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STUDIES ON THE FUNCTIONAL MORPHOLOGY AND BIOLOGY OF THE NOTOSTRACA (CRUSTACEA: BRANCHIOPODA)

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CONTENTS

(In this abstract, numbers in parentheses refer to key figures in the text which facilitate understanding.)

Selected aspects of notostracan morphology are considered from a functional standpoint and related to habits whenever possible.

Scanning electron microscopy and observations on the early stages of development have revealed differences, some of functional significance, between what have been regarded as no more than racially different populations of certain species. These suggest that our taxonomic understanding of the Notostraca is still incomplete.

The natural history and general habits of notostracans are briefly described. Many structural features are related to benthic habits. The development of a dorsal, dome-shaped carapace (2 and 3) has probably influenced the evolution of the trunk and other features involved in maintaining hydrodynamic efficiency when swimming.

Eggs, which in some species are firmly attached to substrata (4), are probably less easily dispersed than often supposed. Besides its ecological significance, this has a bearing on taxonomy, zoogeography and evolution.

The gross morphology of the trunk limbs is re-described as an essential preliminary to interpreting function, and various hitherto undescribed structural features are reported. The anterior series of trunk limbs (5–9) fulfil a multiplicity of roles (in standing, swimming, digging, clambering, food collection and manipulation, egg-carrying, respiration and sensing the environment) and have evolved within the constraints imposed by the overlying carapace, whose presence has, conversely, been exploited. Limbs of the posterior series (10–15) are less constrained by the carapace and have developed large exopodite paddles that set up a respiratory stream, but they are also involved in food handling.

Scanning electron microscopy has revealed details of trunk limb armature previously poorly known and often of great complexity. Many of the spines and setae that play an important part in food handling are hinged at the base in a characteristic manner (21, 24, 33, 34 and 40), a feature of great functional significance.

Spectacular groups of sensillae are present on the trunk limbs of *Lepidurus apus* (54–62). The profusion of sensillae on the trunk limbs of the Notostraca stands in marked contrast to the situation in other branchiopods and is probably related to the versatility of food collecting techniques employed, which necessitates an ability to handle a wide range of food items, ranging from detrital particles to large prey organisms.

An account of the functional anatomy of the head (63–67) is presented. The mandibles are biting appendages (29, 69–71, 87 and 102) that can abduct widely. In this they contrast strikingly with the rolling, grinding and crushing mandibles of most branchiopods whose ability to abduct is extremely limited. Nevertheless they share

many features with such mandibles. Skeletally they have the same hollow, boat-like structure, but their armature is very different, consisting of heavily sclerotized, toothed ridges with additional refinements (69–76). The articulating surface is broad (68), not pointed as in most branchiopods. There is a massive transverse mandibular tendon (64, 81, 82, 85, 87, 88 and 90) homologous with that of other branchiopods but vastly thicker. On each side it is suspended and braced by three dorsal ligaments, and braced by an anteroventral ligament and by four dorsal muscles (66, 67, 87 and 88). It is also supported posteriorly by a pair of complex cuticular apodemes and anchored by fibres to simpler anterior apodemes (64–66, 91 and 93).

The mandibular muscles share many basic attributes with those of other branchiopods but differ strikingly in ways that are related to the different actions that notostracan mandibles and those of the rolling and grinding type have to perform. The transverse muscles originate essentially from the ends of the transverse mandibular tendon (19, 81 and 102). None does so from the main part of its posterior face as they often do in other branchiopods. There are no 5c muscles, in which respect adult notostracan mandibles appear to be unique among branchiopods. Abduction is achieved by dorsally located abductor muscles (66, 67, 86 and 87) that have no counterpart in other branchiopods. The broad articulating surface can slide as these muscles contract, allowing abduction of the molar regions.

The paragnaths, maxillules, maxillae and post-mandibular apodemes make up a functionally integrated complex (64, 66, 67, 94, 97 and 99). The maxillules (100 and 101) are much more complex than hitherto appreciated and far more so than in any other order of the Branchiopoda. Each is two-segmented, the proximal segment having elaborate armature. Intrinsic and extrinsic muscles are involved in maxillulary movements. Among their several roles the post-mandibular apodemes provide firm anchorage for the ventral longitudinal muscles of the trunk (81).

In contrast to the fleshy labrum of most branchiopods with its often conspicuous labral glands, that of the Notostraca is a flattened structure that lacks labral glands (63 and 64).

Standing, swimming and digging are important elements in the life of notostracans and are related to feeding habits. Aspects of trunk limb structure in relation to the feeding mechanism are discussed. Notostracans feed both on finely particulate material and on large items. These food sources call for different handling techniques, both of which are described. In neither case is filtration involved. In both, food is passed forward along, or adjacent to, the shallow food groove from gnathobase to gnathobase and eventually to the mouthparts. The morphological specializations involved in the process and in the actions of the mouthparts are described.

Notostracans hatch as nauplii (119 and 120) (with the possible exception of certain populations of *Lepidurus arcticus* in which this stage may have been eliminated, though the evidence is ambiguous). These do not feed. Feeding begins at stage 2 in *Triops*. Food is collected by the mandibular palps and passed to the oesophagus by a masticatory spine on each mandibular gnathobase (105). At this stage the gnathobase has no armature on the prospective masticatory surface, exactly as in the Anostraca. Proximal masticatory spines of the antennae help to pass food forward but the distal masticatory spines do not collect food and, in *T. cancriformis* at least, seem not to play any part in food handling. In *T. cancriformis* the mandibular gnathobases develop their first masticatory armature at stage 3 (106).

During subsequent ontogeny in *Triops* the naupliar mechanism is gradually replaced by that of the adult. Development is essentially anamorphic but the trunk limbs develop at much earlier stages than in the Anostraca.

Lepidurus arcticus hatches as a non-feeding nauplius that very quickly moults to a stage much more advanced than stage 2 of *Triops*, there being a virtual metamorphosis at the first moult. Although the second instar swims by an essentially adult (though still rudimentary) mechanism, it does not feed. Its mandibles indeed are incapable of

handling food, being in essentially the same state of development as those in stage 2 of *T. cancriformis* but with minute, non-functional gnathobasic spines (122). At no stage do the antennae possess either proximal or distal masticatory spines (121), and the mandibular palps never collect food. There is in fact no naupliar feeding mechanism. When feeding begins, at stage 3, the mechanism involved is already of an essentially adult type.

Although the absence of the 5c muscles of the transverse mandibular series is an outstanding feature of adult notostracans, these muscles are present in the early stages of development (116, 125 and 129).

Swimming of the early stages of *Triops* has been analysed. As in early anostracan larvae the nauplii and early post-naupliar stages inhabit a low Reynolds number environment and have essentially no momentum. Oar-like movements of the antennae propel the larva forwards during the working stroke but, as soon as this impetus ceases, so does forward motion, and during the recovery phase of the cycle of antennal beat the larva moves backwards (130 and 131). Over a series of moults this mechanism is gradually replaced by the adult mechanism as the trunk limbs develop and the antennae atrophy.

A comparison between the early stages of the Notostraca and Anostraca from both functional and evolutionary standpoints reveals striking differences, as well as similarities that are probably indicative of remote common ancestry.

The Notostraca occupy an isolated position within the Branchiopoda. Although primitive, the Notostraca may be less so than the Anostraca.

1. INTRODUCTION

Although, since the pioneering study of Schaeffer as long ago as 1756, branchiopod crustaceans of the order Notostraca have not lacked competent investigators, various aspects of their functional morphology have remained unclear or unstudied. Since Schaeffer's time their primitive nature, long fossil record and evolutionary conservatism have become apparent and their interest to the student of crustacean phylogeny has grown accordingly. Notostracans assignable to the extant genera *Triops* and *Lepidurus* are known from as far back as the Triassic and the group existed in the Carboniferous, though only carapaces of that age are known. Fossilized trackways of Late Palaeozoic age are conceivably the work of notostracans (Pollard 1985). Morphological evolution has been exceedingly slow, some Triassic fossils being inseparable from the extant *Triops cancriformis* (Bosc) on morphological criteria (Trusheim 1938; Longhurst 1955*a*). Eldredge's comments (1984) on the condition of these fossils were uninformed: far more details are preserved than he believed. The fossils of Lower Triassic age described by Gall (1971), likewise attributed to the extant *T. cancriformis*, are also remarkably well preserved. These, fossilized in various postures, reveal details not only of gross form, with the carapace *in situ*, but of trunk segmentation and of the appendages. Notwithstanding criticisms of this concept by Schopf (1981) present-day notostracans can conveniently be referred to as 'living fossils', and certainly as phylogenetic relicts (Fryer 1985).

As a pioneer study, that of Schaeffer was remarkably detailed and, for that early period, well illustrated. Previous references to the Notostraca could have helped him scarcely at all. He not only described the general form of both *Triops* and *Lepidurus*, which he recognized as distinct, but provided details of the limbs supported by better illustrations than those used by such a celebrated zoologist as Lankester (1881) well over a century later, and described not only the trunk limbs but the mandibles and even the minute antennae. Internal anatomy, revealed by dissection, was not ignored and he provided information on development and habits.

Since Schaeffer's time, valuable accounts of the anatomy and development of notostracans have been given for *Triops* by Claus (1873) and for *Lepidurus* by Brauer (1874) and Sars (1896), and the appendages of *Triops* were discussed, with rather crude illustrations, by Lankester (1881). An entire book centring on the Notostraca (Bernard 1892) has also been published but, although not without value, often treats topics at a crude level and is much concerned with now-discredited phylogenetic speculations. Its writer had never seen a living notostracan and, by assuming that these animals always 'swim on their backs', which indicates profound ignorance of the functional significance of many structures, acquired beliefs that are completely erroneous. The paucity of modern studies is epitomized by the reproduction of one of Sars's figures in works published in 1982 and 1983 (in each case borrowed via at least one intermediate author and giving no indication that the true source was known) and, even more amazingly, by the reproduction of a figure 'after Schaeffer' in a textbook the second German edition of which appeared in 1967 and the English edition in 1970. Although a tribute to the lasting nature of Schaeffer's remarkable achievement this, perhaps the most durable example of a scientific illustration re-used in modern times, is symptomatic of current neglect of morphological studies.

Functional aspects, especially in relation to the handling of food, first studied by Schaeffer, have since been investigated by Lundblad (1920), Cannon (1933) and Eriksson (1934). All made useful contributions to our understanding of the processes involved but unfortunately none of them provided many illustrations so it is not always easy to visualize the processes described. Indeed we still lack an illustration that reveals the relation of the trunk limb gnathobases to each other except in so far as they can be seen from the ventral view of the whole animal. Scanning electron microscopy has also revealed hitherto unreported details of functional significance. The skeleto-muscular system has also been neglected, though we have a brief but excellent account of trunk musculature and some information on the cephalic endoskeleton given by Hessler (1964) for comparison with the Cephalocarida. For appendage musculature we have some information on the mandibles by Snodgrass (1950), a system whose function Mahoon (1960) attempted to elucidate, but whose anatomical data are incomplete and inaccurate and whose analysis is therefore defective, and a treatment of the trunk limbs by Preuss (1957) whose usefulness is reduced by the paucity of its illustrations.

The present account deals with selected aspects of notostracan morphology from the functional standpoint, some of which throw light on matters of phyletic interest.

2. Materials and methods

Triops cancriformis was reared from eggs present in dried mud originating in Spain, as was a single individual from the currently only known English locality (a pond in the New Forest). *T. longicaudatus* (LeConte) was similarly reared from mud originating in Texas, U.S.A. Sometimes the early instars were supplied with *Chlorella* but whether this was utilized is uncertain and, after using up their yolk, these stages generally obtained their food from material present in the mud from which they were hatched. Older stages were fed with 'Bemax' (a high protein breakfast cereal) and minute portions of the yolk of hard-boiled eggs. Large adults consumed such material as well as fragments of cooked meat, and were supplied with whatever small animals, usually crustaceans, were available. Adults of *Lepidurus arcticus* (Pallas) obtained from a small pond in Iceland were successfully transported alive to Britain where they flourished for some weeks. These were fed largely on *Daphnia*, which happened to be readily available at the time, and they also did much sifting of the organic bottom material from the habitat that was provided for them. These animals laid many eggs from which early instars were subsequently obtained. These three species provided the live material necessary for a variety of observations on both adults and juvenile stages and also material for fixation, mostly in Zenker's fluid but sometimes in non-alcoholic Bouin's fluid, for anatomical work.

Alcohol-fixed material of *Lepidurus apus* (L.) from Israel was available, as was material from Australia provisionally assigned to this species, though the populations were recognizably distinct (see §3). Similarly fixed individuals of *Triops granarius* (Lucas) from South Africa were also available. Although histologically inferior to Zenker- or Bouin-fixed material, the Palestinian† animals were useful for the muscular system, which was generally well revealed in sections. Skeletal features were perfectly adequate both for work on gross morphology and for scanning electron microscopy.

Sections, mostly thick, were cut from animals embedded in low viscosity nitro-cellulose and stained with Mallory's stain. Dissections were done as required. Scanning electron microscopy was done by orthodox methods on material prepared by critical-point drying and coated with gold palladium. Information was yielded on certain points by high-speed cinematography (100 frames s^{-1}).

3. A NOTE ON TAXONOMY

According to the careful taxonomic review of Longhurst (1955*a*) both the Palestinian and Australian material of *Lepidurus* used in this study should be assigned to *Lepidurus apus* which he says 'has the largest range of any known notostracan and shows very little variation over the whole area'. Longhurst recognized five geographical races or subspecies, Palestinian material being designated as *L. a. lubbocki* Brauer, Australian material as *L. a. viridis* Baird. The differences between these races, as defined by Longhurst, are, however, purely quantitative and would not permit the unambiguous recognition of a single individual whose provenance was unknown.

Although not concerned with taxonomy, this study quite incidentally revealed differences, at least in the material handled, between populations of what I initially regarded as widely separated races of a single species, differences that, moreover, appear to be of functional significance. Although these do not affect most generalized statements that can be made – indeed many such are applicable to the Notostraca as a whole – it is necessary to distinguish between Australian and Palestinian material at times. Unless otherwise stated all references to, and illustrations of, *L. apus* refer to Palestinian material. The morphological differences, and their functional significance, are referred to at appropriate points in the text.

That the situation may be more complex than this is indicated by the recent report of Thiery (1986) on the large branchiopods of western Morocco. Among the notostracans encountered was what is probably the same form as that from Palestine. Indeed North African material of this form has been referred to as *L. a. lubbocki* in the past. Basing his determination on the observations of Brtek *et al.* (1984) on Mongolian material, however, Thiery allocates his animals to *L. couesii* Packard. This species was placed in the synonymy of *L. apus* by Longhurst (1955*a*) but rehabilitated and re-described by Lynch (1972). As recognized at present,

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† This geographical term is used to comply with long-established usage and has no political significance.

L. couesii has a Holarctic distribution and Thiery (1986) attributes its apparent southern extension into Morocco to the influence of the cool, humid climate of the Atlas Mountains. This, however, would hardly apply to Palestine. In addition, examination of what is deemed to be the diagnostic distinction between the two species, namely the form of the exopodite of trunk limb one (Brtek *et al.* 1984) shows that the Australian material displays the same attribute as *L. couesii*, to which species it also should therefore perhaps be referred. If in fact the Australian animals belong to either species the range is enormous. Clearly this problem, which is of zoogeographical and evolutionary interest, requires further consideration from taxonomists, preferably utilizing scanning electron microscopy and electrophoretic techniques. For present purposes the least confusion is probably caused by using the name *L. apus*, even though this may require change in the future. The Australian animals may prove to be distinct from both *L. apus* and *L. couesii.*

That this is only part of a wider problem is indicated by the work of Campan (1929) which revealed differences between individuals of *L. apus* from a population in southwest France and those studied by Brauer (1874) from Germany. These he regarded as racial differences within a single species, but he also noted differences in the pattern of development (see §12) which may be more profound.

The problem is probably not confined to *Lepidurus*. Thus a few minor, but unambiguous, differences in larval morphology have been noted also between individuals from geographically remote populations of *Triops cancriformis* (see §11) of which species Longhurst (1955*a*) recognized three geographical races. At a different level, differentiation in isolation is also indicated by Longhurst's (1955*a*) demonstration of slight differences in protein specificity as manifested in differences in the wavelength of the axis of the oxyhaemoglobin-α band in populations of *T. cancriformis* from widely separated regions of Europe.

Such differences suggest that widely distributed taxa of the Notostraca are perhaps broken up into at least more races than has been supposed, or may even consist of several cryptic species. This would not be unexpected in such an ancient group, some of whose taxa, as currently recognized, appear to have extremely wide geographical ranges. The corollary of this is that dispersal, at least over long distances, is evidently less easily achieved than is sometimes assumed to be the case for organisms with small, drought-resistant eggs. (See also §4).

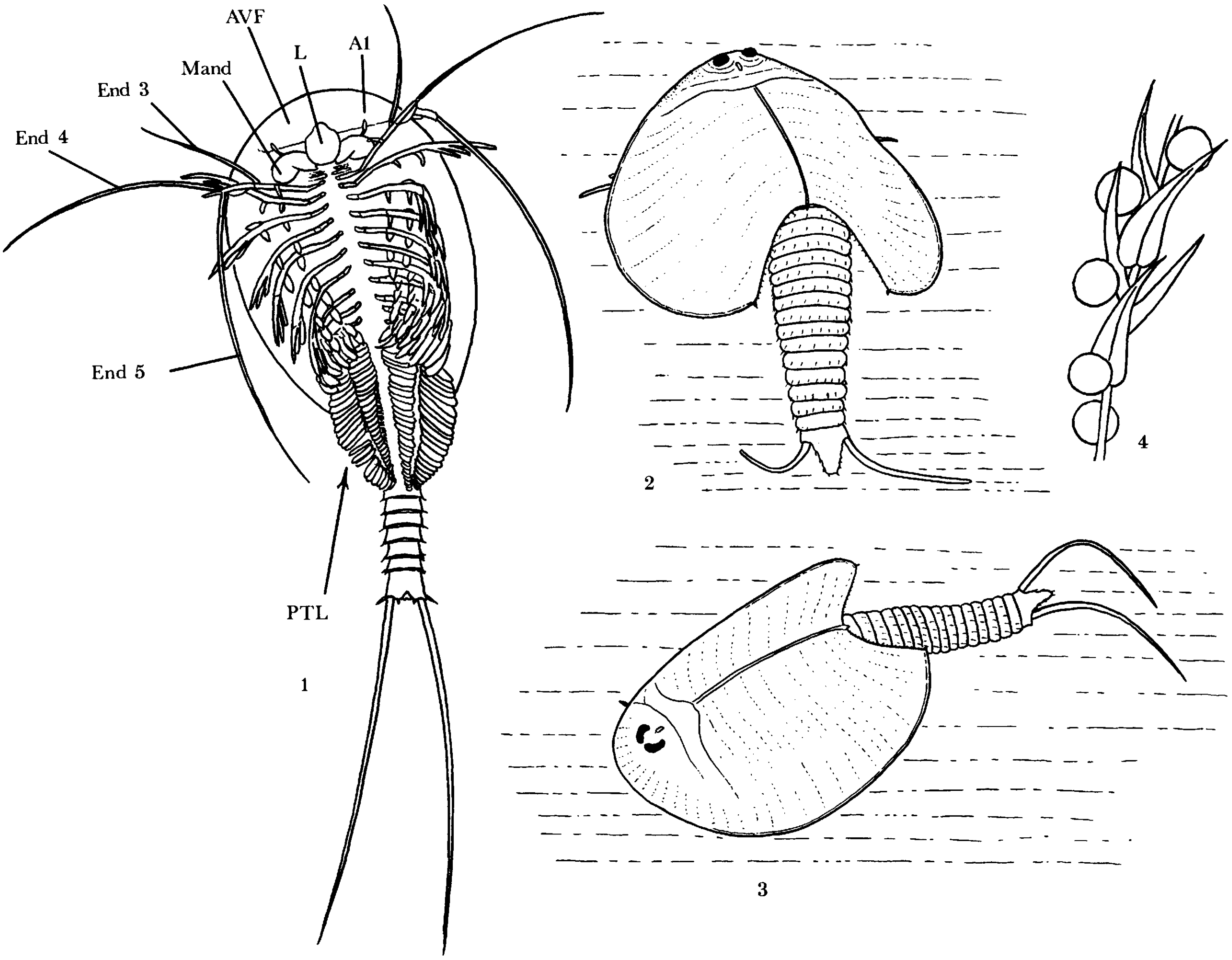
4. Natural history, general habits and some functionally related aspects of morphology

Save for Antarctica, notostracans have a virtually worldwide distribution but are sporadic in their occurrence, are absent from large areas, especially in the wet tropics, and are often rare in regions in which they occur. On the other hand they are sometimes locally common, especially in dry areas, and in some places have become pests of rice fields where they nip off the plumules and radicles of rice seedlings. There are but two extant genera, *Triops*, with four currently recognized species, and *Lepidurus* with seven, all of which are basically similar in major morphological features. All also share many similar habits but often differ markedly in broad ecological preferences. *Lepidurus arcticus* favours cool to cold régimes and is confined to arctic and sub-arctic regions – fossils show that it occurred in Britain during the Quaternary glaciations – whereas all the other species prefer warmer situations. There are hints that, in general, species of *Triops* are more warmth-demanding than those of *Lepidurus*. For example, in Australia *Lepidurus apus* frequents the cooler, moister regions, whereas *Triops australiensis* is widespread in the hot, dry interior from which *L. apus* appears to be absent (Williams 1968). Except for *L. arcticus*, which often lives in permanent water bodies as well as in temporary pools, and perhaps the little-known *L. lynchi*, notostracans are frequenters of temporary waters of various kinds.

Many scattered observations on general habits have found their way into the literature. Some of these were summarized and extended by Lundblad (1920) and Fox (1949). However, little has been done to relate structure to habits or to provide functional interpretations of the morphological features that are so important in the life of these crustaceans.

Notostracans (figures 1–3) are essentially benthic animals that for the most part keep close to the bottom over which they swim ventral surface down, progress usually being slow and intermittent. When occasion demands they climb or scramble over objects. Captive *L. arcticus* spent much time doing so among mosses from their habitat that were available to them, into thickets of which they often penetrated. All species sometimes burrow into soft flocculent deposits in quest of food that consists both of detritus and a variety of small organisms, though habitual burrowing has been disputed by Eriksson (1934). Johansen (1912) and Arnold (1966) report that *L. arcticus* sometimes buries itself completely in soft mud: according to Johansen sometimes only the eyes remain uncovered. This last observation seemed 'phantastisch' to Eriksson, who apparently never saw this species burrow in nature. He also found it difficult to understand the significance of shovelling with the carapace because, as he correctly noted, notostracans are what would now be called members of the epifauna. Nevertheless, shallow burrowing can be used as an alternative to surface skimming in the search for food particles and may unearth buried prey. Certainly individuals of *L. arcticus* (figures 2 and 3) observed during the present study were assiduous diggers and sifters of organic bottom material among which they were often partly hidden. Such habits, combined with the mottled pattern of the greenish brown carapace of this species, render it inconspicuous and help to explain its survival in certain lakes where it is preyed upon by salmonid fishes, and they are an advantage in shallow fishless ponds, where it is eaten by birds. That Eriksson never saw it burrow may reflect the kind of bottom on which he observed it.

Notwithstanding their benthic habits, however, notostracans occasionally make excursions into the overlying water where, as their gut contents sometimes reveal, they capture such swimming organisms as *Daphnia*. Such swimming is, however, slow, and calls for considerable effort, the animals having a greater density than water, no flotation devices, and a morphology adapted for different habits. The posterior, apodous, region of the trunk is extremely flexible as was made apparent by the delightful sketches of *T. cancriformis* given by Brauer as long ago as 1872. As Brauer showed, this ability is necessary to permit mating in bisexual populations. Of the species seen alive, *L. arcticus* in particular revealed the great flexibility of its trunk as it swam, sometimes contorting it rapidly and to a marked degree. The density of notostracans is advantageous as they forage over the bottom. Although they usually swim ventral surface down (figures 2 and 3) they sometimes do so inverted. At least in *T. cancriformis*, as Gaschott (1928), Fox (1949) and Hempel-Zawitkowska (1967), indicate, this is usually associated with visits to the surface beneath which it may swim for a time, charging the haemoglobin-containing blood with oxygen. Schaeffer (1756) had indeed recorded that in nature such inverted swimming took place towards evening on hot days when there had been strong sunshine. He suggested that this behaviour had to do with the cooling of the air or that the



FIGURES 1–4. Some attributes of living notostracans, as sketched largely from photographs, and notostracan eggs.

FIGURE 1. *Triops cancriformis*, ventral (carapace length *ca.* 15 mm). Note the very long antenna-like endites (End 5, 4...) of trunk limb 1. The metachronal rhythm of the anterior trunk limbs is out of phase in the two series as the animal turns. The limbs are merely sketched to give a general impression rather than show fine detail. A metachronal wave is passing along the cluster of posterior trunk limbs (PTL). Although the anterior and posterior series of limbs here appear very distinct – the distal extremities of the posterior series being conspicuous – the endite series in each ipsilateral row is in fact a continuous series. Note that in life the animal swims mostly ventral surface down and that the posterior trunk limbs are better protected by the carapace than appears to be the case in this view. Note: the size of adults is variable. A carapace length of *ca.* 30 mm is occasionally achieved.

FIGURES 2 AND 3. *Lepidurus arcticus* (carapace length *ca.* 15 mm) grubbing among bottom detritus.

FIGURE 2. *L. arcticus* seen from behind, showing the dome-shaped nature of the carapace, the flexibility of the furcal rami, here being used as props (their tips buried in detritus), the anal plate characteristic of the genus, and the shortness of the endites of trunk limb 1 which barely extend beyond the carapace margin (cf. *T. cancriformis*, figure 1).

FIGURE 3. A typical posture when searching surfaces. Another aspect of the flexibility of the furcal rami is shown. Figures 2 and 3 show how the posterior series of trunk limbs is largely hidden and protected by the carapace. Note: the largest adults studied had a carapace length of *ca.* 16 mm.

FIGURE 4. Eggs of *L. arcticus* (diameter *ca.* 700 μm) fixed to a frond of moss.

animals sought 'frische Luft zu schöpfen'. *T. cancriformis* is, however, tolerant of low oxygen tensions (Hempel-Zawitkowska 1967), which must often prevail in some of the habitats frequented. The haemoglobin concentration of the blood varies inversely with the oxygen tension of the surrounding water (Fox 1949), and visits to the surface are probably necessary only under extreme conditions. In vessels with a large surface area in relation to volume such excursions involving inverted swimming (figure 1) are seldom seen.

As is well known, eggs are carried for a time in pouches on the eleventh pair of trunk limbs of females and self-fertilizing hermaphrodites (figure 10), before being shed. Until recently it seemed to be generally assumed that eggs are shed freely and simply fall to the bottom, and this may be true of some species, but captive individuals of *L. arcticus*, which produces fewer, larger eggs than other species, attached them in considerable numbers to fronds of moss (figure 4), a habit that had earlier been noticed by Johansen (1912) and Arnold (1966). Similar attachment of eggs to vegetation was recently reported by Margraf & Maass (1982) for *L. apus*. Burmeister (1982), however, found that this species laid on the bottom, both on hard substrata (whether the eggs were glued down is not stated) and on and in fine sediments. The latter stuck to the egg surface affording, he suggests, additional protection. Each of the pink eggs of *L. arcticus* (diameter *ca.* 700 μm) is invested with a sticky layer which affixes it with considerable tenacity to the chosen site (figure 119). Often two or more eggs adhere to each other.

Even the apparently freely shed eggs of other species are sticky (Longhurst 1955*b*), and Thiery (1985) reports that in Morocco the eggs of *Triops granarius* are laid in clusters of from 5 to 50 and that more than 80% of those laid are glued to gravel on the bottom of the pools in which this species lives. This behaviour is interesting in relation to problems of dispersal and is at variance with what seems often to be accepted, namely that these drought-resistant, diapausing eggs are readily dispersed by wind or biological agents. In *L. arcticus* and *T. granarius* attachment will frustrate dispersal and ensure that eggs remain in a habitat of proven suitability. Such habits are particularly appropriate to a species such as *L. arcticus* that frequents permanent lakes as well as small ponds but, as Thiery (1985) points out, the gluing down of eggs by *T. granarius* avoids their dispersal (doubtless leading almost always to their loss) during sandstorms that are frequent during the dry season. Note, however, that Margraf & Maass (1982), who observed *L. apus* in a pond in Sardinia, think that the attachment of eggs to vegetation may facilitate dispersal by such animals as ducks, and that, when plants dry out, their remains may be scattered by winds. Egg attachment is in keeping with the situation in several anomopods ('cladocerans') of the families Macrothricidae and Chydoridae (Fryer 1972; Fryer & Frey 1981), and there are interesting parallels in patterns of distribution. Anomopods, long regarded as including several cosmopolitan species, are now being shown to be geographically restricted, many allegedly cosmopolitan taxa actually consisting of two or more very similar species or subspecies. (See Frey 1982, 1986, 1987.) Allozyme studies on daphniids confirm the differentiation of widely separated populations, between which there are greater genetic distances than between those of adjacent areas, there being pronounced divergence in stocks from different continents (Hebert 1987). Even adjacent local populations often display marked differences in gene frequencies. (See, for example, Hebert 1974.) The distinctions between isolated populations of notostracans noted in §3 hint strongly at a similar situation.

Paradoxically, in spite of dispersion-frustrating devices, notostracans have colonized even remote oceanic islands. The enormous antiquity of the group may be relevant here.

Eggs of *Triops* are protected by an outer cortex and a thick alveolar layer (Gilchrist 1978; Thiery 1985). They can withstand extreme environmental conditions: desiccation, high temperatures and freezing. Eggs of *Lepidurus arcticus* are different, the alveolar layer, which invests what prove to be two delicate, almost colourless, transparent membranes (§12), being much thinner. The colour is due to the yolky egg contents which are bright pink. These differences provide an interesting example of evolutionary divergence in the early stages of the life history and presumably reflect the great differences between the environments frequented by the cold-loving *L. arcticus* and its warm-water relatives, and probably its frequent habit of living in permanent water bodies.

Many structural features are related to benthic habits. The dorsal, domed carapace is continuous with the equally thickened integument of the head to form a single functional unit, the line of demarcation being indicated dorsomedially by a transverse furrow behind the region of mandibular articulation (figure 3), but is not recognizable laterally. A thickened rim (figures 2 and 3) grants strength and protects against abrasion. The nature and ultrastructure of the carapace cuticle, which has a four-layered epicuticle, a ten-layered exocuticle, and an endocuticle of 60–80 layers, has been studied by Rieder (1972*a*). A row of sclerotized spines guards the posterior emargination (sulcus) of the carapace. The carapace serves as a protective shield for most of the trunk appendages, the anterior margin of the head as a plough for shallow burrowing in soft deposits and is for the most part in close contact with the substratum (figures 2 and 3). Here the headshield integument continues ventrally as a broad, elliptical flat-faced flange (figure 1, AVF) from whose posterior margin arises the labrum (L). The latter is broad and flat and, as a protection against abrasion, well provided with cuticle on its topographically ventral surface. In these respects it differs markedly from that of most other branchiopods – Anostraca, Anomopoda, Ctenopoda and the conchostracan orders Spinicaudata and Laevicaudata† – in which the labrum is typically a fleshy lobe and seldom protected by thick cuticle though a keel is present in some benthic anomopods.

The shape and location of the carapace have probably played a part in determining the form of the trunk and other structures. The dish-like carapace probably requires a 'tail' for hydrodynamic efficiency, which goes some way towards explaining the persistence of the elongate exposed abdomen, protected only by thickened cuticle and cuticular spines. This tends to flick ventrally during open-water swimming (Arnold 1966). Margraf & Maass (1982) also note that although *Lepidurus apus* spends most of its time on the bottom it swims to escape such predators as dytiscid larvae (which it must encounter only towards the end of the season) and in so doing flicks its telson (implying action of the apodous trunk) up and down like the flukes of a dolphin. (Compare the carapace-bearing Spinicaudata, Laevicaudata, Anomopoda and Ctenopoda where the acquisition of an enveloping carapace has led to reduction of the abdomen and its complete withdrawal within it.) The long furcal rami, so different from those of other branchiopods, also become intelligible in the light of selection for hydrodynamic efficiency, though they also serve other purposes (figures 2 and 3), and the anal plate of *Lepidurus* seems more likely to be concerned with such than with protection. The limbless portion of the trunk owes its mobility to the protection of each segment by a narrow hoop of

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† The recognition and definition of two orders, Spinicaudata and Laevicaudata, within the conchostracan assemblage, and of four orders, Ctenopoda, Anomopoda, Onychopoda and Haplopoda within the so-called Cladocera, are documented elsewhere (Fryer 1988), and these ordinal categories are used where necessary in this paper.

cuticle, there being no indication of any division into tergite and sternite, that allows these segments to move freely upon each other.

In an individual swimming over the bottom the carapace tends to be inclined anterior end down (figures 2 and 3). The short, tubular, uniramous antennules (figures 1 and 102, A1), are directed more or less ventrally, must often touch, or lie adjacent to, the substratum, and certainly do so when the anterior rim of the carapace is pushed beneath the mud surface. The smaller, much shorter, antennae (A2) (figure 102), which are apparently lost in large adults of some species, have a similar orientation. The most obvious anterior sensory structures are the elongate endites (End 3–5) of the first trunk limbs (figure 1, see §5 for details), which are longer in *Triops* than in *Lepidurus*. They are shortest of all in *L. arcticus*, in which species they scarcely protrude beyond the carapace margin, possibly a reflection of the fact that this is the only species to be subject to significant predation (except when the habitat is drying out, when the animals are doomed anyhow). Long endites must be vulnerable, and their movements attract attention. The endites are liberally provided with sensillae. In *Triops*, endite 2, much the shortest, is directed more or less ventrally towards the substratum, the elongate, flagella-like endites 3 and 4 extend ahead of the animal and, in the case of endite 4, somewhat laterally, and the even longer endite 5 curves posteriorly – it can reach beyond the posterior limits of the carapace – and extends laterally so that a wide band of substratum ahead of, lateral to, and beneath, the anterior end of the animal is probed. During forward motion the long distal endites tend to be swung somewhat medially, and therefore forward, and even when the animal is at rest there is often some exploratory activity by these endites. The compound eyes and an ocellus lie dorsally and complete a battery of sensory structures anteriorly.

Although the trunk appendages were described by Schaeffer (1756), amazingly well for such an early date, and more recently, e.g. by Lankester (1881), many details have remained undisclosed and except for an appreciation of the use of gnathobases in feeding first noted by Schaeffer and referred to by Lundbland (1920), Cannon (1933) and Eriksson (1934), no functional interpretation of their morphology has been made, yet these appendages are specialized for various roles and many detailed structural features are present that have never been described but whose functions are of great importance. It is therefore necessary to give some account, first of the gross morphology of these limbs, then of certain details.

5. Gross morphology of the trunk limbs

For descriptive purposes the first 11 pairs of trunk limbs are here referred to as the anterior, the remaining pairs as the posterior, series. Differentiation among the trunk limbs was clearly recognized by Schaeffer well over 200 years ago. To the first pair he gave the unfortunate name 'Ruderfüsse', to the next nine pairs 'Kiefenfüsse', to the 11th 'Mutterfüsse' (eggs being carried here), and to the rest 'geblattetten Kiefenfüssen'. The limbs described here are those of *Lepidurus apus*. Comparisons with those of *Triops cancriformis* are made where appropriate.

Trunk limb 1 (figure 5) comprises an elongate corm in the form of a flattened cylinder, which bears what have been interpreted either as six endites or, as here, five endites and an endopodite, an exopodite, and an epipodite. The basal endite (G) is a gnathobase whose armature of spines and setae, as revealed by scanning electron microscopy, are described in §6. Endites 2–5 (End 2–5), especially the fifth, are elongate, filiform structures that fulfil a largely sensory role. Endite 2 is instructive in showing a transitional condition between the extreme filiform type and the broader endites of the more posterior limbs. In the more distal regions of the three longest endites, especially in the fifth, elaborate pivot joints are developed between segments that permit the necessary flexibility of these antenna-like structures. The endites are liberally provided with groups of sensillae whose nature is discussed in §6*b*.

The endopodite (figure 5, EN) is a short, unsegmented plate that articulates via a robust, sclerotized hinge joint, so stout that movement is clearly possible in essentially one plane only. The exopodite (EX) is a flattened plate whose shape is tailored to fit the confined space between the limb and the adjacent under-surface of the carapace. Its margins are sparsely setose. A bulbous epipodite (EP) is present.

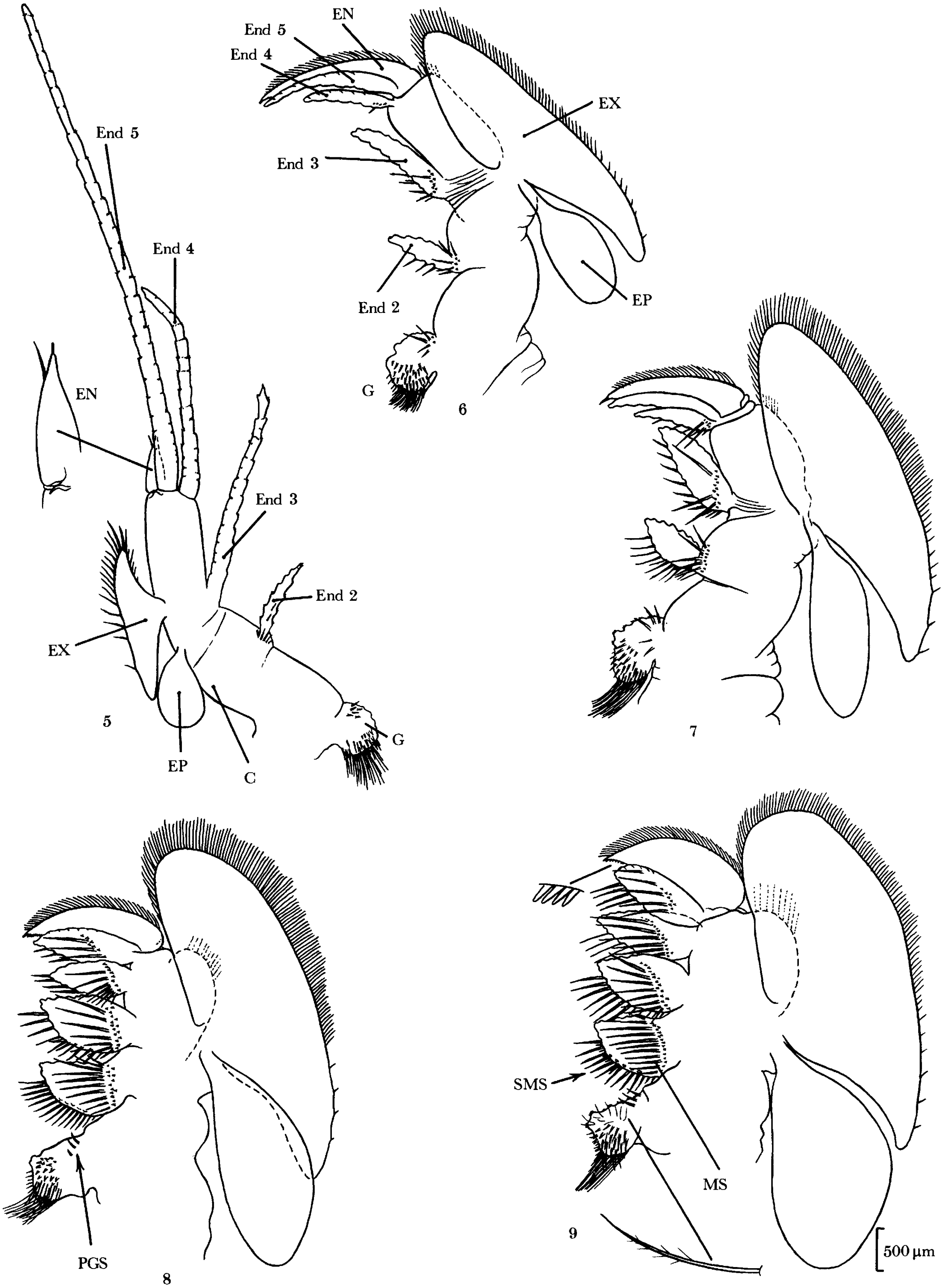
Trunk limb 2 (figure 6) is similar in essential structure to limb 1 but its endites are much shorter, its endopodite much better developed, and its exopodite larger. The gnathobase is very similar to its predecessor. Endite 2 is flattened and similar to, but broader than, that of trunk limb 1 and bears more, but still few, and larger spines. Endite 3 is larger, but much shorter than its homologue on trunk limb 1, and bears several spines. Endites 4 and 5 are elongate and virtually devoid of spines. The endopodite is a specialized structure whose nature is clear from figure 6. It articulates with the corm via a well-developed pivot joint.

