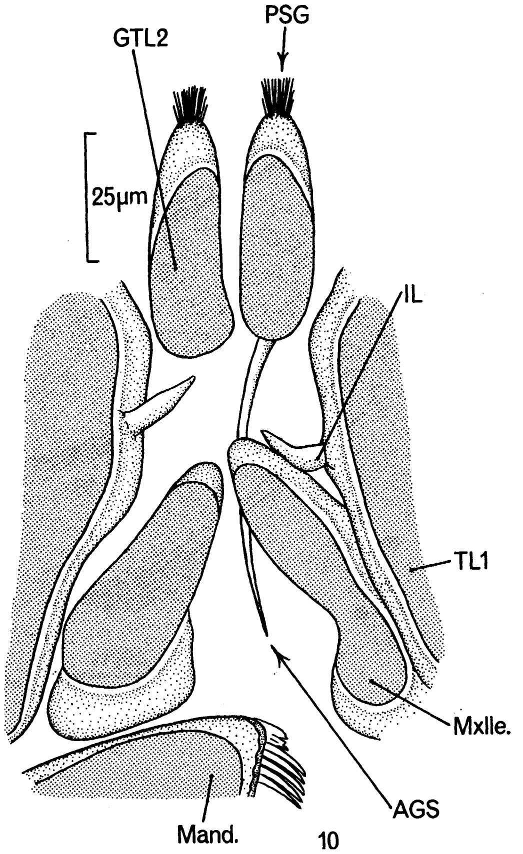
FIGURES 8, 9. *Alonopsis elongata.*

FIGURE 8. Horizontal section through the distal portion of the posterior trunk limbs, looking into the filter chamber from below. Note that endite spine no. 6 of trunk limb 2 (SP 6) is a scraper and pusher.

FIGURE 9. The same, much deeper, with the anterior gnathobasic spines of trunk limb 2 added from the next, even deeper, slice. Note the great posterior reach of the scrapers of trunk limb 2 as a result of fore-shortening of the filter chamber. The inset shows a section through the gnathobase of trunk limb 2 (i.e. deeper than the rest of the figure) to show the posterior spinules and the orientation of the anterior setae.

Within the corm of trunk limb 4 of *Eurycercus* is a large secretion-filled reservoir which discharges via an aperture on the inner face of the limb (Fryer 1963). A similar reservoir is present in *Alonopsis* (figure 14, R4). The discharged secretion is, however, much less easy to demonstrate in *Alonopsis* than in *Eurycercus*. Apart from technical difficulties imposed by small size, the probable reason is that the secretion is discharged distally. A section in which it is clearly seen reveals that it is discharged towards the distal scraper-like spines of trunk limbs 3 and 4, i.e. near the aperture of the carapace chamber. In fixed material therefore, unless it becomes entangled by these scrapers, as it sometimes does, the secretion will pass outside the carapace chamber and be lost. Secretions sometimes accumulate near the base of the fourth trunk limbs, but as these include those discharged from the first pair, any contribution from the fourth cannot be recognized. Within the reservoir Mallory-stained secretions are almost always more purple than those of the reservoir which opens on trunk limb 1. The secretion of both, however, stains blue after discharge.



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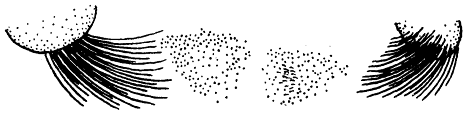

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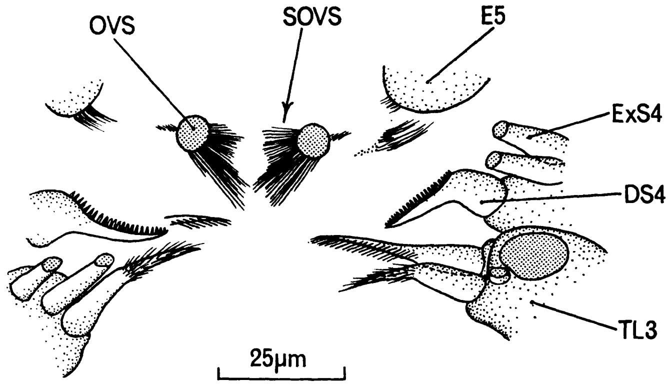

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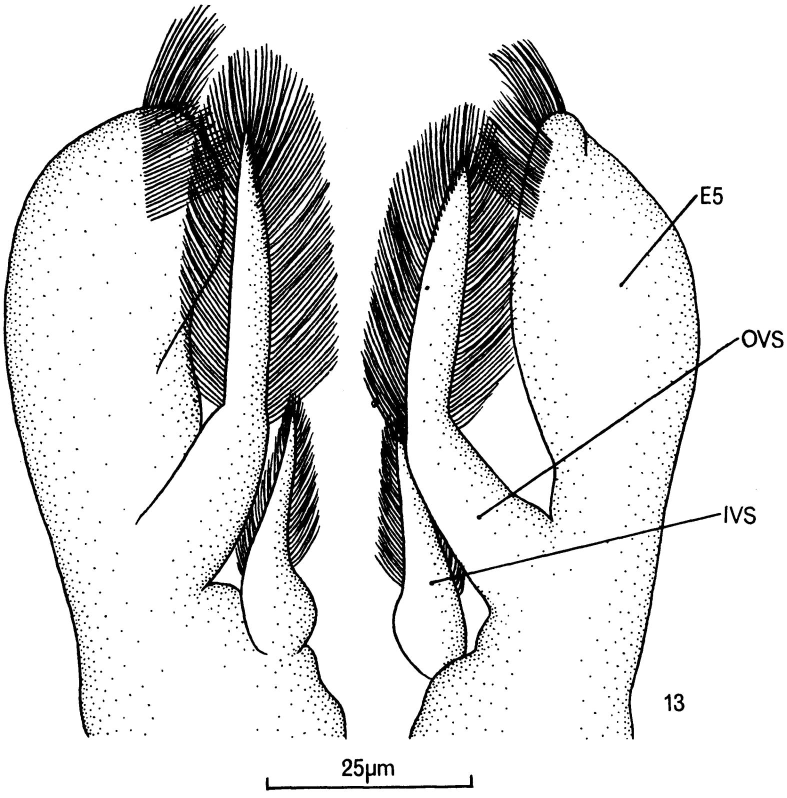
FIGURES 10 to 12. *Alonopsis elongata.*

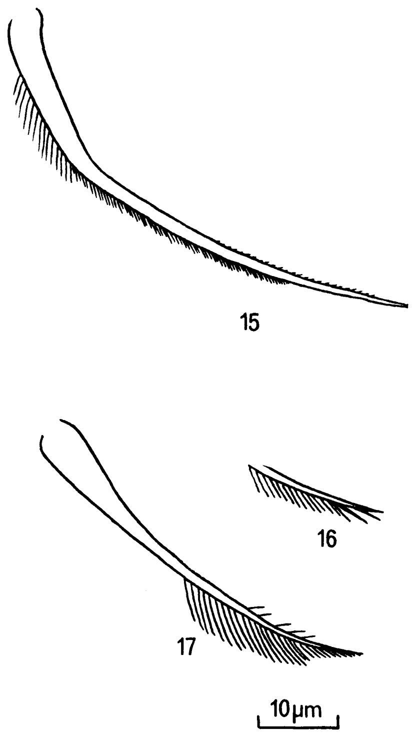
FIGURE 10. Horizontal section through the anterior appendages just ventral to the food groove; ventral. The anterior gnathobasic seta (AGS) of trunk limb 2 is somewhat displaced but serves well to fix the orientation of the appendages shown.

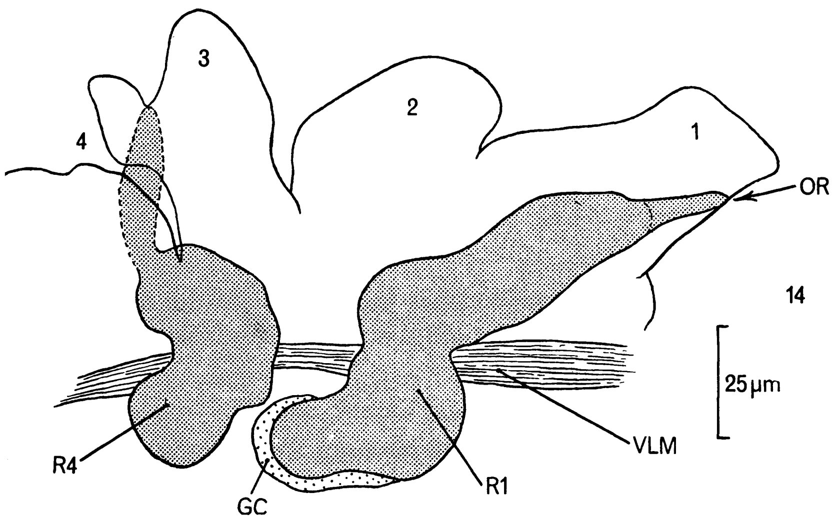
FIGURE 11. Horizontal section through the extreme tip of trunk limb 5; ventral.

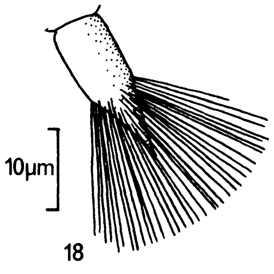
FIGURE 12. Horizontal section through the distal portion of the posterior trunk limbs taken a little deeper than in figure 11.

The exopod of trunk limb 4 is large and flap-like and is provided around its margins









Figures 13 to 18. *Alonopsis elongata.*

Figure 13. Transverse section at the level of the fifth trunk limbs showing how their leaf-like endites and vertical setae seal the posterior end of the filter chamber.

Figure 14. Longitudinal section cutting through the bases of the anterior trunk limbs, as seen from the outside, and showing the secretion-containing reservoirs which discharge on limbs 1 and 4.

Figures 15 to 17. Setae of the gnathobase of trunk limb 2.

Figure 15. Anteriormost seta.

Figure 16. Tip of the third seta.

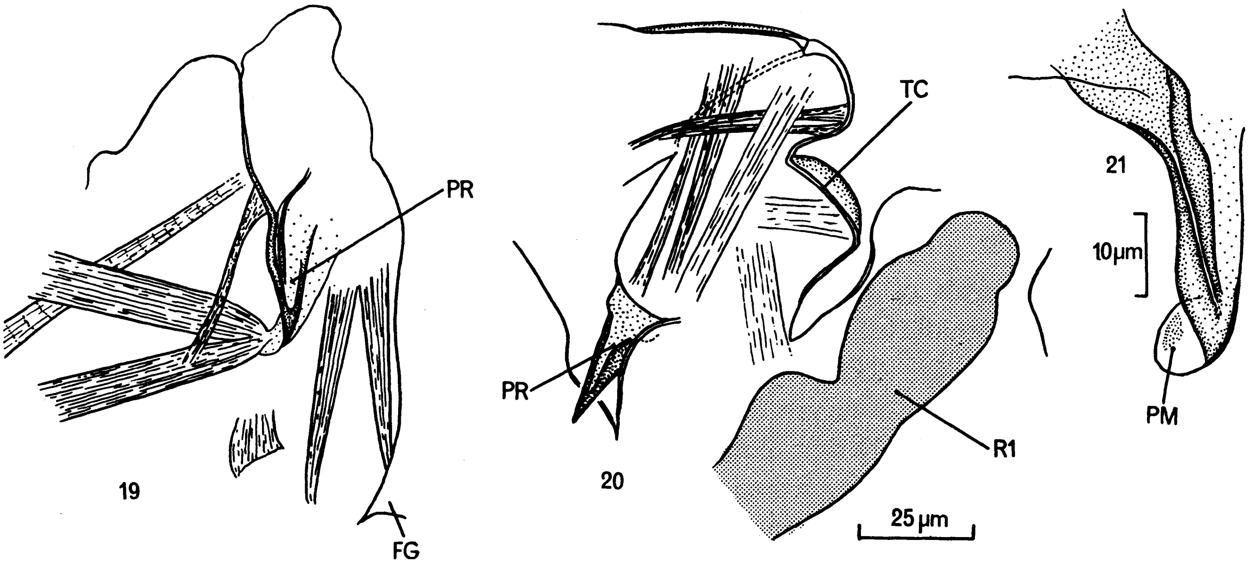
Figure 17. Fifth seta.

Figure 18. Shaving-brush seta.

with the same kind of setae as are present in *Eurycercus*. Each seta has two fringes of setules all of which lie in the same plane as the exopod and effectively increase its surface area.

The fifth trunk limbs (figure 7, TL5) while recognizably similar to those of *Eurycercus*, are much reduced in all parts save the exopod. The corm of each is reduced to a simple lobe with a setose margin. There is no gnathobasic filter plate, and the armature of the corm consists of two setae only. Of these one (figures 7, 8, 12, 13, OVS) is much the longer, is directed vertically, and is provided with lateral setules. Adjacent to and slightly in front of it, and sealing a gap near the level of the food groove, stands the second, smaller, seta (figures 7, and 13, IVS). The exopod is, however, well developed, being similar to that of trunk limb 4 but more elongate.

The sixth trunk limbs are reduced to simple setose lobes.



Figures 19–21. *Alonopsis elongata.*

Figure 19. Transverse section through the posterior extremity of trunk limb 2, from behind, showing the posterior rib of thickened and sclerotized cuticle (PR) and the way in which muscles are inserted on it.

Figure 20. Longitudinal section through trunk limb 2, from the inside to show the posterior rib.

Figure 21. The posterior rib, drawn from a moulted cuticle.

(iv) *The filter chamber*

The filter chamber (figure 7) is similar in many ways to that of *Eurycercus*, but the number of components is reduced. Reduction of filtratory elements is seen particularly at the posterior end but, because the gnathobasic armature of trunk limb 2 is non-filtratory, the number of filtratory elements involved anteriorly is also less. Posteriorly trunk limb 5 plays no part in the composition of the filter chamber and there is no outer filter plate on trunk limb 4. The chamber is therefore made up only from the gnathobasic filter plates of trunk limbs 3 and 4, assisted by modified and not true filter setae borne by the corm of trunk limb 3. It is sealed posteriorly by the flap-like setule-fringed lobes of the corms of the fifth trunk limbs and the vertically standing setae which arise near the base of each (figures 7, 11, 12 and especially 13). Trunk limb 6 plays no part in sealing the chamber (cf. *Eurycercus*).

The setule-lined food-groove is similar to that of *Eurycercus*. Behind the filter plates on each side is a wide exhalent canal. Currents set up by the exopod pump of trunk limbs 4 and 5 enter the carapace chamber, and ultimately the filter chamber, anteriorly and ventrally. The direction of flow, in so far as it can be shown in one plane, is indicated by numbered arrows in figure 3. The stream of water drawn from the antero-ventral region diverges, some (arrow 2) passing dorsal, and some (arrow 3) ventral to the bulk of the labrum. This is the result of the close association of the two anterior margins of the carapace with the labrum (figures 5, 6) described in section (ii), which, dorsally, leaves open a narrow channel on each side of the pedicel of the labrum. Water entering the filter chamber by this route (arrows 1 and 2) passes between the bases of the first trunk limbs and flows backwards through the chamber, ventral to the food groove. Water passing ventral to the labrum (arrow 3) joins that entering from below (arrow 4). Currents entering in the vicinity of trunk limb 4 (arrow 5) are particularly strong and some water is drawn from regions posterior to the filter chamber. The exhalent stream passes out posteriorly, spreading as it does so.

(v) *The feeding mechanism*

Alonopsis is capable of extracting fine particles from suspension. If supplied with a suspension of the small, unicellular green alga *Chlorella*, it filters the cells in the manner described below, passes them to the mouth, and quickly packs its alimentary canal. Nevertheless, the nature of its gut contents, its structure and habits, and the situations in which it lives, leave no doubt that in nature most of its food is collected by scraping material from surfaces. This is accomplished by the scrapers of trunk limbs 2 and 3, perhaps assisted directly by the distal, scraper-like spine at the tip of trunk limb 4.

Trunk limbs 2 and 3 scrape together. Of the scrapers of trunk limb 2, number 6, which is large, stout and somewhat coarsely toothed, is the most important dislodger and collector of material. After this has passed over the substratum it is followed by two longer and more finely toothed brushes (nos. 7 and 8) which sweep up dislodged and straying particles just as in *Eurycercus*. This principle, repeatedly exemplified by anomopods, is used by various substratum-scraping crustaceans of diverse affinities (Fryer 1960, 1963, 1965, 1966). Scraping by trunk limb 2 is towards the mid-line and dorsally, i.e. towards the food groove.

Movement of the scrapers of trunk limb 3 is predominantly backward and dorsal, i.e. they are retracted within the carapace, but also at times inwards towards the mid-line. Such movements scrape or dislodge particles and drag them towards the filter chamber. Movements of trunk limb 3 in animals immersed in a viscous medium (and not feeding) reveal that this limb is very versatile. Movements which cannot be seen when the animal is feeding, including some which are perhaps not used in this process, have been seen, and leave no doubt that the scrapers of this limb play an important part in the collection of food. Sections reveal that the secretion of trunk limb 4, not detected in the living animal, is poured out in the vicinity of the scrapers of trunk limb 3, and particles dislodged by them will inevitably become entangled by it. The mass so accumulated is dragged within the carapace chamber by lunging movements of trunk limb 3 and then pushed towards the filter chamber by trunk limb 4. Whether the distal spine of trunk limb 4 actually participates in scraping or serves only to pass inwards the material scraped by trunk limb 3 is difficult to ascertain. Certainly, however, its structure is very different from that of the other three spines of trunk limb 4, whose function is to push material towards the food groove, and in life it lies in close proximity to the scrapers of trunk limb 3 and appears often to touch them. Its fine denticulation suggests that it serves to sweep up particles dislodged by the scrapers of trunk limb 3, and sections reveal that it can be held parallel to the substratum.

Food is thus collected over much of the length of the ventral embayment of the carapace. That collected by trunk limb 2 is pushed into the rapidly narrowing filter chamber (figures 8, 9) and towards the food groove by the more proximal scrapers (nos. 5, 4 and 3) of that limb so as to be brought within reach of spine number 2, which is large and very coarsely toothed (figure 7) and functions as a rake. This drags material still further towards the food groove and forward, a process which is continued by the similarly specialized, but shorter, spine number 1. As the limb swings forward this spine rakes material along the floor of the food groove. Trunk limb 3 is less important in forcing food into the filter chamber than in *Eurycercus*. The outer 'filter plate' of this limb will deflect inwards any particles which drift towards the filter chamber after being dislodged by trunk limb 2.

Material scraped by trunk limb 3 and entangled by secretions of trunk limb 4 is brought within reach of the spines of trunk limb 4 which push it towards the food groove as they move towards each other in a manner characteristic of many chydorids. Their efforts are aided by the strongly flowing currents which enter the filter chamber in this region (section iv). Material thus comes to lie at the posterior end of the food groove where drifting particles also accumulate.

Because of the currents which flow between the first trunk limbs, secretions discharged from them are carried backwards until they reach the posterior end of the filter chamber and join those produced by the fourth trunk limbs when the animal is feeding. The swinging movements of the second trunk limb perhaps momentarily arrest the backward flow of secretions from time to time because, as they swing forward, they lie very close together. Although water can pass between them a sticky secretion may not so easily do so. It is because of the accumulation at the posterior end of the filter chamber of material exuded from the first (and perhaps fourth) trunk limbs that filtered particles can be agglutinated here. No scraping movements are involved in this, and material accumulates even when the second and third trunk limbs remain stationary.

Because of the foreshortening of the filter chamber and the angle of inclination of the gnathobasic filter plates of trunk limb 4 to the food groove, the distance between trunk limb 2 and the posteriorly-accumulating food mass is not great. Its spines can in fact reach back to the region where food accumulates and, with a single swing, can clear this material and carry it forward. Small particles could not be so handled unless agglutinated into a single mass. This forward transport of the food *en masse* thus differs from the more gradual forward movement in *Eurycercus* and several other anomopods, but in each case transport is effected entirely by mechanical means and against a strongly flowing posteriorly directed current.

Material passed anteriorly is then swept forward by the heavy gnathobasic armature of the second trunk limbs, including the posterior (sweeping) spinules (figures 7, 9 (inset) and 10, PSG). These work in conjunction with the sweeping shaving-brush seta and all swing forward with their tips adjacent to the floor of the food groove. Food is then rammed between the mouthparts by the long gnathobasic spines which reach forward to the level of the mandibles. The tips of these spines from both limbs lie close together as a compact bunch and function as a single ramming unit. Such a compound unit has evolved more than once in the Crustacea, for similar pushing setae made up from elements of right and left proximal endites of the maxillae occur in the thermosbaenacean *Monodella* (Fryer 1965). Orally directed transport of food material is assisted just behind the mandibles by the maxillules.

Although a single swing sometimes suffices to transfer a considerable accumulation of food from the posterior end of the food groove to its anterior regions, many ramming movements of the second trunk limbs may be used to force it between the mandibles. Sometimes particles carried forward break away and slip back to the posterior end of the food groove, thus clearly demonstrating that anteriorly directed currents have no part in food transport.

When excess food accumulates at the anterior end of the food groove the labrum is lowered and the excess removed by the ejector hooks of the first trunk limbs as in *Eurycercus*. This is then kicked clear by the post-abdomen whose denticulate claws reach well forward.

Mandibular movements of the kind described for *Eurycercus* (Fryer 1963) enable food to be dragged between the molar surfaces, rolled forward, and passed to the oesophageal entrance. Peristaltic movements suck food up the oesophagus and discharge it into the wider portion of the alimentary canal.

(vi) *Conclusions*

The locomotion of *A. elongata* is unspecialized and its ventral carapace margins display a primitive condition. The principal differences between its feeding mechanism and associated structures and those of *Eurycercus* are: food is collected by trunk limbs 2 and 3 (by trunk limb 2 alone in *Eurycercus*); the filter chamber is shorter; there is no gnathobasic filter plate on trunk limb 5 or outer filter plate on trunk limb 4, and the setae which comprise the outer filter plate of trunk limb 3 in *Eurycercus* here form a deflector plate rather than a true filter; the main gnathobasic armature of trunk limb 2 is non-filtratory and is used solely for sweeping and pushing; and entangling secretions are exuded from trunk limb 1 as well as from trunk limb 4 and possibly from the labrum. (See also table 3.)

V. THE STRUCTURE, AFFINITIES AND HABITS OF *ACROPERUS HARPAE* (BAIRD)

Although Sars (1862) pointed out the similarity of certain features in *Alonopsis elongata* and *Acroperus harpae*, these species have been unhesitatingly assigned to different genera until Smirnov (1966) re-emphasized the similarity, especially of the limbs, and went so far as to transfer *A. elongata* to the genus *Acroperus*. The present study confirms this similarity of the limbs, though there are slight differences of an adaptive nature which are related to the nature of the food and to habitat preferences. If trunk limb anatomy alone is considered there is no doubt that both species should be assigned to the same genus. Differences are of a quantitative nature, e.g. the two most proximal scrapers of trunk-limb 2 are coarser in *Alonopsis elongata* (figure 7) than in *Acroperus harpae*. Although trivial in the morphological sense such differences reflect important differences in ecology.

Masking these similarities are the carapace and headshield which exhibit mutually incompatible specializations. *A. elongata* has adopted the habit of carrying one or more moulted carapaces while *A. harpae* has developed a chitinous, plate-like, dorsal crest, especially well developed on the head, but which extends also along almost the entire length of the carapace. Carapace shape is also different, being higher (shorter) and narrower in *A. harpae* than in *A. elongata* and there are differences in ornamentation. The ventral margins, however, are so similar in form and armature that the description given for *A. elongata* applies equally well to *A. harpae*, except that here the number of setae is less. Both species are at the same primitive level. Even closely related chydorids sometimes differ widely in this feature in relation to habits (see below), yet here two species with different habitat preferences are similar. The inevitable conclusion is that the similarity reflects affinity, not convergence. There are fewer marginal setae in both the median and posterior series than in *A. elongata*—51 to 58 in all (*ca.* 68 in *A. elongata*).

The genus *Alonopsis* (in which '*A*' *ambigua* has no place—Frey 1965; Smirnov 1966) is here retained solely on account of the striking divergence shown in the form of the headshield and carapace.

A. harpae is common in the littoral region of lakes and smaller bodies of water. While there is some overlap in the type of habitat frequented by it and *A. elongata*, their different preferences are well marked. Although *A. harpae* is occasionally to be found on bare rocky shores (Smyly 1958) such as are regularly frequented by *A. elongata*, or over sand (Flössner 1964), it is much more frequent among vegetation of various kinds where, in England at least, *A. elongata* is of infrequent occurrence. This difference is reflected in the distribution of the two species in Britain: whereas *A. elongata* is absent from the Midlands and S.E. England, *A. harpae* occurs throughout the British Isles.

Like *A. elongata*, *A. harpae* settles on the ventral carapace margins and, under suitable conditions, can balance effectively by extending the long antennae posteriorly and using them as props. When so balanced it can move forward efficiently without moving the antennae and can, for example, creep over the leaves and stems of *Elodea* at any angle. As it balances, the antennules, which share with those of *Alonopsis*, but not most chydorids, the distinction of having one terminal sensilla much longer than the rest, extend laterally and the long sensillae reach out to explore the substrate well beyond the limits of the body. The subterminal sensilla of the antennule explores the substrate ahead of the crawling animal (figure 22). Potential obstacles to the antennal props can therefore be detected in advance.

The dorsal crest of the headshield and carapace, while perhaps also protective, acts like a fin and grants stability when the animal is crawling and perhaps also swimming. This compensates for the narrowness of the 'base' on which a crawling animal rests. Crawling is effected by the first trunk limbs as in *A. elongata*, and food is collected and dealt with in much the same way as in that species. The composition of the food has not been studied in detail and doubtless varies from one habitat to another, but certainly includes both detritus and relatively large algal cells. Large lumps of detritus such as are taken by *Alonopsis* have not been seen in the few guts examined.

The post-abdomen is similar to that of *A. elongata* but lacks the stout marginal denticles so conspicuous in that species (though minute, and perhaps vestigial, denticles are present) and has longer submarginal spinules. These extend beyond the margin so that contact is made with the substrate by many minute spikes which are also directed to a considerable extent outwards. This difference reflects the habitat preferences of the two animals: *A. elongata* often pushes against stones while *A. harpae* generally frequents much softer substrates.

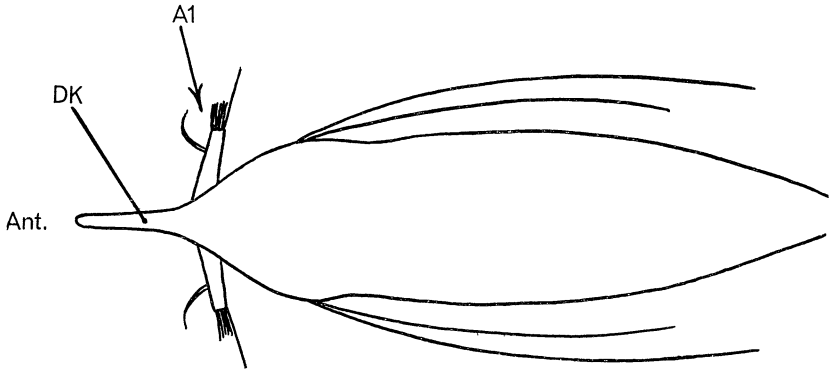


FIGURE 22. *Acroperus harpae*. Diagrammatic sketch showing the orientation of a balanced individual and its antennules. The antennae, which are extended as props, are omitted but their setae are indicated.

The antennae are very similar to those of *A. elongata* but are relatively longer and more slender. They are armed with shorter and more slender spines than the scrambling spines of *A. elongata* but no real evidence has been obtained to show that they serve the same functions.

A. harpae is an active species and can swim rapidly as well as crawl, though it seems to be a less persistent swimmer than *A. elongata*. The best swimming speed recorded for a female 0·609 mm in length over a distance of 5 cm was 8·33 mm (*ca.* 13·7 body lengths)/s, which is very similar to the maximum recorded for *A. elongata*, but was sustained for a shorter period of time.

Other morphological features are indicated in table 3. No secretions originating from the first trunk limbs and no secretion-filled reservoir, such as is readily seen in *Alonopsis*, have been demonstrated.

(i) *Conclusions*

The obvious differences in carapace form between *Acroperus harpae* and *Alonopsis* mask a close similarity in the form and armature of their ventral margins. Both have similar feeding mechanisms.

VI. THE STRUCTURE AND HABITS OF *CAMPTOCERCUS RECTIROSTRIS* SCHODLER

This species shows evidence of relationship with *Alonopsis* and *Acroperus* in several respects, such as the nature of the post-abdominal articulation and head-pore arrangement. Although the trunk limbs differ in details from those of *Alonopsis* and *Acroperus*, their structure is broadly similar, as is the feeding mechanism. Bilateral compression is more extreme than in *Acroperus*, and permits the penetration of narrow gaps among vegetation, but may have more general adaptive value—as in locomotion—of which we are yet unaware. The danger of correlating such a body form with a particular way of life is illustrated by comparing the ecology of this species with that of the equally compressed *C. lilljeborgi* Schödler. Flössner (1964) found that while *C. rectirostris* occurred occasionally among those types of vegetation to which *C. lilljeborgi* was largely confined, it also occurred among plants not frequented by this species and in non-vegetation covered situations both over mud and detritus-covered sand, from which *C. lilljeborgi* was completely absent.

Like *Acroperus harpae*, *C. rectirostris* has a conspicuous dorsal crest which grants stability in a bilaterally compressed animal. The ventral carapace margins are similar to those of *Alonopsis* and *Acroperus*, and the embayment is relatively wide so that, in spite of the narrowness of the body, *C. rectirostris* has no difficulty in balancing on, and crawling over, a surface when the antennae are extended as props, even though these are relatively shorter than those of *Acroperus*—provided the first trunk limbs can grip. It is unable even to balance satisfactorily on a clean glass surface but can do so easily if a bacterial film has developed. The first trunk limbs are each provided with powerful grasping spines distally and also have a fleshy distal lobe such as is not found in any other genus examined. When the animal is balanced on the ventral carapace margins, the antennules, of whose distal sensillae two are elongate, extend laterally much as in *Acroperus*.

The post-abdomen can be deflected outside the carapace, whose outer surface it can wipe, and can be swung rapidly through a very wide angle. This mobility depends upon a highly specialized pivot joint between the trunk and the post-abdomen, and specialized musculature of which some account has been given by Green (1956). By use of this mobile post-abdomen *C. rectirostris* can propel itself with great violence from a position of rest, and this may serve as an escape mechanism.

Certain anatomical characteristics of this species are shown in table 3. The exopod of trunk limb 5 only is involved in the pumping of water through the carapace chamber. Of the species studied *C. rectirostris* is unique in this respect. Of the scrapers of trunk limb 2, number 6 is short and stout and armed with particularly large teeth such as suggest the ability to dislodge attached particles. The few guts examined, however, indicate only that, like most chydorids, *C. rectirostris* scrapes up both very finely particulate detritus and larger lumps of debris and also collects algal cells.

(i) *Conclusions*

Camptocercus exhibits specializations of the carapace which are similar to those of *Acroperus* and different from those of *Alonopsis*. The ventral margins, however, are of the same grade of organization in all three, and in all is the feeding mechanism similar.

These genera exhibit progressive specialization of the post-abdomen: trunk joint. Simplest in *Alonopsis*, this reaches its highest point of refinement in *Camptocercus*. A much less specialized joint is found in many chydorids which exhibit considerably greater overall specialization.

VII. THE STRUCTURE, HABITS AND FEEDING MECHANISM OF *ALONA AFFINIS* LEYDIG

Alona affinis (adult females length 1 mm) may be regarded in some ways as a smaller version of *Eurycercus*, but also shares with *Alonopsis* certain features not found in *Eurycercus*. In this it exemplifies the mosaic-like pattern of evolution found within the Chydoridae. Its filter chamber is made up from almost exactly the same components as that of *Eurycercus* but it also bears distal scrapers on trunk limb 3 as does *Alonopsis*. It also differs from both, sometimes in ways which, while superficially trivial, nevertheless give an insight into the manner in which radiation within the Anomopoda has been made possible.

In the armature of the ventral margins of the carapace *A. affinis* to some extent bridges the gap between *Alonopsis elongata* and *Peracantha truncata* (see below). For this reason it is convenient to describe *A. affinis* first.

(i) *Ecology and habits*

While tolerant of a wide range of conditions *A. affinis* shows a preference for life on or among bottom sediments in the littoral zone of lakes and smaller water bodies. Although found among vegetation it does not appear to scramble among those parts of higher plants which are far removed from the bottom to the same extent as several other chydorids, and often occurs in situations from which higher plants are absent. This was the experience of Smyly (1958) who found it in more than eighty tarns, while Flössner (1964) found it to be more abundant on sandy and muddy bottoms than among various types of vegetation. I have frequently found it by scraping the surface of detritus- or algal-covered stones. Its structure and locomotion are well suited to life in such situations for it has a stout post-abdomen capable of transmitting powerful thrusts (section ii) and uses its antennae for scrambling and forcing its way through detritus, which it does with great agility. When conditions are suitable it settles on the ventral carapace margins of the embayment region and can balance by gripping with the first trunk limbs alone. Crawling is always jerky and not particularly effective, and receives assistance from the antennae which may either make swimming-type rowing movements or be used independently of each other to push on the bottom.

Although Lilljeborg (1900) describes its movements as sluggish it is capable of rapid movements among debris when these are necessary, and it swims well, though slowly, and usually for short distances only. Over a distance of 9 cm a female, 0·94 mm in length and carrying eggs, maintained a speed of about 4·3 body lengths (just over 4 mm)/s. The average speed recorded was very similar to this and even over considerably shorter distances appreciably faster speeds were seldom recorded, nearly 5·2 body lengths/s over 3·5 cm, being the best save for a record of over 5·5 body lengths/s over only 1·1 cm. The swimming speed is therefore only about one-third that of the similarly sized *Alonopsis elongata*. The difference clearly reflects the different habits of the two species.

The food consists of material scraped from the substratum and, as in many chydorids, its composition varies according to the situation in which the animal is living. It is therefore difficult to compare different species. *A. affinis*, however, sometimes ingests large particles. These include naviculoid diatoms whose length is considerably greater than the diameter of the gut, and large inorganic particles. Other large diatoms, including centric species, are also eaten, and other algae have been seen in the gut. These almost always lie in a matrix of indeterminate detritus and inorganic particles. Specimens living in Esthwaite Water on the surface of a stone on which *Melosira* had settled had eaten much more of this centric diatom than any other food, 53 cells being counted in one gut. The maximum number of cells per chain was four. Specimens living on the stony bottom of a tarn in close association with *Pleuroxus uncinatus* had collected very similar food though the particles of inorganic material ingested by *A. affinis* tended to be larger than those ingested by *P. uncinatus*. Specimens of these species and of *Camptocercus rectirostris* kept in the same dish, the bottom of which was covered with the fine grit and detritus collected with the animals, collected essentially the same mixture of organic and inorganic material though *A. affinis* ingested some particles of a larger size than were collected by the other species.

(ii) *Anatomy*

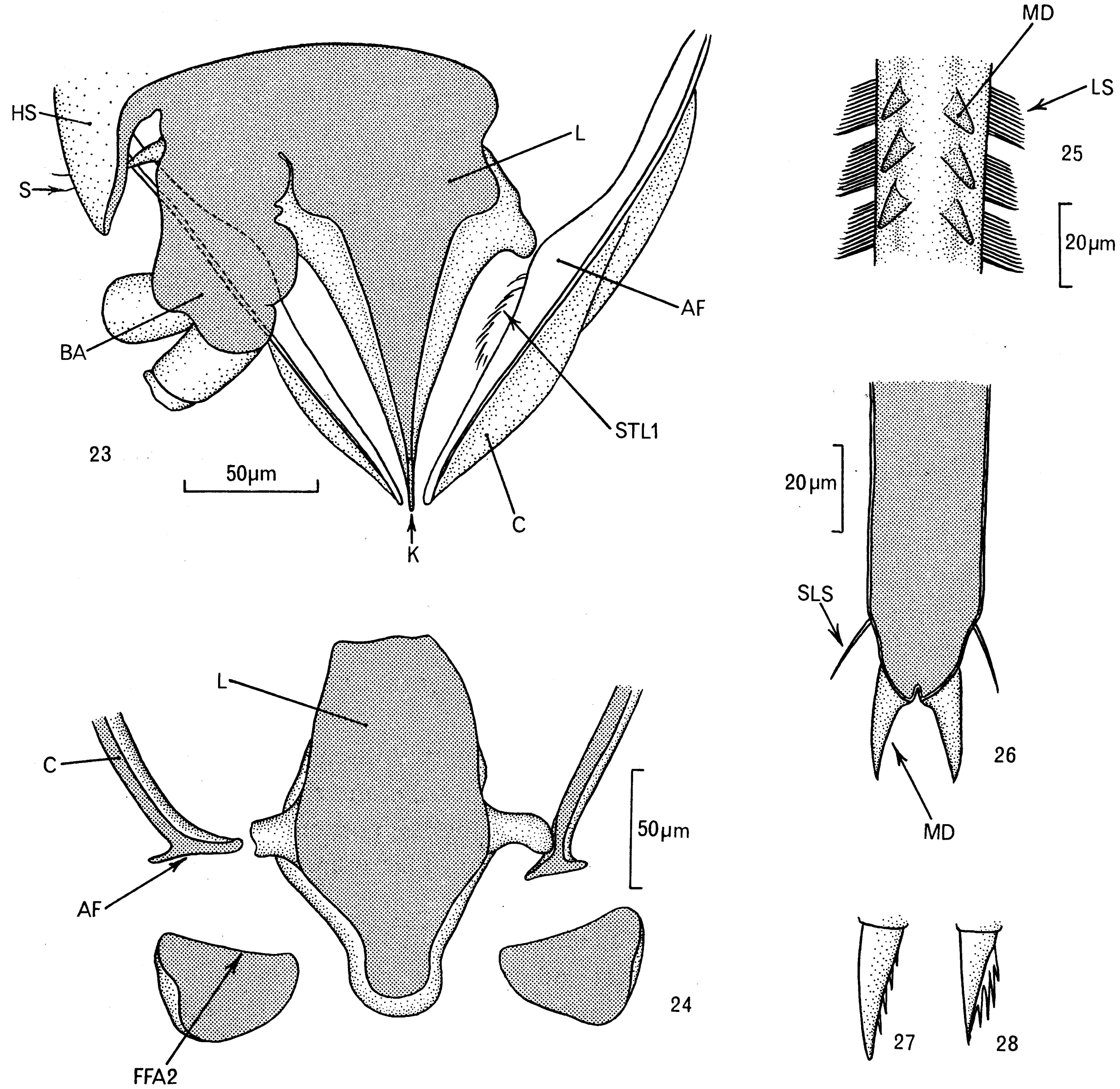
The headshield and carapace resemble those of *Alonopsis elongata* in general form but the carapace is shorter (higher) and less bilaterally compressed. The ventral carapace margins are straight fore and aft of the obtuse angle which lies somewhat anterior to the middle. Anterior to the angle there is an embayment, anterior and posterior to which the carapace margin is produced inwards as a narrow flange which almost disappears in the region of the embayment itself. Anteriorly there is a well-developed flange of great functional significance (figures 23, 24, AF) where, in *Alonopsis*, there is no more than a thickening of the carapace margin (figure 5, ACM).

The carapace margins are armed with about 75 setae. Although these are only slightly more numerous than in *A. elongata* and extend along the anterior margin (unarmed in *Alonopsis*) as well as the ventral margin, those fringing the post embayment region of the ventral margin are closer together than in *Alonopsis*. This reflects the relatively shorter carapace of *A. affinis*.

Anteriorly are some 23 long setose setae of which about 10 are truly anterior and about six arise on the curve between the anterior and ventral margins. These follow the curve of the carapace and are directed somewhat inwards. Each has two rows of setules of which on the anteriormost setae the posterior is the longer and stronger. The rows are about equally well developed on the long ventral setae. Numbers 24 to 36 fringe the embayment and are much shorter. Their orientation is as in *Alonopsis*. Posterior to the embayment the arrangement and armature of the setae is as in *Alonopsis* but, because the setae are closer together, the posteriorly directed row of setules extends back so as just to touch the seta next behind. It is in this respect that the condition in *A. affinis* bridges the gap between *Alonopsis* and *Peracantha*.

The setae which fringe the anterior carapace margins appear to serve as a grid to prevent the ingress of large particles which may slip between the carapace valves anteriorly as the animal scrambles among detritus. Clumps of carmine particles are so excluded in specimens watched under artificial conditions.

In nature it seems probable that the coxae of the antennae seal the dorsal region of the anterior apertures of the carapace (on each side of the labrum) by lying against the anterior flange as they undoubtedly do in *Graptoleberis* (p. 314). Certainly the anterior flange is markedly widened dorsally (figure 23, AF) and the posterior face of the antennal coxa is



Figures 23 to 28. *Alona affinis.*

Figure 23. Transverse section just anterior to the anterior carapace margin—here a distinct flange. Note the relationship of the basal region of the antenna to the anterior carapace flange.

Figure 24. Horizontal section through the anterior region of the carapace. Note especially the elaboration of the anterior carapace margin into a flange and the flattened face of the basis of the antenna which lies opposite this flange.

Figure 25. Ventral aspect of part of the post-abdomen. Note especially the wide lateral spread of the lateral squamae.

Figure 26. Transverse section of the post-abdomen, relatively proximal. Proportions can be appreciated by noting that approximately half the height of the body of the post-abdomen is shown in the illustration.

Figure 27. The third marginal denticle from the distal end of the post-abdomen, seen from the side.

Figure 28. The ninth marginal denticle likewise.

flattened in such a way that, when flange and coxa make contact, an effective seal could be produced (figure 24). Observation of currents in freely moving animals of this size, however, is almost impossible. In individuals whose movements are restricted so that currents can be observed, struggling inevitably ensues and water then does enter by the anterior dorsal apertures as well as more ventrally, but this may be abnormal.

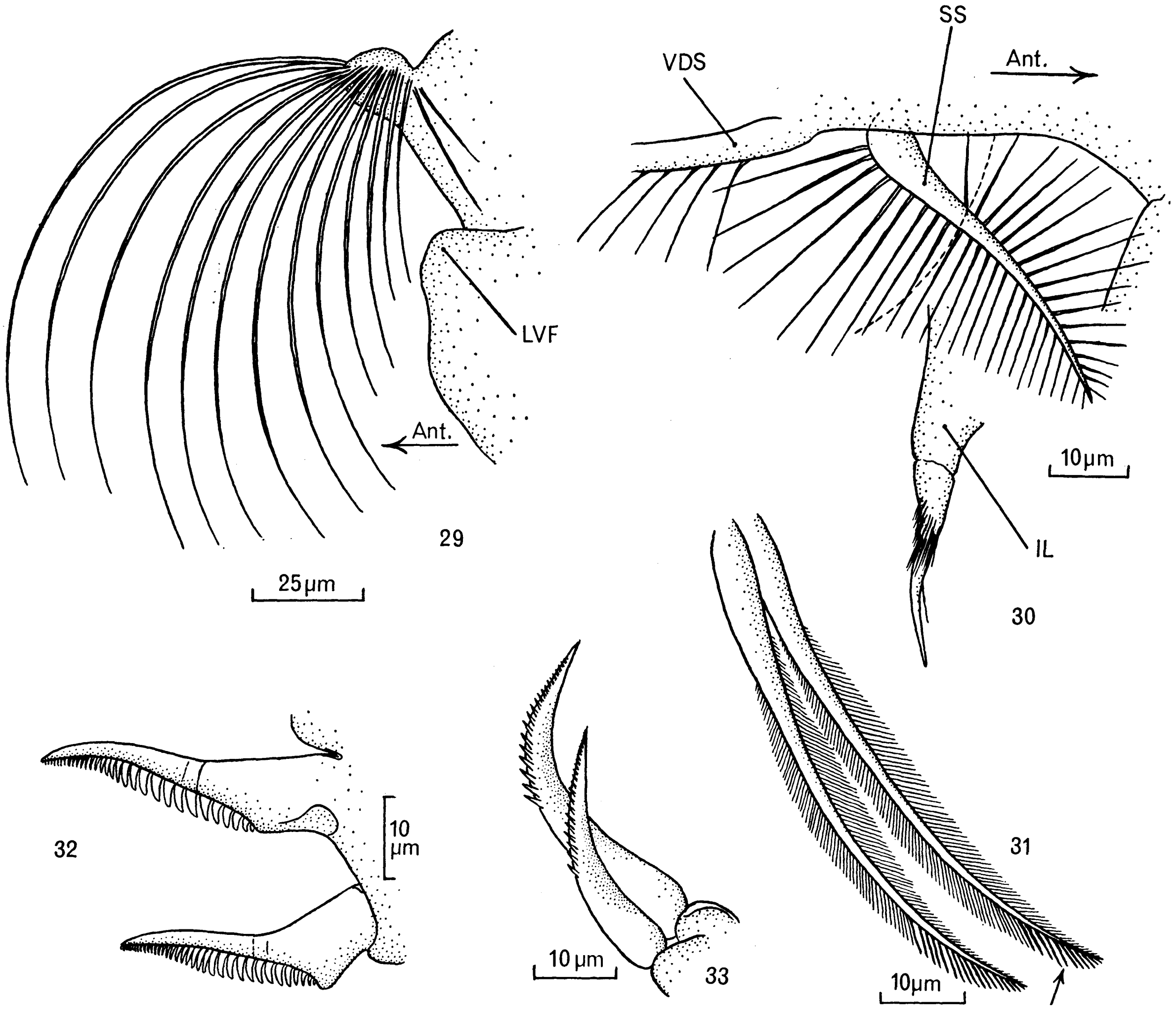
The post-abdomen (figures 25 to 28) is robust and also wide. Its width is not apparent in published illustrations which show it from the side (cf. the narrow post-abdomen of *Eurycercus* with its single row of marginal denticles—Fryer 1963, text-fig. 44). It is armed with two well-spaced rows of stout marginal denticles (MD) and, submarginally, with what in taxonomic works are often called lateral squamae (LS). Each marginal denticle is provided posteriorly with a row of spinules (figures 27, 28). Each group of lateral squamae consists of a row of up to about 12 spinules (figures 25, 26, LS) which are directed outwards as well as ventrally. This orientation is very striking when the post-abdomen is seen from below (figure 25) or in transverse section (figure 26). Such an armature is suitable for use on both hard and soft bottoms over both of which *A. affinis* occurs. On hard bottoms pushing is effected by the stout marginal denticles and neither their posterior spinules nor the relatively delicate spinules of the lateral squamae bear any load. On soft bottoms, or hard bottoms covered with soft detritus, into which the stout marginal denticles will sink, the outspread spinules of the lateral squamae, which present a large total surface area to the substratum, are well suited to prevent sinking and to give purchase. In these functions they are aided by the posterior spinules of the marginal denticles and by the divergent terminal claws. The functional significance of the lateral squamae in *A. affinis* and other chydorids seems hitherto not to have been appreciated, though they have long been used as taxonomic characteristics. Flössner (1964) records that the post-abdomen of individuals living on muddy bottoms, tends to be slighter deeper and to have longer marginal denticles than that of individuals found elsewhere.

The antennules are similar to those of *Alonopsis* save that the subterminal sensilla is not far removed from the tip. The antennae are used both for scrambling and swimming and have both scrambling spines and swimming setae. The exopod bears a stout scrambling spine on its basal segment and a somewhat less stout spine on its distal segment as in *Alonopsis*, but the endopod bears a stout spine only on its distal segment. Segment 2 of the endopod, however, bears an arc of stout spinules distally which grant purchase and which may well be more effective in muddy situations than a single spine (cf. *Leydigia*). Both the exopod and endopod bear three swimming setae distally and in each case the basal section is provided with a row of spinules, again related to the use of the antennae as props and during scrambling.

The labrum (figures 23, 24 L,) is a source of entangling secretions; mandibular articulation is of type A; and the maxillules are similar in form to those of *Alonopsis*.

The trunk limbs and the arrangement of the filter chamber are basically similar to those of *Eurycercus*. There is a gnathobasic filter plate on trunk limb 5 and an outer filter plate on trunk limb 4, both of which are absent in *Alonopsis* (table 3).

Internally and towards the anterior distal extremity of trunk limb 1 is a lobe from which arises a fan of long fine inwardly- and anteriorly-directed setae (figure 29)—the anterior distal fan. Its setae resemble those which arise in six rows on the ventral face of the limb. It in no way interferes with the free passage of any small particles that may be drawn in with the inhalent current entering the carapace chamber anteriorly at each side of the ventral part of the labrum. It serves as a cleaning device and, like the anteriormost of the groups of setae on the corm of the limb, wipes the sides of the labrum. Any detritus which finds its way inside the carapace and is not carried back by the inhalent current is inevitably pushed posteriorly by the successive rows of setae of this limb.



Figures 29 to 33. *Alona affinis.*

Figure 29. Anterior distal fan of setules of trunk limb 1.

Figure 30. The screening seta of trunk limb 1 as seen from a dissection. The dotted line shows the anterior margin of trunk limb 2 and has been sketched in from a longitudinal section.

Figure 31. Anterior gnathobasic setae numbers 2 and 3. Note the stouter spinules distally on the posterior margin (indicated by arrow).

Figure 32. Endite spines 1 and 2 of trunk limb 2.

Figure 33. Distal spines of trunk limb 3.

Arising from the inner dorsal face of trunk limb 1, and directed towards the food groove and anteriorly, is a seta provided anteriorly and posteriorly with a row of well-spaced setules of considerable length (figure 30, SS) and arranged in one plane. Anteriorly a few of the basal setules are deflected ventrally: otherwise all lie more or less at right angles to the seta whose position is such that it lies across, and prevents particles from slipping through, the gap between trunk limbs 1 and 2. It is therefore called a screening seta. The deflexion of the anterior basal setules enables them more effectively to cover the aperture adjacent to them. A similar end has been achieved by different means in *Eurycercus* where a gap to the exhalent canal is sealed by a modification of the anteriormost gnathobasic seta of trunk limb 2 (Fryer 1963, text-figs 27, 28, 45, 47 inset (*a*), and 52), and by means which are different again in *Peracantha* (figure 47). The 'inner lobe' is reduced to a single seta (figure 30, IL) as in *Alonopsis*, but is here thicker and more conspicuous than in that species, and is prolonged into a very delicate finger which is not easily seen.

Several of the gnathobasic setae of trunk limb 2 serve both as filter setae and as brushes for sweeping food along the food groove. The anteriormost is like a normal filter seta but a trifle broader particularly near its tip. It is a little shorter than the next and is inclined forward so that the gap between the tips of the first two setae is wider than that between the second and third. Setae 2 to 4 are in most respects typical filter setae but distally a few of the posterior setules are replaced by stouter, spinule-like structures (figure 31). The fifth is shorter and its tip is unmodified, the sixth shorter still, spine-like, and armed basally with filtratory setules, distally with stouter setules. Posterior to the filter plate is a 'shaving brush' seta like that of *Alonopsis* but a little longer.

Modifications for the mechanical transportation of food along the food groove occur in several chydorids and do not always take the same form. Thus the brushes of the gnathobasic setae of *A. affinis* differ from those found in *Eurycercus* where, near the tip of the setae, there is a supernumary row of spinules behind the rows of filtratory setules (Fryer 1963, text-figs. 29–31).

In its orientation with respect to the filter plate of trunk limb 3 and to the food groove the filter plate of trunk limb 2 is much more like that of *Eurycercus* and *Peracantha* (figure 47) than that of *Alonopsis*, and cannot be swung forward to the same extent as that of *Alonopsis*. Correlated with this is a difference in the denticulation and function of the more proximal scrapers of this limb which are much less coarsely toothed than those of *Alonopsis*. (Compare figures 32 and 7.)

The outer plate of trunk limb 3 is reduced to four setae (seven in *Eurycercus*) which bear longer and more widely separated setules than do the gnathobasic filter setae of trunk limbs 3 and 4. While not strictly a filter plate this will inevitably act as a strainer of relatively coarse particles (though the gaps between adjacent setules are very narrow) as well as a deflector plate. The outer filter plate of trunk limb 4 is reduced to three setae (six in *Eurycercus*) whose setules are more closely set than those of the outer plate of trunk limb 3, but are slightly wider apart than those of the gnathobasic filter setae. Near its base and ventrally the most distal has a row of long and exceedingly fine setules which are a continuation of the more distal filtratory setules of its side.

A pair of well-developed scrapers is present distally on trunk limb 3 as in *Alonopsis* (figure 33). The distal spine of trunk limb 4 is very similar to that of *Alonopsis* shown in figure 7, and has the appearance of a scraper but is unable to reach the substratum. It and the next most distal spine, which is armed with long spinules, serve to seize and pass inwards to the filter chamber material collected by the scrapers of trunk limb 3.

(iii) *The feeding mechanism*

In several basic features the feeding mechanism resembles that of *Eurycercus* and *Alonopsis* but differs from both in various ways. Currents set up by the posterior exopod pump flow through the filter chamber and are an essential component of the feeding process. A longitudinal section of the filter chamber resembles that of *Eurycercus* (Fryer 1963, text-fig. 45) and that of *Alonopsis* (figure 7), but exhibits a condition intermediate between them. (See also the filter chamber of *Peracantha truncata*, (figure 47).) The gnathobasic filter plate of trunk limb 4 is less well developed than that of *Eurycercus* but better developed than that of *Alonopsis*, and the gnathobasic filter plate of trunk limb 5 (well developed in *Eurycercus* but absent in *Alonopsis*) is represented by three setae. An outer filter plate of trunk limb 4 (composed of five setae in *Eurycercus* but completely absent in *Alonopsis*) is present but is reduced to three setae. In its position, and in the extent to which it can be swung forward, trunk limb 2 lies between the two extremes presented by *Eurycercus* and *Alonopsis*.

Food is collected by the distal armature of trunk limb 2 and the distal scrapers of trunk limb 3 and passed to the filter chamber in a similar manner to that of the species already described. Pushing by trunk limb 4 is important. Food is passed forward along the food groove by the gnathobasic filter setae of trunk limbs 3 and 4, especially the former. Whether those of trunk limb 5 (three only) contribute actively to this or serve merely as passive sieves is not known. If they make a contribution, and they presumably move slightly to be cleaned, it must be small. That made by trunk limb 4 is probably not great. The gnathobasic filter plate of this limb curves round the posterior end of the filter chamber and is the most important element in sealing this region.

As in most chydorids trunk limb 2 is very versatile and can perform movements suitable both for collecting material from the substratum and for transferring it towards and forward along the food groove. The two actions can be performed independently. Food collection necessitates movement towards the mid-line of the distal portion of the limb where the scrapers are arranged more or less in the horizontal plane, the outer brushes lying further from the mid-line than the scrapers. These elements lie more or less at right angles to the three proximal scrapers. For inward and forward transport of the food the limb is swung well forward. From the amount of swing to be observed and from the anatomy of the limb it is deduced that the tips of the filter plate setae reach forward only to just beyond the posterior limits of the maxillules and not to the level of the mandibles as they do in *Alonopsis* (figure 7).

In *Alonopsis* the shaving brush seta is short and its setules do not interfere as the gnathobasic armature is swept along the food groove (figure 7). In *A. affinis* this seta is longer and protrudes beyond the heavy armature. The latter can therefore never sweep along the food groove, and its function must be confined to forcing food towards it as in *Eurycercus*, and not forward along it as in *Alonopsis*. The same applies to the more ventral spinules. The seta which is part of this armature does sweep along the food groove, but only along its side, towards which its setules are directed. Even if it brushes material its contribution must be very small, and it appears to be sensory. Sections reveal that although the shaving brush seta protrudes beyond the heavy gnathobasic armature it never sweeps along the food groove. Considering the masses that accumulate there it is in any case too delicate to be so employed. Its main function is therefore to assist in sweeping particles towards the food groove and it probably also helps to clean the tips of the anterior setae of the filter plate of trunk limb 3.

The way in which the brush-like modification of the tips of the gnathobasic filter setae of trunk limb 2 (figure 31) sweep is apparent from their position in relation to the food groove, and can be seen in the living animal. The most anterior seta does not have a brush-like tip. Because this seta is inclined forward its tip lies further from the bottom of the food groove than those of its fellows. This difference in orientation facilitates the pushing of food particles on a broad front. It is to prevent the escape laterally of food particles in the vicinity of trunk limb 2 that the grid seta of trunk limb 1 (figure 30) has been developed.

Other features of the feeding mechanism are similar to those of *Eurycercus* and there are similar refinements such as the use of ejector hooks for clearing excess food from the anterior end of the food groove.

Entangling secretions are employed by *A. affinis*, although their origin has not been proved in the clear and unequivocal manner so easily accomplished in certain other species by means of adequate techniques. No secretion-containing reservoir is present in trunk limb 4. Whether trunk limb 1 produces secretions is not known with certainty. In the living animal, what appears to be a reservoir similar to that of *Alonopsis* can sometimes be made out. What appears to be its narrowing neck leading to a position similar to that at which the reservoir of *Alonopsis* discharges suggests that it is of similar nature. In sections, however, such a reservoir, easily seen in *Alonopsis*, is seldom to be discerned. In one longitudinal slice the outlines of what appear to be a reservoir can be seen but no trace of any secretion, which always stains very positively in *Alonopsis*, is present. The labral glands certainly produce secretions which have been seen clearly within their ducts, but the only discharged secretion seen was a mass trapped at the posterior end of the filter chamber whose origin cannot be established.

(iv) *Conclusions*

A. affinis and *Alonopsis* are equally adept at crawling over surfaces but differ in the armature of their ventral carapace margins.

Apart from the employment or non-employment of scrapers of trunk limb 3 for food collection, the feeding mechanisms of *Eurycercus*, *Alona affinis*, and *Alonopsis* differ in the manner in which food is passed forward along the food groove. In *Eurycercus* the gnathobasic filter plates of trunk limbs 2, 3, 4 and 5 are involved in this: in *A. affinis* the contribution made by trunk limb 5, if any, is negligible and that of trunk limb 4 is reduced: in *Alonopsis* only trunk limbs 2, 3 and 4 are involved and of these trunk limb 2 plays by far the most important role, and here elements other than the gnathobasic setae are actively involved.

VIII. A COMPARISON OF SOME SMALLER SPECIES OF *ALONA*

As at present constituted, the genus *Alona* contains numerous species which exhibit considerable adaptive radiation both in structure, e.g. of the post-abdomen, and in the range of habitats frequented. Morphological differences between species may be very small, as between *A. affinis* and *A. quadrangularis* (O. F. Müller), or considerable. The size ranges from about 1 mm in length (*A. affinis*) to as little as about 0·3 mm (*A. protzi* Hartwig) among British species. Some small species, such as *A. guttata* Sars, which occurs in both large lakes and very small bodies of water, and even in springs, are tolerant of a wide range of physico-chemical conditions, provided detritus, muddy or otherwise, or moss, is available as a substratum. Others appear to have more specialized requirements if investigation is confined to one locality. For example, in an area in which I collected extensively in a variety of habitats, I found *A. rustica* Scott only in very small pools in which *Sphagnum* was present, on or adjacent to acid moorland. Here it was often not uncommon and in the situations in which it occurred was the only anomopod found. Elsewhere in the same district it was never seen (Fryer 1953). Such a clear-cut ecological distribution is not, however, so apparent if the wider distribution of the species is considered, for *A. rustica* is recorded from other habitats elsewhere, even including lakes (Frey 1965). The possible existence of local races or of cryptic species such as Price (1958) has demonstrated for the copepod '*Cyclops vernalis*', and the influence of such factors as competitive exclusion, of which we are still ignorant, make it difficult to define the ecological preferences of such animals.

This is true of three common small species studied alive during this study; *A. costata* Sars (length *ca.* 0·6 mm), *A. rectangula* Sars (*ca.* 0·5 mm) and *A. guttata* (*ca.* 0·4 mm). All are common in Britain but vary in abundance in different localities. In the English Lake District *A. guttata* is very common, *A. rectangula* common, and *A. costata* distinctly uncommon (Scourfield & Harding 1958; Smyly 1958), but it is difficult to see which requirements of *A. costata*, which is common in certain other areas, are not met in this locality. Langhans (1911), Smyly (1958), Flössner (1964) and others, have provided ecological data for all three species, but neither these nor personal observations reveal clear-cut differences which are applicable over their entire range of distribution.

All are creeping species which also swim when necessary, and all are associated with such a variety of substrates, except for bare rock and perhaps exposed sand, that no consistent pattern of preferences is discernible. All can use the ventral carapace margins for balance, but *A. guttata* for long failed to demonstrate this when watched. This species flourished in vessels on whose bottom a layer of flocculent detritus had accumulated and into which it freely burrowed. Under such conditions, which it evidently appreciated, the need to balance never arose. Both antennae and post-abdomen are used to enable it to plough through detritus. Both the exopod and the endopod of the antenna are armed with stout scrambling spines.

By contrast *A. costata* is a persistent crawler which reveals its habits even in a glass vessel. It balances well on the ventral carapace margins where the arrangement of setae is similar to that in *A. affinis* (though there are no anterior setae) and uses the antennae as props. Antennal scrambling spines are present as in *A. guttata* and the terminal setae are spread to facilitate balancing. Trunk limb 1 is provided on its outer lobe with well developed grasping claws similar in many respects to those of *Chydorus sphaericus* (figure 125).

A. rectangula uses the ventral carapace margins but has not been studied in detail. The long lateral squamae of its post-abdomen (relatively longer than those of *A. affinis*) suggest better adaptation to muddy bottoms than in the other two species, but published ecological data do not at first sight always support this. Consideration of the work of Langhans (1911), Johnson (1951), Smyly (1957, 1958), and Flössner (1964), however, suggests that it prefers detritus-rich situations at the base of plants.

A. guttata and *A. costata* have been sectioned in all three planes and morphological data are given in table 3. The maximum swimming speed of *A. guttata*—6·94 body lengths (2·5 mm)/s, achieved by a female 360 μm in length and carrying embryos, over a distance of only 8 mm—is shown in figure 148. This species sometimes swims more persistently but more slowly, e.g. 5 cm covered at about 4·86 body lengths (1·75 mm)/s and 2·7 cm at almost 6·4 body lengths (about 2·3 mm)/s.

IX. THE STRUCTURE, HABITS AND FEEDING MECHANISM OF *PERACANTHA TRUNCATA* (O. F. MÜLLER)

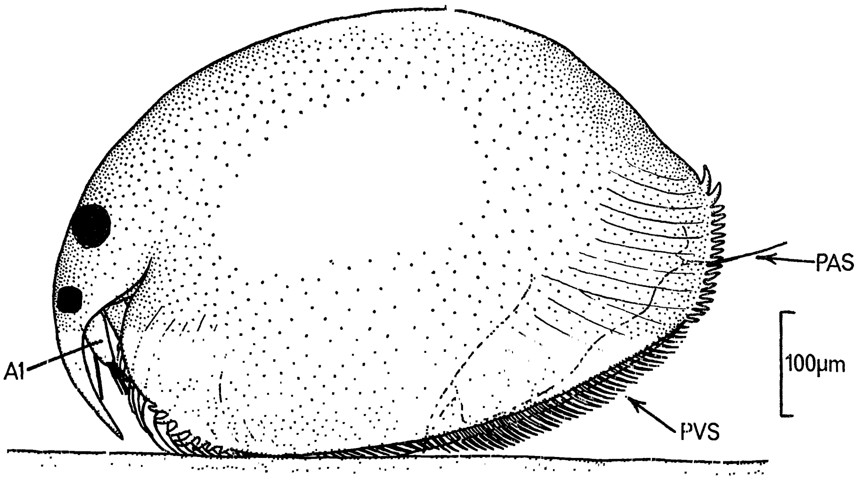
In the structure of the limbs used for the collection and manipulation of food, and in the composition of the filter chamber, *Peracantha truncata* is similar to *Alona affinis* and *Eurycercus* though there are many small but significant differences. In the elaboration of the carapace margins it is specialized in relation both to locomotion and to food collection. The most important of these specializations foreshadow those of a more highly developed nature in other species. The feeding mechanism is therefore dealt with briefly and in a comparative manner but locomotion and the structural features on which it depends are described in more detail.

(i) *Structure, ecology and habits with particular reference to locomotion*

P. truncata (length *ca.* 0·65 mm) is common in Europe, is usually found among vegetation (see Smyly (1957, 1958) and Flössner (1964) for recent references to habitats), and occurs both in the littoral region of lakes and in smaller bodies of water. Although it can swim rapidly and effectively, its habit is to crawl over the surfaces of plants, and perhaps over the bottom also for this it does in vessels. Given suitable conditions it habitually settles on the ventral margins of the carapace and crawls (figures 34 to 36).

Its appearance as seen from the side is well known, but orientation with respect to a substratum (figure 34) is not apparent from figures in taxonomic texts. Very characteristic is the row of teeth which line the posterior margin of each carapace valve and the equally stout incurved teeth which are present on the anterior margin. Although conspicuous the anterior and posterior carapace teeth are not of such great functional significance as are some less apparent elaborations of the carapace. Less well known than the lateral view, but equally characteristic when the habits of the animal are understood, is the dorsal view (figure 35) which is obtained when *Peracantha* balances on the ventral carapace margins. Because of its width (maximum about half the length) and of elaborations of the ventral margins of the carapace, balance is easily accomplished, though the portion of the margins whose setae are in contact with the substratum is small (figure 34).

The 'ornamentation' of the carapace shown in taxonomic works is a very distinct corrugation of the cuticle, seen clearly in sections. This will strengthen the carapace and may thwart attacks from small predators (I have seen *P. truncata* seized by *Macrocyclops fuscus*). The ventral margins are more widely separated than in *Alonopsis elongata* and *Alona*



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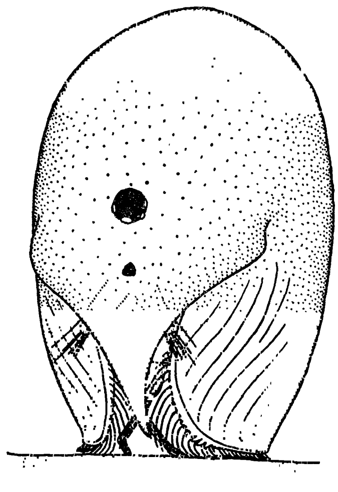

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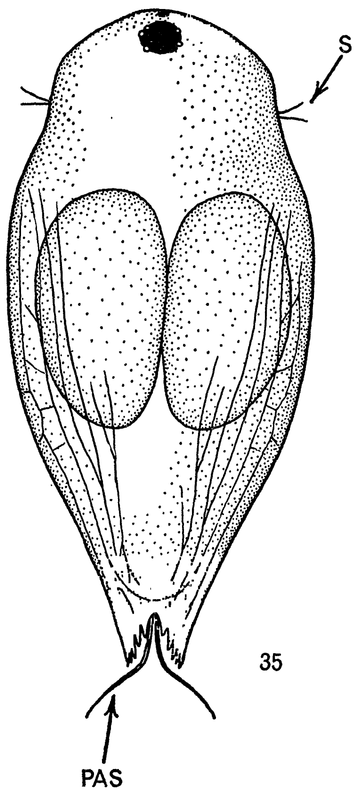

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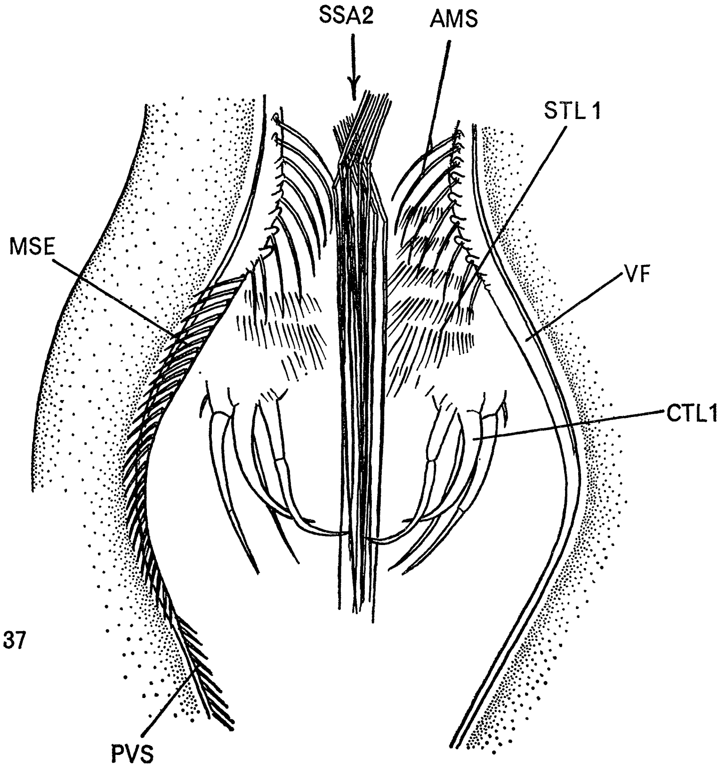


Figures 34 to 37. *Peracantha truncata.*

Figure 34. Adult female (autumn form) seen from the side as it crawls over a firm surface.

Figure 35. Adult female seen from above as it crawls over a firm surface.

Figure 36. Oblique anterior aspect of an adult female crawling over a firm surface. Note especially how it rests on the setae of the ventral carapace margins and how it folds the antennae across each other and tucks them and their long swimming setae inside the carapace when crawling.

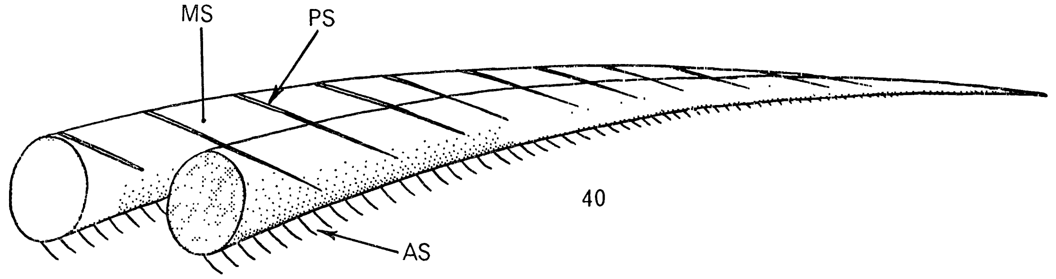
Figure 37. Ventral aspect of the embayment region, based on a photograph of an individual momentarily creeping on glass. Note the intucked antennal setae. The posterior ventral setae (PVS) are the anteriormost members of this series. *Note.* These figures are based on photographs of the living animal and thus portray with complete accuracy the orientation in life.

affinis and in particular the gape in the region of the embayments is much wider and more extensive (figure 37). It is the margins of the anterior portion of the embayments which lie parallel to the substratum when the animal is resting on or moving over surfaces. From about the middle of the embayment and posteriorly each margin inclines away from the substratum and passes as a straight edge to the posterior ventral corner (figure 34). The margin of the straight posterior region is somewhat thickened as is the posterior portion of the margin of the embayment. From the point where the embayment reaches its maximum depth, and extending forward from it, is a gradually widening flange with a flat ventral surface (figure 37, VF). This is widest at the anterior end of the embayment and continues up the anterior margin, narrowing as it passes dorsally. From the flange arise the stout teeth so characteristic of this species (figure 38).

The lower part of the anterior, and the whole of the ventral, margin of each carapace valve is fringed with conspicuous setae. Although they differ in size, armature and orientation, all are based on a common plan. As in *Alonopsis* and *Alona affinis*, each bears a row of closely spaced posteriorly directed setules (PS) of considerable length. There is also an anterior row (AS) though in some cases this is only feebly developed. The orientation (figures 34, 36 and 37) and armature (figures 38 to 42) of these setae is of functional importance and throws light on the evolution of habits in other chydorids. In all there are about 88 to 90 setae. Each anterior seta arises outside a chitinous tooth of which numbers 11 to 14 are the largest. These are the conspicuous anterior teeth (figure 38, MT) whose setae (MS) are long. More ventrally both seta length and tooth size diminish. All the anterior setae are armed with two rows of long setules (figure 38, AS and PS). Ventrally the row of chitinous teeth continues for some way along the margin of the embayment (figure 37). Posterior to about seta 18 only the row of posteriorly directed setules is conspicuous, but a second row of fine setules is present on each seta in the embayment region. The anterior setae of this series arise very close together and are directed outwards (figure 37, MSE). The arrangement of their setules is shown in figure 39 and, diagrammatically, in figures 40 and 41. Posteriorly the setae are more widely spaced and directed inwards (figures 34, 37, PVS). Here the setules of the posterior row (figure 42, PS) are long and conspicuous and reach back over, and to the outside of, the seta next behind.

The headshield is broad (figure 36). Ventrally the rostrum is recurved so that its tip is directed backwards between the antennules. When the animal is crawling over a level surface the tip of the rostrum lies near to the substratum but does not touch it (figures 34, 36).

As an exponent of crawling *Peracantha* is much more accomplished than *Alonopsis* or *Alona affinis*. The use of the antennae as props is not necessary and *Peracantha* has dispensed with their use for this purpose. Nor are they used as levers to assist crawling. Antennae not so used would be an encumbrance if they protruded, e.g. in confined spaces, and also vulnerable to predators. Like several other species *Peracantha* has solved this problem by stowing them inside the carapace during crawling. Here they are folded one above the other so that their distal setae (SSA2) lie between the first trunk limbs, by whose outer distal spines they are covered (figures 36, 37). Sometimes the setae of the right antenna overlie those of the left; sometimes the reverse, and an individual has been seen to change this relationship of the two antennae.



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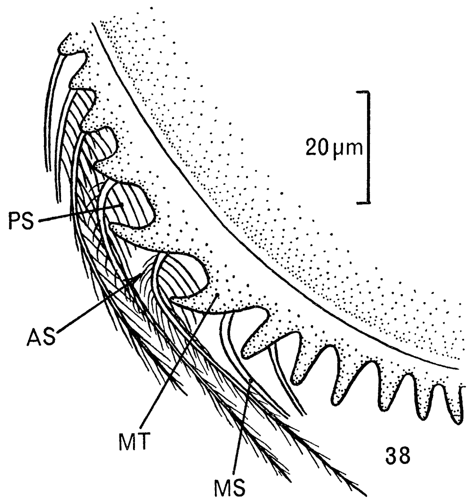

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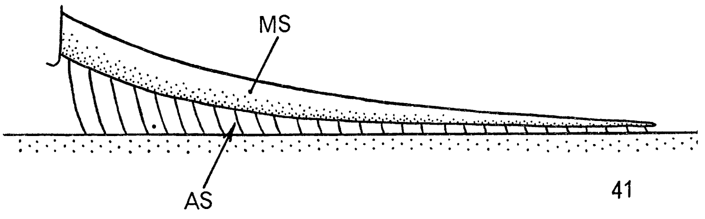

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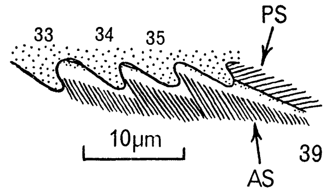

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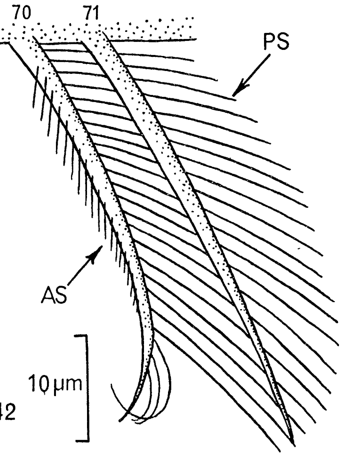

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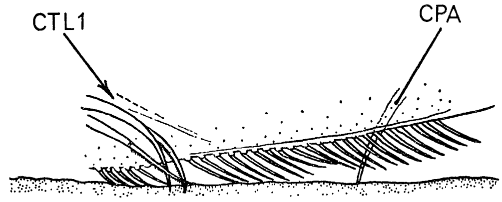

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Figures 38 to 43. *Peracantha truncata.*

Figure 38. Antero-ventral region of the carapace, from inside.

Figure 39. Marginal setae nos 33 to 35 as seen from inside showing the posterior (now dorsal) and anterior (now ventral) setules.

Figure 40. Diagrammatic illustration of the distal portions of an adjoining pair of marginal setae in the embayment region (setae 23 to 44) in a crawling animal, showing how the anterior (now ventral) setules make contact with the substratum, and how the posterior (now dorsal) setules overlie the seta next behind.

Figure 41. Diagrammatic illustration of a single marginal seta from the embayment region as seen from behind in a crawling animal, showing how the anterior (now ventral) setules make contact with the substratum (cf. figure 36).

Figure 42. Marginal setae nos. 70 and 71 (i.e. of the posterior series) from the inside, showing how the posterior setules overlie the seta next behind to the outside.

Figure 43. Sketch, based on a photograph, of the carapace margin in the embayment region, seen from one side as the animal negotiates a difficult situation. Note especially how the claws of the first trunk limb grip the substratum.

The antennae do sometimes, but not often, assist crawling, but only by being used as if the animal were swimming over the bottom. They lack the scrambling spines so conspicuous in *Alonopsis* and *Alona affinis* and the distal spines are weak.

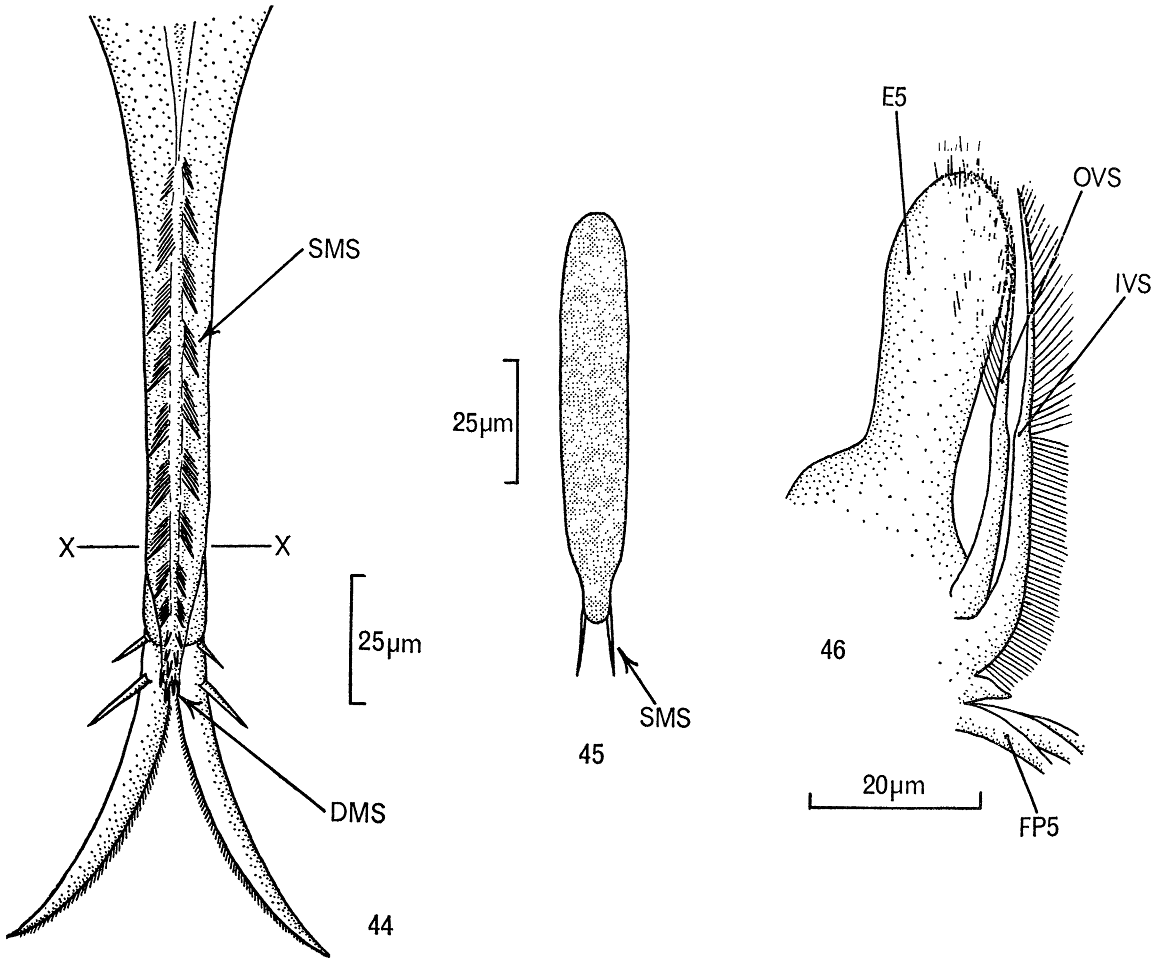
The location of the ocellus enables it to perceive light intensities just ahead of a crawling animal and the compound eye can receive visual stimuli from ahead and above (figures 34 to 36). The orientation of the antennules is shown in figures 34 and 36. The lateral sensory setae at the base of the antennae (figure 35, S) complete a ring of sensory structures anteriorly. At the hind end of the body the sensory setae of the post-abdomen have a characteristic shape (figures 34, 35, PAS) which ensures that their field of detection is wide. Now that the habits of *Peracantha* are understood, the functional significance of these setae and of their orientation is clear.

It is upon the setae which fringe the anterior portion of the embayments of the carapace margins that *Peracantha* balances when at rest and when it moves over surfaces (figures 34, 36). Observation of the setules of these setae in a living, settled animal is very difficult but, particularly as the setae curve from base to tip (figures 40, 41) it is apparent that much, if not all, the contact with the substratum is made by setules, rather than setae (see also figure 39).

Progression on a flat surface may be more or less straight, but a drift to right or left is sometimes noticeable, and always there is a certain amount of wobbling, particularly, but not entirely, in the lateral plane. Although the whole body is involved the posterior end in particular swings rapidly from side to side. An animal moving steadily forward on a smooth surface can cover a distance equal to its own length in less than 3 s, but progress is often slower than this, particularly when the animal is actively feeding, at which times it often spends long periods at rest. The motive force, as in all creeping chydorids, is provided by the first trunk limbs which are armed ventrally with rows of long setules (figure 37, STL 1). The post-abdomen is used for pushing when necessary, including take-off when an animal leaves a surface and begins to swim, but pushing is not a normal component of crawling.

Although not capable of the feats performed by *Alonella exigua* and *Graptoleberis testudinaria* (§§ XI and XVI) *Peracantha* can move easily on the under surface of an object provided it is sufficiently rough. This applies to at least some broad leaves. *A. exigua* and *Graptoleberis* rely for attachment on the setting up of a region of low pressure within the carapace chamber and such a system may to some extent assist *Peracantha* to move inverted. All the elements needed for this are present in incipient form. The zone of contact between carapace margin and substratum is partially sealed, and water is expelled, posteriorly, by the pump made up of the exopods of trunk limbs 4 and 5. Because of the close association anteriorly of the carapace, labrum, first trunk limbs and infolded antennae, the channels through which water enters the carapace chamber are restricted (compare even *Alonopsis*, p. 233, in which the precursor of this situation is seen), and water would have to enter with a very high velocity to replace that expelled posteriorly if pressure was not to be reduced. Reduced pressure must facilitate inverted locomotion, and *Peracantha* is able to hang for several seconds with its ventral carapace margins lying against the under surface of a cover slip, a situation in which it is unable to crawl. A small individual has also been seen thus suspended beneath a dirty film on the water surface. Otherwise *Peracantha* seems when inverted to rely for attachment largely on the claws of the first trunk limb (figure 42). The weight to be borne is small as the specific gravity of the animal is not much greater than that of water.

When creeping on plants *Peracantha* exhibits great agility and acrobatic prowess and can easily move over any part of a stem or leaf, collecting food as it does so. The facility with which it creeps and negotiates obstacles appears to be independent of its orientation, provided the claws of the first trunk limb can grip the substratum. By use of the same claws it can also move along thin strands against which it is not possible for the ventral carapace setae to be pressed.



Figures 44 to 46. *Peracantha truncata.*

Figure 44. Post-abdomen as seen from below (summer form).

Figure 45. Transverse section of the post-abdomen at about the level indicated by XX in figure 44.

Figure 46. Trunk limb 5 as seen from the inside, to show the ventral setae which have been cut short in figure 47.

The armature of the post-abdomen, which is incorrectly shown in all the illustrations seen, is very different from that of *Alonopsis* and *Alona affinis* and its functional nature is best appreciated when it is seen from below (figure 44). Because of flexure this is morphologically the dorsal surface. Distally, at the base of the terminal claws, it is armed with a group of long, extremely sharp-pointed spines, often figured more or less correctly in lateral aspect, which arise in a cluster (figure 44, DMS). More proximally the armature consists of a double row of groups of spinules akin to those of the lateral squamae of *Alona affinis* but orientated differently (figures 44, 45, SMS). Although they are deflected somewhat outwards (figure 44) they point essentially towards the substratum. Of each group the anteriormost spinule is the longest and stoutest. Distally the groups arise from the margin of the narrow post-abdomen; more proximally somewhat submarginally and here perhaps qualify as lateral squamae. Although they arise in pairs distally, they are staggered proximally (figure 44) and it is to this that errors of illustration in the lateral view are often due. The entire arrangement is well suited to pushing on plant surfaces on which the sharp points can push without slipping and without the risk of breaking, but is probably less suited to pushing on hard bottoms (cf. *A. affinis*).

While the distal portion of the post-abdomen is narrow (figures 44, 45) the proximal portion is very wide, much wider than is apparent when seen from the side. When seen from below the relationship of the proximal portion to the carapace is very similar to that of *Alonella exigua* shown in figure 51.

One specimen observed at rest near a leaf edge swung back its post-abdomen so that it lay more or less at right angles to the substratum and used the tips of the claws to form the third point of a tripod-like balance. Presumably the claws of the first trunk limbs were gripping but this was not observed. The use of the terminal claws of the post-abdomen in this or other ways has seldom been seen, but figure 43, which is based on a photograph, shows how the tips of these claws are occasionally used in the negotiation of an irregular surface, and how the claws of trunk limb 1 are used for gripping.

Although undoubtedly specialized for crawling, *Peracantha* is also an efficient swimmer. Over distances of up to about 10 cm an individual 0·65 mm in length carrying embryos maintained a speed of about 14 body lengths (9 mm)/s. The best recorded performance, over a distance of 8 cm, covered in 8·4 s, exceeded 14·5 body lengths/s. These speeds are slightly underestimated as no account was taken of slight deviations from the straight course along which measurements were made.

The food consists of material removed from the surfaces over which the animal crawls. Although inorganic particles are included, the gut contents usually consist of finely comminuted detritus much of which appears to be of organic origin and among which occasional algal cells, including diatoms, can be recognized, but which for the most part is an amorphous mixture. Although not readily definable other than on the basis of its less 'gritty' content, this material is almost always recognizable as being of a different texture and composition from that ingested by, for example, *Alona affinis* adjacent to which *Peracantha* may be living. This reflects the greater preference for plant surfaces shown by *P. truncata* and for the bottom by *A. affinis*, as well as the finer-toothed and less robust food collecting apparatus of the former.

(ii) *Appendages and labrum*

Most of the salient features of the trunk limbs, in so far as the feeding mechanism is concerned, are shown in figure 47 which shows the composition and structure of the filter chamber. Certain important attributes are summarized in table 3. Only those features which are not thus readily apparent or which require special emphasis are referred to here.

The labrum (figures 47, 48) is the source of copious secretions whose extrusion has been clearly demonstrated (figure 48, LGS). The ducts which carry the secretion are dilated to form conspicuous reservoirs (RLG) such as are not present in many other chydorids. Within the reservoirs the secretion stains red with Mallory's stain as in the daphnid *Simocephalus* (Cannon 1922) but blue after extrusion. In *Eurycercus* the secretion stains blue throughout (Fryer 1963). The production of copious secretions by the labral glands is undoubtedly correlated with the complete absence of any secretion produced by either the first or fourth trunk limbs. (See table 3 for comparative data on secretions.) The mandibles are of the usual form; articulation is of type B.

Trunk limb 1 has an 'inner lobe' which consists of a single seta (figure 47), difficult to discern in longitudinal slices. There are co-ordinated specializations of trunk limbs 1 and 2. In *Alona affinis* there is a specialized antero-median spine directed towards the food groove whose function is to prevent food particles from slipping through the gap between trunk limbs 1 and 2 (figure 30). A similar spine is present in *P. truncata* (figure 47, SS). Very characteristic is the elbow-like bend near its tip which adds to its effectiveness. Like those of its homologue in *A. affinis* its elongate anterior and posterior setules are arranged in one plane. The setules of the posterior row are sufficiently long to permit considerable movements of trunk limb 2 during the feeding process without opening the gap, and this attribute is enhanced still more by specializations of trunk limb 2. On this limb, adjacent to the seta of trunk limb 1, is an array of fine setules (figure 47, SS2), not present in *A. affinis*, but whose homologues exist in *Eurycercus* as what, on the basis of their function, were described as screening setules (Fryer 1963). In *Peracantha* these are very long, are arranged in a single row in one plane, and lie behind (outside) the setules of the seta of trunk limb 1. This arrangement results in the formation of a definite grid (figure 47) of which the shape of the holes varies according to the relative positions of trunk limbs 1 and 2, but which are always of small dimensions and, in adult individuals, will always exclude particles as small as 3 μm or even less in diameter.

Although the main gap is sealed there is a narrow space between the basal portion of the inner face of trunk limb 1 and the anterior portion of the filter plate of trunk limb 2. This is sealed by the anterior row of setules of the anterior seta of the filter plate of trunk limb 2 (figure 47, NFS). This row of setules, unlike the rest, is directed not towards the mid-line but away from it and towards the inner face of trunk limb 1, thereby sealing the gap. This row is not continued so far towards the base of the seta as is the posterior row, but for clarity a few additional basal setules have been omitted in figure 47.

Of the filtratory setules of the filter plate of trunk limb 2 those of the two anterior setae are somewhat wider apart and those of the three posterior setae somewhat closer together than setae 3 and 4 (figure 47). Those of the posterior row of the first setae are about 1 μm apart in an adult individual; those of the three posterior setae are so fine and so close together as to defy an accurate estimation of the distance between them.

The difference in degree of sealing of the gap between trunk limbs 1 and 2, ranging from none at all in *Alonopsis*, to considerable screening in *Alona affinis*, and elaborate screening in *Peracantha*, reflects differences in the feeding mechanisms of these species.

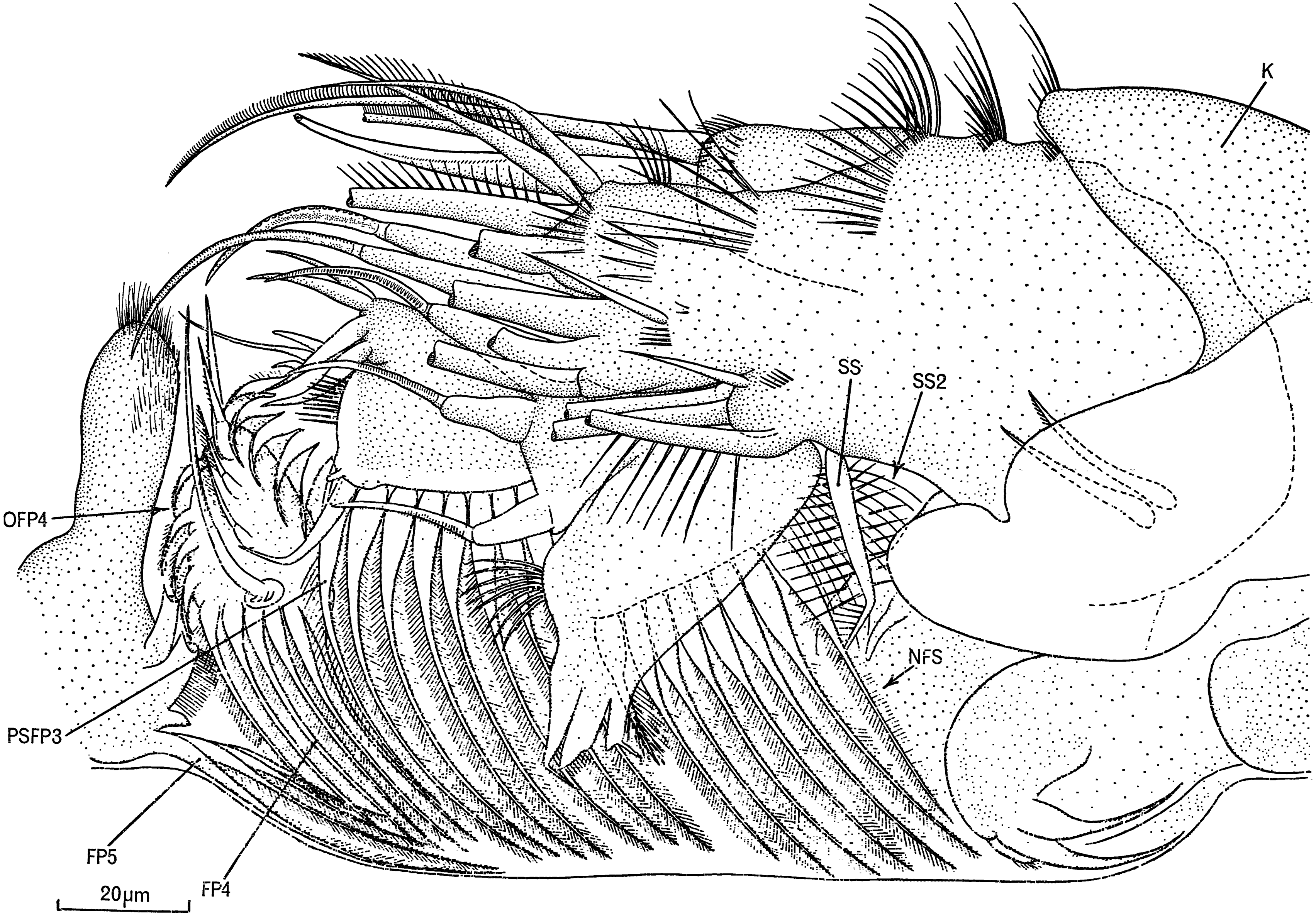
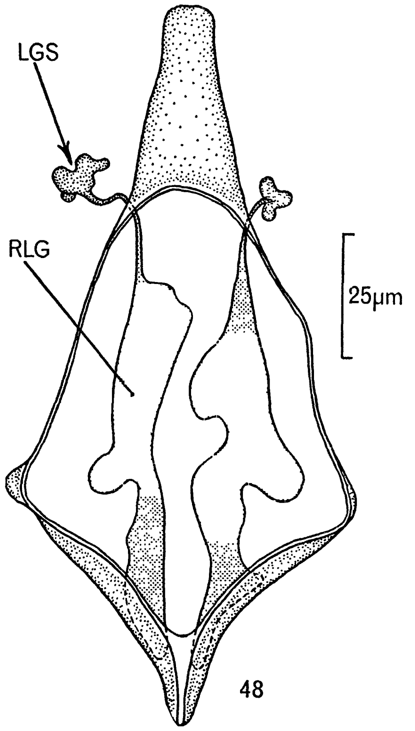


Figure 47. *Peracantha truncata*. Median longitudinal slice through the trunk limbs to show the filter chamber. In order not to obscure the figure only those structures whose identity cannot readily be ascertained by reference to figure 7 are labelled. Note the non-filtratory setules (NFS) of the anteriormost gnathobasic seta of trunk limb 2 which seal the gap between the filter plate and the base of trunk limb 1.

The vigorous anterior swing of trunk limb 2 of *Alonopsis* and the remoteness of the gnathobasic plate from the gap (figure 7) renders such a screen unnecessary. The more elaborate (finer) screening in *Peracantha* than in *A. affinis* is probably correlated with the utilization of smaller particles.

The scrapers of trunk limb 2 are very finely denticulate. The two most proximal (nos. 1 and 2), which are bent in a distinctive manner, have coarse-toothed homologues in *Alona affinis* (figure 32), and especially in *Alonopsis* (figure 7). These differences reflect differences in the habits and habitat preferences of the animals as well as in the nature of their food and feeding mechanism. Close association with plant surfaces neither brings *Peracantha* into contact with the kind of food collected by *A. affinis* and *Alonopsis* nor permits the use of a mechanism that could deal with it. Scrapers 6, 7 and 8, which lie slightly more distal and more lateral than no. 5, are not shown in figure 47. No. 6 is an extremely fine scraper; nos. 7 and 8, which are the longest of the series, are even more finely denticulate than no. 1 and serve as whisks. Fine as the denticulation is on all the scrapers it conforms in this respect, and in respect of relative length, to the comb and brush principle.



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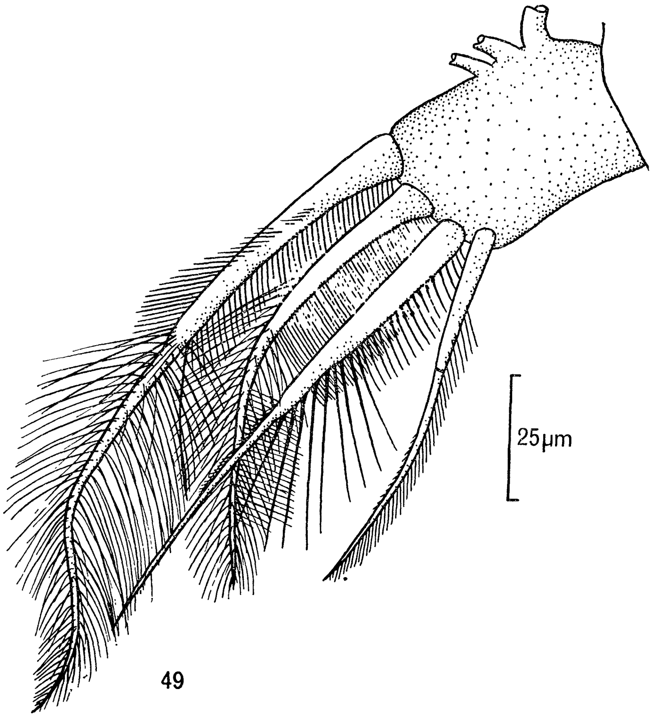

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FIGURES 48, 49. *Peracantha truncata.*

FIGURE 48. Horizontal section of the labrum to show the reservoirs which store the entangling secretions, the ducts which carry the secretions to the exterior, and secretions in the process of extrusion.

FIGURE 49. Exopod of trunk limb 3.

The posteriormost of the gnathobasic filter setae of trunk limb 3 (figure 47, PSFP3) bears posteriorly a row not of filtratory setules but of longer, more widely separated, and brush-like setules. To reveal these more clearly the filtratory setules of the underlying filter setae of the limb behind have been omitted.

There are no distal scrapers on trunk limb 3. Instead of the coarse-toothed scrapers present in *Alonopsis* (figure 7) and *Alona affinis* (figure 33) there are two long slender spines sparsely provided with fine spinules. These are inserted too far to the outside to appear in figure 47.

Trunk limb 3 has a well-developed exopod, plate-like and rectangular in shape and armed distally with four setae (figure 49). In life the disposition of these setae and their relationship to the post-abdomen closely foreshadow those found in *Alonella exigua* (figure 51) and *Graptoleberis testudinaria* (figure 89) and which in these species are of profound functional significance. This disposition adds to the conviction that *Peracantha* can utilize to some degree the ability of adhering by suction to suitable surfaces which has been brought to differing degrees of perfection in these species.

The gnathobase and more distal endites of trunk limb 4 bear delicate, elongate, whisk-like spines. That of the gnathobase is especially long. In *Alonopsis* the elements of this series are short and stout and there is no gnathobasic spine. The setae of the outer filter plate (OFP4) are very long: in figure 47 they appear greatly foreshortened as they are seen end-on.

Trunk limb 5 has a well-formed gnathobasic filter plate (FP5) of four setae, and two long setae (figure 46, IVS, OVS, and cut short in figure 47 so as not to obscure the outer filter plate of trunk limb 4) which seal the posterior end of the filter chamber medially.

(iii) *The feeding mechanism*

That the filter chamber very effectively strains small particles from the current which flows through it is shown by the ability of *Peracantha* to filter cells from a suspension of *Chlorella*. This it does with great rapidity, and the movements of the green mass which accumulates can be followed relatively easily. Nevertheless, it is certain that in nature, food collection by the filtration of suspended particles is subservient to scraping or sweeping material from surfaces, for the most part from plants. This is apparent from the habits of the animals and from the nature of the material in the gut. Pertinent also is that, where weed beds are abundant, the amount of suspended material is often much less than in open water. *Peracantha* can be kept, and will reproduce, in shallow dishes in which the amount of suspended material is negligible and in which food has to be collected by scraping.

In specimens balanced on the ventral carapace margins, currents enter the carapace chamber anteriorly, water being drawn from the anterior and antero-lateral regions ahead of the animal. Particles near the substratum have also been seen to be drawn inwards from the lateral regions and from behind, the latter moving forward more or less parallel to the animal before being drawn in at the level of the filter chamber. Water therefore flows into the filter chamber anteriorly and to some extent ventrally. As in *Alonopsis* (figure 3), and for the same reason, the powerful anterior current does not enter the carapace chamber along the whole of the anterior aperture. Some enters and passes dorsal to and some ventral to the bulk of the labrum.

Food is collected by trunk limb 2. Considering the finely denticulate nature of the scrapers it is probably more correct to refer to the process as brushing or sweeping than scraping. As in *Eurycercus*, particles thus collected are pushed into the filter chamber by the proximal elements of the armature of trunk limb 2, assisted by those of trunk limb 3 whose gnathobasic armature in particular is well suited to forcing particles deeper into the filter chamber. The movements of trunk limb 3 are synchronized and usually (always?) occur simultaneously with those of trunk limb 2. The outer filter plate of trunk limb 3 helps to strain out and deflect particles as in *Eurycercus* and these are whisked towards the food groove by the spines of trunk limb 4, whose brush-like armature is suited to sweeping fine particles and which swings inward in the characteristic chydorid manner. This activity by trunk limb 4 is often very vigorous: when the animal is feeding on a *Chlorella* suspension its rate of beat is about 140/min, and this is often maintained with no more than brief pauses for several minutes and for up to at least 25 s without pause. As movements of trunk limb 3 are relatively few and intermittent, scouring of its outer filter plate is not a passive process but must be carried out actively by trunk limb 4 whose cleansing setules are particularly prominent at its anterior proximal corner (figure 47, just beneath PSFP 3).

The function of the brush-like posterior row of setules on the most posterior filter seta of the gnathobasic filter plate of trunk limb 3 (figure 47, PSFP 3) cannot easily be observed. It must, however, help to sweep particles which accumulate in this vicinity towards the food groove and to some extent forward. Sweeping, however, is performed only intermittently.

The copious secretions produced by the labrum are carried back by currents and accumulate, as do many particles, posteriorly. (Compare the similar accumulation of secretions from trunk limbs 1 and 4 in *Alonopsis*.) In *Eurycercus* entanglement posteriorly is effected particularly by the secretions of trunk limb 4, and although it cannot be observed in the living animal, it seems probable from fixed and sectioned animals as well as from the structure and disposition of the structures concerned, that the labral gland secretions are deflected towards the food groove just behind the maxillules by the well-developed inner lobes of the first trunk limbs and there entangle the food mass, some of which is pushed directly into the anterior portion of the food groove (Fryer 1963). In *Peracantha* there is no posteriorly produced secretion yet it is necessary to entangle particles posteriorly. This presumably explains the greatly reduced, almost rudimentary, nature of the inner lobe of trunk limb 1, which is incapable of deflecting the labral gland secretions, which therefore drift posteriorly. (Compare *Alonopsis* which in this respect is similar in structure and function.) Food accumulated posteriorly is moved forward along the food groove by the tips of the gnathobasic filter setae as in other species, the ramming action of trunk limb 2 being very noticeable.

Although alined in a different plane from its fellows on the more anterior limbs, the gnathobasic filter plate of trunk limb 5 contributes to this forward movement. As the exopod of this limb beats against the post-abdomen, which it does as its contribution to the pumping mechanism, there is a definite forward component to the movement of the gnathobasic region, and the filter plate is in active motion and pushes regularly and appreciably along the food groove.

Food accumulating at the anterior end of the food groove is pushed by the second trunk limbs to the maxillules which transfer it to the mandibles. The mandibles roll in the typical manner. Often they roll many times with a very regular rhythm. The rate of rolling and the duration of a series of consecutive rolls apparently depends on the nature of the food. From 120 to 150 rolls/min, maintained for more than 30 s at a time, have been recorded when food is collected by the second trunk limbs. When the anterior end of the food groove is packed with *Chlorella*, more rapid and sustained rolling has been observed—between 160 and 170 rolls/min, sometimes maintained for well over a minute without pause. *Chlorella* is moved forward relatively rapidly along the food groove, 29 or 30 swings/min of the intermittently-moving trunk limb 2, having been recorded in an animal feeding on this alga.

Although each limb is capable of only a certain range of movements, feeding behaviour in *Peracantha* is not stereotyped. For example a specimen has been seen pulling into the filter chamber part of a colony of *Volvox*. On this occasion trunk limb 1, which normally plays only passive roles in the feeding process, appeared to hold the alga until portions of it could be dragged in by trunk limb 2.

(iv) *Conclusions*

By elaboration of the carapace margins and their setae *Peracantha* shows many advances over *Alona*, *Alonopsis* and related genera, and is more specialized for crawling. As a frequenter of the leaves of plants it enjoys many advantages over these genera, and its feeding mechanism is specialized for the collection of the fine particles found there rather than for the collection of coarser bottom material.

X. A COMPARISON OF TWO SPECIES OF *PLEUROXUS*

Pleuroxus trigonellus (O. F. Müller) and *P. uncinatus* Baird, have been compared. Most specimens came from one locality (Urswick Tarn) where they co-existed. Structurally they are very similar, and are similar in many respects to *Peracantha truncata*, which some would assign to *Pleuroxus*. They differ markedly from *Peracantha* in their ecological preferences as they appear to shun vegetation and occur on bare substrates in situations which *P. truncata* certainly avoids. A similar clear-cut difference was found by Flössner (1964). Both species occur over soft bottoms covered with muddy detritus and over stones with mud-covered surfaces, but observations on living animals indicate that they are members of the epifauna and do not persistently burrow as do certain truly mud-frequenting chydorids such as *Leydigia*. Indeed all their structural adaptations are for creeping over surfaces, and when a firm substratum—which need be no firmer than a piece of decaying leaf—is available they balance on it by use of the ventral carapace margins as does *Peracantha*. Both species ingest bottom detritus, which sometimes includes large quantities of inorganic matter if collected from stones, and among which occasional algae, including diatoms, have been seen. In this they differ markedly from *Peracantha*. Insufficient observations have been made to demonstrate food preferences. In several collections *P. uncinatus* was more common over stones than *P. trigonellus* and the reverse held good for soft bottoms, but in one collection from a soft bottom *P. uncinatus* was the more plentiful.

As Smyly (1958) noticed, the carapace of *P. uncinatus* is usually covered with detritus while that of *P. trigonellus* is clean. *P. uncinatus* seems to owe its 'dirtiness' to a secretion of the carapace surface to which particles adhere. This can be made out in Mallory-stained sections as a pale blue, flimsy pellicle, which usually becomes detached and on which a replication of the reticulations of the underlying carapace can be made out in completely detached portions. The surface of the cuticle of both species stains blue with alcian blue which suggests that both produce a secretion. In *P. uncinatus* this apparently has the property of stickiness.

No detailed anatomical study was made after the similarity of the filter chamber to that of *Peracantha* and *Chydorus* had been ascertained, but certain details are given in table 3.

P. trigonellus swims actively and for long periods (certainly for more than a minute without apparent fatigue), but seldom follows a straight course for more than a few millimetres. Speeds have therefore been obtained in a crude manner and those given (for a female 0·61 mm in length) are definitely underestimates. A speed of at least 7·7 body lengths (4·7 mm)/s was sustained for over 1 min, and higher speeds were recorded over shorter distances, the maximum being 10·6 body lengths (6·5 mm)/s over 13 s. The abilities of *P. uncinatus* appear to be similar. A female, length 0·59 mm, sustained a speed of 14·1 body lengths (8·33 mm)/s for over 19 s.

XI. The structure, habits and feeding mechanism of *Alonella exigua* (Lilljeborg)

Alonella exigua (figures 50, 51) is a little known species whose habits and abilities have not hitherto been appreciated. Although superficially very similar to *A. excisa* (Fischer), so much so that many early records of *A. exigua* in Britain certainly refer to that species, its habits and attributes are very different. These differences serve to a large extent to explain the different ecological preferences of the two species.

A. exigua is small. Various lengths are quoted in the literature, 0·45 mm being the greatest (Scourfield & Harding 1958), but most authorities give the maximum as 0·42 mm or less. Adult females used in this study seldom exceeded about 0·32 mm, which is in keeping with information given by Lilljeborg (1900) and Birge (1918).

Although from the point of view of understanding the evolution of habits within a genus it would be best to consider this species after *Alonella nana* (Baird) and *A. excisa*, the more detailed treatment given to *A. exigua* makes it more convenient to discuss this species first. This is no disadvantage if it be remembered that, in respect of the use of the ventral carapace margins as an adjunct to locomotion, it is more specialized than either *A. nana*, which has assumed different habits, or *A. excisa*, which is probably rather less specialized in this respect than *Peracantha*.

Like several species already described, *A. exigua* has adopted the habit of balancing on the ventral carapace margins when it crawls. In addition, it has developed and perfected a method of attachment to the surface over which it moves to such an extent that, like a fly on a ceiling, it can move upside down just as easily as when attachment is assisted by gravity. The feeding mechanism differs only in details from that of several other chydorids, and interest centres therefore on the means of attachment and locomotion and on the structural and physiological specializations associated with these habits. This is further illuminated by a comparison of its structure, habits and ecology with those of the closely related *A. excisa*.

(i) *Ecology and habits*

Little is recorded concerning the ecology of this species save that it usually occurs among vegetation. Smyly (1957, 1958), however, makes the pertinent observation that he found it associated particularly with the floating leaves of *Potamogeton*, a situation in which most chydorids would not be expected. The abilities here described enable us to appreciate this unexpected habit in terms of functional morphology.

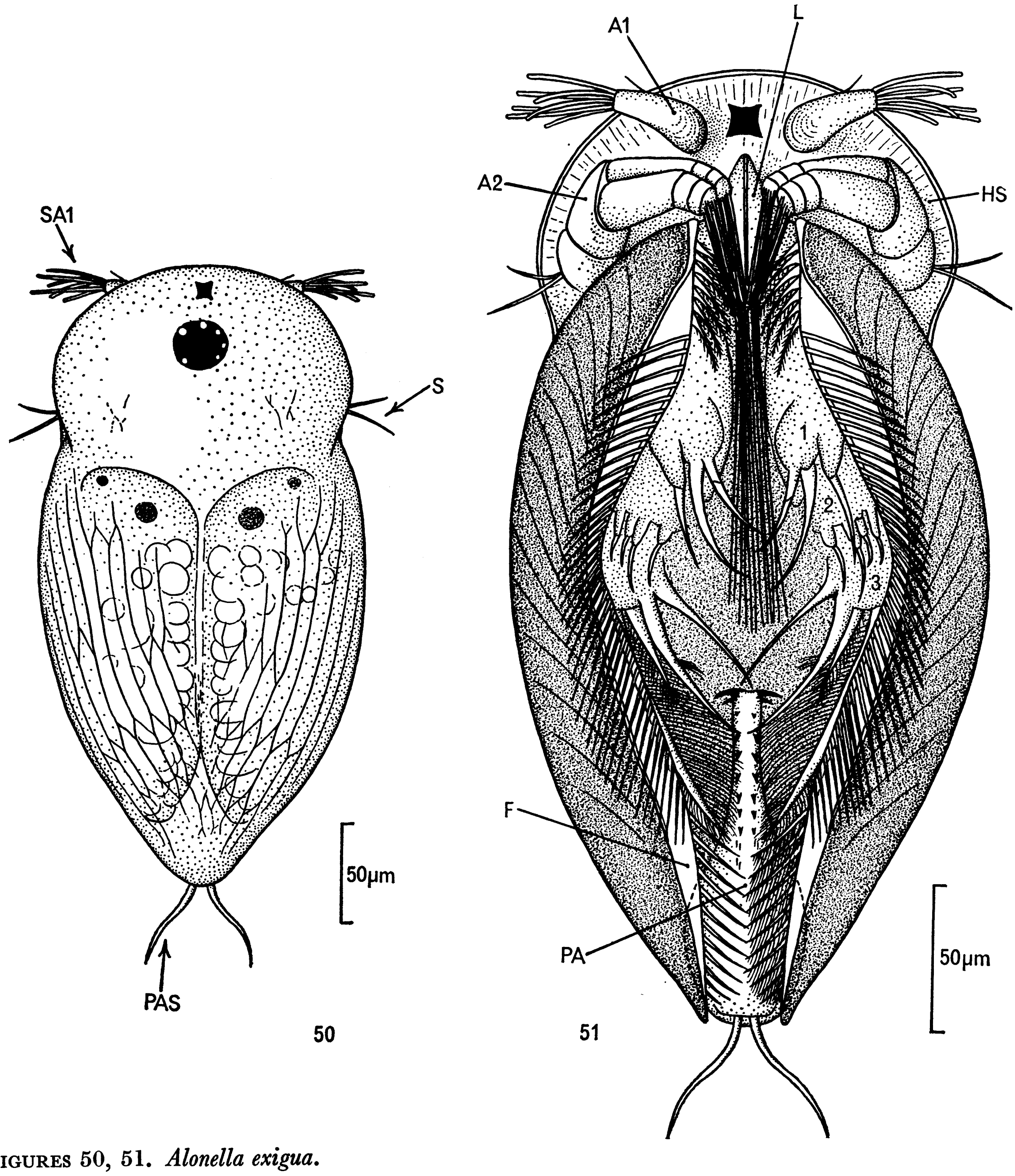
The key to the way of life of *A. exigua* is the form of the ventral margins of the carapace and their associated setae, and the use to which these are put. Its habit is to settle on surfaces, particularly of plants, and to move briskly over these, collecting its food as it does so. It can move with equal facility on surfaces orientated in any plane, and its association with the under surface of floating leaves of *Potamogeton* is explained by its ability to crawl there. (It can crawl along the under surface of a propped-up cover glass—section iv.) In these situations competition is likely to be minimal.

When crawling, *A. exigua* moves forward rapidly for a short distance, pauses, and moves again, the setae of the ventral margins of the carapace being kept in contact with the substratum throughout the movement, as in *Peracantha*, whose habits and abilities foreshadow those of *A. exigua*. Each forward movement is the summation of numerous small forward jerks (section iv). The course followed is usually erratic, changes in direction being very frequent.

Scrambling has never been seen, and crawling invariably involves the infolding of the antennae (figures 50, 51). As in the non-scrambling *Peracantha* the antennae are devoid of scrambling spines though there is a minute spinule on the basal segment of the endopod in the position occupied by the powerful scrambling spine of *Alonopsis* and *Alona affinis*, and there is a short distal spine on both endopod and exopod. Because of its small size and infolded antennae *A. exigua* can doubtless pass through gaps, as among plants, which are inaccessible to larger species and creep over and around obstacles which cannot be negotiated by larger forms without recourse to scrambling.

A. exigua is also an extremely agile swimmer. It swims readily but usually for short distances only, though it always moves with great rapidity, and frequently follows an erratic course. Because of this, accurate estimates of swimming speeds are difficult to make, but a female carrying embryos certainly achieved a speed of more than 31 body lengths (1 cm)/s over a period of 2·6 s. Considerably greater speeds have been measured over short periods of time. Thus distances of at least 8 and 9 mm have been traversed in 0·6 s giving speeds for the individual concerned of almost 42 and almost 47 body lengths/s respectively. Even allowing for considerable errors, these speeds, which are probably underestimates, are very great. Indeed, in spite of its small size, *A. exigua* achieved the highest absolute speed recorded for any chydorid tested—though only over short distances. To enable these speeds to be achieved the antennae beat with great rapidity, and are provided with very long swimming setae.

It is impossible to define the food of *A. exigua* precisely, but the gut contents have a 'consistency' which is characteristic and which is very different from that of, for example, *Alonopsis elongata* or *Alona affinis*, and which differs from that of those specimens of the closely related *Alonella excisa* that have been examined (§ XII (iii)). Particles of very small size predominate in the gut, which often contains minute dark particles scattered through a matrix with a greenish yellow hue, which suggests carotenoid pigments. Most of the material is unrecognizable, but occasional spherical objects, presumably algal cells, are present, and once a relatively large naviculoid diatom was seen, as was a spine-like object.



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Figures 50, 51. *Alonella exigua.*

Figure 50. Adult female seen from above as it creeps over a flat surface.

Figure 51. Adult female seen from below as it creeps beneath a cover-slip. Note especially the greatly expanded embayment, bordered by a very wide flange, and the orientation of the setae which arise from the flange; the position of the labrum relative to the carapace; the way the post-abdomen fits like a plug into the posterior portion of the carapace chamber; the intucked antennal setae; and the nature and orientation of the very long exopod seta of trunk limb 3 which arises from this limb just inside the flange.

These latter give clear evidence of scraping. Considering the minute size of the scrapers it seems possible that bacteria are also collected and some must certainly be obtained inadvertently.

(ii) *Structure, other than that of the appendages used in feeding*

General form is best appreciated from figures 50 and 51, which give an impression very different from the lateral view usually illustrated in taxonomic works. Interest in the carapace centres upon the ventral and anterior margins which are greatly modified in relation to specialized and hitherto undescribed habits. In life there is an extremely wide ventral aperture between the carapace valves (figure 51), much wider than the anterior embayment of many species, and also more extensive from front to back. Posterior to this the ventral margins are widely separated, being for the most part straight in the horizontal plane though they incline slightly dorsally towards the posterior end. Each is extended inwards as a flange whose distinctive shape is shown in figure 51 (F) (cf. the rudimentary flange in *Alonopsis* (figure 4), and the small flange in *Peracantha* (figure 37)). At the antero-ventral corner the carapace margin is broadly curved and here the flange virtually disappears. The anterior margin is almost straight and inclined backwards. Ventrally there is a narrow flange. More dorsally it gradually widens, attaining its maximum width at the level of the labrum and then narrowing somewhat but remaining wide right up to its junction with the headshield (figure 52, AF).

There are no setae on the wide, dorsal, portion of the anterior flange. The curved antero-ventral region is provided with a row of inwardly and backwardly directed setae 7 in number (figure 51) and the margin of each ventral flange is armed with a row of specialized setae, here called the median setae. When the animal is moving over a surface those arising from that part of the flange which lies in the horizontal plane are directed obliquely outwards and lie more or less parallel to the flange itself. This series of setae, about 40 in all, extends over much of the ventral margin of each carapace valve (figure 51). The anterior 11 or 12 setae, and particularly the first 4, are widely separated and are directed outwards and only a little backwards. Posterior to these they arise closer together and, while still directed outwards, become inclined more and more posteriorly so that the last few point essentially backwards (figure 51).

Behind the median series there is an abrupt change and the next seta, which is longer than the last of the median series, is directed obliquely inwards and somewhat ventrally. This is the first of a series of a dozen such setae of which most reach towards and sometimes touch their fellows of the opposite margin, though the last three or four gradually diminish in size. These comprise the posterior series. Although not evident from figure 51 these are inserted not at the margin of the flange but inside it, the first only just inside, the rest progressively further from the margin so that the last is inserted well within the carapace.

The armature of the seven anterior setae is shown in figure 51. That of the median setae on which the animal balances and moves is basically the same as that of their homologues in *Alonopsis* and *Peracantha*. Each has a row of posterior (dorsal) setules which extends backwards and overlies dorsally the seta next behind, and a row of anterior (ventral) setules, detectable only with difficulty at high magnifications. It is upon the minute anterior (ventral) setules that the animal rests on the substratum as in *Peracantha*.

The setae of the posterior series are also basically the same as those of *Alonopsis* and particularly *Peracantha*. If it be imagined that a seta of the median series be folded inward through 180°, the nature of the posterior setae is readily appreciated. The dorsal (posterior) setules, which overlie their fellows dorsally in the median series, now do so ventrally. These posterior setules are considerably stouter than those of the setae of the median series. The anterior setules are very fine.

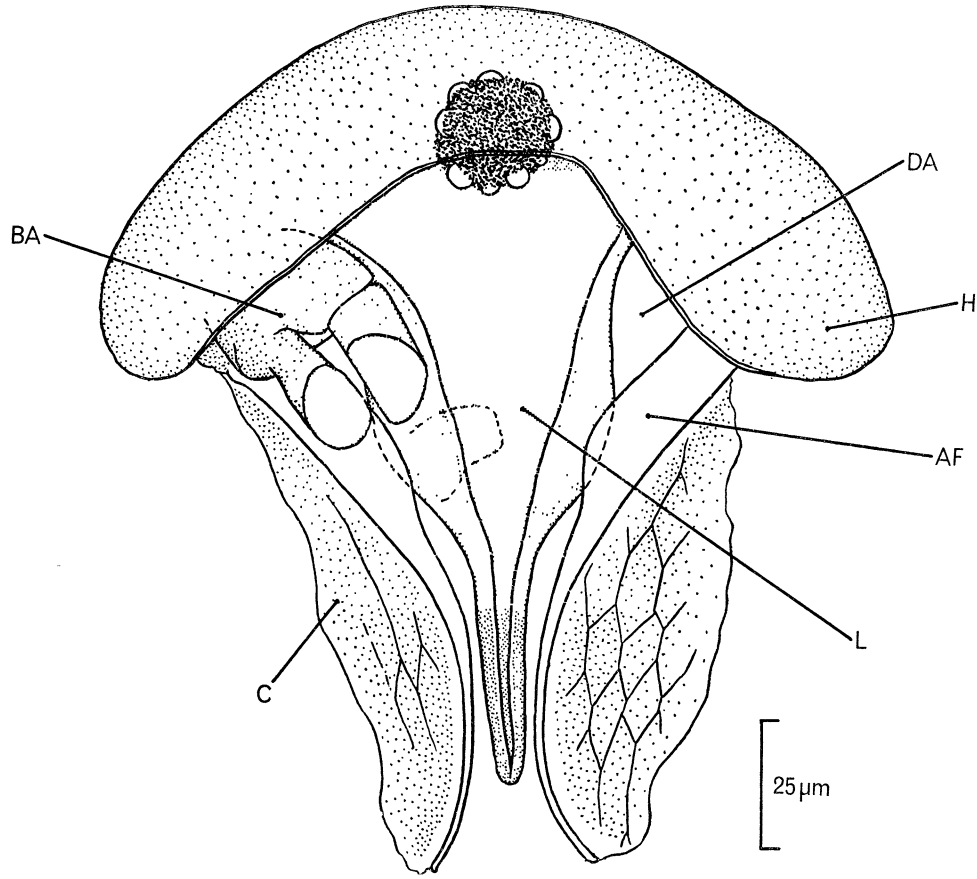


FIGURE 52. *Alonella exigua*. Transverse section at the level of the anterior carapace margins (here flanges) and which slices through the tip of the labrum.

Many features of the headshield, antennules, antennae, labrum and post-abdomen are evident from figures 50 to 52; others are mentioned in connexion with habits. Particular attention is directed to the great width of the proximal portion of the post-abdomen (PA) as this is a feature of functional significance not apparent when this structure is viewed laterally.

(iii) *Labrum, appendages and filter chamber*

The form of the fleshy portion of the labrum and its relationship to the anterior margins of the carapace are shown particularly in figures 51 and 52. The functional significance of this relationship is explained in section (iv). Although gland cells are present, the exudation of secretions from the labrum has not been demonstrated. If secretions are produced all the evidence suggests that they are much less important than those produced elsewhere.

Mandibular articulation is of type B.

In essentials the filter chamber resembles that of *Peracantha* shown in figure 47 (see also table 3) but is relatively smaller, the distance from the posterior extremity of the labrum to the posterior end of the chamber being less than 70 μm in a specimen 0·32 mm in length. This is only about 60 % of the comparable measurement in *Peracantha*, and the volume of the filter chamber is therefore much less. Exact calculations cannot be made but the volume of the similarly constituted filter chambers of *Peracantha truncata* and *Eurycercus lamellatus* are respectively perhaps 3 and at least 200 times as great as that of *A. exigua*. Such differences in absolute size are seldom considered by ecologists. All the dimensions are small. The setae of the filter plates are extremely fine and no filtratory setules have been detected on them. These may be present but be beyond the limits of resolution of available optics, but it is also possible that they are not needed since the gaps between the setae are of the order of only 3 μm or less and, with copious secretions to help, must filter out extremely fine particles.

Trunk limb 1 has a gap-closing spine similar to that of *Peracantha*, and similarly bent, but no co-operating setules have been detected on trunk limb 2. The first trunk limb is the source of a secretion similar to that of *Alonopsis*. A voluminous reservoir containing this secretion lies beneath the ovary and its wide duct runs obliquely forward, ventral to the carapace adductor muscle, to the narrow orifice on the limb. Gland cells apparently attached to the reservoir presumably produce the secretion.

The denticulation of the scrapers of trunk limb 2 is exceedingly fine, finer than in *Peracantha*. In a measured example the 'scraping' portion of scraper number 6, which is a 'coarse' collecting scraper, had a length of about 17 μm and bore about 30 denticles. The more proximal scrapers are more finely denticulate.

The exopod of trunk limb 3 is plate-like and armed with four setae whose size, armature and orientation are shown in figure 51. Of these the outermost is armed with an array of long, extremely fine setules arranged all around the seta, and which are finer and more numerous than it is possible to show in the figure. These are spread across what would otherwise be a gap between the post-abdomen and the carapace margins. (See section (iv) for further details.)

(iv) *Attachment and locomotion*

As in *Peracantha* contact between the animal and the substratum is made by the setae which fringe the carapace margins. In *A. exigua* the region of contact is much longer in relation to the length of the carapace than in *Peracantha* (about 58 % of the carapace length compared with about 25 %) and the number of setae is greater. When an animal is attached to, or rests on, a surface the antennules are widely spread and their sensory aesthetascs make contact in a postion which enables the surface in front of the animal to be explored to a width about equal to that of the body (figures 50, 51). This represents an advance over the condition in *Peracantha* whose antennules do not actually explore the substratum (figures 34, 36). The antennules of *A. exigua* are also relatively larger than those of *Peracantha*. The coxal sensory setae of the antennae project laterally (figures 50, 51), and the eye and ocellus are well situated for the perception of optic stimuli ahead of and dorsal to the animal. The lateral view shown in taxonomic works gives little impression of the true position of the ocellus and obscures its functional significance. The sensory setae of the post-abdomen provide an early warning system of the approach of enemies from behind.