The carapace overlying this limb is here wider and higher than that portion overlying trunk limb 1, permitting the development of a larger exopodite, whose shape is again tailored to suit the space in which it operates. Reflecting its role in propulsion during swimming it also bears a fringe of close-set setae such as are lacking on the exopod of the preceding limb. There are cleaning setae dorsally. An epipodite is again present. Although rather flattened and lying transversely across the animal, the limb is convex anteriorly and concave posteriorly.

Between trunk limbs 3 and 10 there is a gradual change in form, as seen from figures 7–9, which show limbs 4, 8 and 10 respectively. The gnathobase is basically similar throughout the series but endites 2–5 become broader and leaf-like. The proximal endites of the more anterior limbs, and all the endites of the more posterior limbs, are armed with rows of widely spaced, medially directed, long, slender spines. With some variants, the basic arrangement of these is a row of sub-marginal spines (SMS) (on the anterior face) and a row of what are here called meshwork spines (MS) on both the anterior and posterior faces of each endite. The two latter rows differ in location from endite to endite (figures 6–9), are often far removed from the sub-marginal row, and in the case of endite 2 of the more anterior limbs, arise from the adjacent part of the corm rather than from the endite itself (figures 6 and 7). Sub-marginal spines are seen on several endites in figures 19–21, plate 1. These lie more or less in the flat plane of the endites that bear them. The meshwork spines can also be seen. These are directed obliquely away from the endite and interdigitate with the spines of adjacent limbs, thus forming a coarse-meshed network that spans the gaps between consecutive limbs. Details of these spines and of the band of spinules that accompany them are given in §6.

The endopodite is similar on legs 3–10 but becomes broader on the more posterior members of the series. Flattened in section rather like the blade of a knife, the equivalent of the cutting edge terminates in a stout claw (figure 50, plate 4), its inner margin is fringed distally by a row of almost contiguous smaller denticles and its outer by a row of setose setae. It articulates with the corm via a well developed and robust hinge joint. The more anterior of the endopodites bear the stoutest marginal denticles: the tenth has fewer, less robust, denticles.

The endopodite, with its distal claw and row of inner denticles, is remarkably similar to the dactylus of the posterior walking limb of certain lightly built decapod prawns such as the atyids



FIGURES 5–9. For description see opposite.

Caridina (Fryer 1960), *Jonga* and *Potimirim* (Fryer 1977). In both these very different groups the animal stands on the terminal claw, but the prawns use the marginal denticles, not for digging as do the Notostraca (§8) but for grooming the carapace.

Adjacent to the endopod, the distal part of the corm of trunk limb 2 bears a few setae. This region is progressively expanded in more posterior limbs to form a sub-apical lobe that lies in front of the exopodite. In each case its margin is provided with a few setae distally. The exopodite is large, is broader towards the end of the series than at the beginning, and always fits neatly into the available space beneath the overlying carapace.

In males trunk limb 11 is very similar to limb 10 but in the female of *L. apus* and in self-fertilizing hermaphrodites of *T. cancriformis* it is modified for the reception of eggs (figure 10). Its basic structure is well known from earlier descriptions but not all have suggested the same homologies. Those of Lankester (1881) appear to be correct. The cup in which eggs are stored is derived from an expansion of the sub-apical lobe, its lid from the exopodite (the flabellum of Lankester). What is not always clear from descriptions is that, like the cup, the lid of the egg-holding receptacle is concave, so the eggs are pressed against the concave face of the cup by the convex face of the lid. The epipodite (the bract of Lankester) is minute and hardly visible in figure 10 in which its basal portion is obscured.

Irrespective of any modifications for egg storage, that part of the limb concerned with food handling (the gnathobase and the four succeeding endites) is similar to that of limb 10 and in no way interrupts the functional continuity of the limb series in this respect. The endopodite is, however, different from that of trunk limb 10 in both sexes. That of the female is shown in figure 10. In the male it is similar, but free laterally as in the limbs anterior and posterior to it. It lacks both the terminal claw and row of denticles on its inner margin. This reflects differences in function between trunk limbs 10 and 11, the former being involved in digging (§8), the latter not.

Behind trunk limb 11 the limbs, sometimes more than one pair per segment, gradually diminish in size but their gnathobases and their four more distal endites are continuous with the functional series of more anterior limbs as figure 11, of trunk limb 14, makes plain. The endopodite is now more paddle-like, and the exopodite, with plenty of space in which to operate as the carapace here rises somewhat, takes the form of a large paddle, roughly circular at the beginning of the posterior series, more ovate posteriorly (figures 12 and 14). Because, in an animal walking or swimming over the bottom or digging in it, contact with the substratum is made via the endopodites of the anterior trunk limbs (§8), the posterior limbs are held clear of it and can beat unhindered to set up a respiratory stream.

The number of limbs is variable (see Longhurst 1955*a*), usually 40 or more in available individuals of *L. apus*. Towards the posterior end of the series the size of the endites diminishes

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FIGURES 5–9. Trunk limbs of *Lepidurus apus*. Trunk limb 1, a right-hand limb, has been somewhat flattened to reveal the endites: all others are left-hand limbs showing their natural orientation. All limbs show their posterior faces.

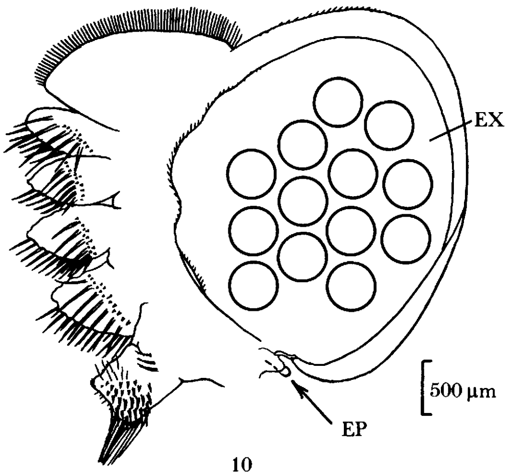
FIGURE 5. Trunk limb 1.

FIGURE 6. Trunk limb 2.

FIGURE 7. Trunk limb 4.

FIGURE 8. Trunk limb 8.

FIGURE 9. Trunk limb 10.



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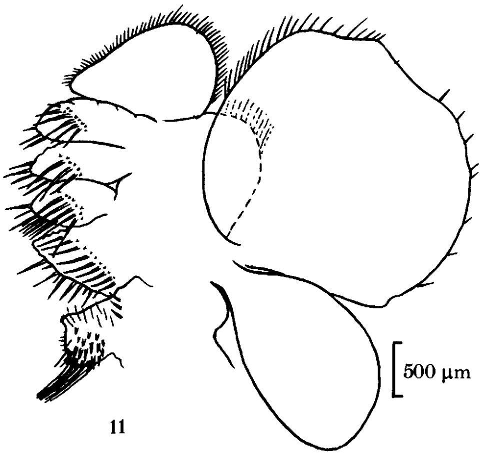

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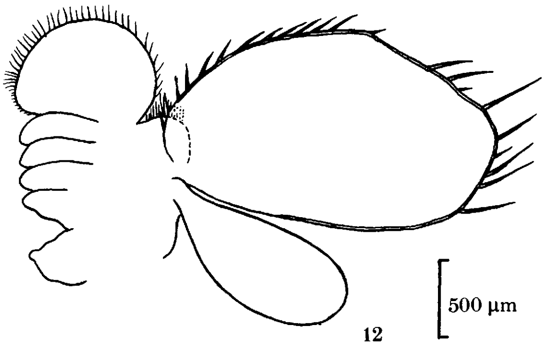

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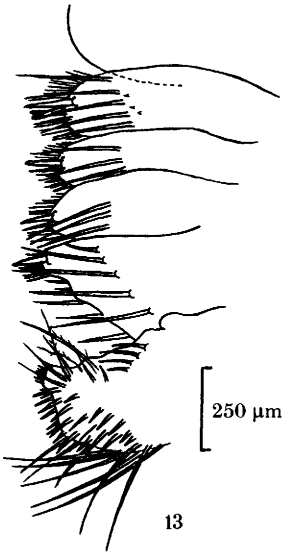

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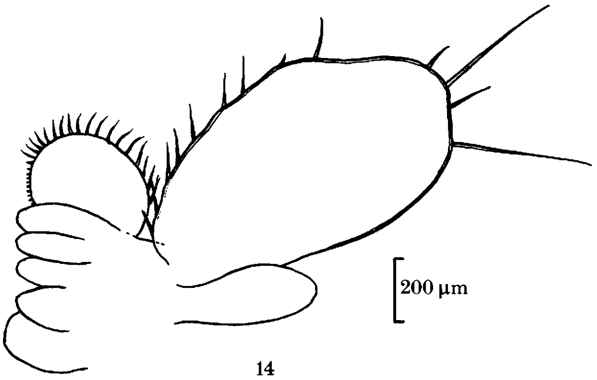

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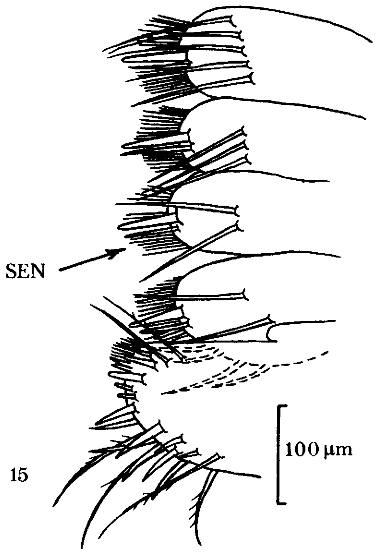

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Figures 10–15. For description see opposite.

both absolutely and in relation to the size of the exopodite which, posteriorly, dominates the limb (figures 12 and 14). Each exopodite has a somewhat thickened rim that grants the necessary rigidity to what is otherwise a soft flap. The endite armature, although similar in many ways to that of the anterior limbs, shows subtle changes from limb to limb within the series. These are best appreciated by reference to figures 13 and 15, which show the armature of trunk limbs 22 and 36 respectively.

As figure 13 shows, endites 2–5 of trunk limb 22 are each provided with a row of long slender spines on their posterior face as is the case on more anterior limbs, though the spines are here more distally located. Endite 2 also has a sub-marginal row of spines, like the endites of anterior limbs, and a row of spines on its anterior face. The latter, however, are shorter and finer than their counterparts on the posterior face. Like endite 2, endite 3 has a row of spines on its posterior face and a row of sub-marginal spines. The latter, however, especially distally, arise further and further from the margin on the anterior face. An anterior row of spines is present but these are short, fine and only three in number. Additionally, there is on the anterior face a somewhat irregular row of seven slender spines that arises not far from its distal end.

Endites 4 and 5 have the usual row of spines on the posterior face, but the anterior row is missing. The distal members of the sub-marginal row have, however, migrated away from the margin and arise from the anterior face of the endite, and again a distal row of fine spines is present. The distal row is seen on several endites of trunk limbs 18 and 19 in figure 27, plate 1.

Trunk limb 36 (figure 14) is similar but smaller. Its endite armature (figure 15) follows the same pattern but differs in details. Because the posterior limbs are congested (figures 26 and 27, plate 1) and the gaps between them are narrow, the spines of both anterior and posterior faces are inevitably directed more or less in the flat plane of the endite, that is medially and somewhat posteriorly. The result is that, on each side of the mid-line, the endites make up a wall armed with hundreds of fine, sharp spines, and copiously provided with sensillae.

The gnathobase of trunk limb 22 (figure 13) resembles that of more anterior limbs but has fewer spines and sweeping setae. Gnathobases of this region are seen *in situ* as viewed from the median side in figure 26, plate 1. Gnathobase 36 (figure 15) is more simplified, and reduction in the size and complexity of the gnathobase continues posteriorly along the series. Some of the most posterior gnathobases are seen *in situ* from the median side in figure 37, plate 3.

Additional details of trunk limb structure and function are given in §6.

FIGURES 10–15. Trunk limbs of *Lepidurus apus*. All limbs show their posterior faces.

FIGURE 10. Trunk limb 11 (female).

FIGURE 11. Trunk limb 14.

FIGURE 12. Trunk limb 22; endites shown in outline only.

FIGURE 13. Trunk limb 22; details of endites.

FIGURE 14. Trunk limb 36; endites shown in outline only.

FIGURE 15. Trunk limb 36; details of endites.

6. Some details of trunk limb armature

(*a*) *Mechanical armature*

Trunk limb armature is far more complex than early accounts indicated. Rieder (1974, 1978, 1979), working on *Triops cancriformis*, was the first to reveal this complexity by use of scanning and transmission electron microscopy. He recognized seven different types of 'bristle' some of which are sensory in function. Rieder was concerned with the nature of those bristles deemed to be sensory, with their ultrastructure and with events taking place during moulting and not with the roles of spines and setae during food handling. Where appropriate reference is made to his numbering of the various spines, setae and sensillae.

The mechanical armature is described and illustrated here with reference to *Lepidurus apus*, but is essentially similar in *Triops*. The anterior series of trunk limbs is considered first.

The gnathobases are equipped both for handling large food masses and for sweeping finer particles forwards (§10). Large food masses are dealt with by stout spines (Rieder's types 2 and 3) that are always directed somewhat medially, i.e. towards their partners on the opposite limb, but also in directions that enable those located posteriorly to grip and drag material forward, and those located anteriorly to push it forward. These spines can be seen, mostly end-on, in a series of gnathobases *in situ* in figure 29, plate 2, on a single gnathobase in figure 39, plate 3, and figure 55, plate 5, and in more detail in figures 51–53, plate 4. They differ in length according to their location. They are not simply cuticular elaborations but are hollow structures that articulate in a very precise manner with the cuticle that supports them.

The exact form of the articulation differs somewhat from spine to spine according to its size and location, but the principles are the same in each case. Each spine is circular in section at its base and arises from a dome-like mound, here called the basal mound. That side of the mound from which the posterior region of the spine arises is raised into a thickened ridge or collar. Although the thickened region may extend for about half the circumference of the mound (figures 42 and 43, plate 3) there is usually an elevated region that occupies a smaller portion of its periphery, here termed the boss (B), (e.g. figures 16 and 17; figure 40, plate 3; and the short spine at the extreme right in figure 46, plate 4). On the opposite (anterior) side there is an expanse of thin cuticle. The spine is hinged against the boss as is conveniently revealed by a broken spine (figures 42 and 43, plate 3). The spine can be tilted forward, the thin cuticle that binds it to the cuticle of the limb then being intucked anteriorly. Forward tilt is best seen in endite spines (e.g. figure 21, plate 1) that employ the same principle. Backward tilting of the spine is prevented by the boss and by tension in the thin binding cuticle, so the spine can be erected but not forced back beyond a certain position. The spines are normally

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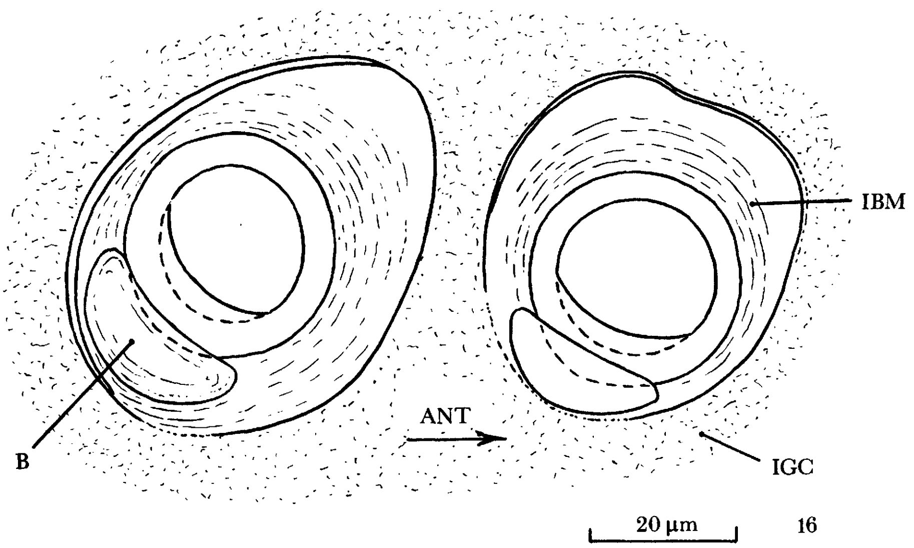
Figures 16–18. *Lepidurus apus*.

Figure 16. Basal regions of two gnathobasic spines of trunk limb 2 as seen in a longitudinal slice of the animal and viewed from inside the limb so that the inner face of the gnathobasic cuticle (IGC) and the inner face of the basal mound (IBM) of the spines are seen.

Figure 17. The same, focused more deeply, i.e. slightly more distal from the spine bases. An indication of the living tissue that occupies the centre of the cavity of each spine is given in one case. The limits of the mound, now out of focus, are indicated by a dashed line around each spine.

Figure 18. The same, slightly more distally. The spines are now seen in transverse section. As at this level they are directed almost medially, they appear in section as almost perfect circles. Their more distal regions curve anteriorly as indicated for one spine by dashed lines.



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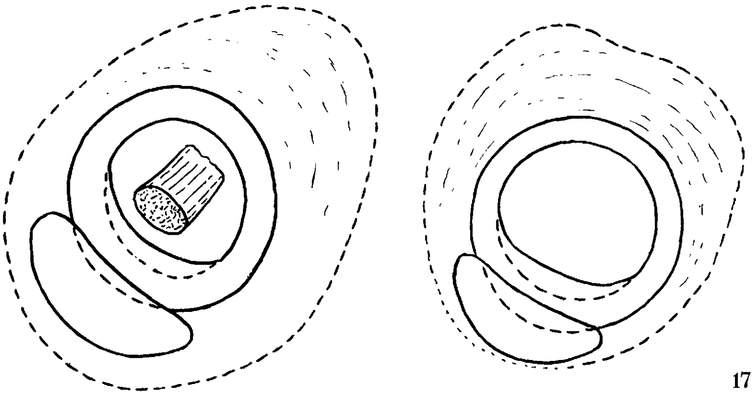

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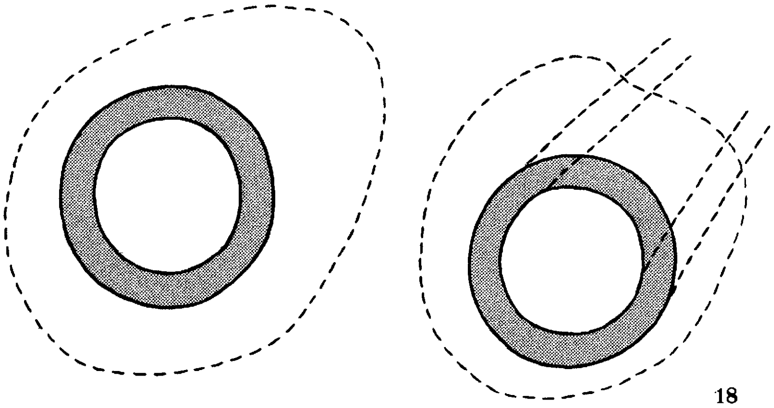

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held in the erect position. This is probably ensured by the binding cuticle. It is unlikely that the turgor pressure of the haemocoele, with which the hollow spines are in continuity, is involved. Such pressure is certainly involved in the erection of the highly complex cheliped bristles of certain atyid prawns (Fryer 1977; Felgenhauer & Abele 1983) that have a somewhat similar, though more complex, hinge, and by the filter setae of certain isopods (Wägele 1987), but here the bristles are normally folded and are erected by a hydraulic mechanism when required. The hinge mechanism of the spines of the Notostraca, although clearly independently evolved from that of atyids, indeed shows some striking similarities but is much simpler. The functional significance of the hinging of the spines is described in §10.

The spines are often somewhat denticulate. The denticles, whose development differs from spine to spine, are always located on the opposite side of the spine to the boss on what is frequently the 'concave' side of a slightly curved spine. Denticles, seen from the posterior side of a spine, are seen, for example, in the right-hand spine in figure 46, plate 4.

Although the above description embraces the majority of the stout spines of the gnathobases,

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Description of plate 1

Lepidurus apus. Details of limb structure and armature (scanning electron micrographs).

FIGURE 19. Endite 2 (edge on) and part of endite 3, left trunk limb 3, and their relations to their homologues on trunk limbs 2 and 4. Median view. Note how the gaps between adjacent limbs are spanned by long meshwork spines originating near the base of the endites or in the case of endite 2 on the adjacent corm. The location of the sensory pads on the various endites is well seen. (Australian material.)

FIGURE 20. The same, different inclination. (Australian material.)

FIGURE 21. Details of the sub-marginal spines and sensory pads of endite 2, trunk limb 3. (Australian material.) Note the trident spines near the bases of the sub-marginal spines.

FIGURE 22. Endite 2, trunk limb 6, median view.

FIGURE 23. Endite 2, trunk limb 8, showing the bases of some of the sub-marginal spines and the arrangement of the tri- and 5-dentate spinules located near them.

FIGURE 24. Endite 3, trunk limb 4, sub-marginal spines, 5-dentate spinules and sensory pads of the median margin.

FIGURE 25. A 5-dentate spinule.

FIGURE 26. Posterior trunk limbs, right-hand side, in median view, showing the endopodites (EN), endites 2–4 and some of the gnathobases (G). The most posterior endopodite (left side of photograph) is that of trunk limb 27. (See figure 12 for general form of limbs in this region.) (Australian material.)

FIGURE 27. Median view of the endites of trunk limbs 18 and 19. All four endites of trunk limb 19 can be seen, at least in part: only endites 1–3 of trunk limb 18 are shown. (Australian material.)

FIGURE 28. Details of the distal armature of an endite of a posterior trunk limb, showing the stout spine and tuft of sensillae. (Australian material.)

Description of plate 2

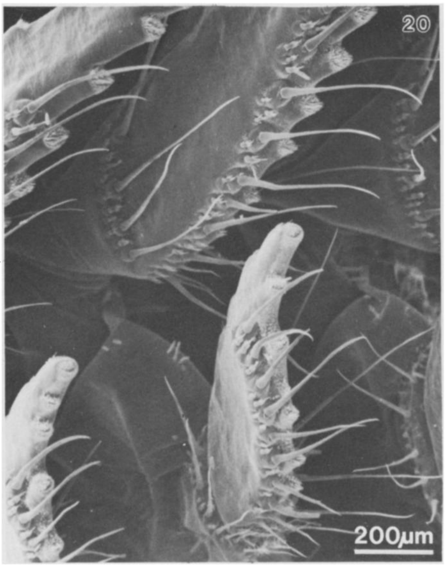
Lepidurus apus. Trunk limb gnathobases, and mouthparts (scanning electron micrographs).

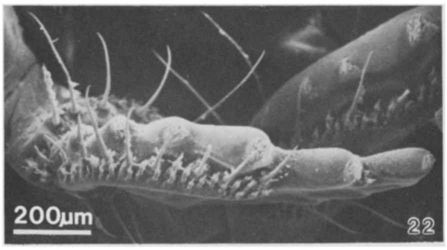
FIGURE 29. The gnathobases of the first six right-hand trunk limbs and the mouthparts *in situ* and seen in median view after bisection of the animal.

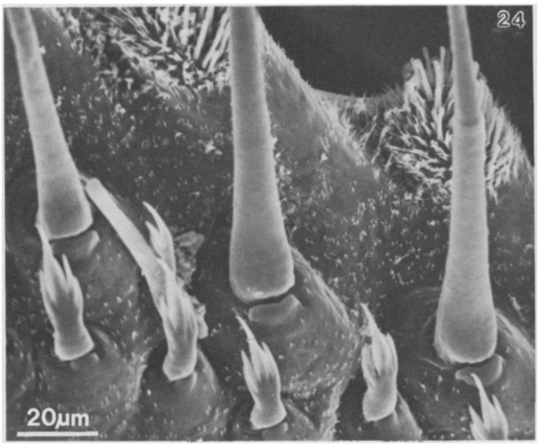
FIGURE 30. The long sweeping setae (SS) of the gnathobases; left-hand appendages. Note the cleaning bristles (CB) that line the margin of the food groove (FG).

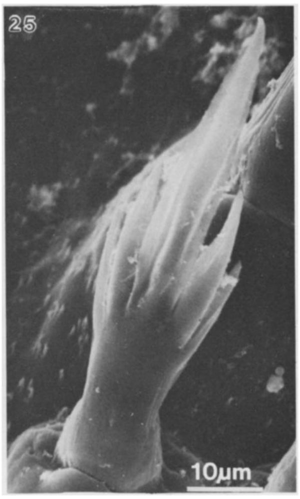
FIGURE 31. The anterior gnathobases of an Australian specimen, showing how the sweeping setae are more slender and more setose than in Palestinian animals.

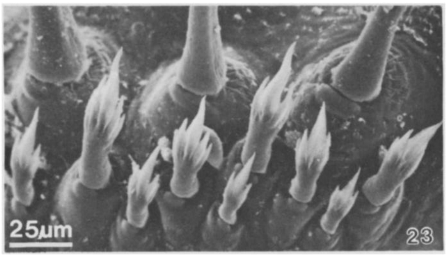
FIGURE 32. Details of the sweeping setae of an Australian specimen showing the long setules not present in Palestinian animals.

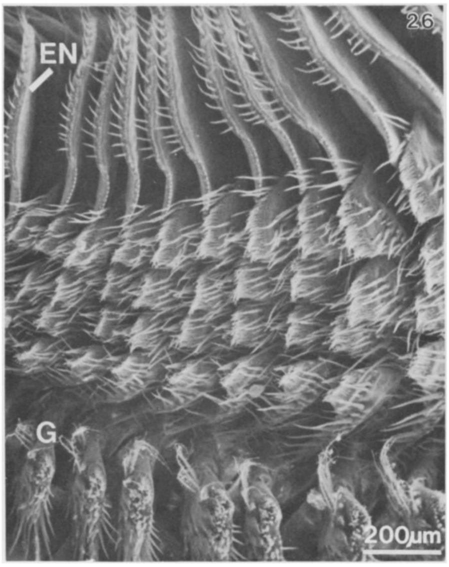


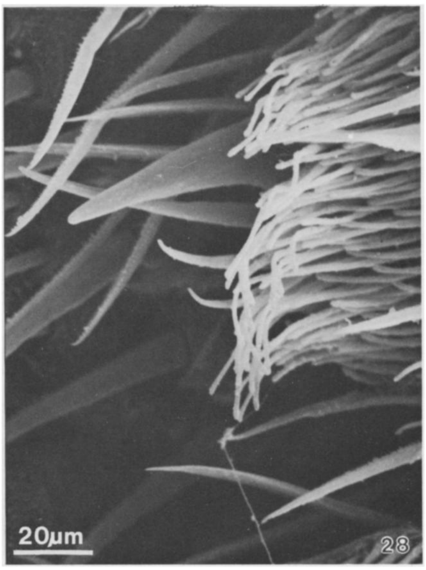




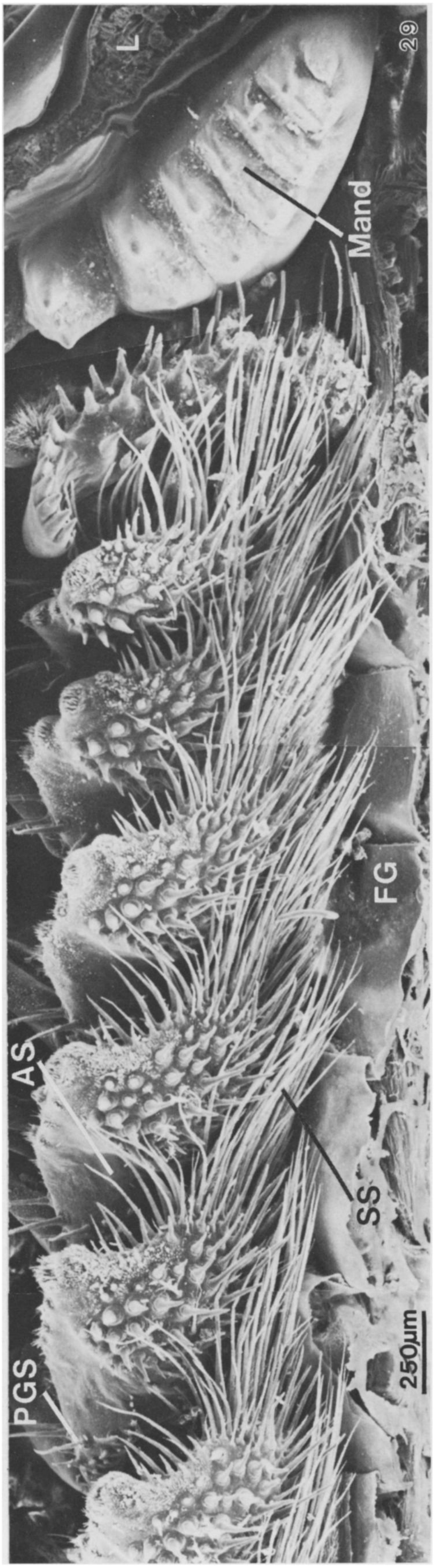








FIGURES 19–28. For description see opposite.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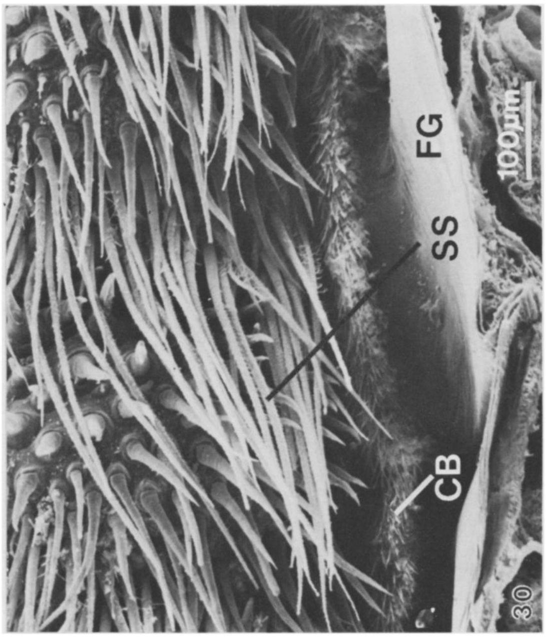
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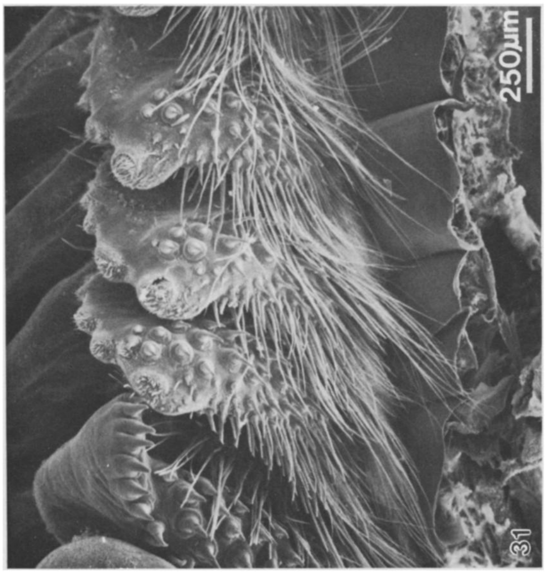
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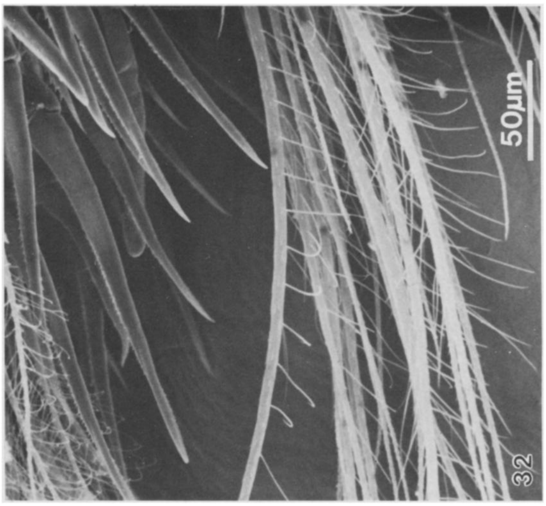
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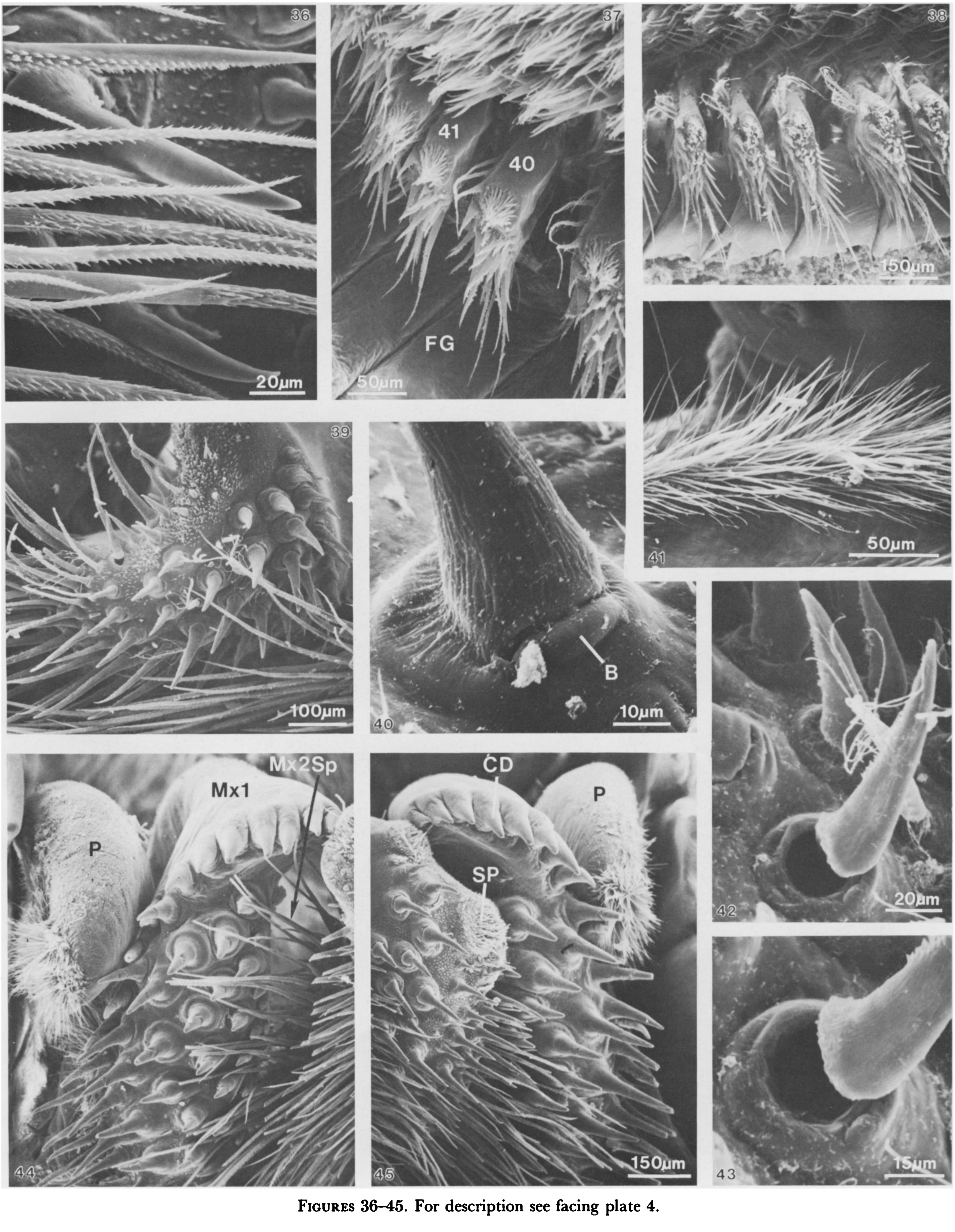
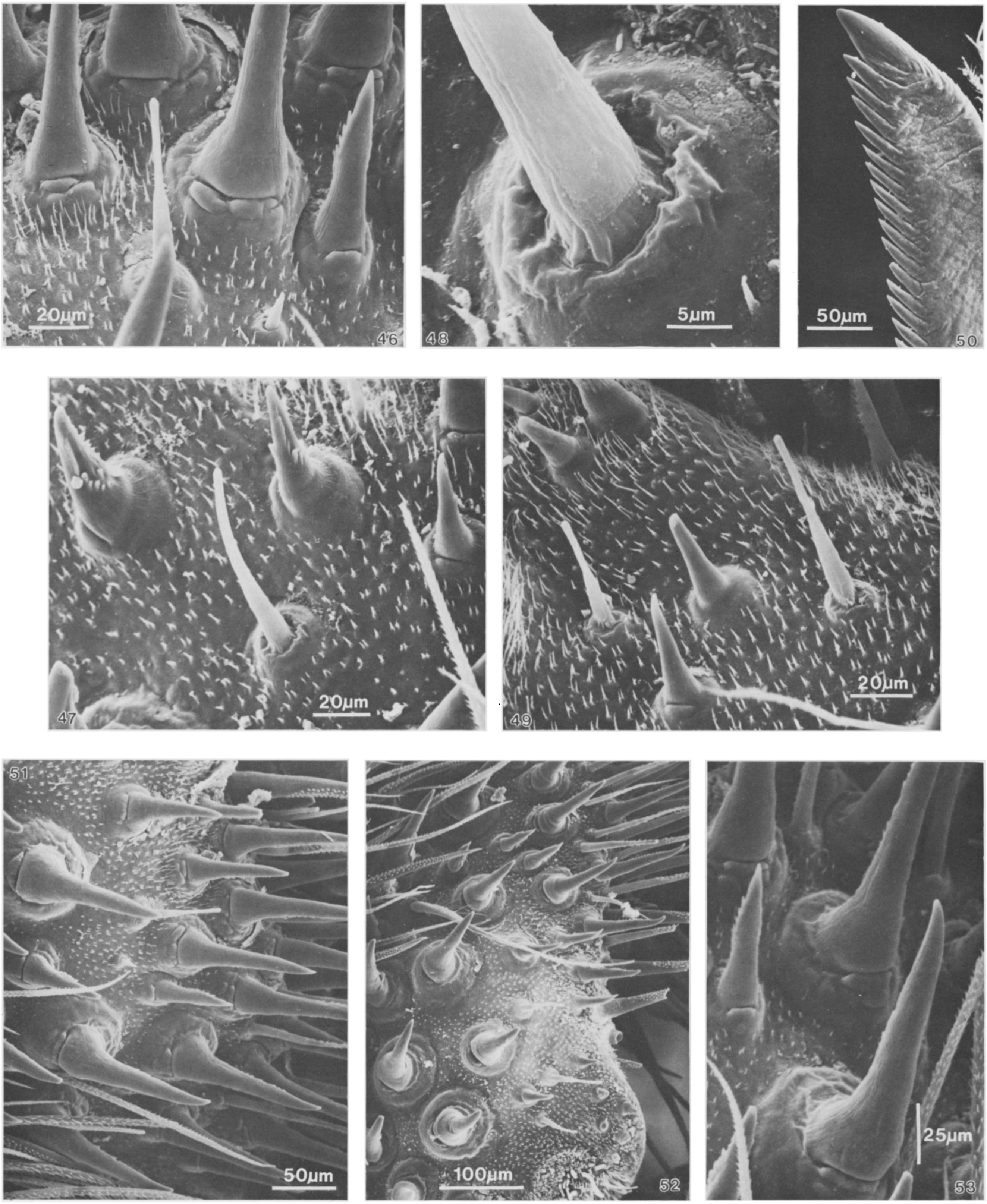
Figures 29–32. For description see p. 46.



Figures 36–45. For description see facing plate 4.



FIGURES 46–53. For description see opposite.

DESCRIPTION OF PLATE 3

Lepidurus apus. Gnathobases, posterior mouthparts and associated structures (scanning electron micrographs).

FIGURE 36. Gnathobase of right trunk limb 3, coarse sweeping spines. Spines of the heavy armature lie beneath the sweeping spines. (Australian material.)

FIGURE 37. Gnathobases and some of the more proximal endites of some of the posterior members of the trunk limb series. Right-hand side. The way in which the gnathobasic armature is directed into the food groove (FG) is clearly seen. (Australian material.)

FIGURE 38. Gnathobases of right trunk limbs 20–23. (Australian material.)

FIGURE 39. Left gnathobase 5 to show particularly the heavy armature. The broken spine indicates the hollow nature of the spines. The long sweeping spines of gnathobase 6 are seen beneath gnathobase 5.

FIGURE 40. Base of a spine, trunk limb 4, to show aspects of the hinge mechanism. The boss (B) is clearly seen.

FIGURE 41. Cleaning bristles that line the margin of the food groove. (Australian material.)

FIGURE 42. A gnathobasic spine, broken at the hinge (compare the hinge of the spine above) to reveal the complex cuticular elaboration at its base. A plumose sensory seta is located just behind the spine.

FIGURE 43. The same, more highly magnified.

FIGURE 44. Distal parts of the paragnath (P) and maxillule (Mx1). Left-hand side. The spines of the maxilla (Mx2 Sp), that protrude between the maxillule and the gnathobase of trunk limb 1, have also been exposed by cutting short some of the spines of the latter. The close association of the paragnath with the mandible can be seen at the top left corner of the photograph where a small portion of the mandible can be seen. Note the robust armature of the maxillule.

FIGURE 45. The posterior mouthparts (distal) and part of the gnathobase of trunk limb 1. Right-hand side. The spines of the maxilla can scarcely be distinguished from those of the gnathobase of trunk limb 1. The distal arc of cutting denticles (CD) of the maxillule is well displayed. Note the sensory pads (SP) of the gnathobase of trunk limb 1.

DESCRIPTION OF PLATE 4

Lepidurus apus. Spines, sensillae and an endopod. Orientation of the photographs is purely for convenience. (Scanning electron micrographs.)

FIGURE 46. Gnathobasic spines, from behind, to show their bases, and two of the simple sensillae, one long, one very short, that are scattered among them. (Australian material.)

FIGURE 47. Short, stout gnathobasic spines, from behind, and a long sensory seta. (Australian material.)

FIGURE 48. The base of the sensory seta seen *in situ* in figure 47. Puckering of the cuticle is a result of fixation.

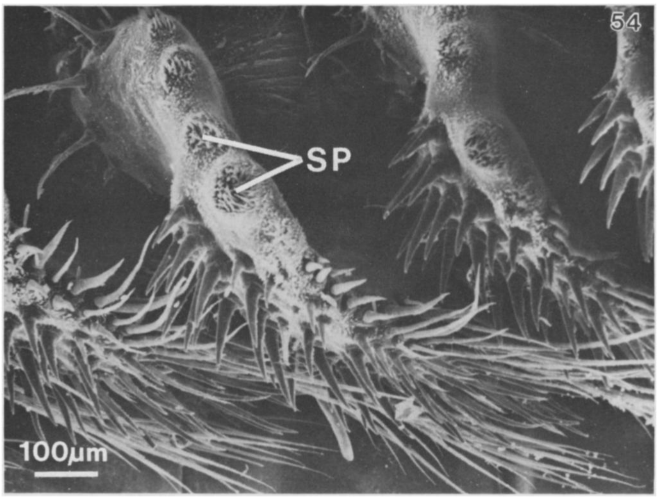
FIGURE 49. Short gnathobasic spines, with and without a basal hinge, and two simple sensory setae of different lengths. Note the scattering of tiny spinules on the cuticle of the gnathobase. (Australian material.)

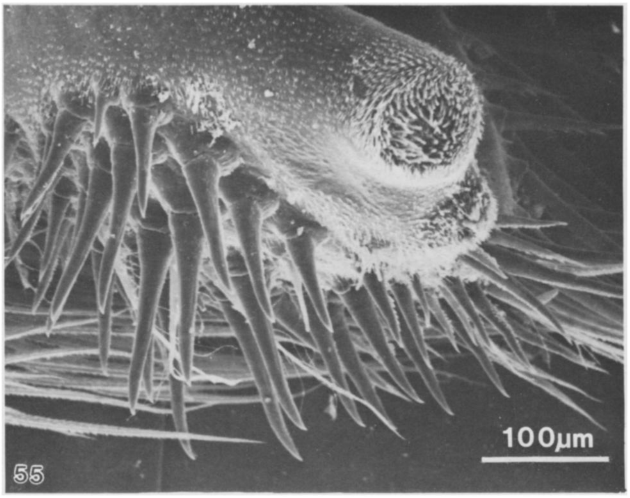
FIGURE 50. The distal part of the endopod of trunk limb 4. Note the massive distal denticle and the row of digging spines along the ventral margin.

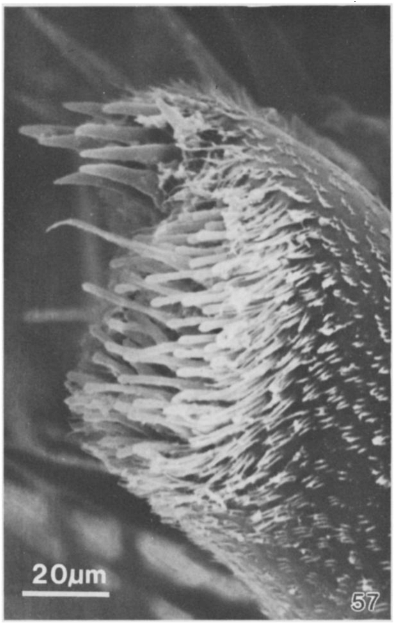
FIGURE 51. Part of the array of spines of the gnathobase of trunk limb 1. The basal hinge is seen from a variety of angles. (Australian material.)

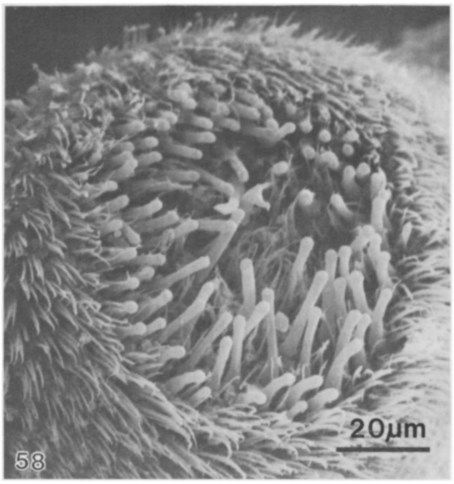
FIGURE 52. Further details of the gnathobasic armature of trunk limb 1 (Australian material.)

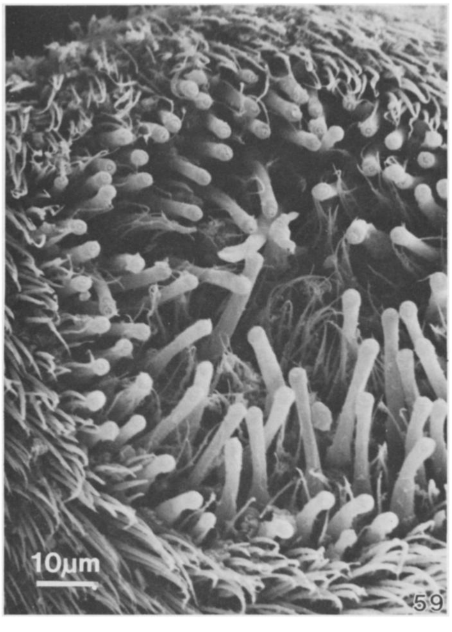
FIGURE 53. Oblique views of gnathobasic spines. (Australian material.)

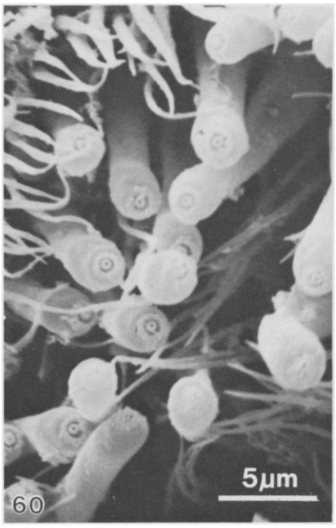


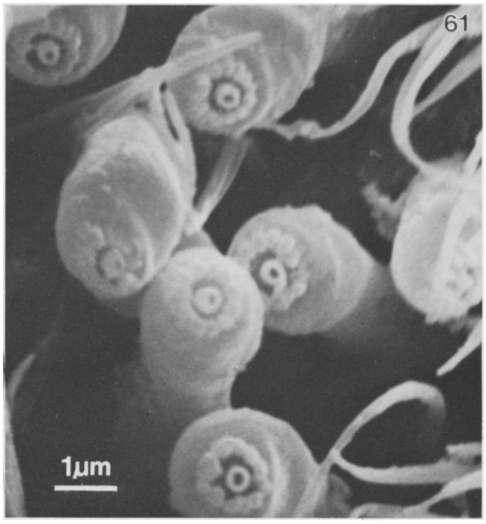












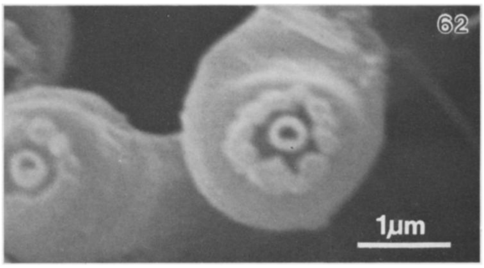
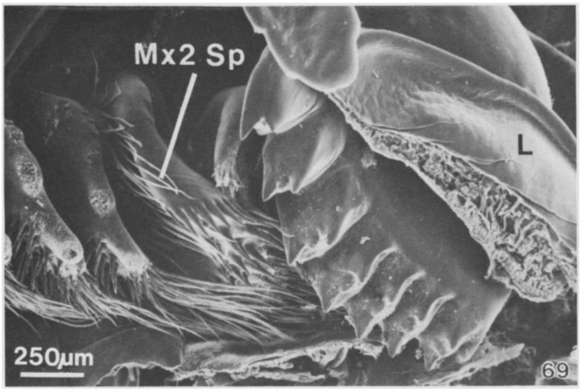
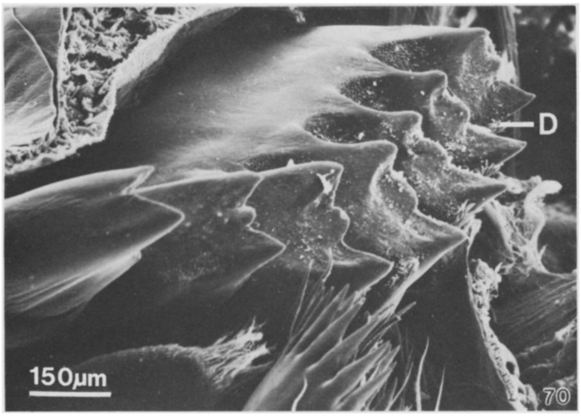
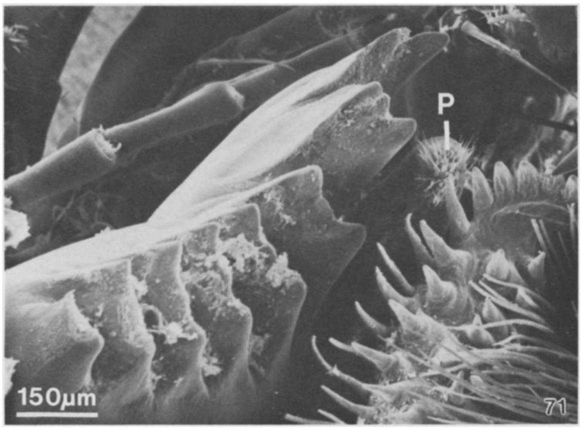
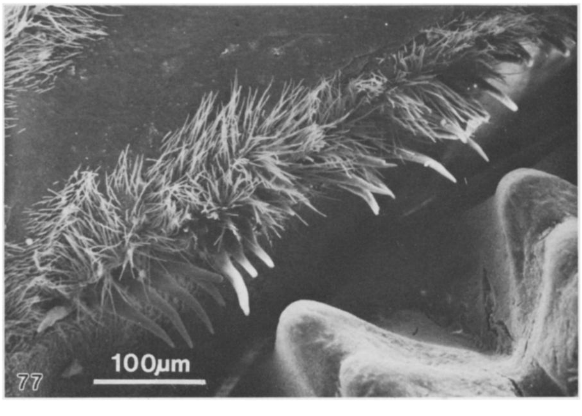


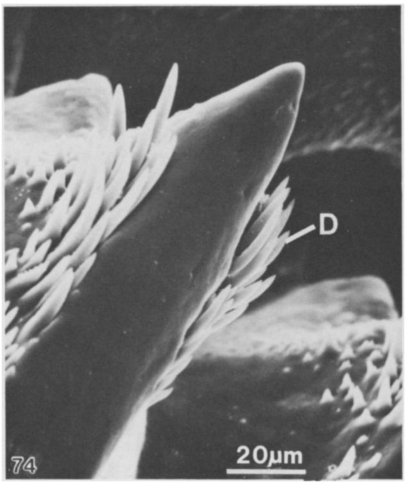
FIGURE 54–62. For description see p. 47.

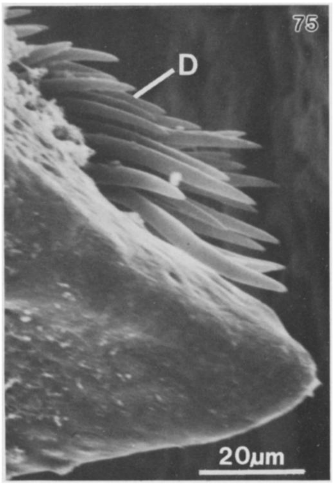


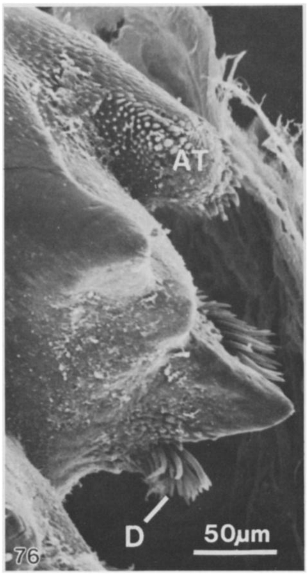




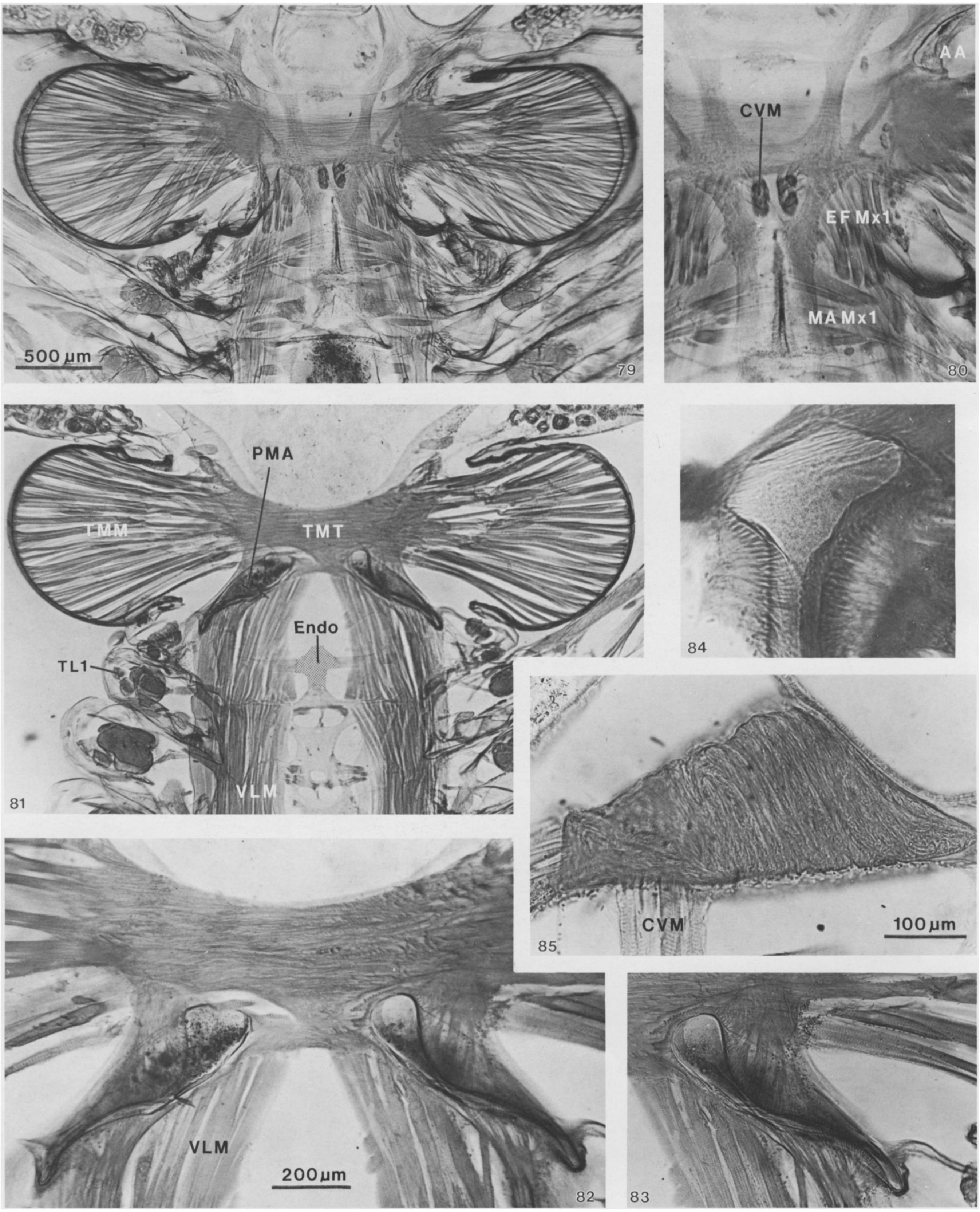








FIGURES 69–78. For description see p. 47.



FIGURES 79–85. For description see opposite and p. 48.

Description of plate 5

Lepidurus apus. The sensory pads of the gnathobases and their sensillae (scanning electron micrographs).

Figure 54. Gnathobases of adjacent right-hand trunk limbs *in situ*, viewed somewhat obliquely from the median side to show the location of the sensory pads (SP).

Figure 55. Gnathobase of right trunk limb 4, viewed from the median side to show the location of the two most proximal sensory pads. The arrangement of the stout gnathobasic spines is also clearly shown. Note the various sensory setae located among these spines.

Figure 56. Opposing gnathobases of the fourth trunk limbs, ventral, to show the most median sensory pads. Some of the opposed stout gnathobasic spines are also seen.

Figure 57. The most median sensory pad of trunk limb 4, ventral.

Figure 58. A sensory pad from the gnathobase of trunk limb 4, showing its array of sensillae.

Figure 59. As figure 58, showing the arrangement of the sensillae.

Figure 60. As figure 59; a group of sensillae more highly magnified.

Figure 61. Details of the sensillae of a sensory pad, showing their distal elaboration.

Figure 62. Sensillae tips, more highly magnified.

Description of plate 6

Lepidurus apus. Mandibles, maxillules and adjacent structures (scanning electron micrographs).

Figure 69. Mouthparts, right-hand side, and adjacent structures. Median view. The labrum (L) has been cut longitudinally. The spines of the maxilla (Mx2 Sp) can be seen protruding between the maxillule and the gnathobase of trunk limb 1. The full complement of transverse ridges of the mandible and the way in which these are drawn out into teeth can be seen.

Figure 70. Right mandible *in situ*, viewed somewhat obliquely from behind. The ventral surface lies uppermost. Note the denticles (D) on the dorsal teeth of the more anterior ridges.

Figure 71. Left mandible *in situ*, viewed from in front. Note the wider gaps between the ridges posteriorly than anteriorly, giving an almost incisor process-like arrangement posteriorly. The paragnath (P) and maxillule can be seen to the right of the photograph.

Figure 72. Masticatory region of the mandibles, ventral; posterior end nearest to observer. The masticatory region of the right mandible (left side of photograph) has been pulled beneath that of the left during fixation revealing the full extent of the more posterior ridges of the left mandible. Note the denticles on the ventral teeth of the more anterior ridges of the left mandible.

Figure 73. Posterior extremity of masticatory region of the mandibles, ventral.

Figure 74. Oblique view of the ventral tooth of the fifth ridge (counting from behind) of the left mandible, showing its armature of denticles (D).

Figure 75. Denticles of a dorsal tooth of an anterior ridge of the right mandible.

Figure 76. The two anteriormost teeth of the right mandible viewed ventrally. Note the denticles (D) on the dorsal tooth of the ridge and the bluntly rounded nature of the small anteriormost tooth (AT).

Figure 77. The mandibular cleaning rakes (see figures 86–91 for location) and associated setules. (Australian material.)

Figure 78. The ventral cutting denticles (CD) of the right maxillule. The upper part of the photograph is anterior. Some of the robust spines of the appendage are also partly visible.

Description of plate 7

Lepidurus apus. Anatomical details of the mandibles.

Figure 79. Horizontal slice through the mandibles, seen from the ventral side, and cutting just ventral to the massive transverse mandibular tendon whose ventral surface can be seen beneath the various elements of the nervous system that lie above it. Note the way in which the transverse mandibular muscles radiate from the ends of the transverse mandibular tendon and the oblique inclination of some of the muscles that insert on the posterior face of the mandibular cuticle.

there are, particularly near the periphery of the spinous area, a few short spines that, although they arise from a basal mound, are not hinged at the base. Such a hingeless spine, adjacent to another of about the same length but with a basal hinge, is seen in the centre of figure 49, plate 4, and others are to be seen to the top left of this photograph.

A few spines fit neither pattern. Two such, seen in figure 47, plate 4, are very short, have relatively stout denticles, and appear to be developing a hinge, and perhaps indicate how such might have been evolved. That to the left appears to have gone further towards acquiring a hinge than does that to the right.

The cuticle of the spine-bearing region of the gnathobases is also provided with a coat of fine spinules, always inclined anteriorly, whose length differs in different regions (e.g. figures 46, 47 and 49, plate 4).

Each gnathobase is also armed with an array of much longer, more slender spines, here called sweeping spines. These are essentially the type I bristles described by Rieder, though he included in this category other spines, situated elsewhere, that although similar in nature, are functionally distinct. Proximally the gnathobase curves forward as a somewhat flattened laterally extending plate and it is on this that the sweeping spines are borne (figures 29–31, plate 2: SS). There is, however, no clear line of demarcation between these and the stout spines, members of the latter series lying adjacent to the sweeping spines being longer than those remote from them.

The sweeping spines are directed anteriorly, and to some extent medially, along the food groove and the longest, most dorsal, members of each assemblage extend forward beyond the limits of the gnathobase in front (figure 29, plate 2). The sweeping spines are articulated at their bases in the same way as are the stout gnathobasic spines (figures 33 and 34). The hinge

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Description of plate 7 (*cont.*)

Figure 80. A detail of figure 79 at a slightly different focus to show some of the extrinsic musculature of the maxillules. The median adductors of the maxillules (MA Mx1), which appear to originate on the ridge of cuticle that lies between the left and right sets of muscles, in fact pass over it to unite in the mid-line or originate on the endoskeletal sheet or both. (See figure 94.) Note the cuticular vaulting muscles (CVM) that descend vertically from the transverse mandibular tendon, and are therefore cut in transverse section. They are here seen passing through a nerve commisure *en route*. Part of the anterior apodeme of the mandible (AA) is seen at the top right of the photograph.

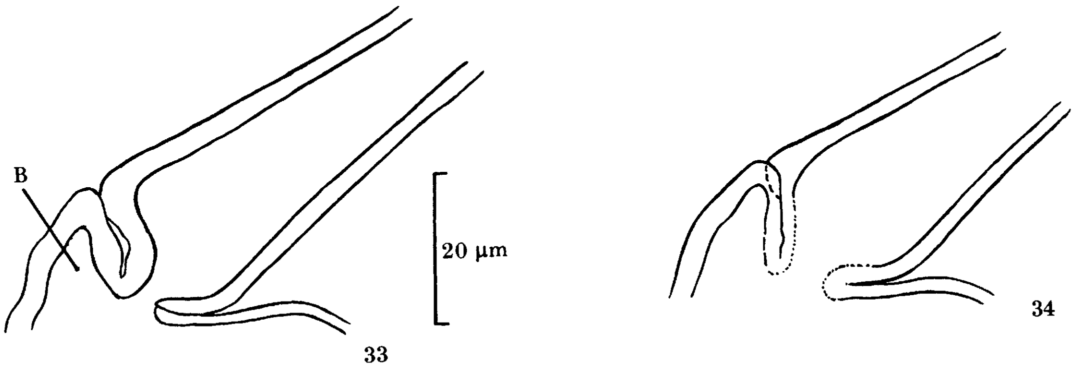
Figure 81. Horizontal slice through the mandibles, seen from the ventral side, immediately dorsal to that in figure 79. Note the massive transverse mandibular tendon (TMT), the post-mandibular apodemes (PMA) with which they are associated, and the anchorage of the anterior ends of the ventral longitudinal muscles (VLM). The ventral endoskeletal sheet of the first trunk segment is clearly seen. A more anterior extension of the endoskeleton (Endo), as seen by deeper focusing in figure 79, is indicated by stippling. Note the way in which the transverse mandibular muscles (TMM) radiate from the ends of the transverse mandibular tendon.

Figure 82. As figure 81. Details of the transverse mandibular tendon and post-mandibular apodemes. Note the fibrous texture of the tendon. Note also how the hollow nature of the apodemes (basically cuticular invaginations) is revealed by the particles of detritus that have found their way into them. The anchorage of the ventral longitudinal muscles (VLM) is clearly seen.

Figure 83. As figure 82. Details of the post-mandibular apodeme as seen at a different level of focusing. Its relation to the transverse mandibular tendon and ventral longitudinal muscle of its side are clearly shown.

Figure 84. Expanded dorsal portion of the post-mandibular apodeme as seen in a longitudinal slice of the whole animal. Being a thick slice this reveals something of the three-dimensional shape of the apodeme.

Figure 85. Transverse section of the transverse mandibular tendon, anterior end to the right (from a longitudinal slice of the entire animal) to show its massive nature and its texture. The anchorage of the ventral longitudinal muscle on its posterior margin and that of the vertically descending cuticular vaulting muscles (CVM) on its ventral margin are also seen.



FIGURES 33–34. *Lepidurus apus.*

FIGURE 33. Basal region of a sweeping spine of a trunk limb gnathobase as seen in optical section. (From a longitudinal section of entire animal.)

FIGURE 34. The same, focused at a level nearer to the observer.

is located at the posterior or dorsal margin of the spine so that the spine is 'locked' on the forward, working, swing of the gnathobase (§10).

Between populations of *Lepidurus apus* which, according to current taxonomic criteria, are conspecific, (but see §3) there are considerable differences in the nature of the sweeping spines. In individuals of what Longhurst (1955*a*) designates as *L. a. lubbocki* from Palestine these spines make up a compact group, are stout, and are armed with short, fine spinules (figures 29 and 30, plate 2). None of them bears long spinules. Australian animals, deemed to be only racially or subspecifically distinct by Longhurst, and designated as *L. a. viridis*, have a less compact group of spines whose dorsal members are more slender and are armed with long slender setule-like bristles (figures 31 and 32, plate 2).

Even in the Australian animals the transition between the region of long sweeping spines and the stout spines is not abrupt. Towards the dorsal extremity of the region armed with stout spines and towards its anterior margin there are long stout spines armed wtih stiff spinules (figure 36, plate 3). Such spines of intermediate length can be seen in Palestinian material in figures 29 and 30, plate 2, and figure 39, plate 3.

Along the anterior margin of the gnathobase, and arising in the region where the groups of stout spines and sweeping spines merge with each other, is a row of singly standing spines, long distally, diminishing in length proximally, that extends across the gap between adjacent gnathobases, whose disposition is best seen in figure 29, plate 2. Members of this row are referred to simply as anterior gnathobasic spines (AS).

Proximally, well removed from the rest of the mechanical armature, the gnathobases also bear (both anteriorly and posteriorly) a row of spines which are here called the proximal gnathobasic spines (PGS). The posterior row is seen in figures 6–9 and, showing its orientation in an undisturbed series of gnathobases, in figure 29, plate 2. The hidden anterior row is similar but tends to consist of more numerous and more slender spines. Rieder (1978) reveals these spines in one of his photographs but assigns them (and some associated sensory setae) to his type I: the sweeping spines. Their function is, however, very different. They are probably homologues of the rows of spines that arise on both the anterior and posterior faces of the more distal endites (or on the corm in the more anterior limbs).

The long sub-marginal spines that are so conspicuous a feature of the more distal endites of

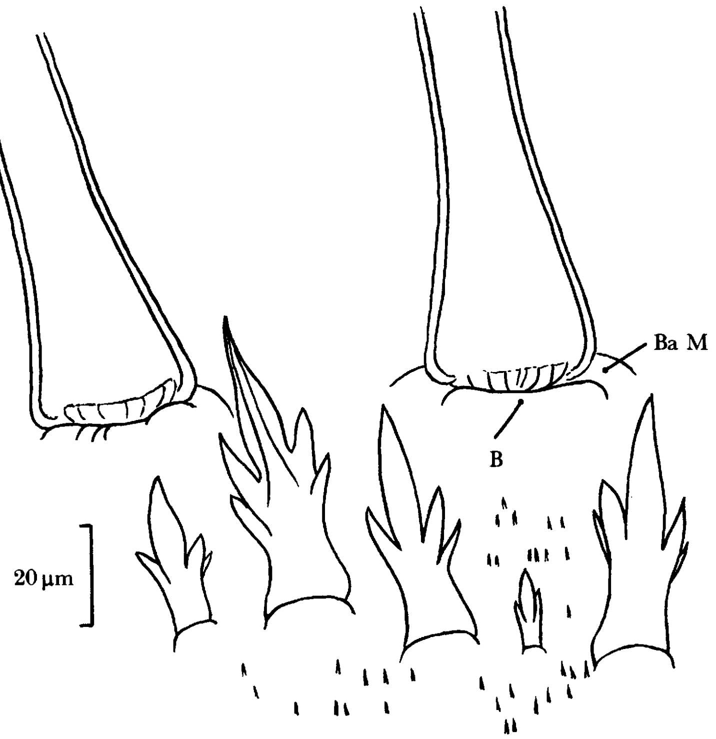


FIGURE 35. *Lepidurus apus*. Bases of meshwork spines of a trunk limb endite and their accompanying trident and 5-pointed spinules.

all save trunk limb 1 are hinged in a similar manner to the stout gnathobasic spines. The hinge always lies to the anterior side of the spine so that the spine itself can incline posteriorly (figures 21 and 24, plate 1) but locks in a more or less vertical position relative to its base if pushed forward.

The meshwork spines that make up the uniseriate rows on the anterior and posterior faces of endites 2 to 5 or, in the more anterior limbs, in some cases arise from the corm, are also hinged (figure 35). These protrude so as to make an acute angle with the endite that bears them (figures 19 and 20, plate 1) and are held erect. Erection is here due to tension in the cuticular hinge for, even in a detached and preserved appendage, each spine can be pushed towards the face of the endite but, on release, flicks back to the erect position, beyond which it cannot be forced. Hydrostatic pressure is clearly not involved. Their orientation, and that of their basal springs, enables them to fold against the face of the endite as the limbs come together, and return to the erect position as the limbs move apart. This enables the meshwork system they make up to be maintained at all positions of adjacent limbs relative to each other.

Proximal to the rows of both submarginal and meshwork spines are rows, sometimes two-deep and staggered, of minute spinules that arise from the endite cuticle (figures 6–9). These are not simple spinules but for the most part elaborate tridents or five-pointed structures and each of these too is hinged at its base (figures 23–25, plate 1; figure 35). Their size differs according to location and the size of the animal but, as a rough approximation, the smaller spinules (30 µm or less in length) tend to be tridents. Of their three teeth or cusps the central is much the largest. Close inspection reveals that many apparent tridents have minute teeth laterally and are in fact five-pointed. Larger denticles, sometimes 60–70 μm in length, generally have five teeth of which the central is the largest, the two outer on each side the smallest. Occasional denticles are seven-pointed and a few are asymmetrical, having more teeth on one side than the other. Each central tooth is long and pointed, and drawn out on each lateral margin into a thin, broad lamella so that its width is effectively doubled. The smaller, lateral teeth also have lamellae, but only on the inner margin. Each spinule is thus a scoop-like structure. In the case of the spinules that stand near the bases of the sub-marginal spines, the hollow face lies posteriorly, the hinge and boss, like those of the sub-marginal spines, anteriorly (figures 21 and 24, plate 1). Spinules that accompany the meshwork spines have their hollow faces opposed to the flat surface of the endites.

The gradual transition in armature of the posterior series of limbs from limb 12 backwards, referred to in §5, is apparent in figures 11–15. Details of the armature are seen in figures 26–28, plate 1, and figures 37 and 38, plate 3. On the gnathobases there is a gradual reduction in the size and number of both the stout spines and the sweeping spines. Towards the posterior end of the series the stout spines tend to be more denticulate than their anterior homologues (figure 37, plate 3). The row of anterior spines is well developed, as can be seen very clearly in figure 38, plate 3. These spines are directed obliquely forward and appear not to be hinged at the base. They are therefore rigid. Proximal gnathobasic spines are present on the posterior face of the gnathobase as in the anterior series and can be seen in figures 37 and 38, plate 3, but the equivalent series on the anterior face diminishes in degree of development posteriorly and is found no further back than gnathobase 22 in the material studied.

The nature and arrangement of the meshwork spines is self-evident from figures 19 and 20, plate 1 and comparison with descriptions of their anterior homologues. The close packing of adjacent limbs posteriorly means that the meshwork spines are directed in a direction very similar to the endites that bear them. Trident spinules are present on the endites of anterior members of the posterior series of limbs. Their number diminishes posteriorly and they are not present on the more posterior limbs.

The inner margins of the endopodites bear denticulate spines (figures 12 and 14; figure 26, plate 1). More ventrally and laterally these give way to longer, soft setae each of which has marginal fringes of setules in the plane of the endopodite.

Further anatomical information on the trunk limbs is given in §9.

(*b*) *Sensillae*

For the certain identification of a structure as a receptor it is necessary to demonstrate the presence of nerve cells and to establish function electrophysiologically (Bush & Laverack 1982). However, structure and location are sometimes such as to make function self-evident at least in a general way. For descriptive purposes a more practical difficulty is the designation of structures known to be innervated but which serve a predominantly mechanical function. Thus the stout gnathobasic spines of the anterior trunk limbs of notostracans are innervated (Rieder 1978, 1979) but their role is that of food-handling. They have thus been treated here as elements of the mechanical armature of the limbs.

The trunk limbs of notostracans are provided with a profusion of sensillae. Some are clearly tactile, others equally obviously serve as chemoreceptors. Sensory setae of various kinds are present on the gnathobases. Ventral to the region of heavy armature are several long, slender, sparsely plumose setae, tending to be more numerous on the posterior than on the anterior limbs of the anterior series (figure 9, inset). Scattered among the stout gnathobasic spines are other sensory setae of several kinds. A few are very long and extend forward and towards the food groove. Three such can be seen in figure 55, plate 5, and such a seta can be seen extending across much of the visible portion of the gnathobase in figure 52, plate 4. These setae are sparsely provided with setules, a few of them long. A few shorter, more profusely setose setae, whose setules are also very long, are also present, one being seen behind the spine shown in figure 42, plate 3. These are probably tactile in function (mechanoreceptors).

Also present are thin-walled, smooth, rod-like setae of various lengths. These arise from a socketed base and extend, either straight or somewhat curved, in more or less the same direction as the spines among which they occur (figures 46–49, 51 and 52, plate 4). These are superficially like the rod setae described by Thomas (1970) in the crayfish *Austropotamobius pallipes* but are much shorter. Long examples are 60–70 μm in length: others (figure 46, plate 4) are very short: only about 15 μm long. They could probably be classified into several categories on purely morphological criteria. Their socketed base perhaps hints at a tactile function, but chemoreception cannot be ruled out. Their tips show some elaboration but this may not be a significant indicator of function. As Ball & Cowan (1977) and Laverack & Barrientos (1985) point out, some apparent chemoreceptors lack terminal pores, and pores have been found in many setae that are almost certainly mechanoreceptors. A clue as to function may be given by size and location. Although sensory setae that are about the same length as adjacent spines may function as either chemo- or mechanoreceptors, very short setae, such as that seen in figure 46, plate 4, surrounded by long spines, must seldom make contact with food items and can therefore scarcely have a tactile function during feeding.

Laverack & Barrientos (1985) have illustrated short sensory structures in *Homarus* that they suspect are chemoreceptors for oxygen and carbon dioxide. These are somewhat similar to the short receptor seen in figure 46, plate 4, and, superficially at least, perhaps even more like the short, robust, hingeless structures seen near the top left, and in the centre, of figure 49, plate 4. These latter are, however, larger than the structures illustrated by Laverack & Barrientos. In neither case are they thin-walled like 'obvious' sensillae.