An individual so orientated with respect to a surface can move rapidly and easily even on the under surface of a cover slip provided the film of water is sufficiently deep, and it is largely from photographs of animals so attached, and which therefore accurately portray the disposition of the ventral setae and other structures when in use, that figure 51 has been produced. The position shown for trunk limb 1 is typical of an animal at rest, but sometimes the distal spines cross over each other. Trunk limb 2 is shown at the end of the recovery stroke.

When *A. exigua* is attached to a surface the posterior exopod pump is in vigorous and incessant action. Never has an attached individual been seen in which the pump stopped even briefly and, if the means of attachment has been correctly elucidated, this is to be expected as the pump plays an indispensable part in the process.

In an attached animal the carapace chamber is for the most part sealed and in a manner which foreshadows similar but more complete sealing in *Graptoleberis*. Anteriorly the gap between the carapace margins is largely sealed by the labrum (figures 51, 52, L), though apertures remain dorsally and ventrally. Whether the dorsal aperture is sealed has not been established, but the ventral aperture is certainly unsealed and extends posteriorly in the region through which pass the swimming setae of the infolded antennae and where the ventral carapace margins are lined by the short row of anterior setae. These can obviously do no more than restrict, and are certainly unable to prevent, the inflow of water. It is through this limited aperture that the inhalent current enters. Much of the ventral surface is sealed by the row of median setae on each side. (An account of the sealing principle is deferred until the habits of *Graptoleberis* have been described.) Posteriorly the posterior setae serve as a one-way valve on each side. Water forced out backwards between them will lift the overlapping rows of posterior setules, but any tendency for water to flow in the reverse direction will close them. In practice the pump draws water from the anterior end of the carapace chamber and forces it backwards in such a constant stream that the sealing action of the valve must be called into play only momentarily.

Posteriorly the post-abdomen is jammed into the gap between the carapace lobes as a plug (figure 51, PA) which very effectively seals this region: this is why the proximal region is wide.

There remains to be sealed the wide region across the ventral surface where, at the point of transition between the median and posterior series of marginal setae, the carapace flange inclines away from the substratum. Here the gap is bridged very largely by the conspicuous outermost seta of the exopod of trunk limb 3 described in section (iii), whose long fine setules extend across the wide aperture between the carapace margin and the post-abdomen and make contact with both (figure 51). In this it is to some extent assisted by the shorter setae alongside it.

Because the carapace chamber is sealed in the manner described, the vigorous action of the pump, which beats with a frequency too great to be counted by eye, drives out water posteriorly and sets up a region of low pressure within the chamber. To counteract this, water flows in through the antero-ventral aperture. For an animal so small, and with a density only a little greater than that of water, the pressure difference necessary to maintain attachment need be very small. Although pumping is rapid and incessant when the animal is attached, it is intermittent, being sometimes fast, sometimes slow, and sometimes stops altogether, in healthy individuals observed under other conditions. These observations, in conjunction with those on other Anomopoda—*Graptoleberis* (this paper) and the macrothricids *Streblocerus* and *Drepanothrix* (unpublished observations)—show that a constant current is not always necessary for respiration, or for feeding, and emphasize that it is essential for attachment. (See also Smirnov (1968) on *Rhynchotalona* and *Monospilus*.)

An attached animal can move with great rapidity. The motive force is provided by the first trunk limbs, traction being achieved by the setules of their ventral surfaces. Movements of these limbs appear to be essentially the same as in other crawling chydorids, their ventral faces moving in an antero-postero direction, but take place with such rapidity that detailed analysis is impossible without recourse to elaborate apparatus. Certainly, however, they can give a long 'pull'. These movements reveal that although the claws of this first trunk limb appear to serve as a clip for the infolded antennal setae they do not in fact do so.

The post-abdomen is protruded in the usual anomopod manner when the animal defaecates. This action inevitably breaks the seal yet is performed with such rapidity that re-attachment presents no difficulty and is presumably a less difficult feat than is original settlement in an inverted position which, as when a fly alights on a ceiling, involves a complex manoeuvre. Occasionally the post-abdomen has been seen to press against the substratum and lift the carapace a little, possibly to overcome an obstacle. It is possible that the claws of the first trunk limbs are used for gripping on such occasions, and perhaps in other situations, as they are in *Peracantha*, but this has never with certainty been observed and for the most part these claws are not used during crawling. When the substratum is smooth glass, such grasping is impossible.

A. exigua can also suspend itself from the surface film of water which it uses in the same manner as a solid substratum. This has been seen several times in small vessels, but never in nature, and is perhaps seldom practised. That *A. exigua* is capable of this feat is informative: it reveals a potentiality of straight flanged carapace margins which has been exploited by *Dadaya* (Fryer 1956; and this paper) and, in a somewhat different manner, by certain daphnids.

(v) *The feeding mechanism*

What has been seen of limb movements and the collection of food particles indicates that the mechanism is the same in essentials as that of *Peracantha* and *Eurycercus*. However, whereas *Peracantha* uses labral gland secretions, the major, and possibly sole, source of entangling secretions in *A. exigua* is trunk limb 1. These must inevitably be carried by the powerful current which flows through the filter chamber and accumulate at its posterior end. (Cf. *Alonopsis* where this has been demonstrated.) That filtration is very effective, even if no setules are present on the filter plates of the trunk limbs (section iii), is readily apparent from the ability of *A. exigua* to filter cells of *Chlorella* from a suspension. This is done as the animal moves over surfaces in the typical manner. Cells enter the carapace chamber via the antero-ventral aperture, pass into the filter chamber between the first trunk limbs, and accumulate posteriorly. Nevertheless, the habits and the nature of the gut contents leave no doubt that this species feeds mainly by sweeping material from the surfaces over which it crawls, and this has often been observed. Limb movements are essentially the same as those of other chydorids. Movements of trunk limbs 2 and 3 are co-ordinated; those of trunk limb 2 involve a forward 'ramming', component of the gnathobasic setae; trunk limb 4 beats inwards in the typical chydorid manner; and there is a definite forward component to the movement of the filter plate of trunk limb 5. Scraping takes place both as the animal is being propelled forward by the action of the first trunk limbs, and when it is still.

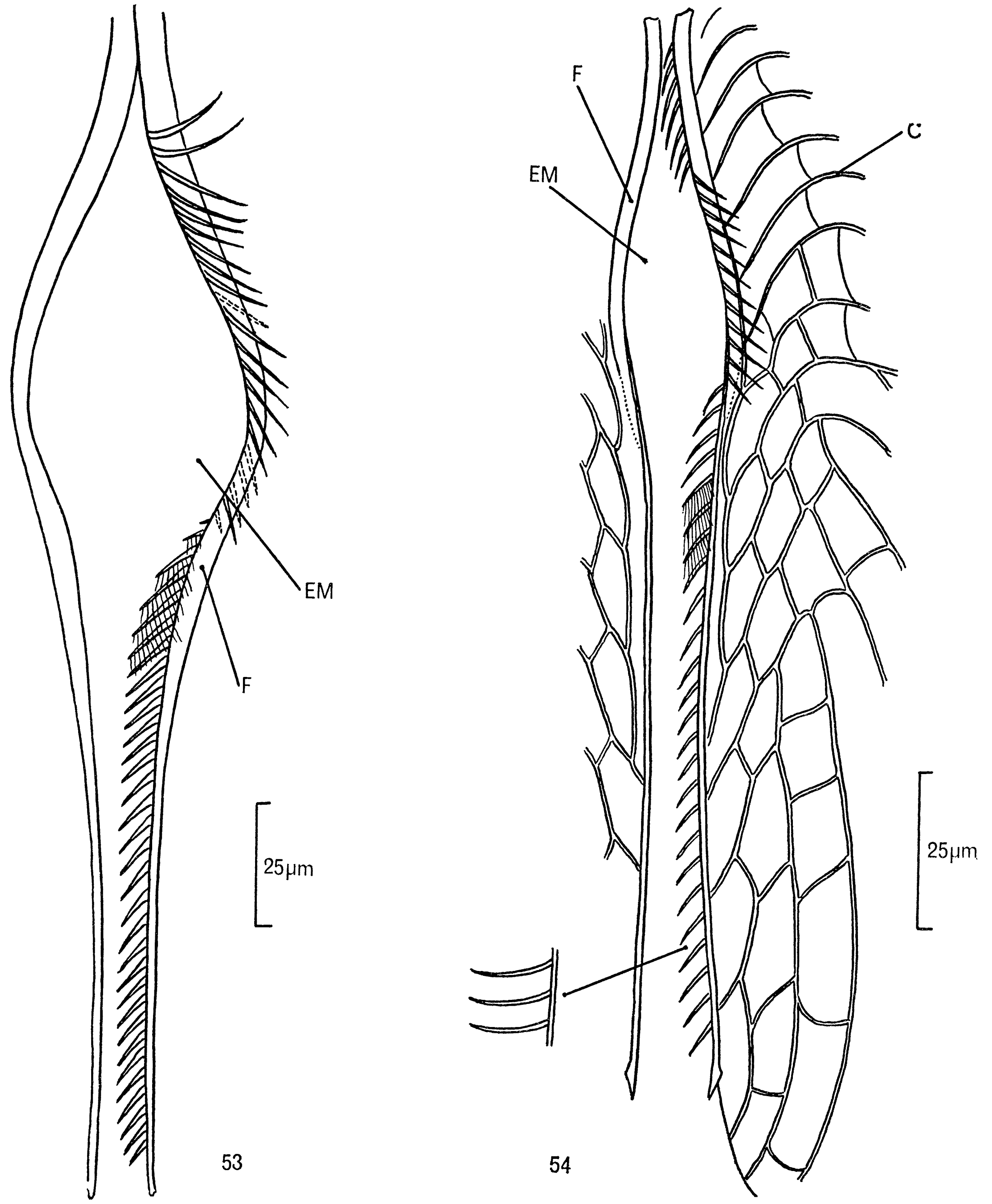
XII. THE HABITS AND ABILITIES OF *ALONELLA EXCISA* (FISCHER) COMPARED WITH THOSE OF *A. EXIGUA*

(i) *A major difference in ability*

From an evolutionary point of view study of the comparative ecology of closely related species is a fruitful field of investigation and may indicate how different specializations were initiated. Ecological differences need not necessarily have a morphological basis (though an apparent lack of significant morphological differences may sometimes indicate only insufficient study), but in some cases structural differences whose significance is not readily apparent may be the basis of profound differences in habits. This is so in *A. exigua* and *A. excisa* whose close relationship is undoubted. Although *A. excisa* (length to about 0·44 mm) has a distinct flange on the ventral carapace margins, and uses this and its associated setae as a stable base when it crawls, just as does *A. exigua*, it is incapable of performing the most characteristic feat of that species and cannot move upside down on the underside of an object. Its limitations are made clear when it is confined in a cavity dish. Here, by preference, *A. excisa* settles on the ventral carapace margins and balances with obvious ease. It crawls like *A. exigua* but, unlike this species, when it ascends the ever more steeply sloping sides of the dish it is unable to move on the steeper parts. When it rests with its long axis at right angles to the slope it topples sideways.

(ii) *Structural and functional bases of differences in ability*

The key to the difference in ability between *A. exigua* and *A. excisa* is the difference in structure of the ventral carapace margins and associated differences in their setae. The salient differences can be seen when a horizontal slice, cut to reveal the carapace margins of *A. excisa*, is compared with the same region in *A. exigua*. Figure 53 shows such a slice. The most important differences are that the flange is narrower, and that the embayment, and setae which fringe it and which are used for balance, occupy a smaller proportion of the total length than in *A. exigua*. This is readily seen by the more anterior position at which the carapace margin begins to incline away from the substratum when the animal is viewed laterally, as well as by the extent of the flat 'balancing zone' readily ascertained by focusing on a horizontal slice. Inevitably the posterior region is more elongate in *A. excisa* and bears about 32 inwardly directed posterior setae (about 12 in *A. exigua*). *A. excisa* (width about 46 % of length) is also slightly narrower than *A. exigua* (width about half the length). Specialization for close association with a substratum is thus less apparent in *A. excisa* than in *A. exigua*. In this respect it is at about the same level as *Peracantha truncata*. On the anterior margins, however, the flange is broad and similar to that of



Figures 53, 54. *Alonella excisa* and *Alonella nana.*

Figure 53. *A. excisa.* Ventral carapace margins as seen from below. From a sectioned animal.

Figure 54. *A. nana.* Ventral carapace margins as seen from below. The figure is prepared from a sectioned animal but the orientation of the setae in the embayment region has been ascertained and drawn from a living animal. The marginal setae of the posterior series are drawn from the preparation but their orientation in life is indicated in the inset. The length of these setae is greater than is apparent from the main figure as here they are directed towards the observer. Note how the ornamentation of the carapace consists in fact of cuticular ribs.

A. exigua, and from its relationship to the labrum and antenna it is evident that the anterior entrance to the carapace chamber is equally well sealed.

The development of a close association between the ventral carapace margins and the substratum is a prerequisite to the establishment of a chamber which can either be sealed, or sufficiently well sealed to ensure that water enters over a restricted region and pressure within the chamber can be reduced, be it ever so slightly. In *A. excisa* the anatomical specializations on which such a system can be based have not been fully acquired though all appear to be present in incipient form.

(iii) *The anatomy and ecology of* Alonella excisa

A. excisa is an active species which frequents a variety of habitats and occurs both among vegetation and on vegetation-free bottoms.

The swimming setae of the antennae are both relatively and absolutely shorter than in *A. exigua*. In specimens whose antennal rami were approximately the same length, the longest swimming setae of *A. excisa* had a length only about 82 % of those of *A. exigua*. A rudimentary denticle is present on the basal segment of the exopod but, as in *A. exigua*, no scrambling spine is present. There are spines, a little longer than those of *A. exigua*, distally on both rami. These differences are reflected by, and presumably correlated with, differences in swimming abilities, though other factors are probably also involved, and *A. excisa* swims less swiftly than *A. exigua*. Nevertheless, it is exceeded in swiftness only by this species among those investigated. When swimming it usually moves forward only a few millimetres, then pauses: only seldom does it swim persistently. Over a short distance (9 mm) a female 0·34 mm in length attained a speed of 18·9 body lengths (6·43 mm)/s. Somewhat slower speeds were sustained for considerably greater distances.

The trunk limbs of *A. excisa* are similar to those of *A. exigua* and the arrangement of the filter plates is the same. Secretions are produced from the first trunk limbs. Although not so finely denticulate as in *A. exigua*, the scrapers of trunk limb 2 are nevertheless minutely toothed. In spite of this the size of the food particles collected is much greater than in *A. exigua*. This was apparent in all the specimens examined and seems to reflect the nature of the habitats frequented rather than the fineness of the denticulation, though the scrapers are presumably capable of collecting also minute particles. Ingested material included relatively coarse detrital particles and spherical green algae. Specimens living in a moorland pool among stands of *Fontinalis* had eaten, among other items, numerous specimens of the epiphytic diatom *Epithemia* whose cells were as long as the diameter of the more posterior portion of the alimentary canal. That such a diatom, which attaches itself by the whole of its ventral surface, can be collected testifies to the efficacy of scraping. *A. excisa* can filter cells of *Chlorella* from a suspension, at which times the employment of secretions is apparent, for the algae which accumulate in the food groove are evidently bound together into a string. Food collection and manipulation take place much as in *Peracantha*.

XIII. *ALONELLA NANA* (BAIRD), THE SMALLEST ANOMOPOD: ITS STRUCTURE AND HABITS COMPARED WITH THOSE OF RELATED SPECIES

(i) *Some aspects of minute size*

Adult females of *A. nana*, which is the smallest anomopod and one of the smallest arthropods, have a maximum length of about 0·26 mm. Males are slightly smaller. Females of the largest chydorid, *Eurycercus glacialis* Lilljeborg, attain a length of about 6·0 mm. These differences are most readily appreciated by reference to figure 55 and by a comparison of volumes. The volume of *E. glacialis* is some 7000 times that of *A. nana.*

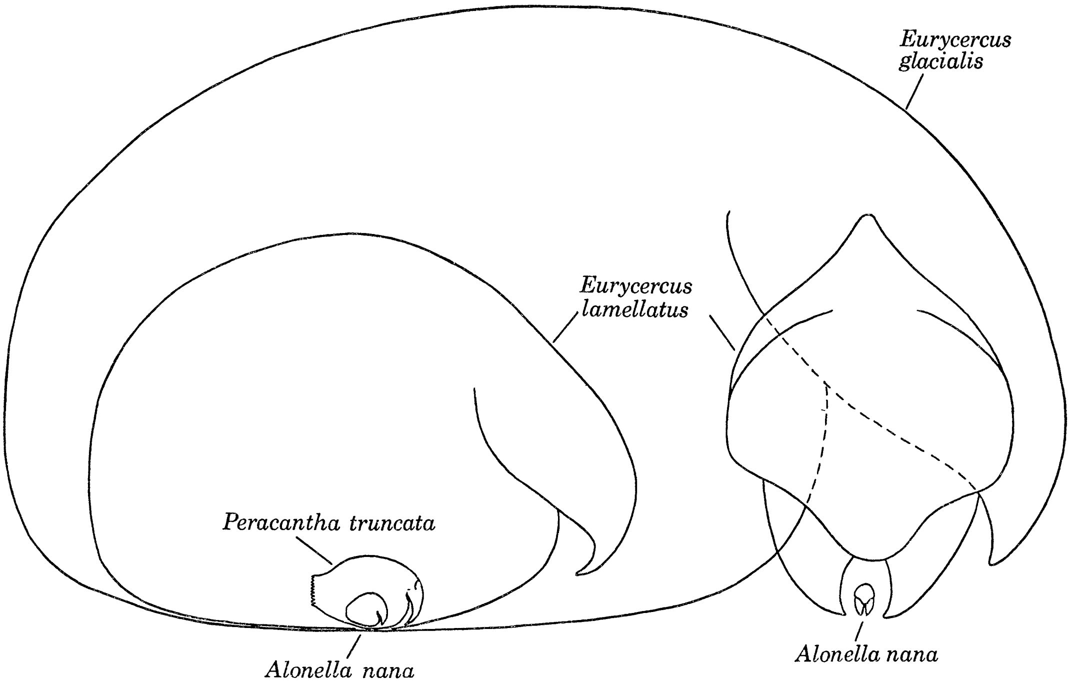


FIGURE 55. The relative sizes of certain Chydoridae. The outline of *Eurycercus glacialis* is that of a female 6 mm in length, which is the maximum attained by this species. The approximate lengths of the other species shown in the figure are *E. lamellatus* 3·1 mm, *Peracantha truncata* 0·64 mm, and *Alonella nana* 0·24 mm.

That such organisms must have different ways of life and exploit different niches is clear. Differences between the volume of the filter chamber are even more striking. Only crude calculations are possible but the filter chamber volume of *Eurycercus lamellatus* is some 18000 times that of *A. nana*. If the ratio, filter chamber : body volume in *E. glacialis* is the same as in *E. lamellatus*, then its filter chamber volume may be more than 140000 times that of *A. nana*. This figure will be exceeded if males or early instars of *A. nana* are used in the comparison. Although so different in volume, the filter chamber is similar in essentials in the largest and smallest species. This strikingly reveals the successful nature of the basic chydorid feeding mechanism.

It is obvious that *A. nana* cannot collect particles of the size utilized by larger species (and that the scrapers of the latter probably leave untouched some of the material collected by *A. nana*), and that it can penetrate cracks and crannies, both among vegetation and detritus, which are inaccessible to larger species. It can co-exist with them yet make entirely different demands on the environment. To an animal so small most objects must present an irregular surface, and as in nature many surfaces are covered with a layer of micro-organisms and fine detritus—in some cases in the interstices of coarser material—situations favourable for creeping and scrambling (section ii) must be almost ubiquitous. This may in part explain the great ecological tolerance of this species.

(ii) *The habits of* Alonella nana *and their structural basis*

A. nana occurs in many different situations in the littoral zone of lakes and in smaller bodies of water. Flössner (1964) found it in so many littoral habitats that he designated it as ubiquitous. The only other species to qualify for this epithet was *Chydorus sphaericus*. Mr W. J. P. Smyly has found it regularly on a soft bottom at a depth of 24 m in Buttermere where conditions are very different from those in the littoral zone.

This wide tolerance is accompanied by a lack of that specialization of the ventral margins of the carapace which is seen to varying degrees in *A. excisa* and *A. exigua*, and by less specialized means of locomotion. Although *A. nana* settles on the ventral carapace margins and moves over surfaces by means of the first trunk limbs, these appendages are also assisted by the antennae, which are not, however, as specialized for scrambling as they are in some chydorids and which make their contribution by slow sweeps.

The ventral margins are shown in figure 54. There is only a rudimentary embayment—less developed than in *A. excisa* and negligible in comparison with that of *A. exigua*—and about two-thirds of the length is occupied by the more or less straight posterior region. It also shows the 'ornamentation' of the ventral portion of the carapace. The characteristic 'striations' of the carapace of this species are in fact distinct thickenings of the cuticle which give strength with lightness and are better termed cuticular ribs. Firm anchorage for the ribs is necessary ventrally and is provided by the more or less hexagonal reticulation of thickened cuticle. Cross-struts strengthen the ribs at intervals, some being as thick as the ribs themselves, others (shown by a single line in figure 54) being thin.

The headshield is broad. Seen dorsally it is similar to that of *A. exigua*. The endopod of the short antenna bears a short terminal spine and the exopod has short spines on the basal and distal segments; that on the basal segment in particular being very small. These appendages are used for scrambling among detritus into which, if it be of suitable consistency, the animal penetrates. Versatility rather than specialization is a feature of the locomotion of this species which has also been seen to take an algal filament between its carapace lobes and move along it by use of the first trunk limbs in the manner frequently exhibited by *Chydorus sphaericus*. The antennal setae are not folded within the carapace as they are in *A. exigua* and *A. excisa*, but the antennae can be held close to the carapace margins—perhaps indicating a step towards the habit of protecting these appendages.

A. nana is an active but not a persistent swimmer and often moves erratically. Swimming speeds are therefore not easily measured. When illuminated from below it gives the misleading impression that it swims upside down. When illuminated from above it swims ventral surface down and is negatively phototactic. In part because its size is small, absolute speeds are low, rather less than 0·2 mm/s being the best recorded for an individual 0·257 mm in length, but speeds relative to size are also low—maximum about 7·6 body lengths/s sustained for 21 s. Even if these err considerably on the low side, *A. nana* is much slower than *A. exigua*, a difference which reflects two different ways of life practiced by members of the same genus.

(iii) *Adaptive radiation and specialization as shown by* Alonella nana, A. excisa *and* A. exigua

Three species of *Alonella* occur in Britain. (Reasons for excluding *Disparalona rostrata* are given in § XIV.) All employ the same basic kind of feeding mechanism. All are closely associated with substrates and all utilize the ventral margins of the carapace for balance, though they can also swim well. The degree of specialization of these margins varies greatly, being least in *A. nana* which uses the antennae to assist crawling, greater in *A. excisa* which folds the antennal setae inside the carapace and uses only the first trunk limbs for propulsion over surfaces, and greatest in *A. exigua* which can move over surfaces even when inverted, a feat which the other two cannot emulate. These and other features are tabulated in table 1.

TABLE 1. SOME MAJOR DIFFERENCES IN THE HABITS AND ABILITIES OF THREE SPECIES OF *ALONELLA*, AND THEIR STRUCTURAL BASES

A. nana	*A. excisa*	*A. exigua*
Embayment very feebly developed; occupying about 40 % of length of ventral margin	Embayment well developed; occupying about 50 % of length of ventral margin	Embayment enormously developed; occupying over 60 % of length of ventral margin
Ventral marginal flange feebly developed around embayment	Ventral marginal flange well developed around embayment	Ventral marginal flange enormously developed over most of its length
About 15 or 16 embayment setae	About 21 embayment setae	About 40 embayment setae
Antennal setae not infolded when crawling	Antennal setae infolded when crawling	Antennal setae infolded when crawling
Antennae used to assist crawling	Antennae not used to assist crawling	Antennae not used to assist crawling
Unable to crawl inverted	Unable to crawl inverted	Able to crawl inverted
Swims slowly. Max. 7·6 body lengths/s	Swims quickly. Max. 18·9 body lengths/s	Swims extremely rapidly Max. *ca.* 47 body lengths/s
Ecologically euryvalent	Ecologically euryvalent	In a more restricted range of habitats

In their ecological preferences they show definite differences. Besides exhibiting different substrate preferences *A. excisa* and *A. exigua* tend to frequent waters which differ chemically. *A. excisa* occurs particularly in acid waters, is tolerant of very acidic conditions, and sometimes occurs among *Sphagnum*. Lowndes (1952) found it over a pH range of 3·4 to 4·6, and all the 48 tarns (of 144 surveyed) in the English Lake District in which Smyly (1958) found it had a total ionic concentration of less than 1·0 mequiv./l. Less is known of such environmental relationships in the less common *A. exigua* but it is certainly rare in the more acidic waters. It does, however, sometimes inhabit the same body of water as *A. excisa*, and did so in two of the 144 tarns surveyed by Smyly. *A. nana* is tolerant of a wide range of chemical conditions, and is more common in Britain than either of the other two species, with both of which it co-exists. Smyly (1958) found all three in a tarn only about 300 m^2 in area.

A. exigua is designated as a phytophile by Flössner (1964) and its specialized accomplishments enable it to feed even beneath floating leaves, while *A. excisa*, although unable to frequent some of the situations exploited by *A. exigua*, lives both among plants and in vegetation-free habitats, though its tolerance is less than that of *A. nana*. Size differences, and the fact that *A. excisa* ingests larger particles than do the other two, means that co-existence is possible without exploiting the same resource.

(iv) *Conclusions concerning three species of* Alonella

The structure and abilities of *A. nana*, *A. excisa* and *A. exigua* (summarized in table 1) are related to different ways of life. *A. nana* frequents bottom detritus into which it can burrow by use of the antennae while *A. excisa* and *A. exigua* are associated with surfaces, particularly of plants in the case of *A. exigua*, over which they crawl by use of the first trunk limbs. Specialization of the ventral carapace margins and an ability to reduce the pressure within the carapace chamber enables *A. exigua* to crawl inverted. *A. excisa* cannot do this. These different abilities are of great ecological significance. Those of *A. exigua* add another dimension to its habitat and enable it to live in situations which *A. excisa* cannot exploit and where competition is minimal. From an evolutionary point of view they illustrate, perhaps in a phylogenetic sense (though it is not claimed that the two species have an ancestor–descendant relationship), how one habit can give rise to another, that of *A. excisa* being the more primitive.

XIV. *DISPARALONA ROSTRATA* (KOCH), AN INDICATOR OF PHYLETIC DIVERGENCE

(i) *Disparalona* gen.nov.

Chydoridae of the subfamily Chydorinae, of more or less elongate form. Carapace with a broadly rounded postero-ventral corner with or without one or more denticles, and either striated or reticulated. Ventral margins of carapace with a narrow flange showing no elaboration in the region of the ill-defined embayment, and fringed over the whole of their length by setae of more or less uniform type, which show little differentiation among themselves on the basis of function. Flange on anterior margin of carapace widened dorsally. Headshield drawn out into a distinct, sometimes markedly elongate, rostrum, and with head-pores showing the arrangement found in several chydorid genera (*Alonella*, *Dunhevedia*, *Chydorus*, *Pleuroxus*, *Peracantha*, *Anchistropus*), namely two major pores between which are situated two close-set minor pores.

Antennae with seven natatory setae and three stout scrambling spines, one on the distal segment of the endopod and one each on the basal and distal segments of the exopod. Five pairs of trunk limbs. Trunk limb 3 in almost constant, active motion in life, with a fine gnathobasic filter plate and a coarse outer sieve, and with a large sweeping seta arising at the posterior dorsal corner of the gnathobase and directed forward along the food groove.

Post-abdomen with sharply pointed marginal denticles and minute lateral setules but no lateral squamae. Alimentary canal with rectal caecum.

Type species: *Lynceus rostrata* Koch, 1841.

The species here placed in a new genus has undergone many taxonomic vicissitudes, having been shuffled several times between *Alona* and *Alonella* and, since 1909, having been assigned to *Rhynchotalona* by European workers. Because of similarities in the arrangement of the head-pores, however, Frey (1959) transferred it to *Alonella* and (1961) expressed the opinion that it 'is clearly a member of the genus *Alonella*'. Previously (Frey 1959) he felt that 'if the species (of *Alonella*) do not belong in the same genus, at least they belong in a number of closely related genera'. While the usefulness of head-pore arrangement as an indicator of relationship is undeniable, the limitations of this characteristic, whose function remains unknown, should not be ignored, and similarity in head-pore arrangement must not be allowed to obscure other differences. In this section of the family, the arrangement of head pores does no more than indicate general relationships for it is essentially the same in several genera—*Alonella*, *Dunhevedia*, *Chydorus*, *Pleuroxus* and others, including *Disparalona*, and cannot be used as a generic characteristic.

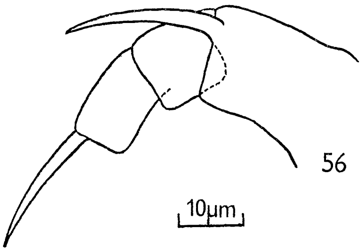
In the more fundamental aspects of its anatomy, and in the way in which it uses its appendages for the collection of food, *D. rostrata* differs markedly from the species of *Alonella* and has no place in that genus, as Lilljeborg (1900), who was familiar with many structural details of the animal, recognized and unequivocally stated many years ago.

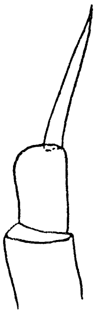
While several genera may share a common head-pore arrangement, striking differences in this feature do indicate phyletic distinctness, and on this basis Frey (1959) recognized that *D. rostrata* was not closely related to *Rhynchotalona falcata*. This was confirmed by Smirnov (1966*a*) on the basis of trunk limb setation and is here supported by the revelation of morphologically based functional differences.

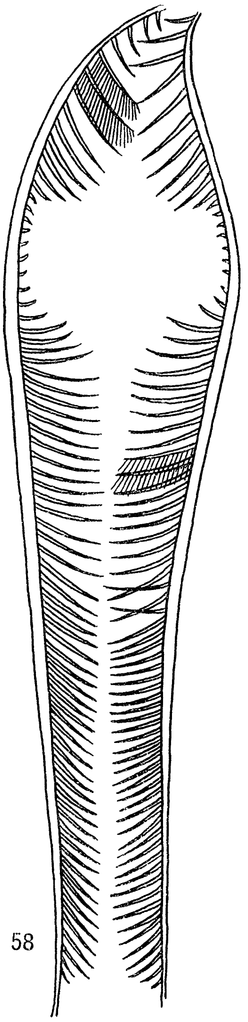
No living specimens of *Rhynchotalona falcata* (Sars) have been available, but thanks to Dr Deitrich Flössner, I have been able to dissect and section material collected by him in Germany. This species occurs particularly on sandy bottoms in the littoral regions of lakes, (Flössner 1964, and others) and might therefore be expected to differ adaptively from the mud-frequenting *D. rostrata*. The differences, however, are not merely those which reflect different habits but are more deep-seated. Head-pore arrangement, which cannot at present be related to any particular way of life, is one such feature. It is also evident that the feeding mechanism of *R. falcata* cannot be the same as that of *D. rostrata* (section v).

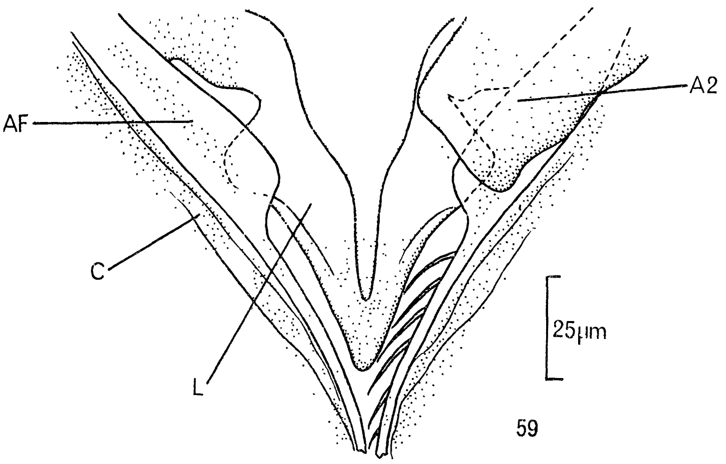
(ii) *Ecology and habits and some associated anatomical features*

References to the ecology of this species are usually somewhat vague, but recent work indicates with greater precision the kind of situation which it prefers. Flössner's (1964) careful comparison of littoral habitats reveals it as a mud-loving species. He noted its absence from associations of higher plants and its occurrence only rarely on sand. Lilljeborg (1900) found it in situations 'mit sandigen Boden, unter Pflanzen', which probably implies sandy bottoms with a covering of detritus. Among littoral habitats in which Langhans (1911) found it, one, 'über fast nackten Steinen' is noteworthy. Berg (1929) comments on the fact that previous authors have referred to it as occuring on sandy bottoms by saying that 'this does not seem to be the case to any marked extent', and he found it several times on a 'miry bottom', as did Ramult (1930). I have found it in four places myself. It occured plentifully in the film of mud covering the surface of stones in a vegetation-free region of a canal in Yorkshire where it was the most abundant crustacean (Fryer 1953, 1955). Its close association with the mud was shown by the large number of individuals obtained by scraping a small area and by its absence from net collections. When material was required for this study some 10 years later a visit to the same spot produced abundant material. It has since been found under similar conditions on the surface of stones in an alkaline tarn (Urswick) in Lancashire. The canal was acidic. It has also been found in a stony-shored reservoir, and in a bog pool on limestone in Ireland. Precise details of the bog pool habitat—which had a different fauna from that found in bog pools in England—were not ascertained but here it seemed to be living among flocculent detritus. *D. rostrata* therefore seems to prefer muddy bottoms—perhaps where









Figures 56 to 59. *Disparalona rostrata.*

Figure 56. Exopod of the antenna showing the massively developed crawling spines. All swimming setae omitted.

Figure 57. Distal segments of the endopod of the antenna. Swimming setae omitted.

Figure 58. The ventral carapace aperture as seen in a living animal. Note the virtual absence of a flange and how some of the marginal setae are directed outwards—a feature clearly correlated with the animal's way of life.

Figure 59. Transverse section through the head region at a level just anterior to the anterior carapace margins, showing the well-developed flange dorsally and the way in which the antennae apparently seal the dorsal apertures into the carapace chamber.

the mud is of no great depth and overlies a hard substratum. Such preferences would account for its occurrence both on stones and, in suitable situations, over sand.

That it actively penetrates mud is clear, and into a thin layer of flocculent mud or detritus it readily burrows when kept in dishes. It is negatively phototactic, and illumination from below (as when it is observed by transmitted light under a microscope) tends to drive it out. The headshield is bluntly rounded and suited to penetrate between flocculent particles. The body is longer with respect to both height and width than in European species of *Alonella* and this is related to differences in habits. Movement through the mud is achieved by means of the antennae, assisted by the post-abdomen. The first trunk limbs are unimportant in locomotion: often there is nothing that could be grasped by them. Although the antennae are used to propel the animal through the mud their action is very different from the well-known rowing of the mud-frequenting macrothricid *Ilyocryptus*. The exopod is provided both distally and on its basal segment with long, stout, scrambling spines (figure 56) and a similar spine is present distally on the endopod (figure 57). These contrast markedly with the small terminal spines and rudimentary spinule of the basal exopod segment in species of *Alonella*. The scrambling spines are greatly used to assist progression and the 'swimming setae' also help to push against particles. The antennae often move independently of each other. They are very versatile and their action is often rapid.

The post-abdomen is frequently used for pushing. Its ventral (morphologically dorsal) margin is armed with moderately stout spines of considerable length. Long spines may be an asset when the post-abdomen probes a thin layer of mud in search of a firm substrate on which to push, and they make provision for wear.

As *D. rostrata* moves through flocculent mud its orientation varies greatly. When denied access to mud, however, as in a smooth-bottomed dish, it abandons crawling and swims, but always keeps near the substratum and almost always keeps its ventral surface against the bottom. Crawling over firm substrates by use of the first trunk limbs is not practised. In nature it almost certainly swims only infrequently.

Material found in the gut consisted essentially of mud particles of unknown origin, though a definite greenness, indicating plant pigments, was present, and occasional algae, including naviculoid diatoms as long as the diameter of the middle portion of the alimentary canal, have been seen. In general the particles were small, any large objects, such as diatoms, being for the most part edible, suggesting that selection may be practised.

(iii) *Carapace morphology*

The carapace height ranged from about 59 to 67 % of the length in specimens measured, but may exceed 70 % according to reliable illustrations in the literature. Behind the broadly curved antero-ventral corner, beneath which lie the first trunk limbs, the ventral margins are more or less straight, though usually slightly concave until, posterior to the level of the last trunk limbs, they incline dorsally in a gentle curve.

The ventral margins are elaborated into only a narrow flange which extends over the whole of their length (figure 58). The embayment has ill-defined limits but in the vicinity of the trunk limbs the carapace margins are wider apart than elsewhere. There is no elaboration of the flange in this region such as is seen to some extent even in *Alonella nana*, and in fact it is here slightly narrower than in its more posterior portion. This, and the fact that the marginal setae of this region are not deflected outwards, reflect the habits of *Disparalona* and the lack of specialization for balancing on surfaces. The arrangement of the marginal setae is shown in figure 58, which is based largely on photographs and shows the orientation in life of a specimen lying free. A further six or seven setae occur on the anterior margins which lie deeper than the level of focus. With the exception of those which fringe the widest part of the embayment region, the setae are directed essentially inwards towards their partners on the opposite flange. Those not so directed are somewhat shorter than most of their associates but appear greatly foreshortened as they are directed more or less towards the observer. Each seta bears a row of posterior setules, shown on a few setae only in figure 58, which form a screen to prevent the ingress of mud particles in regions where these are undesirable. Such a screen is probably particularly necessary in the antero-ventral region which is constantly pushed through flocculent deposits.

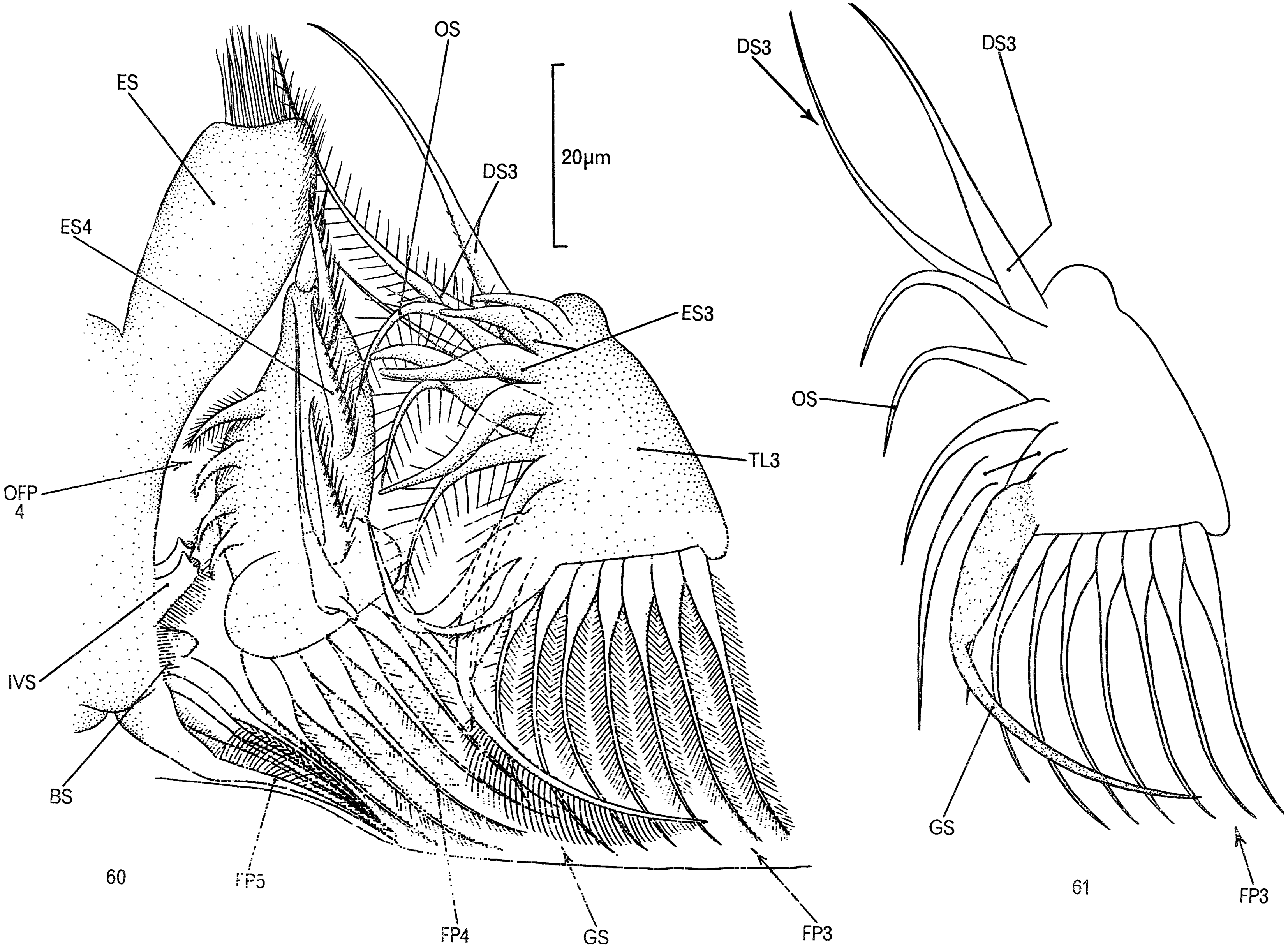
The anterior margins are shown in figure 59 (AF) which reveals the way in which they are widened into a broad flange dorsally, and shows the armature of setae ventrally, and the topographical relation of the flanges to the labrum (L) and antennae (A2).

(iv) *Trunk limb morphology*

The basic arrangement of the filter chamber is much as in *Peracantha truncata* (figure 47) but with certain notable differences. The first and second trunk limbs are sufficiently similar to those of *Peracantha* to render an illustration unnecessary, though they exhibit numerous small differences of which one is very significant. Because, unlike *Peracantha*, *Disparalona* does not crawl by means of its first trunk limbs, grasping spines on the outer lobe are unnecessary and the spines here are in fact elongate, as in other mud-frequenting chydorids—*Chydorus piger*, *Leydigia* and *Monospilus* (q.v.) An antero-median spine directed towards the food groove is present on trunk limb 1. The denticulation of the scrapers of trunk limb 2 is exceedingly fine, and the setae of the filter plate of this limb are definitely filtratory.

In the structure of trunk limb 3 *D. rostrata* exhibits a departure from the arrangement found in the species previously described. A typical gnathobasic filter plate is present (figures 60, 61, FP3) and this is continuous posteriorly and distally with an outer row of setae (OS) undoubtedly homologous with the outer filter plate of many species but which is made up of four setae provided, not with close-set filtratory setules, but with widely separated setules which make up only a coarse grid. This is here termed the outer sieve. Distally and outside this group of setae is another similarly armed seta (figure 60, DS3) which, although very different from it in structure and function, is homologous with one of the distal scrapers in species such as *Alonopsis* and *Alona affinis* (cf. figure 60 with figure 7). Adjacent to this is the second terminal spine, here slender, and very different from the stout scraper of several species (cf. these structures with the scrapers shown in figure 33). The different nature of these spines in different species is a clear example of the way in which homologous structures have been modified in accordance with functional demands during the evolution of the Chydoridae.

Even more noteworthy, and very different from anything to be found in any other chydorid yet examined, is the nature of one of the setae at the posterior corner of the



Figures 60, 61. *Disparalona rostrata.*

Figure 60. Longitudinal section through the posterior end of the filter chamber showing the specialized gnathobasic sweeper and outer sieve of trunk limb 3. Some of the filtratory setules of the posterior setae of the filter-plate of trunk limb 3 and of the anterior setae of trunk limb 4 have been omitted in order more clearly to show the gnathobasic sweeper.

Figure 61. Outline of the endopod of trunk limb 3 from the same position as shown in figure 58 with all spines and setae save those of the filter plate, outer sieve and gnathobasic sweeper, omitted, as are all setules. The gnathobasic seta is shown stippled so as more clearly to show its spatial relationship to the other structures present.

gnathobase. This takes the form of a large seta (figures 60, 61, GS) which, from its origin, is directed towards the food groove and which, more distally, curves sharply forward and extends about two-thirds of the way along the gnathobasic filter plate. On its dorsal edge, that is adjacent to the food groove, its distal portion is armed with a row of long, curved setules which make a very obvious brush. This seta, here called the gnathobasic sweeper, is shown stippled in figure 61 which also shows in outline the gnathobasic filter plate and the outer sieve unobscured by the heavier armature. These anatomical peculiarities are correlated with a unique mode of operation of trunk limb 3 (section v).

Trunk limb 4 is shown in figure 60. The spinules of its vertical endite spines (ES4) are located more anteriorly than in, for example, *Peracantha* (compare figures 60 and 37), but the similarity of this limb to its homologue in *Peracantha* and other species is obvious. Trunk limb 5 is illustrated in figure 60. The row of fine spinules on the basal portion of the innermost gnathobasic filter seta is continuous with a row of spinules which crosses the gnathobasic portion of the limb (BS) and is itself continuous with the row of fine spinules on the innermost sealing seta (IVS). These setules lie adjacent to their counterparts on the opposite limb and make a very efficient screen at the base of the limb.

The usual plate-like exopod is present on trunk limb 3, and the fourth and fifth trunk limbs are provided with large paddle-like exopods which make up the exopod pump.

(v) *Limb movements and the feeding mechanism, with a note on niche exploitation*

In life, although brief pauses are frequent, trunk limb 3 is in almost incessant, rapid and regular motion. This is not so in any other chydorid examined. In other genera this limb moves only intermittently and seldom completes more than a few cycles of movement in any one bout of activity. Similar regular activity of trunk limb 3 is, however, a feature of the Bosminidae and Daphniidae. Movement consists essentially of a swing such as occurs during intermittent movement in other species and which, on remotion, carries the gnathobasic region forward. This causes the gnathobasic sweeper to sweep forward along the food groove. The rate of beat is variable and, because speeds are sometimes great and pauses intermittent, is not easy to measure. Up to at least 20 cycles of movement may be completed at a rate of about 5 beats/s, but the average rate is less than this. During more sustained beating 60 and 50 cycles of movement were completed in 18·2 and 15·8 s (about 3·3 and 3·2 beats/s respectively) but slower movements have been recorded, for example 46 cycles of movement at just over 2·8/s. Pauses are sometimes connected with clearing of the anterior end of the food groove; sometimes no reason is apparent.

When the animal is lying freely, trunk limb 2 usually, but not invariably, moves at the same time as trunk limb 3. This movement, which is of small amplitude, is not associated with scraping, nor is it apparently necessary to move forward material pushed along the food groove by trunk limb 3, for when food accumulates in the region of trunk limbs 1 and 2 movement further forward than this is accomplished by a bigger swing. Trunk limb 4 moves in a typical chydorid manner and appears to be synchronized with trunk limb 3.

Because, although associated with a substrate, *D. rostrata* scrambles rather than crawls over it, and burrows in mud, it is not easy to observe the limb movements involved in food collection when the animal is behaving in a natural manner. Although this may be in part the reason why no definite act of scraping has been seen, it is probable that scraping is less important than the collection of suspended particles. The scrapers of trunk limb 2 are very finely denticulate and are probably used at most to whisk loose particles and not to dislodge attached material, which in any case is probably not necessary in the habitats frequented. The nearest approach to a scraping movement that has been seen is a reaching out of trunk limb 2 in an animal held in a compressorium. That trunk limb 2 may be used at times for food collection is, however, perhaps indicated by the presence of occasional large diatoms in the gut.

D. rostrata lives in situations where flocculent matter is inevitably stirred up as it moves forward—a process accentuated by its method of locomotion—and a constant stream of particles is therefore probably drawn into the carapace chamber. Material thrown into suspension is more likely to be flocculent organic matter than inorganic particles, which are more difficult to stir up and which settle quickly. It seems likely therefore that, by employing a modification of the basic method used by the scraping species, *D. rostrata* has been enabled to exploit a different kind of niche.

Currents set up by the animal can only be observed in detail in individuals whose movements have been restricted, so the results obtained need to be interpreted with care. Certainly, however, water enters the carapace chamber, and ultimately the filter chamber, from the ventral side in the vicinity of the trunk limbs. A powerful current has also been observed entering the carapace chamber anteriorly and dorsally, the general direction of flow of all the currents being much as in *Alonopsis* (figure 3). In the antero-ventral region of the carapace no water enters. Whether the antero-dorsal current is a true component of the feeding mechanism is uncertain. If it is, it is difficult to understand why the anterior flange of the carapace is widened here (figure 59, AF) as if, by collaboration with the labrum (L) and antennae (A2), it is specifically intended to seal the aperture through which water enters. The ventral carapace setae inevitably serve as a screen in the region in which water enters the carapace chamber, and will exclude most of the large flocculent particles which must almost always be present in the situations in which *D. rostrata* lives. Such a function is incompatible with their employment as aids to balance, which is their function in species which crawl over firm substrates.

So far as it can be observed (which is less than in most species) and deduced from limb movements, the feeding mechanism appears to be as follows. Particles enter the carapace chamber ventrally in the 'embayment' region as a result of movement through mud and the action of the feeding/respiratory current. Others may perhaps enter antero-dorsally but this is not proven. Some scraping of material by trunk limb 2 may take place, but this is also unproven and material can certainly be collected without scraping. Movements of this limb may, however, at times help to force material towards the food groove.

Suspended particles are carried backwards into the filter chamber. Of these the larger will be caught by the outer sieve of trunk limb 3. Although this is 'coarse', the gaps between its constituent setae are no wider than about 10 μm in an adult female, and their setules effectively close these gaps to all save very small particles. Those with a diameter greater than 4 μm will certainly be retained. Very small particles, which are likely to prove embarrassingly abundant, will pass through it. The coarse nature of the sieve may also be related to the rapid movement of the limb: a fine sieve so orientated may offer too much resistance, especially when loaded, to permit such rapid beating. A similar situation prevails in *Bosmina* where the rapidly beating outer filter plate of this limb is coarser than the gnathobasic filter plate (Fryer, unpublished observations).

The orientation of the setules of the outer sieve of trunk limb 3 is such that any particles which they entrap will be pushed towards the food groove on remotion of the limb. On promotion the mere movement of the limb will tend to 'leave behind' any such particles even without the assistance which is received from trunk limb 4. Particles are then actively pushed towards the food groove by the anteriorly located vertical endite setae of trunk limb 4 and by the two gnathobasic spines which arise near the gnathobasic sweeper of trunk limb 3.

Any fine particles not trapped by trunk limb 3 will inevitably be retained by the fine-meshed outer filter plate of trunk limb 4 and, if required, will be passed to the food groove in the usual manner. Presumably *D. rostrata* like several other chydorids, can release unwanted material from the posterior end of the filter chamber by the simple expedient of opening the gap between the fifth trunk limbs. If so then any excess of fine particles can be released and only the larger particles retained by the outer sieve of trunk limb 3 need be dealt with. In a muddy environment this will enable considerable selection for size to be achieved (which may lead to economy of effort), will perhaps make for ease of handling, and will reduce the risk of clogging the entire mechanism (cf. *Leydigia*). Should the need to utilize very small particles arise, this can easily be achieved.

No secretions are produced by the trunk limbs, nor has the production of labral gland secretions been established, but it is difficult to see how fine particles can be dealt with, at least anteriorly, if these are not produced.

Movement of food along the posterior part of the food groove is greatly facilitated by the almost constantly sweeping gnathobasic sweeper of trunk limb 3. From time to time material is moved forwards from the region of trunk limb 2 by the gnathobase of that limb, the whole accumulated mass being swung forward as a result of a deliberate movement.

In *Rhynchotalona*, as in many other genera, the homologue of the gnathobasic sweeper of *Disparalona* is bent in the opposite direction to that of *Disparalona* and is obviously used for pushing food towards the food groove and not for sweeping it forward. Although living specimens have not been studied it may be predicted with confidence that rapid and almost incessant beating of trunk limb 3 is not practised by *R. falcata*.

Smirnov's recent observation (1968) that although the exopod pump of *Rhynchotalona* is present there is no feeding/respiratory current, reveals a further striking difference between it and *Disparalona*, and shows that the feeding mechanisms of the two genera differ considerably. In *Rhynchotalona* food must be scraped and pushed entirely by mechanical means as in *Graptoleberis* (§ XVI). Observations on certain macrothricid genera suggest that in the environment frequented by *Rhynchotalona* the lack of a respiratory stream will be no embarrassment.

It can be suggested with considerable confidence that '*Alonella*' *acutirostris* (Birge) should be assigned to *Disparalona*. When various features have been checked it may well be shown that *Alonella dadayi* (Birge) and *Alonella hamulatus* (Birge) belong here also.

(vi) *Conclusions*

Disparalona rostrata has no place in either *Rhynchotalona* or *Alonella*. Its habit is to penetrate flocculent mud though not, apparently, deeply. Major specializations in relation to this habit concern the ventral carapace margins, trunk limbs and feeding mechanism. Food is not collected by scraping but is extracted from stirred up particles. The gnathobase of trunk limb 3 is armed with an enormously developed sweeping seta which in life is in almost incessant motion, sweeping along the food groove. In this *Disparalona* is unique among the genera studied.

XV. *DADAYA MACROPS* (DADAY) AND THE EXPLOITATION OF A NOVEL NICHE

The habits of this essentially tropical species reveal a most interesting further way in which the ventral carapace margins can be used. By virtue of the arrangement of their carapace margins and associated setae both *Alonella exigua* and *Graptoleberis testudinaria* (q.v.) can, under certain conditions, crawl not only over firm substrates but also beneath the surface film of water, though there is nothing to suggest that this is practised in nature. *Dadaya macrops*, however, exhibits definite specializations for this way of life. Four living specimens were found in Central Africa long before the present study was commenced and, although information on previously unknown habits was obtained (Fryer 1956), the evolutionary interest of this species and the means whereby its habits might have evolved were not appreciated at that time, nor were opportunities available for studying the setae of the carapace margin in detail. Although not even preserved specimens have since been available, certain features are now apparent in the light of what has been learned of other species.

Each carapace valve of *D. macrops* has a long straight region which is drawn out into a flange (figure 62). The resemblance to *Alonella exigua* (figure 51) is obvious. The marginal setae, however, arise 'on the inside surface of the posterior part' of the carapace, (Smirnov 1966*b*), i.e. in a similar manner to those of *Chydorus sphaericus* (figure 136). That crawling beneath the surface film is a persistent habit is indicated by the inverse coloration of *Dadaya*, which is very darkly pigmented ventrally. Other features are related to this habit, for example the sensillae of the long antennules must make contact with the surface film, as do those of *Alonella exigua* with the surface over which it crawls. The large eye and ocellus—both relatively by far the largest in the predominantly benthic Chydoridae—suggest that, as in the swimming Bosminidae and Daphniidae, the perception of light is important. The film-hanging *Notodromas* and *Oncocypris* (Ostracoda) and *Tropocyclops prasinus* (Copepoda) all have very large eyes.

Functionally, the evolutionary route to the way of life practised by *Dadaya* is made clear by the habits of other chydorids. No great morphological changes need be entailed in a change from specialized substrate crawling to film-hanging (as is shown by the abilities of *Alonella exigua*). More information on the locomotion of *Dadaya*, which apparently swims beneath the surface film, is however, required. Although among the Anomopoda many evolutionary steps were apparently initiated by a change in habits, which preceded morphological changes (§ XXIII) *Dadaya* may have been pre-adapted to its present way of life, which could have arisen by the exploitation of morphological specializations associated with other habits.

Smirnov (1966*b*) has for the first time given sketches of the trunk limbs of *Dadaya*. These show that the distal portion of the corm of trunk limb 1 is long and more slender than in most crawling species and, especially interesting, that the 'scrapers' of trunk limb 2 are slender and extremely elongate—apparently more so than in any other species yet studied. The likelihood is that these do not serve as true scrapers but perhaps as whisks.

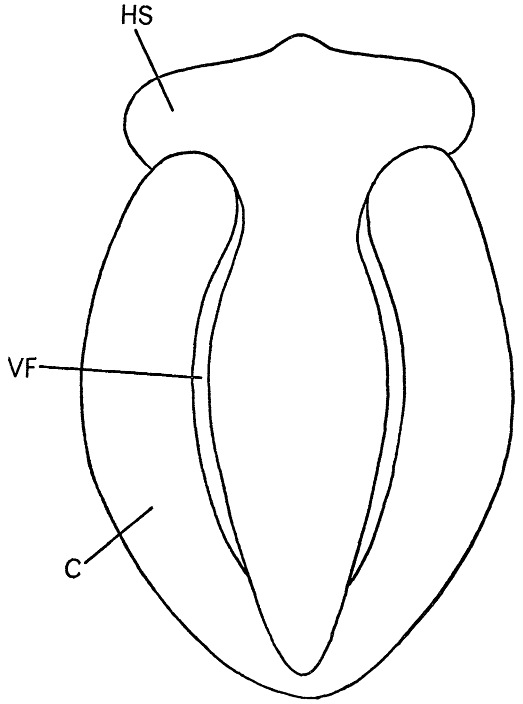


FIGURE 62. *Dadaya macrops*. Outline of the carapace and headshield as seen from below. Note the great breadth of the carapace, the wide embayment, and the well-defined ventral flange. (Redrawn from Fryer 1956.)

XVI. THE STRUCTURE, HABITS AND FEEDING MECHANISM OF *GRAPTOLEBERIS TESTUDINARIA* (FISCHER), A CHYDORID WITH THE HABITS OF A GASTROPOD MOLLUSC

(i) *The gastropod-like habits*

Although its structure must be understood before its way of life can be fully appreciated, an account of the remarkable and hitherto undescribed habits of this species must be given first. It is not possible to give an absolute measure of the degree of specialization of an animal but, considering what has so far been revealed, *Graptoleberis* has strong claims to be regarded as the most specialized chydorid, or perhaps even as the most specialized anomopod. Its structure and habits are directed almost entirely towards one specialized way of life.

Among the Chydoridae, *Graptoleberis* has carried to the furthest limits the utilization and modification of the ventral carapace margins. These it habitually uses when, as it does by preference, it moves over surfaces, particularly of plants, in a manner reminiscent of a gastropod mollusc, figures 149 and 150, (plate 18, facing p. 378). Although the entire principles of feeding and locomotion are vastly different in *Graptoleberis* and a gastropod, convergence had led to the acquisition of remarkably similar habits, and the analogy is the most useful way in which to convey an impression of the way of life of this crustacean. As does a gastropod, *Graptoleberis* glides over surfaces, this being accomplished by the combined use of the carapace margins, of their setae, which serve as do the runners of a sledge, and of trunk limb 1. The whole headshield–carapace complex has taken on a protective function analogous to that of the gastropod shell. The antennae can be used to enable *Graptoleberis* to overcome obstacles without losing contact with the substratum, but on smooth surfaces locomotion is effected exclusively by the first trunk limbs and the animal glides forward in a snail-like manner. The slow and deliberate nature of progress—so different from the rapid and apparently erratic movements of most chydorids—enhances the similarity to a gastropod. On a very smooth surface *Graptoleberis* can, by use of the first trunk limbs alone, traverse a distance equal to its own length in a little less than 6 s but usually moves considerably more slowly than this, feeding as it goes. Even without pausing, which it frequently does, it may take as long as 25 s to traverse one body length. During its advance it collects food by the use of scrapers borne on the second trunk limbs, the movements of which are slow and deliberate and, when seen from below at low magnifications, bear a superficial similarity to the rasping movements observable in a gastropod radula as the animal glides over a surface.

Many observations of *Graptoleberis* settled on *Elodea*, on which plant it is sometimes abundant, show that it is almost sedentary in habits, and that rasping of food sometimes takes place when the animal is stationary. Attachment (section v) is very firm. Attempts to remove by suction with a fine pipette an animal gliding over a glass surface are completely ineffective. Individuals can be pushed so that they slide over the surface but retain their grip. If specimens are attached to the walls of a vessel which is tilted so that they are exposed to the air for a time then swilled with water they usually remain attached.

Thus, by employing completely different principles, *Graptoleberis* has exploited a niche comparable with that of a typical herbivorous gastropod mollusc but, by virtue of its small size (maximum length *ca.* 0·7 mm) one in which it will encounter no molluscan competitor. It also has certain advantages over a mollusc with similar habits in that it can use its antennae both to assist gliding and to enable it to swim (see below).

(ii) *Ecology*

The ecological preferences of *Graptoleberis* are intimately related to its structure and habits. Flössner (1964) has recently pointed out that his observations are not in agreement with the statements of most previous authors (whom he cites) who claim that this is a bottom-dweller. Flössner found it to be associated particularly with dense stands of vegetation, and with these findings my own observations, both in England and tropical Africa, are in full agreement. Lilljeborg (1900), that most careful of workers, also laid particular stress on the association of this species with vegetation and even suggested that it might be transported with plants, but makes no reference to bottom-dwelling habits. I have found it in particularly large numbers in dense stands of *Elodea canadensis*—whose flat leaves offer particularly suitable surfaces for attachment and grazing. Although

Ramult (1930) also noted that it was particularly abundant in '*Elodea*-Wiese', though without being aware of its true habits, it has possibly been overlooked at times by those collecting in such situations as, if undisturbed for some time, it usually attaches itself to the walls of the vessel in which the collection is placed and there easily escapes detection. Its habits and adaptations seem ill-suited to the conditions prevailing among most bottom deposits.

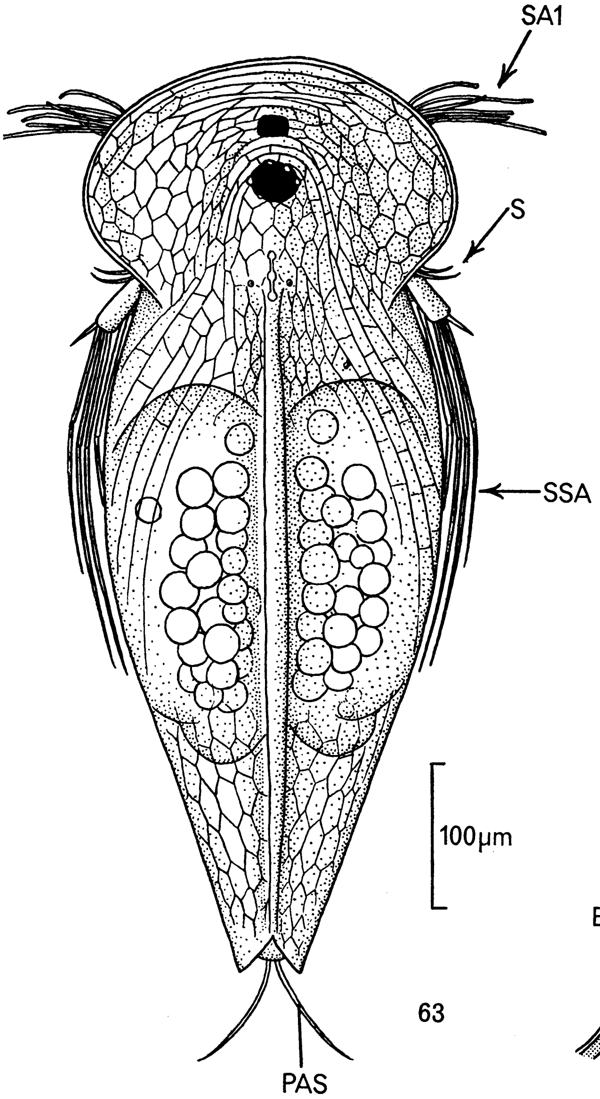
It is suggested that the existence of suitable vegetation is of much greater importance as an ecological requirement of this species than are the frequently measured physical and chemical variables. Its wide tolerance of the latter is shown by its occurrence in waters of diverse types from the arctic to the tropics, and Lowndes (1952) found it in nature in waters with a pH range of from 4·2 to 9·2.