That notostracans are provided with olfactory (or gustatory) receptors is obvious from their behaviour when supplied with certain foods that, without being touched, elicit searching behaviour. (Disturbance caused by live prey may, however, be detected by pressure receptors.) What can scarcely be other than chemoreceptors are also conspicuous on the trunk limbs. As long ago as 1930, Seifert demonstrated that *Triops* was able to 'taste'. For example, gelatin, pure and containing either sugar, salt, acetic acid or quinine, was accepted or rejected to different degrees. Pure gelatin was accepted most and rejected least; gelatin containing acetic acid and quinine was least acceptable. Small worms were usually accepted readily; after soaking in quinine they were almost always vigorously rejected. Although Seifert felt that his feeding experiments threw no light on the localization of chemoreceptors, he went on to say that on the gnathobases and endites are 'feine stumpfe Härchen, die in kleinen Gruppen auf flachen Erhebungen des Chitins stehen und als Chemorezeptors in Frage kommen könnten'. He cautiously concluded, however, that his findings did not enable him to corroborate this conjecture.

Scanning electron microscopy has revealed much more of the nature of these undoubted receptors, which occur in conspicuous groups. Rieder (1978) illustrates those of *Triops cancriformis*, but those of *Lepidurus apus* are much more spectacular. In this species, on the anterior series of trunk limbs, they occur on both the gnathobase and more distal endites. Each group of sensillae makes up a circular pad. Several such pads are present on each gnathobase ventral to the armature of spines and setae. On the more anterior limbs the three most distal are particularly large and circular, the more proximal smaller, and although tending to be circular, form no more than tufts.

The appearance and location of these pads is best appreciated from figure 45, plate 3: SP, and figures 54–56, plate 5. A particularly well-developed pad lies just ventral to the mass of gnathobasic spines (figure 55, plate 5). This is ringed by a coronet of densely arranged, stiff, slender pointed setae that display no particular cuticular elaboration. These surround a central area within which arise numerous tubular sensillae from an undergrowth of pointed setae shorter than those covering the peripheral coronet (figure 58, plate 5). These are the type 4 bristles described by Rieder (1978) who showed that they are innervated. Size is variable according to the size of the animal but, to give some idea of dimensions, the central area of the pad in an 'average' sized adult is about 70 μm, the diameter of the entire pad 100 μm or a little over. Boundaries are ill-defined. Under low magnifications a pad presents an almost sea-anemone-like appearance.

Each tubular sensilla (figures 58–62, plate 5) has a diameter of about 2 μm or a little more. Because the base of each is hidden, the length is not easy to measure, but many of them are at least 20 μm long. Each tends to swell slightly at its blunt tip. The somewhat domed, but not far from flat, distal face of the sensilla displays considerable elaboration (figures 61 and 62, plate 5). Arising from the centre is a tubular structure, about 0.4 μm in diameter and 0.3 μm long. Its walls are thick so its internal diameter is less than 0.15 μm. Whether it opens to the exterior or is spanned by a membrane is not known. Surrounding this terminal tube but separated from it by a space, is a ring of 14 or 15 papillae whose length is about the same as that of the terminal tube. These are regularly arranged in the main but an occasional papilla is as it were partly squeezed out of the ring. The outside diameter of the ring is about 1 μm or slightly more.

The position of even the most proximal such pad on the gnathobase is such that, when small food particles are being handled, direct contact with the food seldom takes place. When larger items are being dealt with and held between the limbs (§10) contact with the grasped item must at times be inevitable. Towards the posterior end of the anterior series of trunk limbs the more ventral pads of the gnathobase are smaller than on more anterior limbs but the dorsalmost pad persists as the major large pad. This trend continues in the posterior series of trunk limbs so that on limb 18 the ventral pads are reduced to small tufts. Small groups of sensillae persist in these locations as far back as at least limb 24 but here the major dorsal pad dominates (figure 38, plate 3) and this is even more obviously so more posteriorly (figure 37, plate 3).

Sensory pads are present along the margins of all the more distal endites. The inner margin of each endite is drawn out into a series of mounds, each of which is surmounted by a sensory pad (figures 19, 20 and 22, plate 1). These are seen in greater detail in figures 21 and 24, plate 1. Although including fewer sensillae than the large pads on the gnathobases, these are essentially similar to the latter. Similar, but smaller, pads are present on the outer margins of the endites, these being more numerous on the proximal than on the distal endites. Often one sensilla is longer than the rest in these pads. In some cases, on both inner and outer margins, the pad is accompanied by a somewhat longer, presumably tactile, seta.

Towards the posterior end of the anterior series of trunk limbs the distalmost pad of sensillae on each endite is accompanied by a small spine. Progressively more posterior limbs, that is the anterior members of the posterior series, here bear a spine that becomes not merely relatively but actually larger the more posterior in the series it is located, so that on trunk limb 16 this is stout and conspicuous and becomes even more so more posteriorly. Although the spines diminish in size on the most posterior, very small, limbs, they remain relatively robust throughout. This development is accompanied by a progressive increase in length of the tubular sensillae and a gradual shift of the presumed chemosensory armature towards the distal ends of the endites of the more posterior trunk limbs. That is, the more proximal pads tend to be reduced in size and disappear whereas the distalmost pad, in particular, becomes larger. At the level of about trunk limb 18 the bulk of the sensory structures are concentrated at the distal extremity of each endite though more proximal pads persist on endite 2 more posteriorly in the series. The concentration of sensillae distally, and the accompanying large spine of each endite, are seen in figures 27 and 28, plate 1. The result of the arrangement of mechanical and sensory armature is the wall of close-set spines and dense array of sensillae seen at low magnification in figure 26, plate 1, and, in more detail, in figure 27, plate 1.

(*c*) *Sensillae in the Notostraca and Anostraca: a brief comparison*

The profusion of sensillae on the trunk limbs of the Notostraca stands in marked contrast to the situation in other branchiopods. This is readily apparent by comparison with the Anostraca. In the latter, each of the first ten of the eleven gnathobases of the trunk limb series bears a long, presumably tactile, seta that projects into the food groove. This is seen in scanning electron micrographs of a large *Branchinecta ferox* in figures 133–136, plate 6, of Fryer (1983) and is representative of the situation in other species. Apart from this seta no other receptors are apparent on the gnathobases. Possibly sensory structures are sometimes present distally on trunk limb one, but often the more distal endites bear at most a single seta that may have a sensory function, and some endites appear to be devoid of receptors. This paucity of sensory structures is typical of particle-eating branchiopods with relatively stereotyped limb movements (Anostraca, Ctenopoda), and even the Anomopoda, with their often considerable versatility of limb movements, have relatively few sensillae in relation to the Notostraca.

This difference can be related to the nature of the food and to the way it is collected. Anostracans, which generally abstract particles from suspension but sometimes supplement this source by scraping, are generally restricted to the intake of relatively fine particles. With small modifications, the limbs follow a set sequence of activity. This is so even in the giant species of *Branchinecta* that, as adults, are carnivores. Relatively few sensillae are needed. The same applies to the conchostracan orders Spinicaudata and Laevicaudata, to the Ctenpoda, and in part to some suspension-feeding anomopods. Even scraping anomopods are generally restricted to fine particles or, in exceptional cases, secondarily acquired specialized diets such as carcasses (*Pseudochydorus*) or tissues torn from *Hydra* (*Anchistropus*). By contrast notostracans delve into a wide range of deposits, sift particles of various sizes, ingest detrital material of diverse origins, and seize a wide range of prey, large and small. The value of sensillae is readily apparent. Moreover, although other branchiopods are unlikely often to encounter noxious material, the digging habits of notostracans offer no such insurance. Thus in their long histories, anostracans and notostracans have acquired very different armouries of sensillae to serve their very different feeding mechanisms.

7. The functional anatomy of the head

(a) General features

A general impression of the nature of the head can be obtained from figure 63 which is a longitudinal slice very near the mid-line. The shovel-like anterior extremity is readily apparent. On each side, and not far from the mid-line, is a stout tendon, the cephalic bracing tendon (CBT) that runs more or less dorsoventrally between the dorsal and ventral cuticle, inclining a little posteriorly dorsally where it fans out into an array of anchoring fibrils (AF). Ventrally there are no such fibrils and it merely widens somewhat adjacent to where it anchors on the cuticle. It is entirely tendinous, no muscle fibres being present. In its posterior dorsal portion each tendon provides the origin for a few short muscles that dilate the dorsal part of the oesophagus (D Oe DM). Dorsally (indicated by an arrow) part of the anterior extremity of the midgut wall is firmly bound to each bracing tendon that thus help to support it. Ventrally the oesophagus (Oe) also lies close against the tendons at one point, though such intimate union

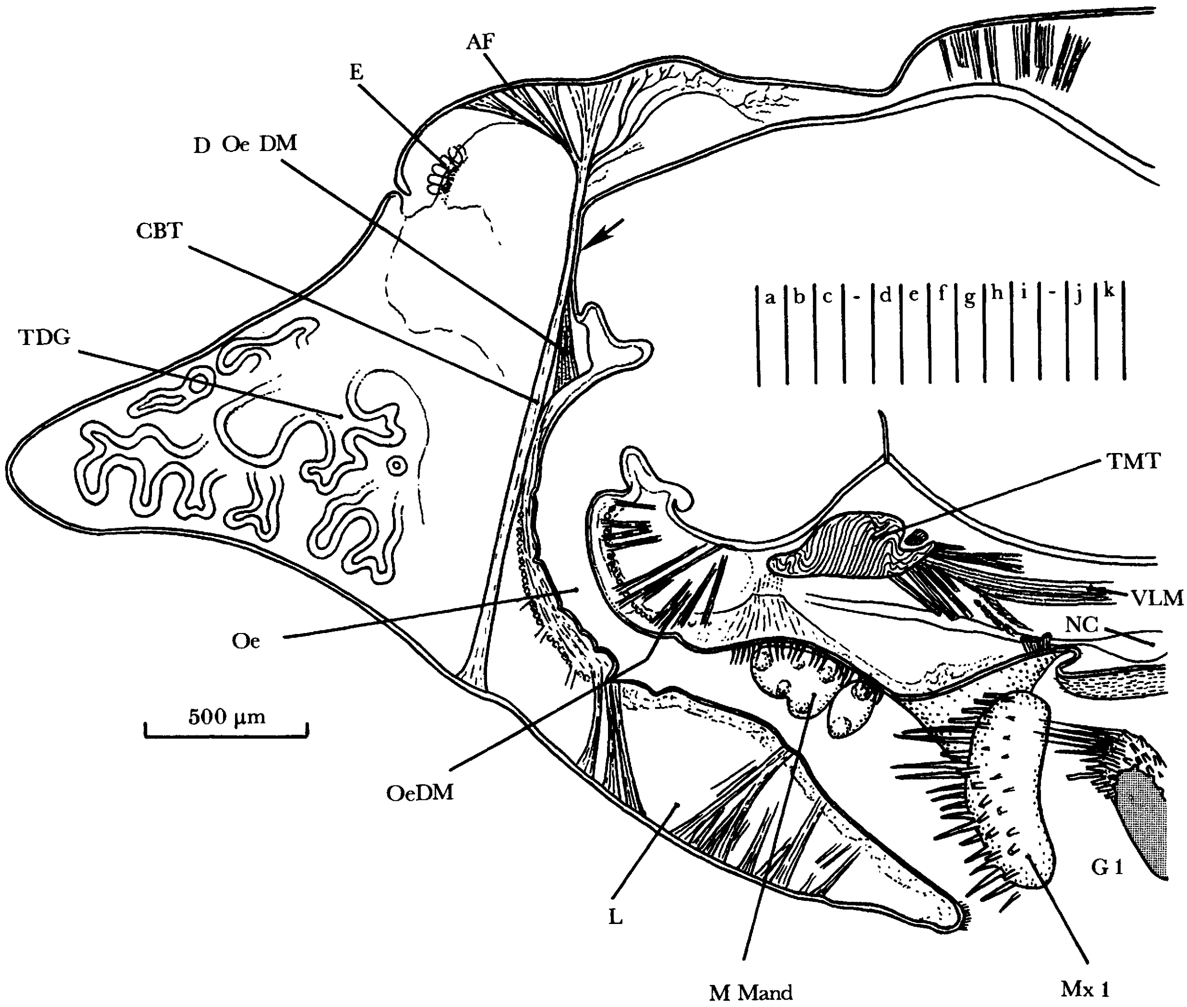


Figure 63. *Lepidurus apus*. Longitudinal section of head almost along the mid-line. The paragnath (except for a trace of its base) and maxilla lie too far lateral to be seen. The approximate location and thickness of the transverse sections shown in figures 86–99 are indicated by letters a–k. The arrow indicates where the midgut wall is bound to the cephalic bracing tendon on each side.

as that shown by the tendons and midgut wall is precluded by the need for the oesophagus to undergo peristaltic movements.

The course of the oesophagus is seen in figure 63. More of the dilator muscles (Oe DM) can be seen in figure 64 which is a little more lateral. Too lateral to be seen in figure 63 are two dilator muscles of its dorsal end that originate dorsally just behind the eye. The oesophagus is lined by soft cuticle. On each side, and extending anteroventrally, this gives rise to a long, apodeme-like, hollow prolongation on which some of the dilator muscles insert.

From the midgut extend forward two ducts that break up into a mass of tubules (TDG) of the digestive gland, the so-called hepatopancreas. These extend to the anterior extremity of the head and largely occupy the region anterior to the cephalic bracing tendons except for the region occupied dorsally by the compound eyes (figures 63 and 65).

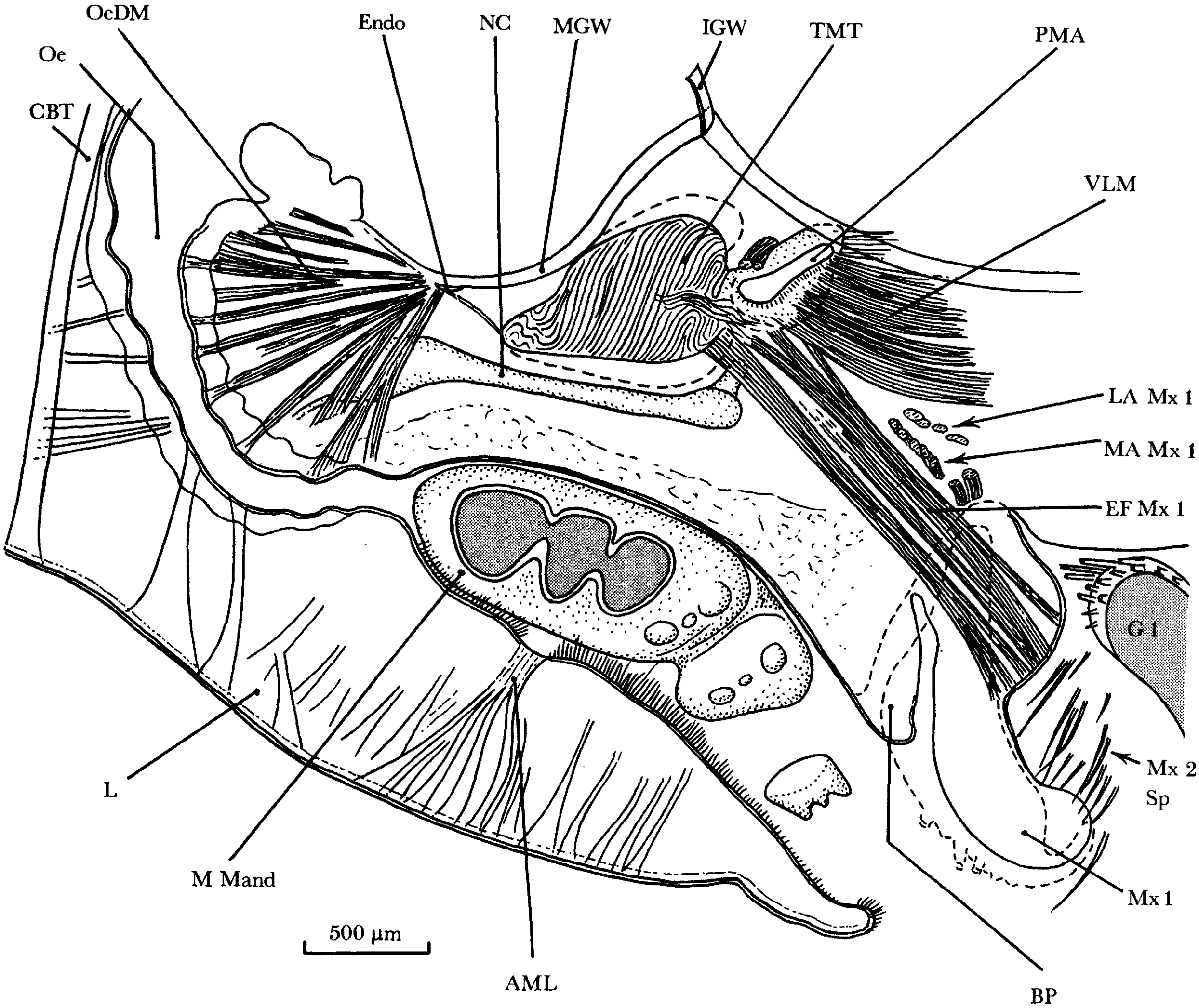


FIGURE 64. *Lepidurus apus*. Longitudinal section in the region of the mouthparts, immediately lateral to that shown in figure 63. Note the intimate association of the transverse mandibular tendon (TMT) and the post mandibular apodeme (PMA). The gut wall is cut obliquely and therefore appears thicker than is the case. The dashed lines around the maxillule show its outline as seen by focusing towards the observer. For convenience the oesophagus, shown in outline only, is focused at a slightly different level from the maxillule.

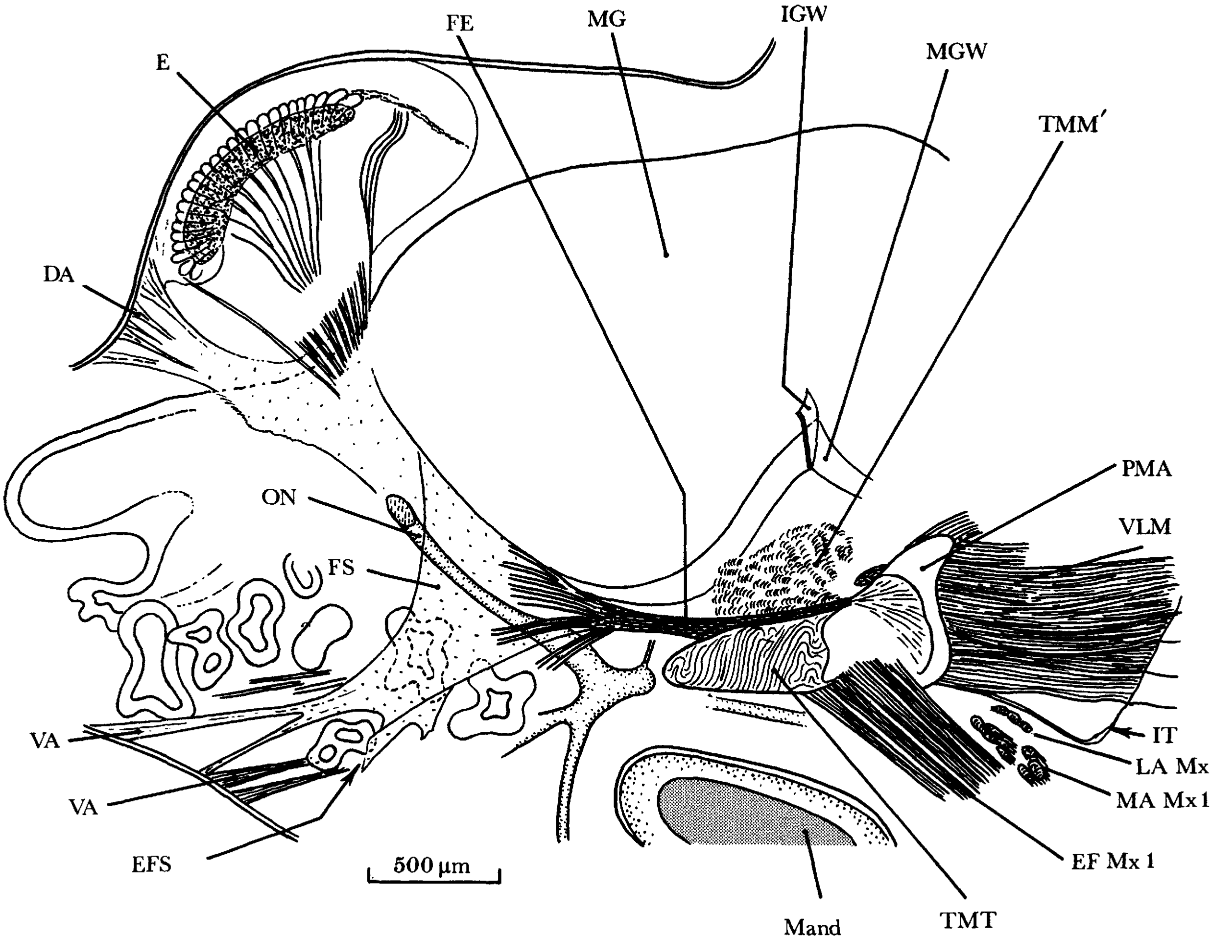


Figure 65. *Lepidurus apus*. Lontitudinal section showing the transverse mandibular tendon (TMT) and adjoining features immeditaely lateral to that shown in figure 64. Note how some of the muscle bundles of the ventral longitudinal muscles are anchored on the post-mandibular apodeme (PMA) which, with the closely associated transverse mandibular tendon, provides the sites of origin of the extrinsic flexor muscles of the maxillule (EFMx1). Note the fibrous anterior extension (FE) from the transverse mandibular tendon on which oesophageal dilator muscles originate, and the fibrous sheet (FS) extending anteroventrally with which this is continuous and which itself is anchored (VA) on the ventral cuticle. As the sheet is very thin, and lies in different planes at different levels, no more than an indication of its disposition can be given in a two-dimensional illustration. Other structures in its vicinity are shown in outline only merely as topographic markers. The midgut wall (MGW) is cut obliquely and thus appears to be thicker than is actually the case.

(*b*) *The labrum*

The broad, flattened nature and thick ventral cuticle of the labrum were noted in §4 and various internal features can be seen in figures 63 and 64. Although the junction between the labrum and the ventral head cuticle is evident when the whole animal is viewed from below, and the labrum can pivot slightly about its anterolateral corners, there is no well defined hinge, nor are there any levator muscles, such as occur for example in the Anomopoda, that can lift it. The fibrous cephalic bracing tendons have been mistakenly thought to be such in the past. Manipulation suggests that the labrum can be forced away from the mandibles slightly if large food masses are pushed into the pre-oral space, but its ability to swing is extremely limited. The elasticity at the lateral pivots takes it back to the position indicated in figures 63 and 64 when it is released. Its topographically dorsal surface, which is armed with numerous short spinules in places, is mobile, as can be deduced from the numerous strands, some fibrous some muscular, that span its thickness. This gives scope for some increase in the volume of the pre-oral space.

No labral glands have been detected even in Zenker-fixed material of *Triops*. This is in marked contrast to the situation in particle-eating branchiopods with rolling and crushing mandibles belonging to several orders. Here labral glands, and sometimes secretion-storing reservoirs, are often a conspicuous feature of the bulky fleshy labrum.

(*c*) *The mandibles and associated skeleto-musculature*

The mandibles of the Notostraca are biting appendages. In this they differ markedly from those of the Anostraca, Lipostraca, Spinicaudata, Laevicaudata, Ctenopoda and Anomopoda which, although they have sometimes developed secondary modifications that enable them to bite to a limited extent, are basically grinding and crushing appendages that sweep particulate food forward. (Manton 1964; Fryer 1963, 1968, 1974, 1983, 1985). Notostracan mandibles nevertheless exhibit many similarities in their skeletal features, and in the nature of their tendons and muscles, to the rolling, grinding type of branchiopod mandibles. Herein lies one of the great puzzles of the notostracan mandibular mechanism. Although a limited degree of biting can be accomplished without adduction of the mandibles, as is the case in certain large anostracans (Fryer 1966, 1983), such a mechanism is of restricted versatility, and true biting demands a degree of direct mandibular abduction and adduction, a feat of which mandibles of the rolling, crushing type are incapable. Although abduction of notostracan mandibles has been inferred it has not, apparently, previously been reported. As described here abduction–adduction movements can be performed. How this is achieved is an hitherto undescribed notostracan specialization.

The cuticular element of each mandible has the same hollow, boat-like nature as the rolling, crushing type of branchiopod mandible, but its specializations are of a very different nature. The articulating surface is broad (figure 68), not pointed, and the masticatory region is drawn out into a relatively narrow, gently curved prolongation, the margin of which is deeply incised so that there are eight well-separated transverse ridges (figures 69–73, plate 6). Of these, all save the anteriormost on the right mandible, are drawn out into two, sometimes three, teeth or cusps, there being slight differences between species. In the vicinity of the teeth the cuticle is thick and heavily sclerotized. In life, when at rest, the ridged masticatory prolongation of each mandible lies at an angle of approximately 45° to the long axis of the body, and therefore to the food groove, its posterior end lying ventral, its anterior end dorsal (figure 29, plate 2) a matter of great relevance to the feeding mechanism. The masticatory regions of the right and left mandibles are not quite symmetrical but much generalization is possible. In *Lepidurus apus*, to which these descriptions specifically refer, the widest gaps and deepest clefts between adjacent ridges are those between the three posteriormost (figures 69–71, plate 6). On each mandible the posteriormost ridge lies at the extremity of the masticatory prolongation and is drawn out into two conical teeth to form a rather sharp bifid structure (figures 69–71, plate 6). The second ridge is produced into three conical teeth of which the median is smaller than its outer partners. Each of the five succeeding ridges of the right mandible is also produced into three conical teeth, the median tooth being in each case the smallest (figures 69–70, plate 6). A similar arrangement prevails on the left mandible save that rather than a conical tooth, the middle region of the ridge resembles a blunt blade running transversely across the masticatory surface (figure 71, plate 6). (There is some variation here, some of it apparently size-related.) The anteriormost ridge of the right mandible, takes the form of a small, bluntly rounded tooth (figure 76, plate 6: AT), that of the left is more elongate and indistinctly bicuspid (figure 71, plate 6). The arrangement in *Triops* is very similar. Here the posteriormost ridge tends to have what are in effect two cutting blades of chitin, one of which arises from the side of the main tooth, but similar blades are sometimes seen in small individuals of *Lepidurus*.

Some of the teeth of the mandibular ridges display a further elaboration. Counting from the posterior end, the ventral teeth of the third and, more especially, succeeding ridges of the left mandible are provided with groups of short, stout, bluntly pointed, spinous denticles whose location and arrangement are seen in figure 72, plate 6. Details of these denticles are shown for a single tooth in figure 74, plate 6:D. Similar clusters of denticles are present on the more anterior ridges of the right mandible, but here it is the dorsal teeth that are so armed (figures 70, 75 and 76, plate 6:D). Thus when the ridges of the opposed mandibles come together, their ability to grip and to force food forward is enhanced by an array of teeth near the dorsal margin of the right masticatory region and near the ventral margin of the left.

The skeleto-musculature of notostracan mandibles is much more complex than the outline descriptions of Snodgrass (1950) and Mahoon (1960) indicate. Both give simple sketches indicating the promotor and remotor roller and transverse muscles (for which they use different nomenclature) and both show the transverse mandibular tendon, but neither of them gives any details of the muscles and neither indicates any suspensors of the transverse mandibular tendon. Mahoon in fact states that such suspensory ligaments are absent. He also makes the surprising statement that the musculature is 'much simpler' than that of other branchiopods, perhaps because of the absence of any transverse 5c muscles linking the posterior margins of a pair of mandibles. Important muscles, vital to the functioning of the mandibles, were overlooked.

Each mandible articulates dorsally not by a pointed tip as in many branchiopods but by a flat, broadly U-shaped distal extremity (figure 68). The open ends of the Us of the two mandibles more or less face each other. Each lies in a hollow which is reflected by a small mound on the upper surface of the carapace. Strength is given to this region by a groove encircling the outer part of the region of articulation that is continuous with a transverse groove, itself continuous with the median ridge of the carapace which it joins at right angles. In large individuals these grooves are noticeably sclerotized and the whole complex clearly forms a series of strengthening ribs. It is the presence of a dorsal carapace that has permitted the development of such a robust articulation and of a specialization in the mandibular musculature unique to the Notostraca, so, in considerable measure, the dorsal carapace has enabled the group to develop powerful biting mandibles.

There is a massive transverse mandibular tendon (TMT: figures 63–66; figures 82, 83 and 85, plate 7; figures 86–91) much thicker than that of other groups of branchiopods, where indeed, as in anomopod cladocerans, it is often thin and strap-like (Fryer 1963, 1968). Notwithstanding Mahoon's (1960) statement that there is no suspensory ligament, the tendon is so suspended and braced – by no fewer than three dorsal ligaments on each side – as well as being braced by an anteroventral ligament and by four dorsal muscles. It is also supported posteriorly by a pair of complex cuticular apodemes, whose presence was noted by Hessler (1964) but whose complexity and functions have not previously been investigated, and is anchored by fibres to a pair of simpler anterior apodemes.

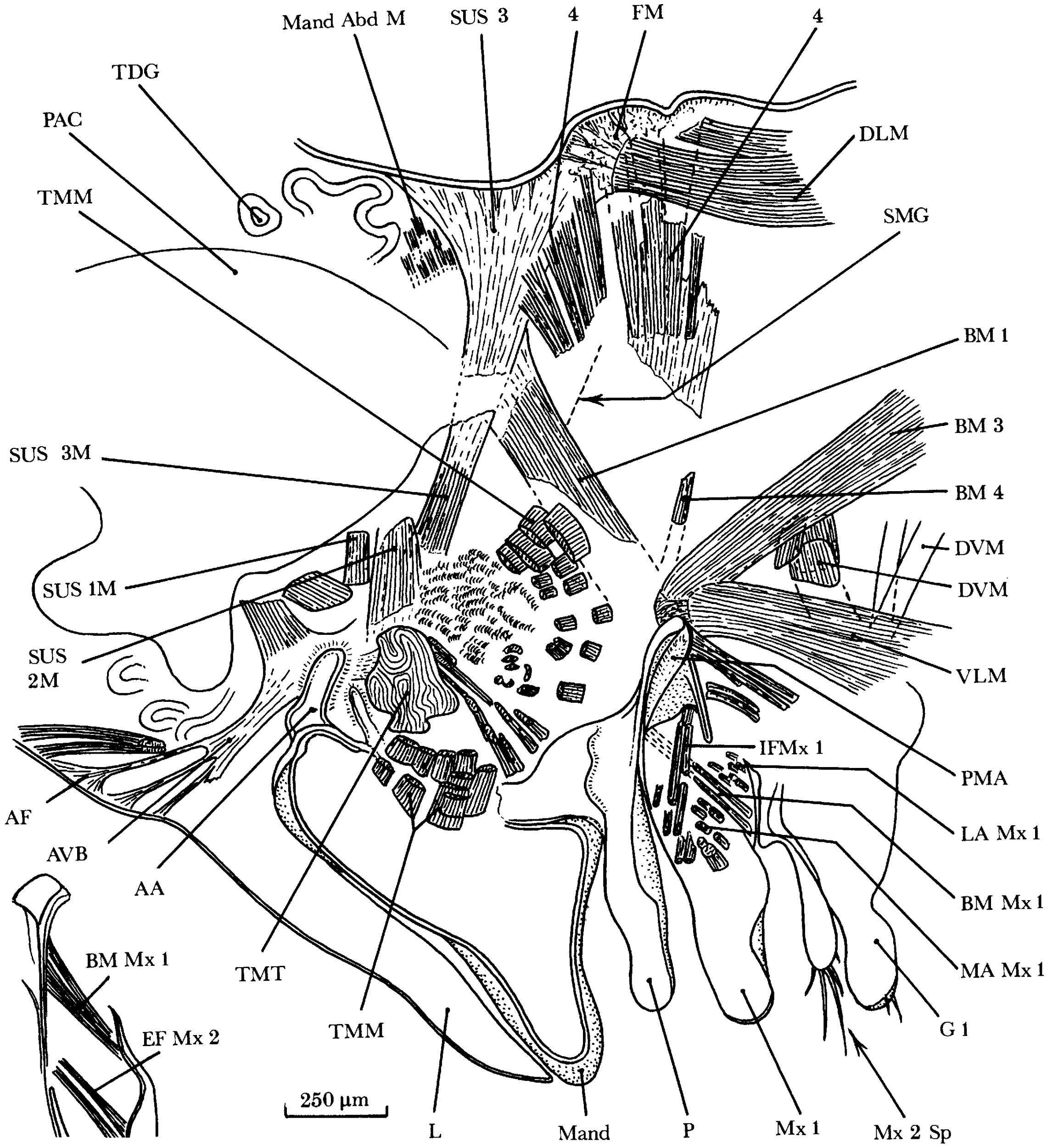


FIGURE 66. *Lepidurus apus*. Longitudinal section in the region of the mouthparts more lateral than in figure 65. Suspensor 3 (SUS 3) – note its muscular basal region (SUS 3M) – and the muscular basal regions of suspensors 1 (SUS 1M) and 2 (SUS 2M) of the transverse mandibular tendon are shown. Note the anterior apodeme (AA) and the thick cuticle of the posterior face of the paragnath (P). The inset, to a slightly smaller scale, and located a little less laterally, shows the bracing muscles (BM Mx1) near the base of the maxillule that originate on the ventrally extending rib of the post-mandibular apodeme, the dorsalmost portion of which is seen in figure 84, plate 7. The fragment of the extrinsic flexor muscle (EFMx2) seen here is the extreme lateral margin of this muscle.

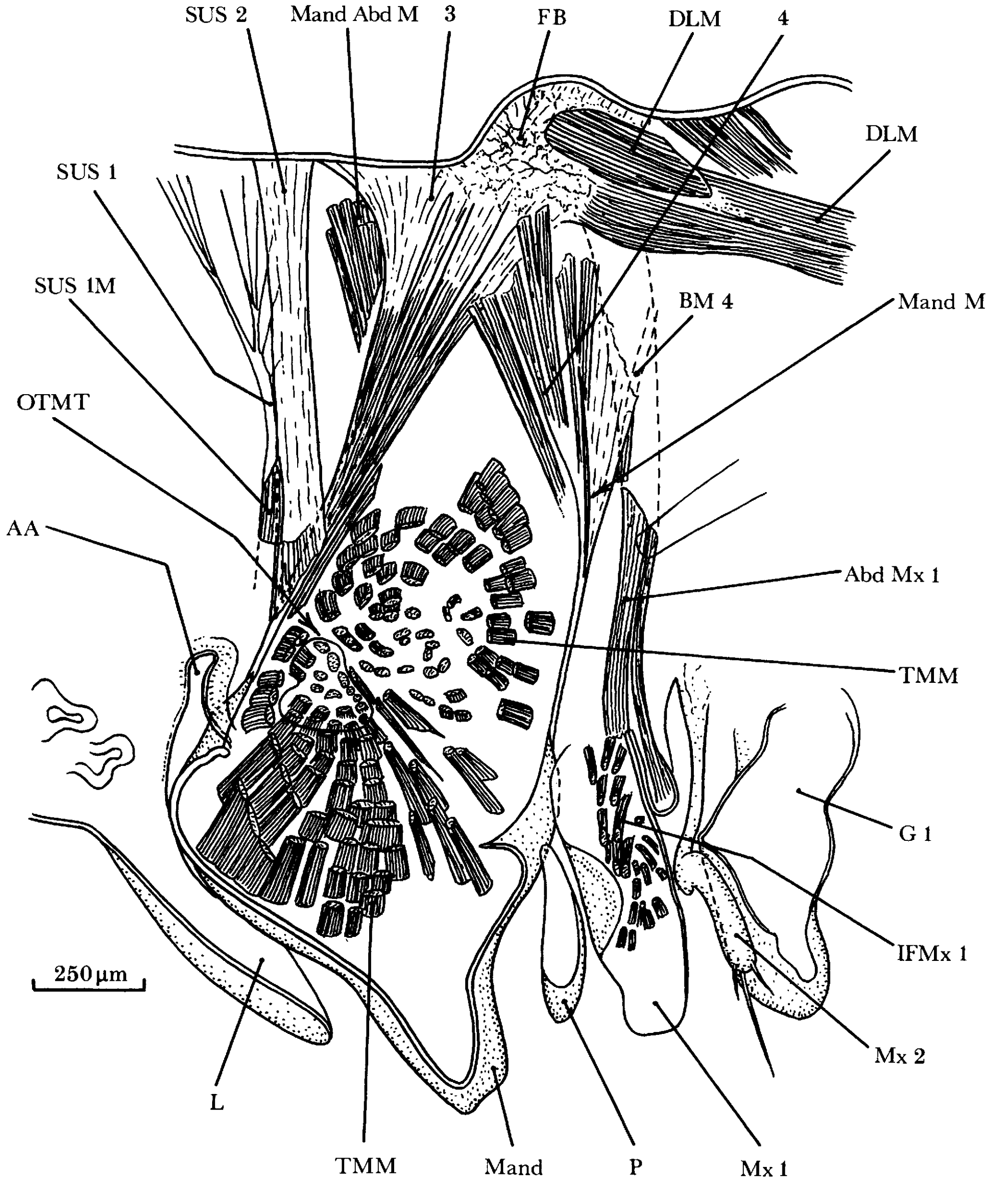


FIGURE 67. *Lepidurus apus*. Longitudinal section through the mouthparts immediately lateral to that shown in figure 66 and at the lateral extremity of the transverse mandibular tendon which in fact is seen only by focusing on the extreme upper surface of the section. Its outline (OTMT) is indicated, but the transverse mandibular muscles (TMM) that are here seen converging upon it from their more lateral insertions are drawn from a deeper level of focusing. At the level of focus of the rest of the section the tendon would not in fact be seen. The mandibular abductor muscle (Mand Abd M) can be seen dorsally. The distal part of suspensor 1 (SUS 1), whose muscular basal region (SUS 1M) is present in this section, has been added from the next, more lateral, section, and the lateral continuations of the abductor muscle of the maxillule (Abd Mx1) and bracing muscle 4 (BM4) are indicated by broken lines.