The food consists for the most part of minute particles which are usually so small that their origin cannot be ascertained. Minute algae are certainly taken in at times but these never comprise more than a very small proportion of the food. Even the coarsest scrapers of trunk limb 2 (no. 6) (section iv, figure 85) are only about 25 μm long in large individuals and the gap between adjacent teeth is considerably less than 2 μm at its widest point, so that, even if particles do not adhere, very small fragments can be collected. In fact much smaller particles must inevitably be swept to the mid-line by the outer scrapers (nos. 7 and 8) (figure 85) whose teeth are very fine and separated by gaps of less than 0·5 μm. Masses of such material can easily be handled so it appears that material down to the dimensions of bacteria can be collected, and it seems possible that bacteria adherent to minute organic particles comprise an important part of the diet. Although it is seldom possible to identify individual items in the gut it is very apparent that *Graptoleberis* ingests smaller particles than do several other weed-frequenting chydorids. This is not the result of particularly efficient trituition by the mandibles. This difference reinforces the niche specificity so apparent from habits alone.

(iii) *Form and function of the carapace and headshield*

From an ecological point of view the function of the headshield–carapace complex is the same as that of the shell of a gastropod mollusc. In fulfilling this role it has, however, also to serve as the actual structure which glides over the substratum. Further, it has to continue to fulfil the long established functions of providing attachment for certain muscles and to permit the utilization of appendages which have themselves taken on specialized functions. The reconciliation of these various requirements represents one of the great achievements of anomopod evolution.

The external form of the carapace is best appreciated by reference to figures 63, 64 and 68. In transverse section it has for the most part the form of a tall ogee arch (figures 64, 77) but becomes more nearly triangular anteriorly (figure 66). Dorsally the cuticle, besides being slightly thickened, is sharply folded on itself, and is therefore for a short distance essentially of double thickness (figure 65), and thus forms a thickened dorsal ridge to the carapace. This is very noticeable in the living animal (figures 63, 64). Here, too, a difference in staining reactions perhaps indicates that the dorsal ridge has physical properties different from those of the rest of the cuticle. In Mallory-stained sections the carapace cuticle is for the most part differentiated into a thin, amber-coloured, non-staining



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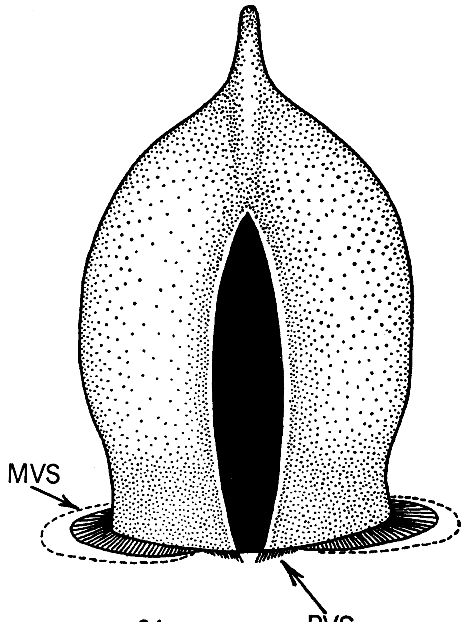

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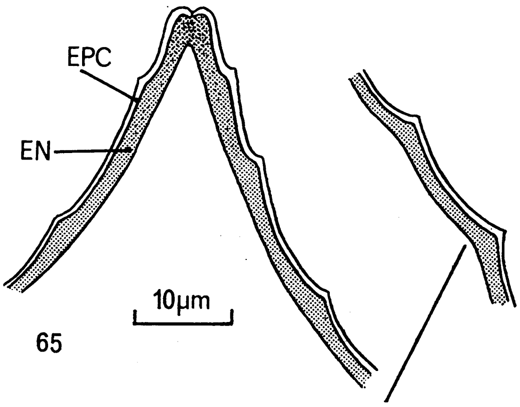

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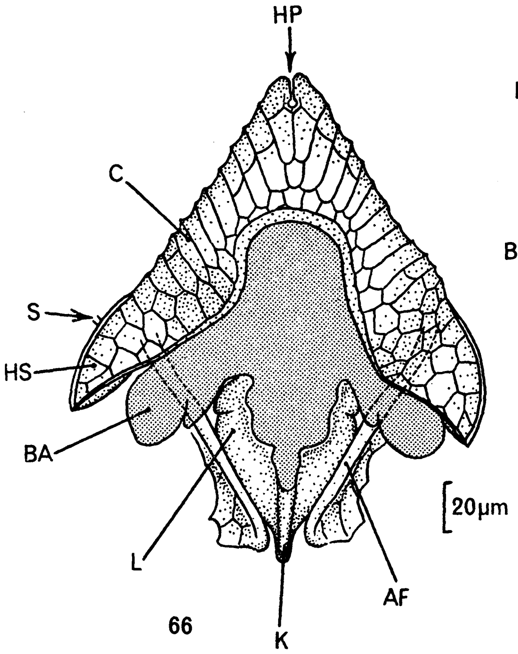
Figures 63 to 65. *Graptoleberis testudinaria.*

Figure 63. A gliding animal seen from above. Note the array of tactile sense organs both around the head and posteriorly.

Figure 64. A gliding animal seen from behind, the observer being slightly above the level of the substratum. The outline of the animal is taken from a photograph focused somewhere near the middle which gave an accurate silhouette, and the posterior aperture, shown in black, was added from another photograph. The general appearance of the median ventral setae is correct but the setae themselves are shown only diagrammatically.

Figure 65. Transverse section through the cuticle of the carapace showing the dorsal ridge and, inset, a portion of the more lateral region of the carapace. The dark stippling indicates those portions of the endocuticle which stain red-purple with Mallory's stain. Otherwise the endocuticle stains pale blue.

epicuticle (figure 65, EPC, but see below) and a thicker blue-staining endocuticle (EN), traces of red-staining material being sometimes detectable in the endocuticle at the region of juncture of the two layers. In the dorsal ridge the epicuticle is unmodified but the slightly thickened endocuticle stains red-purple over much of its thickness. Ventral to the ridge the red-staining zone rapidly narrows and merges imperceptibly with the rest of the blue-staining endocuticle (figure 65). When seen in surface view the apparently non-staining epicuticle is red, which suggests the presence of an extremely thin film of material of different properties external to the epicuticle.



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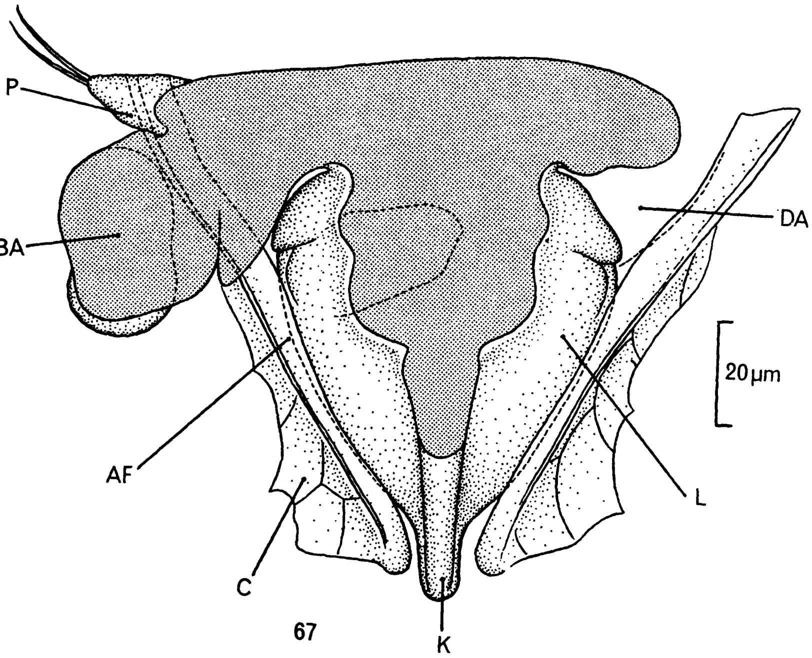

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Figures 66, 67. *Graptoleberis testudinaria.*

Figure 66. Transverse section through the head region at a level just anterior to the anterior carapace margins, showing how the labrum fits as a plug into the anterior carapace aperture and how the antennal coxa seals the dorsal aperture of its side above the labrum. The joint between the basis and coxa of the antenna can be seen ventrally.

Figure 67. The same, showing the seal in greater detail. The outline of the deeper-lying mandible is shown on the left. Had the dotted line showing the outline of the antennal rami (which are directed backwards alongside the carapace—figures 63 and 68) been drawn at the level of this section, it would, because of the position of the antenna in the fixed animal, have partly overlain the anterior flange of the carapace, but it has here been drawn so as not to do so. The dorsal aperture (DA) is sealed by the coxa of the antenna. The dotted line indicates the limits of the deeper-lying mandible.

The dorsal ridge strengthens the carapace and presumably affords some protection from abrasion and perhaps even against small predators. A gliding *Graptoleberis* was not disturbed when 'bumped' by a carnivorous cyclopoid copepod, nor did the latter hunt excitedly as happens when an actively swimming cladoceran is encountered but not immediately seized. In the embryo there is a distinct ectodermal ridge, presumably responsible for the elaboration of the cuticular ridge during development.

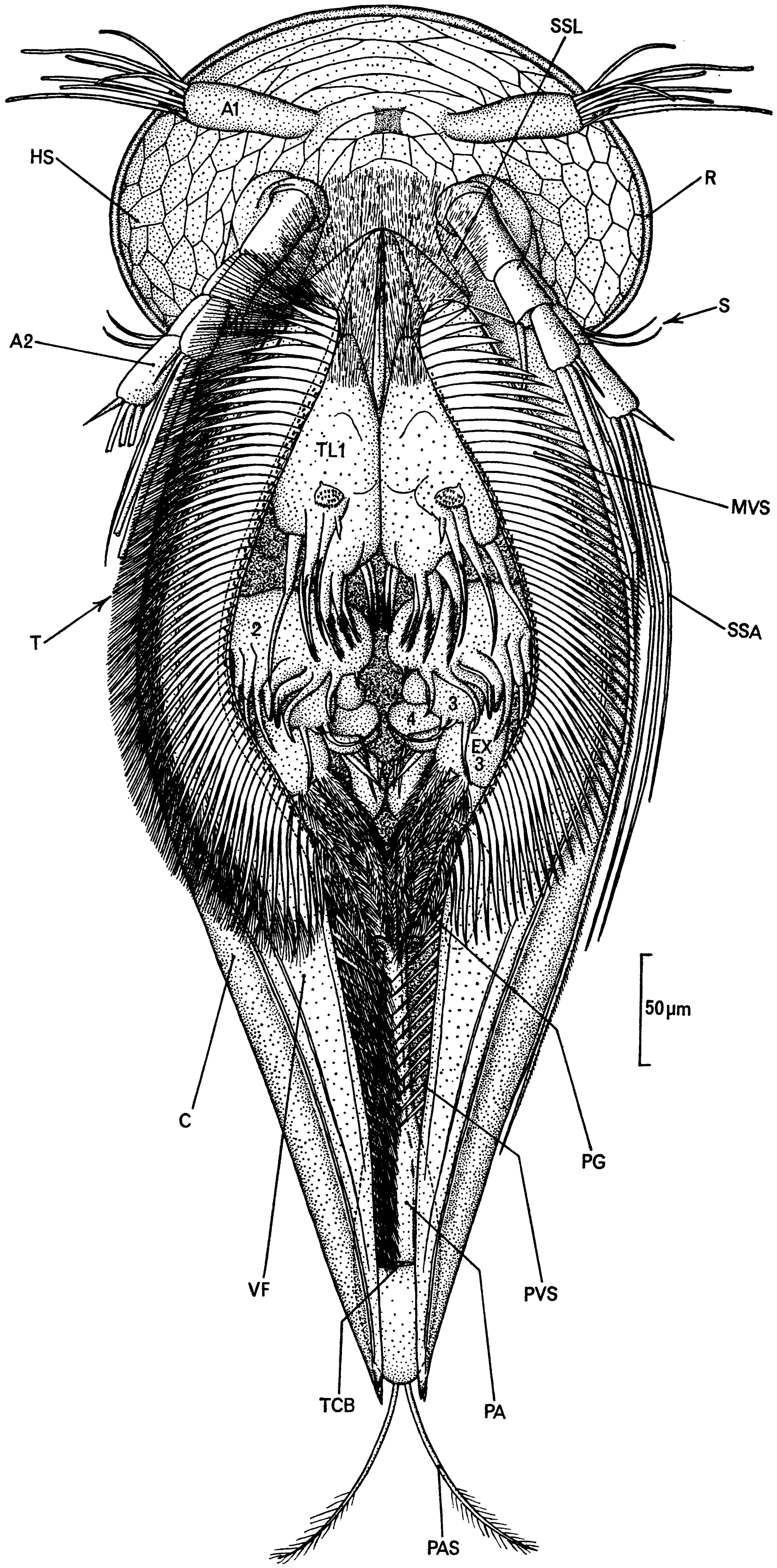


Figure 68. *Graptoleberis testudinaria.* An individual seen from below as it glides over a surface. The setules of the median ventral setae on which it actually rests are omitted. The first trunk limbs are at the end of their forward movement and the second trunk limbs are in the position from which they begin their working stroke. Note the posterior gap (PG) of the suction chamber which is sealed largely by the exopod setae of trunk limbs 3 and 4.

The carapace and headshield are conspicuously reticulated (figures 63, 66 and 68). This is no mere ornamentation but a means of giving strength with little increase in weight, and is achieved by local thickening of both epi- and endocuticle (figure 65).

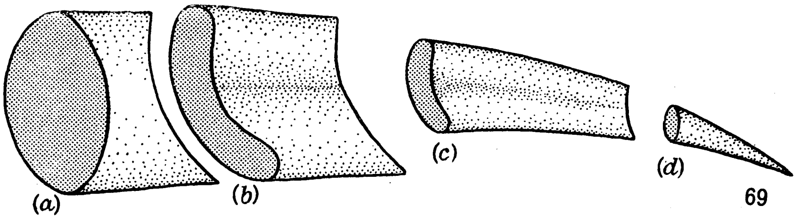
The anterior carapace margins are straight and slope backwards from the anterior ventral corner. Their relationship to each other is shown in transverse sections in figures 66 and 67. Each is elaborated into a simple flange (AF).

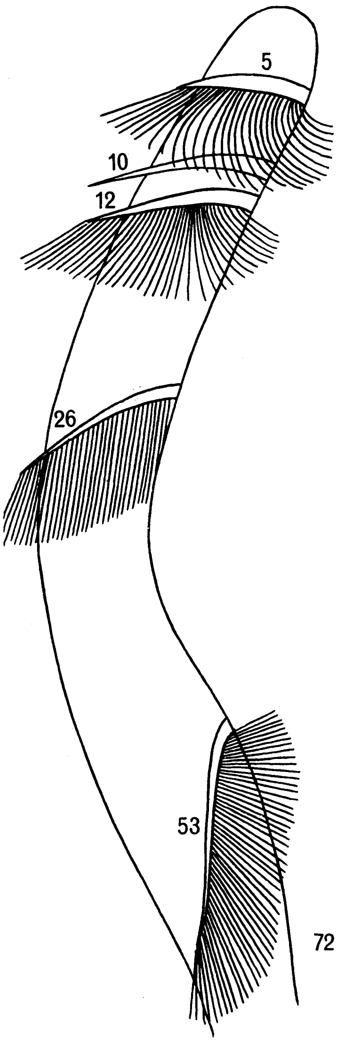
Posteriorly the carapace lobes approach each other and there is a narrow posterior aperture, bi-convex in section (figure 64). At the posterior ventral corner of each carapace valve are two or three sharp, sclerotized denticles (figures 149 and 150, plate 18) which may offer protection against small predators.

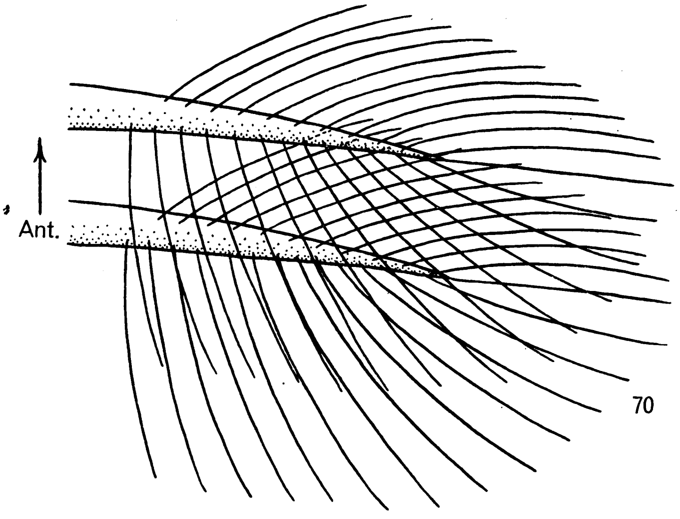
The most remarkable feature of the carapace is the modification of its ventral margins (figure 68). Each is straight in the horizontal plane over much of its length, and the cuticle is bent inwards more or less at right angles to form a broad flange (figures 68, 75, VF) which therefore lies in the horizontal plane and parallel to the substratum when the animal is crawling (cf. the unelaborated margin of *Alonopsis*, the rudimentary flange of *Peracantha*, and the well-developed flange of *Alonella exigua*). Because there is a wide ventral embayment, each flange is markedly curved anteriorly. The flange is approximately constant in width in the embayment region, though it widens a little posteriorly. It then gradually narrows towards the posterior end of the carapace where it virtually disappears (figure 68). In the narrowing region the flange is deflected slightly from the horizontal and the carapace margin rises as it approaches the posterior corner (figures 149, 150, plate 18). Although this broad base makes for stability in an animal with the habits of *Graptoleberis* it does not in fact come into contact with the substratum.

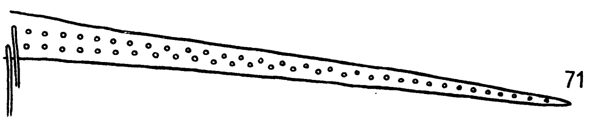
Arising from the inner margin of each flange is a row of highly specialized setae. Beginning at the anterior end and fringing the embayment, these setae, approximately 60 in number and here termed the median series, are close-set, so much so that proximally they are enabled, by virtue of their shape, to overlie each other, and are directed for the most part outwards and backwards (figures 68, MVS, 80 and 81). The more posterior the location of a seta in the series the more it is directed backwards; the last few are directed almost straight back. When the animal is lying free each seta is somewhat curved so that its tip is directed ventrally (figure 75, MVS) and the whole seta springs somewhat ventralwards from the base. When, as is usually the case in life, the animal is attached to some object, all these setae with the partial exception of the first five, lie parallel to and apparently in contact with, the substratum though in fact there are setules between setae and substratum. Distally the first five also lie parallel to the substratum but, because the flange of the carapace margin here curves very slightly upwards, the basal portion is somewhat curved in the transverse plane.

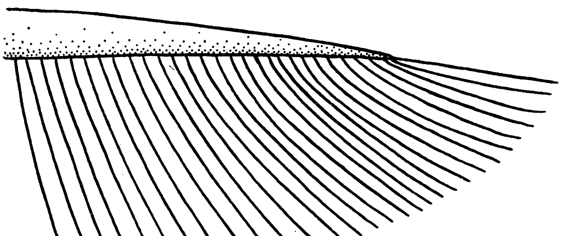
The median setae are long and tapering, the distal portion being very slender. Each is flattened and curved in the manner shown in figures 68, 69, 80 and 81. Near its base each is approximately oval in section (figure 69 (*a*)), the long axis being directed somewhat obliquely in the dorso-ventral plane, the dorsal end being anterior. This axis has a length of up to about 5 μm in a well-grown female. Very quickly this shape changes so that, while still near its base, each seta is flattened in the anterior–posterior direction and is markedly convex anteriorly and concave posteriorly (figure 69 (*b*)). Because these setae lie so close

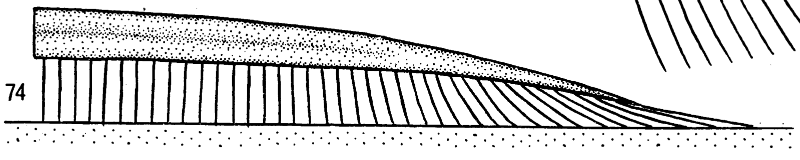












FIGURES 69 to 74. *Graptoleberis testudinaria.*

FIGURE 69. Diagrammatic representation of one of the median ventral setae of the carapace (from the middle region) showing the change in shape from base to tip.

FIGURE 70. Diagrammatic representation of the tips of two adjacent median ventral setae as seen from above, showing the arrangement of the posterior (dorsal) setules. Note how these setules, which form a single posteriorly directed row over most of the length of the seta, here extend around its tip and form a short anteriorly directed row.

FIGURE 71. The arrangement of the anterior (ventral) setules on a median ventral seta. Extremely diagrammatic.

FIGURE 72. Examples of some of the median ventral setae, whose position in the series is indicated by numbers, to show the orientation and length of the rows of ventral setules. Diagrammatic.

FIGURE 73. Diagrammatic representation of the tip of a median ventral seta as seen from above, showing the arrangement of the ventral setules.

FIGURE 74. Diagram showing the distal portion of one of the median ventral setae and the way in which its setules (which are very much more numerous than are shown here) make contact with the substratum.

together and the ventral portion of each extends beneath part of the seta next behind (figure 80) they misleadingly appear to be circular when seen from below (figure 68). Their shape is such as to give rigidity in the dorso-ventral plane and permit some flexibility in an antero-postero direction. Arising from the dorsal surface of each, and extending over the length of the seta, is a single row of long and extremely fine dorsal (posterior) setules, homologous with those described for *Alonopsis*, *Peracantha* and others. The orientation and diameter of these varies according to their location. Those arising proximally are the stoutest and most widely separated, though the gap is very narrow. The more distally located the setule, the more slender it is and the nearer to its neighbours is it situated. The most distal are exceedingly fine. Most of the setules are directed to a large extent posteriorly. Those located in the proximal 75 % or so of the seta (there is variation according to the location of the seta) are directed backwards so as to overlie the seta behind (figure 80) and often extend over the two setae posterior to that on which they arise. Their distal portions are so slender that their tips are difficult to discern. Towards the tip of the seta the setules not only become finer but directed more and more laterally rather than posteriorly (figure 68, T) and those at the extreme tip project in more or less the same direction as the seta itself. Furthermore, they not only extend to the tip along the posterior margin of the seta but as it were continue round it and extend for some way as a distinct row along the anterior margin from which they project forward (figure 70). Because of this the dorsal setules of the distal portions of adjacent setae present a complex meshwork which is best understood by reference to figure 70.

Ventrally on each seta arise setules homologous with the ventral (anterior) setules of *Alonopsis*, *Peracantha* and others, but much finer and which can be seen only at high magnifications. Their diameter is about 0·2 μm. The electron microscope reveals that, unlike the dorsal setules, these are not arranged in a single row. Over much of the length of the seta they arise, very close together, in two rows, possibly more at the extreme base. Towards the tip of the seta they appear to arise in a zig-zag manner (figure 71) this perhaps being determined by the limited area available for attachment as the seta becomes more slender. Most of the exceedingly numerous setules are very long. When seen from below as the animal glides beneath a cover slip they look like the pile of a carpet (figures 152, 153, plate 19) for, as in *Peracantha*, it is on these setules that the animal rests. Their orientation differs from seta to seta and according to their position on the seta (figure 72). Those of the anterior setae are extremely long. Here the distal portions of the proximal setules curve inwards, protrude into the carapace chamber, and lie between the anterior portion of trunk limb 1 and the substratum (figure 72, seta 5). Some of these make contact with the setules of the sealing seta of trunk limb 1 described below and with setules of the limb itself. The arrangement of the distal setules is shown in figure 72. The most distal merge imperceptibly with the distalmost, very fine, dorsal setules. On setae towards the middle of the median series the ventral setules are directed posteriorly (figure 72, seta 26). More posteriorly, where the setae themselves are directed posteriorly, the proximal setules are again directed into the carapace chamber (figure 72, seta 53) and here make contact with sealing setae of trunk limb 3 described below.

At the posterior end of the row of median setae the form and orientation of the marginal setae changes. There is here a short zone of transition, most conveniently mentioned below, posterior to which is a posterior row of setae (figure 68, PVS) some two dozen in number, which fringes the margin of the straight-edged posterior portion of the ventral flange but which, for reasons given below, does not extend to the extreme posterior end of the carapace. In the living, gliding, animal it is in this region that, as they pass posteriorly, the carapace margins gradually leave the substratum. The posterior setae are widely separated and directed inwards, ventrally and posteriorly (figure 68). Except at the extreme anterior and posterior ends, the tip of each makes contact with that of its homologue on the opposite carapace margin. They thereby form an arc beneath the post-abdomen. Each bears a row of close-set setules, homologous with the dorsal (posterior) setules of the median setae. These extend backwards and overlie the seta next behind on its outer side (figure 68) just as in *Peracantha* and several other species. That these setules are more close-set than their homologues in the median series is of great functional significance.

The size and orientation of the setae of the short transition region between the median and posterior series is best appreciated by reference to figure 68. The attributes of the setae in this region are determined by their relationship to the sealing setae of trunk limb 3 and the need to seal the wide ventral gap in this region (section v).

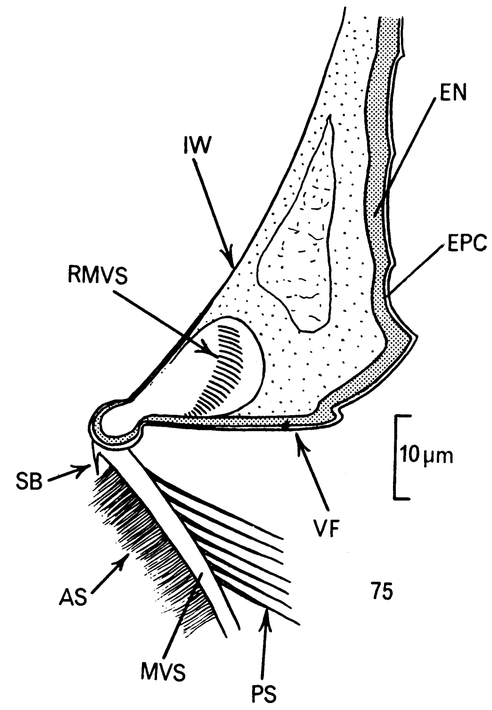
The headshield of *Graptoleberis* (figures 63, 68) is possibly more specialized than that of any other anomopod but, specialized as it is, it is not difficult to understand how it evolved from a generalized chydorid type. Instead of being produced antero-ventrally into a rostrum as in many chydorids, the antero-ventral margin is broadly rounded and the lateral portions are expanded. The rim is distinctly thickened. When the animal is gliding, most of the antero-ventral region lies close to the substratum figures 149 and 150, (plate 18). The whole shovel-like structure acts in a manner akin to a snowplough. The stout cuticular hoop which forms the rim will help to give the required rigidity to the whole structure, and will protect the margin against crumpling and abrasion when it makes contact with obstacles. The rim is elaborated as well as thickened in the vicinity of the fornix, this being related to mandibular articulation.

The incorporation of the compound eye and ocellus into the cephalic arrangement of *Graptoleberis* presents few problems yet here both are admirably situated to receive optical stimuli from a wide field and particularly from the anterior and antero-dorsal directions.

The headshield of *Graptoleberis* is about as different as can be imagined from that of *Acroperus*, and the two represent very different end-terms in the evolution of this structure within the Chydoridae; yet both animals are adapted to a weed-frequenting way of life. Ecological studies have hitherto largely ignored the niche-specificity so obviously implicit in such striking differences.

(iv) *The appendages, labrum and post-abdomen*

The antennules are adapted, particularly by their orientation, to assess the suitability of the substratum over which *Graptoleberis* is to glide and from which it is to collect its food. From an evolutionary point of view they were to some extent pre-adapted for this by virtue of their primitive function, and structural modification in response to gastropod-like habits has been slight. The antennules are completely covered and protected by the headshield (figures 63 and 68). In *Alonella exigua* they project slightly from beneath it (figures 50 and 51). Each is set obliquely on the head and is directed outwards, downwards and slightly



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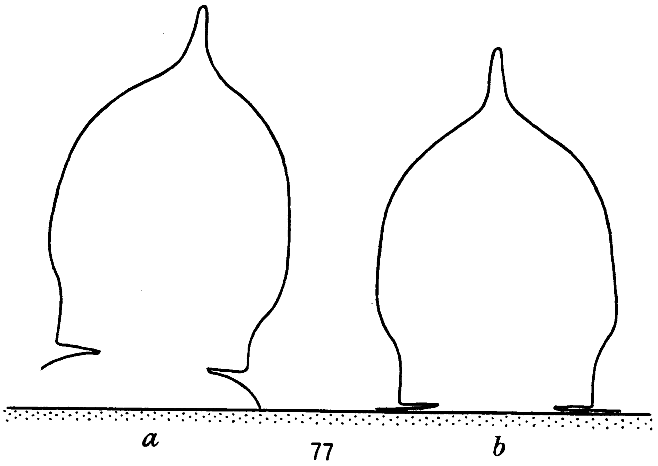

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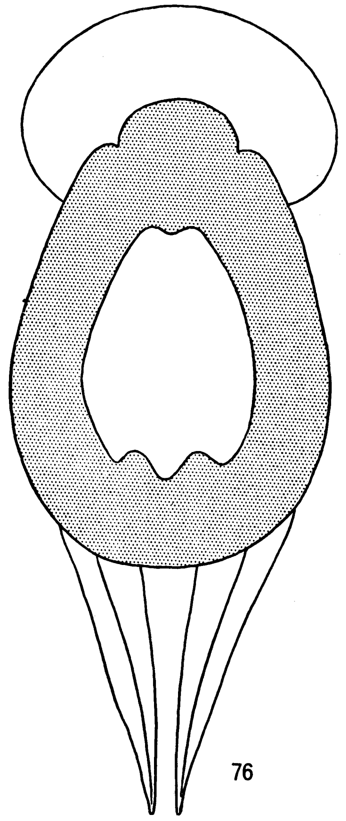

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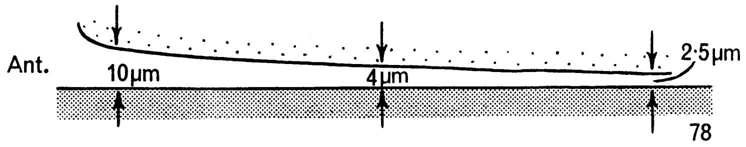

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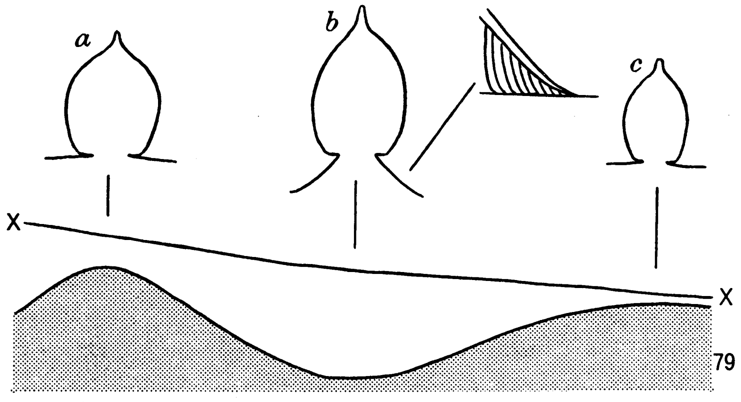

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Figures 75 to 79. *Graptoleberis testudinaria.*

Figure 75. Transverse section through the ventral carapace margin in the region of the median ventral setae, showing the ventral flange, the 'elasticity' of the seta (though its orientation is not necessarily exactly that of an unattached animal in life), and the channel in which the seta which will be used after the next moult is developing.

Figure 76. Outline of an animal seen from below. Stippling indicates the limits of the setose cushion on which, laterally, it rests, and which, all round, seals the ventral margin of the carapace chamber.

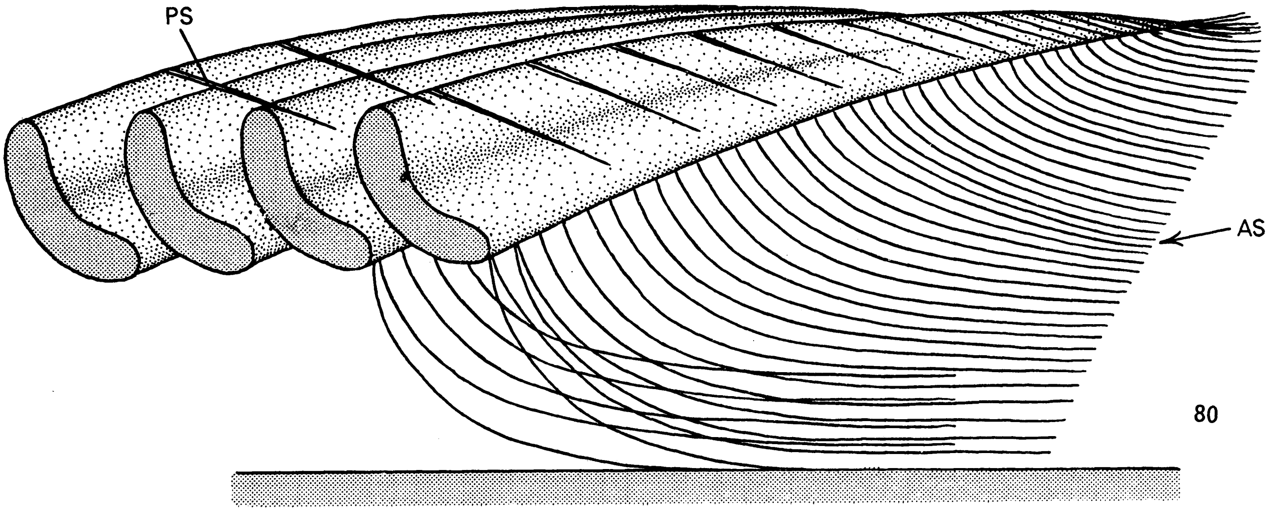
Figure 77. Diagrammatic sections through the middle region of an animal (*a*) 'wobbling' over a surface to which it is not attached, and (*b*) after being suddenly sucked down against the surface. Note the change that takes place in the curvature of the median ventral setae.

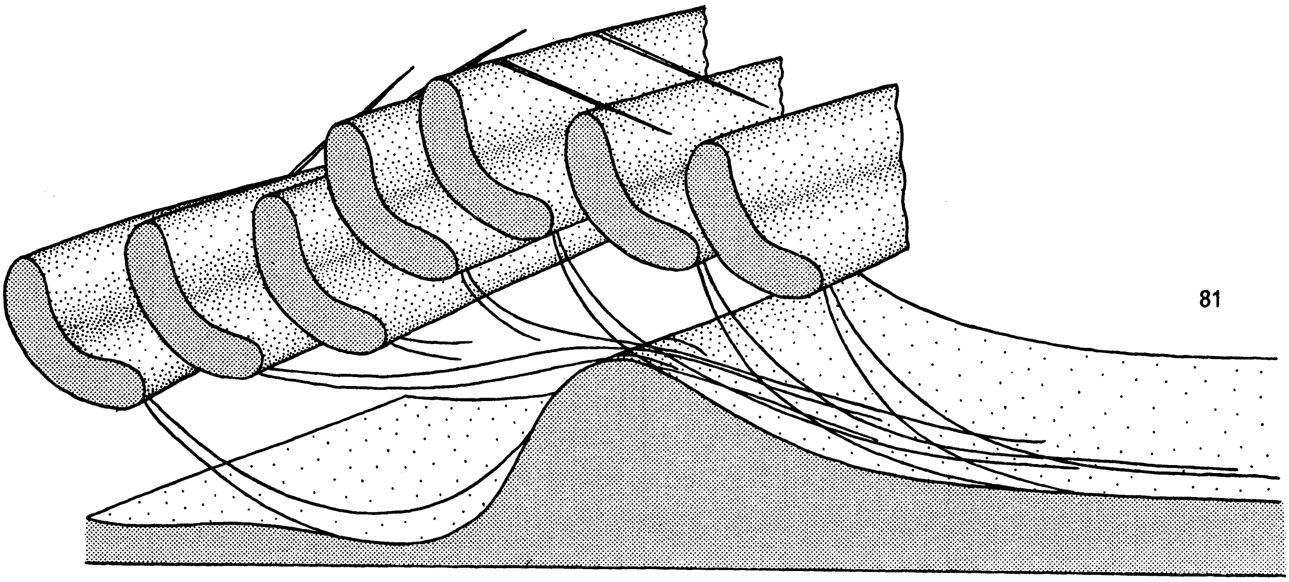
Figure 78. Diagram showing the distance, spanned by the cushion of ventral setules, between the median ventral setae and the surface over which an animal is gliding. Note how the gap narrows from the front of the row to the back.

Figure 79. Diagram showing how, by their elasticity, the median ventral setae and their setules can

(*Continued on p.* 307)

forwards. The olfactory setae protrude well beyond the confines of the headshield and are directed for the most part laterally and ventrally, though the dorsalmost curves dorsally. The tip of the ventralmost appears to be always either in contact with or extremely close to the substratum when the animal is resting or gliding (figure 88, and figure 150, plate 18) which suggests a tactile as much as an olfactory function.





Figures 80, 81. *Graptoleberis testudinaria.*

Figure 80. Diagrammatic representation of the distal portion of a group of median ventral setae of the carapace showing a few of the exceedingly numerous ventral setules and their relationship to the surface over which the animal is gliding.

Figure 81. The same showing how, by displacement both of the ventral setules and of the setae which bear them, an irregularity of the surface over which an animal is gliding can be negotiated without breaking the seal of the carapace chamber.

Figure 79. (*Contd.*)
cope with irregularities over which the animal glides. The line XX represents that portion of the ventral flange which is armed with median setae and figures *a*, *b*, and *c* are diagrammatic sections through the anterior, median and posterior regions of this part of the animal. The inset from *b* shows the relationship of a seta and its ventral setules to the substratum.

The antennae are illustrated in figures 63 and 66 to 68. These serve several functions and this is reflected in their structure. Distally the exopod, which is the longer of the two rami, bears a stout claw and three jointed setae (figure 68, SSA). The endopod is similarly armed distally and bears a jointed seta on the second segment. Towards its base the distal segment of each seta is armed with stout spinules. More distally these become more slender. For clarity these are not shown on all the setae in figure 68.

Near the base of each antenna is a papilla (figure 67 (P)) bearing two laterally directed sensory setae which protrude beyond the edge of the headshield (figure 66, S) not far from its union with the carapace and curve somewhat dorsally (figures 63, 66 to 68). These, which are presumably tactile, complete a ring of sensory structures around the headshield.

The labrum, while of familiar structure, has to meet specialized demands which are reflected in its shape. Its anterior portion, which appears triangular when seen from below, is very broad (figure 68) and is also triangular in transverse section (figures 66, 67, L). There is the usual posterior extension. Other features, including the keel (K), are shown in the illustrations and become intelligible when sealing of the anterior end of the carapace chamber is understood.

The mandibles have the same basic structure as those of other anomopods. Articulation is of type A. Muscular asymmetry is particularly well marked, being of about the same magnitude as in *Chydorus sphaericus* (figure 128). The right mandible has once been seen to swing very markedly while the left appeared to remain motionless, but both are usually in action together. For the maxillules see figure 82 (Mxlle).

The form of the first trunk limbs (figures 68, TL1, and 82) reflects their function as the main organs of propulsion in a specialized type of locomotion, and their further function of contributing to the sealing of the anterior end of the carapace chamber during gliding, irrespective of their position in relation to the carapace. Because the method of propulsion makes no demands on the inner distal lobe, whose armature is used for grasping in many species, this part of the limb has been freed to take on another function apparently unique within the Chydoridae. Salient anatomical features are apparent from figures 68 and 82 to 84, but description of certain points is necessary.

These limbs lie close together and touch in the mid-ventral line (figure 68). Each is borne on pedicel and the bulky distal portion is elongate in an anterior-posterior direction (figure 82). Much of the ventral surface is flat (FTL1). In life this flat face makes contact with the substratum and acts like the sole of a foot (section vi). It is armed with numerous short, curved rows of minute denticles detectable only at high magnifications. Anteriorly the flat face decreases in width to a narrow point (figure 68) and also inclines slightly away from the substratum. Here it is clothed with a carpet of exceedingly fine setules (figures 68, 83: not shown in figure 82). From its apex, and therefore near to its ventral face, arises a short soft, tapered seta, bent as shown (figures 68, 82 and 83, SL) and from which radiate numerous extremely long and extremely fine setules. This seta is probably homologous with the anterior distal fan of *Alona affinis*. It is directed forwards through a narrow gap whose walls, when the animal is gliding, are made up dorsally by the labrum, laterally by the carapace margin to the outside and the ventral portion of the labral keel to the inside, and ventrally by the substratum. Because of its function it is called a sealing seta.

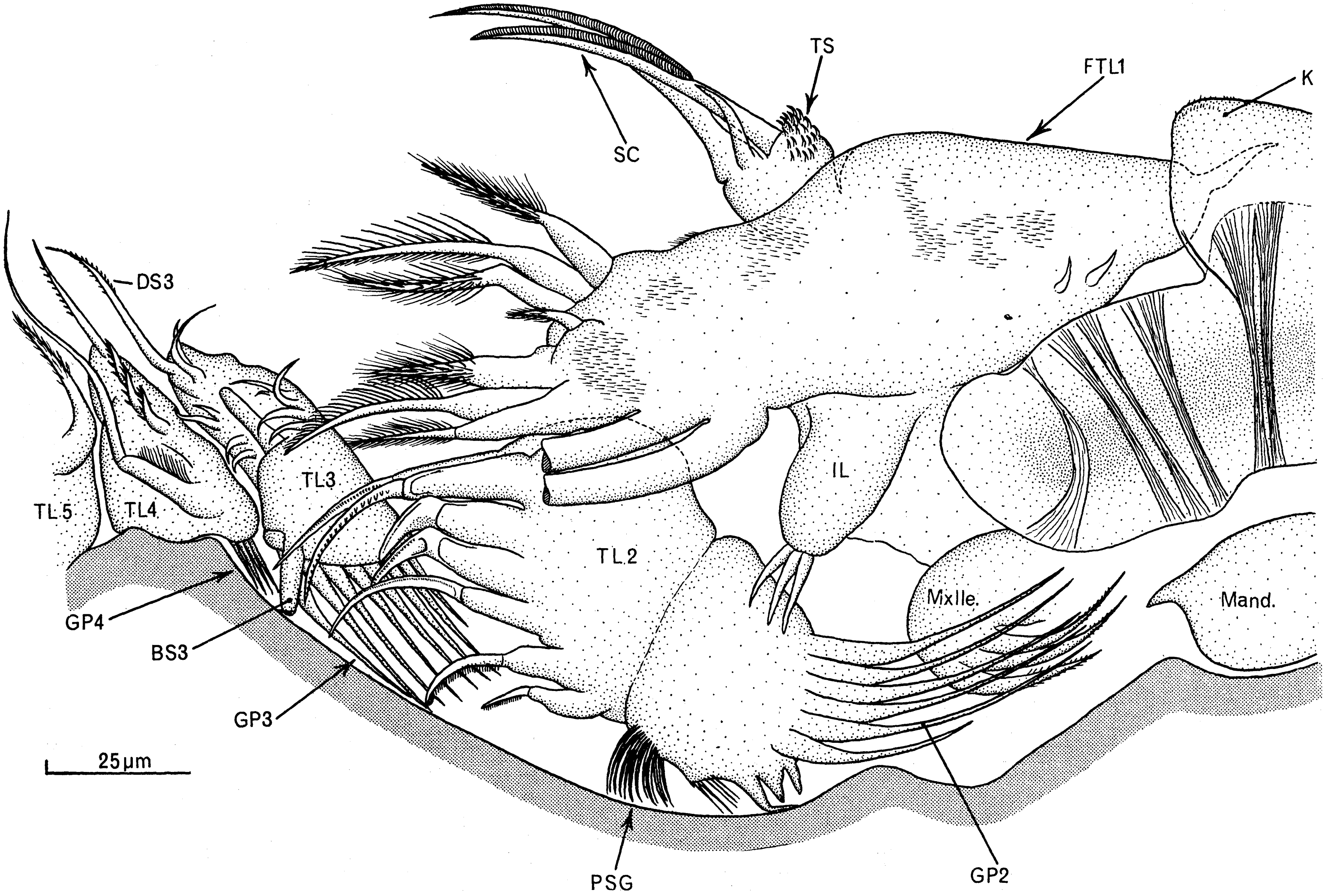


Figure 82. *Graptoleberis testudinaria*. Longitudinal section through the trunk limbs showing the equivalent of what in many chydorids is the filter chamber. Note the great reduction of the posterior trunk limbs and the swing of trunk limb 2.

Towards the posterior distal portion of the limb, and from its ventral face, arises a lobe which bears three posteriorly directed spines, two long and one very short, which lie in the horizontal plane (figures 68, 82 and 84). The distal portions of the long spines are excavated on the inner side, and to the outside have a blade-like edge (figure 84) which, because of the orientation of the spines, lies parallel to the substratum when the animal is gliding. The blade, although functioning as a single unit, is made up of numerous close-set spinules of appropriate form. At the base of the long spines is a tuft of minute, but robust spinules (figures 68, 82 and 84, TS). The rest of the distal armature is evident from the illustrations.

An inner lobe, smaller than in *Eurycercus* but much better developed than in many genera, is present (figure 82, IL). Because of the proximity of the members of a pair of limbs it protrudes but little from the corm. Ejector hooks are also present (figure 82).

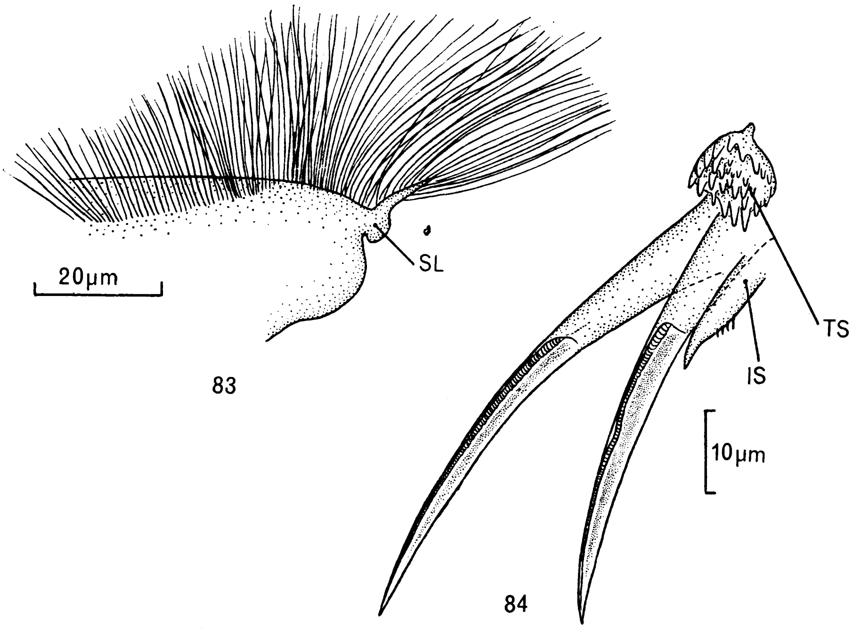
The second trunk limbs (figures 68, 2 and 82, TL2) exhibit many specializations. The gnathobase bears a typical row of setae, six in number, homologous with the filter plate of many species (figure 82, GP2). They are, however, spiniform and although Lilljeborg (1900), who shows only five, indicates that they are setose, no setules of any kind have been detected on them. In life they are directed anteriorly along the food groove (figure 82). The rest of the gnathobasic armature is shown in figure 82. Note its relationship to the food groove.

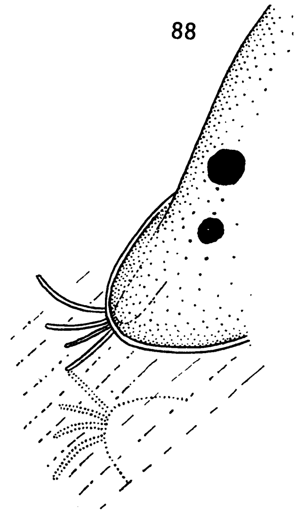
The scrapers are shown in figures 68, 82, 85 and 86. The shortness of nos. 4 and 5 is emphasized. When these are viewed from below in the 'resting position' (see section vi) in an attached animal (as in figure 68) they appear toothless. In fact each has a broad toothed blade which is directed towards the substratum when the limb is in this position, but which is clearly seen at the end of the working stroke (figures 85, 86). Spines 4, 5 and 6, which perform the heaviest duties, are darkly sclerotized.

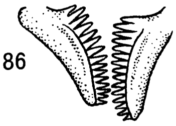
As in many chydorids part of the limb is covered by thickened sclerotized cuticle which here covers the ventral portion like a hood and curves up the anterior face. Posteriorly there is a plate of thickened cuticle in the form of a broad-based and elongate V which runs like a tongue along the face of the limb (figure 87, PR) and which grants strength as well as a firm insertion for the massive dorsal adductor muscle (D Add) (cf. *Alonopsis*). In *Graptoleberis*, unlike other genera, movements of trunk limb 2 are stereotyped and not versatile (section vi) and the rib and muscle arrangement is related to the achievement of maximum efficiency in one kind of movement rather than to an ability to perform many.

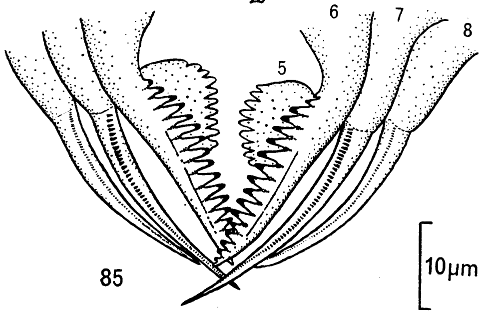
In comparison with those of other genera the third trunk limbs (figures 68, 3 and 82, TL3) are much reduced. The gnathobase bears a plate of eight setae (nine in one specimen) (figure 82, GP3). Unlike their counterparts on trunk limb 2 these are setose, but the setules are difficult to detect and the setae are not filter setae (section vi). Internal to each and located near the most posterior seta is a short stumpy seta (BS3) whose short, feebly setose tip is much narrowed and bent sharply inwards. This is called the brush seta (cf. *Disparalona*). The rest of the armature of the limb is illustrated in figures 68 and 82. There is no outer filter plate, but a row of four short setae obviously represent this. There is a large, flap-like exopod (figure 89) whose setae can easily be homologized with the exopod setae of *Peracantha* (figure 49), *Alonella exigua* (figure 51) and others. The three longest are clothed with long and extremely fine setules of the kind found on the sealing seta of trunk limb 1.

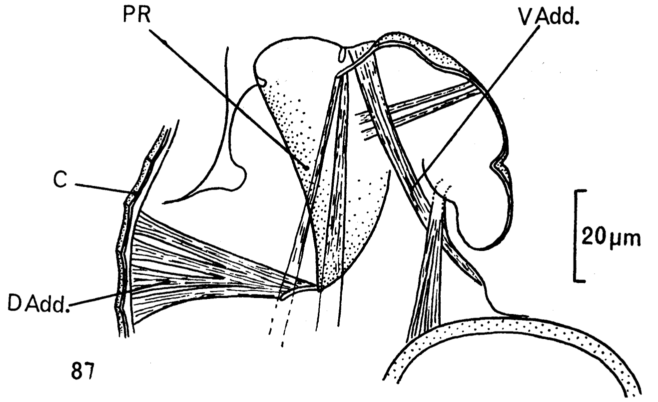
The fourth trunk limbs (figures 68, 4 and 82, TL4) are greatly simplified versions of the basic type. The gnathobasic plate (GP4) is reduced to a row of four short setae. The gnathobase bears a long vertically directed spine, and the usual four spines standing in line one above the other are present on the more distal endites. Their armature is simple. A flat exopod is present though this is not the large paddle-like structure seen in many











FIGURES 83 to 88. *Graptoleberis testudinaria.*

FIGURE 83. Distal portion of trunk limb 1 seen from the side. The length of the setules is correct but far more are present than are actually shown.

FIGURE 84. The scrapers of trunk limb 1 and the adjacent tuft of spinules.

FIGURE 85. The scrapers of trunk limb 2 as seen at the end of their working stroke.

FIGURE 86. Scraper no 4 of trunk limb 2 as seen by deeper focusing when the limbs are in the position shown in figure 85.

FIGURE 87. Transverse section through trunk limb 2, from in front, to show the posterior rib and some of the muscles of the limb.

FIGURE 88. Oblique dorso-lateral view of the headshield of an animal gliding over a surface. The figure is based on a photograph of an animal gliding on glass so that a reflexion of the sensory setae of the antennule was obtained. This showed that only one seta was actually in contact with the surface over which the animal was gliding.

chydorids. It can be seen in part in figure 68. Some of its setae resemble those of the exopod in trunk limb 3.

The fifth trunk limbs (figure 82, TL 5) are again simplified versions of the basic type. The gnathobasic region is obsolete. There is no gnathobasic filter plate. The corm stands vertically and its anterior margin is bent inwards as in many species. Its armature is reduced to a single vertically standing seta. Posteriorly it is continuous with an exopod flap which is somewhat elongate in the anterior-posterior direction. There are no sixth trunk limbs.

The post-abdomen is small and feebly armed. It is illustrated from the side by various authors, being reasonably well depicted by Lilljeborg (1900), and is seen from an unusual, but from a functional point of view more revealing, angle in figure 68 (PA). Only the submarginal groups of spinules (seen end-on in figure 68 where they appear as rows of dots) have previously been illustrated. Proximally these spinules become much finer and close-set and continue in an unbroken line along the margin of that portion of the post-abdomen on which the anus opens. Above (morphologically ventral to) these spinules are more, extremely fine, spinules or setules, detectable only at high magnifications. Distally these occur in groups, somewhat irregularly arranged, but more or less in a single row. Here they are probably best designated as spinules. Proximally they are setules and occur in two more or less continuous rows, those furthest from the margin overlapping those which arise nearer to it. Although apparently less fine, and certainly more rigid, than the sealing setules of trunk limb 1 and elsewhere, these proximal setules appear to have the same function as these structures. Near their bases adjacent setules are so close together that no gap can be resolved between them. Posterior to the anal orifice when the animal is gliding, is a transverse bar of chitin (figure 68, TCB), henceforth called the transverse chitinous bar, which runs across the post-abdomen and forms the apex of the posterior elbow. The proximal part of the post-abdomen and adjacent parts of the trunk are inflated and fit neatly into the posterior end of the carapace chamber. This, and features not described, are apparent from figure 68.

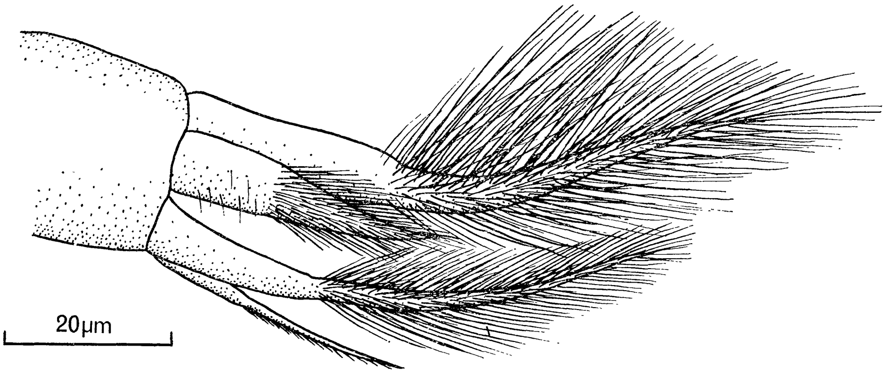


Figure 89. *Graptoleberis testudinaria*. The armature of the exopod of trunk limb 3. In life the longest seta is the outermost (see figure 68). It is these setae which play an important part in sealing the posterior gap between the two sets of marginal carapace setae. The similarity to the homologous structure of *Peracantha* is made obvious by comparison with figure 49.

(v) *The mechanism of attachment and the watertight seal*

Perhaps the most remarkable feat which can be performed by *Graptoleberis*, and the one on which its whole way of life is based, is that of attaching itself to surfaces as described in section (i). Its abilities are even greater than are usually displayed in nature and are demonstrated most strikingly when, as with patience it can be coaxed to do, it glides beneath the surface of a suitably elevated coverslip. (A large rectangular cover slip raised on smaller slips and also specially constructed cells were used.) Here it sometimes glides or remains motionless for long periods and enables observations to be made at high magnifications on both the disposition of the various parts during attachment and on appendage movements used during feeding. Figure 68 was prepared from photographs of an animal so attached, details being added from direct observations, and is therefore accurate in its portrayal of shape and the disposition of parts in the living animal.

Ample evidence shows that adhesion is achieved by lowering the pressure within the carapace chamber. This demands a means of rendering the chamber more or less watertight and some means of driving out water both to produce the original low pressure and to counteract the effect of water which leaks in.

The regions to be sealed are anterior, posterior and ventral. Anteriorly the carapace margins are straight and the gap between them is V-shaped in transverse section (figures 66, 67). This gap is largely sealed ventrally by the bulky anterior portion of the labrum (L) which fits between the carapace lobes like a plug. In chydorids not needing such a seal there are wide gaps laterally between labrum and carapace. This is so in *Eurycercus*, for which species text-fig. 7 in Fryer (1963) shows a section in a region roughly corresponding to that shown for *Graptoleberis* in figure 67. In *Alonella exigua*, the one other species studied in which such a seal is a partial necessity, a similar but less well developed arrangement is found (§ XI).

The anterior gap in *Graptoleberis* is not entirely closed ventrally by the labrum. A complete seal would involve contact between the labrum and substratum, would necessitate adjustment to irregularities of the surface over which the animal crawled, and would inevitably involve abrasion of the labrum during locomotion. Protection against abrasion is provided by the labral keel which persists ventrally (figures 66, 67, K) and intervenes between labrum and substratum, though its depth is small and the gap between labrum and substratum at each side of it is therefore narrow (figures 66, 67). Compare the large, protective, ventrally projecting keel of *Eurycercus* (Fryer 1963, text-figs. 10, 11 and 45) and other species. Protection is still desirable anteriorly and here the keel is well developed in relation to the size of the labrum, as it is posteriorly (figure 82, K). The two ventral apertures beneath the labrum, and at each side of the keel, are sealed by the sealing setae of the first trunk limbs, one of which passes through each aperture (figure 68). (In figures 66 and 67 the sealing setae have slipped from the apertures as a result of fixation and are not seen.) In this they are assisted posteriorly by the fine setules which arise on the ventral face of the first trunk limbs. The structure of the sealing setae is such that, during locomotion, the setae and apertures move relative to each other yet maintain a seal throughout (section vi).

Dorsally, where the V-like aperture is widest, there is a region at each side which the labrum does not seal. This gap is shown on the right-hand side of figure 67 (DA). Here sealing is accomplished, not from inside the carapace, but from outside by the coxa of the antenna. This arises beneath the headshield immediately in front of the anterior flange of the carapace and extends obliquely across the gap which exists dorsal and lateral to the labrum. As sections reveal, it fits closely against the anterior (outer) face of the flange. The coxa need not move when the antenna is used and can therefore serve as a plug without rendering the appendage immobile. Because of the manner in which the protopod is directed and, particularly, because of the oblique insertion of the exopod and endopod on the basis, these two rami can be directed backwards outside the carapace (figures 63 and 66 to 68). The precursor of this arrangement is to be seen in *Alonopsis* (figure 5). *Alona affinis* (figure 23) exhibits greater elaboration, and in *Graptoleberis* the device has achieved perfection, but this does not constitute a phyletic series.

Sealing of the ventral surface is accomplished by the median and posterior setae of the ventral margin, assisted in the region of transition by specialized setae of trunk limbs 3 and 4. The median setae serve not only as a seal but as runners (analogous to those of a sledge—here the carapace) a function for which they are remarkably well adapted. Because attachment is effected by the setting up of a region of low pressure within the carapace chamber, the natural curvature and the springiness of each seta is overcome when contact is made between the setae and the substratum (as when one flattens a curved flat spring) and the setae are drawn against the substratum over the whole of their length. This has been observed repeatedly in the living animal (figure 77*a*, *b*). The setae themselves only make indirect contact with the substratum via their ventral setules, and it is on these that the animal glides (figure 80). Frictional resistance between the substratum and the sliding carapace will be slight as contact is restricted to a series of 'lines' of minute width. The animal in fact slides forward on a thin film or cushion of water. The thickness of this film is not uniform along the lines of contact. Ignoring the four or five anteriormost median setae whose basal portions are separated relatively widely from the substratum, the gap between the substratum and the anterior members of the series was of the order of about 10 μm or a little more in a specimen in which this was measured as accurately as possible by two-level focusing. In about the middle of the series the gap was reduced to a little over 4 μm and towards the extreme posterior end was less than 2·5 μm (figure 78). These dimensions apply to a well-grown adult and are presumably less in the earlier instars. With this can be correlated variation in the length of the ventral setules, those of the anteriormost setae being longer than those arising more posteriorly (figure 72). That the gap is widest anteriorly can be detected in the photographs in figures 151 and 152, plate 19, where the anterior setae can be seen to be less clearly in focus than those in the middle of the picture.

Thus the film of water on which the animal glides is wedged-shaped. Now, in bearings, optimal conditions for lubrication obtain when the bearing surfaces are separated by a wedge-shaped space through which the lubricant passes from the wider inlet to the narrower outlet. In *Graptoleberis* therefore, optimal conditions for lubrication will obtain in an animal moving forward. (For experimental evidence of this principle, for a very different application in the climbing organ of the bug *Rhodnius*, and for references to the theory of film lubrication and its practical applications, see Gillett & Wigglesworth (1932).)

Sealing of this zone depends upon the behaviour of water in very small spaces (see below). This device is not only well suited to gliding over flat surfaces and making a watertight seal but is also able to take care of small irregularities of the surface over which the animal glides without breaking the seal. Elevation or depression of setae of the median series and a change in the angle of inclination of the ventral setules permit such obstacles to be negotiated while maintaining an unbroken seal (figures 80, 81). The great length of the ventral setules is perhaps in large part an adaptation to such a function. Even if a marked irregularity is encountered (and the sensory equipment presumably allows an unnegotiable object to be avoided) some lifting of one or both carapace margins can be dealt with by the springiness of the setae (figure 79).