The transverse mandibular tendon is broader from front to back than from top to bottom (figures 63–65; figure 85, plate 7) and is narrowest towards its anterior margin, at least medially. Towards each end it is suspended by two stout fibrous ligaments (SUS 2 and 3) of which the former runs more or less dorsoventrally whereas the latter inclines posteriorly as it passes dorsally (figures 66, 67 and 86–88). Both are muscular ventrally (SUS 2 M and 3 M,

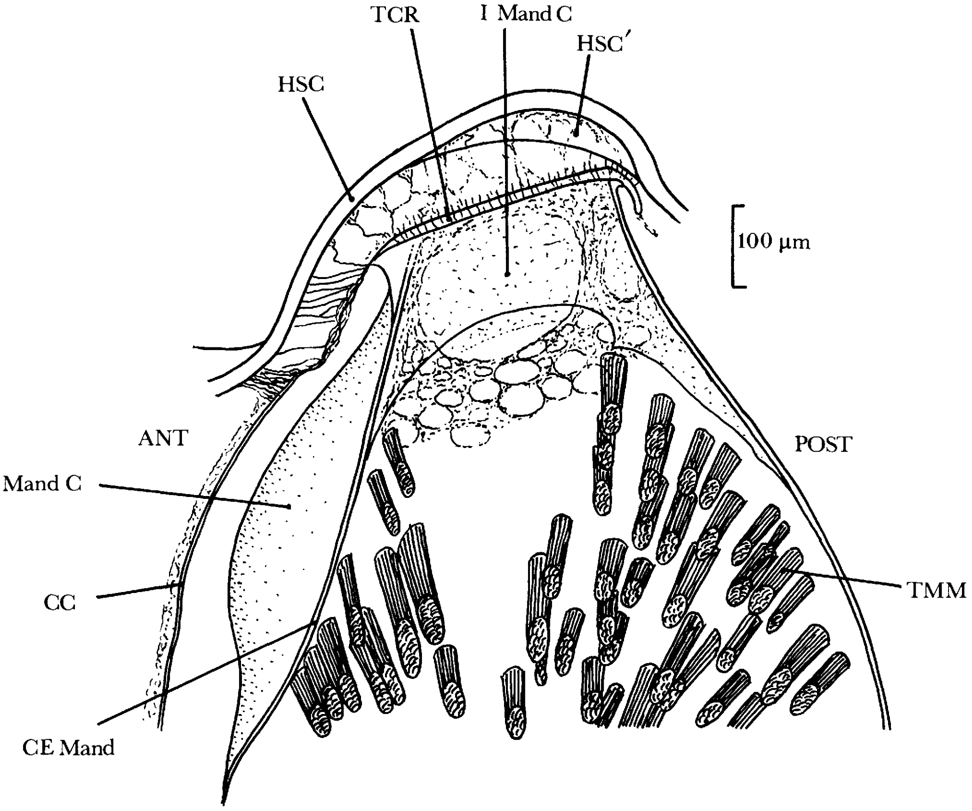


Figure 68. *Lepidurus apus*. Longitudinal section showing the mandibular articulation, seen from the inside. Note the thickened cuticular ridge (TCR) at the dorsal extremity of the mandible which forms the zone of articulation. The headshield cuticle (HSC) is seen in section and to the right it is also seen in face view (HSC′) in this thick slice. The epicuticle, which is sclerotized, and golden brown in colour, is not indicated.

same figures). Being flattened, suspensor 3 is not always easy to see in transverse sections (see figures 66 and 88) but is in fact a robust ligament with a broad dorsal anchorage. Anterior to these is another ligament (SUS 1) again with muscle fibres ventrally. This inclines laterally as it passes more or less vertically to fan out dorsally into an array of fibrils that anchor over a wide area of the exoskeleton (figure 67). A similar bracing tendon (AVBT) extends anteroventrally (figure 66).

At its anterior lateral extremities the transverse mandibular tendon is anchored by fibres to a simple apodeme (figures 66, 67 and 86: AA), referred to here as the anterior apodeme. At each end the tendon is also firmly attached posteriorly to a much more complex apodeme, the post-mandibular apodeme, (PMA: figures 64–66; figures 81–83, plate 7; figure 91–94). This arises between the paragnath and the maxillule, (not between the maxillule and maxilla as stated by Hessler), and is described in §7 *e*.

In transverse section the transverse mandibular tendon has a characteristic laminar appearance (figure 85, plate 7) presumably resulting from the nature of its secretion. In the anostracan *Branchinecta ferox*, whose tendon is much less massive, a laminar structure is very apparent in the early stages of development, in which the cells that secrete it can readily be seen (Fryer (1983): figures 71, 74 and 75). A similar process, but involving more cells, is presumably involved in the Notostraca. In thick slices the tendon stains red–purple with Mallory's stain.

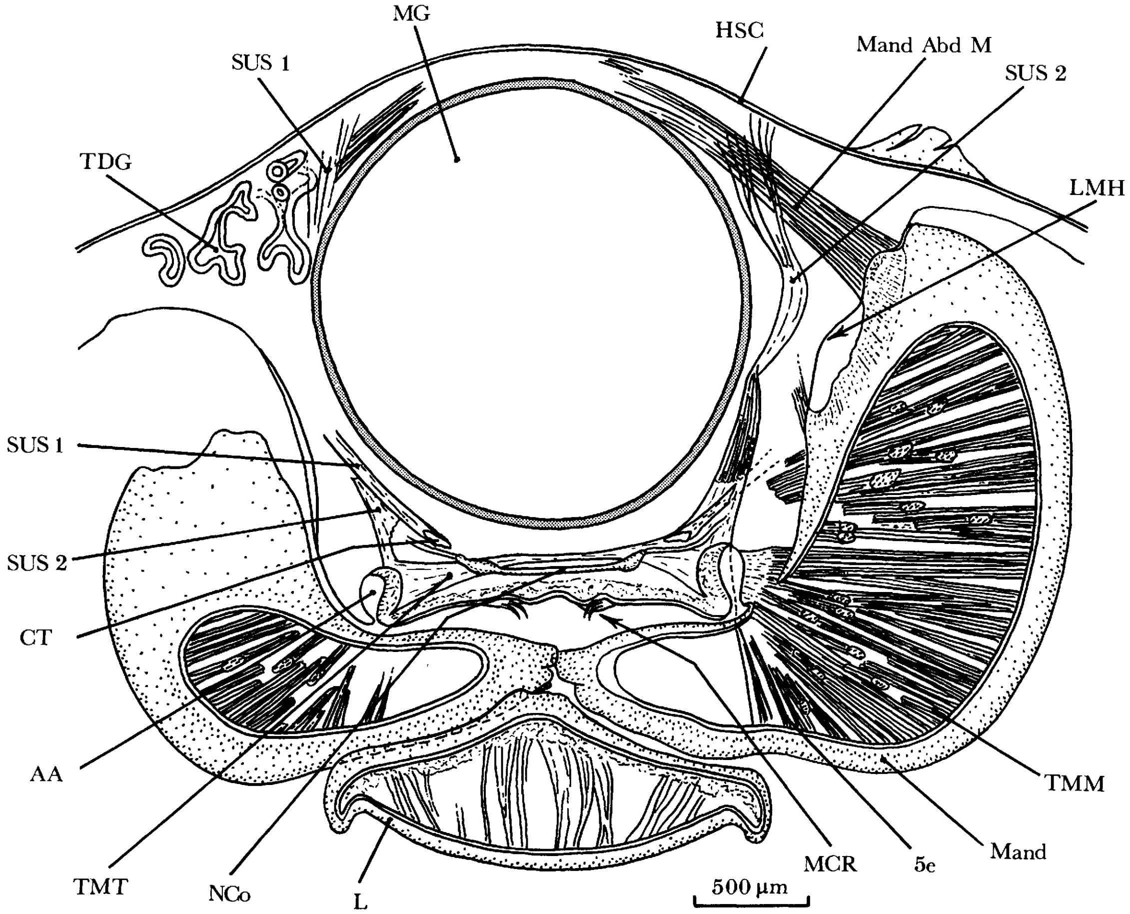


FIGURE 86. *Lepidurus apus*. Transverse section through the anterior extremity of the mandibles, seen from in front, at approximately the level indicated by a in figure 63. The section cuts the right mandible (left-hand side of figure) more anteriorly than the left. Only the extreme anterior edge of the transverse mandibular tendon (TMT) is seen. The slight buckling of suspensor 2 (SUS 2) is an artefact. Note the muscular region near the base of this suspensor. It is in this slice and the next (figure 87) that the mandibular abductor muscle (Mand Abd M) of the left mandible is clearly seen.

Extending anteriorly through the transverse mandibular tendon from each posterior mandibular apodeme there is a strand of material of seemingly different texture from the rest of the tendon. This, here called the 'core' of the tendon (CT), can be recognized in longitudinal slices, but most easily in transverse slices (figures 86–88 and 90) (and more easily in formalin-fixed material of *Lepidurus apus* than in Zenker-fixed *Triops cancriformis*). Anteriorly this strand emerges from the tendon and it is to it that the anteriormost suspensor (SUS 1) is attached (figure 86). At its lateral extremites the transverse mandibular tendon is drawn out into fibrous sheets and narrow tendons on which the transverse mandibular muscles originate. As these radiate outwards, the ends of the tendon appear to have a ragged appearance when seen in both transverse (figure 87, 88 and 90) and horizontal (figures 81 and 82, plate 7) sections.

The transverse mandibular tendon is part of the endoskeleton, with other elements of which it is continuous anteriorly and posteriorly. Anteriorly, near the mid-line, there is a fibrous extension (figure 65:FE) from whose anterior margin radiates a series of oesophageal dilator muscles (figures 64 and 65). The posterior extension of the endoskeleton is noted in §7*e*.

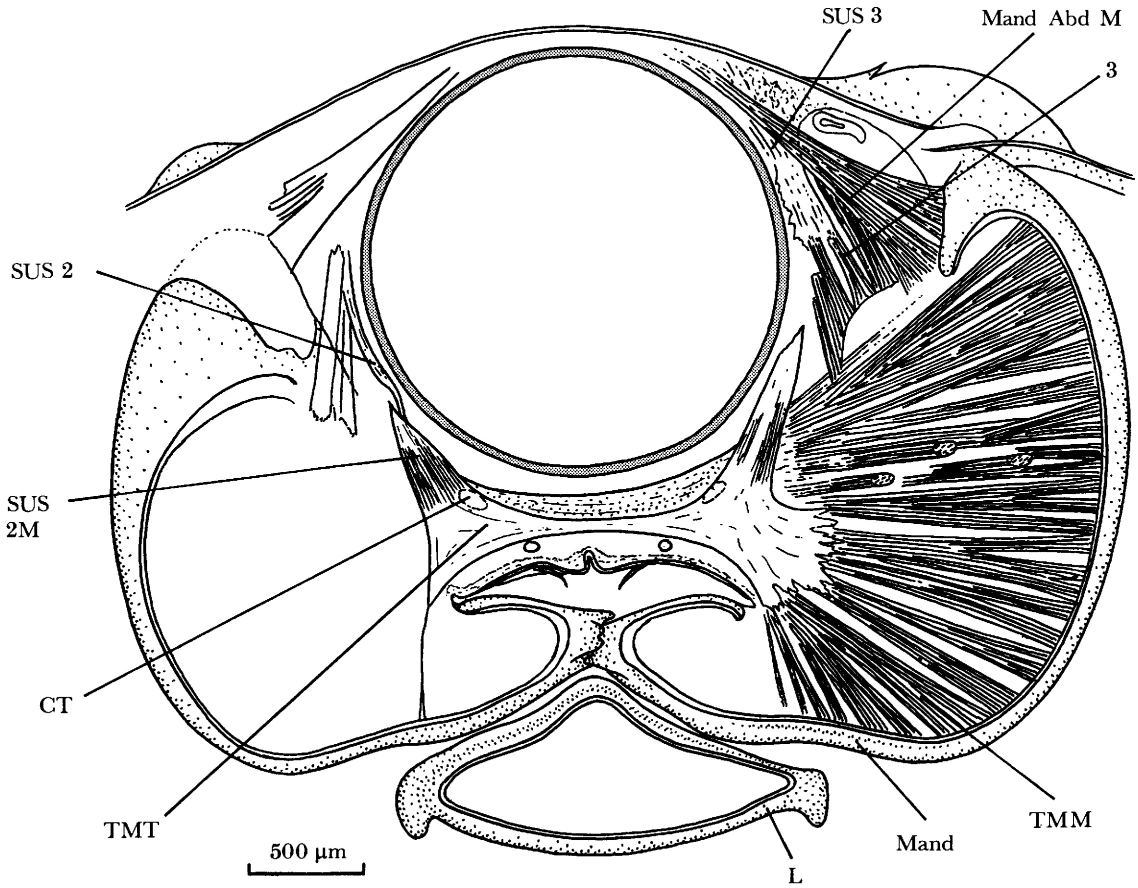


FIGURE 87. *Lepidurus apus*. Transverse section of the mandibles immediately behind that shown in figure 86, at approximately the level indicated by b in figure 63. Much more of the transverse mandibular tendon (TMT) is now seen. The tendon is wedge shaped in section over much of its length (see figures 63–65). This being a thick slice, the way in which it thickens in the vertical plane behind its anterior margin can be seen.

The arrangement of the mandibular muscles is similar in certain basic respects to that found in other branchiopods, but there are many striking differences related to the very different actions of which the mandibles of notostracans and those of branchiopods with rolling mandibles are capable. As in other branchiopods the transverse mandibular tendon serves as the origin of numerous transverse mandibular muscles. These, however, all originate from its lateral extremities (figures 79 and 81, plate 7; figure 102). None of them originates on the face of the tendon as do various muscles in the Anostraca (Manton 1964; Fryer 1983), Anomopoda (Fryer 1963, 1968, 1974), Ctenopoda, Spinicaudata and Laevicaudata (G. Fryer, unpublished observations). This difference is related to differences in the tendon: thick and not very deep in the Notostraca; thin, strap-like and deep in Anostraca, Anomopoda and others.

An outstanding distinction of notostracan mandibles is that the number of muscle fibres, and therefore the power that can be developed by the transverse series, is much greater than in other branchiopods. This is clearly related to functional requirements when biting large, tough, food items.

The transverse muscles (TMM) are extremely numerous (figures 79 and 81, plate 7; figures 88–93 and 102) and do not differ greatly in size from each other. This contrasts

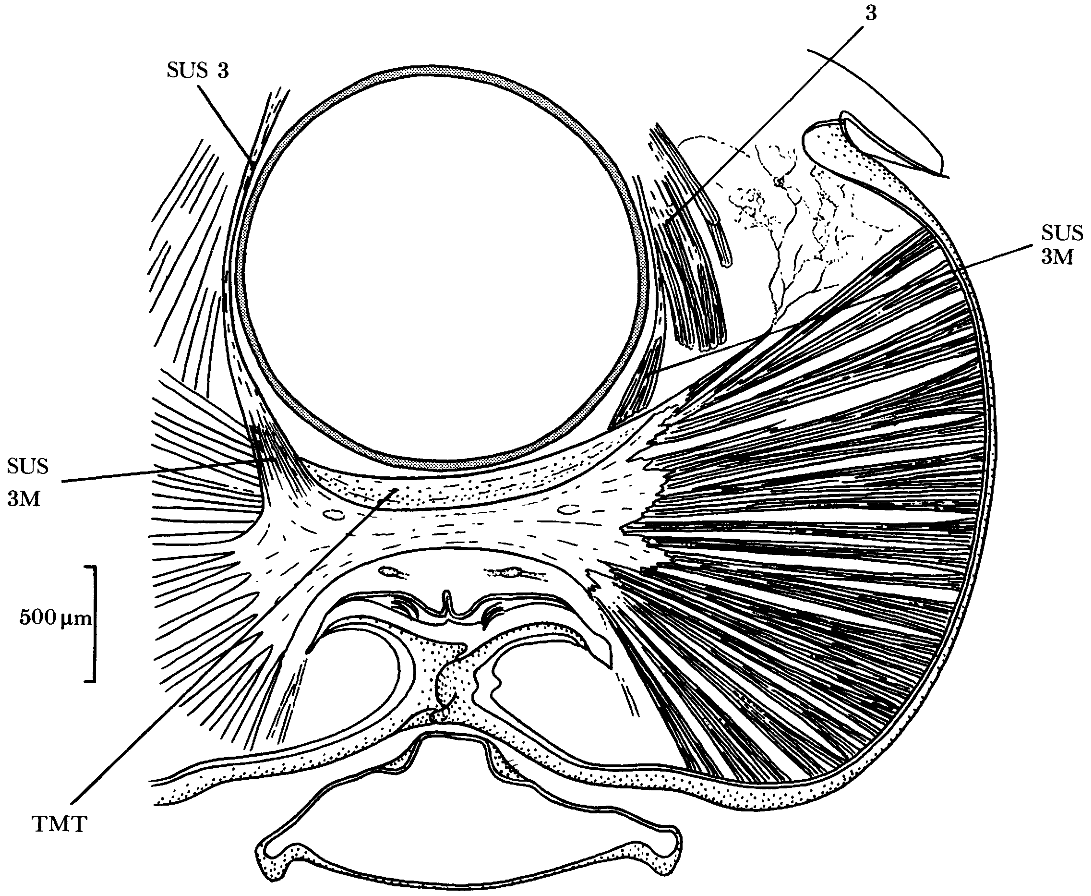
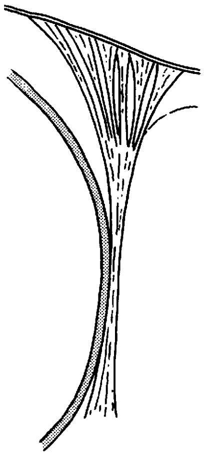


FIGURE 88. *Lepidurus apus*. Transverse section of the mandibles immediately behind figure 87, at approximately the level indicated by c in figure 63. The massive nature of the transverse mandibular tendon (TMT) is clearly shown.

markedly with the situation in the Anostraca, Anomopoda, Ctenopoda and conchostracan orders where there are a few long, sometimes massive, transverse muscles and many very short, small muscles that radiate from the expanded ends of the tendon, which comes much nearer to the mandibular cuticle than it does in the Notostraca. In branchiopods with rolling mandibles there is also a marked concentration of transverse mandibular muscles posterior to the mid-line, related to the need for greater power when the mandibles swing on their working stroke than on the return. This is much less the case in the Notostraca (figures 79 and 81, plate 7). Here, although certain ventrally located muscles that run obliquely backwards from the transverse tendon have no anterior counterparts (figure 79, plate 7), and although there is a tendency for the posterior muscles to be longer than their anterior equivalents, the general arrangement is relatively uniform fore and aft. All the transverse muscles converge on a relatively small area at each end of the transverse mandibular tendon.

As in other branchiopods there are several muscles that, originating on the transverse mandibular tendon, incline ventrally, some almost vertically, to insert on the ventral wall of the mandible (figure 86–88). These, the equivalent of the 5e muscles in anostracans and anomopods, and so named here, clearly have a levator function and enable small adjustments of the masticatory prolongations of the mandibles to be made in the vertical plane.



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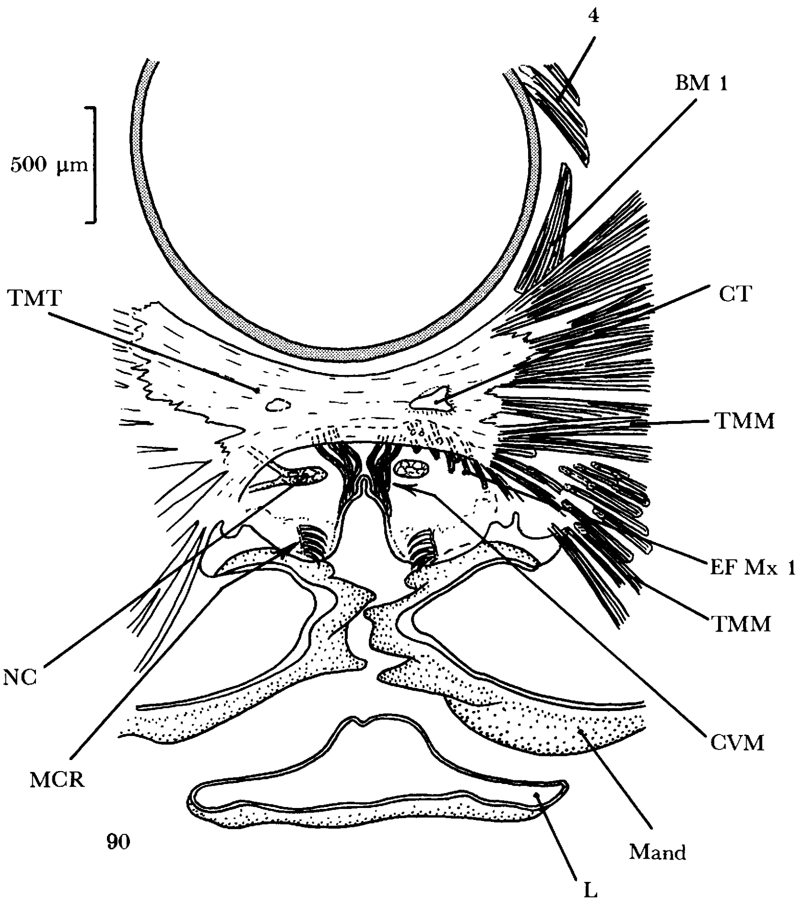

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FIGURES 89 AND 90. *Lepidurus apus.*

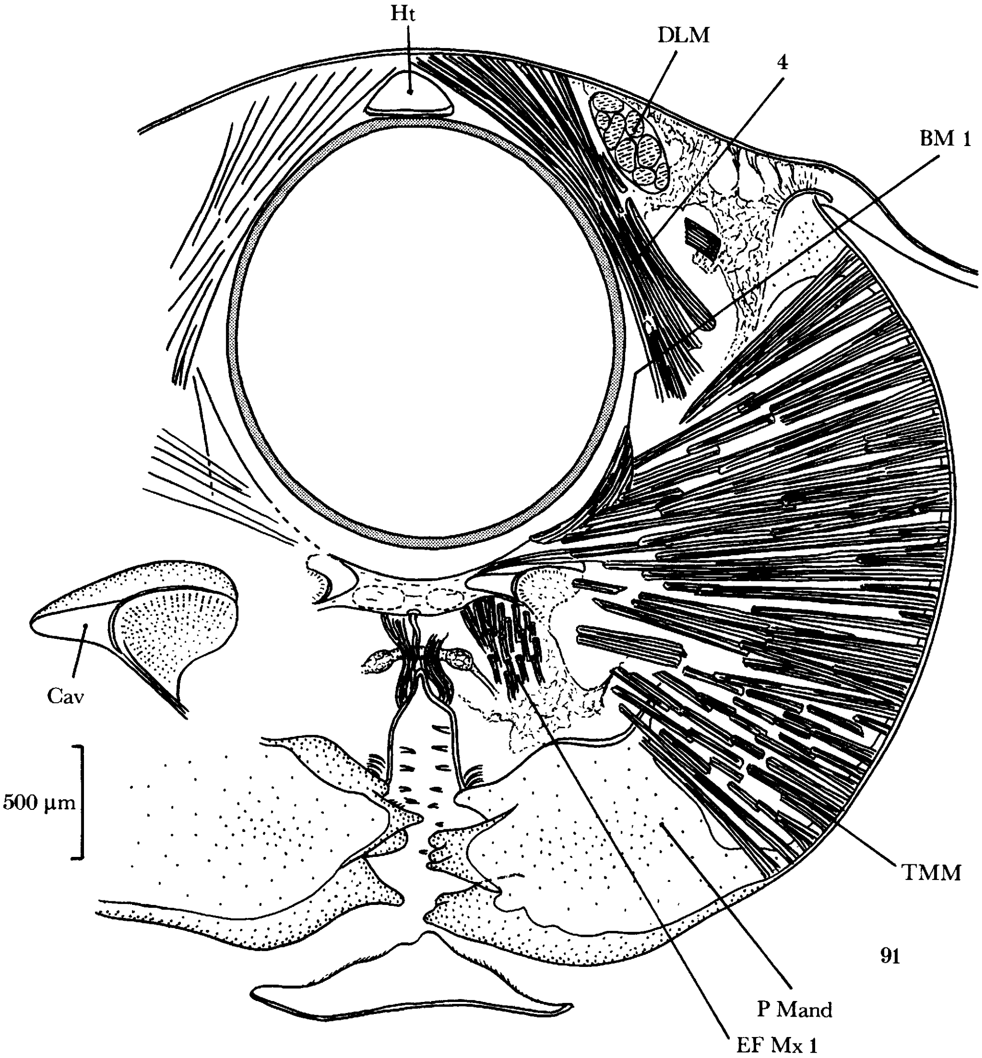
FIGURE 89. Left suspensor 3 of mandible from a transverse section of a different individual from that shown in figure 88 to show the dorsal anchorage.

FIGURE 90. Transverse section of the mandibles at a level posterior to that shown in figure 88, at approximately the level indicated by d in figure 63. Note that this section does not lie immediately behind that shown in figure 88 but somewhat further posteriorly. The origin of the cuticular vaulting muscles (CVM) and the extrinsic flexor muscles of the maxillule (EF Mx1) on the ventral face of the transverse mandibular tendon is seen. Note the long fibrous attachments of the transverse mandibular muscles (TMM) to the transverse mandibular tendon (TMT).

FIGURES 91 AND 92. *Lepidurus apus.*

FIGURE 91. Transverse section of the mandibles immediately behind that shown in figure 90 and near the posterior limit of the transverse mandibular tendon. Its approximate level is indicated by e in figure 63. The inset shows the left post-mandibular apodeme to a larger scale and focused slightly deeper through a partly obscuring muscle.

FIGURE 92. Outline as in figure 91, but to a larger scale, of the transverse mandibular tendon region to show the anchorage of the ventral longitudinal muscles (AVLM) on its posterior face (seen by deep focusing and indicated by broken lines), the bracing fibres (BF) and the cuticular vaulting muscles (CVM) that originate on its ventral surface, and the supporting post-mandibular apodemes (PMA).



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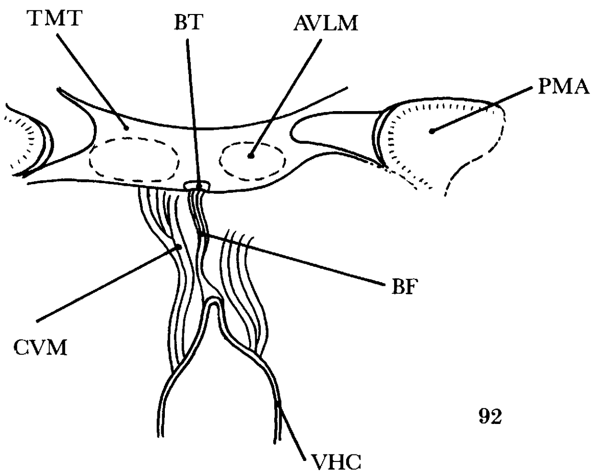

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FIGURES 91 AND 92. For description see opposite.

There are no 5c muscles. Such muscles, which unite the posterior margins of the opposed mandibles, are present in the Anostraca, Spinicaudata, Laevicaudata, Ctenopoda and Anomopoda, and even in the biting mandibles of the Onychopoda and in the highly specialized mandibles of the Haplopoda (*Leptodora*) (G. Fryer, personal observations). Their absence, although in agreement with other features that suggest an isolated systematic position among the Branchiopoda for the Notostraca, has to be interpreted with care as they are present in the early stages (§12). Their absence (loss), like the lack of concentration of other transverse muscles posteriorly, reflects functional requirements, in particular the smaller emphasis on mandibular swing than in other branchiopods.

Of the other mandibular muscles, pairs of promotor rollers (3) and remotor rollers (4), whose location and robust nature are readily seen in the illustrations, are present as in other branchiopods (figures 66, 67 and 87–96). An additional muscle, apparently unique to the Notostraca, is also present dorsally. This is the mandibular abductor (Mand Abd M), seen in figures 66, 67, 86 and 87. It is easy to see how mandibular adduction is achieved by contraction of the appropriate transverse mandibular muscles. These are sufficiently numerous and robust to give a powerful bite, to which the crushing of food of various kinds by the mandibles bears witness. How abduction might be accomplished has not hitherto been explained. A small degree of abduction can be achieved even in branchiopods with rolling mandibles by contraction of the appropriate dorsally located transverse muscles, and such muscles doubtless play a part in the Notostraca, but greater abduction than can be achieved by this means is required for true biting and is here produced by a muscle that originates near the mid-line and dorsally above the alimentary canal and inserts on the anterior margin of the mandible very close to its dorsal articulation (figures 86 and 87). This distal location relative to the pivoting region at the extremity of the transverse mandibular tendon gives it a good mechanical advantage, and contraction inevitably abducts the masticatory regions of the mandibles. This action demands a capacity for sliding on the part of the mandibular articulation. This is permitted by the broad articulating surface of the mandible, bound by fibrils within a fibre-cushioned cup (figure 68). Such sliding would be difficult or impossible for the generally pointed articulation of other branchipods. The broad articulation is thus necessitated as much by this requirement as by the need to bear heavy loads.

The transverse mandibular tendon has also been used as a point of origin for other muscles. Towards its posterior margin there are, on each side of the mid-line, groups of slender muscles (CVM) that descend vertically and insert on the ventral head cuticle (VHC) where it overlies the masticatory surfaces of the mandibles (figures 80 and 85, plate 7; figures 90–92). *En route* they pass through the aperture of a nerve commissure. These are here called cuticular vaulting muscles. In the region of their insertion the cuticle forms a barrel vault over the mandibles. More anteriorly it becomes more or less flat (figures 86–88). When the mandibles abduct and swing backward, the gap between them is greatest posteriorly. The anterior apodemes cope with matters anteriorly but as the masticatory regions move apart posteriorly, the roofing ventral head cuticle inevitably has to span a widening cavity. This is catered for by its vaulted nature. The arch can become shallower. As the masticatory surfaces adduct and swing forward, the narrowing span is made possible by deepening the vault, via the action of the cuticular vaulting muscles. The cuticle is also braced in the mid-line by a number of fibres (BF) that descend from a button-like structure (BT) inserted into the ventral surface of the transverse mandibular tendon (figures 91 and 92). This arrangement presumably ensures an even straightening of the arch on each side of the mid-line and prevents the apex of the arch from being drawn down too far as the mandibles abduct and swing. This folding and straightening of the cuticle cannot be observed, but that the deductions drawn from anatomy are correct receives support from the presence on the roofing cuticle of two rows of short, curved spines, the mandible-cleaning rakes (figures 86–91: MCR; figure 102, inset), that run fore and aft. Were the cuticle immovable, so too would be the spines, which could serve no significant function other than perhaps preventing slippage of food during its mastication. If, as suggested, the cuticle is alternately drawn up and spreads laterally, then the rows of spines can also help to clean the upper surfaces of the mandibles and conceivably even tear food masses to a slight extent as they move laterally.

(*d*) *Distinguishing features of notostracan mandibles and their skeleto-muscular system*

The mandibles of adult notostracans differ in so many ways from those of other branchiopod orders that it is convenient to list their distinguishing features. Although they share a biting function and certain skeletal similarities with the Onychopoda they differ in many ways even from the mandibles of that group. Their salient features, many of them unique among branchiopods, are as follows.

1. The ability to undergo abduction and adduction movements and thereby bite food items directly.
2. A relatively narrow, elongate, masticatory region armed with a small number of transverse ridges, each drawn out into a few sharp, heavily sclerotized, biting teeth.
3. Dorsal articulation broad.
4. Transverse tendon massive, very thick, and not extending so far laterally as in branchiopods with rolling mandibles; with three pairs of suspensors and associated with elaborate apodemes.
5. Intimately associated with simple anterior, and complex posterior apodemes.
6. Transverse mandibular muscles numerous, comprising more muscle fibres, and therefore with the ability to develop greater force, than other branchiopods. All relatively long, and originating from the ends of the transverse mandibular tendon. None originating from its posterior face.
7. Less obvious concentration of transverse mandibular muscles posteriorly than in branchiopods with rolling mandibles.
8. No 5c muscles present.
9. Mandibular abductor muscles present dorsally.
10. Transverse mandibular tendon used for anchorage of muscles not concerned with movements of the mandibles.

Most of these features are directly related to the functional ability listed as item 1.

(*e*) *The post-mandibular complex*

Immediately behind the mandibles lies a complex of structures made up of the paragnaths, maxillules and post-mandibular apodemes, so closely associated that they are best described together. Close behind these lie the maxillae.

Viewed from in front the paragnaths (P) are more or less crescent-shaped (figure 94); seen

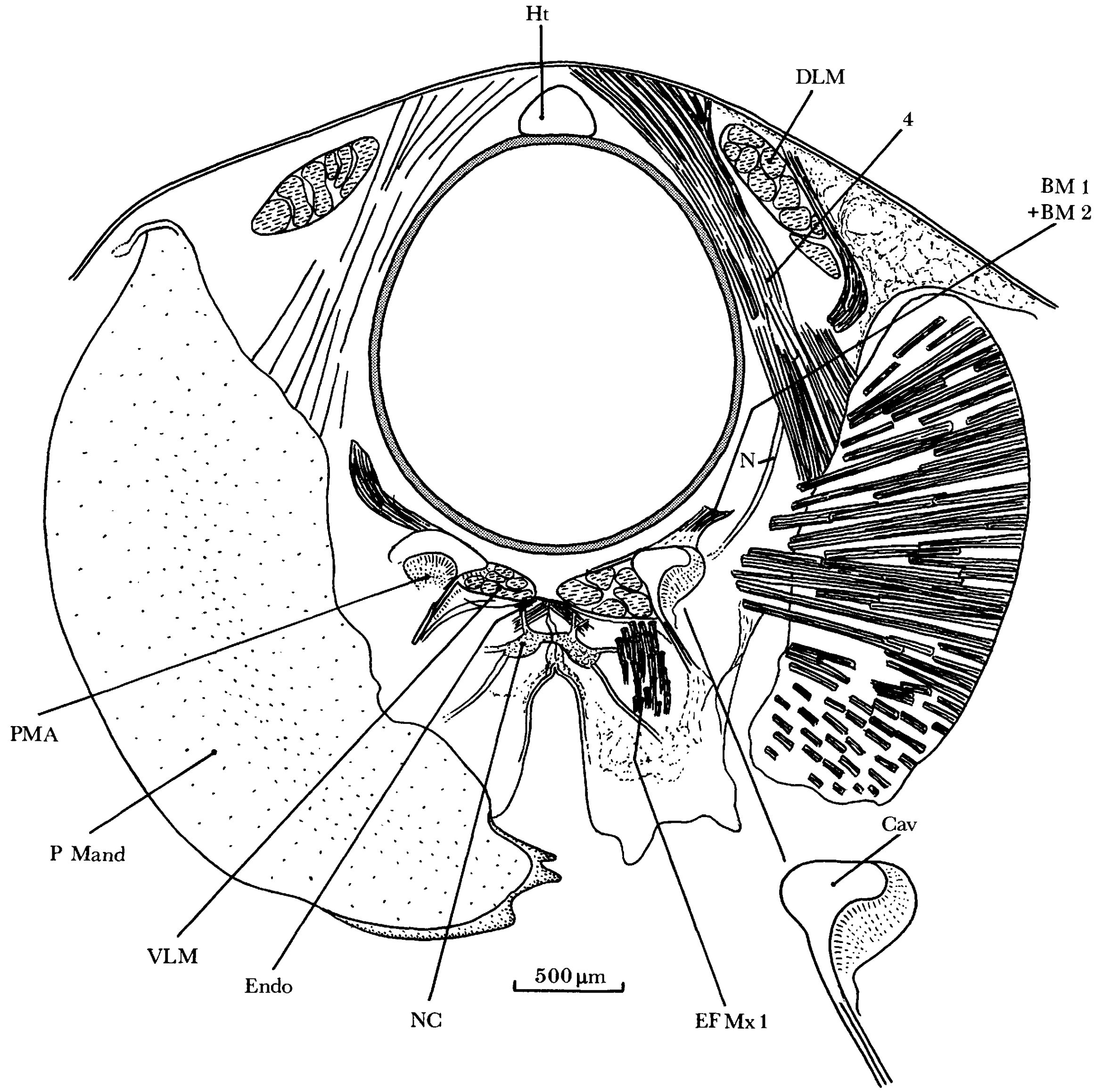
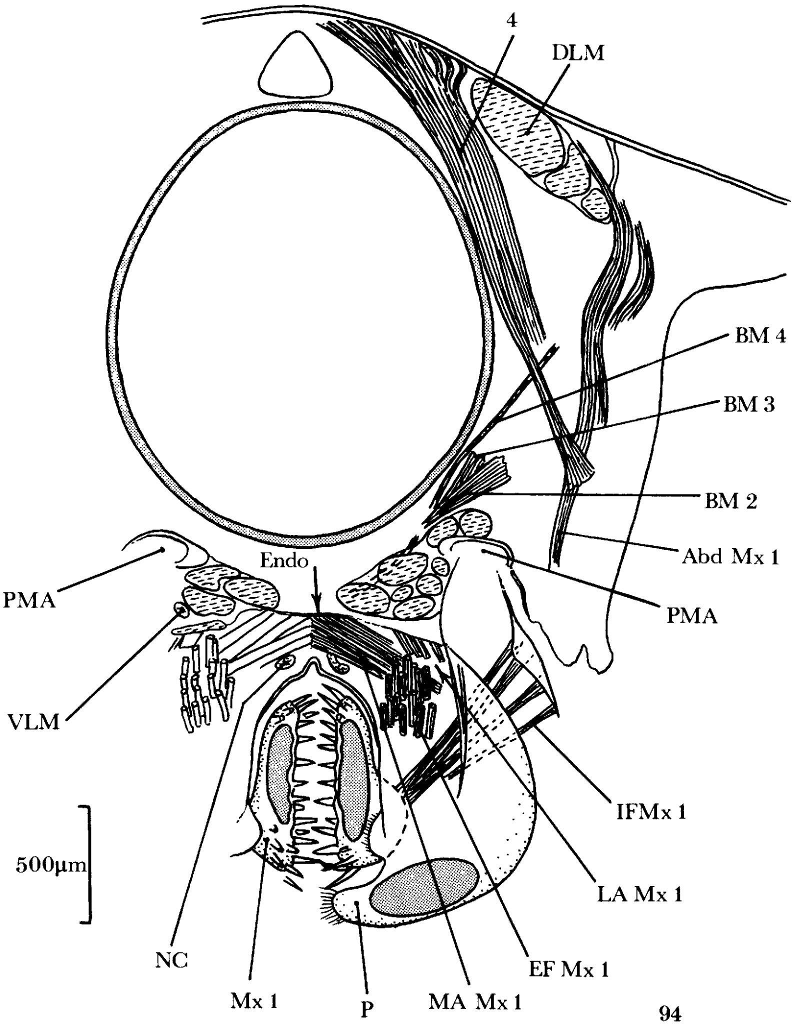


FIGURE 93. *Lepidurus apus*. Transverse section of the mandibles immediately behind that shown in figure 91, at approximately the level indicated by f in figure 63. This is at the extreme posterior limits of the mandibles, the mandibular cuticle (P Mand) seen here being the inner face of the posterior wall. The section falls posterior to the transverse mandibular tendon but reveals much of the post-mandibular apodemes (PMA) and shows those bundles of ventral longitudinal muscles (VLM) that are anchored to the transverse mandibular tendon. Other bundles insert on the posterior face of the apodemes. The left posterior mandibular apodeme is reproduced at a larger scale in the inset to show its hollow nature.

laterally their compressed nature is apparent (figures 44 and 45, plate 3; figures 66 and 67). Each arises from a broad base (BP) just behind the mandible and at about the level of the distal extremity of the labrum (figure 64). Each bears a tuft of short setules distally and there is also a sub-terminal pad of setules (figure 94). Unless they move slightly when the cuticular vaulting muscles contract, they are immobile. The posterior wall of each is thickened proximally and is continuous with a fold of cuticle that extends into the head as a cuticular apodeme, the post mandibular apodeme (PMA). The posterior wall of the paragnath is also closely associated with



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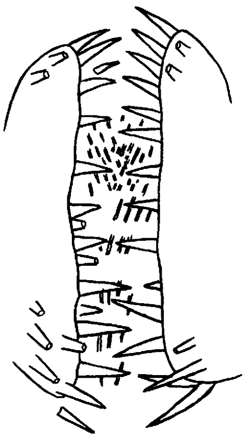

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Figures 94 and 95. *Lepidurus apus*.

Figure 94. Transverse section immediately posterior to that shown in figure 93, at approximately the level indicated by g in figure 63, revealing the paragnaths (P) and, immediately behind them, the anterior extremities of the maxillules (Mx1). The long slender setae of the maxillae and the long sweeping spines of the gnathobases of the first trunk limbs that protrude between the stout denticles of the maxillules are omitted for clarity (see figure 95).

Figure 95. Outline of part of figure 94 more highly magnified, to show the slender spines of the maxillae and, particularly, the sweeping spines of the gnathobases of the first trunk limbs, protruding between the maxillules.

the anterior wall of the maxillule, so closely that several observers assumed the paragnaths and maxillules to be parts of a single structure.

The maxillules (figures 44 and 45, plate 3; figures 63, 64, 66, 67, 94–98 and 100–102) are more complex than even the best of previous accounts suggest. Proximally each is continuous with the post-mandibular apodeme (PMA), with which it articulates by a lateral hinge joint (figure 100: PMA/Mx1). Each consists of two segments (figure 100) of which the proximal is unarmed. The distal segment articulates with the proximal at a lateral hinge joint (LHJ). It has a broad face directed anteriorly and medially towards its partner, and this is armed with

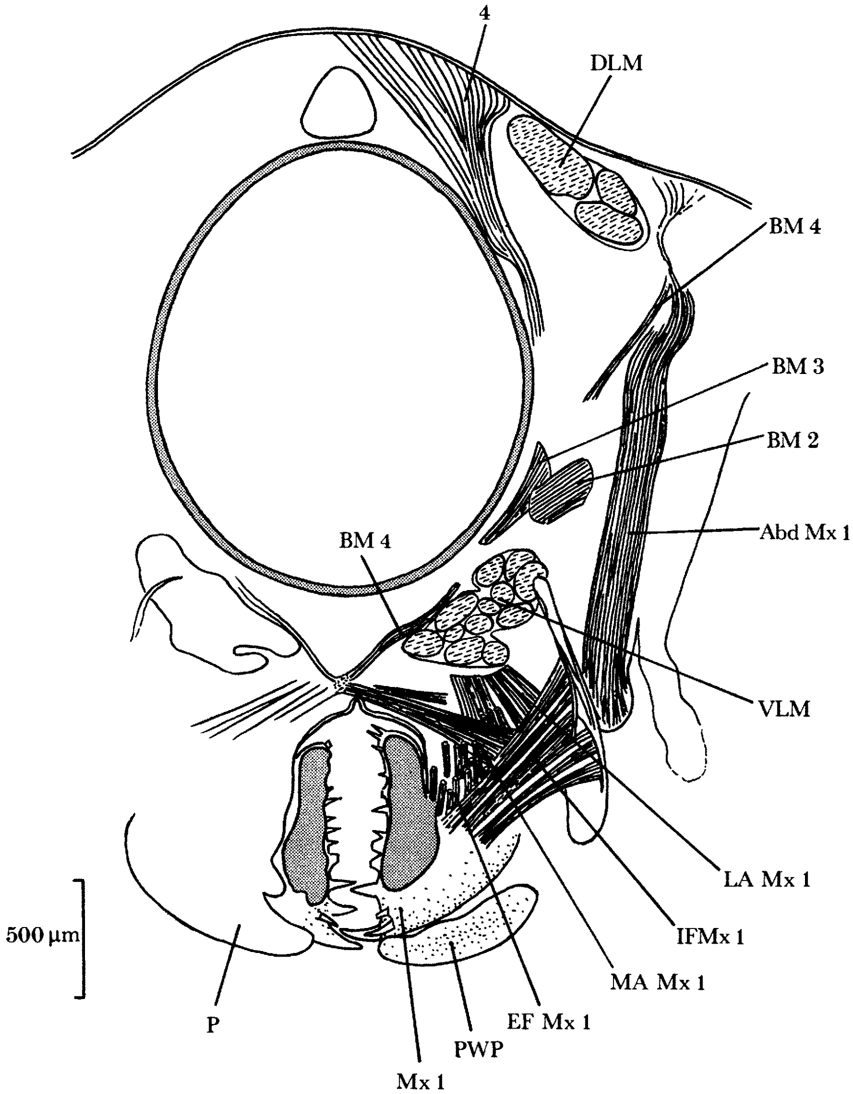


FIGURE 96. *Lepidurus apus.* Transverse section immediately behind that shown in figure 94, at approximately the level indicated by h in figure 63, and cutting through the maxillules, much of whose musculature is seen in the left appendage (right-hand side of figure). The fragment of the left paragnath remaining in the section is the cuticle of its posterior wall (PWP).

an array of denticles and spines of which the more robust denticles are located distally. It terminates ventrally in a curved uniseriate row of stout denticles (CD) that make up a cutting blade, which, when it meets its counterpart on the opposing appendage (figure 97), comprises a pair of shears. The nature of this cutting blade (and the armature of the broad face) as revealed by scanning electron microscopy are shown in figures 44 and 45, plate 3 and figure 78, plate 6. More proximally and anteriorly the armature of the distal segment consists of an array of long, slender, robust spines that are directed anteriorly along the food groove adjacent to which they lie These, some of which can be seen in figure 29, plate 2, are functionally a continuation of the series of sweeping spines of the trunk limb gnathobases.

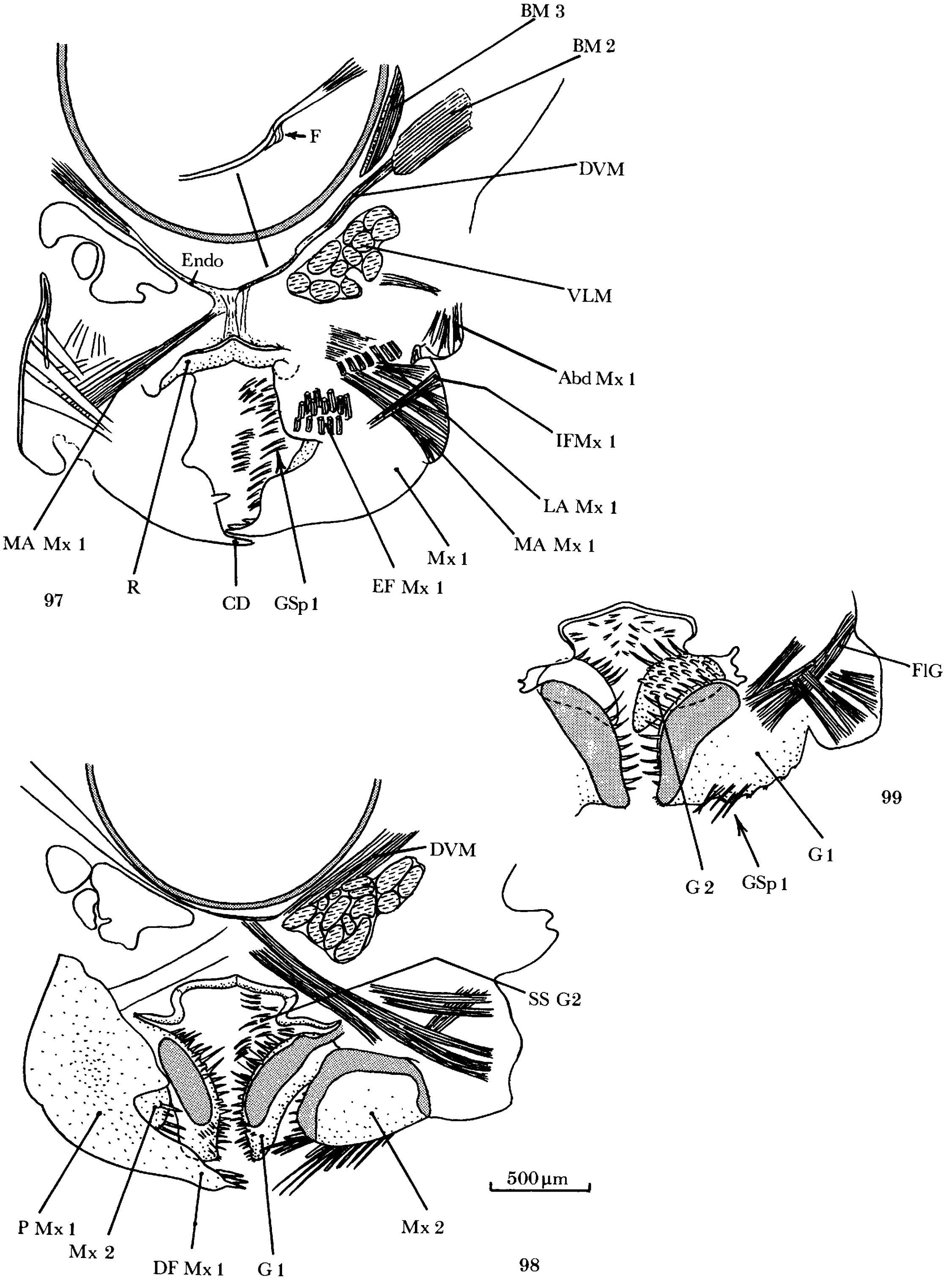
The entire appendage is inclined backward. The orientation of some of its armature in relation to the mandible can be seen in figure 29, plate 2. Because of their musculature the maxillules have a wide gape, slightly less than the maximum observed gape of the mandibles.

Each maxillule is actuated by both extrinsic and intrinsic muscles. Some of these are easily provided with suitable descriptive names: the names given to others are inevitably somewhat arbitrary. Originating on the transverse mandibular tendon adjacent to the dorsal elaboration of the post-mandibular apodeme and inclining steeply backward and ventrally, is a robust muscle (EFMx1) whose full course is seen in figure 64, and can be traced in figures 91–96. It is seen in a different plane in figure 102. This inserts on the posterior face of the distal segment of the maxillule. Although a pulling forward is clearly a component of the action of this muscle it is best described as an extrinsic flexor. Contraction pulls the distal segment of the maxillule, partly towards its partner and somewhat forward. The forward component is small, less than the strong anterior–posterior orientation of this robust muscle might lead one to suspect. Little directly forward swing of the maxillule is indeed possible because of its close association with the paragnath and mandible (see figure 102). The orientation of the mandible, however (figure 29, plate 2), is such that contraction of this muscle causes the distal segment of the maxillule to be pulled obliquely inwards and somewhat forward, more or less parallel to the long axis of the masticatory armature of the mandible. This muscle works in conjuction with an intrinsic flexor (IFMx1) that originates on the thickened lateral wall of the proximal segment and inserts on a ridge developed on the distal segment for this purpose. The orientation of the maxillules is such that flexure of the distal segment brings the opposed spine-bearing margins together in a biting action.

Combined with flexure is adduction of the entire appendage, effected by two sets of extrinsic adductor muscles the median (MAMx1) and lateral (LAMx1) adductors. The former originate partly on the ventral endoskeletal sheet of the head, partly on a thin ventral prolongation of this that enables them to pull against each other (figure 94), the latter more laterally on the endoskeletal sheet (figures 94 and 96). The course of both sets of muscles can be traced in these figures and figure 97. They insert laterally and, in the case of the lateral adductor, somewhat more anteriorly, on the proximal segment. They adduct the entire appendage about the lateral hinge joint at its base. Abduction is achieved by a powerful muscle (Abd Mx1) that originates dorsally in the same mass of fibrous tissue as the dorsal longitudinal muscle of its side (figure 67), and extends ventrally to insert in a cup of cuticle (figures 67, 94, 96 and 97) that receives it on the lateral margin of the basal segment of the maxillule. Its full course is seen in a transverse slice in figure 96, and most of it in a longitudinal slice in figure 67, the cup in which it inserts being readily seen in each case. The cup itself is seen in figure 100 (CAM).

There are no extensor muscles of the proximal maxillulary segment. Extension, which is not a working movement and therefore demands little energy, must be effected either by hydrostatic pressure or by elasticity of the relevant cuticle or by a combination of these methods. Although hydrostatic pressures are low in such arthropods as have been investigated, and insufficient to grant extension on a working stroke, as in the pushing of a limb, they suffice to extend limbs that are not so loaded (see Manton 1958). As the cuticle in the region of insertion of the extrinsic flexor is thick, cuticular elasticity may be involved in counteracting the action of this muscle.

Near the base of the maxillule, and with a similar orientation to the extrinsic flexor muscles, with which they are easily confused in longitudinal sections though they lie more lateral, are



Figures 97–99. For description see opposite.

muscles originating on a ventrally directed rib of the post-mandibular apodeme. These insert on the posterior face of the proximal segment (figure 66 and inset: BM Mx1). It is not easy to assign a function to these muscles, that are difficult to detect in transverse sections. Their contraction may grant slight adjustment of the orientation of the appendage, or they may serve merely to brace its proximal region, that at times must bear considerable loads. Although they may have other minor functions, they can conveniently be designated as bracing muscles.

The maxillules of the Notostraca are much more elaborate than those of any other branchiopod order and their muscular system has no parallel there. For example, the massive, dorsally originating abductor muscle has no homologue in other orders. The nature of this system emphasizes the isolated phyletic position of the Notostraca among the branchiopods, as does the post-mandibular apodeme, which is also unique within the subclass.

The maxillae are smaller and much simpler than the maxillules. Each consists of an inner, flattened lobe armed with setae, and an outer, tubular portion that carries the duct of the maxillary gland whose exit is at its tip. The setae of the inner lobe are directed medially and anteriorly through the gap between the maxillule and the gnathobase of the first pair of trunk limbs (figure 64: Mx2 Sp; figure 102) and can be seen *in situ* in figure 29, plate 2, and, more clearly, in figure 44, plate 3 (Mx2Sp) where some of the obscuring spines of trunk limb 1 have been cut short.

The post-mandibular apodemes (PMA) have a complex shape that can only be appreciated from illustrations. Each rises as a narrow slit behind the paragnath of its side and expands forward and inwards into an elaboration whose shape as seen in longitudinal section at different levels is shown in figures 63–66 and figure 84, plate 7; in transverse section in figures 91–94, especially the insets; and in horizontal section in figures 81–83, plate 7. The hollow nature of the apodemes, whose cavities are open to the exterior, is conveniently revealed by the particles of detritus that find their way even to their dorsal extremities.

The apodemes fulfil several functions. Besides being bound to the transverse mandibular tendon, which they support, they provide anchorage for many muscle bundles of the ventral longitudinal muscles (VLM) (see especially figures 64 and 65, and figures 81–83, plate 7), and several other muscles converge upon them from above. Three of these (BM 1–3) appear to be bracing muscles (figures 66, 90, 91, 94, 96 and 97) and muscles 1 and 2 are evidently homologous with two of the suspensory muscles of the cephalic endoskeletal sheet of the

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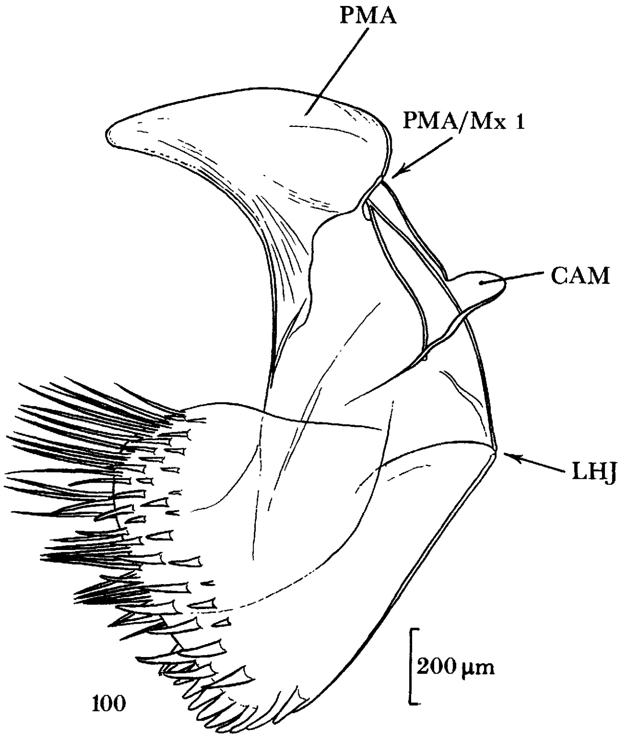
FIGURES 97–99. *Lepidurus apus.*

FIGURE 97. Transverse section immediately behind that shown in figure 96, at approximately the level indicated by i in figure 63, and cutting through the posterior part of the maxillules. The endoskeletal plate (Endo) is here broad and its extremities provide anchorage for dorsoventral trunk muscles (DVM). The inset shows the fibrous nature of the muscle anchorage, slight buckling of the preparation revealing the individual fibres (F). (Simplified.)

FIGURE 98. Transverse section posterior, but not immediately posterior, to that shown in figure 97, at approximately the level indicated by j in figure 63. The right maxillule from the section immediately behind that shown in figure 97 has been superimposed upon it. Much of the distal part of this appendage is in fact the inner face of its posterior wall (P Mx1) here shown without some fragments of muscle that are still visible in the section. The gnathobases of the first trunk limbs (G1) are now visible. Only part of the musculature present is indicated, and, for simplicity, only a few of the sweeping spines of the gnathobase of trunk limb 2 (SS G2), that are also visible, are shown.

FIGURE 99. Transverse section immediately behind that shown in figure 98, at approximately the level indicated by k in figure 63. This cuts through the gnathobases of the first trunk limbs (G1) and reveals the anteriormost portions of the gnathobases of trunk limb 2 (G2). Most spines of the right gnathobase 2 omitted.



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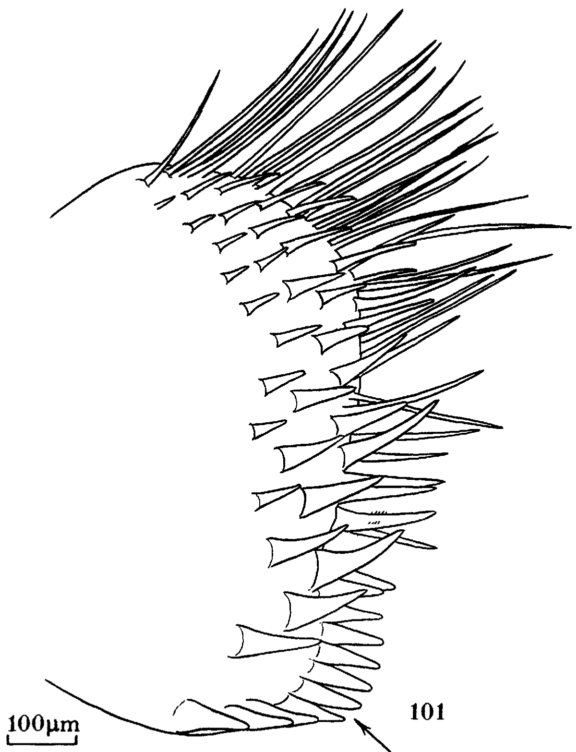

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Figures 100 and 101. *Triops cancriformis*, maxillule and post-mandibular apodeme, from a moulted exuvium.

Figure 100. Right maxillule, seen from behind, and the post-mandibular apodeme (PMA). The distal portion of the maxillule is somewhat twisted so that its armature is well seen. Although the appendage is slightly distorted, the transparency of the exuvium permits ready appreciation of the relation between the maxillule and the apodeme and makes it easy to see the armature of the former. The cup (CAM) in which the abductor muscle inserts is well displayed.

Figure 101. Left maxillule, showing the armature as seen from behind and viewed somewhat obliquely. The row of distal cutting denticles (CD) is well displayed.

anostracan *Branchinecta* (Fryer 1983, figure 42) (but see §7*f* for some problems of homology). Another, slender muscle (BM 4) to which it is difficult to assign a function, also originates here and inclines outwards and backwards as it rises to a dorsal insertion. For convenience as much as conviction it is also categorized as a bracing muscle. It may help to maintain posture when the trunk is flexed.

Just as it has connections with more anterior elements of the endoskeleton (§7*c*) the transverse mandibular tendon is continuous posteriorly with the ventral endoskeletal sheet. This changes in shape over short distances. Just behind the mandibles, where it is anchored laterally, it is broad and provides the site of origin for the median and lateral adductor muscles of the maxillules though some of the former also meet at the mid-line on a thin ventral prolongation of the endoskeletal sheet (figure 94). It then narrows (figure 96) before widening again. Its shape as it approaches the maxilla/first trunk limb intersegment is shown in figure 81, plate 7, which (Endo) also shows its shape in the first thoracic segment. It is in various places anchored to the ventral cuticle by fibrils or muscles. In figure 81, plate 7, several muscular anchors can be seen rising towards the observer from the posterior section of that part of the endoskeletal sheet that lies within the first thoracic segment.

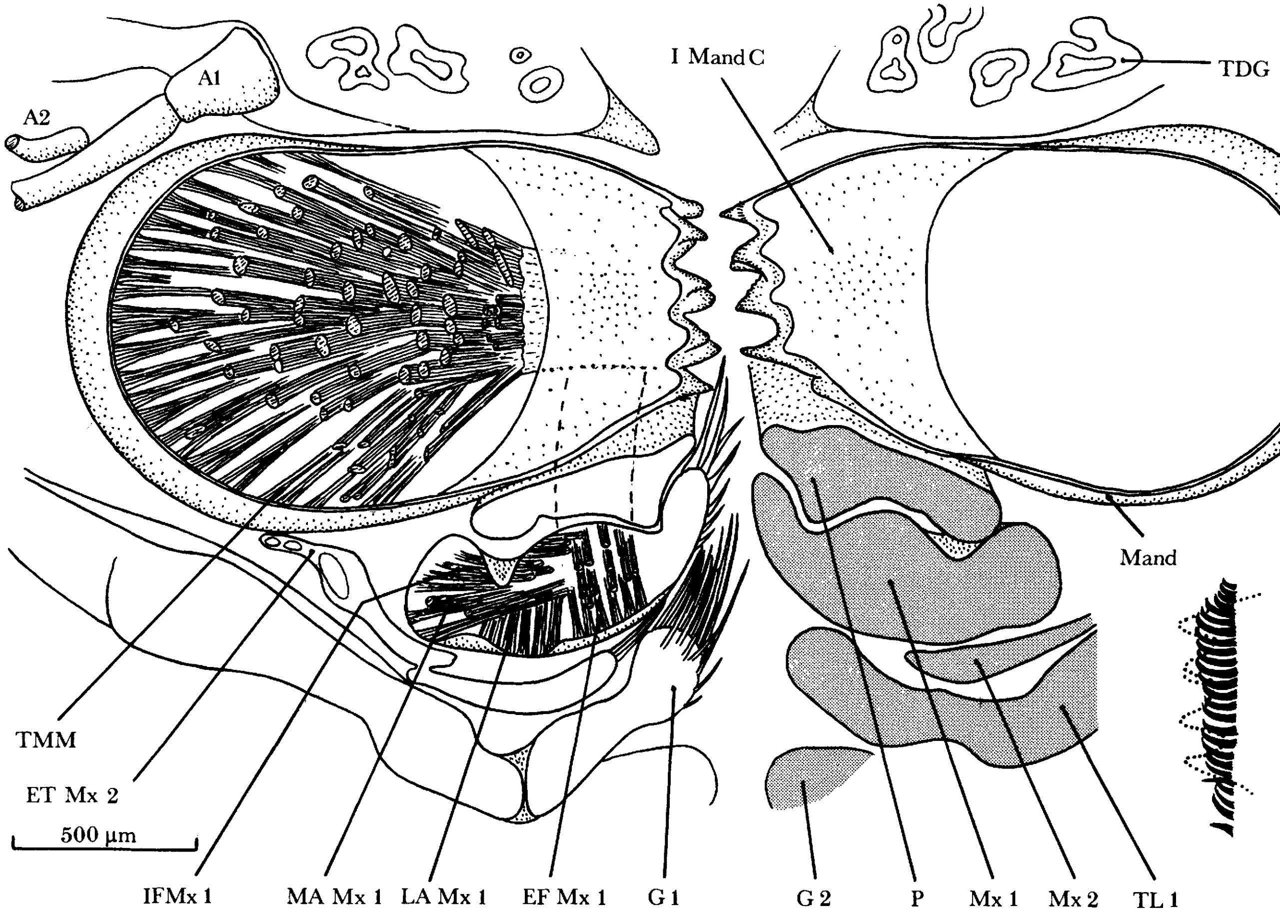


FIGURE 102. *Lepidurus apus*. Horizontal slice through the mouth parts, at the level of the dorsal part of the masticatory region of the mandibles. Ventral view. Some of the spines and setae of the maxillule (Mx1) maxilla (Mx2) and gnathobase of trunk limb 1 (G1) are omitted for clarity. The inset shows the row of hooks that make up the mandible-cleaning rakes on that part of the cuticle that forms a roof over the masticatory regions of the mandibles. (See figures 86–91: MCR.) These are seen by deeper focusing than in the main figure. The teeth of the mandible, that largely obscure them, are indicated by a dotted line.

(*f*) *Suspensors and braces: a comparison with the Anostraca and a problem of homology*

What are here called bracing muscles (see especially figures 66, 91 and 96: BM 1–4) are similar to, and in some cases apparently homologous with, the suspensor muscles of the ventral endoskeletal sheet of the anostracan *Branchinecta ferox* (compare figure 66 here with figure 42 of Fryer (1983)), but present intriguing problems. In the Notostraca, as exemplified by *Lepidurus*, all converge on each side at the post-mandibular apodeme: in the Anostraca two of them converge at what appears to be the ventral intersegmental node of the maxilla/first trunk segment. This node was so designated in *Branchinecta* partly because the node immediately behind it is clearly that of trunk segments 1 and 2, and the dorsal nodes confirm the nature of those of the trunk. In *Branchinecta* this ventral node lies well behind the transverse mandibular tendon.

In *Lepidurus* the post-mandibular apodeme arises between the paragnath and the maxillule, an anatomical observation confirmed by the ontogeny of the maxillules (figure 107; §11). Also, it is closely associated with the transverse mandibular tendon (e.g. figures 64 and 65; figures 81–83, plate 7). (The apparently wide separation of apodeme and tendon seen in figure 66 is deceptive: here only the extremities of both are seen.) The ventral longitudinal muscle is anchored to the post mandibular apodeme, just as it is to the maxilla/first trunk limb intersegmental node in *Branchinecta*. There is no sign of any intersegmental tendinous sheet anterior to that which demarcates trunk segments 1 and 2.

The similarity in arrangement in both Notostraca and Anostraca is striking and, bearing in mind the different functional demands made upon each system, seems more likely to be indicative of ancient ancestry than the result of convergence. A claim that bracer 1 (BM 1) of *Lepidurus* and suspensor 1 (SPM 1) of *Branchinecta* are homologous would be difficult to refute, and BM 2 and 3 (there are two muscles here in *Lepidurus*) are so like SPM 2 in *Branchinecta* in location and function that homologies are hard to deny. Even so, the complete homology of the nodes is uncertain. As shown by the situation in *Lepidurus*, where the location of the post-mandibular apodeme is unambiguous, the fact that no intersegmental tendinous sheet can be seen in the ventral longitudinal muscle anterior to that between trunk segments 1 and 2 need not mean that the node in front of it represents the intersegmental boundary between the maxillary and first trunk segments. If the node in *Branchinecta* is indeed located in the same position as in *Lepidurus*, the homology is established but, notwithstanding the availability of a good deal of anatomical information (Fryer 1983), the matter remains debatable.

8. Standing, swimming and digging

A resting notostracan is supported on the tips of the endopodites of trunk limbs 2, 3 and 4, each of which terminates in a strout sclerotized claw reminiscent of that present in a diversity of crawling and walking arthropods. Curiously, this use of the anterior endopodites, and hence the significance of their claws, appears not to have been reported. Schaeffer (1756) referred to the endopodite and distal endite as 'obere' and 'untere Scheere' respectively (in modern German 'Schere'), and one of his figures gives an erroneous impression of pincer-like claws, an interesting example of the influence of preconceived ideas on a careful observer. Probably influenced by Schaeffer, Brauer (1877) referred to the majority of the anterior trunk limbs as 'Scheerenfüsse' each terminating in an 'Endscheere' and his illustrations have a distinctly pincer-like appearance. As Eriksson (1934) pointed out, such a conception could only be held by those unfamiliar with the method of food collection. In other respects Brauer was also a careful observer.

Depending on the nature and configuration of the substratum, adjacent denticles of the endopodite margin probably assist in support at times. Each endopodite can be flexed on the corm according to need. The endopodite of trunk limb 5 is generally directed inwards and is seldom used to give support, and this is even more the case in the successively more posterior pairs of the first ten trunk limbs, though in each the endopodite bears a terminal claw, progressively shorter in the more posterior limbs. These are used at other times for scrabbling or for gripping objects.

Between these opposed limbs is a tunnel, very wide anteriorly, narrowing posteriorly, and no more than a narrow elongate slit from behind the 11th pair. This slit is bordered on each side by rows of small, numerous, posterior limbs which form a dense cluster at the posterior end of the limb-bearing segments. The arrangement of the limb armature lining the walls of the tunnel is of great functional significance and is described in §9.

In a stationary individual a current of water is drawn into this tunnel from in front and anterolaterally, passes posteriorly, and is discharged posterolaterally where, when an animal is standing on fine detritus, its course is easily seen by the cloud of fine particles in this vicinity. Prime agents in the setting up of this current are the numerous posterior limbs whose exopodites (figures 12 and 14) beat with great rapidity but small amplitude, but they are assisted by the exopodites of the more posterior members of the anterior series of trunk limbs, activity becoming progressively less towards the anterior end of the series and of only scant importance in the fifth pair. The anterior pairs are not involved in the setting up of this current. Nevertheless, these limbs, like their posterior homologues, have a foliaceous exopodite or flabellum whose shape differs from limb to limb (figures 5–7). The differences are a functional necessity. The exopodites wipe the under surface of the carapace as the trunk limbs beat, the position and region swept by each differing from limb to limb. The differences in size and shape of the exopodites thus receives a functional explanation related to cleaning and locomotion. Each is exquisitely fitted to its position beneath the carapace.

The distal claw and marginal denticles (figure 50, plate 4) of the anterior trunk limbs, especially the anteriormost, are used when it is necessary for the animal to crawl or gain purchase.

Swimming involves the use of all the trunk limbs of the anterior series save the first. Ironically, following Schaeffer's designation of the first pair of trunk limbs as 'Ruderfüsse', the belief persisted long that this pair of limbs alone was responsible for locomotion, movements of the more posterior limbs being deemed to be concerned with respiration and feeding. During swimming the limbs beat in metachronal rhythm. Although the broad exopodites are of prime importance, the endopodites, armed with a row of setae on their dorsal margins (figures 5–8), which increases their effective surface area, also contribute. Progression over the bottom is generally by swimming but usually involves contact. On a pristine surface of fine mud the endopodites leave two broad parallel grooves with, as noted by Fox (1949) and Arnold (1966), a narrow median ridge between them. Both then, and especially when deliberate digging takes place, the discharge of a cloud of particles along the route followed by the respiratory stream is clearly seen. On 'take-off' a stationary animal sometimes flicks the abdomen downwards and the long caudal filaments of the furca leave two impressions in the mud. When necessary, locomotion can be reversed, enabling an individual to back away from an undesirable situation.

Notostracans bear a superficial similarity to xiphosurans, a striking example of convergent evolution in distantly related organisms. Both have a rigid protective dome covering the anterior part of the body and its ventrally located appendages, and a slender, elongate posterior region. It might therefore be expected that the mechanics of swimming would be similar. In fact, orientation during swimming is very different. Except for brief excursions usually for a visit to the surface where they swim inverted with the body aligned horizontally, notostracans habitually swim ventral surface down, the body usually being held horizontally or with the anterior end depressed (figures 2 and 3). Xiphosurans swim inverted with the body inclined obliquely, anterior end uppermost. Nevertheless, notwithstanding the inversion, the two situations are hydrodynamically similar. Fisher (1975) has analysed the swimming of the xiphosuran *Limulus polyphemus*, mostly by using legless models mounted in a flume, and believes that a vortex is set up ventrally that assists the swimming limbs on their return stroke, though this seems not to have been demonstrated in living animals. Apart from the problem of alignment in the correct plane, (and the inevitable extra load imposed on the working stroke) it would be difficult for such a vortex to assist the return stroke of the locomotory limbs in a swimming notostracan. Here the anterior end of the headshield is often close to, and frequently touches, the substratum, which interferes with, or precludes, any regular posterior flow ventrally from the anterior extremity. The powerful respiratory streams set up by the posterior trunk limbs would also prevent the establishment of such a vortex.

Although they have many similarities in shape, the Notostraca and Xiphosura swim in different ways and emphasize the importance of basing comparisons of living animals whenever possible rather than on hypothetical deductions, which in this case could be misleading. This does not mean that all inferences of function from structure are dangerous. Used with discretion and experience they can be very fruitful, and in some cases, as in palaeontology, they may afford the only possible approach. Nevertheless, it is clear that whatever selective forces led to the convergent acquisition of similar shapes in the Notostraca and Xiphosura, they appear not to have been related to orientation of the animals during swimming. Protection as the animals forage over the bottom – which occupies most of their time – may be the key.

Although notostracans spend much time in swimming, most of it over the bottom, and the posterior limbs are in constant motion, it is not strictly true to state, as did Fox of *Triops cancriformis*, that 'the limbs beat continuously throughout life' for the first four are not infrequently still as the animal rests on the bottom, and the first pair does not participate in the incessant activity of the most posterior limbs.

The posterior, apodous, section of the body is extremely mobile, an attribute perhaps helpful at times in extricating an individual from an awkward situation or throwing off a predator (of which, however, few occur in the habitats frequented by most species), as well as in steering. The entire trunk can be flexed ventrally so that the posterior end of the carapace is in effect elevated.

Much of the activity over the bottom is concerned with the quest for food. A variety of organisms, some several millimetres in length, is seized, and Arnold (1966) reports cannibalism and the eating of dead congeners in *L. arcticus*. However, notostracans of all sizes also feed on fine particles. These are acquired as a result of digging in the substratum, which is done with vigour by the endopodites of the anterior series of trunk limbs. Although difficult to observe directly, except to some extent from the side (even with an inverted microscope an obscuring layer of mud is necessary to allow digging to proceed) it is clear that the marginal rows of denticles are important here. They not only facilitate digging but prevent abrasion of the endopodite margins. The structure and role of the endopodites in this connection seems hitherto to have been underestimated or ignored. The ability to flex the endopodite on the corm enables appropriate adjustments to be made to the angle of attack. When working on flocculent deposits an individual sometimes stands, digs vigorously for a few cycles of movement with the anterior trunk limbs, then passes back a large amount of material which rises as it proceeds. Most such material is passed back quickly and dumped behind the trunk limbs where a pile may accumulate before the animal moves on. Large inedible items can be passed back quickly from limb to limb and rejected.

The versatility of the trunk limbs requires emphasis. Although they display a regular metachronal beat in a swimming individual, other activities are often irregular and movements are adjusted to circumstances.

The fate of such particles as are obtained from the mud is discussed in §10: much fine material is carried backward by the respiratory stream.

9. Trunk limb structure and arrangement in relation to the feeding mechanism

(a) *Trunk limb structure and arrangement*

The trunk limbs are described in §§5 and 6 and their general form is shown in figures 5–15. The size, shape and armature of the endites are related to the feeding mechanism. On the first trunk limb the endites, other than the first (the gnathobase), are tubular and, especially distally, elongate, and serve an essentially sensory role. On succeeding limbs of the anterior series there is a gradual transition to a more flattened, more or less oval, form. These endites, although not rigidly flat in life, lie approximately transverse to the long axis of the body so that, depending on the degree of lateral spread of the limb, their median margins either face the substratum or those of their partners on the opposite side of the body, and are also directed slightly posteriorly. The angle that they, and the corm of the limb, make with the ventral surface of the trunk changes throughout a cycle of movement but is generally acute posteriorly and becomes more so as the limb swings backwards.

The endites can be flexed somewhat on the corm and can therefore adjust a little to circumstances, and the endopodite, with its robust hinge joint and powerful flexor muscles, is capable of greater flexion. Preuss (1957) noted that the distal endites and the endopodite had flexor muscles but no antagonists. He therefore suggested that, although this seemed to him to have a certain improbability, extension is a consequence of the resistance of the water during the backward stroke of the limb. Extension can in fact only be achieved by hydrostatic pressure.

The medially or posteromedially directed spinous armature of the endites and, on the more anterior limbs, that of the adjacent part of the corm, is described in §6*a* and illustrated in figures 5–10. When the limbs are not widely spread laterally but are directed more or less ventrally, the meshwork spines transform the median space between the two series of trunk limbs into a cage whose walls are armed with a medially directed array of sub-marginal spines (figures 19 and 20, plate 1). It is readily apparent that these two profusely spinous walls can entrap any large objects brought into the median cage and that, should a current be drawn through them, only coarse particles can be retained.

On the posterior series of limbs the endites are close together, adjacent limbs lie closely packed, and the two rows are separated by only a narrow slit. Here each opposing wall of endites is also profusely armed with spines (figures 13 and 15; figures 26–28, plate 1). These are directed posteriorly and somewhat inward and, although less suited to holding large items than the anterior limbs, are capable of dealing with small particles.

The arrangement of the gnathobases along the trunk limb series is readily appreciated from figures 29–31, plate 2, figures 37 and 38, plate 3, and figures 54 and 55, plate 5. These show how, in the anterior series of trunk limbs, the gnathobases project markedly from the corm, and are directed inward and forward at an angle of about 45° to the longitudinal axis. Figures 54–56, plate 5, show how they are compressed over much of their length so as to appear narrow when seen end-on or from below. Figure 29, plate 2, in which they are viewed at right angles to the long axis of the body, shows the arrangement of their heavily armed regions and their relations to each other. This figure alone, although extremely informative, does not adequately convey a sense of their narrowness, which can be obtained by comparison with figures 54–56, plate 5 (see also figure 31, plate 2). Figure 29, plate 2, figure 39, plate 3, and figure 56, plate 5 show how the heavy armature of each is directed towards the mid-line and forward. Each of the anterior gnathobases lies ventral to the food groove but their long, slender, anterior and distal spines lie within it and some of them, the sweeping spines, actually sweep along its wall. Figures 29–31, plate 2, also show how these long spines extend anteriorly beneath the gnathobase in front to near the posterior limits of the gnathobase next but one in front. The view obtained by looking directly into the food groove from below (figure 56, plate 5) shows how these long sweeping spines arise in part from the anterior margin of a plate-like extension of the gnathobase.

These illustrations also show very clearly how the space immediately beneath the anterior series of gnathobases (above them in the illustrations), which forms part of the median cage, is much wider than the gap between the rows of gnathobases. They also show the position of the sensory pads on the ventral margins (e.g. figure 54, plate 5: SP) and on the median margins of the more distal endites. Thus the walls of the cage are profusely provided with sensillae.

The gnathobases of the posterior series of trunk limbs are directed more medially than those of the anterior series (figures 37 and 38, plate 3).

An account of trunk limb musculature is given by Preuss (1957), who gives names to the major muscles. Although his illustrations are few and small, and show only part of the limb, they give some idea of the arrangement and complexity of both intrinsic and extrinsic musculature.

(*b*) *The food groove and associated structures*

The notostracan food groove is broad and shallow (figure 103: FG). In this it stands in marked contrast to that of other branchiopods. In the Anostraca, Lipostraca, Spinicaudata, Laevicaudata, Anomopoda and Ctenopoda it is essentially narrow: the raptorial Haplopoda and Onychopoda lack a true food groove.