By their contact with the seta or setae next behind, the dorsal setules must give some rigidity to the sliding seal as a whole, and they perhaps serve to protect the underlying setules from particles of detritus, but over much of the length of the seta they probably play little part in the sealing process. Distally, however, they collaborate with the ventral setules in sealing the important region at the outer margin of the fringe. Sealing of the transition region is described after reference to the posterior series of setae.

When the animal is attached, and pressure within the carapace chamber is low, the dorsal setules (now topographically ventral) of the posterior setae must always be sucked against the seta next behind (as in figure 68) and thus, because they are close-set, largely seal the gap between adjacent setae. When, as a result of pumping (as in the combined feeding/respiratory stream of many species) there is a temporary local increase in pressure, the setules will be forced outwards and water enabled to flow between adjacent setae. Thus each row of setules functions as a simple non-return valve.

In order to be watertight the carapace must have a complete seal ventrally. How sealing is achieved medially and posteriorly is now apparent and the way in which the small anterior ventral gap is sealed by the sealing setae of the first trunk limbs has been noted, though the full subtlety of these setae will not be apparent until locomotion is described (section vi). At the posterior end of the embayment the carapace inclines away from the substratum (figures 149, 150, plate 18) and there is a wide gap, the sealing of which represents one of the most astounding achievements of anomopod evolution. The gap is sealed largely by the setae of the exopods of trunk limbs 3 and 4 whose long setules make up a continuous and largely watertight carpet whose arrangement can be appreciated from figure 68 and figures 154 and 155, plate 19, which also show how the few marginal transition setae (between the median and posterior series) lie at the lateral margins of the seal. More posteriorly a deeper-lying (i.e. more dorsal) seta of the exopod of trunk limb 5 may also make a contribution. It is in this region also that the ventral setules of the median setae of the carapace margins begin to be directed inwards (figure 72, seta 53) and thus make a contribution. The complete seal is shown diagrammatically in figure 76.

Posteriorly the carapace chamber narrows and has a narrow aperture (figure 64), and is sealed by the post-abdomen and adjacent parts of the trunk. Although the distal, pushing, portion of the post-abdomen is narrow, the more proximal parts and the adjacent trunk region are inflated (figure 68, PA), and fit into the narrow posterior end of the carapace chamber like a plug (cf. *Alonella exigua*). Sealing is made easier dorsally by the steep descent of the dorsal carapace ridge, which here is very wide, thus reducing the height of the gap that is to be sealed. Rows of fine spinules which run around this portion of the trunk are probably not connected with sealing the carapace chamber but with grooming or preventing the ingress of detritus. The inner surface of the carapace is covered by a layer of living tissue overlain by a thin cuticle and this, by its pliability, will be conducive to the establishment of a good seal between parts which make contact. This lining layer is particularly thick ventrally (partly of necessity to house the sacs in which the marginal setae are formed prior to each moult (figure 75)) and this facilitates sealing there.

The transverse chitinous bar of the post-abdomen (figure 68, TCB) spans the gap between the opposed ventral margins of the carapace, here narrow, and forms the posterior limit of the ventral seal. No marginal setae occur posterior to this point. Just anterior to it, fine setules continuous with the submarginal denticles of the post-abdomen perhaps help to seal the region in which they occur.

Thus the carapace chamber is sealed wherever there is a gap. To summarize, it is sealed anteriorly by the coxae of the antennae, the labrum, and the carapace and, at the most ventral point, by the sealing setae of the first trunk limbs. At the anterior end of the ventral surface it is sealed by the carapace margins and trunk limb 1; more posteriorly by the carapace margins alone; still further back by setae of the exopods of the posterior trunk limbs and of the carapace margins; most posteriorly by the posterior series of setae of the carapace margins, and ultimately by these and the post-abdomen. The posterior gap is sealed by the post-abdomen and adjacent trunk, working in collaboration with the carapace.

Although such movements have not been detected in a living animal it is easy to see how pressure can be equated inside and outside the carapace chamber so that the animal can release its hold. All that is necessary is a slight contraction of the carapace adductor muscle, which will reduce the size of the chamber. The natural springiness of the setae of the median series will then tend to throw the animal clear of the surface on which it rests (figure 77 in the order *b*, *a*).

Suction is probably initiated in a settling animal by relaxation of the adductor muscle. Again this is almost impossible to prove, but an animal seen more or less from behind as it moved away from the observer on a vertically standing sliver of cover-glass provided useful evidence. It left and then resettled on the surface. When not in close contact it 'wobbled' with one set of marginal setae in contact with the glass, the other well removed from it (figure 77 *a*). Distinct curvature of these setae was apparent. It then 'flopped' down in a manner suggestive of sudden suction and the setae flattened out (figure 77 *b*). Only a sudden relaxation of the adductor muscle seems capable of producing the effect observed, though conceivably brisk pumping movements of the posterior trunk limbs are also involved.

Sealing of the carapace chamber need not be complete, nor indeed is this desirable as changes of water within it are necessary not only for the respiration of the animal itself but also for that of the eggs and embryos which, in summer, are almost always present in the brood pouch. What is necessary is that there should be some means of driving out water which enters and raises the pressure within the chamber. This need is exactly the same as in *Alonella exigua* except that in *Graptoleberis* the seal is much more effective so the amount of water to be driven out is small. Expulsion of water is effected by the exopod pump of the posterior trunk limbs whose sealing setae are not disturbed by the pumping movements, and perhaps by movements of the carapace. Currents set up by the exopod pump are much weaker and less sustained than in many chydorids, and are not easy to detect. Whether movements of the carapace regularly play a part or whether those observed were involuntary and caused by contraction of limb muscles is uncertain, but such movements have sometimes been seen, and were such as could have helped to accomplish the desired end. When the pump was expelling water a small steady movement of the posterior portions of the ventral carapace margins towards each other was clearly seen. This would reduce the volume of the chamber but, as water was being expelled, would not increase the pressure. At the end of the expelling phase of pumping the margins moved apart with a jerk. This would increase the volume of the carapace chamber and reduce the pressure.

Observations which confirm that low pressures prevail in the carapace chamber of an attached animal were made on individuals gliding beneath a 'dirty' surface film at which bacteria were present. Although the limbs went through the motions of locomotion, progress was negligible. Some of these individuals were observed at magnifications of up to ×100, and a distinct depression in the region of the wide ventral embayment was clearly seen. By shining a light obliquely across the water surface, chromatic effects in the region of curvature were easily obtained. Small elevations of the surface film caused by the scrapers of trunk limb 2 were also clearly seen within the depression, which was obviously not a capillary depression and could only have been produced by the drawing of the surface film into a region of low pressure.

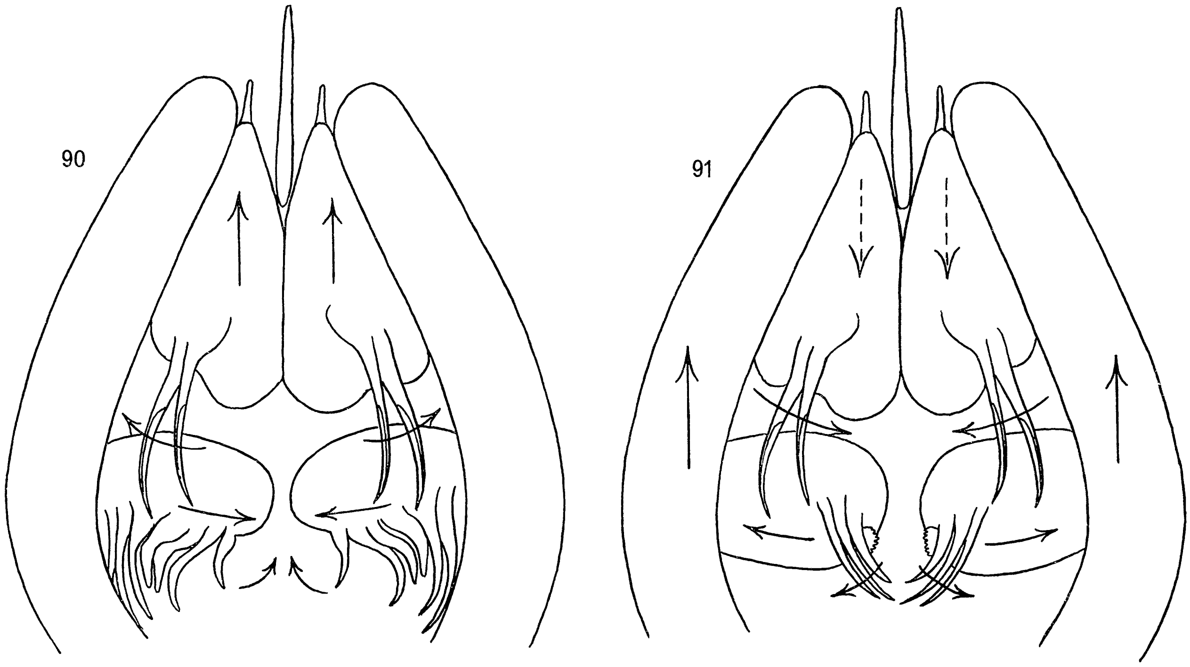
Where the carapace chamber (functionally the suction chamber) is not completely sealed from the external water (as it is by the antennae, labrum, post-abdomen and posterior setae of the ventral carapace margins) it is sealed by a mass of extremely fine setules between which minute interstices exist and through which water can pass only very slowly. (For the principles of flow through narrow channels see standard texts on hydrodynamics.) This is equally true of the carapace setae, the sealing setae of the first trunk limbs, and the exopod setae of the more posterior trunk limbs.

Graptoleberis is apparently not the only animal to have utilized this principle. No detailed survey has been made but it seems that a similar device is used by animals as diverse as protozoans and insects. What appear to be the requisite constituents of a system capable of producing a low-pressure chamber fringed by restraining setae or bristles are present in peritrich protozoans (*Trichodina*), in several torrential stream insects in some of which a mechanism for the expulsion of water exists (Hora 1930), and in the suckers of psychodid larvae (Diptera), (see figures in Feuerborn 1933).

(vi) *Locomotion and the feeding mechanism*

The feeding mechanism and the most consistently exhibited method of locomotion of *Graptoleberis* are so intimately related that it is not possible to describe one without the other. An unattached animal is unable to feed.

Locomotion is effected primarily by the first trunk limbs, assisted under certain circumstances by the antennae. The means of propulsion is in essence extremely simple. The first trunk limbs are slid forward to their maximum extent, at which point they abut against the labrum (figure 90). They are then pressed against the substratum, and drawn back. However, because of the traction obtained between limb and substratum (a reflexion of its flatness and armature of minute spinules) and the well lubricated runners of the carapace margins, the ventral faces of the limbs remain pressed against the substratum and the carapace slides forward (figure 91). This process, constantly repeated, results in forward progression. An even pull by both trunk limbs carries the animal straight forward: a full cycle carried out by one limb while the other reaches forward for less than the maximum distance enables the animal to turn to the left or right. Turning by the employment of the limbs alone is frequent when the animal is gliding beneath a cover slip. It is easy to see how this specialized form of traction has been derived from that of chydorids which employ the first trunk limbs for more orthodox crawling.



FIGURES 90, 91. *Graptoleberis testudinaria.* Diagram showing the co-ordinated sequence of movements of the trunk limbs and of the entire animal in an animal gliding over and feeding from a flat surface. In figure 90 the carapace remains stationary while the first trunk limbs slide forward (and have here reached their anterior limit) and their scrapers swing outward. At the same time the scrapers of the second trunk limbs (the major food collectors) move medially and deeper into the food chamber, thus being swept over the substratum while the animal is stationary. Having completed these movements the sequence is, in essence, reversed (figure 91). The first trunk limbs grip the substratum and pull. Because their 'soles' remain stationary, the carapace, and therefore the animal as a whole, slides forward. Simultaneously the scrapers of the first trunk limbs swing towards the mid-line (perhaps collecting material for the next working stroke of the second trunk limbs) and the second trunk limbs, here seen near the end of their working stroke, reverse their previous movement, thus making their non-working movement as their scrapers move forward over the substratum.

Movement of trunk limb 1 is essentially in one plane, but observations from the side show that there is also a small dorso-ventral component. This enables the sealing seta at its apex to slide easily back and forth within the hole, the sealing of which is its function. When the limb is extended forward, much of the seta protrudes and its setules splay out into a large tuft (figure 68, SSL) which can often be rendered conspicuous by treatment with a trace of Alcian blue. As the carapace slides forward the seta disappears into the hole and its setules are drawn against it much as the stays of an umbrella are drawn against the shaft when it is closed. By this means the hole is plugged either by simple blockage (at the end of the back stroke) or by a combination of blockage and the use of the sealing setules at other positions.

The antennae are used from time to time to assist a gliding animal to overcome obstacles, or to increase its speed, and to assist in turning by what is obviously a modified form of scrambling. When not in use they are directed posteriorly along the sides of the carapace (figures 63, 68). The exopod lies dorsal to the endopod. Observations and photographs of animals gliding beneath a cover-glass show that much of the armature of the endopod, but not of the exopod, is then in contact, or very closely associated, with the substratum (figure 68). When necessary, however, the antennae are so swung that, in addition to the armature of the endopod, that of the exopod also comes into contact with the substratum. This is made possible by the greater length of this ramus and by the flexure of the joints in both rami. The exopod arches over the endopod so that its armature makes contact with the substratum outside that of the endopod. Flexure of the distal joint of the endopod allows the seta of its second segment to be used. The absence of anything but terminal armature on the exopod is now easy to understand. Only terminal spines and setae are able to reach the object over which the animal is scrambling. Leverage is effected not merely by rowing movements but by flexure and straightening of the antennae about their joints. Indeed *Graptoleberis* may be said to 'walk' by means of its antennae when occasion demands. This can be achieved without breaking the coxal seal. Each antenna operates independently according to the demand of the moment. There is no stereotyped simultaneous usage when gliding is being supplemented, and when the animal turns sharply only one antenna is used. With a few slow, deliberate strokes it can turn neatly in a small space. The stout spinules of the basal portion of the terminal segment of the swimming setae of the antennae grant purchase when these appendages are so used, and their presence thus receives a functional explanation. The antennae are also used for wiping the outside of the carapace, much of which can be reached by their setae.

Body form in *Graptoleberis* is not designed for efficient swimming, and the animal swims only with reluctance. Nevertheless, speeds of up to about 6 body lengths/s over 22 s have been recorded for a female 0·56 mm in length and carrying embryos, and slightly in excess of 6 body lengths/s over about 15 s. Almost 7 body lengths/s was achieved over less than 3 s. These speeds are about half those of *Alonopsis*.

Feeding takes place either when the animal is gliding forwards or, and apparently much less frequently, when it is stationary. Food collection is effected mainly by trunk limb 2 as is usual in scraping species—but is assisted to some extent by trunk limb 1. In crawling species the spines of the inner distal lobe of trunk limb 1 are used for grasping the object over which the animal is crawling: in *Graptoleberis* this lobe and its spines fulfil no such function and are therefore free to assume another role, food collection. In crawling species the first trunk limbs move according to the demands of the moment: in *Graptoleberis* both the whole limb and the inner distal lobe move rhythmically and their movements are synchronized with those of trunk limb 2. The inner distal lobe swings in one plane about its base so that its scrapers describe an arc, the working stroke being that during which the scrapers are swung inwards. Because of the position and orientation of their blades (figures 68, 84, 90 and 91) material over which the animal is gliding is swept towards the mid-line by this movement and lies in a position ready for collection by trunk limb 2.

In a gliding individual the scrapers of trunk limb 1 are swung outwards as the limb moves forwards (figure 90). It is at this time that the scrapers of trunk limb 2 are moved inwards, and therefore make their working stroke when the animal is stationary. As trunk limb 1 is dragged back, thus propelling the animal forwards, its scrapers are swung inwards and therefore scrape when the limb, although working, is stationary relative to the substratum (figure 91). As the scrapers of trunk limb 1 operate, those of trunk limb 2 make their recovery (non-working) stroke, to the successful accomplishment of which the forward movement of the animal is no impediment. Thus the scrapers of both limbs make their working stroke when the limb on which they are borne is not moving forward over the substratum. The scraping rate is variable and there are often brief pauses. In specimens gliding over glass, under which circumstances counting is relatively easy, sustained rates in excess of 170 strokes/min can be achieved. Over short periods (29 and 15 s) rates of 186 and about 200 strokes/min were measured, the last being the fastest recorded. On leaves of *Elodea*, where with suitable illumination the scraping rate of trunk limb 2 can be measured easily though details cannot be observed, its frequency is lower, presumably because of greater resistance to the scrapers. Here, in a moving individual, a maximum rate of 140 strokes/min, over a period of 30 s was measured. In almost stationary individuals the highest rate recorded was only 80 strokes/min, but this was sustained for 111 s. On some occasions a minute lift of the carapace, without breaking the marginal seal, has been detected as the scrapers of trunk limb 2 swing inwards and the first trunk limbs slide forward.

The movement of the second trunk limb is a complex swing which brings the distal scrapers (nos. 6 to 8) towards each other in the mid-line and at the same time swings them through an arc so that their tips make contact while their bases remain wide apart (figures 85, 90 and 91), and also pushes them, and particularly the more proximal scrapers, deeper into the median chamber. The same movement swings the spines of the gnathobasic plate forward along the food groove (partially indicated in figure 90). As the scrapers approach each other in the mid-line nos. 4 and 5 are turned by the swing of the appendage so that their flat blade-like faces push towards the food groove (figures 85, 86 and 91). Thus food is scraped by scraper no. 6, which in conformity with the principle which seems to apply to all such devices, is followed by two fine-toothed brushes (spines 7 and 8) of greater length than itself which whisk loosened material to the mid-line and inwards in readiness for the next stroke. This material is concentrated in a small area by virtue of the coming together of the tips of the scrapers (figure 85) and is then pushed towards the food groove by spines 4 and 5 whose shortness is now easy to understand. As is clear from figures 90 and 91, the further towards the food groove the food is pushed, the more it becomes compacted in the mid-line. Although trunk limb 3 swings in such a manner that its endite armature must force towards the food groove particles which escape backwards from trunk limb 2, the indications are that any such material is small in quantity and that trunk limb 2 handles successfully the bulk of the material which it scrapes.

As food passes deeper into what in filter feeding species would be called the filter chamber, the gnathobasic plates of trunk limb 3 help to funnel it into the posterior end of the food groove. These plates are directed obliquely forward and their tips converge. They function in part as shutes, but also play an active part in food transport. Here the median gap is narrow and food is dragged through it largely by scrapers 1, 2 and 3 of trunk limb 2 whose tips lie against or very near to the evenly curved floor of the posterior end of the food groove (figure 82). This contrasts strikingly with the condition in *Eurycercus* (Fryer 1963, text-fig. 45), *Peracantha* (figure 47) and others in which even scraper no. 1 never makes contact with the floor of the food groove, and in which the food groove extends much further back relative to trunk limb 2. The functional significance of the difference in length of scrapers 1 to 3 of trunk limb 2 in *Graptoleberis* is now apparent. The swing of the limb is such as to keep them near the floor of the food groove at all stages of the cycle of movement. The precise length of each scraper is therefore important. In this forward movement of food near the posterior end of the food groove trunk limb 2 is assisted by the gnathobasic plate of trunk limb 3.

The median gap between the gnathobasic plates of the third trunk limbs (figure 82, GP 3) is narrow, and as they swing forward together their tips actually meet, as do the inwardly directed tips of the stumpy brush setae (BS 3). These latter inevitably sweep forward any particles which lie in the mid-line at the posterior end of the food groove. Trunk limb 4 appears to play no active part in pushing food forward. Its gnathobasic setae possibly help to seal the posterior end of the food groove, though even this function appears to be taken over almost entirely by their homologues on trunk limb 3. The endite armature of trunk limb 4, used for forcing material towards the food groove in most chydorids, seems here to serve essentially as a barrier to the backward passage of particles, though very little material seems to find its way here. Thus food particles are pushed forward mechanically at the posterior end of the food groove by trunk limbs 2 and 3.

Just anterior to scraper no. 1 of trunk limb 2 is a tuft of long spinules located on the gnathobase (figure 82, PSG). These, like the proximal scrapers, are of such a length as to skim the surface of the food groove as the limb swings forward, and therefore continue the process of forcing food anteriorly. Anterior to these spinules, and separated from them by a gap, is the rest of the gnathobasic armature, and it too skims the surface of the food groove (figure 82). Material pushed by this armature is finally brought within reach of the spinous setae of the gnathobasic plate (GP 2), this being facilitated by the fact that the most posterior of these is the shortest. These push the food between the first trunk limbs and forward at least to the level of the maxillules. Sections indicate that they can push food even further forward than this—right up to the posterior margin of the mandibles (figure 82)—so it seems that here they combine with the maxillules in moving food forward at the extreme anterior end of the food groove. Thus trunk limb 2 is largely responsible for the transport of food from one end of the food groove to the other. Whether labral gland secretions are involved is uncertain. If the function of the inner lobe of trunk limb 1 has been correctly interpreted then its presence implies the production of such secretions.

That currents are not involved in the feeding mechanism is no bar to their employment. No secretions are produced by trunk limb glands.

A specimen scraping food from a leaf of *Elodea* and watched from the side revealed that the whole operation of scraping and transfer of food to the mandibles can be accomplished in four cycles of movement of trunk limb 2. The passage of a dark mass of particles along the route just described was clearly seen to take place in four distinct stages though the exact location of the food mass in relation to the various scrapers at the end of each cycle could not be ascertained. Four successive swings of trunk limb 2 took the food to the level of the posterior margin of the mandibles where it remained for some time before being passed between them and taken up the oesophagus.

Important features of the feeding process are that filtration is not involved either in the collection or handling of the food, and that there is a reduction in the number of appendages directly involved, the reduction being effected posteriorly. Even trunk limb 4 plays only a minor part.

(vii) *Conclusions and the evolution of gastropod-like habits*

By the adoption of habits akin to those of a gastropod mollusc *Graptoleberis* has been able to exploit a very distinctive ecological niche. Morphological specializations are comprehensible only in the light of these habits.

Although a phylogenetic series showing the evolution of gastropod-like habits, and of the suction chamber which makes them possible, does not exist among extant Chydoridae (and all known fossils are of still extant species) it is nevertheless possible to illustrate the stages in such evolution by reference to representatives of four genera. These, in order of progressive specialization, are *Alonopsis elongata*, *Peracantha truncata*, *Alonella exigua* and *Graptoleberis*. The trend was undoubtedly initiated by the habit of balancing on the carapace margins as *Alonopsis* does to this day. The arrangement of marginal setae and setules in *Alonopsis* contains in essence all the features utilized by *Graptoleberis*.

From the *Alonopsis* condition it is a small step to that in *Peracantha* where, by developing a definite flange, the ventral margins have become somewhat elaborated to facilitate balance, where a well-marked embayment serves the same ends, and where the setae have also been modified for this purpose but are still similar in all essentials to those of *Alonopsis*. In an animal so constructed, pumping to establish a respiratory stream inevitably leads to at least intermittent establishment of reduced pressure within the carapace chamber, and this also facilitates attachment. There is evidence that this is to some extent the case in *Peracantha*.

Such a situation requires for its exploitation only an improvement of the seal and, initially, more efficient expulsion of water from the carapace chamber. Both are seen in *Alonella exigua* in which, in addition to the setae of the carapace margin, those of the exopod of trunk limb 3, whose functional precursors are present in *Alonopsis* and *Peracantha*, have been exploited.

The more efficient the seal, the less effort need be expended on pumping, and such a trend has led from the *A. exigua* condition to that of *Graptoleberis*. Such a sequence involves the loss of a regular current through the former filter chamber, prohibits filter feeding, and has necessitated important changes in the feeding mechanism. As a functional sequence this is valid, but it is not a phyletic series.

Factors which have probably contributed to the successful accomplishment of such evolutionary steps include the small difference in density between the animal and the water in which it lives, and the small size of the structures involved. Only a slight diminution in pressure is needed for attachment, and irregularities of the substratum present fewer problems than they would to a large organism.

Reduction of the respiratory stream in *Graptoleberis* has probably been facilitated by sluggish habits, though the situation in the macrothricids *Streblocerus* and *Drepanothrix*, which have dispensed completely with the so-called respiratory stream (Fryer, in preparation), suggests that, in the Anomopoda generally, the stream is concerned more with feeding or, in some cases, with attachment, than with respiration. This is further borne out by the observations of Smirnov (1968) on *Rhynchotalona* and *Monospilus* (the two genera of which I was unable to study live material) in neither of which is there a respiratory stream. Comparison with *Graptoleberis* reinforces the evidence that rapid and incessant pumping by *Alonella exigua* when attached is concerned not so much with respiration as with establishing and maintaining low pressure to permit attachment, though it also continues to subserve an earlier-developed function and is a component of the feeding mechanism.

XVII. The structure, habits, and feeding mechanism of *Pseudochydorus globosus* (Baird), a scavenging chydorid

(i) *Pseudochydorus* gen.nov.

Chydoridae of the subfamily Chydorinae, of globular form. Ventral margins of carapace thickened, but without flange, and meeting each other over their entire length when the carapace chamber is closed, so that there is no embayment. With a distinct flange on anterior carapace margins which widens dorsally. Marginal carapace setae arise everywhere from within the carapace. Headshield drawn out into a pointed rostrum: its ventral portions fit closely against the adjoining anterior carapace margins so as to convert the entire animal into a subspherical ball. Cuticle of carapace and headshield greatly thickened and sclerotized, and amber in colour; often with a dark, almost black, spot in the centre of each carapace lobe. Head pores of the type found in *Alonella*, *Peracantha*, *Chydorus* and several other genera.

Mandibles with a wider gape than in anomopods in general and lacking a posterior apodeme. Articulation as in other Chydorinae. Transverse mandibular muscles slender and showing little asymmetry. Muscle 5c absent. Accessory remotor muscle present.

First trunk limbs bearing a massive hook distally. Trunk limbs 2 to 5 without filtratory setae; their gnathobases bearing spiniform setae which are fewer in number (5 on trunk limbs 2 and 3, and 4 on trunk limb 4) than in all chydorid genera with filters and, in the case of trunk limbs 2 and 3, than in all investigated genera except *Anchistropus*, irrespective of feeding habits. Trunk limb 2 with distal spines modified for dragging large food masses.

Post-abdomen moderately long and narrow, parallel sided, and bearing numerous long marginal denticles and very fine movable lateral squamae. Claws with two basal spines of which the more distal is long and slender.

Alimentary canal with enlarged stomach region.

Type species *Chydorus globosus* Baird, 1850.

The feeding habits of *Pseudochydorus* (figures 92, 93) differ markedly from those of all other chydorids save to some extent *Anchistropus* (§XVIII) which feeds on the living tissues of hydrids. The food consists, not of algae and detritus scraped from surfaces, but of larger masses of dead animal tissue. *P. globosus* is a scavenger. Such habits demand means of food collection and manipulation different from those practised by species which feed on small particles.

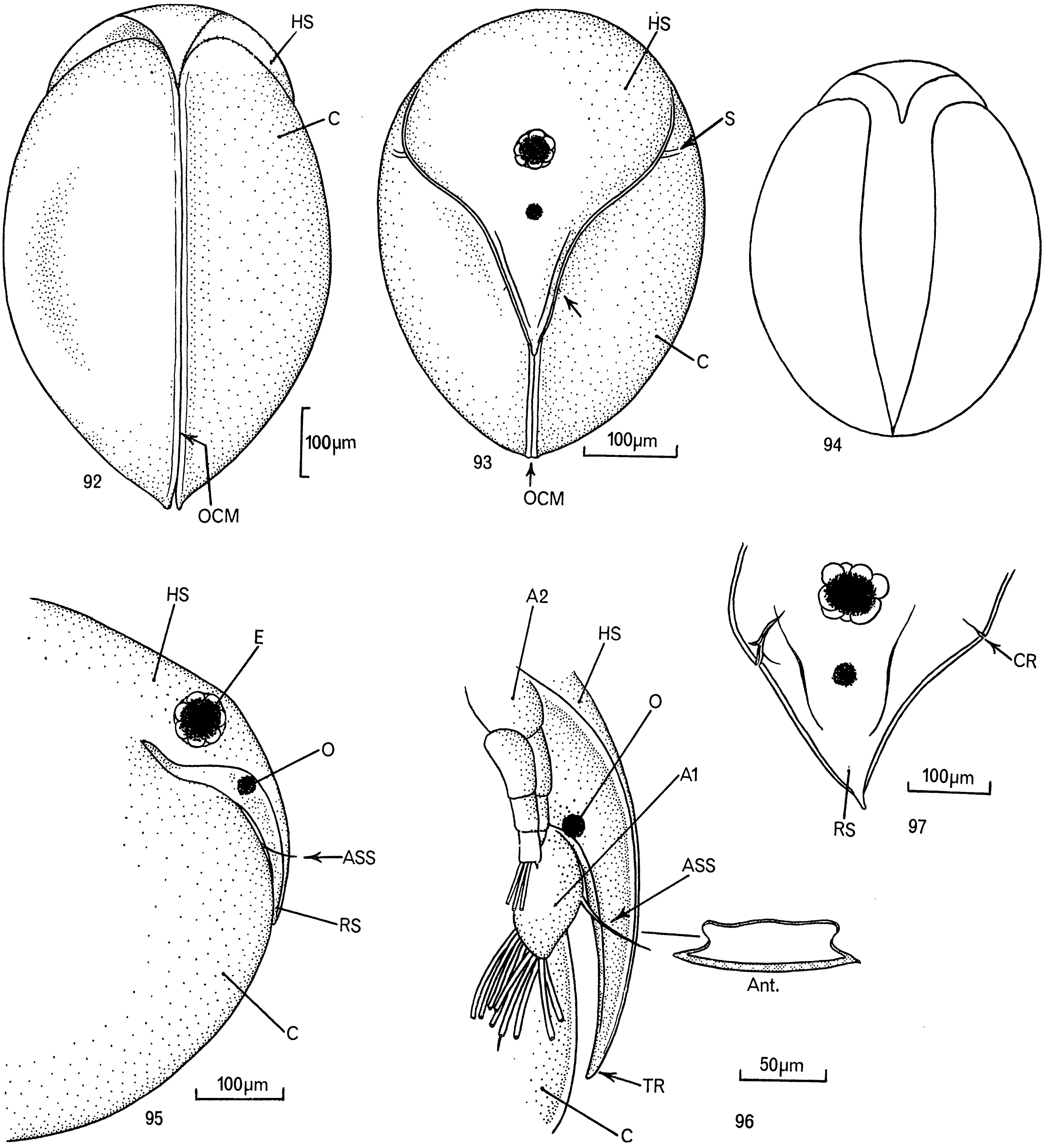
Concomitantly with the evolution of scavenging habits *P. globosus* has adopted a defence mechanism involving encasement in a ball of greatly thickened and sclerotized cuticle. This influences both locomotion and the feeding mechanism. For example, the formation of a closed sphere is incompatible with the provision of a ventral carapace embayment such as plays an important part in crawling in several chydorids and which also often facilitates contact between the food-collecting second trunk limbs and the substratum. Particular attention is directed to the ways in which these various and apparently conflicting demands have been reconciled in the organization of this species.

On the basis of features apparent to the systematist several authors, e.g. Lilljeborg (1900) and Birge (1918), have expressed doubts as to the wisdom of regarding this species as a member of the genus *Chydorus*, and subgeneric status has been suggested. Dr D. S. Johnson tells me it was his intention eventually to place it in a separate genus on the basis of features used in taxonomy, but as his work is not ready for publication he has kindly agreed that this transfer should be made here. That the same conclusion should be reached from different standpoints is gratifying. Many fundamental, but hitherto unknown, differences between *P. globosus* and members of the genus *Chydorus* in both external morphology and internal anatomy, as well as in habits, are described below and the conclusion is inescapable that, a similarity in head-pore arrangement and mandibular articulation notwithstanding, the two genera are only remotely related.

(ii) *The nature of the food and its bearing on ecology*

The alimentary canal of most anomopods is almost invariably well filled with food. This is not so in *P. globosus* which seems almost always to have little or no food in the gut. The explanation is that it obtains its food not as an almost continuous supply of small particles but in the form of occasional large masses. Even allowing for rapid digestion, the field data indicate that such meals are usually infrequent. This goes a considerable way towards explaining the fact, noted by several observers, e.g. Langhans (1911), that where it is to be found this species usually occurs only in small numbers. Smirnov (1963) gives figures of numerical abundance and biomass.

The food consists largely of the dead and decomposing bodies of other organisms. All food items so far seen in process of collection have been small crustaceans—*Diaphanosoma* (seen being eaten on four separate occasions), *Sida* (twice), *Daphnia*, and a cyclopoid copepod—but it is assumed that what is eaten is largely determined by what is available. Such large items are dragged *en masse* into what in many species constitutes the filter chamber, here designated simply as the median chamber. Data on the mortality of such food organisms and of the availability of their corpses are scanty. Indeed the relative infrequence of *P. globosus* is possibly as good an indicator of their lack of abundance as any other evidence.



Figures 92 to 97. *Pseudochydorus globosus.*

Figure 92. Ventral aspect showing the complete absence of any embayment when the adductor muscle brings the two carapace lobes together.

Figure 93. Anterior aspect of an individual in the 'closed' position. The unlettered arrow indicates the anterior seta of the antennule, here protruding between headshield and carapace.

Figure 94. Diagrammatic figure of an individual seen from below with the ventral aperture open.

Figure 95. Anterior region, lateral, to show the general form and the absence of any flat balancing region on the ventral carapace margins.

Figure 96. The anterior cephalic appendages revealed by removal of the right lobe of the carapace. The inset shows a transverse section through the rostrum at the level indicated and drawn to the same scale but from another individual, not necessarily exactly the same size.

Figure 97. Headshield dissected from the carapace and slightly flattened. Note how the flattening has produced distinct cracks at each side.

This species occurs in a variety of situations in ponds and lakes, particularly among macrophytic vegetation in the littoral zone. Provided a suitable substrate is available it can grip with the first trunk limbs and even move forward slowly, but seldom does so for more than a very short distance. A striking characteristic is its habit of closing up when disturbed (section iii). When this happens it inevitably falls to the bottom. This presumably enables it to avoid being eaten by enemies, such as Odonata nymphs, capable of ingesting it, but experiments are desirable.

Very noticeable in the living animal is the rapid beat of the exopod pump whose beat rate exceeds that of all other chydorids examined save perhaps *Anchistropus*. The heart also beats with great rapidity. The direction of currents entering the carapace chamber is much the same as in many chydorids, but the most powerful current enters ventrally and only weak currents anteriorly.

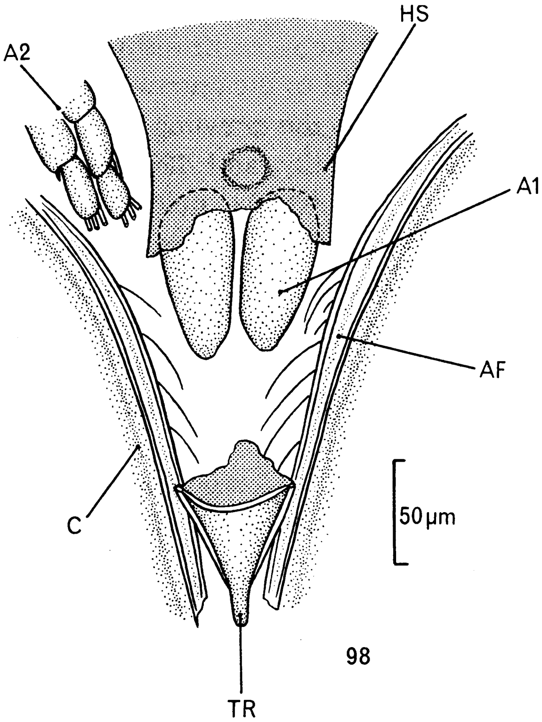
Pseudochydorus can swim well and does so frequently over the bottom with the ventral side down. A female 0·68 mm in length carrying embryos covered distances of 8·5 and 15 cm at speeds of 8·93 body lengths (*ca.* 0·61 cm)/s and 8·49 body lengths (*ca.* 0·58 cm)/s respectively, and over a short distance (2·5 cm) a speed of about 9·2 body lengths (0·63 cm)/s was achieved.

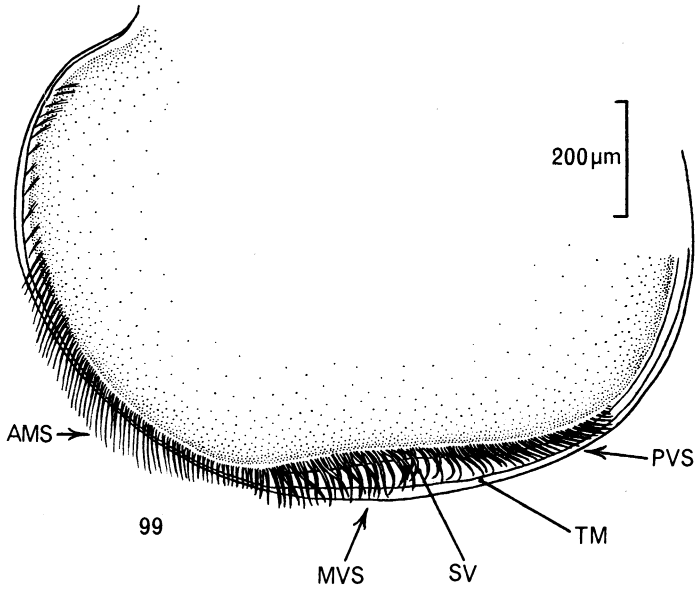
(iii) *Headshield and carapace and a note on cuticle*

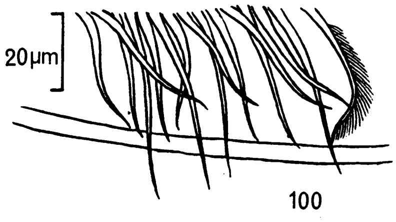
The specific epithet 'globosus' aptly describes the general form of the headshield–carapace complex. Each carapace lobe is essentially a hemisphere, and because each is evenly curved ventrally (figures 95, 99) there is no sign of the straight (flat) anterior portion which, bounding the embayment, is so characteristic of the Chydoridae as a whole. This feature alone is indicative of distinctive habits different from those of most chydorids. Equally striking is the complete absence of any embayment (figures 92, 93). Ventrally the carapace margins can be brought into contact over the whole of their length except at their anterior and posterior extremities. Posteriorly, however, divergence is only slight (figure 92) and the posterior aperture is no more than a narrow slit. Elaboration of the ventral margin is different from that of many species. Its form over most of its length is best appreciated from transverse sections (figures 101, 102). Anteriorly and dorsally the margin is widened (figure 98, AF) for reasons described below.

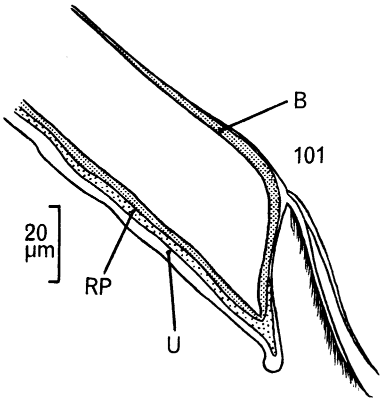
When the opposed carapace margins are brought together, as they are at times in life, they completely close, but probably do not seal, the ventral region. The curvature of the headshield is continuous dorsally with that of the dorsal surface of the carapace, and its elongate anterior ventral prolongation, the rostrum, curves towards the ventral carapace margins. Its shape is such that when the carapace lobes are pulled together by the adductor muscle, the rostrum fits neatly into the anterior gap and protects the only large aperture of the carapace chamber (figures 92, 93 and 98).

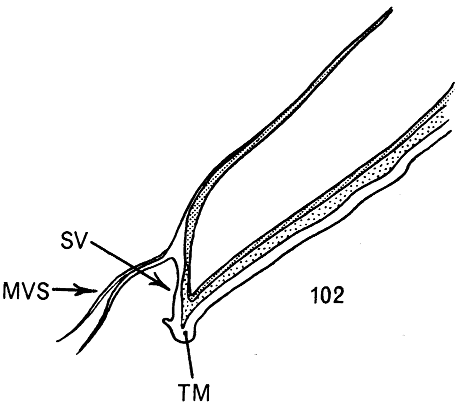
Not only is there a close correspondence between the shape of the headshield and the contour of the anterior aperture of the carapace chamber when the carapace lobes are opposed, but the opposed margins of each are elaborated. It is here that the anterior marginal flange of each carapace lobe widens (figure 98, AF). Each margin of the flange is bordered by a rib of thickened cuticle between which is a shallow groove. Except near its tip each margin of the headshield has a rim (figures 93, 98) which is not so much a thickening as a lateral extension of the thick anterior (outer) cuticle. In section (figure 96, inset) the shape of the rostrum, which has considerable thickness, is such that its inner portion fits between the carapace lobes, and its rim rests against the flange. This can to some extent be seen from figure 98.











FIGURES 98 to 102. *Pseudochydorus globosus.*

FIGURE 98. Transverse section through the anterior part of the head. Sufficient of the headshield has been sliced away to reveal the anterior flange of the carapace which, in life, it obscures. By comparing this figure with figure 95 some idea can be obtained of how the headshield fits into the anterior, V-shaped aperture of the carapace.

FIGURE 99. Right lobe of the carapace seen from inside.

FIGURE 100. Details of some of the median ventral setae.

FIGURE 101. Transverse section through the ventral carapace margin showing the thickness and staining properties of the cuticle when stained with Mallory's stain, and the arrangement of the median ventral setae. In life these are directed more inwardly, towards their fellows on the opposite lobe, than they are here.

FIGURE 102. The same more posteriorly.

When not in use the antennae can be folded so that their setae and much of their rami lie inside the carapace chamber. Proximally they are protected by the lateral expansion of the headshield. The antennules can be swung inwards to lie parallel to each other and are then completely overlain anteriorly by the rostrum and, on each side, are entirely protected by the carapace (figures 95, 96 and 98, A1) though the lateral sensory seta (figures 95, 96, ASS) is so curved as to pass through the chink between headshield and carapace (see also figure 93). More protection is therefore afforded to the anterior appendages in a 'closed' animal than in such well-protected species as the crawling *Peracantha truncata* (figures 34, 36), in which the antennules are exposed laterally, and *Alonella exigua* (figure 51) where, although overlain and protected by the headshield, neither of the anterior appendages (other than the antennal swimming setae) are directly protected. In *Pseudochydorus* protection is almost complete and a closed animal is in effect protected by a sphere of cuticle. In that the same end has been achieved, though by very different means, *Pseudochydorus* exhibits convergence in its defence mechanism to such dissimilar arthropods as the isopods *Armadillidium*, *Caecosphaeroma* and some of its relatives, to the pill millipede *Glomeris*, and to ostracods and conchostracans.

In order to form a completely enclosed sphere *P. globosus* has had to forego the development of a ventral embayment yet reconcile this with the needs of the feeding mechanism, which include provision of an adequate, and in this case considerable, gape. The spherical form permits such a reconciliation. The margins of the carapace are more free anteriorly than posteriorly. Anteriorly they are fixed at two points which, because the body is wide, are widely separated, and which are dorsally located. Posteriorly they are fixed at a common point which is less dorsally located. Relaxation of the carapace adductor muscle therefore produces a wider gape anteriorly than posteriorly: a gape which is wider than can be achieved by narrow-bodied forms (figure 94).

Clearly correlated with the evolution of a defensive sphere is a thickening and sclerotization of the cuticle which is much thicker than in any other anomopod. The thickness varies, being greatest near the middle of the carapace lobes where, in an adult female, it is about 12 μm. It is thinnest in the postero-dorsal region where it may be as thin as about 5 μm. Even this is very thick for a chydorid: the cuticle of an adult female of the robust *Alona affinis* has a maximum thickness of less than 2 μm, and the thickened ventral parts of the carapace of *Graptoleberis* only attain a thickness of about 3 μm. In *Anchistropus*, whose cuticle shows similar thickening, the maximum thickness is about 4 μm.

Sclerotization is evident even to the naked eye by virtue of the golden amber colour of the outermost layer of cuticle. Mallory-stained sections reveal three zones of cuticle characterized by different degrees of tanning, but the boundaries are not very distinct and the degree of development of each differs in different parts of the carapace. The outermost layer, which presumably includes the epicuticle, in places occupies more than half the total thickness. The innermost zone is blue-staining, and therefore soft and unsclerotized. Beyond it is a zone of red-purple staining, and therefore somewhat sclerotized, cuticle, and to the outside is a zone of unstained cuticle which varies from golden amber to brown in different regions and is therefore considerably sclerotized. The blue zone is present everywhere and occupies from about 10% of the total thickness, in the centre of the carapace lobes, to about 25% posteriorly. The red-purple zone is virtually absent posteriorly but comprises up to 30 % or even more of the thickness towards the centre of the lobes. The amber zone makes up 70 % or a little more of the thickness posteriorly, where, however, it is pale and its total thickness is not great, and, in some individuals, about 60 % of the thickness in the centre of the lobes where it is much darker and brownish in colour. In this region in other (less recently moulted?) individuals it usurps much of the red-staining zone. It is to the sclerotization in this region that the dark blotches, one on each carapace lobe, which are so characteristic of this species, are due. A difference between the properties of the cuticle of this and other species is that the cuticle of *P. globosus* is distinctly brittle and cracks rather than crumples under pressure. (See, for example, figure 97.)

The arrangement of the marginal setae of the carapace is shown in figures 99 and 100. Unlike those of many species, these arise not at the margin itself but internal to it. Where they lie most remote from the margin, the inside rim of the carapace is elaborated by the development of a flattened region, the selvage (figures 99, 101 and 102, SV). Three groups, anterior, median and posterior, can be recognized. Those of the anterior series (AMS) are short, extremely fine, and form a single row whose tips protrude beyond the carapace margin. So fine are they, however, that they do not prevent the close opposition of the margins when the carapace is closed. The median group (figures 99–102, MVS) consists of longer, soft setae which in life are directed essentially inward towards the mid-line, though their curvature is not the same in each case. This being so, although they arise in a single row, they produce a pad-like effect. When the carapace is closed they meet their fellows of the opposite lobe and form a 'tangle' which is then pressed between the opposed selvages and flattened. As the carapace opens they disengage. The posterior series is arranged as shown in figure 99 (PVS).

(iv) *Appendages, labrum and post-abdomen*

Although it is necessary to describe the structure of the appendages before giving an account of the feeding mechanism, it is helpful to bear in mind that many of the peculiarities described are directly related to the nature of the food, which is very different from that of all species so far described, and with the problems involved in its collection and manipulation. Some of these correlations are sufficiently evident to render the descriptions meaningful from the point of view of function even before the feeding mechanism is considered, and reference is at times made to function.

The antennules and antennae are shown in figures 96 and 98. The very broad labrum contains large gland cells which produce copious secretions. Discharged secretions are shown in figure 103 (LGS). Although of the basic anomopod type, the maxillules (figures 103, 110, Mxlle) show certain specializations, obvious in the illustrations, which befit them for pushing large masses of food.

Salient features of trunk limb 1 are shown in figure 103 (TL1). Most noteworthy is the presence of powerful, heavily sclerotized spines, including a stout hook (H) in the posterior ventral region. An 'inner lobe' has not with certainty been detected, but is mentioned as being very rudimentary by Lilljeborg (1900).

The second trunk limbs (figure 103, TL2) are clearly modified in relation to the nature of the food. The gnathobasic plate is reduced to five spines, of which only three are directed anteriorly, and of which none is filtratory (GP2). (In *Alonopsis* (figure 7), although these

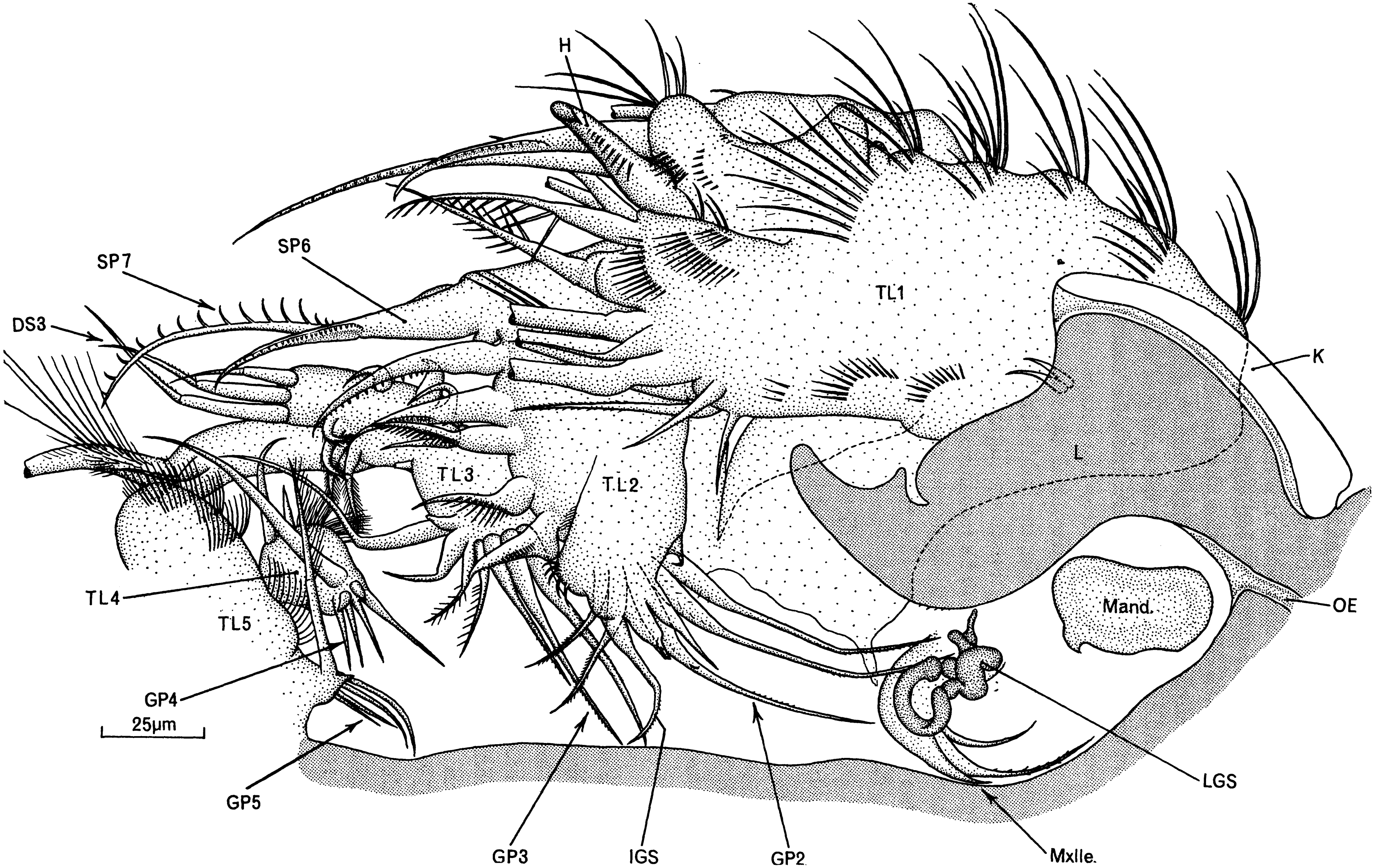
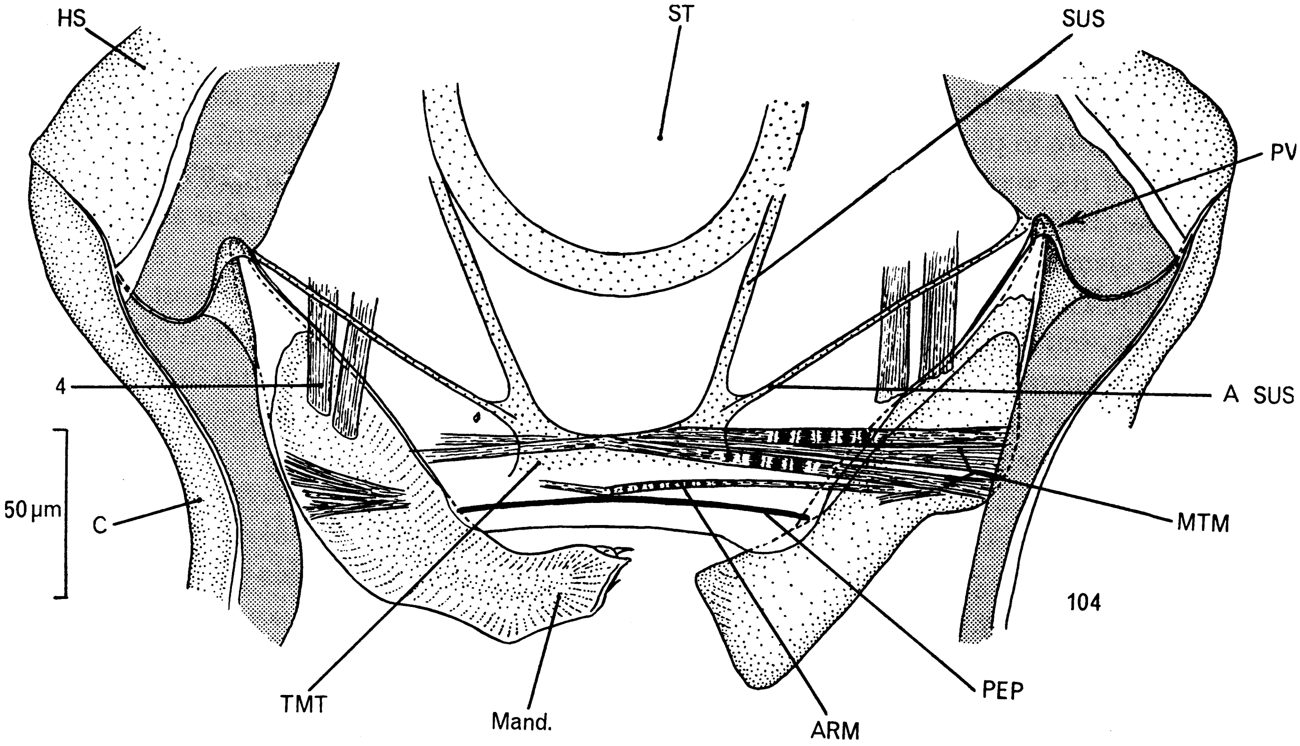
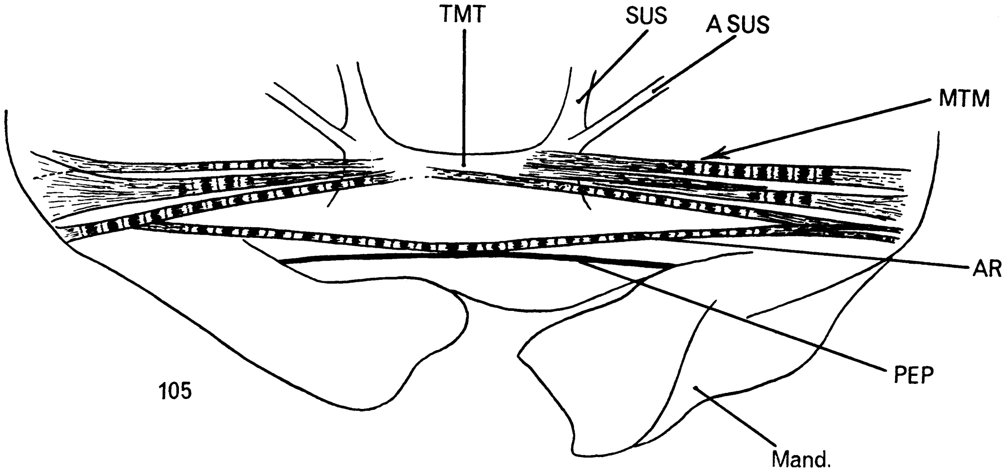


FIGURE 103. *Pseudochydorus globosus*. Median longitudinal section to show what in many chydorids is the filter chamber. Note the absence of any filters and the modification of all the limbs for grasping, dragging, pushing and forking. Note how endite spine no. 7 of trunk limb 2 (SP7) is modified for dragging, and how no. 6 (SP6) is modified for pushing.





FIGURES 104, 105. *Pseudochydorus globosus.*

FIGURE 104. Transverse section through the mandibular region. This is a relatively thick slice and is very slightly oblique so that on the right is seen the outer face of the anterior surface of the left mandible, and on the left the inner face of the posterior surface of the right mandible. In order to reveal muscles the mandibles are treated as if transparent. Note the wide gape of the mandibles, the double nature of their suspension, the details of mandibular articulation (shown enlarged in figure 106), the absence of the 5c muscles and their apodemes, the reduced, elongate and slender nature of the major transverse muscles and the small degree of asymmetry which they exhibit, and the accessory posterior remotor muscle (ARM) which inserts on the posterior endoskeletal plate (PEP). Such parts of the promotor roller muscles as can be seen in the section are omitted for clarity. The major suspensory ligaments incline steeply into the plane of the paper as can be appreciated by reference to figure 107.

FIGURE 105. Transverse section through the mandibular region from another preparation to show further details of the major transverse muscles. Other features are shown in outline only.

structures have a pushing function, six are directed anteriorly.) The anteriorly directed spines are widely separated and their fork-like action is easily appreciated. The two posterior spines are directed backwards in such a way as to enable them to assist the more distal armature to push food towards the food groove, and to force it forward. The nature and role of the rest of the gnathobasic armature is apparent from figure 103. Note the long spine (IGS) which reaches into the food groove and the small hook-like spine anteriorly.

Of the armature of the corm all save the two outermost (most distal) spines are shown in figure 103. The three outermost are shown in figure 109. Of these the outermost is short and simple, but the next two, which are used for dragging food into the median chamber, are the most modified of all the spines of this limb and are very different from those of any other chydorid yet examined. Each is flexible and is armed along its distal portion with a row of long, widely separated hook-like spines.

The gnathobasic armature of trunk limb 3 (figure 103 TL3) is also reduced and that portion of it which is the homologue of the filter plate of many species (GP3) much resembles that of the preceding limb. Two spines are used for pushing food towards the food groove and three for forking it anteriorly. The armature of the posterior dorsal corner is shown in the figure. Four anterior endite spines take the form of hooks. In this they differ from those of their homologues in other species (see appropriate illustrations of *Alonopsis*, *Peracantha*, *Graptoleberis*, etc.). There is also the equivalent of an outer filter plate consisting of four setae which are cleaned by setules borne on trunk limb 4, and long distal spines (DS3).

The fourth trunk limbs (figure 103 TL4) are greatly reduced, especially by the loss of spines in the vertical row. The gnathobasic armature (GP4) is also reduced and is non-filtratory. Reduction is also apparent in trunk limb 5 (figure 103, TL5), but rudimentary gnathobasic spines are present (GP5).

The limbs are widely separated. Strict comparisons cannot be made, but in *Pseudochydorus* the gap between the second trunk limbs, which is narrow in most species is at least twice as wide as in *Eurycercus*.

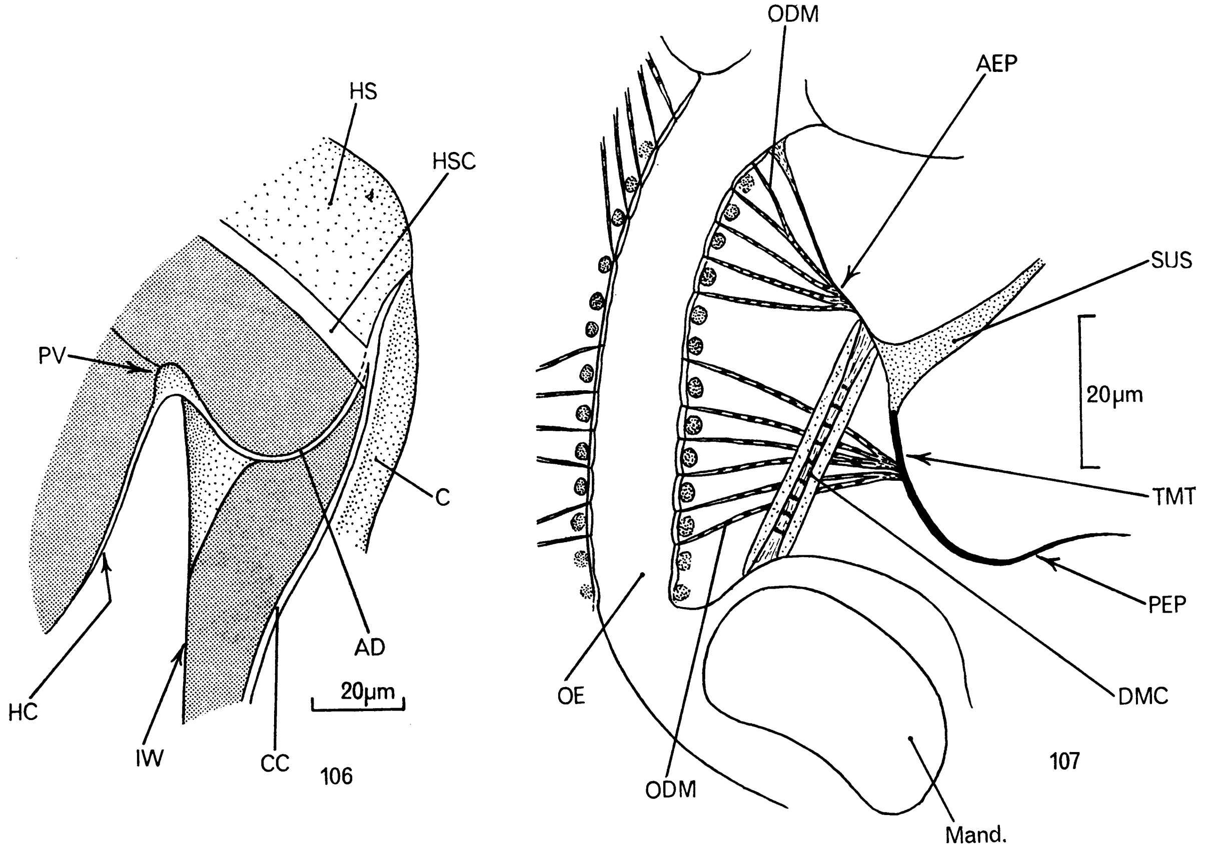
(v) *The mandibles*

Of skeletal features of the mandibles related to the specialized diet the most obvious is the development of curved spines at the posterior dorsal corner of the masticatory surface of each (figures 103, 104 and especially 110, PH) whose function is obviously that of dragging and pushing. Such spines, which would serve no useful purpose in a detritus- or algal-feeding species, are the homologues of the teeth described in *Eurycercus* (Fryer 1963, text-fig. 16) and of the biting teeth of the anostracan *Branchinecta gigas* (Fryer 1966). Like the teeth of *Eurycercus* these exhibit asymmetry. The left mandible bears several teeth; the right a single tooth. This asymmetry, and asymmetry of the major transverse mandibular muscles, ensures that the hooks of the left mandible drag material forward into the field of action of the right-hand tooth, whose smaller arc of rotation and more rapid movement enables it to push material yet further forward between the molar surfaces. This can easily be visualized by reference to figure 110.