The segmental nature of the groove is clearly apparent. Each segment is represented by its own sternite of thick cuticle, with an intucking at intersegmental boundaries which grant flexibility (figures 29 and 30, plate 2: FG). A continuous sheet of thin cuticle such as makes up

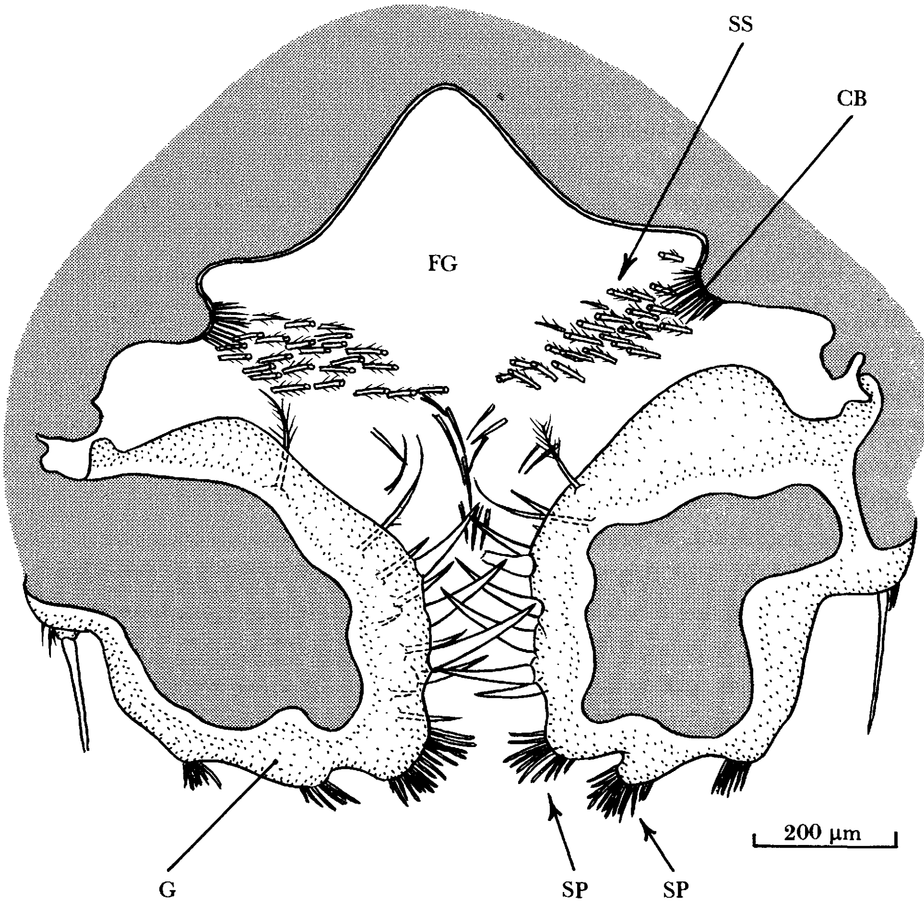


FIGURE 103. *Triops cancriformis*. Transverse section through the gnathobasic region of a pair of anterior trunk limbs, anterior view. The hidden heavy armature is indicated by dashed lines for one gnathobase only. The sweeping spines (SS) that lie dorsal to the gnathobases are those of the next posterior pair of limbs. Note the location of the sensory pads (SP) ventrally on the gnathobases.

the food groove in, for example, small anomopods is flexible: the stout cuticle demanded here by the nature of the food and feeding mechanism would be far too rigid if it were in a continuous sheet. The intuckings are so arranged that the anterior margin of each sternite overlies that in front, thus minimizing the danger of food material finding its way into the joints.

The surface cuticle of the food groove is smooth, but along each lateral margin is an array of cleaning bristles (figure 30, plate 2: CB; figure 41, plate 3), that serve to clean the spines of the gnathobases. These bristles are longer in Australian than in Palestinian animals currently assigned to *L. apus*.

The cuticle that forms a roof over the masticatory region of the mandibles is provided with similar bristles (figure 77, plate 6) in Australian, but not in Palestinian, individuals of *L. apus*. These are additional to the mandibular cleaning rakes that are present in both.

10. The adult feeding mechanism

Larval notostracans eat finely particulate material, and post-naupliar instars and small adults continue to do so. Large individuals, whose versatile feeding mechanism permits this, are opportunistic and consume a wide range of small organisms, but particulate material thrown up by the digging activities of the anterior trunk limbs continues to be taken in. The feeding mechanism has therefore to cope with material of two kinds.

Schaeffer's (1756) account of the feeding of notostracans earned the accolade of 'schöne Beobachtungen' from Lundblad (1920), and Eriksson (1934), who thought it probably the best account available almost two centuries later, concurred. The account given here amplifies those of these workers, and the observations of Cannon (1933), draws upon more detailed morphological information than has hitherto been available, and provides the illustrations, hitherto lacking, that are essential for an understanding of the mechanisms involved. How large items are handled is dealt with first.

Adults, which feed on such animals in nature, (see, for example, Einarsson 1979), seize and devour small crustaceans and tiny chironomid larvae when these are supplied, and readily accept a proprietary breakfast food 'Bemax', lumps of which they handle in the same manner. Although tactile stimuli are clearly involved in the detection of live prey, gustatory organs assist the location of inert foods. As Seifert (1930) showed by feeding gelatin containing various substances, pure gelatin was generally accepted but that containing things like acetic acid and quinine was rejected. Small worms were normally readily accepted, but after soaking in quinine were usually vigorously rejected. 'Bemax' offered with fine forceps is quickly seized, and hunting for isolated lumps indicates that their presence has been detected.

Large food masses are enveloped by the anterior limbs. When necessary the endopodites can curl around active prey to prevent its escape, but this is in any case almost always ensured by the grasp secured by the spines of the endites that, directed medially and somewhat backwards, enclose it in a cage whose walls are beset by numerous spines. The ventral opening of the cage is generally closed by the substratum, but when the prey is firmly grasped this is probably irrelevant. The space within the cage is commodious and adjustable and is wide dorsally where the corm of each limb arises lateral to the gnathobase at an elbow-like joint (figures 29 and 31, plate 2). Its width more ventrally is easily adjusted by lateral inclination of the limbs. The back and forth swing of the trunk limbs is such that the sub-marginal endite spines, as well as inflicting damage on the prey, tend consistently to force it backwards and dorsally towards the gnathobases.

The arrangement at the base of the spines is important here. Because the hinge always lies to the anterior side of the spine, whenever the limb is on its working stroke the spines are erected and, when necessary, push large items of food backwards, towards the mid-line, and dorsally. Depending on what is being handled they can push either with their tips or with more extensive distal regions that are armed with suitably oriented spinules, some of which can be seen in figure 21, plate 1. On the recovery stroke any resistance inevitably causes the spines to flex, thereby allowing them to slip over any adjacent portion of material being handled, only to be erected again on the next working stroke. Hinging may also be helpful whenever two adjacent limbs need to make contact.

Ample opportunity is provided for testing the acceptability or otherwise of seized material by the rosettes of sensillae on the inner margins of the endites and on the ventral margins of the gnathobases. Unsuitable, or excessive, material is rejected by being passed back quickly from limb to limb to just behind the anterior series of trunk limbs and then discharged.

Acceptable material is gradually forced towards and between the gnathobases. Contrary to the statement of Eriksson (1934), these, which have their own musculature (Preuss 1957), can swing independently of the more distal parts of the limb. Contrariwise they are often stationary when the limbs beat. The gnathobases are also capable of abduction–adduction movements. Although it is not possible to observe this directly, it is clear that a forward and inward swing by the heavily armed gnathobases will inevitably tear, or in some cases perhaps merely crush, material held by the more distal endites. Such tearing or crushing is indeed necessary before some kinds of food can be forced deeply between them. Material so torn or crushed is then passed forward from gnathobase to gnathobase. It is largely prevented from passing right into the shallow food groove by the long gnathobasic sweeping spines that lie between the gnathobases and the groove (figures 29–30, plate 2; figure 103) and screen out large items. The passage of food forward is easily seen in an individual feeding on 'Bemax' which, having taken material from a pair of forceps, sometimes obligingly handles it while lying in an inverted position. Such material can accumulate over a distance spanned by several gnathobases where it is held until it can be accommodated by the mouthparts, an example of the independence of the gnathobases from the rest of the appendage. Most large chunks of material are thus handled anteriorly. Any particles of 'Bemax' that pass more posteriorly are generally forced towards the food groove there, and then passed forwards to join the bulk of the material, and this is presumably the case when detritus is handled. No doubt large items that extend well back are similarly treated, there being no sharp point of demarcation between the anterior and posterior series of trunk limbs.

Large lumps of food are passed forwards by the opposed armature of stout denticles of each pair of gnathobases (figure 103) assisted (figure 39, plate 3) to some extent by the more proximal and more dorsal curved spines that arise from the posterior face of each, though not all these can gain access to it. Although some of these must inevitably come into contact with large food masses at times, their role in handling large items is clearly small. The significance of the articulated gnathobasic spines (§6*a*) is now readily apparent. Their arrangement is such that, as the gnathobase swings forward, they are erected, present their working face to the food mass, and sweep or carry it forward. On the return stroke any resistance they encounter from material being gripped by adjacent gnathobases causes them to flex and enables them the more easily to ride over it without any tendency to move it backward. Erection will automatically result from contact with an obstacle and it is unlikely that hydrostatic pressure is important. The proximal gnathobasic spines (figure 29, plate 2: PGS), probably help to prevent detached fragments from slipping though the gaps between adjacent trunk limbs.

The danger of material being carried back along the food groove as the gnathobases make their return stroke is also obviated by the fact that, at least in the anterior series, the gnathobases are capable of abduction–adduction movements. This can sometimes be seen most clearly in the first pair. Thus adduction assures the gnathobases of a firm grip during the working stroke; abduction ensures that what has been achieved by the working stroke is not negated as they complete their cycle of movement.

Large items proceed forward to the mouthparts, by which time some maceration of soft tissues has occurred. The maxillae appear to play a very minor role in food handling, perhaps serving less as manipulators than as agents to prevent slipping back of material as the gnathobases of trunk limb 1 swing back and to prevent its escape laterally as the maxillules abduct.

The maxillules are very important. They are capable of wide abduction (figure 104) so that large items can pass between them, are stoutly armed, and provided with powerful muscles (§7*e*). Their orientation (figure 29, plate 2; figures 44 and 45, plate 3) is such that as they adduct, which they do in a very positive manner, their armature of stout denticles bites the food and forces it forwards between the paragnaths to the mandibles. The distal (ventral) arcs of cutting denticles (CD) on each maxillule (figures 44 and 45, plate 3; figure 101) that between them make up a pair of shears, cut off material at about the level of the most ventral teeth of the mandible. Any material so severed that lies ventral to the mouthparts can pass backward and be returned to the feeding stream posteriorly or discharged. This shearing action, at the appropriate level, is particularly important and has no counterpart in the maxillules of any other group of branchiopods. Indeed in no other extant branchiopod order are the maxillules capable of abduction.

Observations on an individual recovering from partial asphyxia that several times swung its maxillules while no food was present between them, suggested that (cf. mandibles) towards the end of adduction they met dorsally and that this provided a fulcrum for the final cutting action of the shears which met in the mid-line. When food is being bitten a more effective fulcrum may be provided.

Slight abduction–adduction movements of the paragnaths take place as the maxillules operate. These, which are purely passive as the paragnaths have no independent musculature, reflect the close association of these structures and the maxillules.

Thanks to the dorsal abductor muscles, the ventral (masticatory) portions of the mandibles can be swung apart in a way not possible in branchiopods with rolling mandibles. The gape can also be somewhat increased posteriorly by contraction of the anterior muscles of the transverse mandibular series, as it can in other branchiopods. This inevitably involves some sacrifice of the gape gained anteriorly by abduction. The abductor muscles are aided by the most dorsal elements of the transverse series whose equivalents grant a small measure of abduction in non-biting branchiopods.

Movements of the mandibles are indicated in figure 104 During abduction the most posterior, ventralmost, masticatory teeth can be swung almost to the level of the lateral margins of the labrum. As they bite, the massive body of each mandible swings inward and the posterior teeth approach their partners just behind the posterior margin of the labrum. Adduction, and a slight forward swing, are the results of the work of the more or less transversely oriented transverse mandibular muscles and their somewhat obliquely inclined posterior companions. Although overshadowed by abduction–adduction movements, there is a rolling component to mandibular action that, powered by the remotor roller muscles, contributes to forward movement of the food. Towards the end of the cycle there is a slight swing forward that causes the biting region to move forward somewhat. This is clearly the result of contraction of those transverse muscles that insert on the posterior face of the mandible and incline more anteriorly than do the majority of their associates (figure 102; figure 79, plate 7). It seems likely also that, if the more anterior parts of the toothed region bite into food first, they will act as a fulcrum and enhance the swing and the power of the bite of the posterior teeth. In an individual recovering from partial asphyxia, reflex biting, not normally seen in a non-feeding animal,

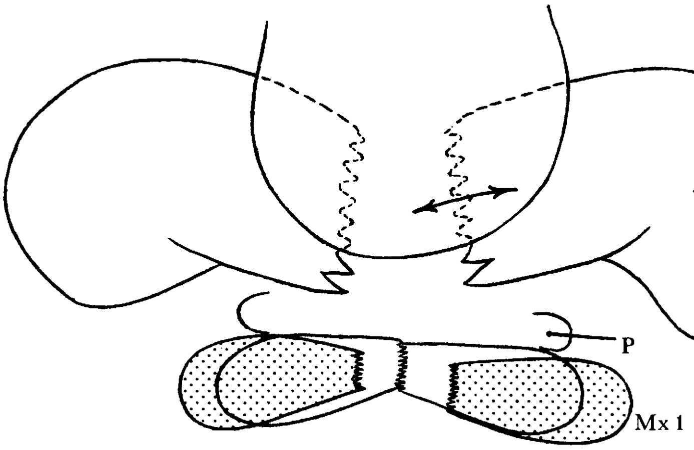


FIGURE 104. *Triops longicaudatus*. Outline of the mandibles, partly abducted, and of the maxillules in the abducted and adducted positions; ventral. Sketched from a cine film of a very young adult (more transparent than large individuals). The maxillules actually lie just behind the mandibles but are shown further behind them for clarity. The position of the paragnaths is indicated in relation to the maxillules.

showed that the posterior teeth met in the mid-line, even with no food between them. The power of the bite is attested by the enormous array of muscles that converge, many of them at only a slight angle, on the ends of the transverse mandibular tendon (figure 102; figures 79 and 80, plate 7). Minor adjustments are possible during the cycle as in non-biting branchiopods. For example, the biting regions can be pulled dorsally a trifle by contraction of the 5e muscles (see figures 86 and 87). The promotor roller muscles reverse the roll. Any material that arrives at the mandibles without having been broken up more posteriorly can be cut into manageable pieces as they bite. This is the case with lumps of 'Bemax' and is presumably so in the case of such prey as a chironomid larva, whose body may have been crushed by the trunk limb gnathobases but whose cuticle may by too tough to be torn by more distal endites or by the gnathobases.

The motion of the mandibles is slow and deliberate. Biting at an average rate of about 1.3 bites s^{-1} was recorded in *Triops cancriformis* over several sequences in an individual ingesting 'Bemax', and the longest sequence, 110 consecutive bites, was at about the same rate, approximately 1.38 bites s^{-1}. Shorter sequences (max 54) when chewing *Daphnia* averaged about the same rate, 1.23 bites s^{-1}. Chewing is, however, sometimes slower e.g. 43 bites in 46 s when chewing a piece of cooked meat.

In the lobster, *Homarus gammarus*, whose mandibles are sufficiently large to enable electromyograms to be obtained, Wales *et al.* (1976) have shown that after these appendages have come to the closed position during biting there is further isometric contraction of the adductor muscles. Although not proven, it seems probable that this is the case also in the Notostraca, though the muscles involved are different. It seems likely to be so also in the case of the maxillules where such a device would increase the efficiency of the distal shears.

The mandibles are wiped ventrally by the spinules on the adjacent face of the labrum whose muscles suggest some degree of mobility (§7*b*). The mobility of the overlying cuticle and probable roles of the two longitudinal spine rows located there has been noted in §7*c*. Food passed anteriorly from the mandibles is sucked up the oesophagus by peristalsis.

Feeding on small particles involves many of the same processes as does the handling of large items, but there are also differences. The gut contents of notostracans often include large amounts of particulate matter and, notwithstanding its strongly carnivorous proclivities, *Triops cancriformis* can, as Fox (1949) noted, be reared to maturity on particles that it extracts from mud. Often these are brought into suspension as the animal works its way over the bottom, scraping and digging with the endopodites of the anterior trunk limbs, and are drawn into the median cage by the rhythmic beating of the limbs. They are also obtained by scraping the surfaces of stones or plants as noted for *Lepidurus arcticus* by Arnold (1966). Individuals of this species that I kept in captivity spent much time clambering among clumps of mosses, fronds of which they repeatedly scraped, presumably removing attached algae and detritus. Many of the particles obtained by these different means appear to be flocculent, which doubtless facilitates handling. They appear to enter the cage in the region posterior to the anterior series of trunk limbs. Sometimes *T. cancriformis* stands on its four anterior pairs of trunk limbs, which are therefore stationary, and whisks up material more posteriorly. This passes posteriorly and dorsally and there is sometimes a distinct delay as it is manipulated ventral to the food groove before being passed to the groove and forward. The spines of the inner margins of the endopodites of the posterior series of limbs are probably involved in holding such material but this is not proven.

As Eriksson (1934) observed, there is no device whereby the anterior trunk limbs can retain very fine particles. The same is true even of the compact array of finely denticulate posterior limbs. The animals have no filter plates. Fine particles are expelled by the pumping activity of the trunk limbs, mostly in two backwardly directed streams that were aptly likened to clouds of smoke by Eriksson (1934) and to 'smoking motor exhausts' by Fox (1949). The endites of the anterior trunk limbs are provided with a meshwork of spines suitable for retaining coarse particles. However, when an animal is digging and foraging over the bottom these limbs are widely spread laterally and their endite rows are not directed towards their partners on the opposite side as is the case when large food masses are being handled. Thus they cannot easily handle even relatively coarse particles while engaged in such activities though some such, especially irregularly shaped lumps of detritus, are doubtless retained and passed backward, medially and dorsally to the food groove, as is flocculent material.

The seizing and handling of any coarser particles encountered would presumably be facilitated by rising slightly above the bottom, which would allow opposed sets of endites to operate as they do when seizing prey, but such rising would be difficult to detect and has not been observed.

Stirred up fine particles or flocculent accumulations move posteriorly. Here the spine-armed endites of the posterior limbs are so closely packed (figures 26 and 27, plate 1) that they can retain relatively small particles. Also, unlike those of the anterior limbs, these endites are not widely spread when the animal is digging but face their counterparts on the opposite side. Their armature is inclined dorsally in the vertical and medially in the horizontal plane of the longitudinal axis of the trunk, and directed obliquely towards the food groove, in the direction of which it drives particles posteriorly and dorsally. Thus although the entire trunk limb series is involved in the feeding mechanism there is a strong tendency for large food items to be handled particularly by the distal parts of the anterior limbs and for particulate material to be handled by the distal parts of the posterior limbs.

Particles collected by the posterior trunk limbs are forced towards the shallow trough that constitutes the food groove. On the way, and possibly even in the food groove, there may be some triturition of small items by the stouter elements of the endites and, more posteriorly, of the gnathobases (figures 13 and 15; figures 37 and 38, plate 3). Material is swept forward along the food groove by the armature of long sweeping spines of the gnathobases that becomes more profuse towards the anterior end of the series (compare figures 11, 13 and 15). Well forward in the posterior series, as in limbs 20–23 (figure 38, plate 3), even the spines of the stout armature that are directed into the food groove can propel small particles forwards as a glance at the scale of this figure reveals. More anteriorly, especially in the anterior series of trunk limbs, the distal, most dorsal, spines of the gnathobases make up a dense brush-like array of sweeping spines (figures 29–31, plate 2), so dense that there is probably little risk of even small items falling from the food groove as they proceed forward. This is particularly the case in Australian animals currently assigned to *Lepidurus apus*, whose sweeping spines are profusely armed with fine setules (figures 31 and 32, plate 2), but even the stouter, more coarsely armed spines of Palestinian animals (figures 29 and 30, plate 2) are so closely packed that they can handle fine particles. There is no doubt, however, that, at least in the available material, Australian and Palestinian animals are adapted for dealing with finer and coarser particles respectively. Transport is purely mechanical: no currents are involved.

The long sweeping spines of the first pair of gnathobases are capable of sweeping food right to the mandibles (figure 29, plate 2), but their counterparts on the maxillules collaborate with them in this region just as the heavy armature of the maxillules collaborates with that of the trunk limb gnathobases. Although less specialized for handling fine particles than are the mandibles of non-biting branchiopods, those of the Notostraca are able to deal with the relatively coarse material passed to them in this manner and do so by the action described in connection with large food items. The groups of spines on the teeth of the more anterior ridges (§7*c*; figures 70, 72 and 74–76, plate 6) are probably particularly helpful here.

As the ability to feed on large and very small items shows, the feeding mechanism is very versatile. It can also be adapted to other circumstances. For example sand grains are picked up, passed posteriorly and dorsally, and there manipulated, presumably being scraped of adhering material, before being rejected. A small individual of *T. cancriformis* was seen to straddle a thin, twig-like stem longer than the length of the anterior series of trunk limbs, and to do so for some time with the limbs beating, and presumably scraping, before rejecting it posteriorly with a few rapid movements of the limbs, and small individuals of *L. arcticus* have also been seen to scrape elongate objects taken between the trunk limbs. An individual of *T. cancriformis* that had siezed a piece of 'Bemax' from a pair of forceps hung inverted from the forceps with its anterior trunk limbs while the food was manipulated posteriorly and passed forward to the mandibles, incidentally a good illustration of the ability of the gnathobases to move independently.

As well as animal prey, flocculent detritus and particulate material, vegetable matter is also eaten. The guts of specimens of *Lepidurus apus* from Australia were packed with small fragments of grass. Whether this had been picked up as detritus or torn from living plants – notostracans sometimes frequent grassy pools – is unknown.

The role of the trident and 5-pointed spinules (§6*a*) in the feeding mechanism is not clear. Like the major spines, these are hinged in such a manner that they erect during the working stroke of a limb and flex on the return stroke. Those of the posterior series of limbs can probably assist adjacent spines. Those on the anterior series of limbs inevitably trap a few small particles that they may then assist on their way to the more posterior limbs and they can perhaps help to retain flocculent masses of material, though their location behind the sub-marginal spines seems ill-suited to such a role. They possibly at times clean the anterior face and meshwork spines of the limb behind, but a satisfactory explanation of the function of these elaborate structures is still elusive.

11. DEVELOPMENT AND THE ONTOGENY OF THE FEEDING MECHANISM IN *TRIOPS*

As in so many aspects of the biology of the Notostraca the pioneering observations on development were made by Schaeffer (1756) who saw and described hatching eggs, nauplii and several of the early instars of *Triops cancriformis*. Later, the gross features of development of the same species were described with his usual skill by Claus as long ago as 1873, and the development of *Lepidurus apus* was described by Brauer (1874). Campan (1929) also followed the development of the latter species and provided valuable information on the ontogeny of individual cephalic appendages. These, and subsequent observations on other species, revealed that the pattern is not identical in all species.

The feeding mechanisms of the early stages have not hitherto been investigated. These mechanisms are of intrinsic interest and the ontogeny of the process not only reveals how the animal maintains functional continuity in an essential process from larva to adult, but provides information of phyletic value in assessing the relationships of the Notostraca and other branchiopod orders. The following account refers mostly to *Triops cancriformis* but makes comparisons with *T. longicaudatus* whose development is basically similar but involves more early instars. Although hatching, which is the first event in this process, has been observed in *Lepidurus arcticus*, an account of this is deferred until this species is dealt with in §12.

Eggs of *T. cancriformis* hatch as a plump feebly swimming nauplius about 600 μm in length that frequently sinks to the bottom. As Brauer (1872) noted long ago the first nauplius is less active than its counterparts in *Branchipus* (Anostraca) and *Estheria* (Spinicaudata). Richly provided with yolk that, as Claus (1873) observed, serves it not only as a source of food in this and the second, but probably even in the third instar, it does not feed. Indeed the mandibular gnathobases are not developed. Anlagen of the mandibular palps, each armed with six short setae, are present but as yet have no role in feeding. The antennae of *T. cancriformis* have five, of *T. longicaudatus* seven, unjointed natatory setae on the endopodite, three on the exopodite, a number that never increases as development proceeds (see §14). Each antenna is also armed on its posterior margin with the homologues of what, in the Anostraca, were described as proximal and distal masticatory spines (Fryer 1983), whose structure and functions in later instars are referred to below.

Development proceeds very rapidly, an adaptation to the temporary pool habitat. Under warm conditions the duration of each early instar in *T. cancriformis* can be much less than a day. In *T. longicaudatus*, whose first nauplius is transient, the stages can be exceedingly brief, fourth and fifth instars having been recovered less than 43 h after wetting the eggs. As several hours were probably involved in the hatching process some of the early instars must have had a duration of at most a few hours each. Moreover, in contrast to the very gradual anamorphic development of the Anostraca, large steps are taken at each moult so development proceeds apace in all respects. The size of the steps differs from species to species (see also §12 for differences between *Triops* and *Lepidurus*).

After the first moult, when the larva of *T. cancriformis* has a length of up to *ca.* 750 μm, the head is covered by a simple headshield, a short carapace rudiment is present, the trunk has begun to extend posteriorly, elongate conical papillae indicate the developing furcal rami, the naupliar appendages are better developed, and not only can the outlines of six or seven trunk limbs be made out but early signs of differentiation into endites can be seen on the first three. Swimming, mostly near the bottom and punctuated by frequent rests, involves sweeps of wide amplitude by the antennae that present a broad face with widespread setae on the working stroke. From the standpoint of feeding, the salient feature of the antennae is the massive proximal masticatory spine (PMS) that curves inwards on each side in the vicinity of the mandibles (figure 105).

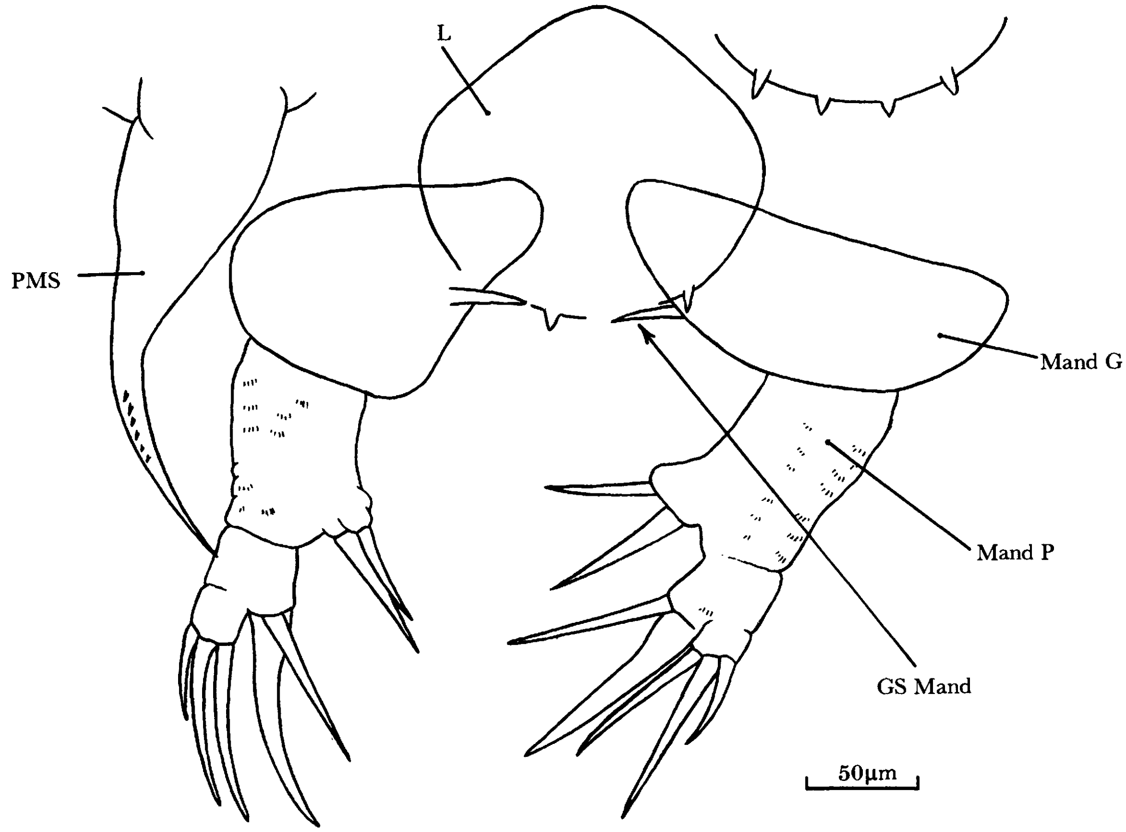
The labrum (L) is short and flat (figure 105), in this respect being very different from the elongate, fleshy naupliar labrum of the Anostraca, Spinicaudata and Laevicaudata. It only partly covers the mandibular gnathobases. The latter (Mand G) are substantial structures but their presumptive masticatory regions, which are widely separated (figure 105), are as yet devoid of armature. On its posterior margin each bears an inwardly directed spine, the gnathobasic spine (GS Mand.). From each gnathobase there also arises distally a now well developed palp (Mand P) whose structure and armature are apparent in figure 105. Just behind the mandibular gnathobase it is possible in moulted cuticles to make out the earliest Anlagen of the maxillules.

The gut, which now undergoes peristalsis, is still packed with yolk, but Claus (1873) noted that detrital particles are taken up. Certainly the mandibular palps are active at this stage. They swing inwards and can be flexed to give a forward component to the movements of the distal armature. It is this whisking action of the mandibular palps that is responsible for food collection in this and later stages, particles being so collected as the nauplius swims over the bottom. Their angle of attack can also be varied. Their structure suggests that they may sometimes grasp material, as in a pair of forceps, and pass it forward, but this has not been observed.

The dense mass of yolk in the gut prevents observations on the mandibular gnathobases, but moulted cuticles enable their structure and arrangement to be seen, and it is clear that their presumptive masticatory regions are neither suitably armed nor sufficiently close together to enable them to deal with particles in the way they will in subsequent instars (figure 105). However, if observations on naupliar anostracans be taken as a guide (Fryer 1983), and as can be deduced from movements of the gnathobases in later instars, the swing of the gnathobases will enable the gnathobasic spines to push forward any particles swept towards them from behind, just as they do in naupliar anostracans. The presence and employment of these spines in naupliar and early post-naupliar stages, which were present in the Devonian lipostracan *Lepidocaris* (Scourfield 1926, 1940; Fryer 1983), is clearly an ancient branchiopod character.

The forward passage of food beneath the labrum and between the mandibular gnathobases is assisted also by the inswinging proximal masticatory spine of the antenna (figure 105: PMS) of each side, just as it is in the Anostraca (Fryer 1983). This spine is not concerned with the collection of food, but its inward and forward swing is admirably suited to assisting the mandibular palps to pass forward material that they have collected.

The distal masticatory spine of the posterior margin of the antenna is short in *T. cancriformis*, a little longer in *T. longicaudatus*. This spine is the primary food-gathering agent in the naupliar stages of the Anostraca (Fryer 1983). In the Notostraca it either plays no part in food collection or perhaps has a minor role in *T. longicaudatus* (see below). It is lacking in those species of



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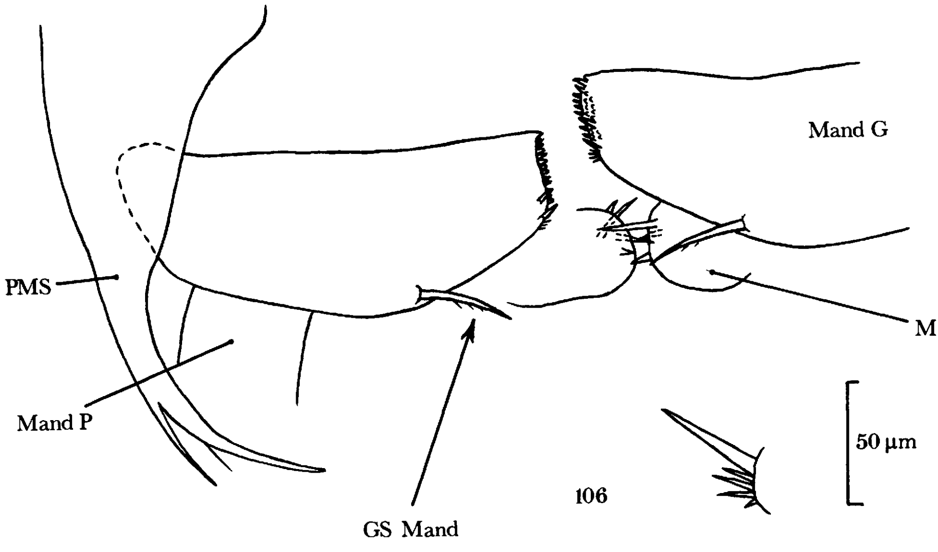

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Figures 105 and 106. *Triops cancriformis.*

Figure 105. The mandibles and their palps, and the proximal masticatory spine of the antenna (PMS) of a stage 2 nauplius, as seen in a moulted cuticle; ventral. To avoid obscuring the gnathobasic spines (GS Mand), parts of the posterior margin of the labrum (L) are omitted and its entire posterior margin is shown in the inset.

Figure 106. The mandibles, maxillules and proximal masticatory spine of the antenna of a stage 3 nauplius, as seen in a moulted cuticle; ventral. The mandibles have beeen slightly displaced. Much of the armature of the masticatory region of the mandibles lies dorsally and is indicated, on the left mandible only, as seen through the transparent cuticle. The inset shows the extreme posteriormost armature of the left mandible more highly magnified.

Lepidurus whose larvae are known (§12). Herein lies an important difference in the feeding mechanisms of the early stages of members of the Notostraca and the other anamorphically developing branchiopods, (Anostraca, Lipostraca, Spinicaudata and Laevicaudata), and is related to the association of the Notostraca with the bottom from the earliest stages of the life cycle.

The labrum (L) is a simple plate and there is no indication that labral gland secretions are produced. The nature of the food seems not to require the use of such. From this early stage relatively coarse particles are collected and these can be handled in a way in which the minute particles collected by filter-feeding branchiopods cannot.

The different nature of the food particles handled by naupliar notostracans and anostracans is clearly reflected in the structure and armature of their mandibular palps, even in these early stages. The remarkable correspondence of the setal armature of the mandibular palp in nauplii of the Anostracan *Chirocephalus* and the Devonian lipostracan *Lepidocaris* was pointed out by Scourfield (1940). The arrangement is precisely the same in the Notostraca but, in accord with functional necessity, the structure of the individual elements of the armature is markedly different. Information on the palp armature is available for the anostracans *Chirocephalus diaphanus* (Scourfield 1940) and, in greater detail, for *Branchinecta ferox* (Fryer 1983, figures 6 and 7), and Scourfield also illustrates that of *Lepidocaris* (Lipostraca). In all cases the three distal spines are long, slender and unarmed. In *Triops cancriformis* they are much shorter and robust (figure 105) as befits their role in sweeping relatively coarse particles. Although slightly more elongate and slender in *T. longicaudatus* they are essentially similar to those of *T. cancriformis*. In the anostracans and *Lepidocaris* the two median spines are long and slender, and in *B. ferox* are armed with two rows of obliquely directed setules that enable them to sweep fine particles over the ventral surface of the head. Their counterparts in *T. cancriformis* are stout. These are the spines that inevitably make most contact with the substratum from which they sweep, and perhaps sometimes even dislodge, coarse particles. In the anostracans and *Lepidocaris* the two proximal spines are long and slender, and in *B. ferox* are armed with laterally extending rows of setules that help to contain small particles between themselves and the ventral surface of the head. In *T. cancriformis* they are short, stout and well adapted to the forward transfer of coarse particles.

The third instar larva of *T. cancriformis*, up to about 1.25 mm in length, is immediately distinguishable from its predecessor by its much longer, but still conical, furcal rami. The headshield is continuous with the developing carapace that extends posteriorly to cover only about the first two pairs of trunk limbs which, like the third pair, show well defined, but still rudimentary, spine-bearing endites. These three pairs of limbs are now capable of feeble movement but are not able to contribute to locomotion, for which the antennae are still entirely responsible, nor do the trunk limbs contribute in any way to feeding.

The antennae are similar to those of the second instar and the proximal masticatory spine is still well developed, but now bears a short, slender spine on its outer face that in effect renders it bifid (figure 106; PMS). The mandibular gnathobases now lie closer together and each has acquired an armature of short, sharp denticles (figure 106). The gnathobasic spine (GS Mand) is retained but is now located relatively more laterally than in the preceding instar but is suitably located to assist the armature of the mandibular palps. The palps are essentially the same as in stage 2 but the larger spines of both the proximal and median pairs and the companion of the latter, bear minute spinules or setules on their median margin. The as yet non-functional maxillules (Mx1) are now readily seen behind the mandibular gnathobases. Each bears four spines, two of them minute.

As in the preceding stage, particles are collected by the mandibular palps, which now display great versatility. Movements of the mandibular gnathobases are largely obscured by the yolk still present in the gut but, now suitably shaped and provided with the necessary armature on their masticatory surfaces, doubtless operate as described for later instars. Any forward swing of the gnathobases will enable the gnathobasic spines to propel material forward and this effect will be enhanced by any adduction component involved, but their role is already less important than in the preceding instar. Sweeping of material to the mid-line and forward is assisted by the now bifid proximal masticatory spines of the antennae.

Fourth and fifth instar larvae, variable in size, the latter more than 1.6 mm in length in the limited material available, show progressive development of the furcal rami and of the trunk limbs. In the fourth instar the first five pairs of trunk limbs, and in the fifth the first seven pairs, that now have well developed endites with a simple spiniform armature (figure 108), are active in locomotion and food collection, and in each case another pair, or two pairs, of limbs are capable of feeble movement. With their developing carapace and abdomen and the habit of swimming over the bottom, larvae now resemble miniature adults, but the antennae are still well developed and active in locomotion. In the present material (from Spain) the smaller, outer, branch of the proximal masticatory spine of the antenna has virtually disappeared in instar 4 and has done so in instar 5. In material described and illustrated by Claus (1873) from central Europe this spine is distinctly bifid in instars 3–5. This evidently is another example of racial differentiation (§3). By stage 4 the mandibular gnathobases have developed a formidable array of teeth on their masticatory surfaces (figure 107). Particularly noteworthy are the two posterior teeth on each mandible that are much the largest of the series. These are well spaced and form in effect the equivalent of an incisor process. The gnathobasic spine is retained (figure 107, inset). The mandibular palps are still essentially the same as in earlier instars. Above the mandibular gnathobases the roofing cuticle is now armed with spinules and with the precursors of the two rows of spines, the mandibular cleaning rakes, that are present in the adult (figure 107:MCR′).

The maxillules are now much better developed (figure 107: Mx1). By stage 4 their two-segmented nature is evident as are clear indications of differentiation of their armature into stout grasping and biting distal teeth, and long, more proximal, sweeping spines. The rudiment of the posterior apodeme (RPMA) is readily seen in a moulted cuticle of this stage.