The molar surface of the left mandible is drawn out into a row of about 11 rake-like spines (cf. *Eurycercus*, Fryer 1963, text-fig. 16). Of these the most posterior four or five are more or less pointed, the more anterior spatulate, there being a gradual transition from one type to the other. Another striking skeletal feature is the absence of a posterior apodeme (see below).

The gape of the mandibles is wider in *P. globosus* than in any other chydorid yet examined and is related to the ingestion of large food masses. It is doubtful whether the mandibles could cope with small particles even if the means existed for their collection.

Mandibular articulation is of type B (figures 104, 106). Details of this type of articulation are conveniently given for this species. Where headshield and carapace unite, the cuticle, which here is relatively thin, is drawn inwards into a plate-like apodeme (AD) curved as shown in figures 104 and 106, at whose inner extremity is a cup of chitin (PV) continuous with the cuticle of the head (HC). The inner part of the apodeme is braced by an arc of somewhat thickened, but still thin, cuticle which is morphologically part of the inner cuticular face (IW) of the carapace. The pointed proximal tip of the mandible articulates in the cup (figure 104). The cup itself can be thought of as being like that of *Eurycercus* (whose articulation is of type A) which has been carried inwards by growth of the apodeme.



FIGURES 106, 107. *Pseudochydorus globosus.*

FIGURE 106. The region of mandibular articulation as seen in transverse section. (Compare figure 104). Note that the headshield cuticle (HSC) is cut obliquely and therefore appears to be thicker than is in fact the case. The inner wall of the carapace (IW) is here seen in section, but its surface is seen a little more dorsally.

FIGURE 107. Longitudinal section through the mandibular region to show the endoskeletal system. This is a median slice and does not reveal the accessory suspensory ligament which lies deeper in the plane of the section. The general shape of the entire endoskeletal system of this region can be appreciated by comparing this figure with figures 104 and 108.

Suspension (figures 104, 105, 107 and 108) is by means of a major suspensory ligament

(SUS), which inclines steeply backwards in relation to the transverse mandibular tendon (TMT) (figure 107) and an accessory, more lateral, ligament (A SUS) on each side. The suspensory ligaments and transverse mandibular tendon are continuous anteriorly, and therefore dorsal to the transverse mandibular tendon, with an endoskeletal plate (figures 107, 108, AEP), and the transverse mandibular tendon is continuous posteriorly and ventrally with a similar but more robust plate (figure 107, PEP). The whole complex is difficult to visualize from one figure and is best appreciated by consideration of figures 104, 105, 107 and 108. From both the anterior endoskeletal plate and the transverse mandibular tendon, oesophageal dilator muscles (ODM) take their origin (figures 107, 108) and on the anterior plate also originate a pair of small muscles (DMC) which on contraction must draw in the cuticle just dorsal to the mandibles, thereby presumably helping to suck forward (or even manipulate) the food mass.

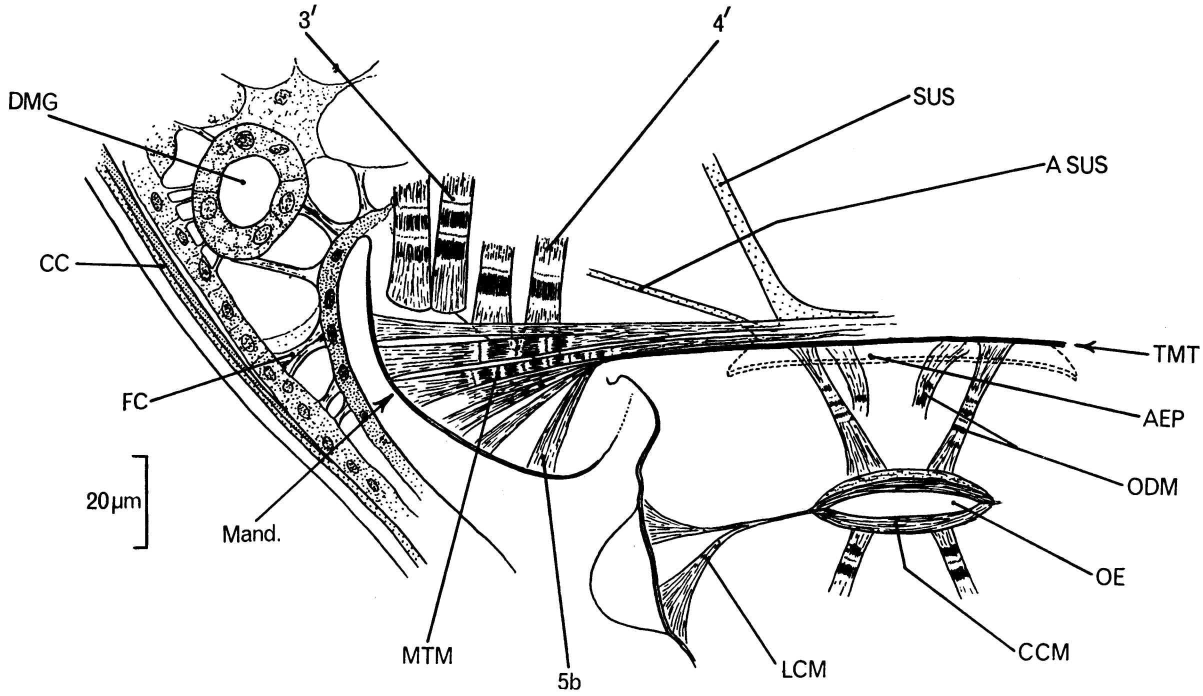


FIGURE 108. *Pseudochydorus globosus*. Slightly oblique horizontal section through the mandibular region, in ventral aspect, to show the mandibular muscles, some of the details of the endoskeleton, and some of the associated non-mandibular muscles. The anterior endoskeletal plate (AEP) is indicated here as it appears as a result of focusing down, for it is a dorsal extension of the transverse mandibular tendon.

It is in their musculature (figures 104, 105 and 108), however, that the mandibles of *Pseudochydorus* show the greatest modification. Some features are unique, others are shared only by *Anchistropus* of the forms studied. Most striking is the absence of muscles of the 5c series which, in most other genera, are massive muscles which unite the mandibles by running between the apodemes of the posterior margin (themselves absent here).

The long transverse muscles of the α, β, γ series (MTM) are much reduced in cross-sectional area and, compared with those of many species, are long and slender. They are also located more ventrally than in, for example, *Eurycercus*. While the homology of the entire series is clear on comparison with, e.g. *Eurycercus* (Fryer 1963, text-figs. 18 and 19) and *Chydorus sphaericus* (figure 126), that of individual muscles is not, and no attempt is made to label these. The degree of asymmetry exhibited by these muscles is much less than that found in all other anomopods examined, with the exception of *Anchistropus* (cf. figures 104, 115 and 126). Great reduction is also apparent in the short muscles of the 5a, d and b series at the lateral extremities of the transverse mandibular tendon and which serve a remotor, adductor and promotor function respectively. Of these the 5a muscles are virtually absent and the 5d series barely recognizable. Complete loss of the 5b muscles is not possible but reduction is apparent (figure 108). The promotor (3) and remotor (4) roller muscles, particularly the latter, are also less massive than in many species.

Pseudochydorus also possesses muscles not observed in any other species. From the inner posterior face of each mandible originates a slender muscle (figures 104, 105, ARM) which inclines somewhat posteriorly and ventrally and inserts on the posterior endoskeletal plate just behind the mandibles. Because of its function (best appreciated by use of three-dimensional models) it is designated as an accessory remotor, though it possibly grants also a small degree of adduction.

Mandibular movements are extremely rapid. Rolling and swinging take place too rapidly to permit visual estimations of the rate, which exceeds that observed in other species. Slow movements sometimes take place, but rapid movements are more usual. If rapidity of movement and the development of muscles with a small cross-sectional area are correlated, the connecting link may be the open blood system. The muscles are bathed in blood and supplied neither by minute blood vessels (as in vertebrates) nor by tracheoles (as, for example, are insect flight muscles). Rapid and sustained activity may therefore present respiratory problems not encountered in slowly contracting muscles. Conceivably these can be overcome by employing muscles whose cross-sectional area is small, so that oxygen has to diffuse for only short distances. In *Eurycercus* the minimum distance between the central fibres of a major transverse mandibular muscle and the periphery may be more than 15 μm—possibly considerably more in a large individual: in the comparable muscle of *P. globosus* the distance is less than 3 μm. In insect flight muscles oxygen has to diffuse 'on the average about 5 microns' (Smith 1965). If this explanation is true then the rapid heart beat, and the brisk activity of the posterior exopod pump which is responsible for the setting up of respiratory currents, also become intelligible.

If this solves one problem it raises others. The power of a muscle is proportional to its cross-sectional area, and the cross-sectional area of a transverse mandibular muscle of *P. globosus* is less than that of other chydorids of comparable size. This discrepancy in power must be accentuated by the absence of the 5c muscles. The wide gape probably enables heavy loads to be avoided (the molar surfaces need not roll across each other) and rapid movement will enable the effort to be spread—one slow strenuous effort being replaced by many smaller efforts. A functional explanation cannot yet be offered for the loss of the 5c muscles, for which, however, some compensation is given by the unique accessory remotors.

(vi) *The alimentary canal*

Posterior to the oesophagus the alimentary canal of chydorids may be somewhat dilated, but never so much as in *P. globosus*. Here it is greatly dilated to form a wide 'stomach', shown in outline in figure 111 (ST), which bulges dorsally and extends posteriorly to about the level of the last pair of limbs. It is extremely conspicuous in longitudinal sections. Almost always it is completely empty. Such a voluminous stomach is necessitated by the diet. Large quantities of food have to be ingested and stored at what, judging from the large proportion of empty stomachs, are irregular, and perhaps long, intervals. Globular form lends itself admirably to such dilatation in all planes. Such a development, and presumable scavenging habits, are not possible in bilaterally compressed forms such as *Leydigia*, *Acroperus* and others.

(vii) *The feeding mechanism*

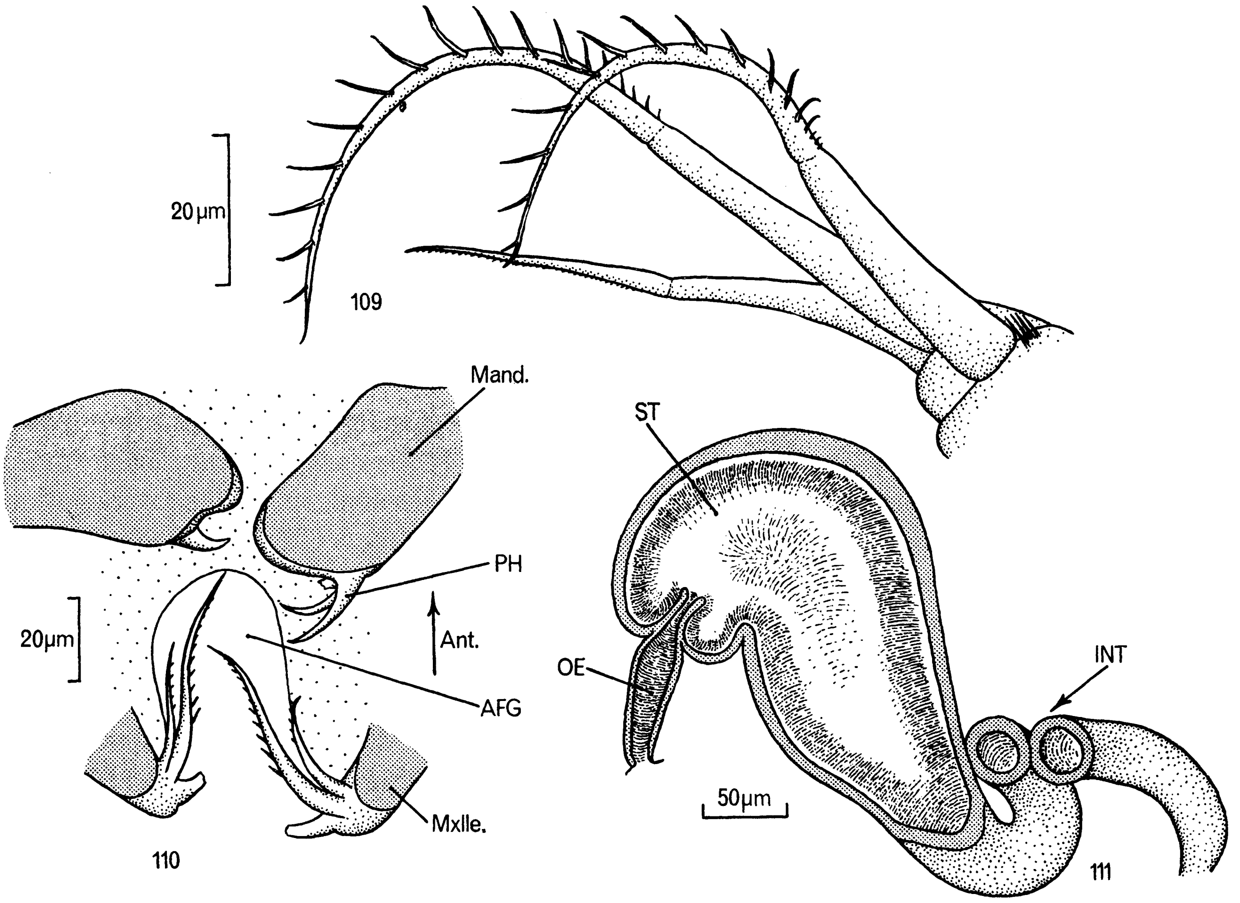
As *P. globosus* feeds on the dead bodies of other animals, feeding is intermittent, but each meal may be prolonged. An individual already feeding on a much decayed *Sida* when first observed continued the process for 14 min during which it pulled in only certain pieces which did not include appendages.

The outer spines of trunk limb 2, which are scrapers in most chydorids, are used for seizing material and dragging it towards the median chamber. Dead animals are grasped by the two long outer spines (nos. 7 and 8), whose flexibility permits the hooks with which they are armed to grip objects of diverse shape. Trunk limb 2 is extremely mobile—more so than in any other species examined—and does most of the handling of the food. This mobility enables it to drag food into the median chamber, push it towards the food groove by the more proximal spines, whose armature, and particularly the long spinules of spines 1 to 3, is well suited to this function, and then fork it anteriorly with the gnathobasic armature. The median gnathobasic spines continue the process begun by the more distal elements and the three anterior spines of the gnathobasic plate push the food towards the mouthparts. This they do with great vigour.

During the process of food manipulation, trunk limb 1, which is also very mobile, has been seen to play no active part. More striking, trunk limb 3 also often remains still or virtually so. Its armature must therefore act as no more than a fence which restricts food to the region covered by the movements of trunk limb 2. Movements have occasionally been seen whereby the gnathobasic spines of trunk limb 3 must assist in the anterior movement of food in the expected manner, but such movement of food is sometimes accomplished by the second trunk limbs alone. The four anterior distal hooks of trunk limb 3 also seem ideally suited to grasping and dragging large food masses into the median chamber and are perhaps so used at times, but his has not been observed.

Although the observed movements of trunk limb 4 can presumably assist slightly in moving food towards the food groove and forward, this limb also plays a negligible part, and sometimes no part, in forcing food into the median chamber. To this its greatly reduced median armature also bears witness.

Food is rammed towards the maxillules, which can be seen reasonably well in this species, and which by their steady, slow swinging, help to pass food to the mandibles. They continue to swing during the period when trunk limb 2 is still. It is in this region that labral gland secretions are discharged. That these are employed even though small particles, for the entangling of which they were probably evolved, are not utilized, suggests that they may have some other function, perhaps lubrication. In their staining and coagulating properties, however, the secretions appear to be the same as those of microphagous species. That such secretions can be employed in the absence of a well developed inner lobe on trunk limb 1 is probably related to the size of the food masses which must be pushed into the exuded material.



Figures 109 to 111. *Pseudochydorus globosus.*

Figure 109. The three outermost endite spines of trunk limb 2 seen from the inside. The spines, here clearly modified for grasping and dragging, are the homologues of what in many species are scrapers or combs.

Figure 110. Horizontal section which slices through the mandibles adjacent to their molar surfaces and shows the posterior hooks which drag food masses between them.

Figure 111. Longitudinal section of the alimentary canal to show the anterior dilatation to form what is at least topographically a stomach.

(viii) *Conclusions*

Pseudochydorus globosus has no place in the genus *Chydorus*. Some similarities, especially the very obvious globular form, are the result of convergent evolution.

Although not at once apparent, *P. globosus* exhibits one of the most divergent suites of characteristics associated with a particular mode of life in the Chydoridae. Specializations are for defence—protection being granted by a greatly thickened sphere of sclerotized cuticle—and for the collection of dead bodies of other animals. The feeding mechanism is therefore very different from that of species which scrape, and often filter, small particles, yet the same elements are employed; this being a striking illustration of the evolutionary potential of the anomopod grade of organization.

XVIII. The structure, habits and feeding mechanism of *Anchistropus emarginatus* Sars, a parasite of *Hydra*

The remarkable habits of *Anchistropus emarginatus*, which lives parasitically on *Hydra*,† were discovered and described by Borg (1935, 1935*a*, 1936) who also gave some account of the feeding mechanism. Prior to this Hyman (1926) had already observed that the N. American *Anchistropus minor* Birge attaches itself to and destroys *Hydra*, though she made no detailed investigations. Many specimens of *A. emarginatus* have recently been available and Borg's findings have been amply confirmed and can be supplemented in certain important respects.

(i) *Structure, with special reference to adaptations for life on* Hydra

The general form of *Anchistropus* is shown in lateral aspect in figure 112. It is rotund, and much resembles *Pseudochydorus globosus* in shape. Ventrally the carapace margins are more or less straight, though each is drawn out into a ventrally directed, spine-like prolongation anteriorly in the region of the embayment (figures 112 to 115, VCT). Although short in length the embayment is extremely wide anteriorly. Posterior to it the margins are straight and provided with no more than a thickened rim (figure 114). Their setation is shown in figures 112 and 114. The setae are stiff and bristle-like. In life they are directed obliquely inwards, and are alternately inclined more and less steeply so that at their tips they effectively form two rows. Each prolongation of the carapace contains what has hitherto been described as a gland of unknown function (figures 112, 113 and 115, CE), but which appears to be simply a cuticular elaboration associated with which I can find no glandular tissue. Its chitinous skeleton has a froth-like appearance. What in lateral view appears to be a duct may in fact be a pair of dividing walls, though there is a suggestion of a terminal pore. Being chitinous, the entire structure is replaced at each moult, and a new structure in process of formation is sometimes to be seen alongside that in use. From its form and location it seems probable that this structure is a rib which gives strength with lightness to the prolongation of the carapace. In *A. minor* the prolongation and adjacent portion of the carapace are hollowed out to form a groove in which the basal portion of the great claw (see below) of the first trunk limb slides. This is certainly not the case in *A. emarginatus* but it seems likely that in both species the prolongation fulfils a purely mechanical function.

The carapace cuticle is relatively thick—up to about 4 μm near the middle of each lobe—and more than twice as thick as in the robust and considerably larger *Alonopsis elongata.*

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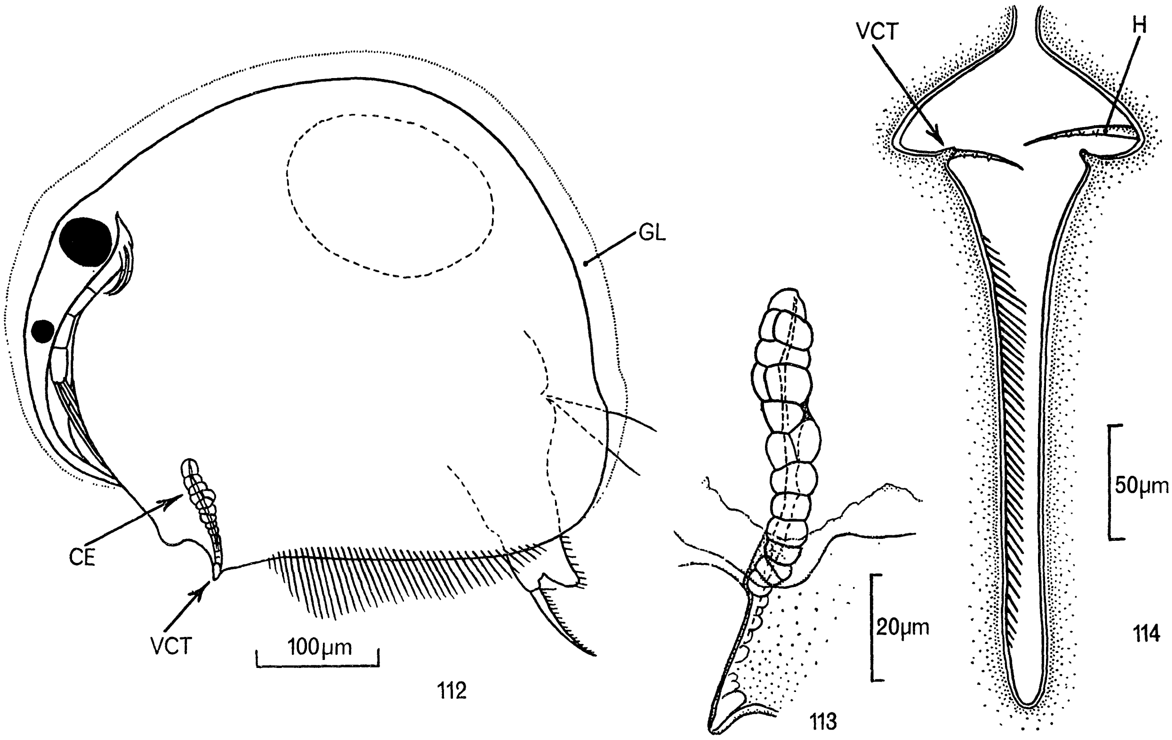
† For convenience the comprehensive generic name *Hydra* is used throughout though, besides living on the brown *Hydra oligactis* and what is probably a second brown species, specimens have been placed on the green *Chlorohydra viridissima* on which they successfully lived.

The cuticle is also well sclerotized, the whole animal being amber-brown in colour, as is *Pseudochydorus globosus*, but is less golden than are adults of that species, and there is a broad almost chocolate, band ventrally which merges gradually with the more amber-coloured dorsal cuticle. Mallory-stained sections reveal an essentially two-layered cuticle, a thin, blue-staining layer being overlain by a thicker amber-coloured, non-staining layer. Brittleness is apparent as in *P. globosus*. Thickening of the cuticle in regions where it is very thin in other species (see below) suggests that the thickening is an adaptation to life on *Hydra* where nematocysts are a hazard, but it may well be that thickening of the carapace and headshield was acquired before parasitic habits.



FIGURES 112 to 114. *Anchistropus emarginatus.*

FIGURE 112. Female seen laterally to show the general form, the chitinous elaboration adjacent to the ventral carapace tooth, and the approximate limits of the hitherto undescribed gelatinous layer.

FIGURE 113. The ventral carapace tooth and the adjacent chitinous elaboration as seen in a longitudinal slice which has cut away the outer cuticle of the carapace in the upper part. Dotted lines indicate chitinous walls visible only by deeper focusing.

FIGURE 114. The ventral aperture of the carapace. Note how the great claws of trunk limb 1 are given freedom of movement by the great widening of the ventral aperture adjacent to them.

There is a further and hitherto undescribed peculiarity of the carapace which is unique within the Anomopoda. Immersion of the living animal in a suspension of indian ink reveals that the carapace is covered externally by a layer of colourless, transparent, gelatinous material, which is stained blue by a very dilute solution of Alcian blue and is therefore presumably a mucin-like substance. The layer can also be observed in individuals settled on a *Hydra* when *Trichodina* is also present. The protozoans from time to time glide over the attached *Anchistropus*. When they do so an apparent gap is revealed between them and the crustacean. The gelatinous material extends over the whole carapace and headshield and attains a maximum thickness of about 20 μm dorsally in an individual about 450 μm in length. Towards the ventral region it thins out and is absent from the ventral margins and from the undersurface of the headshield. Its limits are indicated in figure 112 (GL). While not proven it seems likely that this layer is an adaptation to life on *Hydra*. Borg, who repeatedly watched *Anchistropus* settle on *Hydra*, never saw a nematocyst discharged when this took place, but whether the gelatinous layer prevents their stimulation is not known. That its function is probably not primarily the granting of protection against nematocysts is suggested by the fact that appendages which handle nematocyst-containing tissues are adequately protected by cuticular thickening alone: thickening which is less than that of the carapace and headshield.

Although Borg gave an interesting account of the parasitic habits of *Anchistropus* he did not apparently section the animal and was therefore unaware of its most outstanding adaptations. These consist of thickening and sclerotization of the cuticle of the appendages, labrum and post-abdomen, and of remarkable deepening and armour-plating of the food groove. No comparable modification is found in any other species. Thickening and sclerotization is apparent on the antennules and antennae and on all the trunk limbs. In no case is this more striking than in the distal endite of trunk limb 5 (figure 116, TL5) which, in most species a soft lobe covered with delicate cuticle, is here encased in a thick brown pellicle. In spite of this it is fringed with long setules.

The form and armour-plating of the food groove are shown in figures 116 to 119. Such a food groove is unique within the Anomopoda. The armour plating terminates posteriorly just behind the gnathobasic setae of trunk limb 5 (figure 116, LAP): posterior to this it is not necessary. The great depth of the food groove, particularly in the vicinity of trunk limb 2, is indicated in figures 118 and 119. This is necessary to protect the adjacent limb bases. The cuticle of the base of trunk limb 1 is itself thickened and sclerotized. The food groove cuticle is completely devoid of the long cleaning setules so conspicuous in those species whose gnathobases bear filter plates (e.g. *Eurycercus*—see text-figs. 52 to 55 in Fryer 1963).

In other anomopods the posterior prolongation of the labrum is a fleshy lobe. In *Anchistropus* this lobe is covered by thick sclerotized cuticle on its topographically dorsal surface, i.e. the surface which, with the food groove, makes the anterior tunnel along which food passes to the mandibles. Cuticular thickening extends over the posterior extremity of the labrum and onto its topographically ventral surfaces (figure 116).

The structure of the trunk limbs follows the basic anomopod plan but there are many specializations for attachment to the host and for the collection and manipulation of food. Some of these are evident in figures 115 and 116. Particularly striking is the powerful development of the major distal claw on trunk limb 1 (figures 114, 115, H) which is used for attachment to the host. Although a stout claw is present here in certain other chydorids, and particularly in *Pseudochydorus*, in none is it so well developed as in *Anchistropus* where it has usurped the position usually occupied by three long spines or setae, of which only a rudiment remains. This claw can be swung a great distance laterally, a movement permitted by the great width of the embayment (figure 114). Some of the intrinsic musculature involved in such movements is shown in figure 115. The 'inner lobe' of trunk limb 1 is represented only by a minute seta.

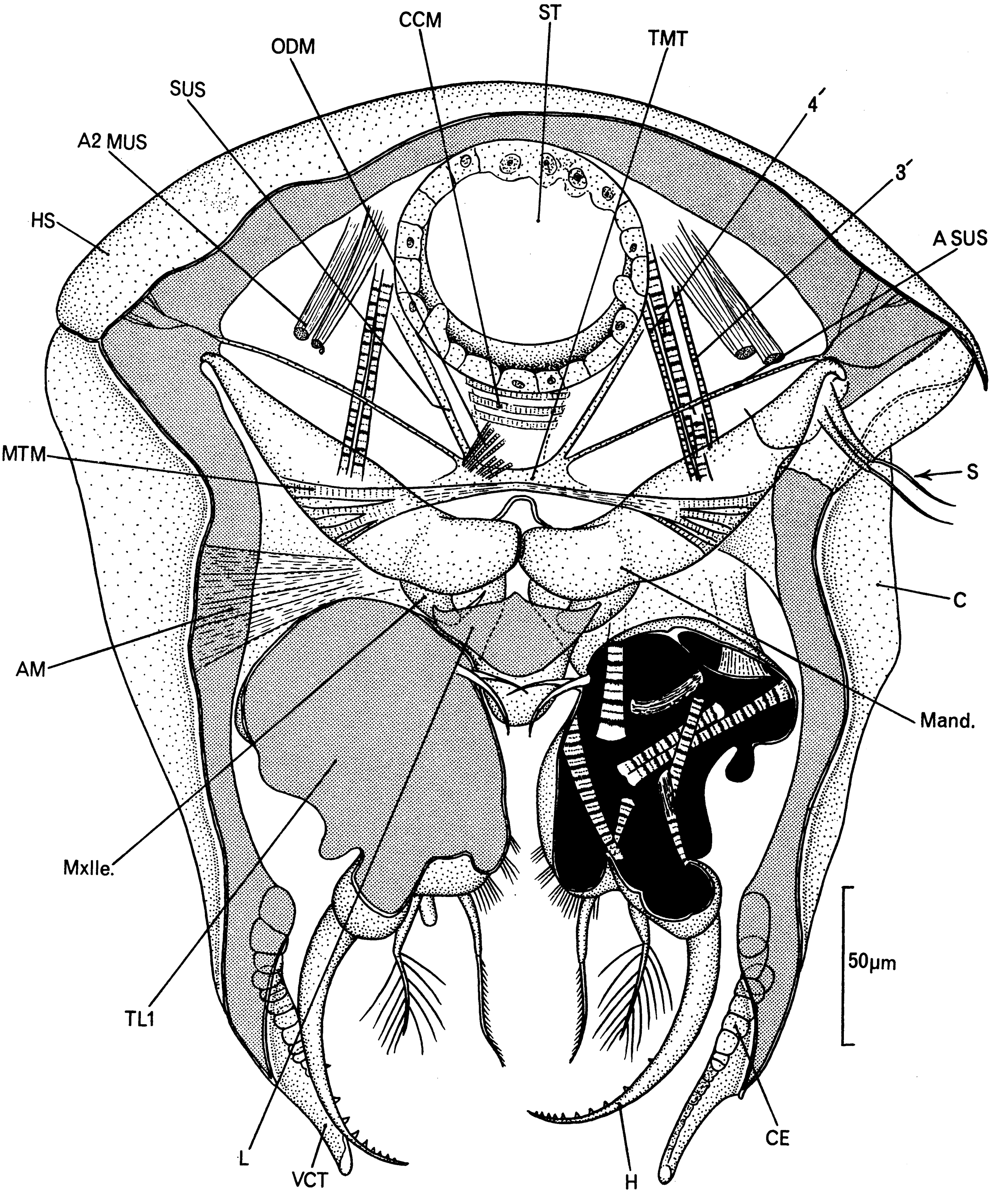
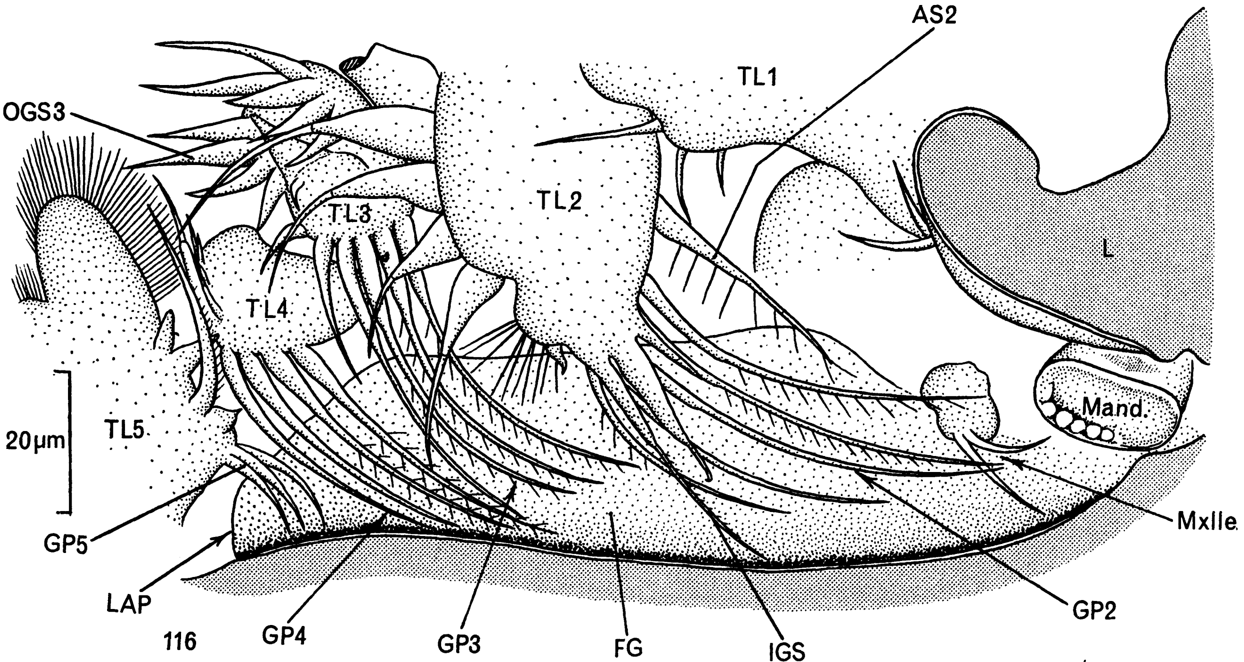
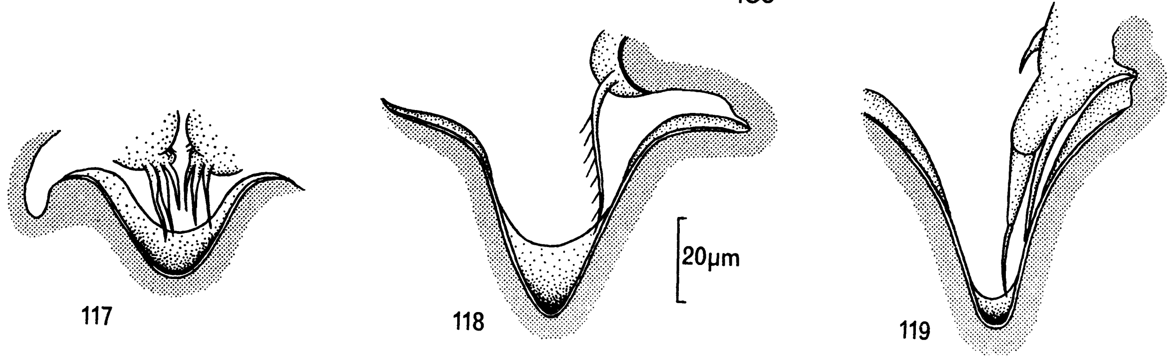


FIGURE 115. *Anchistropus emarginatus*. Transverse section through the mandibular region to show the suspension, articulation and musculature of the mandibles; the arrangement and location of the ventral carapace tooth and the adjacent cuticular elaboration; the massive hook of trunk limb 1, and some of the complex musculature of the same limb. Note the similarities in mandibular musculature between this species and *Pseudochydorus globosus*, especially the slender nature of the major transverse muscles and the small degree of asymmetry which they exhibit, and the absence of the 5c muscles and their associated apodemes. The mandibles are treated as though they were transparent. The apparent anomaly of the remotor roller muscles entering the gut is due to the fact that these incline posteriorly and here the gut narrows.

The gnathobasic region and some of the scrapers of trunk limb 2 are shown in figure 116 (TL2). The scrapers are similar in principle to those of other genera. Each is very finely denticulate and all are basically alike. The gnathobasic plate is represented by a row of spiniform setae (GP2) only five in number and of which some at least bear a single row of widely spaced spinules on the posterior margin. These obviously have a pushing function as have the other elements of the gnathobasic armature, one of whose spines (IGS) reaches to the bottom of the food groove. A robust anterior spine (AS2) is present. Unless this is





FIGURES 116 to 119. *Anchistropus emarginatus.*

FIGURE 116. Median longitudinal section through the basal portion of the trunk limbs to show what in many chydorids is the filter chamber. Note especially the armour-plated food groove whose limits (LAP) are clearly defined; the armour-plating of other structures, which is exemplified by the labrum, here seen in section; the simple endite spines of trunk limb 2 whose structure is suited to dragging, and the anterior spine (AS2) of trunk limb 2. For similarities between this arrangement and that in *Pseudochydorus globosus* compare with figure 103.

FIGURES 117 to 119. Transverse sections through the food groove taken respectively at the level of trunk limb 5, trunk limb 3 and trunk limb 2. These reveal the great depth of the food groove, its armour-plating, and its change in shape from end to end. For clarity only one gnathobasic seta of trunk limb 3 is shown in figure 118.

the homologue of the small hook-like spine present in *Pseudochydorus* (figure 103), it is without counterpart in any other chydorid yet examined. Its presence is directly related to feeding habits. On promotion of the limb (functionally the return stroke) it will sweep down into the food groove any particles, which can include nematocysts, which might otherwise rise above the limits of the armour-plating. As a screen it would be ineffective; as a down-beater of material it cannot fail to be efficient.

Some features of trunk limb 3 are shown in figure 116 (TL3). The gnathobasic plate (GP3) is reduced to five spiniform setae of which only the four anteriormost pass deeply into the food groove. Of these, three at least are similarly armed to their homologues on the limb in front and are obviously specialized for the mechanical movement of material forward along the food groove. There is no outer plate or grid of setae distally.

Trunk limb 4 (figure 116, TL4) is much reduced yet reveals some of the basic elements of this member of the series. The gnathobasic plate (GP4) consists of four well-developed spiniform setae of which the two most anterior at least bear widely spaced spinules anteriorly and posteriorly. These transform at least the anterior region of the gnathobasic plate into a coarse sieve, very different from the fine-meshed filter plate of species which employ true filtration. The only other armature of this limb is a row of vertical setae.

Trunk limb 5 (figure 116, TL5) retains a gnathobasic plate (GP5) of three short spiniform setae.

(ii) *The mandibles*

The general appearance of the mandibles, their articulation, suspension and musclature, are shown in figure 115. Articulation is of type B. Of the musculature the most striking feature is the complete absence of muscles of the 5c series which, in all other species examined save *Pseudochydorus globosus*, take their origin on a large apodeme on the posterior face of each mandible, which here is absent, and unite the mandibles transversely. The major transverse muscles are much reduced in comparison with those of most species and show only slight asymmetry. In this they resemble those of *Pseudochydorus*. Great reduction in muscles of the 5a, b and d series is apparent. Both the promotor and remotor roller muscles are slender.

(iii) *Habits and feeding mechanism*

Although *Anchistropus* can apparently collect certain particles while living freely, it undoubtedly lives by preference on *Hydra*. Particles of detritus have been seen in the alimentary canal of some of the specimens found in field collections. Whether these individuals were living freely when collected or had been dislodged from *Hydra* could not be ascertained. With no other source of food it will live for many days on *Hydra* and produce young which also attach themselves to the coelenterate and feed from the outset on its tissues. Specimens kept without access to *Hydra* never survived for more than a few days, but this may have been due to ignorance of their requirements.

Parasitic habits are not incompatible with efficient swimming, and *Anchistropus* swims rapidly, though usually erratically, so speeds are difficult to estimate. A female 0·43 mm in length and carrying embryos averaged at least 11·6 body lengths (0·5 cm)/s over several runs of at least 7·5 cm and this was certainly an underestimate as no account was taken of wavering. Over 15 cm it maintained a speed of at least 12·5 body lengths (0·53 cm)/s and over 10 cm a speed of about 13 body lengths (0·56 cm)/s.

In spite of these abilities *Anchistropus* has never been seen to leave a hydrid after settling there. As Borg observed, it attaches itself to any part of the body, including the nematocyst-bearing tentacles. Attachment is effected by means of the large hooks of the first trunk limbs which are plunged deeply into the ectoderm of the *Hydra*. When so attached, the ventral surface of the carapace in the embayment region lies against the *Hydra* and the ventral prolongations press against it. Although, as shown in some of Borg's photographs, an attached *Anchistropus* is often tilted forwards, individuals also aline themselves in such a manner that the post-abdomen can reach and push against the host. When thus alined the stout bristle-like setae of the ventral carapace margins inevitably press against the tissues of the *Hydra* and prevent the carapace itself from making contact.

Movements, as Borg described, are accomplished by withdrawing the claw of one of the first trunk limbs, swinging it forward, and plunging it afresh into the *Hydra*. By use of the right and left limb alternately, forward progression is achieved. The wide lateral swing of the claws permits considerable versatility of movement. Although Borg states that movement is achieved exclusively by means of these limbs, occasional pushing by the post-abdomen has been seen. Contact is made by the post-abdominal claws and this perhaps grants stability during movement.

Borg has described how, when food is to be collected by scraping with the second trunk limbs, the ventral surface of *Anchistropus* is drawn close to the *Hydra* by means of the first trunk limbs, the ventral prolongations thereby being pressed into the tissues of the host. The carapace lobes are drawn together and cause an elevation of host ectoderm in the vicinity of the prolongation and which is of easy access to the scrapers of trunk limb 2, which can reach forward for a considerable distance. In an unattached animal they can reach anterior to the ventral prolongations of the carapace.

Borg's observation that the claw of trunk limb 1 is also used for ripping ectodermal tissue from the host has been confirmed and the action has been watched at high magnifications. During this process the carapace prolongations appear to help the animal to maintain balance. Of the chydorids studied, only *Graptoleberis*, *Leydigia* and *Anchistropus* employ the first trunk limbs for food collection. In *Anchistropus* this is obviously a secondary development related to the unusual nature of the food source. With this exception the feeding mechanism is clearly of the basic anomopod type. Food, other than that collected by trunk limb 1, is scratched from the host by the finely denticulate scrapers of trunk limb 2 and pushed towards the food groove by this limb and by trunk limb 3. During this process it is liable to be whisked backwards by powerful currents set up by the exopod pump of trunk limbs 4 and 5 whose rapid beating is characteristic of *A. emarginatus*. Although not truly filtratory, the gnathobasic setae of trunk limbs 3 to 5 form a cage bounded posteriorly by those of trunk limb 5 (figures 116, 117) and laterally by trunk limbs 3 and 4 (figure 116), through which particles down to at least 5 μm in diameter would be unable to pass even if no setules were present. Setules, however, are present on at least some setae (some are difficult to detect even by use of an oil-immersion objective) and enable the cage to retain much smaller particles.

Material collected by the gnathobasic plates is passed mechanically along the food groove by them. The posterior row of setules present on several of these setae of trunk limbs 2 and 3 is well suited for gripping and pushing. As Borg observed, large accumulations of food are transferred forward at the anterior end of the food groove by one or a few movements of trunk limb 2. Both the gnathobasic plate and the rest of the gnathobasic armature are involved in this process, for one spine of the latter (IGS) reaches to the bottom of the food groove. Food can be pushed to the level of the mandibles by trunk limb 2 but assistance is given anteriorly by the maxillule.

(iv) *The origin of parasitic habits in* Anchistropus *and the probable phylogeny of the genus*

Anchistropus is unique among the Anomopoda in its parasitic habits, for which it is highly specialized. The means whereby this habit might have been acquired and the affinities of the genus are indicated by this comparative study.

Sars (1862) noted that at first glance *A. emarginatus* may be mistaken for a juvenile *Pseudochydorus globosus*. Both are very similar in colour, general form, and swimming habits. Besides these apparently superficial similarities, which rest in part on thickening of the cuticle, there are other profound resemblances which are indicative of common ancestry. The similarities, which do no violence to the affinities suggested by Frey (1959, 1967) and Smirnov (1965) on the basis of head-pore arrangement, mandibular articulation, and trunk limb setation, include the following: (See also table 3, p. 374.)

1. Globular form.
2. Thickening and sclerotization of the carapace cuticle.
3. Ventral carapace margins without flange.
4. Long rostrum deflected inwards towards carapace.
5. Rapidly beating exopodite pump.
6. Trunk limb 1 with extremely well developed claw.
7. Inner lobe of trunk limb 1 extremely rudimentary.
8. Non-filtratory feeding mechanism.
9. Gnathobasic plate of trunk limb 2 reduced to five spines, of which the first three are the longest. (Six to eight are present in other chydorids investigated even when, as in *Graptoleberis*, this plate has a pushing function.)
10. Gnathobasic armature of trunk limb 2 (other than the gnathobasic plate) includes a long spine which reaches to bottom of food groove.
11. Gnathobasic plate of trunk limb 3 reduced to five spines. (Seven to nine are present in other chydorids.)
12. Gnathobasic plate of trunk limb 4 reduced to four spines. (Five to nine are present in other chydorids.)
13. Muscles of the 5c series, and their skeletal apodemes, completely lacking from the mandibles. (These features distinguish the two genera from all other investigated anomopods.)
14. Transverse mandibular muscles of the α, β, γ series long and slender and showing only a small degree of asymmetry.
15. Mandibular muscles of the 5a, b and d series feebly developed.
16. The possible homology of the hook-like spine on the anterior face of the gnathobase of trunk limb 2 of *Pseudochydorus* with spine AS 2 of *Anchistropus*.

The similarity in coloration is due in large part to thickening and sclerotization of the carapace cuticle. At least some young individuals of *P. globosus* resemble *A. emarginatus* in this respect even more than do the adults. While adults of *P. globosus* usually have a dark spot in the middle of each carapace lobe, juveniles may have a dark diagonal band across the carapace as does *A. emarginatus*, though this tends to be somewhat black rather than chocolate.

The similarities listed above are not all of equal significance and some may be convergent, or necessary correlates, though care has been taken to avoid the latter save that all the features relating to the gnathobasic armature of the trunk limbs are related to the non-filtratory method of feeding, which, however, merits separate listing. The similarities include shared features which are unique not only within the Anomopoda but, so far as is known, within the Branchiopoda, and indicate phyletic affinity between the two genera. With these two exceptions muscles of the 5c series are present on the mandibles of all Anomopoda, Ctenopoda, Conchostraca, Anostraca and at least young Notostraca investigated (various authors and unpublished observations). Such divergence could have arisen twice but, when other similarities are considered, it seems more likely that the resemblance indicates phyletic affinity.

Such resemblances, and new information on habits, enable the features of the common ancestor and the route to divergence to be reconstructed with some confidence. The ancestor probably had a globular form, a long rostrum, no well marked embayment, and a tendency to close the valves completely, and had begun to specialize in the development of a thick and sclerotized carapace cuticle. In habits it was probably a bottom dweller, able to swim actively, which had begun to develop stout, hooked claws on the first trunk limbs, and had taken to scavenging. In relation to these habits it had reduced the number of elements in the gnathobasic plates of trunk limbs 2, 3 and 4, had developed a long inner spine on the gnathobase of trunk limb 2, and did not indulge in filter feeding. Probably also in connexion with these scavenging habits, though for reasons not fully understood, mandibular specializations, of which the most striking was loss of the 5c muscles, took place. From such a form the derivation of *P. globosus* is easy to envisage. Such a form was also preadapted, by virtue of its protective, thickened carapace, its means of attachment, and its food preferences, to settlement on and removal of food from hydrids. The habit of using the ventral carapace margin for balance was doubtless important here. Subsequent to the acquisition of such habits, specialization would consist largely of great development of the attaching hooks, and concomitant widening of the embayment in their vicinity in order to grant a wide field of action, the development of ventral prolongations on the carapace, and various devices related to protection against nematocysts. It is conceivable that as a parasite of *Hydra*, *Anchistropus* was originally confined to the trunk, and that the ability to frequent the tentacles was acquired later as protection of appendages and food groove against nematocysts was gradually evolved.

Keilhack (1907) drew attention to certain peculiarities of the ephippium of *Anchistropus* and argued that these are older than the elaborations of the ventral carapace margins, and that the latter are comprehensible in the light of ephippial structure. The habits of *Anchistropus* were then unknown and it is now apparent that the argument must be reversed: certain pecularities of the ephippium are the result of accommodation to specialized developments of the carapace.

Although I have not seen an ephippial female of *Anchistropus* (nor had Keilhack who described only the moulted ephippium) I believe that at least one of the peculiarities to which he refers is probably erroneous. According to him the ephippium is unique in that its dorsal margin is not formed from the existing carapace margin but along a special cleavage line. In moulted cuticles of parthenogenetic females the ecdysial line is inclined very steeply backwards so that the split lies almost parallel to the ventral margin—unlike Keilhack's outline of the female but like his figure of the ephippium—and meets the dorsal margin in a very posterior position just as it does in other globular species. This probably constitutes the dorsal margin of the ephippium as it does in *Chydorus sphaericus* (Scourfield 1902, fig. 33) and *Pseudochydorus globosus* (Gurney 1905, fig. 4).

(v) *Conclusions*

A. emarginatus shows many adaptations to life on *Hydra*, especially in the thickening and sclerotization of the cuticle of the carapace, headshield, limbs and labrum, and in its unique armour-plated food groove, as well as in carapace modifications and limb structure.

Phyletic affinity with *Pseudochydorus* is clear, and the two may have had a common proximate ancestor. The habits of these genera have more in common than has either with any other chydorid, and they share many anatomical characteristics, including one, the absence of the 5c muscles of the mandibles and their associated apodemes, which is unique, not only within the Chydoridae but within the Branchiopoda.

XIX. The genus *Chydorus* and the exploitation of globular form

Members of this genus (in which the animal for long called *C. globosus* has no place) are essentially globular or spherical in form, e.g. see figures 120 and 121. That such a body form is successful is indicated by the richness in species of this genus and by the adaptability of *C. sphaericus* (O. F. Müller) which occurs, often abundantly, in a variety of habitats in almost all parts of the world, and in many areas is not only the commonest chydorid but the commonest anomopod. That the success of this body form is not related directly to swimming abilities is shown by a comparison of *C. sphaericus* and *C. piger* Sars. Although the two are similar in size, the former moves actively when necessary, though seldom for more than a short distance, while the latter is slow-moving and 'lumbering' in habits.

While bilateral compression permits penetration between cracks, e.g. gaps in vegetation, small animals can enter small spaces by virtue of size alone irrespective of shape. Members of the genus *Chydorus* are usually less than 0·7 mm in length. Furthermore, for a given height and the same embayment width, a globular animal is just as stable as is one which is bilaterally compressed when both are crawling over surfaces in the typical chydorid manner. The globular form, however, lends itself better to an increase both in embayment width and in the width of the ventral flange, both of which contribute to stability, and in *C. sphaericus* compensate for the lack of a flattened ventral region. Chydorids by no means always move over level surfaces; stability is particularly important when the animal is inclined. As the habits of *C. piger* reveal, a globular form is suitable also for movement through mud and detritus, under which conditions the ventral carapace margins are not used for balance and are free to specialize in other ways. At present our ignorance of the hydrodynamics of very small moving bodies makes it pointless to compare swimming and crawling efficiencies even in animals as different in form as *Chydorus sphaericus* and *Acroperus harpae*, but these problems call for attention.

A globular form affords better protection against certain predators (those too small to engulf the whole animal) than does bilateral compression because a sphere is well suited to withstand compression stresses; a flattened object is more easily squashed. An adult *Macrocyclops fuscus* has been watched by Mr W. J. P. Smyly struggling for more than 30 min with a specimen of *C. sphaericus* which it seemed unable to devour. He also supplied a hungry stage 5 copepodid of this copepod with a specimen of *C. sphaericus* which was immediately seized. This I was able to see. After 1 h the copepod still gripped its prey with its maxillules and maxillipeds but the *Chydorus*, whose carapace was closed, was still alive and apparently undamaged. Only after more than 2 h did the copepod succeed in forcing open the carapace and devouring its contents. The carapace itself was not ingested. Attacked by a smaller or less persistent predator, protection may have been complete. The teeth developed on the labral keel of certain species, most notably *C. barroisi* (Richard), and which protrude beyond the limits of the carapace, may also be concerned with protection, as probably is the posterior ventral spinule of each carapace lobe of this species.

For some reason globular form seems to lend itself better to 'ornamentation'—whose function in some cases is almost certainly to grant strength with lightness—than does bilateral flattening. This is most strikingly shown by the elaborate development of deep polygonal cells, or of cells and ridges, on the carapace of the N. American *C. faviformis* Birge and *C. bicornutus* Doolittle respectively, but other elaborations exist; e.g. in *C. pubescens* Sars (which I have seen, but not reported, in tropical Africa) the carapace is covered with tiny spinules which give the entire animal a hedgehog-like appearance and are possibly protective.

(i) *The habits and abilities of* Chydorus sphaericus

Although this is the commonest chydorid, relatively little of real ecological value has been recorded, though its ability to tolerate a very wide range of conditions is well known. To this, physiological adaptations contribute as well as structural features. Thus Bogatova (1962) found that of six chydorids tested (all of different genera) *C. sphaericus* was much the most tolerant of low concentrations of dissolved oxygen. The lethal concentration at 19 to 21 °C was as low as 0·36 mg/l., or *ca.* 3 % saturation, and less than a third of that lethal to *Peracantha truncata*, *Acroperus harpae* and *Alona affinis* (0·93 to 1·04 mg/l. or *ca.* 10 to 11 % saturation) and a good deal lower than that lethal to *Camptocercus rectirostris* (1·4 mg/l. or *ca.* 15 % saturation) and *Eurycercus lamellatus* (1·69 mg/l. or *ca.* 18 % saturation). While less tolerant of high temperatures than *Alona affinis* (lethal temperature 40·5 °C), *C. sphaericus* (lethal temperature 38·0 °C) can also tolerate higher temperatures than certain other chydorids (Bogatova 1962) and the possibility that physiological races adapted to higher temperatures occur in the tropics should not be overlooked. Lowndes (1952) found it in waters whose pH ranged from 3·4 to 9·2 which, shared by *P. truncata* was the widest range demonstrated for any chydorid and, shared by *Scapholeberis mucronata*, for any anomopod. Later Bogatova (1962) showed that it and *P. truncata* can tolerate a pH of 10·6, and Leloup (1956) recorded it from pools with a pH as low as 3·2.

When a collection of this species is observed in a clean vessel one's immediate impression is of restlessness and almost incessant activity. Such an impression is completely misleading. Conditions are such that normal behaviour is impossible. If, by contrast, *C. sphaericus* is kept in a vessel with even sparse detritus on the bottom and is not disturbed by a bright light, it spends most of its time attached to objects as Franke (1925) observed. Like many chydorids it rests with the ventral carapace margins against a solid surface—though there is no flat ventral region comparable with that of, for example, *Alonella exigua* (see below). Under such circumstances an individual was watched for about 30 min, during which it moved very little and spent most of the time stationary on the bottom, feeding at times. Its habit was to remain stationary for many minutes, then move only once or twice its own length and pause again.

C. sphaericus cannot simply rest on the ventral carapace margins as can the globose, but not spherical, *Alonella exigua*, and depends to a considerable extent on the claws of the first trunk limbs for attachment. It is, however, sufficiently adept to have dispensed with the use of the antennae as balancers and these are folded inside the carapace, as is essential if the protection granted by the spherical form is to be exploited to maximum advantage.

The importance of the claws, and the need for particular conditions, are clearly shown by the following observations. Specimens placed in a clean watch-glass frequently lay on their sides. A few days later, however, the same specimens in the same dish were behaving normally and utilizing the ventral carapace margins; the reason being that a carpet of bacteria had developed on the glass and to this they were able to cling. That they gripped this flimsy carpet was clearly shown by the irregular movement of particles of detritus some way from the animal and which lay on the slime carpet. Although the animals wobbled somewhat as the grip was obviously insecure, they could maintain balance.

To roughened surfaces *C. sphaericus* is extremely adept at clinging. To some flattened leaves at least it is able to cling so effectively that it can clamber on their under surfaces. This feat is accomplished by other means and with greater efficiency by *Alonella exigua*, but certainly not by many species, and is probably of considerable ecological importance. Smyly's numerical data (1957) indicate, however, that *C. sphaericus* is not proficient at colonizing the under surface of the floating leaves of *Potamogeton* which are frequented by *A. exigua*.

When crawling on a flat surface *C. sphaericus* balances on the curved ventral carapace margins and at the point where the ventral gape is widest (section ii). This is the best point for balance, though the area of contact is very small and is in fact the point at which the ventral flange is narrowest (section ii). When it crawls along the edge of a leaf *C. sphaericus* takes it between the carapace lobes and the claws of the first trunk limbs grip its upper and lower surfaces. It often feeds in this position. It can also hang inverted beneath a dirty surface film, i.e. a film strengthened by a raft of bacteria.

C. sphaericus has to a large extent reconciled the conflicting demands made by a spherical form, which grants protection, and by the ventral carapace margins when used as an adjunct to locomotion. While less specialized than, for example, *Peracantha* or *Alonella exigua* in its use of the ventral margins, it is an adequate performer in this respect and enjoys advantages not shared by these species. In comparison with species such as *Alonopsis elongata* and *Acroperus harpae* it is both better protected (though *Alonopsis* perhaps gains protection in a different way) and more adept at creeping over surfaces, and, on a length for length basis, is at least as competent a swimmer (see below).

Although this species occurs particularly in small bodies of water or in the littoral zone of lakes it is not infrequently reported from the plankton. Its structure and adaptations, however, are not those of a planktonic animal, and to regard it as such is misleading. The explanation of its occurrence in open water was given by Scourfield as long ago as 1898. This species frequently takes an algal filament between its carapace lobes and clambers along it (e.g. see Franke 1925) and, as Scourfield pointed out, 'the chief condition necessary for this pelagic habit seems to be the presence in the water of such algae as *Clathrocystis*, to the comparatively large colonies of which it no doubt clings'. Wesenberg-Lund (1908) also reported finding colonies of the blue-green alga *Anabaena flos aquae* which supported three or four individuals of *C. sphaericus* and suggested that this is the reason why this species 'occurs pelagically in Cyanophyceae lakes', a suggestion reiterated in 1939. Records from as far back as Apstein (1896) and Birge (1897) indicate that the occurrence of *C. sphaericus* in open water usually coincides with a bloom of blue-green algae, and Birge drew attention to the correlation and correctly expressed the opinion that this species is 'not properly a limnetic form'. He believed, however, that the blue-green algae were used directly as food, which is probably incorrect. The functional morphology and habits of this species are fully in keeping with Scourfield's neglected suggestion. I do not believe that its occurrence in the plankton is directly related to the optical properties of water under different conditions as recently suggested (Hutchinson 1967). Although not equipped for a pelagic way of life, *C. sphaericus* swims well when necessary, but can seldom be induced to do so for more than a short distance. The fastest speed recorded for a female 0·38 mm in length was 0·56 cm (14·7 body lengths)/s, over a distance of 4·5 cm.

The gut contents of specimens examined consisted for the most part of very fine particles of both organic and inorganic origin, but larger particles are sometimes ingested, and occasional diatoms and one large lump of unidentified material were seen. Franke (1925) noted that the most frequently ingested diatoms were those, such as *Gomphonema* and *Cymbella*, which grow on gelatinous stalks.

(ii) *The anatomy and feeding habits of* Chydorus sphaericus

The general shape is shown in figures 120 and 121. Of these figure 120, which is based on a photograph taken from directly above a living animal, is particularly informative as it reveals the correct orientation of a creeping and feeding individual. From this aspect the orientation of the sensory setae of the antennal coxae and of the post-abdomen is apparent and their function can be readily appreciated.

Figures 120 to 125. *Chydorus sphaericus.*

Figure 120. Adult female seen from directly above as it rests on a horizontal surface.

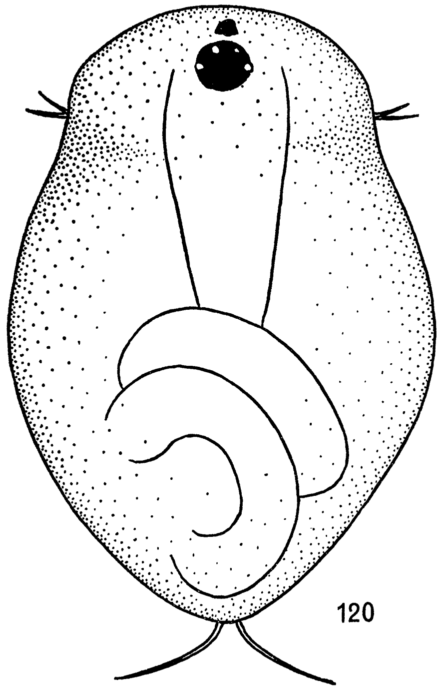
Figure 121. Outline of the same seen from the side, showing the general form of the body and its orientation in life with respect to a horizontal surface. Note the absence of any flattened ventral region.

Figure 122. The ventral carapace margins from below as seen in life. Note the seta-free region of the ventral flange.

Figure 123. Transverse section through the ventral carapace margins in the region which makes contact with the substratum. Slight distortion during processing of the specimen is probable but the relationship of the flat faces of the ventral flange to the substratum is clearly apparent.

Figure 124. Transverse section through the ventral carapace margin posterior to the region of contact.

Figure 125. The claws of trunk limb 1.



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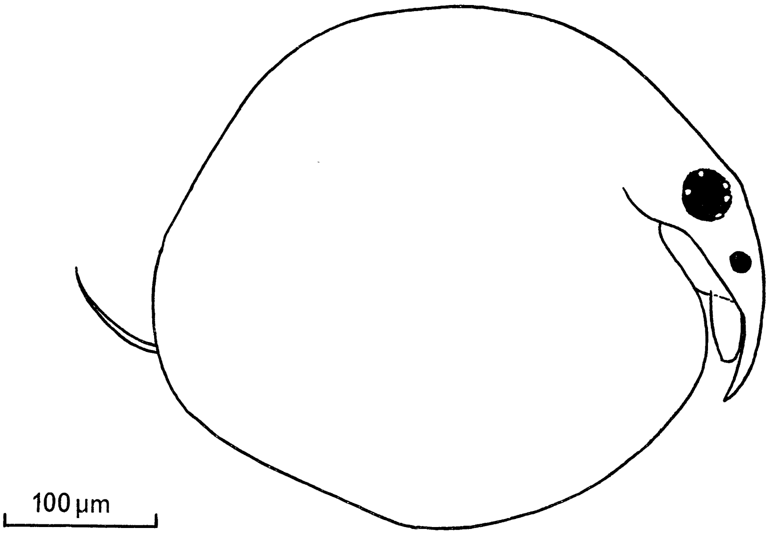

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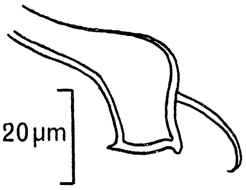

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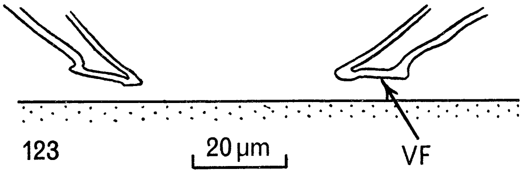

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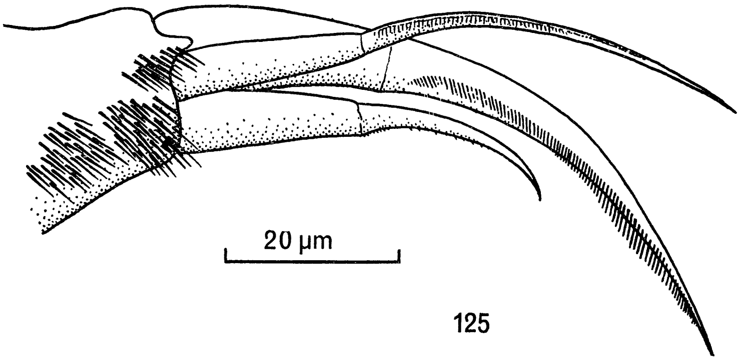

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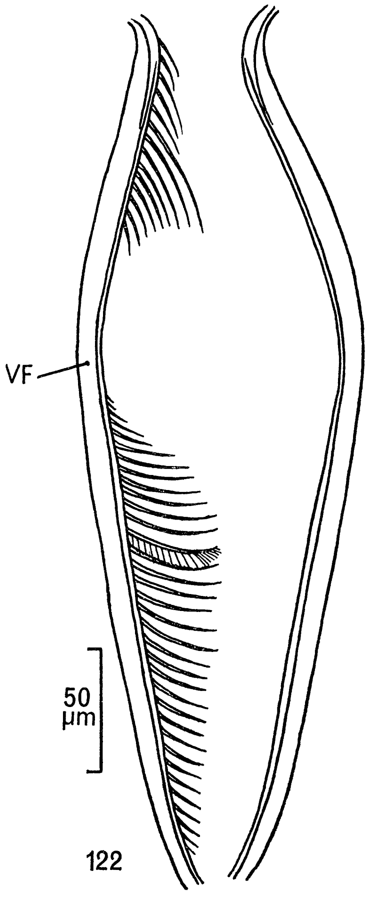


122

FIGURES 120 to 125. For legend see facing page.

As shown by Bravo (1918) body form may vary at different seasons. Likewise, as Flössner (1962 *a, b*) has shown for certain other species of the genus, *C. sphaericus* is somewhat variable in form even within a single population. This applies not only to height in relation to length but also to width, though even the least wide individuals are rotund. The ventral carapace margins are shown in figures 122 and 136. Points of note are the presence of a flange (VF) over the whole of the ventral margin, the wide ventral gape, which is in effect all embayment, and the absence of setae from the margins where the gape is widest. The posterior setae arise inside the rim of the carapace in a manner similar to those of *Pseudochydorus globosus*. Their arrangement and armature is shown in figure 136 from which (inset) it can be seen that the basic arrangement of setules is followed. The length of setae of the anterior series is difficult to ascertain, but is drawn as accurately as their resolution would permit. Although the widest point of the ventral aperture lies anterior to the mid-point of the carapace it is located at the mid-point of a whole animal orientated as in figure 121, and is therefore the point of natural balance. That region of the flange on which the animal rests is shown in transverse section in figure 123. The carapace margins can be drawn much closer together than is shown in this figure but the ventral gap cannot be completely closed.

To the inside of the anterior flange is another flange, the accessory anterior flange (figure 136, AAF) which, whatever may be any other undiscovered function, will help to resist compression exerted on the carapace either dorso-ventrally or bilaterally.

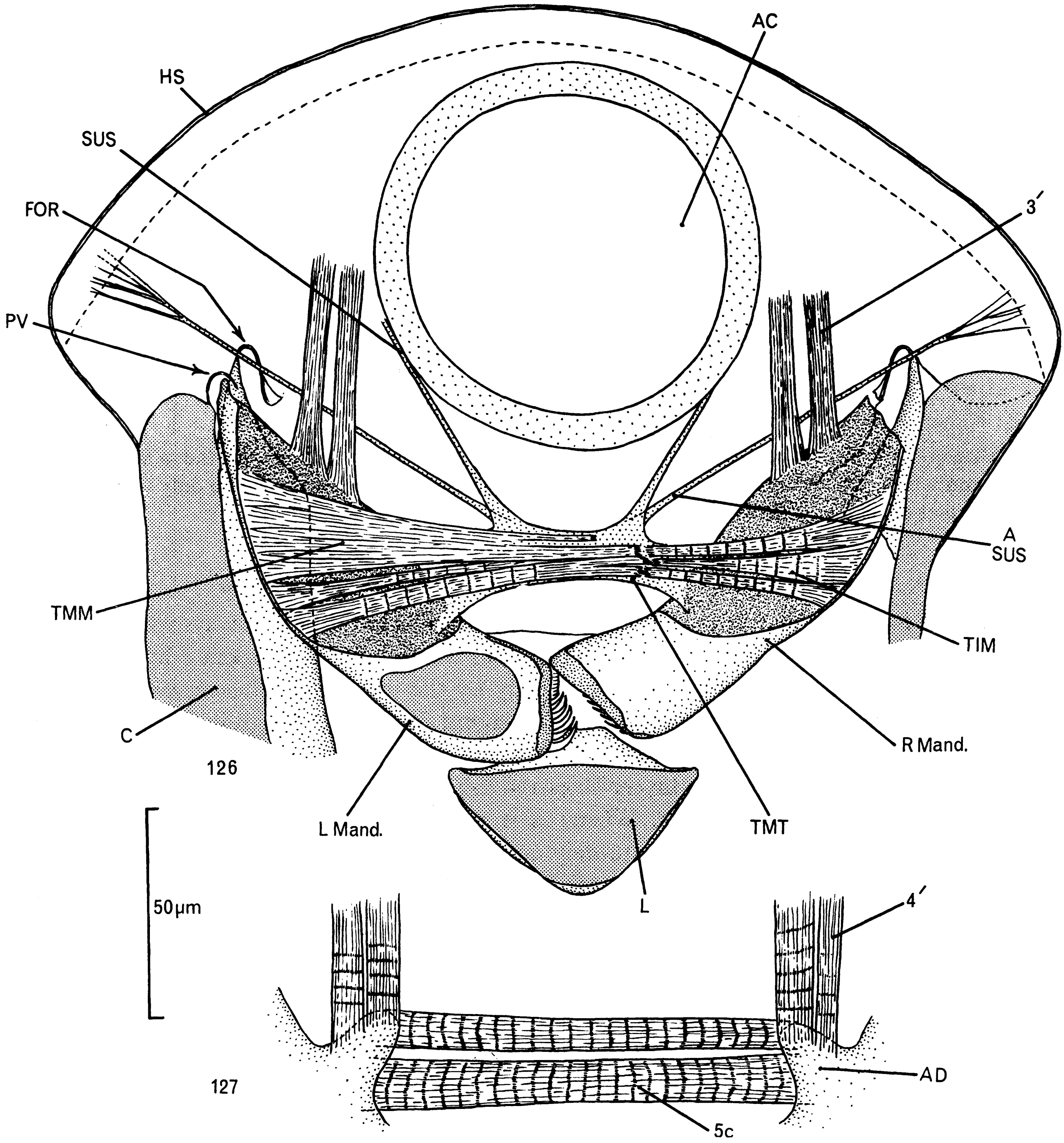
For comparison with *C. piger* it may be noted that both the exopod and endopod of the antenna bear distally a minute spinule.

Figure 125 shows the distal claws of trunk limb 1, whose importance and activities were noted by Franke (1925). In considering their effectiveness their minute size has to be appreciated: in an adult female the largest is only about 80 μm in length. The tips of the two stoutest, which bear the major load, are extremely finely pointed and it is these which can grip minute irregularities. When an object can be partially embraced the fine denticulations of the largest spine must greatly increase its effectiveness.

The filter chamber is sufficiently similar to that of *Peracantha* (figure 47) to render a description unnecessary, but one point is noteworthy. While the large filtering surface presented by the gnathobasic filter plates of trunk limbs 2 and 3 is just as conspicuous in *C. sphaericus* as in *Peracantha*, the filter chamber has been foreshortened by a change in orientation of trunk limb 4 whose gnathobase has swivelled so as to bring the posterior end towards the mid-line.

As might be expected from the minute size of some of the particles found in the gut, feeding involves vigorous scraping (or sweeping) of surfaces—including surfaces to which very small amounts of material appear to be attached. For example individuals vigorously swept fragments of lettuce leaves on whose surface no more than micro-organisms could have developed. When so engaged *C. sphaericus* may whisk its second trunk limbs vigorously over a surface for minutes on end with only brief intermittent pauses. Reasons why the involved and incomplete description of the feeding mechanism given by Franke (1925) cannot be accepted as completely correct have been given elsewhere (Fryer 1963).

The mandibles are shown in transverse section in figures 126 and 127 which serve to illustrate typical chydorid mandibular musculature (which contrasts markedly with that



FIGURES 126, 127. *Chydorus sphaericus.*

FIGURE 126. Transverse section through the mandibular region, seen from *behind*. The posterior face of the mandibles, their apodemes, remotor roller, and 5c muscles have been sliced away (see figure 127), and this permits easy comparison with *Pseudochydorus* (figure 104) and *Anchistropus* (figure 115)—but note that these are seen from in front. On each side the point of union between the headshield and carapace (fornix) is seen just internal, and anterior, to the point of articulation of the mandible, and at first glance looks deceptively like a point of articulation. Note the massive nature of the transverse muscles (not here individually labelled), their great asymmetry (cf. *Pseudochydorus* and *Anchistropus*) and the related skeletal asymmetry of the masticatory region of the mandibles. Because the mandibles are seen from behind, the short muscles of the 5a, b and d series (see figure 128) tend to be obscured.

FIGURE 127. The same a little further back to show the mandibular apodemes, the 5c muscles (cf. *Pseudochydorus* and *Anchistropus*) and the powerful remotor roller muscles. If this figure be superimposed on figure 126 the whole complex of major muscles is represented.

of *Pseudochydorus* and *Anchistropus*), articulation of type B, and typical double suspension. *C. sphaericus* also exhibits extreme asymmetry of the transverse mandibular muscles (figure 128). In *Pseudochydorus* and *Anchistropus* the degree of asymmetry is slight.

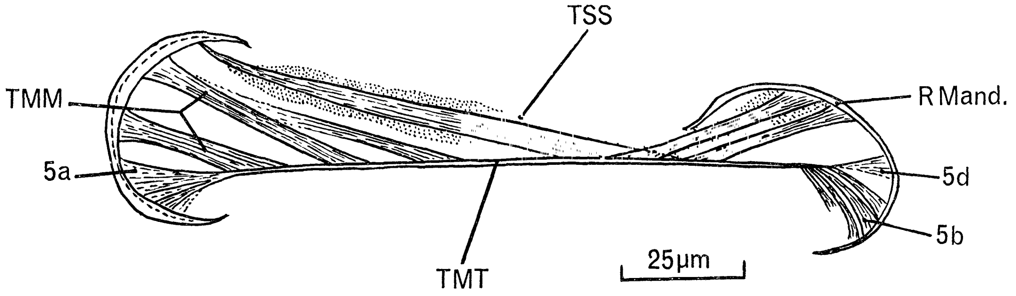


FIGURE 128. *Chydorus sphaericus*. Horizontal section through the mandibles from the ventral aspect and a little ventral to the 5c muscles. The thick sarcoplasmic sheath shown on only two muscles in fact envelops all those of the major series.

(iii) Chydorus ovalis *Kurz: a case of incipient specialization*

C. ovalis is very similar to *C. sphaericus* in many respects but differs in ways which, while apparently trivial, point the way to specializations which have been taken a little further in *C. piger* and are shown even more strikingly by the unrelated *Pseudochydorus globosus*. To the latter it bears a certain amount of convergent similarity, though it differs in many fundamental respects both in structure and habits.

C. ovalis is somewhat golden, brownish or reddish in colour: *C. sphaericus* is usually very light brown, greyish or greenish. When, as is sometimes the case, these species occur together, they can be separated accurately on the basis of colour even at low magnifications. This difference reflects a difference in the cuticle of the carapace and headshield, which in *C. ovalis* is sclerotized and slightly thickened. This confers different physical properties: the carapace of *C. ovalis* tends to crack under pressure, that of *C. sphaericus* to crumple. Sclerotization is apparent also in the cuticle of the antennae and distal portion of the post-abdomen.

C. ovalis has thus gone some way towards exploiting one potentiality of globular form by strengthening the cuticle. As a defence mechanism sclerotization may confer great advantages. This species is also more nearly able to close the ventral aperture of its carapace than is *C. sphaericus*. The ventral margins can be drawn together over most of their length though narrow gaps are left anteriorly and posteriorly. There is, however, no median gap. Protection is also given by a more elongate and pointed rostrum than that of *C. sphaericus* and which more nearly fills the anterior wedge-shaped gap between the carapace lobes (cf. *Pseudochydorus*). Its tip is sliced off in figure 129. Frey (1959), to whom only two specimens were available, says that the rostrum was about the same length as that of *C. sphaericus*. In my material it is definitely longer and has a marginal rim of thickened chitin as has *C. sphaericus*.

An increase in size is probably advantageous in exploiting a mechanism of this sort and adult females of *C. ovalis*, which attain a length of about 0·65 mm, are some 12 % or more longer, and therefore considerably more bulky, than those of *C. sphaericus*, of which indeed a dwarf form of uncertain genetic standing, the so-called variety *leonardi*, also exists.

The ventral carapace margins resemble those of *C. sphaericus* though the flange is narrower, particularly posteriorly, and the armature of setae differs. The setae are more numerous than those of *C. sphaericus* and are present along the whole length of each margin (figure 137), i.e. there is no median seta-free region as in *C. sphaericus*. Although not easy to observe in an intact animal this provides a useful and unambiguous taxonomic character. The arrangement of the posterior setae is shown in figure 137 and their armature of setules in the inset. In this they exhibit a definite specialization. Each seta is armed with two rows of setules of which the posterior consists of a few widely spread spinule-like structures. The anterior setules, however (the homologues of those on which, for example, *Peracantha* rests) are numerous, elongate and close-set, and extend beyond, and pass to the inside of, the seta next in front. Because of this the whole series forms a close-meshed mat of setules which meets its fellow of the opposite lobe when the carapace is closed. The function of this is not known, but one suspects that it is in some way related to the firm closure of the carapace. An accessory anterior flange is present as in *C. sphaericus* and is similar in form but appears to be somewhat sclerotized (figure 137, AAF).

In many other aspects of its anatomy *C. ovalis* is very similar to *C. sphaericus*. In the presence of only a very short spinule on the distal segment of both the exopod and endopod of the antenna it differs markedly from *C. piger*.

The spines comprising the armature of the outer lobe of trunk limb 1 are less robust than in *C. sphaericus* (figure 125) but not so slender as those of *C. piger* (figure 133) and the denticles which fringe the two longest are coarser than those of *C. piger*. Although gripping by means of these spines is possible, one suspects that the grip is less efficient than in *C. sphaericus*, but this has not been tested.

C. ovalis appears to be similar in general habits to *C. sphaericus* and to behave in a similar manner, but I have the impression that it makes more use of its post-abdomen for pushing. It is much less common than *C. sphaericus* and occurs in a narrower spectrum of habitats. Several writers indicate that it is found usually in small bodies of water and apparently not infrequently in those of a temporary nature. I have found it commonly in very small water-filled hollows in the mid-Pennines, which were sometimes peaty and in which *Sphagnum* was often present, but never in the more intensively searched and extremely acid waters of the southern Pennines, and have found it also in a small tarn in the Lake District and in a similar tarn in south-west Ireland. Scourfield (1895) and Galliford (1953) record it from bogs in North Wales. In all these situations the water is probably acidic. In the Lake District tarn it co-exists with *C. sphaericus* both among flocculent bottom material and among marginal mosses and grasses, but in the water-filled hollows either it or *C. sphaericus* were always found alone. It is possibly to some extent a fugitive species in the sense defined by Hutchinson (1951).

Like *C. sphaericus*, *C. ovalis* can seldom be persuaded to swim in a straight course for long distances. A female with no eggs in the brood chamber, and 0·52 mm in length, however, covered 7·8 cm in 14·5 s, i.e. at about 0·52 cm (nearly 10 body lengths)/s. Over short distances much faster speeds can be achieved. A female 0·49 mm in length with no eggs in the brood chamber covered 2·5 cm in 3·0 s, i.e. at over 8·3 mm (17 body lengths)/s.

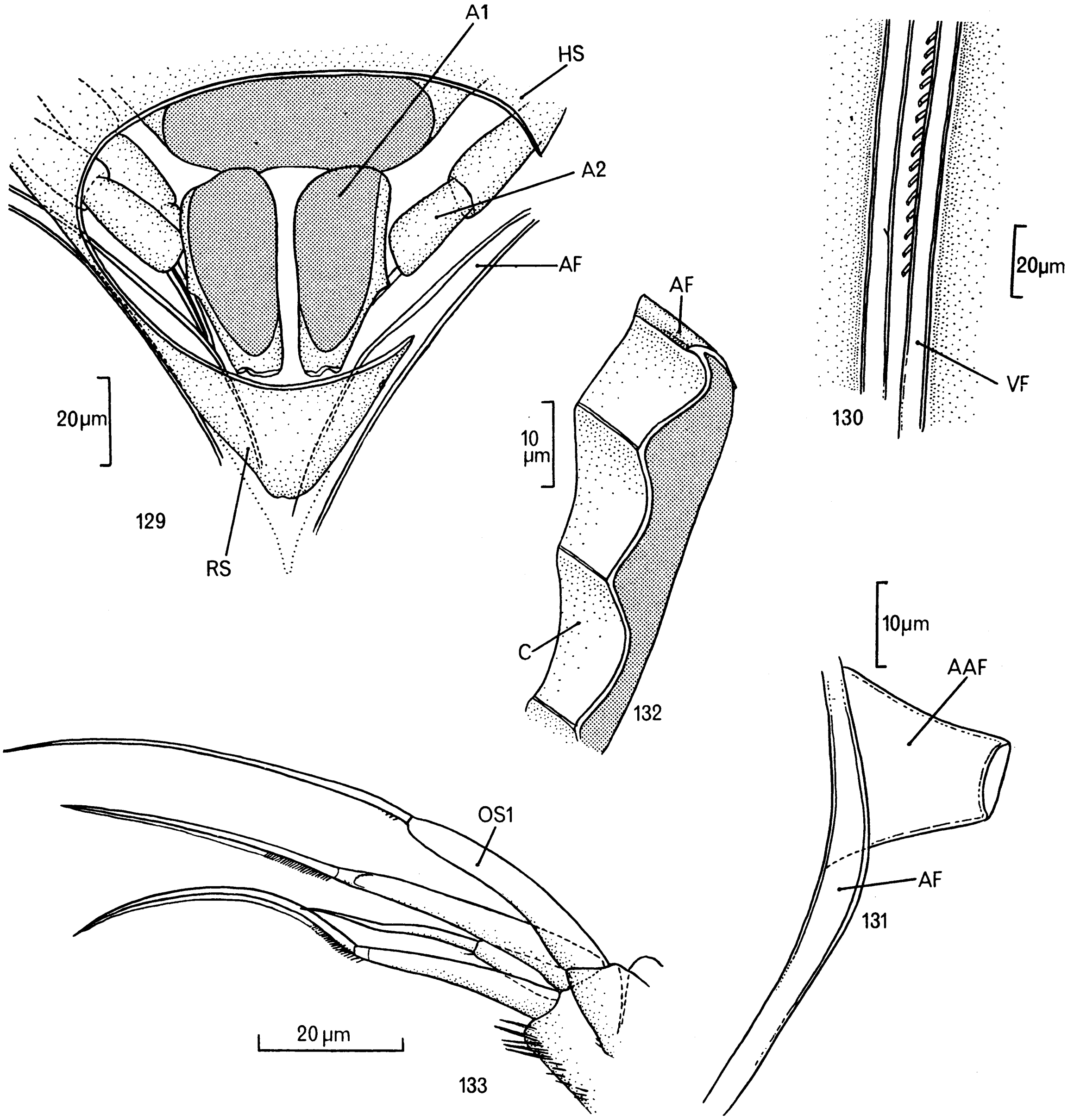
(iv) Chydorus piger *Sars: an example of dual specialization*

While *C. sphaericus* is almost ubiquitous, *C. piger* has exploited a basically similar organization for a more restricted way of life, and exhibits specializations which would be a liability to *C. sphaericus*. Like *C. ovalis* this species is golden amber in colour, and for the same reason: the carapace and headshield cuticle is sclerotized and somewhat thickened, though considerably less so than in *Pseudochydorus* and *Anchistropus*. As a concomitant specialization it is able more perfectly to close the ventral carapace aperture than is *C. sphaericus* or even *C. ovalis*. These specializations lend themselves more to a bottom-dwelling way of life than for clambering over plants or swimming, and *C. piger* is specialized for a benthic existence. This has been appreciated by various workers, e.g. Flössner (1964) who includes it among the true benthic species. It occurs both on hard and soft bottoms, though it almost certainly requires a thin layer of soft detritus on hard bottoms, as when it occurs on mud-covered stones (Fryer 1953), and it frequents both the littoral zone, where I have found it in only a few centimetres of water, and soft muddy bottoms down to depths of at least 24 m. (Information from W. J. P. Smyly.)

Although he recognized it as a member of the benthic community, Moore (1939) stated that it 'has no outstanding modifications for life on the bottom', but this is not so. In its locomotion and in several structural features it shows well-marked adaptations for a benthic existence. As its name suggests, *C. piger* is a slow-moving animal: by comparison with *C. sphaericus* and *C. ovalis* which dash wildly when disturbed, it is slow and lumbering. It moves over the bottom and through mud by swimming-type movements of the antennae which show striking modifications for this way of life, and by frequent pushing movements of the post-abdomen. In its mode of progression over surfaces it differs markedly from *C. sphaericus* and *C. ovalis* in which the first trunk limbs and not the antennae are of prime importance. The antennae are folded inside the carapace chamber when these species are crawling. *C. piger* can perform this feat, but only as part of its defence mechanism and not during locomotion.

The antennae are specialized as much for progression over surfaces and for pushing through mud as for swimming. They are shorter and stouter than those of *C. sphaericus* and *C. ovalis* and each ramus is armed distally with a long stout spine and not, as in these species, by a minute spinule (figures 134 and 135). Short appendages pushing with the tip can exert a greater force at the tip than longer appendages moved by muscles of the same cross-sectional area and with the same angle of swing. When, as in *C. sphaericus*, swimming is important, it is advantageous to have antennae as long as is compatible with other requirements, such as stowage when crawling. As in all chydorids, whose basic features are not those of swimming animals, rapid antennal beat is however still necessary. In *C. piger* the antennae are specialized for other purposes, shorter rami are more suitable, and the bulk saved by shortness is utilized to increase the diameter, and therefore strength, of the shorter segments.

The swimming setae are also used for giving purchase at times, and it is probably because they have such a function, which demands a robust basal segment, that one of the terminal setae of the endopod has been lost (figure 135). In *C. sphaericus* and *C. ovalis* three terminal setae are present on this ramus, one of which is shorter than the other two.



FIGURES 129 to 133. *Chydorus ovalis* and *Chydorus piger*.

FIGURE 129. *C. ovalis*. Transverse section through the anterior part of the head which has sliced away sufficient of the headshield to reveal the anterior flange of the carapace which, in life, it obscures. The tip of the rostrum, which has been sliced away by the posteriormost knife-cut, is indicated by a dotted line.

FIGURE 130. *C. piger*. Part of the ventral carapace margins as seen in a horizontal section of an almost closed individual. This is from the posterior end of the carapace but the arrangement is similar over the entire ventral region. The ventral flange (VF) is here really a thickened rim.

FIGURE 131. *C. piger*. Transverse section revealing the arrangement of the accessory anterior flange to the anterior carapace margin.

FIGURE 132. *C. piger*. Horizontal section showing the anterior carapace margin (anterior flange) and the corrugations and ribs of the cuticle. The thickness of the cuticle cannot be assessed accurately from the figure as it is cut obliquely.

FIGURE 133. *C. piger*. The equivalent of the claws of *C. sphaericus* and also the outermost seta.

Such a short seta would be of little use in pushing and has been lost in *C. piger*. The space at the point of insertion made available as a result has been utilized by an increase in girth of the two remaining setae which, like the two anterior terminal setae of the exopod, are armed with spinules such as are not found in *C. sphaericus* and *C. ovalis* and which must greatly improve the efficiency of purchase (figures 134, 135).

In his figure of the antenna of *C. piger*, Lilljeborg (1900) shows three (not two) terminal setae on the endopod and also a non-existent seta on the basal segment. This has caused confusion and led Meuche (1937), who observed the arrangement correctly, to erect a new species, *C. thienemanni*, which was later even transferred to a new genus, *Paralona*, by Šrámek-Hušek (1962). The confusion has been cleared up by Flössner (1962*a*), but it may be noted that not only did Lilljeborg, a meticulous worker, illustrate two non-existent antennal setae, but, in his figure 26 (plate LXXVII), shows an arrangement of ventral carapace setae which is certainly incorrect for *C. piger*. Thus, although Flössner was able to examine some of his material and show it to have the characteristics described by Meuche, the possibility remains that some of Lilljeborg's figures were prepared from a different, and undescribed, species. In support of this, in a paper not seen by Flössner, Gurney (1915), another careful worker, also clearly shows three terminal setae on the endopod of what he called *C. piger*, as does Stenroos (1897).

C. piger can and does swim, but slowly—an attribute related to the structure of the antennae—and sometimes swims inverted. A female, 0·385 mm in length and carrying eggs, sustained a speed of 3·9 body lengths (1·5 mm)/s for 42 and 58 s, and a speed of 4·68 body lengths (1·8 mm)/s was achieved over 15 s. This is less than one-third of the maxima recorded for *C. sphaericus* and *C. ovalis* (table 2).

The post-abdomen bears longer, stouter, marginal spines than those of *C. sphaericus* and *C. ovalis*, as befits an animal which pushes frequently. The more proximal setules are perhaps used for grooming the limbs either when the post-abdominal claws clean out the food groove, or by a separate action, and are probably related to the frequenting of muddy environments.

C. sphaericus crawls by use of the first trunk limbs, which are specialized for gripping (section ii). In the environment frequented by *C. piger* opportunities for gripping are few and locomotion is effected by other means. Trunk limb 1 is therefore free to develop other specializations. What on the outer lobe of *C. sphaericus* are grasping claws, one in particular of which is robust and stout (figure 125), are in *C. piger* longer and more slender (figure 133). The adjacent outer seta (OS 1) is also long and slender but differs only slightly from its homologue in *C. sphaericus* (not shown in figure 125). The functional significance of the arrangement in *C. piger* is not known but the armature of the outer lobe cannot serve the purpose fulfilled in *C. sphaericus*. The elongate spines, whose marginal fringe of spinules appears to grade into a continuous membrane (figure 133), may be concerned with grooming the inner face of the carapace lobes and marginal setae or, as in the case of another, and even more specialized mud-frequenting species, *Leydigia leydigii* (§XX) with bringing food particles within reach of trunk limb 2.

Modifications of the carapace armature related to bottom-frequenting habits are described at the same time as the adaptations for defence, which represent the second major suite of morphological specializations related to habits.

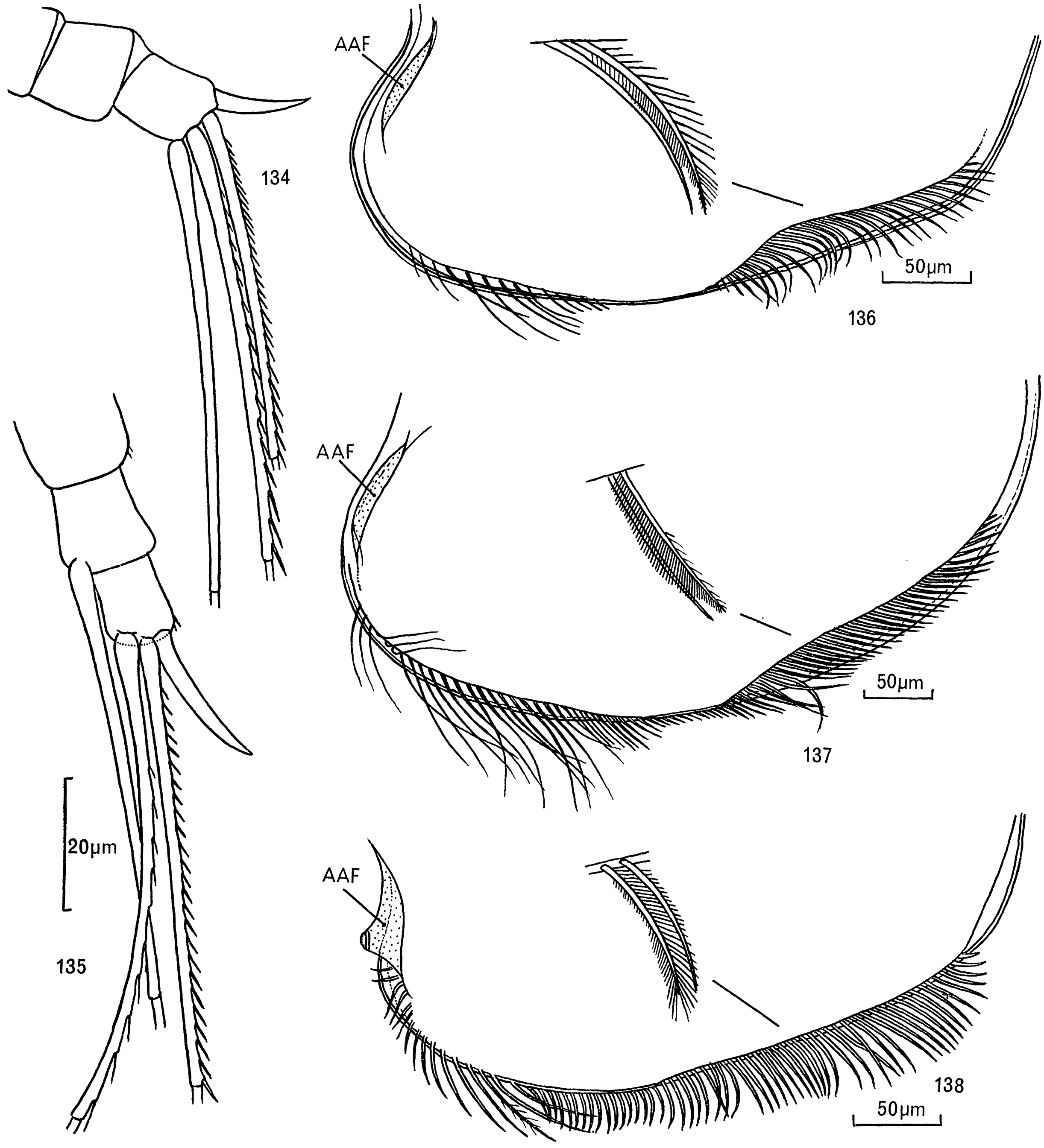
C. piger has carried to greater perfection the trend shown by *C. ovalis* towards closure of the ventral gape of the carapace and in this shows striking similarity to *Pseudochydorus*. Scrambling through muddy detritus does not call for those specializations of the ventral carapace margins seen in many crawling species, and they are therefore free to specialize for other purposes such as the exclusion of particles and close association in the mid-line. There is no ventral embayment. As in *Pseudochydorus*, when the margins come together they close the ventral aperture. There is also a correspondence, perhaps less perfect than in *Pseudochydorus* but certainly greater than in *C. sphaericus* and perhaps than in *C. ovalis*, between the shape of the anterior aperture when the carapace lobes are drawn together, and the form of the headshield, whose sudden widening dorsal to the rostrum thus receives a functional explanation. This helps to seal the anterior region more efficiently. The rostrum has a cuticular rim.

The flange of the ventral margins (figure 130, VF), which is really a thickened rim, is narrower than in *C. sphaericus*, gradually narrows from the posterior to the anterior ends, and is continuous with an anterior flange or rim. *C. piger* balances less efficiently than does *C. sphaericus* but in a muddy environment this is no embarrassment. Towards the posterior end of the ventral margin long setae are conspicuous. In *C. sphaericus* and *C. ovalis* the location of the homologous but somewhat shorter setae is similar to that in *Pseudochydorus* (cf. figures 136 and 137 with figure 99). In *C. piger* (figure 138) the arrangement is different; all the ventral setae arise at the margin (cf. figures 136, 137 and 138). Although *C. piger* shows striking convergent similarity to *Pseudochydorus*, it is in this respect much less like this genus than are *C. sphaericus* and *C. ovalis* whose over-all convergent similarity to it is less. In *C. piger* and *Pseudochydorus* the same end has been achieved by different means, and *C. piger* has combined two specializations—defence and the exclusion of mud particles.

The long posterior setae bear two rows of well-developed setules (figure 138 inset) which are arranged as in many chydorids, and not as in *C. ovalis* (cf. insets of figures 137 and 138). In life the setae are directed not so much medially, as they are in *C. sphaericus* and *C. ovalis*, as ventrally, with only a slight median inclination. They project well beyond the carapace margins and must exclude particles as the animal moves through mud. The two posteriormost, and particularly the last, are modified as sharp, perhaps defensive, spines. In the region where contact is made with the substratum—what in many species would be the embayment region—several setae are directed laterally.

An accessory anterior flange is present as in *C. sphaericus* and *C. ovalis*, but is different in shape (figure 138, AAF), being drawn out towards the mid-line (figure 131, AAF). Sections through individuals whose carapaces are closed indicate that the recurved tip of each flange fits into, and probably makes contact with, a hollow in the side of the labrum just anterior to the lateral projection of its side. This suggests that the function of the flange is to grant strength and rigidity to a closed animal. The carapace is further strengthened by corrugations and 'striations' which are often noticeable in this species, and which are in fact ribs of chitin (figure 132).

Several of the features described for *C. piger*, *C. sphaericus* and *C. ovalis* are useful taxonomic characteristics; e.g. the form and armature of the carapace margins (figures 136 to 138), the presence in *C. piger* of large distal spines on the antennal rami (figures 134 and 135) where only spinules are present in the other two species, and differences in the



FIGURES 134 to 138. *Chydorus piger*, *C. sphaericus* and *C. ovalis*.

FIGURE 134. *C. piger*. Exopod of the antenna. In this and the following figure note especially the short ramus, the powerful terminal spine, and the stout swimming setae armed on the basal segment with spinules.

FIGURE 135. *C. piger*. Endopod of the antenna.

FIGURE 136. *C. sphaericus*. Carapace lobe seen from the inside. The inset shows details of the posterior setae.

FIGURE 137. *C. ovalis*. The same.

FIGURE 138. *C. piger*. The same.

armature of the outer lobe of trunk limb 1. These are all of great functional significance, are intimately related to different ways of life, and refute the oft-repeated claim that taxonomic characteristics should be 'non-adaptive'.

TABLE 2. A COMPARISON OF CERTAIN DIFFERENCES BETWEEN THREE SPECIES OF *CHYDORUS*

C. sphaericus	*C. ovalis*	*C. piger*
Occurs in a very wide range of habitats, large and small. Among vegetation or on bottom. Almost ubiquitous	Occurs usually in small, often very small, and mostly acidic bodies of water. Among vegetation and on bottom. Possibly a fugitive species	A specialized bottom-dweller in large and small bodies of water
Crawls over surfaces. An active swimmer when necessary. Max. swimming speed recorded 14·7 body lengths/s	Crawls over surfaces. An active swimmer when necessary. Max. swimming speed recorded 17 body lengths/s	Pushes through mud and detritus. Slow moving. Max. swimming speed recorded 4·7 body lengths/s
Crawls by use of first trunk limbs	Crawls by use of first trunk limbs	Scrambles by use of antennae
Antennae without spines (minute spinules only are present)	Antennae without spines (minute spinules only are present)	Exopod, and endopod of antennae with a stout distal spine
All swimming setae lacking spinules on basal portion	All swimming setae lacking spinules on basal portion	Four swimming setae of antennae with spinules on basal portion
Three terminal setae on endopod of antenna	Three terminal setae on endopod of antenna	Two terminal setae on endopod of antenna
Armature of outer lobe of trunk limb 1 grasping spines	Armature of outer lobe of trunk limb 1 grasping spines. (More slender than in *C. sphaericus*)	Armature of outer lobe of trunk limb 1 slender spines
Gnathobase 2 with filter setae	Gnathobase 2 with filter setae	Gnathobase 2 with ramming setae
Carapace thin and essentially unsclerotized	Carapace slightly thickened and sclerotized	Carapace slightly thickened and sclerotized
Ventral carapace margins with broad flange and distinct embayment. Narrow aperture remains when carapace chamber is closed	Ventral flange narrower than in *C. sphaericus*. Embayment present but gap closed except for chinks anteriorly and posteriorly when carapace chamber is closed	Carapace margins with a narrow thickened rim. No definite embayment. Can close carapace chamber completely
Accessory anterior flange a simple dorso-ventral plate	Accessory anterior flange a simple dorso-ventral plate	Accessory anterior flange projects towards mid-line
Carapace setae arise inside margins	Carapace setae arise inside margins	Carapace setae arise at margins
No setae in embayment region	Setae in embayment region	Setae along whole ventral margin
Posterior marginal setae of carapace with widely separated posterior setules	Posterior marginal setae of carapace with only a few posterior spinules distally	Posterior setae long and apparent length accentuated by virtue of their site of insertion. With close set posterior spinules, especially proximally

(v) *Convergence in* Chydorus piger *and* Pseudochydorus globosus

Several hitherto unrecognized similarities between *C. piger* and *Pseudochydorus globosus* are now apparent and might be thought to provide additional justification for the former inclusion of both species in the same genus. That the similarities are the result of convergent specialization towards the same ends and are essentially superficial is, however, indicated by many profound, if not immediately obvious, differences. Newly discovered differences indeed greatly outnumber newly discovered similarities: the latter are more obvious because they include similarities in external form. There are many differences in the appendages. For example, the trunk limbs of *C. piger* are in essence the same as those of other species of *Chydorus*– though gnathobase 2 is armed with more spiniform, ramming setae—and the feeding mechanism is based on scraping and filtration: the corresponding appendages of *P. globosus*, while of the same basic design (as are those of all anomopods) are different in almost every detail and the feeding mechanism is based on dragging and forking large food masses. Comparison of the mandibles and their musculature is alone sufficient to indicate the deep seated nature of the differences.

Convergence in carapace and headshield form in chydorids which have begun to exploit the advantages of a globular form is not surprising. Indeed some of the features common to *C. piger* and *P. globosus* are found also in the distantly related ostracods and, in a different phylum and employing unrelated structures, in bivalve molluscs.

(vi) *Conclusions concerning* Chydorus, *and a summary of certain differences between* C. sphaericus, C. ovalis *and* C. piger

Like *Pseudochydorus* the species of *Chydorus* have exploited the globular form. Similarity in gross form has not, however, precluded the exploration of different ways of life by modifications of appendages, post-abdomen, and carapace margins, and the specializations of *C. piger* are very different from those of *C. sphaericus* and *C. ovalis*. Table 2 summarizes some of the differences, most of which have not previously been appreciated. Most are clearly related to different ways of life and several are useful taxonomic characteristics.

XX. LEYDIGIA LEYDIGII SCHÖDLER AND ITS ADAPTATIONS FOR LIFE IN MUD

Leydigia leydigii (figure 139) exemplifies a trend different from those exhibited by any chydorid yet discussed save to some extent *Disparalona*. From the primitive condition in which, as in *Alonopsis*, chydorids balanced somewhat ineffectively on the ventral carapace margins, locomotory specializations (other than swimming) have been largely determined by substrate preferences. Firm substrates, as provided by macrophytic vegetation and stones, have permitted exploitation of the carapace margins and their setae for balance and attachment, as seen in numerous forms; a specialization often accompanied in the Chydorinae by infolding of the antennal setae within the carapace. Muddy substrates, which offer alternative niches, permit no such developments, and a chydorid such as *Leydigia*, which has become adapted to life in such situations, exhibits an entirely different suite of specializations.

Penetration of mud is achieved most readily by chydorids with a bilaterally compressed body and a headshield suitably shaped to push mud particles aside. Such specializations, which affect the entire form of the body, are found in *Leydigia*. As a source of motive force the first trunk limbs are ineffective in mud, against which they can obtain no purchase, and the antennae, which assist scrambling and balancing in some generalized species, are here specialized for forcing the animal through an unstable, yielding substrate. In this they co-operate with the post-abdomen which plays an important part in locomotion and shows striking specializations for obtaining purchase in a soft, shifting substrate. The collection of food in a muddy environment also presents problems. Scraping cannot be practised in the manner so frequent in forms which collect their food from surfaces, and the presence of mud particles poses the constant threat of clogging of any true filter. These problems *Leydigia* has had to overcome. Furthermore, life in mud sometimes takes an animal into regions where oxygen tensions are low, and this calls for physiological adaptations which may also involve morphological specializations.

(i) *Body form, ecology, habits and locomotion*

These features are so intimately related that they are best treated together. *L. leydigii* is a true bottom dweller which frequents soft muddy substrates, but in two separate localities I have found single specimens in a layer of flocculent mud or detritus on the surface of stones. Such a layer need be only a millimetre in thickness to enable the animal to cover itself completely. By use of special samplers Moore (1939) ascertained with considerable precision the nature of the bottom deposits among which he found this species (referred to by him as *L. quadrangularis*). It occurred in the littoral and sublittoral regions of a lake at depths of up to 15 m on bottoms which ranged from sand overlain by a 4 mm layer of 'fine ooze (organic detritus)' to black ooze at least 18 cm thick and of which the upper 2 cm 'were quite liquid'.

The nature of the muddy detritus is of great importance, for while *Leydigia* burrows freely into suitable material and remains perfectly clean, it quickly becomes entangled in material of a different consistency which may occur adjacent to the point at which it was collected. Such unsuitable detritus sticks to the carapace. Differences in substrates are difficult to define but Moore's term 'soft ooze' aptly describes the material in which this species thrived in captivity. From Moore's data it can be calculated that on a day when he collected *Leydigia* at 11 m, the water of the lake was only about 42 % saturated with oxygen at this depth. It would certainly be less well oxygenated at the mud surface, and it is evident that *Leydigia* must be frequently subjected to oxygen tensions lower than this. Leloup (1946), in fact, found it in water only 22·2 % saturated with oxygen. Other members of the genus are similar in general form and, according to the literature, have similar habits. This is certainly so in what I regard as an African form of *L. acanthocercoides* (Fischer) which I found in abundance among organic bottom material in a sheltered marginal area of L. Bangweulu and on the bottom of a richly vegetated pool in the Zambezi Valley.

The body is bilaterally compressed (figure 140) and distinctly wedge-shaped (figure 139). Such a shape must facilitate penetration into mud, into which it is driven by the highly specialized post-abdomen, either alone or with assistance from the antennae. In horizontal section the head-shield has the form shown in figure 140. The carapace cuticle is not more than about 2 μm in thickness in adults, and delicate, the outer sclerotized zone, which presumably includes, if it does not represent, the epicuticle, being very thin and difficult to measure accurately. The inner zone is essentially pale blue in Mallory-stained sections. The ventral carapace margins exhibit almost no elaboration, but a broad flange is present anteriorly whose width increases dorsally. An embayment is scarcely differentiated as such ventrally but the carapace margins are separated from near their anterior extremities by an elongate and never very wide slit which extends posteriorly to about the level of the posterior margin of trunk limb 5. In preserved specimens the carapace margins are often drawn together over the whole of their length. Whether this can take place in life is uncertain, but probable, and the slit does appear to be narrowed when the animal swims. Posteriorly there is an aperture with the contour of a narrow biconvex lens.

The anterior margins are armed with some 13 setae of which all save the five dorsalmost are very long (up to more than 8 % of the carapace length), and there are approximately 80 setae, all long, on each ventral margin. Of these about a dozen at the level of the second trunk limbs are shorter than the rest, but are nevertheless equal to between about 5·5 and 7 % of the carapace length. The rest are longer, as much as 14 % of the carapace length in some cases. Their armature follows the basic plan seen in *Alonopsis*, *Peracantha* and others. On the five dorsalmost anterior setae two rows of setules are readily apparent over the whole length: only the posterior row is obviously developed on the rest, though an anterior row can be detected on most and is not difficult to see on the posteriormost members of the ventral series. The setules of the posterior row are fine, close-set, and relatively long in the basal half of the seta so that, over most of the ventral margin, they overlie the seta next behind and form an efficient screen against mud particles (but see below). The distal portion of each seta, however, appears to be naked. Setules are present on the short ventral setae at the level of trunk limb 2, but are very fine and do not appear to span the gap between adjacent setae.

The labrum appears partially to seal the dorsal part of the anterior aperture to the carapace chamber, and the setose margin of the keel possibly helps to do so ventrally though usually it appears to be too far forward to be of much value in this respect.

In an active animal constructed on the anomopod plan, a brisk respiratory stream is probably a prerequisite for life in muddy bottom deposits where oxygen is often in short supply. *Leydigia* therefore has a powerful pump made up by the exopods of trunk limbs 4 and 5, whose effective surface area is increased by fringing setules both on their setae and margins, as in *Eurycercus* (Fryer 1963). The stream set up by this pump, however, produces its own problems. Were it to flow through a filter chamber such as that of *Eurycercus*, *Peracantha* or *Chydorus sphaericus*, the mud which it must inevitably carry would quickly clog

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FIGURES 139 to 145. *Leydigia leydigii.*

FIGURE 139. Outline of an adult female from the side to show the massive development of the post-abdomen and the course of currents through the carapace chamber, the main flow being shown by solid arrows. For details see text. Marginal carapace setae are omitted. The curved line shows the approximate posterior limits of the cage comprised by the trunk limbs, through which currents do not pass.

FIGURE 140. Outline of an individual in horizontal section at about the level of the ventral part of the mandibles to show the shape of the headshield. Dotted lines complete the headshield from a more dorsal slice.

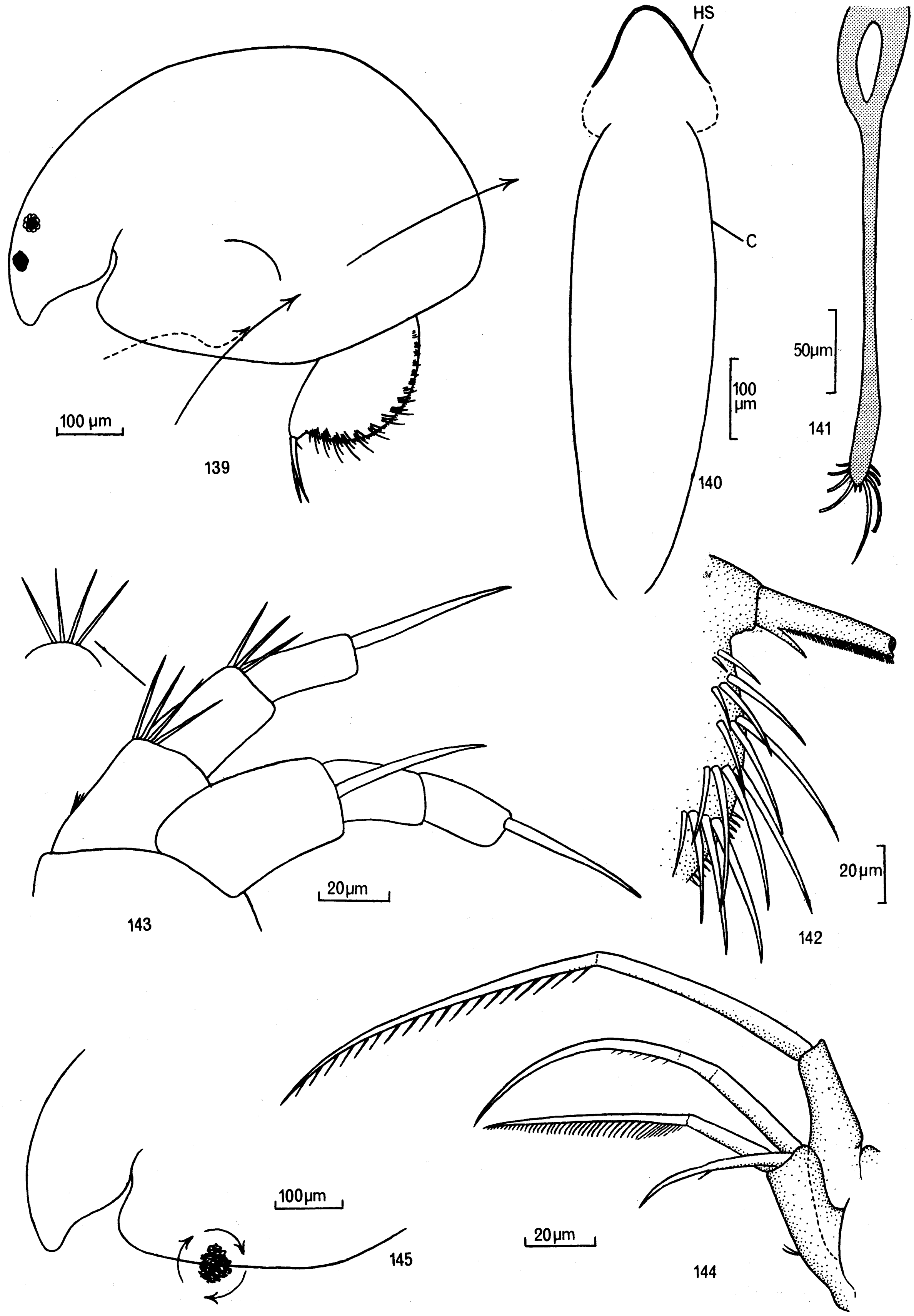
FIGURE 141. Somewhat oblique transverse section through the post-abdomen to show its narrowness and the spread of the marginal setae, here somewhat displaced.

FIGURE 142. Details of the armature of the distal part of the post-abdomen.

FIGURE 143. The antennae, swimming setae omitted, to show the long spines used for ploughing through muddy substrates and also the arcs of long, stout spinules on the endopod (one shown in diagrammatic section in the inset).

FIGURE 144. The outer distal armature of trunk limb 1.

FIGURE 145. Rotation of the food mass at the entrance to the carapace chamber (for details see text).



FIGURES 139 to 145. For legend see facing page.

the filters. Filter feeding as practised by such species is therefore impracticable and is not employed by *Leydigia* which has solved the problem of clogging by diverting the respiratory stream to the outside of the median chamber. Currents enter and leave the carapace chamber as indicated in figure 139. They enter ventrally in one restricted region only, at the level of trunk limbs 2 and 3, and do not flow through the median chamber, which is restricted in size (section ii). The absence of any marked flow other than that indicated by solid lines in figure 139 is shown by the movement of such particles as (dotted line) find their way into the carapace chamber, but do not pass towards the median chamber, and actually drift away from it until they reach the main stream. Likewise there is no real current in front. These observations refer to animals observed at relatively high magnifications on a microscope slide and which may to some extent have behaved in an abnormal manner. However, individuals kept, free from all restraint, in dishes whose bottoms were covered with flocculent mud among which they had been living in nature, have been seen to draw considerable quantities of suspended material into the carapace chamber and immediately discharge it posteriorly. Likewise a specimen placed in a suspension of carmine particles passed large lumps, as well as a stream of fine particles, through the carapace chamber, yet none were collected. Many chydorids quickly fill the food groove under such circumstances.

Although the marginal setae of the carapace may act as a screen anteriorly and may prevent excessive inflow of particles in the restricted region where water enters the carapace chamber, they do not rigorously exclude even large flocculent masses, which have been seen to enter ventrally. As these do not pass through a filter chamber they present no problems. The width of the ventral gap is reduced by the somewhat medially directed marginal setae, and the posterior aperture is sufficiently wide to permit the unimpeded passage of any particles which are drawn in.

A further adaptation to life in mud is the presence of haemoglobin in the blood (Fox 1957). This is sometimes present in sufficient amounts to render the animal distinctly reddish in colour. Although at least some other chydorids have haemoglobin in the blood (Fox 1957), seldom do they appear reddish.

Although it can swim well, *Leydigia* is by preference a scrambling animal which actively penetrates flocculent detritus. In dishes it is sometimes driven out by illumination from below: in nature such negative photo-taxis will reinforce the tendency to burrow. The compound eye is small, but the ocellus relatively large (cf. *Monospilus*), suggesting that while vision is unimportant it is desirable to maintain sensitivity to light.

The post-abdomen is well adapted for pushing. Its adaptations have elicited comment from various writers but the full subtlety of its adaptations has not always been appreciated. It is not only deep but much compressed from side to side (figure 141) and therefore combines strength for pushing with lightness, as does the post-abdomen of *Eurycercus* (Fryer 1963). A great surface area is important in order to grant purchase and is achieved by means of extremely long marginal spinules whose arrangement is readily seen from the side (figures 139, 142), but whose effectiveness can only be appreciated by inspection from the morphologically dorsal aspect or in transverse section (figure 141). This reveals the large area on which they grip. The spinules are movable and give purchase during pushing, which often involves a great swing of the post-abdomen, yet offer little resistance during the return movement, during which the significance of narrowness is apparent. An inflated structure, while suitable for pushing, would offer much resistance during return.

The antennae (figure 143) are also vigorously employed as *Leydigia* burrows. Both the basal and distal segments of the exopod and the distal segment of the endopod bear long outwardly directed spines, similar to those of several scrambling species, but longer than, for example, those of *Alonopsis*. The basal and middle segments of the endopod bear distally an arc of long slender spinules, four in number on the basal, three on the middle segment, whose arrangement resembles that of the spinules of the post-abdomen, and which serve a similar function. These, apparently not previously described or adequately illustrated, represent a striking adaptation to life in mud and soft substrates. The basal segment of each major swimming seta is stiff and armed with a row of widely spaced spinules, and contributes to the efficiency of the antennae as propulsive organs in soft deposits (cf. *Chydorus piger*). The antennal setae are never folded within the carapace.

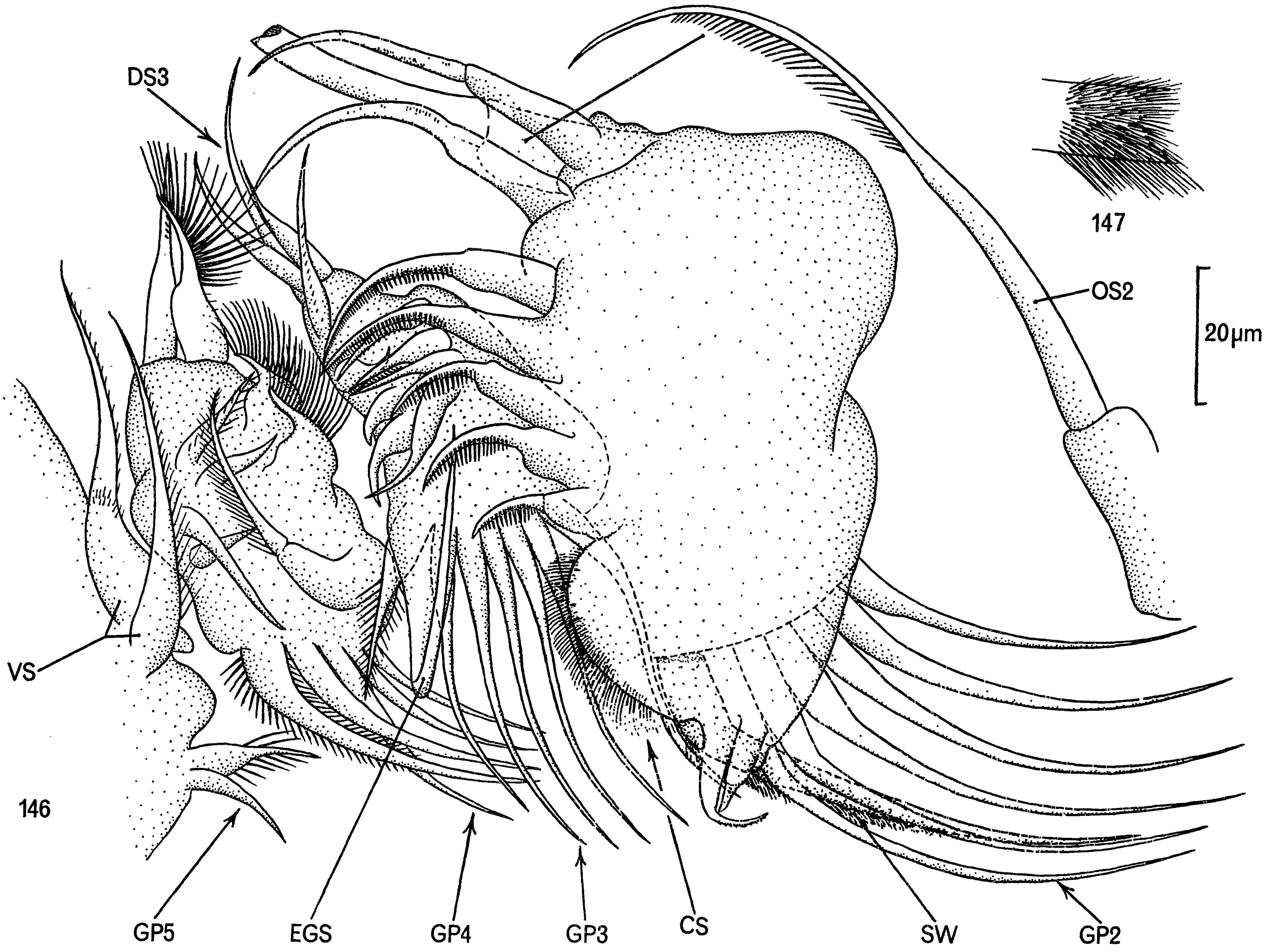
Observations on feeding individuals (section iii) suggest that the material ingested to a large extent reflects the nature of the deposits in which they are burrowing. Gut contents (from one locality only) included dark amorphous masses, innumerable particles of various sizes (but in general rather coarse) of both organic and inorganic origin, and a few algal cells including diatoms. Pacaud (1939) referred to the gut contents of this species as 'brun foncé' and believed that this testified to 'la constante prédominance des débris végétaux allochtones dans le seston qu'ils ingèrent'. The use of the term seston, which means particulate matter in suspension, is somewhat misleading as *Leydigia* in fact feeds on sedimented material—see section (iii).

Although *Leydigia* plunges into deposits with its ventral surface downwards, it swims by preference inverted. It does so effectively but not at great speeds. A female 0·71 mm in length, carrying embryos, sustained a speed of more than 3·52 body lengths (2·5 mm)/s over a distance of 13 cm and certainly increased its speed towards the end. Higher speeds can be achieved over shorter distances. Over a distance of 9 cm a speed of just over five body lengths (3·57 mm)/s was achieved.

(ii) *Trunk limb specializations and the sorting chamber*

Each first trunk limb is notable for the shortness of both the distal portion of the corm and of the armature of this region. By contrast the distal lobes are elongate and bear very long spines and setae (figure 144). The solitary spine borne on the outer distal lobe is longer than in any other chydorid examined. Other specializations of this limb include the presence of a screening seta which fulfils the same function as does that of *Alona affinis* and *Peracantha truncata*.

Trunk limb 2 is clearly of the basic chydorid type but exhibits several striking, and in some cases unique, specializations. The gnathobasic plate (figure 146, GP2) is well developed and consists of seven setae of which the posteriormost (SW) is highly specialized in structure and orientation and is here called a sweeping seta. It is large and setose in a manner not seen in any other genus, being clothed by a dense carpet of setules on its morphologically dorsal and outer faces, i.e. on the surfaces adjacent to the food groove (figure 147), and is so curved as to lie along the food groove to the outside of the adjacent, sixth, seta. It therefore sweeps along a more lateral part of the food groove. This is related to mud-frequenting habits (section iii). Furthermore, the posterior face of the gnathobase itself is covered with a carpet of setules (CS) which is functionally continuous with the setules of the sweeping seta (figure 146). Of the chydorids studied only *Leydigia* and the mud-frequenting *Monospilus* possess such a carpet. The extensive carpet replaces the sparse and usually compact array of spinules of many species (e.g. *Peracantha*, figure 47) and is represented by a few stout spinules in *Pseudochydorus* (figure 103). The median gnathobasic armature is shown in figure 146. Its longest spine is sweeper-like. Of the endite armature the



Figures 146, 147. *Leydigia leydigii.*

Figure 146. The left-hand half of the sorting chamber seen from inside. This figure is based on a dissection in which trunk limb 2 has been deliberately pulled forward. In life this limb to a large extent overlies trunk limb 3, the chamber being very short from front to back. The setae which in many species make up an outer filter plate on trunk limb 4 are somewhat displaced. Note the extremely long distal spine of trunk limb 2 (cut short in the figure and drawn to the same scale in the inset), the setose nature of the posterior face of the gnathobase of trunk limb 2, and the long sweeping seta of this gnathobase which lies *behind* the gnathobasic plate. Although in fact largely obscured by the gnathobase and its spine-like setae the whole of the sweeping seta is indicated by stippling. Note also the absence of filtratory setules on the gnathobasic setae of the trunk limbs and the long distal spines of trunk limb 3.

Figure 147. Details of the setose *outer* face, i.e. the face which sweeps along the lateral wall of the food groove, of the sweeping seta of trunk limb 2 (shown stippled in figure 146).

outermost spine (OS2), which is not a scraper, is extremely long. The rest are relatively short. Not only is the outermost very long but it is borne on a distinct segment which articulates with the corm (figure 146, especially inset). In this respect *Leydigia* is again unique among the Chydoridae examined. This spine is armed with a row of setules; the rest are finely denticulate.

What in many species is an outer filter plate is represented on trunk limb 3 of *Leydigia* by a row of setae which are for the most part unarmed. Of the elements of the gnathobasic plate (GP3) the posteriormost is much shorter than the rest and bears two rows of coarse spinules (figure 146). The seta at the posterior dorsal corner (EGS) is very long and is curved in the manner shown. Distally, in the position occupied by scrapers in some species, are slender spines (DS3).

Of the five setae of the flap-like exopod, the second from the outside is extremely long and reaches back so as to overlie the exopod flaps of both trunk limbs 4 and 5. This seta is armed, not with rows of long setules to increase its efficiency as a pump, but with a sparser array of stiff setules which are directed towards the exopods of trunk limbs 4 and 5. This strongly suggests that the seta serves as a cleaner of the more posterior exopods, and this can again be related to mud-frequenting habits.

Of the gnathobasic plate of trunk limb 4 (GP4) the posterior element is a stout seta armed with two rows of spinules which are coarser and more widely spaced than are filter setules (figure 146). There are four setae in the position occupied by an outer filter plate when this is present, but setules—coarse and widely separated—have been detected only on the outermost. A typical row of vertical setae is present, details of whose armature is shown in figure 146. The exopod is very large (section i).

In those parts of its make-up which are related to the manipulation of food trunk limb 5 follows the typical chydorid plan, and its most striking feature is an extremely large exopod (section i). The gnathobasic armature (GP5) consists of two setae only, of which the outermost is armed with a few spinules on each side.

The limbs are crowded together. Unlike the equivalent figures for other species, which are drawn from sections, figure 146 is drawn from a dissection, and trunk limb 2 is deliberately pulled forward. In life it obscures considerably more of trunk limb 3 than is indicated, so the median chamber is much compressed from end to end. (In figure 146 trunk limb 4 has become somewhat twisted as a result of manipulation and both the anterior and posterior rows of setae are somewhat displaced.)

Except for the spinule-like structures shown on certain gnathobasic setae of trunk limbs 3, 4 and 5 in figure 146 (one seta only in each case) no setules have been detected on the gnathobasic setae which comprise the median chamber, although such are indicated in a vague manner by Lilljeborg (1900). By contrast setules, while fine, can readily be seen on the maxillule in the same preparations by use of an oil immersion lens. If setules are present it is difficult to see how they can fulfil any function as no currents pass through the cage comprised by the gnathobasic setae. An absence of setules is, however, readily understood and is in full accord with the ecological preferences and feeding habits of this species.

Even without setules the gnathobasic setae of trunk limbs 2 to 5 of an adult female are capable of retaining particles at least as small as 5 μm in diameter, and possibly a good deal smaller. Certainly much smaller particles, if they do not escape before they reach this point, will inevitably be retained posteriorly by the spinules of the most posterior gnathobasic seta of trunk limb 4 and the adjacent seta of trunk limb 5 (figure 146), and can then be swept along the food groove, especially by the sweeping seta of trunk limb 2. That some small particles are successfully collected is apparent from the gut contents (the assumption being made that the mandibles do little to fragment the food), but the presence of innumerable large lumps of material such as would easily be retained in the absence of filtratory setules is characteristic of the guts examined. These had 'clean' contents and provided no evidence of the collection of flocculent mud particles. If they entered the median chamber such minute mud particles would, in the absence of filtratory setules, slip through the gaps between the gnathobasic setae of trunk limb 3, down whose length most of the material travels. Such a loss would be advantageous.

Habitat preferences, observed details of the feeding mechanism (section iii), and the nature of the food are therefore all consistent with an absence of setules from the gnathobasic setae of the median chamber, which is perhaps best termed the sorting chamber.

(iii) *The feeding mechanism*

Although a young specimen kept in a dish in which detritus was present was seen to collect food in a manner reminiscent of several chydorids—with the ventral carapace margins against the solid surface, antennae spread and used as balancers, and the limbs apparently scraping material from the surface—this is not the typical method of food collection. Food is usually obtained in situations where such a method cannot be practised.

Although feeding often takes place when the animal is completely buried in mud, and details cannot then be observed, *Leydigia* conveniently feeds with the body lying in apparently any position and, in shallow mud, has sometimes been watched manipulating food while it lay near the surface and only partly buried. When so feeding it reaches out with the first trunk limbs and, with a single rapid movement, pulls material towards the carapace aperture. When the distal spines of trunk limb 1 (figure 144) are swept through flocculent mud, large particles are trapped and dragged towards the carapace chamber while minute fragments are left behind. The use of this trunk limb in food collection is unusual (but compare *Graptoleberis* and *Anchistropus*) and may not always be involved as material has been seen to 'appear' in the position to which the first trunk limbs drag it when no movement of these appendages has been detected. In such cases it has probably been collected directly either by the distal scrapers of trunk limb 2 or the distal spines of trunk limb 3, or by the combined action of both limbs. On one occasion the long spines of the first trunk limbs were seen to hold a large clump of material while it was being dealt with by the other limbs, but this is unusual and, whether concerned with initial collection or not, the first trunk limbs usually play no active part in the subsequent manipulation of the food.

Under the artificial conditions of the observations which, however, employed flocculent mud from the site of collection, relatively large clumps only were utilized. Such masses were 'held' at the distal extremity of trunk limbs 2, 3 and 4, which are located close together, and manipulated vigorously while they remained in this region. It is highly characteristic of the feeding process of this species that the food mass is rotated in the vicinity of these limbs and in the direction indicated in figure 145. As it rotates briskly it must be lying freely yet be enclosed within a cage of spines, and for this purpose the distal spines of trunk limb 3 are well suited.

As material is removed from this rotating mass—and it is presumed that the more distal scrapers of trunk limb 2 are particularly important in this respect, though the point is difficult to ascertain—it is either pushed towards the food groove by the brisk movements of trunk limbs 2, 3 and 4, or is whisked backwards and discharged with particles drawn in from elsewhere. Very small, and therefore light, particles, which could easily become an embarrassment in a muddy habitat, are possibly eliminated in this way. Whether any currents flow through the sorting chamber during the feeding process has not been ascertained, but true filtration need not be employed, and the nature of the gut contents suggest that it is not. The exopod pump, however, is active throughout. Food is transported along the food groove briskly and in large clumps as in many other species. During the forward swing of trunk limb 2 the sweeping seta must inevitably clean the food groove of any minute particles which, perhaps by adhering to other particles, have evaded the currents at the distal extremities of the limbs. The mandibles move rapidly (cf. *Pseudochydorus*) and at a rate difficult to count, though about 250 cycles/min is a rough estimate.

A feature of the feeding process is the rapid action of trunk limb 3 which is reminiscent of that seen in *Disparalona rostrata*, but with the important difference that, while in *Leydigia* such movements take place only while the animal is feeding, in *Disparalona* they are virtually continuous.

(iv) *Feeding and defaecation in* Leydigia *and other anomopods*

Many chydorids defaecate at a brisk rate as food is passed into the gut anteriorly. This is especially noticeable in *L. leydigii* which often produces a rapid succession of faecal ribbons as it feeds. These appear always to be at least twice as long as their diameter and are usually longer; sometimes more than three times as long. One animal, which was feeding when first observed, was watched for 2 min 5 s as it fed, during which time it discharged fifteen faecal ribbons. Rough calculations indicate that at such a rate of ejection the entire alimentary canal could be evacuated in less than 6 min, possibly considerably less. This represents even more rapid passage than is implied by the times taken by various Anomopoda and Ctenopoda to fill the gut with carmine or indian ink particles (Pacaud 1939). Yet when the animal is deprived of food the gut remains full for long periods. Similar behaviour has been observed in several other anomopods, on some of which quantitative measurements should be easy to make if coloured markers are used, and storage of food for at least 2 days has been observed in the minute detritus-eating malacostracan *Monodella* (Fryer 1964).

It is suggested that most anomopods—*Pseudochydorus globosus* is the one exception noted during the course of this study—and at least some other small microphagous crustaceans, maintain a full gut as an insurance against periods of scarcity (which may be associated with daily rhythms of activity, or with the patchiness of available food in nature). When, in the case of an animal such as *Leydigia*, large food masses which cannot be digested in a few minutes, are ingested, the premium is probably at times expensive. Such behaviour, which applies at least in part to certain daphnids, implies that the value of some of the vast number of measurements made on daphnid feeding rates, without agreement being reached, must be regarded as extremely dubious.

(v) *Conclusions*

The whole organization of *Leydigia leydigii* is directed to life in mud. Locomotion is very different from that of species which crawl over firm substrates, and feeding, which is non-filtratory, shows many specializations for avoiding the collection of fine mud particles. Although several chydorids are to a large extent selective feeders, especially *Pseudochydorus* and *Graptoleberis*, and *Anchistropus* is completely so when living on *Hydra*, probably none is so selective as *Leydigia* if judged on the basis of the feeding mechanism alone.

XXI. *MONOSPILUS DISPAR* SARS AND ITS ADAPTATIONS FOR A BENTHIC EXISTENCE

No living specimens of *M. dispar* have been available during the present study, but through the kindness of Mr W. J. P. Smyly I have been able to examine and section a few formalin-fixed specimens collected by him from the benthos of certain lakes in the English Lake District. These came from various depths (maximum 24 m). *Monospilus*, (length to *ca.* 0·5 mm) is seldom seen, but this may be the result of inadequate sampling of suitable habitats, for according to Lilljeborg (1900) it is common in certain localities. It is a true bottom dweller in muddy situations. A detailed account of its way of life cannot be given on the basis of preserved material but certain morphological features related to benthic habits are listed here.

The general form is illustrated by several authors, e.g. Lilljeborg (1900). As in *Chydorus piger*, to which it shows certain convergent similarities, all the setae of the carapace margins are located on the margins themselves and not internal to them as in, for example, *C. sphaericus*, and there is no embayment, so the carapace can be closed completely as in *C. piger* and *Pseudochydorus*. The cuticle also shows signs of thickening and sclerotization and is yellowish in colour. Old carapaces, but not headshields, are not shed but are retained and envelop the functional carapace as they do in *Alonopsis*. Lilljeborg illustrates a specimen carrying eight such carapaces. Such retention is permitted only in species of certain cross-sectional shapes and with a narrow embayment or which, like *Monospilus*, lack an embayment. Such retention would be a mechanical impossibility in, for example, *Peracantha*. Thickening of the cuticle and retention of old carapaces are, like the ability completely to close the carapace chamber, protective, and also increase the specific gravity, which is advantageous in a benthic species.

Crawling, and presumably burrowing, is certainly by means of the antennae and post-abdomen, both of which are adapted for this purpose. Both rami of the antennae bear long, stout spines distally, as does the basal segment of the exopod (cf. *Disparalona*). The post-abdomen is short and broad, and armed, in addition to its marginal denticles, with an array of long spinules on its lateral faces which must grant additional purchase, as must the large spine at the base of each terminal claw. By contrast the first trunk limbs show no adaptations for gripping: as in *Chydorus piger* the outer lobe bears long spines.

The complete absence of a compound eye, unique within the Anomopoda, is related to life in dark situations where vision is unimportant, and suggests persistent burrowing, but the retention of an ocellus indicates that sensitivity to light is still of value (cf. *Leydigia*).

In the few specimens available the long gut was crammed with minute particles of detritus, presumably collected by a feeding mechanism showing many basic chydorid features. Among the anatomical specializations noted is a long fringe of setules on the posterior face of the gnathobase of trunk limb 2 similar to that present in the mud-frequenting *Leydigia* (figure 146), but otherwise not seen in any chydorid yet examined. This is related to life in a muddy environment. There is, however, no sweeping seta on the limb such as occurs in *Leydigia*. Trunk limb 3 bears a long reflexed posterior gnathobasic seta such as occurs also in *Leydigia* (figure 146), but is a little shorter and so located as apparently to sweep down the gnathobasic filter plate of trunk limb 4. Both trunk limbs 3 and 4 have well-developed outer filter plates. In the available material a mound arising in the food groove appears effectively to exclude the small filter plate of trunk limb 5 from participation in the sealing of the posterior end of the filter chamber. As in *Leydigia* the penultimate vertical spine of trunk limb 4 bears a fan of long spinules (cf. figure 146) which appear almost to meet those of their fellow on the opposite limb. In life these may serve either to prevent the posterior drift of large particles or serve as a mutual cleaning device. Mandibular articulation is of type A and, so far as it has been studied, the musculature is of the typical chydorid type, the 5c muscles being present. Further anatomical details are given in table 3.

Smirnov's recent observation (1968) that although the exopod pump is present it does not normally operate, shows clearly how *Monospilus* has coped with the problem of food collection in a muddy environment, but indicates that its respiratory needs are met in a different way from those of *Leydigia*. According to Smirnov, survival without a respiratory stream is achieved at the expense of restriction to the well oxygenated open littoral zone. Penetration to 24 m (as in the English Lake District) may therefore be possible only in oligotrophic lakes such as Buttermere where hypolimnetic oxygen deficits are never great.

XXII. Inter-generic relationships of the Chydoridae

The relationship of the Chydoridae to the other anomopod families will be considered when accounts of these families have been presented.

As a result of recent work by Frey (1959–67) on head-pores and mandibular articulation, and Smirnov (1965*a*, *b*) on trunk limb setation, considerable light has been thrown on major groupings within the family. Frey (1967) recognizes four groups of genera which he has defined as subfamilies, whose validity is here supported. All species dealt with above belong to the Aloninae and Chydorinae. The other two subfamilies contain respectively only *Eurycercus* and *Saycia*. Of the three features on which separation of the Aloninae and Chydorinae are largely based, the type of mandibular articulation and the number of setae on the exopod of trunk limb 4 are the same for all species yet studied, and cannot therefore give information on inter-generic affinities. Head-pore arrangement, while useful, has limitations if considered alone, and only studies of the whole organization of individual genera and species can reveal affinities within the subfamilies. This study indicates, sometimes unequivocally, sometimes tentatively, some such relationships, but also shows that convergence can lead to similar end-points in species which are not closely related, and that closely related species may have very different habits and abilities.

TABLE 3. SUMMARY OF CERTAIN CHARACTERISTICS OF SOME INVESTIGATED CHYDORIDAE

All the species listed have a gnathobasic plate on trunk limbs 3 and 4 and an outer plate, usually filtratory, on trunk limb 3, though this is greatly reduced in *Graptoleberis*. All have a pair of distal spines on trunk limb 3, but only in the species so indicated do they serve as scrapers. + indicates the presence of a particular feature, or the ability to perform a particular feat; −, absence or inability. When a symbol is enclosed in parentheses the indication is probably correct but not proven with certainty. A ? indicates a feature not adequately resolved in spite of considerable effort. Blank spaces are left when the material was inadequate in quantity or quality to permit resolution of the point at issue. *Eurycercus* represents the subfamily Eurycercinae, the next 10 species the Aloninae, the rest the Chydorinae.

	gnathobasic plate on trunk limb 5	outer plate (usually filtratory) on trunk limb 4	distal spines of trunk limb 3 serve as scrapers	trunk limb 6	tubular organ†	able to fold antennal seta within carapace	source of entangling secretions		
							labrum	trunk limb 1	trunk limb 4
Eurycercus lamellatus	+	+	−	+	−	+	+	−	+
Alonopsis elongata	−	−	+	+	−	−	?	+	+
Acroperus harpae	−	−	+	+	−	−	(+)	(−)	+
Camptocercus rectirostris	−	−	+	+	−	−	(+)	−	+
Alona affinis	+	+	+	+	−	−	+	?	−
A. guttata	+	+	+	?	−	−		+	+
A. costata	+	+	+	+	−	−		(+)	
Leydigia leydigii	+	+*	−	−	−	−	(−)?	−	−
Rhychotalona falcata	(−)	+	−	+	−	(−)			
Graptoleberis testudinaria	−	−	−	−	−	−	(+)	−	−
Monospilus dispar	+	+	−	(−)	(−)	−			
Alonella nana	+	+	−	(−)	−	−		(+)	(−)
A. excisa	+	+	−	−	−	+		+	(−)
A. exigua	+	+	−	−	−	+		+	(−)
Disparalona rostrata	+	+	−	−	−	?	?	−	−
Peracantha truncata	+	+	−	−	+	+	+	−	−
Pleuroxus uncinatus	+	+	−	−	+	+	(+)	−	−
P. trigonellus	+	+	−	−	+	+	(+)	−	−
Chydorus sphaericus	+	+	−	−	+	+	(+)	−	−
C. ovalis	+	+	−	−	+	+	(+)	−	−
C. piger	+	+	−	−	+	+	+	−	−
Pseudochydorus globosus	+	−	−	−	−	+	+	−	−
Anchistropus emarginatus	+	−	−	−	(−)	+	?	−	−

* Not a true filter. † Details of this are presented elsewhere (Fryer, in press).

Support for Frey's classification is apparent from table 3. This, while revealing no additional feature on which the Aloninae and Chydorinae can be unequivocally separated, shows that certain features, such as the ability to fold the antennal setae within the carapace, or the possession of a tubular organ (Fryer, in press) are largely or entirely confined to one or other subfamily. Possession of a sixth trunk limb also appears to be largely confined to the Aloninae, though Smirnov (1966*a*) has recently demonstrated its presence in *Pleuroxus striatus*. Of features included in the table some, such as the ability to fold the antennal setae within the carapace, which is a behavioural and not a purely morphological feature—and is certainly functional—are apparently good indicators of affinity at the subfamily level. Others, such as the source of entangling secretions, have to be interpreted with care. The distribution of the latter, so far as yet ascertained, suggests that it might be a guide to affinity within the Chydorinae, but this is not borne out by the situation among the Aloninae. Although not always completely proved, *Peracantha*, *Pleuroxus* and *Chydorus*, which on other grounds appear to be closely related (see also Smirnov 1966*a*) appear to employ only labral gland secretions. In this they differ from the three studied species of *Alonella* which all produce secretions from trunk limb 1. *Disparalona rostrata* differs from *Alonella* in this respect. Within the Aloninae, however, the apparent difference between *Alonopsis* and what appear to be its close relatives *Acroperus* and *Camptocercus* will suggest, if they are eventually proved, that differences in this respect can arise among even closely related species—probably in accordance with functional demands.

Inter-generic relationships indicated by the entire study and not merely by the facts shown in table 3 include the following. *Pseudochydorus globosus*, formerly included in *Chydorus*, is not in fact closely related to that genus. Its nearest relative is undoubtedly *Anchistropus*, and these genera were perhaps even derived from a common ancestor. *Chydorus*, *Pleuroxus* and *Peracantha* are closely related. *Disparalona rostrata* is generically distinct from *Alonella*. The close relationship of *Alonopsis*, *Acroperus* and *Camptocercus* is confirmed.

While Smirnov (1966*a*) emphasized the similarity of the trunk limbs of *Pleuroxus* and *Alonella* and showed that distinctions between these genera could not easily be drawn, two differences are indicated in table 3, at least for the species studied. These are the presence of a tubular organ in *Pleuroxus* (and *Chydorus*), and its absence in *Alonella*, and a difference in the site of entangling secretions.

XXIII. Adaptive radiation

Adaptive radiation in the Chydoridae has been of a spectacular nature. Although the same basic apparatus (carapace and appendages) is employed throughout the family, whose unity is clear, its end-points include species which differ markedly in form, size, habits and feeding mechanism. Radiation has produced plant-frequenting scrapers and filterers of fine particles (*Peracantha*, *Alonella exigua* and others) which differ among themselves in form and habits so that a variety of habitats has been exploited, a snail-like scraper of leaves (*Graptoleberis*), several benthic species which frequent a variety of substrates over or through which they crawl or scramble, and where they collect particles of different sizes (*Alonopsis*, certain species of *Alona*, *Chydorus piger*, etc.) or in which they burrow (*Disparalona*) or live as true mud-dwellers in soft or semi-liquid deposits (*Leydigia*). Other end-points of adaptive divergence include a species specialized for creeping inverted beneath the surface film of water (*Dadaya*), a scavenger which eats the dead bodies of other small crustaceans and is also specialized for defence (*Pseudochydorus*), and a parasite which ingests the living tissues of *Hydra* against whose nematocysts it is specially protected (*Anchistropus*). Adaptation towards a particular end has sometimes led to convergent similarity in body form (*Chydorus* and *Pseudochydorus*) or attributes (such as the retention of moulted carapaces by *Alonopsis* and *Monospilus*) which, however, mask important differences in anatomy and ways of life.

These changes involved whole suites of characteristics, as in *Graptoleberis*, almost every feature of which is related to its habit of gliding over and grazing from surfaces. The number of mechanically inter-related features is always great, sometimes exceedingly so, and co-ordination is of a high order. Indeed, at the purely mechanical level, the Anomopoda, of whose total diversity the Chydoridae represents only one segment, can perhaps claim to exhibit a correlation between structure and function whose complexity is scarcely exceeded elsewhere in the animal kingdom. This contradicts the not infrequent assertion that small arthropods are simpler in structure, both externally and internally, than are related larger forms.

In addition to specialization of the whole animal the evolution of particular organ systems has taken place, as in the specialized trunk/post abdomen joint of *Alonopsis*, *Acroperus* and *Camptocercus*, so that an otherwise generalized species may exhibit great specialization in one feature (this joint in *Camptocercus*, the dorsal keel of *Acroperus*, etc.). So integrated are these constellations of anatomical features that without a single seta or even the setules on it, a complex mechanism may be rendered inoperative. Even minute differences may reflect considerable differences in function. For example, the hooks on the posterior dorsal corner of the mandibles of *Pseudochydorus* are minute and are not apparently greatly different from their homologues in detritus-feeding species, yet their function is completely different.

The significance of an apparently trivial feature may be revealed only intermittently. For example, the ejector hooks of trunk limb 1 are used by all species only when excess food accumulates at the anterior end of the food groove. Likewise, in *Graptoleberis* the spinules on the basal segment of the swimming setae of the antennae *would* be a 'meaningless ornamentation' if the animal was a persistent swimmer, or even if it swam and moved over surfaces in the way it habitually does but did not occasionally use its antennae in order to overcome obstacles.

Form is never 'bizarre' as often stated but is intimately related to habits and habitat preferences. The habits concerned are mostly those involving a relationship with a substrate and not those related to swimming abilities but this does not mean that swimming is not practised efficiently. Figure 148 shows that there is no apparent relationship between body form, or size, and swimming ability. Of the eight species which attain speeds of more than 12 body lengths/s, and which encompass a considerable size range, some are among the most rotund and others among the most elongate species. *Alonella exigua* is outstandingly swift by any criteria, and is specialized for swimming as well as creeping. If one discounts *Alonella nana*, *Chydorus piger* and *Graptoleberis*, whose slow swimming speeds reflect specialized habits, there is perhaps a trend towards an increase in swimming speed in terms of body lengths (but not absolute speeds) with decrease in size. *Alonella exigua*, by far the swiftest, is one of the smallest species.

Although adapted particularly for life on the bottom or among vegetation, many chydorids are nevertheless more efficient swimmers than fishes in terms of the number of body lengths which they can cover per unit of time. For fishes the best authenticated speed is 13·4 body lengths/s for the tuna, and although several species can sustain speeds in excess of 10 body lengths/s, for 1 min (Bainbridge 1958) many cannot. *A. exigua* can sustain over 31 body lengths/s for what is perhaps as long a period as it usually swims in nature and can achieve almost 47 body lengths/s for short bursts. Apart from the metabolic limitations of fishes, this difference is related to differences in bulk in obvious ways. For example, slowing down would present serious problems to a large fish travelling at such speeds. So many factors are involved in the determination of swimming speeds, such as

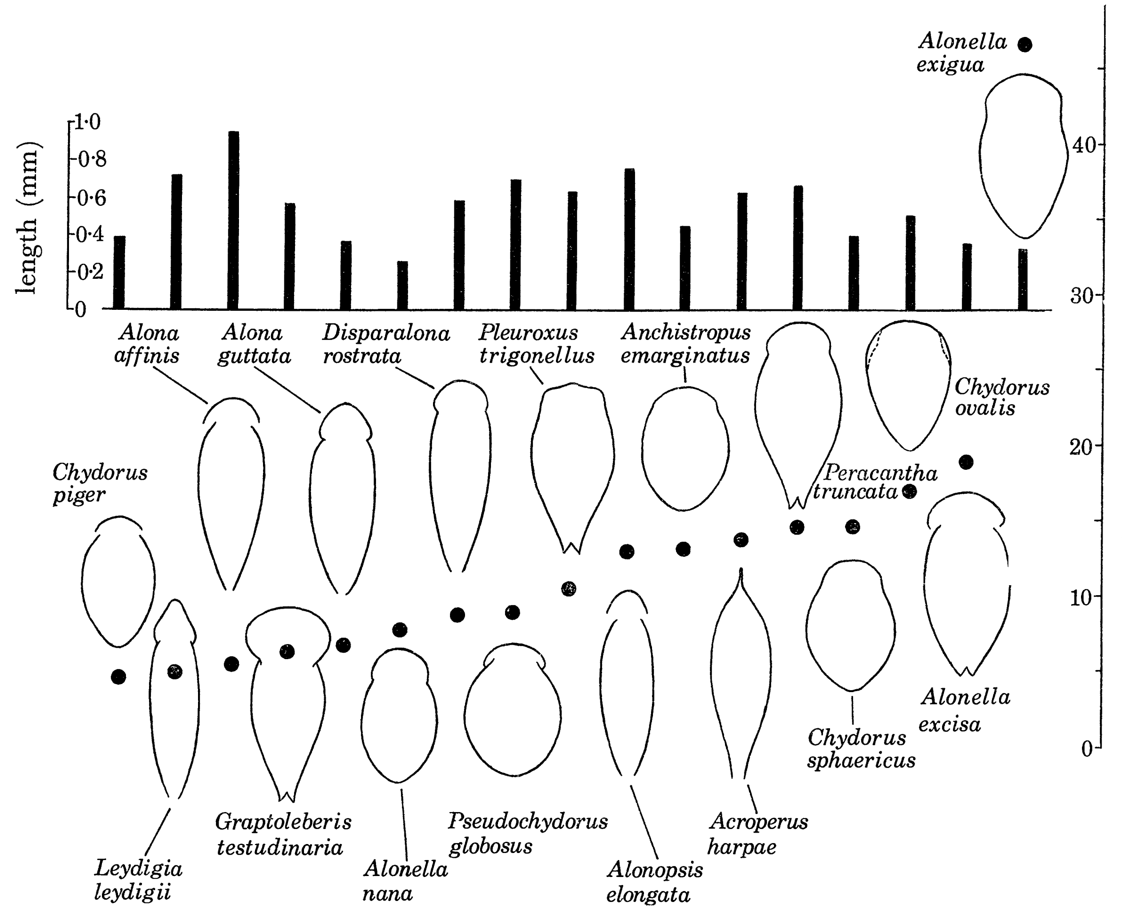


FIGURE 148. Form, size, and swimming speed in certain Chydoridae. The outlines, which are not all drawn to the same scale, show either a dorsal view or the animal in horizontal section at or near its maximum width. The species tested are ranked in order of speed (black circles). The speeds given are the maxima recorded, and in perhaps all cases are probably exceeded at times (see text). Lengths are those of the individuals used in tests (always parthenogenetic females) and, while giving a good indication of the relative size of the species concerned, do not represent the maximum achieved by a particular species. Reliable measurements are available also for *Pleuroxus uncinatus* (not shown). Its size and shape are almost exactly the same as those of *P. trigonellus*. The maximum recorded speed is 14·1 body lengths/s (10·6 for *P. trigonellus*).

body form (which influences the volume : surface area relationship as well as the magnitude of drag), length of the antennae and their swimming setae, and frequency of antennal beat, that detailed investigation would be necessary to render intelligible the facts obtained. Hydrodynamic problems presented by these small moving bodies are intriguing; not least in potential interest being the way in which species such as *A. exigua* can overcome inertia and accelerate so rapidly, for total drag increases greatly with increase in velocity.

It is clear that, in the evolution of the Chydoridae, a change in habits must sometimes have preceded structural changes. This is most clearly exemplified in the progressive specialization of the ventral carapace margins, which trend must have been initiated by the habit of supporting the body on unelaborated ventral margins, much as *Alonopsis* does today. This is an example of an evolutionary change of the kind recognized by Watson (1949) and Manton (1963) but of which no crustacean example appears ever to have been quoted. Such changes, while not imposed by the environment, have been more important in relation to major steps in evolution than changes associated with ever increasing specialization for the exploitation of a particular niche. It is also one of those adaptations which 'facilitate particular habits of life, which lead to better and easier living in a variety of habitats' and which 'result in persistent and far-reaching evolutionary advance' (Manton 1963). 'It is not easy to recognize which, among the many things an animal does, represent the habit or habits of real evolutionary importance' (Manton 1963) but the use of the ventral carapace margins by the Chydoridae appears to be one such habit.

Correlations between structure and environmental preferences of the Chydoridae have hitherto been largely ignored. Much effort has, however, been made to demonstrate correlations between the occurrence of particular anomopods and chemical conditions of the environment, often with equivocal results. This study demonstrates the supreme importance of structure in determining whether or not a chydorid can live in a particular situation. On the other hand, when correlations between distribution and water chemistry appear to exist, they are often likely to be indirect and to reflect the chemical needs of plants among which chydorids live—or shun. Many species are tolerant of a wide range of such environmental variables as temperature, oxygen content, pH, and salt content. A direct correlation in some cases is not denied, and extreme conditions will obviously exclude species, but many are relatively indifferent to chemical conditions, provided 'grosser' features of the environment are satisfactory. These include the nature of the substratum—whether muddy, sandy, rocky or otherwise—the presence of particular kinds

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DESCRIPTION OF PLATE 18

FIGURES 149, 150. *Graptoleberis testudinaria.*

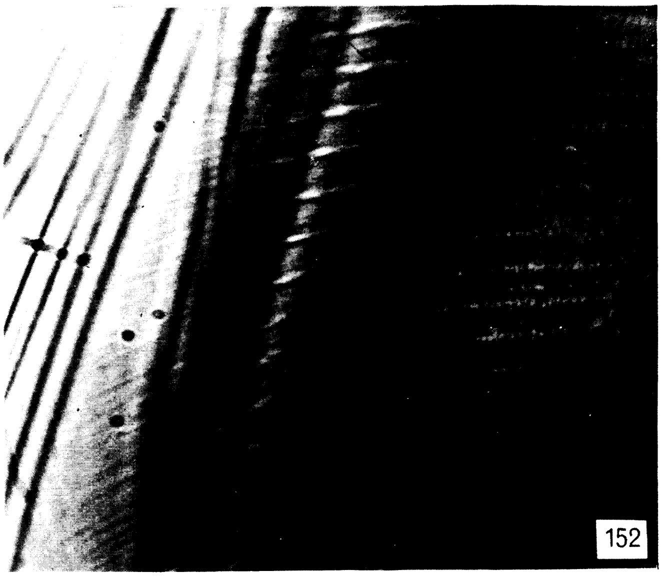
FIGURE 149. An individual (length *ca.* 0·56 mm) attached to and gliding over a surface. The surface on which it is moving is a strip of glass cut from a cover slip whose cut end can be seen at the bottom of the picture. Although here gliding horizontally on a vertical face *Graptoleberis* can move with equal facility in any direction on surfaces orientated in any plane.

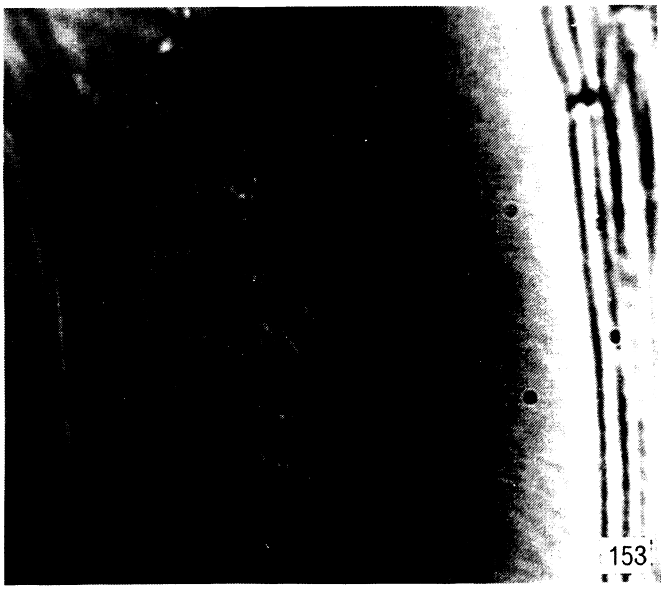
FIGURE 150. Another attached individual seen from a slightly oblique angle. The animals reflexion is clearly seen on the glass surface over which it is gliding. Although the reflected light mars the clarity of the ventral parts of the animal itself, the existence of a reflexion is particularly informative in indicating where the animal makes contact with the substratum. Note, for example that the outstretched sensory seta of the antennule touches the substratum anteriorly and that the claws of the post abdomen do not quite do so. The reflexion also reveals the under surface of the right-hand side of the headshield and in fact portrays the shape of this part of the body more clearly than does the image of the animal itself. In each photograph the animal is in focus at a level which does not permit the antennae to be seen although they lie outside the carapace.

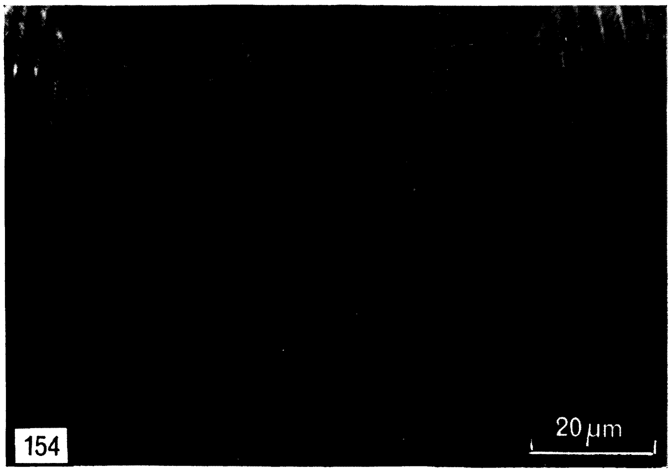
149

150


151


152


153


154


155

of vegetation, adequate supplies of food, and so on. All these are intimately related to structural features, and it seems curious to look for differences of a few milligrams/litre of calcium as an explanation of the distribution of animals whose structure and habits are as different as those of *Graptoleberis*, *Pseudochydorus* and *Leydigia*. As old inhabitants of freshwater, chydorids must long ago have made the physiological adjustments necessary to allow them to tolerate such differences in their chemical environment as are generally experienced. The claim is therefore made that structural features and the habits with which they are inseparably linked, together with biotic factors, such as the presence of particular predators, are in general more important than chemical factors in the ecology of the Chydoridae. Study of these factors seems likely to be more fruitful than attempted correlations with the chemistry of the environment have proved to be.

During the course of this investigation I have received both practical and clerical assistance first from Miss A. Cumbus (Mrs Walling) and later from Miss O. Forshaw. Dr D. Flössner and Mr W. J. P. Smyly kindly provided preserved material of species which I was unable to collect myself, and Mr Smyly has allowed me to refer to his unpublished data on the depth distribution of certain benthic species. Dr H. Y. Elder prepared for examination with the electron microscope sections of the carapace setae of *Graptoleberis* which provided much useful information. Helpful and stimulating suggestions were made by Mr F. J. Mackereth when I was attempting to elucidate the method of attachment of *Graptoleberis* and Mr J. E. M. Horne kindly translated papers written in Russian. To Dr Sidnie M. Manton, F.R.S., and Dr J. P. Harding I am particularly indebted for reading the manuscript. Their criticisms and suggestions have been extremely helpful. To all these I express sincere thanks.

Description of plate 19

Figures 151 to 155. *Graptoleberis testudinaria.*

Figure 151. Ventral carapace setae of the median series seen from below as a living animal glides beneath a coverslip. The level of focus is such that the setae are seen in optical section. This and the next two photographs were obtained by use of an oil immersion objective.

Figure 152. The same at such a level of focus that the fine ventral setules on which the animal rests can be seen. Note how the setae at the top right-hand corner of the photograph, i.e. the more anterior setae, lie deeper than the posteriormost (cf. figure 78, p. 306).

Figure 153. Another specimen at the level of focus which gives some impression of the length of the ventral setules and shows how some of those on the more anterior median setae curve inwards (cf. figure 72, p. 303).

Figure 154. The gap at the posterior limit of the embayment and the setae of trunk limbs 3 and 4 which seal it (cf. with figure 68, p. 301). The setae seen here are essentially those of trunk limb 3. The level of focusing is such as to show how the gap is sealed by a continuous wall of fine setules.

Figure 155. The same focused to show some of the setae in optical section. One of the setae of trunk limb 4 is now clearly seen. The dark structures at the bottom of the photograph are the claws of the post-abdomen. Here on both sides the long seta of trunk limb 3 passes between them; in figure 154 the seta of the left limb passes to the outside of the claws.

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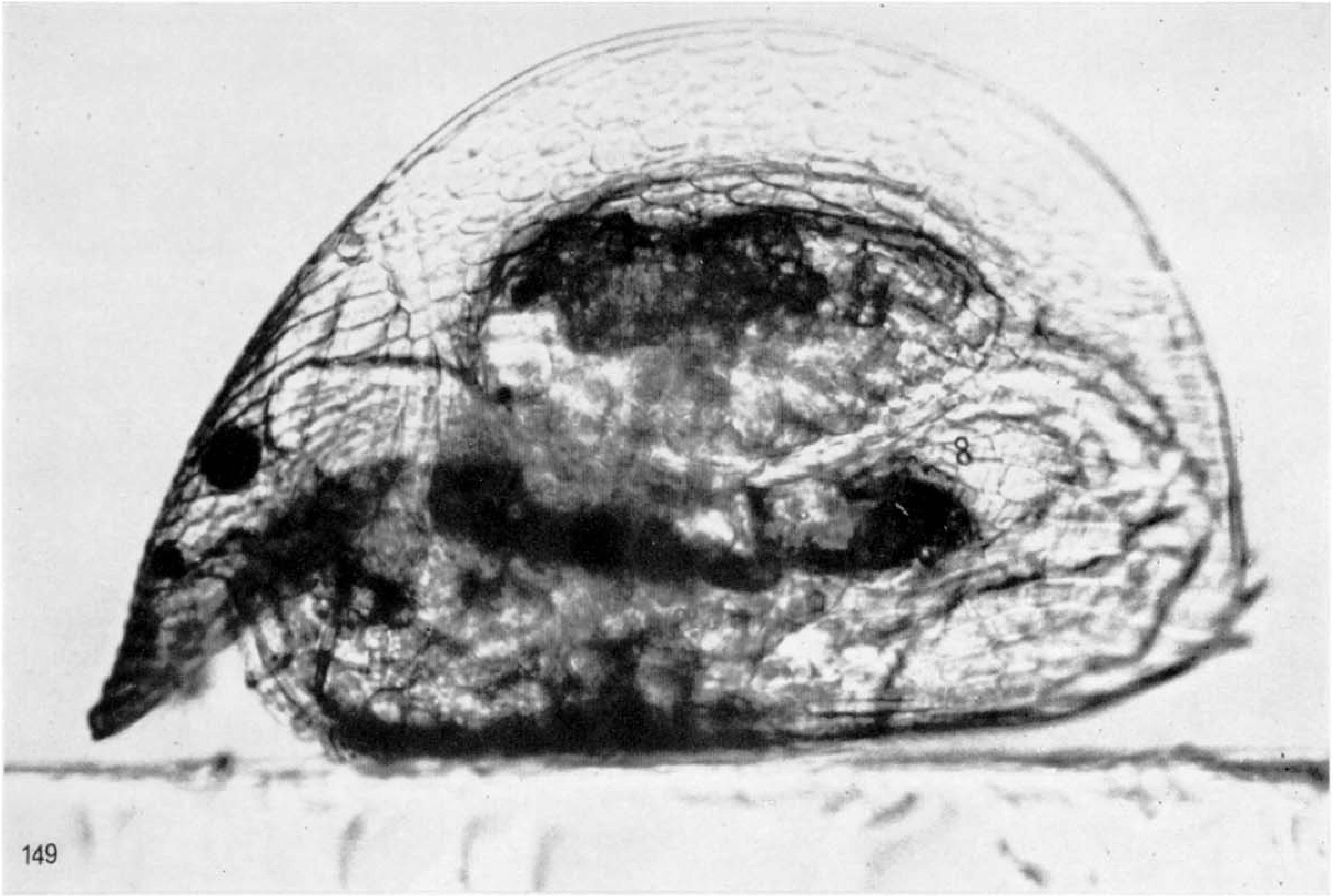
List of abbreviations used on figures

A1	Antennule
A2	Antenna
AAF	Accessory anterior flange
AC	Alimentary canal
ACM	Anterior carapace margin
AD	Apodeme
ADGC	Anterior distal gland cells
AEP	Anterior endoskeletal plate
AF	Anterior flange of carapace
AFG	Anterior end of food groove
AGS	Anterior gnathobasic seta of trunk limb 2
AM	Adductor muscle of carapace
AMS	Anterior marginal setae
A2 MUS	Antennary muscles
AR	Articulation
ARM	Accessory remotor muscles
AS	Anterior (ventral) setules of marginal seta
AS2	Anterior spine of trunk limb 2
ASS	Anterior sensory seta of antennule
A SUS	Accessory suspensory ligament
B	Blue-staining endocuticle
BA	Basipodite of antenna
BS	Basal spinules of trunk limb 5
BS3	Brush seta of trunk limb 3
C	Carapace
CC	Carapace cuticle
CCM	Circular oesophageal constrictor muscles
CE	Chitinous elaboration within carapace
CPA	Claw of post-abdomen
CR	Crack
CS	Carpet of setules clothing posterior face of gnathobase of trunk limb 2
CTL1	Claws of trunk limb 1
DA	Dorsal aperture
D Add	Dorsal adductor muscle
DG	Duct of labral glands
DK	Dorsal keel
DMC	Dilator muscle of mandibular cavity
DMG	Duct of maxillary gland
DMS	Distal marginal spines
DS	Ventralmost distal spine
DS3	Distal scrapers (spines) of trunk limb 3
DS4	Distal spine of trunk limb 4
E	Compound eye
E5	Endite of trunk limb 5
EFC	Entrance to filter chamber
EGS	Elongate gnathobasic seta of trunk limb 3
EH	Ejector hooks of trunk limb 1
EM	Embayment
EN	Endocuticle
EP	Epidermis
EPC	Epicuticle
ES3, 4	Endite spines of trunk limbs 3, 4
EX3	Exopod of trunk limb 3
EXS4	Exopod setae of trunk limb 4
F	Flange
FC	Fibrillar cells
FFA2	Flat face of basis of antenna
FG	Food groove
FOR	Fornix
FP3, 4, 5	Gnathobasic filter plate of trunk limbs 3, 4, 5
FTL1	Flattened ventral face of trunk limb 1
GC	Gland cells; presumed origin of secretions
GL	Gelatinous layer
GP2, 3, 4, 5	Gnathobasic plate of trunk limbs 2, 3, 4, 5
GS	Gnathobasic sweeper of trunk limb 3
GS2, 4, 5	Gnathobasic setae of trunk limbs 2, 4, 5
GTL2	Gnathobase of trunk limb 2
H	Large hook of trunk limb 1
HC	Cuticle of head
HP	Head pore
HS	Headshield
HSC	Headshield cuticle
IGS	Internal gnathobasic spine
IL	Inner lobe of trunk limb 1
INT	Intestine
IS	Inner spine
IVS	Inner vertical seta of trunk limb 5
IW	Inner wall
K	Keel of labrum
L	Labrum
LAP	Limit of armour-plating of food groove
LCM	Longitudinal oesophageal constrictor muscles
LGS	Labral gland secretions
L Mand	Left mandible
LS	Lateral squamae
LVF	Lobe from which first ventral fan arises
Mand	Mandible
MD	Marginal denticle
MS	Marginal seta
MSE	Marginal setae of embayment region
MT	Marginal tooth
MTM	Major transverse muscles of mandibles
MVS	Medium ventral setae
Mxlle	Maxillule
NFS	Non-filtratory setules

O	Ocellus
OCM	Opposed carapace margins
ODM	Oesophageal dilator muscles
OE	Oesophagus
OFP3, 4	Outer filter plate of trunk limbs 3, 4
OGS3	Outer grid of spines of trunk limb 3
OR	Opening of reservoir of trunk limb 1
OS	Outer sieve of trunk limb 3
OS1	Outermost seta
OS2	Outermost spine on trunk limb 2
OVS	Outer vertical seta of trunk limb 5
P	Papilla of antenna
PA	Post-abdomen
PAS	Post-abdominal seta
PDGC	Posterior distal gland cell
PEP	Posterior endoskeletal plate
PG	Posterior gap
PH	Posterior hooks of mandibles
PM	Plate-like extension for insertion of muscles
PR	Posterior rib
PS	Posterior (dorsal) setules of marginal seta
PSFP3	Posterior seta of filter plate of trunk limb 3
PSG	Posterior spinules of gnathobase of trunk limb 2
PV	Pivot
PVS	Posterior ventral setae
R	Thickened rim of headshield
R1	Reservoir of trunk limb 1 containing entangling secretion
R4	Reservoir of entangling secretion which discharges on trunk limb 4
RLG	Reservoir of labral gland
R.Mand	Right mandible
RMVS	Rudiment of median ventral seta
RP	Red-purple staining endocuticle
RS	Rostrum
S	Sensory setae of antenna
S1	Entangling secretion issuing from first trunk limb
SA1	Sensory seta of antennule
SB	Spinule at base of median ventral seta

SBS	Shaving-brush seta of trunk limb 2
SC	Scrapers of trunk limb 1
SL	Sealing seta
SLS	Seta of lateral squama
SMS	Sub-marginal spinules
SOVS	Setules of outer vertical seta of trunk limb 5
SP1	Proximal endite spine (no. 1) of trunk limb 2
SP6, 7	Endite spines no. 6, 7, of trunk limb 2
SS	Screening seta
SS2	Screening setules of trunk limb 2
SSA	Swimming setae of antennae
SSL	Setules of sealing seta of trunk limb 1
ST	Stomach
STL1	Setules of trunk limb 1
SUS	Suspensory ligament
SV	Selvage
SW	Sweeping seta of trunk limb 2
T	Tip of posterior (dorsal) setules of median ventral setae
TC	Thickened and sclerotized cuticle
TCB	Transverse chitinous bar
TL1, 2, 3, 4, 5	Trunk limbs 1, 2, 3, 4, 5
TM	Thickened margin
TMM	Transverse mandibular muscle
TMT	Transverse mandibular tendon
TR	Tip of rostrum
TS	Tuft of spinules of trunk limb 1
TSS	Thick sarcoplasmic sheath
U	Unstained, amber-coloured epicuticle
V Add	Ventral adductor muscle
VCM	Ventral carapace margin
VCT	Ventral carapace tooth
VDS	Ventralmost distal spine
VF	Ventral flange
VLM	Ventral longitudinal muscle
VS	Vertical setae of trunk limb 5
1, 2, 3, 4,	Trunk limbs 1, 2, 3, 4
3′	Promotor roller muscles
4′	Remotor roller muscles
5c	Transverse muscles of mandible
5a, b, d	Minor transverse muscles



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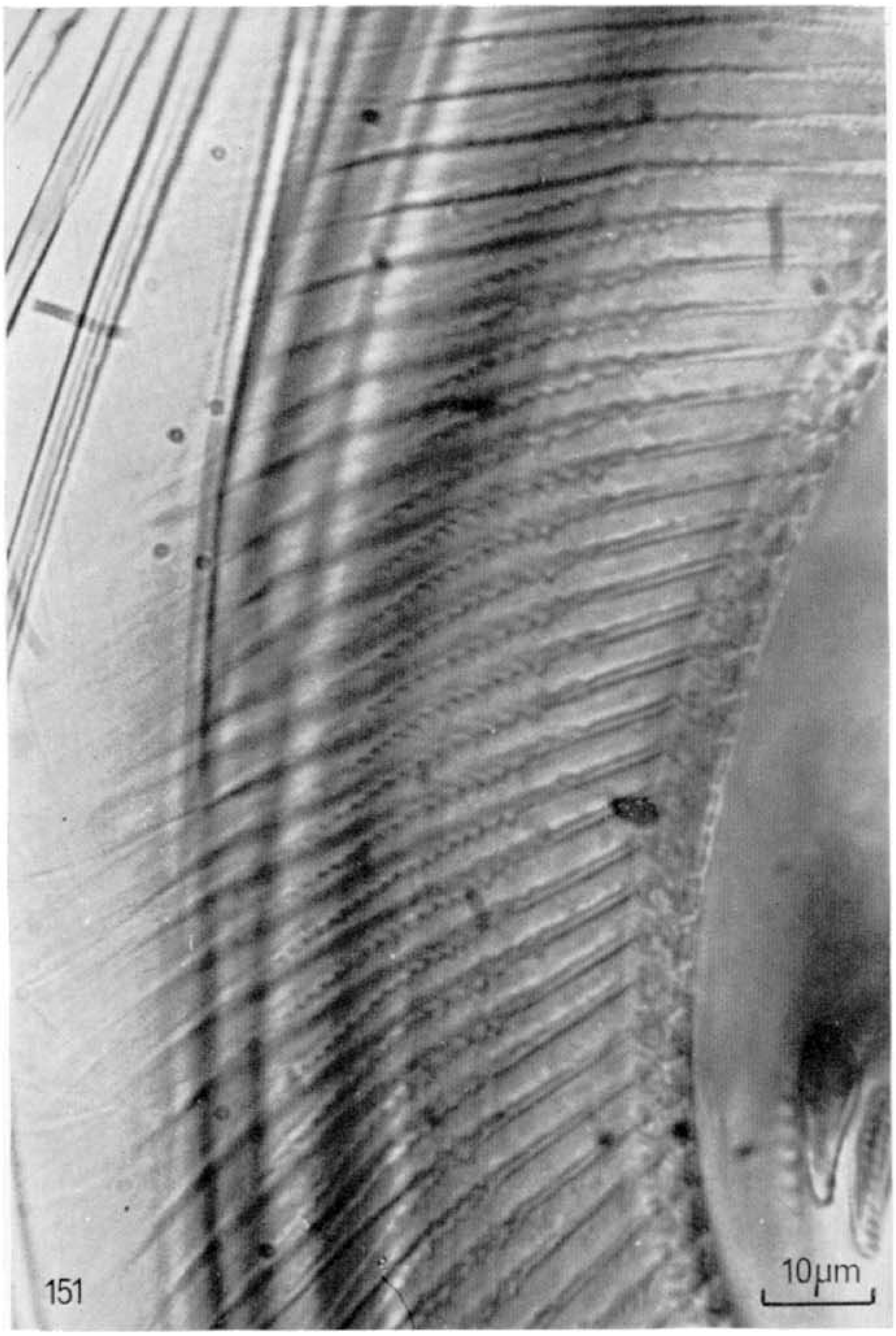
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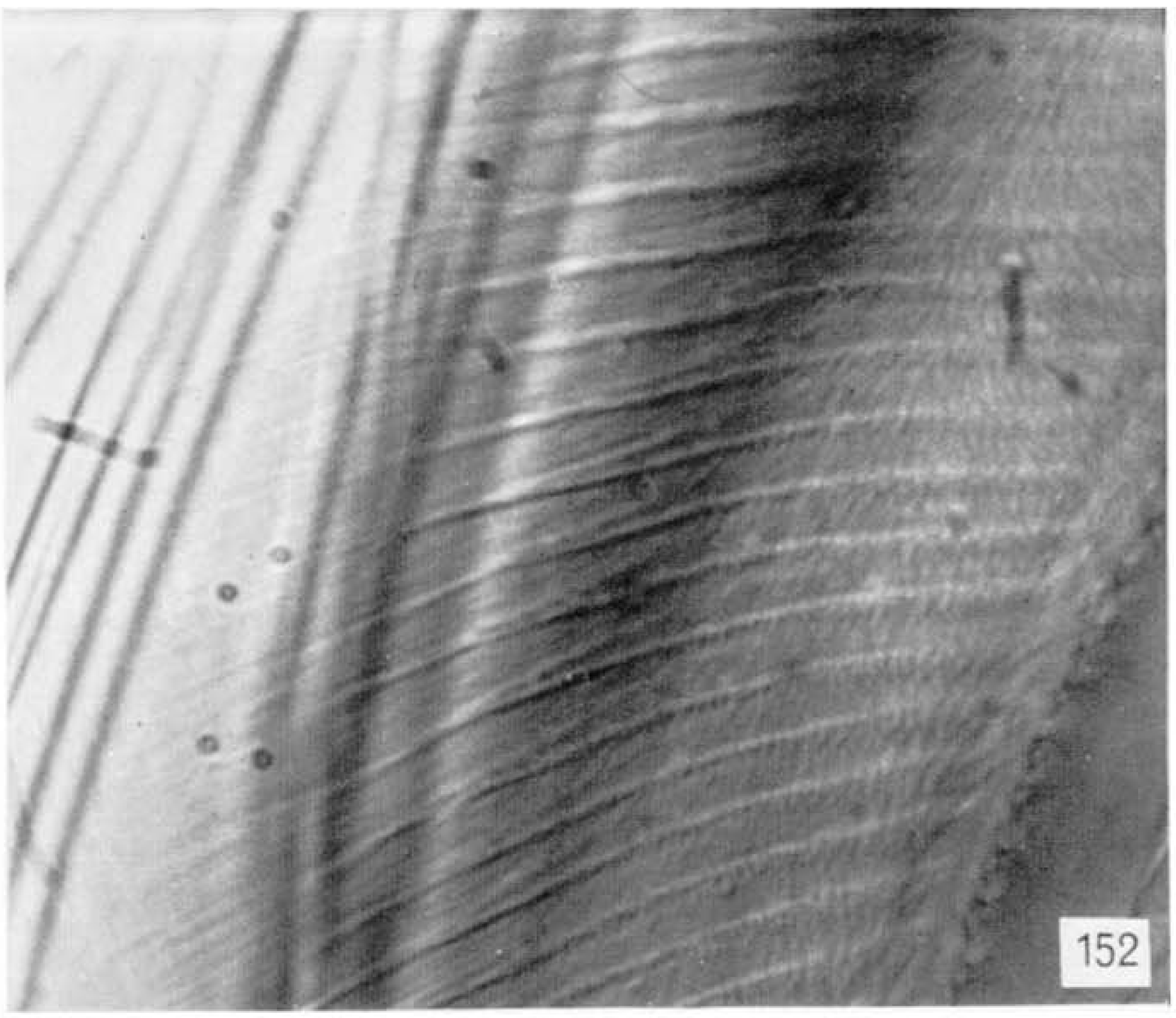
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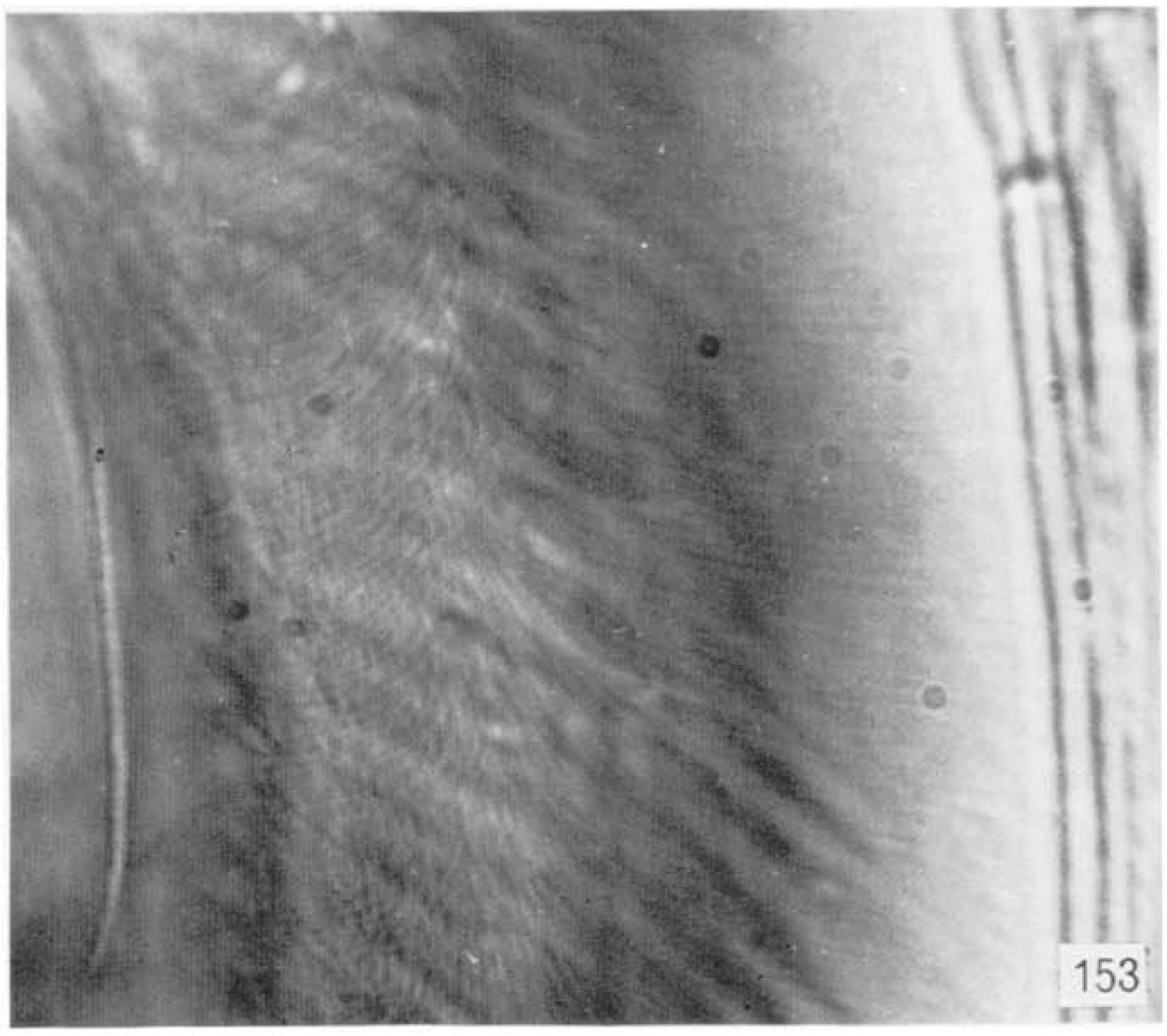
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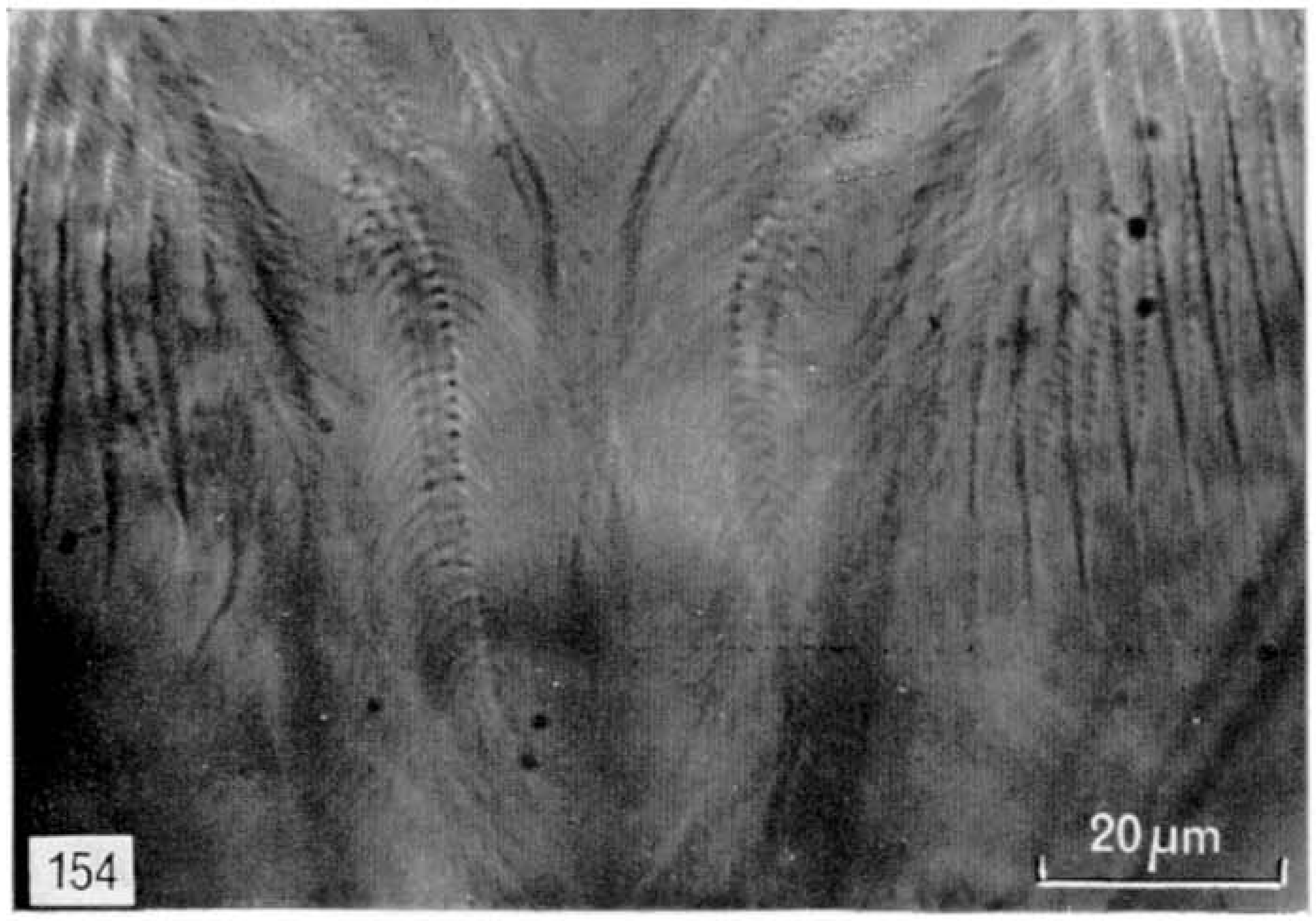
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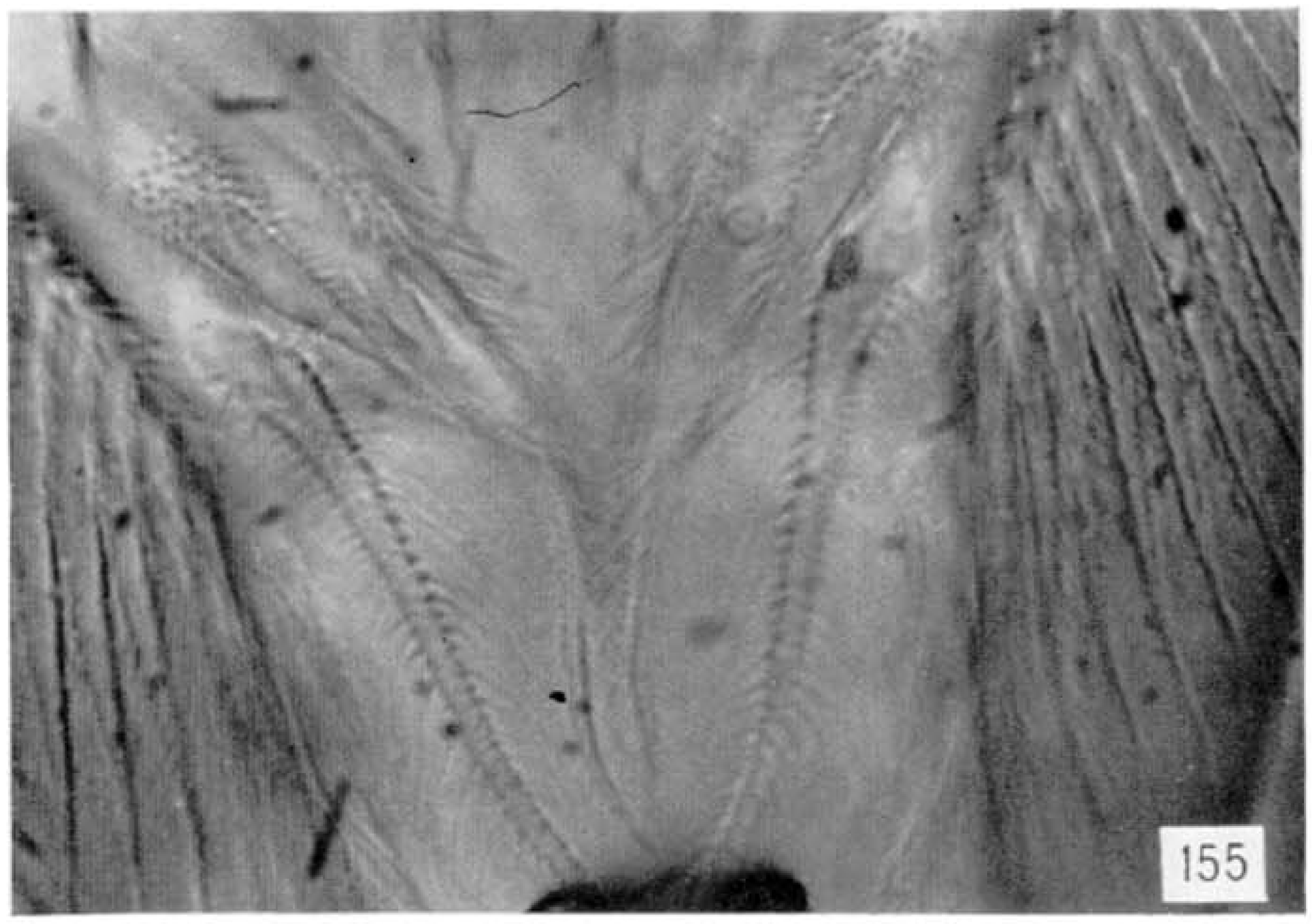
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