The active, anterior, trunk limbs have endites (End) armed with simple spines, and their endopodites (EN) are provided with three or four claw-like spines (figure 108). The sensillae that are such a conspicuous feature of the adult trunk limbs are now represented for the first time, as a single sensilla (SEN) on each endite. Propelled both by the antennae and the currently active trunk limbs, the larvae swim over the bottom in an adult-like manner. The antennae beat rapidly but, particularly in stage 5, with smaller amplitude than in stage 2, the limits of the posterior swing being restricted by the developing trunk limbs. In contrast to their behaviour in the adult, at this stage the first pair of trunk limbs contribute to the propulsive thrust and do so vigorously, but noticeably less so, than the next two pairs.

An undisturbed larva frequently halts and scrapes the substratum with its trunk limbs. Although difficult to see, it is probable that the endopodites of the first pair are at times used for gripping, but sometimes these limbs are active and it is not always clear how the animal

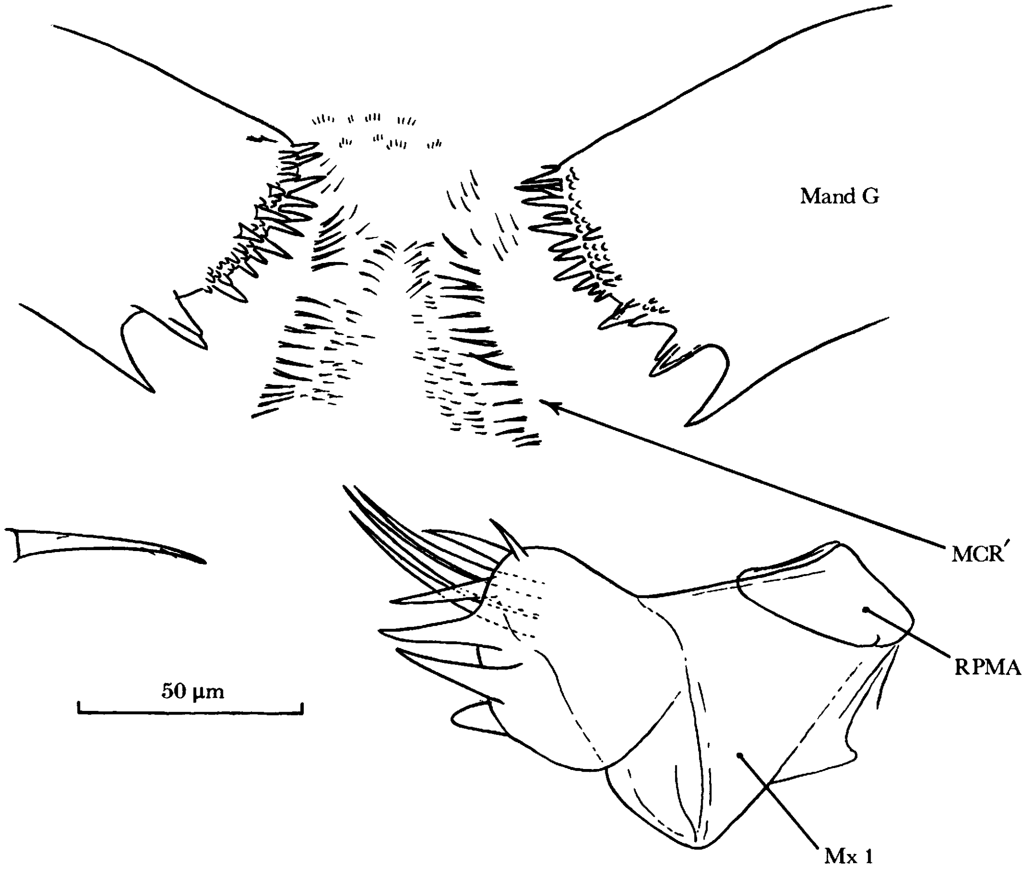


Figure 107. *Triops cancriformis*. The mandibles and a maxillule of a stage 4 nauplius as seen in a moulted cuticle; ventral. The mandibles are more widely separated than in life and the shape and position of the maxillule are somewhat altered by compression, but the nature of the armature is clear. The inset shows the gnathobasic spine of the right mandible.

maintains station. The other functional limbs are active, and their endopodites, that can grant purchase when required, may help to sweep particles at this time. In a stationary individual engaged in scraping, the antennae are sometimes at rest, at others they beat rapidly but with much smaller amplitude than when used for swimming and with their long axes inclined backwards at approximatley 45° even at the point of maximum promotion. Although movements of the proximal masticatory spine cannot be seen from above, antennal activity in a stationary individual is clearly indicative of its use in food transfer.

By stage 4 food is collected by the combined efforts of the naupliar feeding apparatus and the precursor of the adult mechanism. It is difficult to assess the relative importance of the two at this or the next stage but, as development proceeds, the former method is gradually replaced by the latter. Particles are whisked towards the mid-line by rapid movements of the currently functional trunk limbs and passed forwards by their gnathobases as is the case in the adult. The armature of spines involved is much simpler than in the adult. Like that of the maxillules, however, the armature of the trunk limb gnathobases of the functional limbs already shows differentiation into stout grasping spines remote from, and long sweeping spines adjacent to, the food groove, even in stage 4 when the number of spines is few. At this stage for example the gnathobase of trunk limb 1 bears four short stout grasping spines and three long sweeping

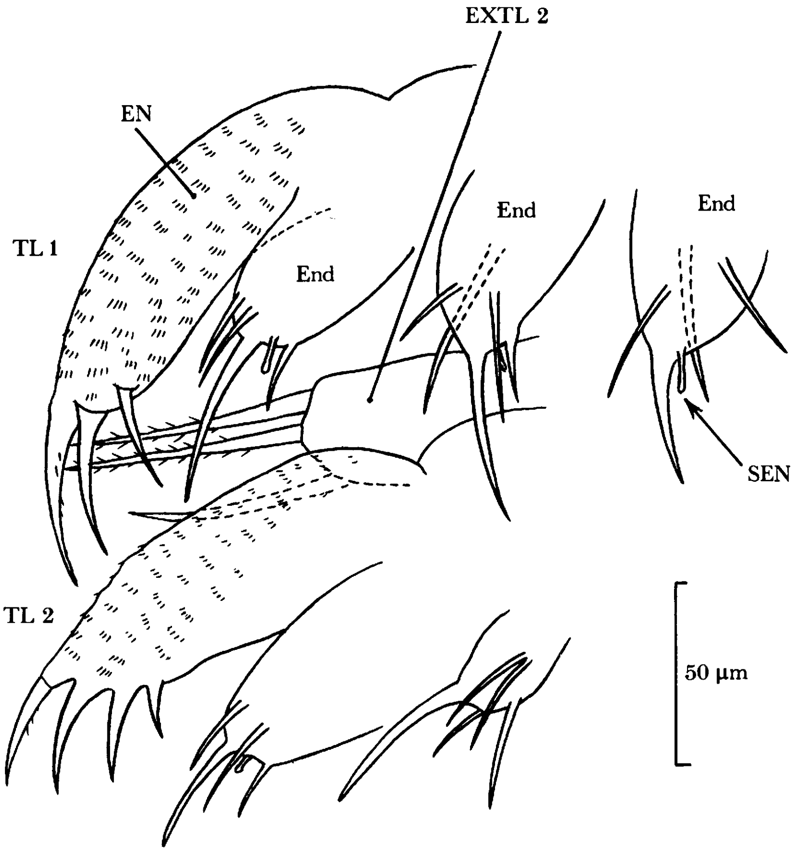
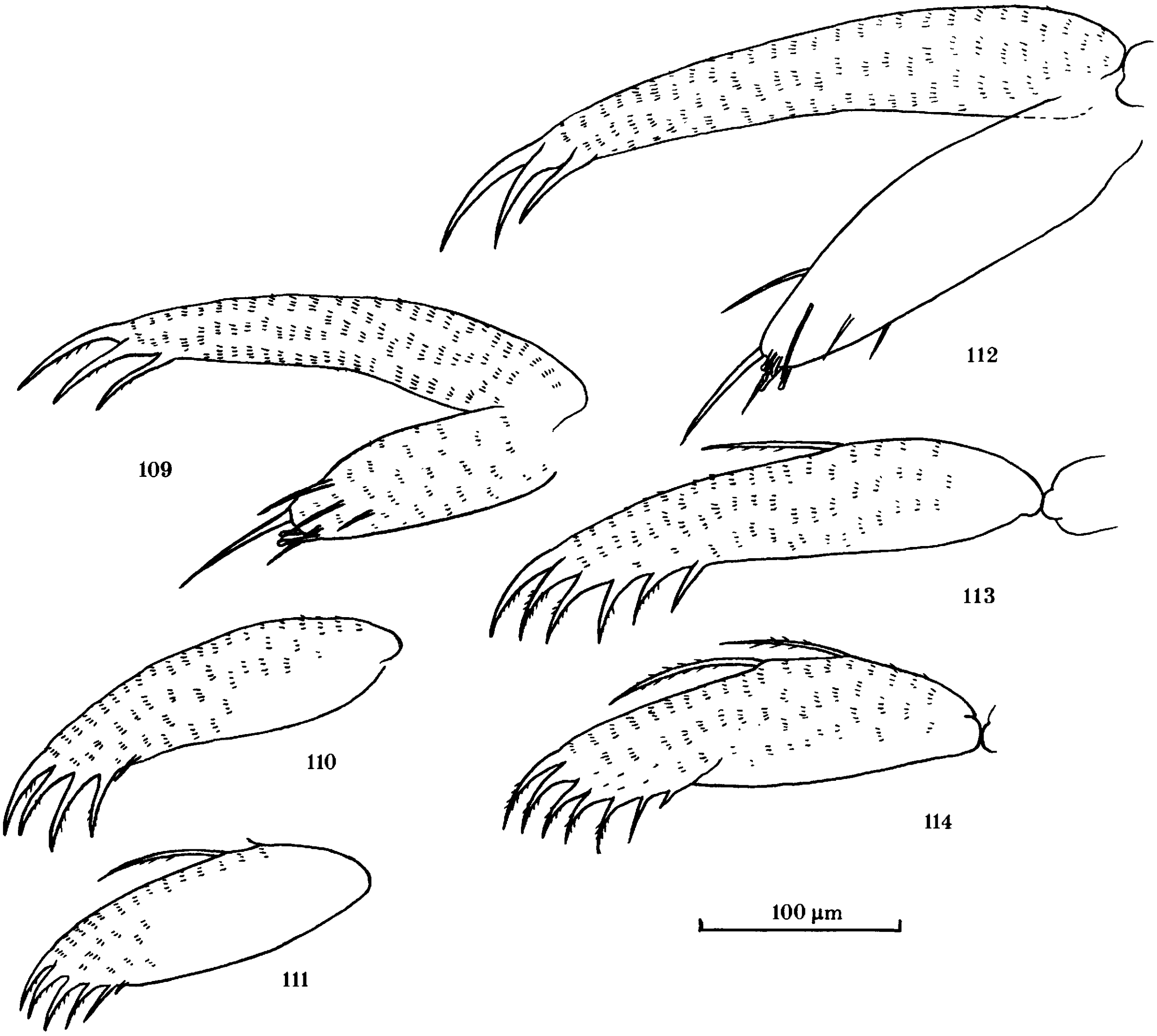


FIGURE 108. *Triops cancriformis*. The distal portions of trunk limbs 1 and 2 of a stage 4 larva, ventral. Note how at this stage the differences between these limbs are trivial. It is from these simple beginnings that the complex endites and endopodites of the adult develop.

spines. The gnathobases are very active and display much abduction–adduction as well as the necessary swing. Collected material is passed forwards, via the maxillules, which appear to contribute to only a small extent in the fourth instar but are very actively involved in the fifth, to the mandibular gnathobases. Here it joins any collected by the mandibular palps. Although these function as in earlier instars a palp has been seen entangled in a large lump of detritus that was merely moved back and forth by its action so it may be that they are occasionally used for gripping. Food arriving in this region is also assisted on its passage to the mandibles by the proximal masticatory spines of the antennae that, as in earlier stages, sweep inwards and forwards.

The distal masticatory spine of the antenna is the collector of food particles in the Anostraca, Spinicaudata (Fryer 1983 and unpublished observations) and, by inference, Laevicaudata. In *T. cancriformis* it is a simple spine whose role is at best trivial. In *T. longicaudatus* it is somewhat better developed, but still simple, and possibly helps occasionally to sweep or push material towards the mid-line. It has muscles that enable it to be swung, but even here its role is at best very small. No such spine is present in *Lepidurus* (§12).

The mandibular gnathobases are very active and a cycle of movement takes place much more rapidly than in the adult. Abduction–adduction movements, so unusual in branchiopods, are very pronounced, being even more evident than in the adult, but the usual branchiopod swing is also displayed. This swing enables the large posterior teeth (figure 107) to bite the food and swing it forward much in the manner of an incisor process. The posteriormost tooth of each mandible is even more accentuated in size in *T. longicaudatus*. Such a device has been exploited by certain adult anostracans that are incapable of any substantial abduction of their mandibles (Fryer 1966). The same swing enables the gnathobasic spines to force food medially and forwards. Slipping back of the food as the mandibles abduct and make their return swing is impeded by spinules (figure 107) on the cuticle that roofs the gnathobases. These include the precursors of the mandible-cleaning rakes (MCR′).



Figures 109–114. *Triops cancriformis*. Stages in the development of the endopodites and endites of the trunk limbs.

Figure 109. Endopodite and distal endite of trunk limb 1, instar 6.
Figure 110. Endopodite of trunk limb 2, instar 6.
Figure 111. The same, trunk limb 3.
Figure 112. Endopodite and distal endite of trunk limb 1, instar 7.
Figure 113. Endopodite of trunk limb 2, instar 7.
Figure 114. The same, trunk limb 3.

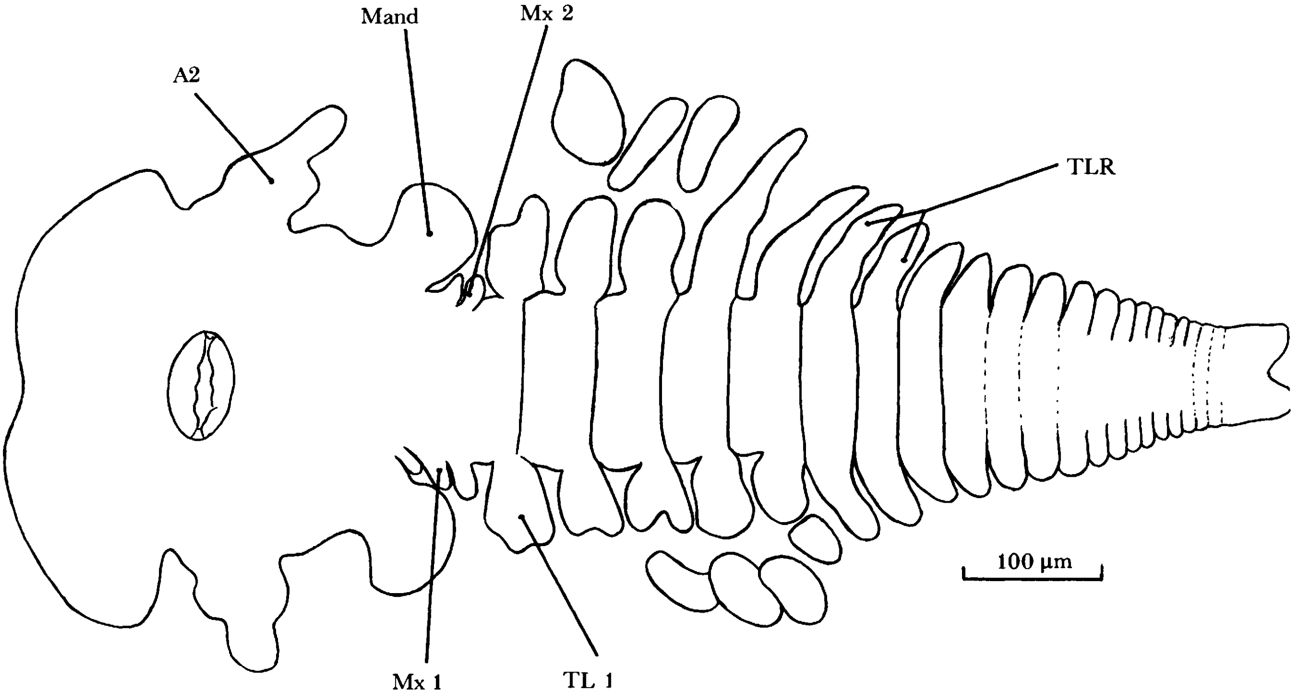


FIGURE 115. *Triops longicaudatus*. Outline of a horizontal slice through a stage 4 larva to show the anterior–posterior gradient in the differentiation of the appendages. The animal is viewed ventrally and the slice is cut at a level dorsal to the developing endites of the trunk limbs, and through the dorsal parts of the maxillules and maxillae, all of which are considerably more differentiated than is apparent at this level. Details of the cephalic organization of the same individual are shown in figure 116.

Stage 6 larvae (length *ca.* 2.3 mm) resemble their predecessors but have more elongate furcal rami, more trunk limbs are active, and differentiation continues along the anterior–posterior gradient. The endopodites of limbs 1 and 2, especially of the former, are now more elongate (figures 109 and 110), and the first natatory seta has appeared on limb 3 (figure 111). Well-developed exopodites ensure effective swimming. The antennae are still well developed and contribute actively to locomotion. The proximal masticatory spine of each is still well developed but, in the available material, is a simple curved spine, having lost the minor outer spinule earlier in development.

Mandibular palps are still present but are now small in relation of the gnathobase and are located so far laterally that they are effectively removed from the scene of operations and almost certainly never contribute to food collection. Likewise, the gnathobasic spine of the mandible is still present but is now relatively smaller than in the previous instar. The masticatory regions of the mandible resemble those of the previous stages but three teeth, now clearly the precursors of the ridges of the adult mandible, are recognizable, though the anteriormost is close to the array of smaller denticles that is still present. The maxillule is better developed and now has six robust spines and three shorter companions and five long sweeping setae (see stage 4, figure 107).

By stage 7 (length to 3.0 mm or a little more, but sometimes considerably less) the ever elongating furcal rami show articulations for the first time and the trunk limbs continue their differentiation (figures 112–114). There are problems of identifying stages from now on, though these are not important in the present context. For example a specimen slightly smaller than

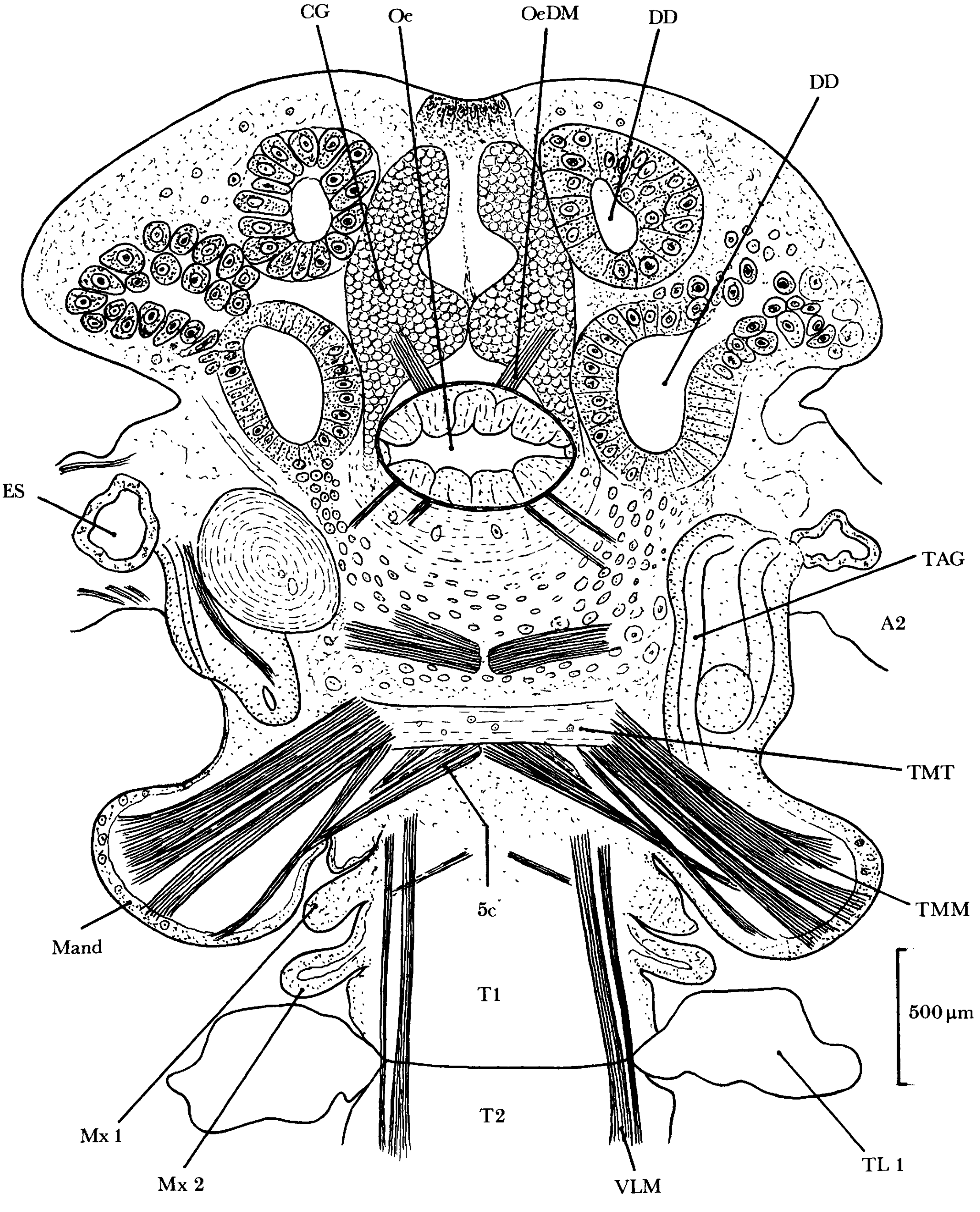


FIGURE 116. *Triops longicaudatus.* Horizontal slice through the anterior region of a stage 4 larva to show the development of the mouthparts, and the presence in these early instars of 5c muscles in the transverse mandibular series. The section also reveals an early stage of development of the digestive diverticula (DD) in the head (the precursor of the digestive gland of the adult), shows the location of the transient antennary gland on each side, both its tubules (TAG) and end sac (ES) being seen, and shows how the ventral longitudinal muscles (VLM) are laid down at an early stage. Note that the maxillules are better developed than is apparent from a section at this level, as revealed by the more ventral slice shown in figure 117.

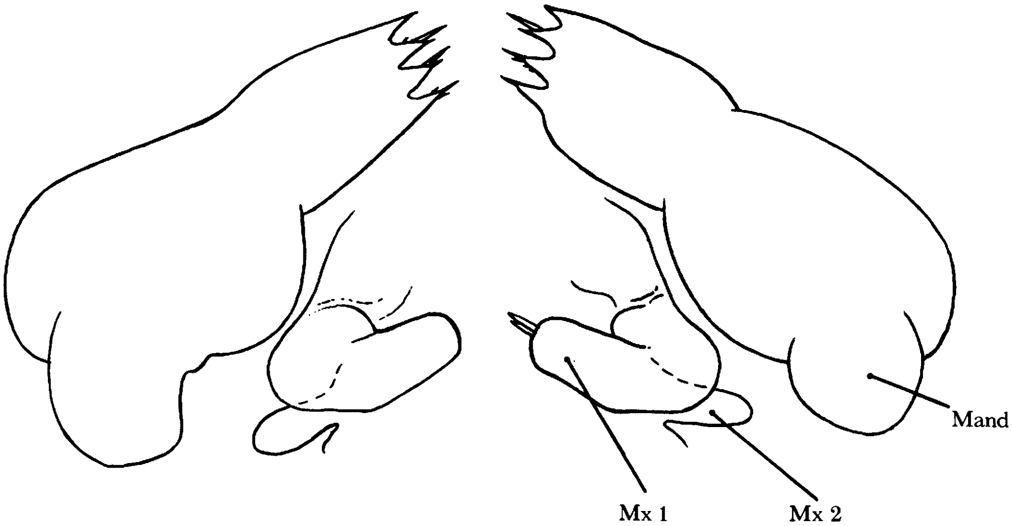


FIGURE 117. *Triops longicaudatus*. The mouthparts as seen in the next ventral slice, of the stage 4 larva seen in figure 116. Outline only. The more distal parts of the mandibles and maxillules are seen at this level.

that used to prepare figures 112–114 had four distal spines on the endopodite of trunk limb 1 and two natatory setae on that of trunk limb 2, indicating more advanced development.

Although the antennae still contribute to locomotion they no longer have a proximal masticatory spine. As the mandibular palps have also been lost, the animal now collects its food entirely by means of an adult-type mechanism though the full refinements of that mechanism are not yet developed. The mandibles have also lost the gnathobasic spine.

An elongation of the distal endite of trunk limb 1 is now evident and the sensillae, now five in number, form a rudimentary tuft.

From this stage on, the antennae begin to atrophy and to play an ever diminishing role in locomotion, the process being essentially similar to that followed by Campan (1929) in the first 13 instars of *Lepidurus apus*, though the condition in each instar of *T. cancriformis* has not been studied. By stage 8 the contribution of the antennae to locomotion is probably insignificant. Figure 127, from an individual at about stage 8, shows the transition in mandibular armature between that of a fourth instar larva and the adult.

Some anatomical features of early notostracan larvae are shown in figures 115 and 116. These are of a stage 4 larva of *T. longicaudatus*, which is less advanced in development than is this instar in *T. cancriformis*. Figure 115 is an outline of an individual sliced horizontally at a level dorsal to the food groove and therefore reveals only the dorsal parts of the trunk limbs. Figure 116 gives some details of the anatomy of the head region (see caption for details). Reference is made to the mandibular musculature in §13. At this stage the antennary glands are well developed and presumably functional: they begin to function in stage 2 of *T. cancriformis* (Grasser (1933), q.v. for the development of the excretory organs), but the maxillary glands are already developing, their tubules being housed within the lobes of the carapace fold. In *T. cancriformis* they are functional at stage 4 (Grasser 1933).

That the feeding mechanism of juveniles is essentially a simplified version of that of the adult is evident from the arrangement of the mouthparts and anterior trunk limb gnathobases of an individual at about stage 9 seen in longitudinal section in figure 118. It is also easy to appreciate how, from this stage on, the complexity of the gnathobasic armature gradually

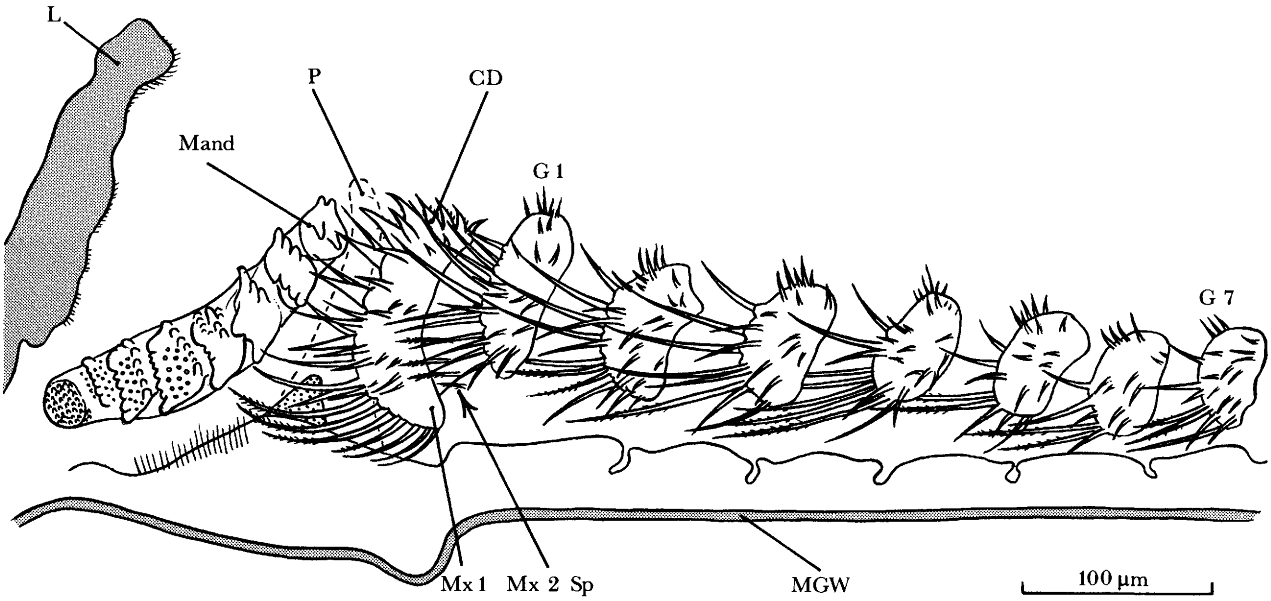


FIGURE 118. *Triops cancriformis*. Longitudinal slice through a young individual (about stage 9 but smaller than some individuals an instar younger) showing the incipient development of many of the adult features of the feeding mechanism. The paragnath (P) is located too far laterally to be seen but part of its base (stippled) is visible and its outline has been added as a broken line from the adjacent slice.

increases until the adult condition is achieved. Even in this, and earlier stages, food is handled entirely mechanically. Although the particles collected are often small, filtration is not involved. Figure 118 also shows the early stages of development of what will become the ridges of the adult mandible, and makes clear the important role of the maxillules from an early stage of development. At this stage they are more massive, and have a more complex armature, than even the most anterior trunk limb gnathobases. The sequential development of the latter is also evident. Gnathobases posterior to those illustrated become progressively smaller and less well differentiated from fore to aft.

12. DEVELOPMENT AND THE ONTOGENY OF THE FEEDING MECHANISM IN *LEPIDURUS ARCTICUS*

According to Johansen (1912) and Poulsen (1940), both of whom studied the life cycle of *Lepidurus arcticus* in the field in Greenland, Olofsson (1918), who did likewise in Spitzbergen, and Longhurst (1955*a*), who hatched eggs received from Iceland, this species, which has larger eggs than other notostracans, hatches at a later stage of development than, for example, *Triops cancriformis*. Longhurst says 'equivalent to about instar 3 of *Triops* larvae'. Likewise Sars (1896) encountered only similar larvae, and never nauplii, in Norway, though his collections were evidently sporadic, and the earliest stage encountered by Brehm (1912) in material collected by an expedition to Greenland were similar larvae. However, Borgstrøm & Larsson (1974) found that in populations in southern Norway the eggs hatched as nauplii, as was the case in a population from northern Iceland studied by Einarsson (1979). This larva moults into a stage much more advanced than the second instar of *T. cancriformis*.

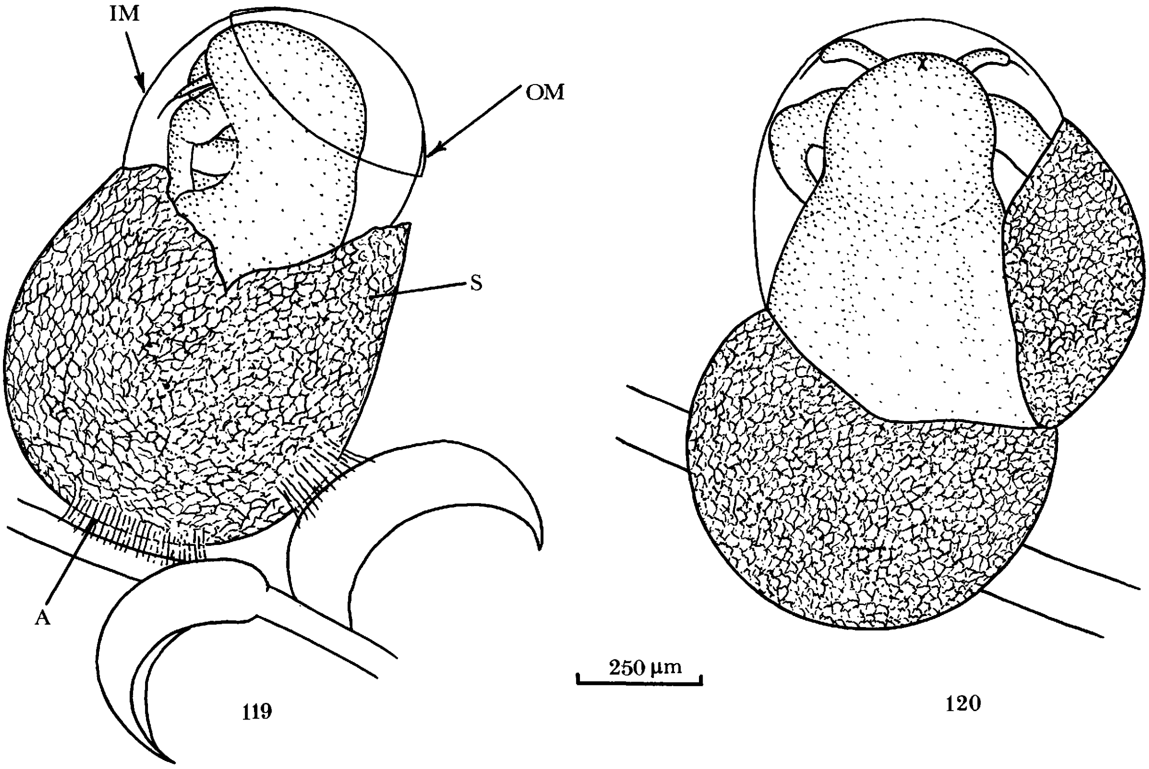
Borgstrøm & Larsson (1974) record that the naupliar stage of their Norwegian animals lived for less than 80 min at room temperature before moulting, whereas Einarsson (1979) reports that Icelandic nauplii moulted after about 1 h, which suggests that earlier workers, all of whom were careful observers, could easily have missed such a transient stage. This I would have done myself in *T. longicaudatus* but for an accident. In warm weather, individuals of this species were recovered from egg-containing mud in a very short time: less than 19 h in one case. These were the equivalent of stage 2 in *T. cancriformis*. Because of the short time involved I would have assumed that these had hatched at this stage had I not earlier obtained nauplii that, perhaps because the ionic content of the water was too low, died, presumably immediately after hatching. These were at the equivalent stage of development to stage 1 nauplii of *T. cancriformis*. This species therefore moults within a very short time of hatching. This is also the case in the population of *Lepidurus apus* studied by Campan (1929) in which the duration of the first instar was 'de quelques minutes seulement'.

Live material of *L. arcticus* obtained from southern Iceland enabled light to be thrown on this matter, provided the opportunity to make observations on the hatching process, and yielded additional ontogenetic data. The remarkable achievements of Schaeffer (1756) are emphasized by the fact that since he observed, and provided a minute illustration of, the hatching egg of *Triops cancriformis*, very little information on the process of hatching in the Notostraca appears to have been recorded. Various workers have hatched eggs in the laboratory but few of them appear to have studied the process. Zaddach, however, (in a thesis of 1841 that I have not seen) apparently refers to it, as, briefly, does Baird (1850), whereas Grasser (1933) provides certain details. The process in *L. arcticus* is somewhat different from that which he describes for *T. cancriformis*. There is no mention of notostracans in the reviews of hatching mechanisms in aquatic invertebrate eggs given by Davis (1968, 1981).

It is often difficult to locate dried eggs among mud. *L. arcticus* eggs are easy to observe. Not only are they relatively large but they will hatch without previous drying. Eggs attached to moss fronds (figure 4) remained dormant for several months when kept at *ca.* 4 °C and dimly illuminated for several hours a day during what would be their normal overwintering period, but began to develop when brought to room temperature. Marked progress in the hatching process was evident within 5 or 6 days when the outer egg membranes (the alveolar layer and its enveloping outer cortex, for convenience called the shell) split and the developing larva could be seen within. Hatching is evidently initiated by osmotic swelling of a fluid-filled capsule bounded by what the process reveals to be the inner of two thin, transparent membranes (figures 119 and 120) that enclose the larva. This ruptures the thick protective shell, sometimes by an irregular split, sometimes by a split that lifts a 'lid', and the capsule expands beyond its limits. It also splits the outer of the thin membranes cleanly on what is evidently a predetermined line of weakness. Part of this outer thin membrane remains within the shell: the other part sometimes sits like a cap on the inner membrane (figure 119) but is often lost.

The arrangement of the shell and membranes appears to be the same as in the resting eggs of other branchiopod orders (see Davis (1968, 1981) for summaries) and the origin of the membranes is probably the same as is the case in *Limnadia lenticularis* (Spinicaudata) (Zaffagnini & Minelli 1970). It is interesting that in the Anomopoda, where the place of the outer shell is taken by the non-homologous protective carapace valves, the same two inner membranes are present and a similar initiation of hatching by osmotic swelling takes place (Fryer 1972).

According to Grasser (1933) the outer shell of the egg of *T. cancriformis* splits and a lid-like



FIGURES 119 AND 120. Hatching eggs of *Lepidurus arcticus*.

FIGURE 119. An egg that has ruptured irregularly. The nauplius can be seen to be enclosed by the inner of two delicate membranes; the outer (OM) has split cleanly and one segment of it sits like a cap on the inner (IM). Note how the sticky layer that invests the egg adheres to the chosen site of oviposition, here a moss leaf.

FIGURE 120. An egg of which the shell has split to give a 'lid'. The cap-like portion of the outer of the two delicate membranes has been lost.

portion is lifted. From it emerges what he describes as 'eine weisslichgraue, schwammige Masse' that he suggests, presumably by swelling, is responsible for the splitting of the egg. No such mass of material has been seen in *L. arcticus*. In *T. cancriformis* the inference is that it forces the developing nauplius, still surrounded by the inner membrane (Grasser refers only to one) out of the shell. Splitting of this membrane takes place shortly thereafter.

As did the eggs of Borgstrøm & Larsson (1974) and Einarsson (1979) the Icelandic eggs produced nauplii. These were seen moving within the egg membrane for about 4 days after the rupture of the egg shell. Nauplii always lay with the anterior end towards the emerging end of the capsule and rotated in either direction about their long axis. Activity is deceptive. It is stimulated by the bright light needed for observation. In dim light larvae show little activity. Whether emergence is due to further swelling of the capsule or activity by the larva is not known.

The bright pink, yolk-packed nauplius that emerges has been illustrated by Borgstrøm & Larsson (1974) and Einarsson (1979). It swims slowly, with but few pauses, by active beating of the antennae. Duration of this stage is brief but sometimes exceeds 2 h.

The nauplius does not feed. Moulted exuviae reveal that there are neither proximal nor distal masticatory spines on the antennae. In this it differs strikingly from the nauplius of *Triops*.

The stage 2 larva, almost 2 mm in length, is illustrated by Borgstrøm & Larsson and by Einarsson. Although in many respects a miniature adult, this stage does not feed. The well-developed antennae lack both proximal and distal masticatory spines (figure 121), the gnathobases of the mandibles are unarmed, widely separated and clearly incapable of handling food, the gnathobasic spine is minute and non-functional, and the palps, although armed with the same complement of spines as are the functional palps of *Triops*, show signs of degeneration (figure 121). Even if the mandibular palps could collect food, there is no means whereby it could be dealt with. The lack of any means of handling food anteriorly is rendered all the more striking by the precocious development of the trunk limbs of which several anterior pairs are active in locomotion, and by the development of the rudiments of food-handling spines and setae on several of the anterior gnathobases and on the maxillules (figure 122).

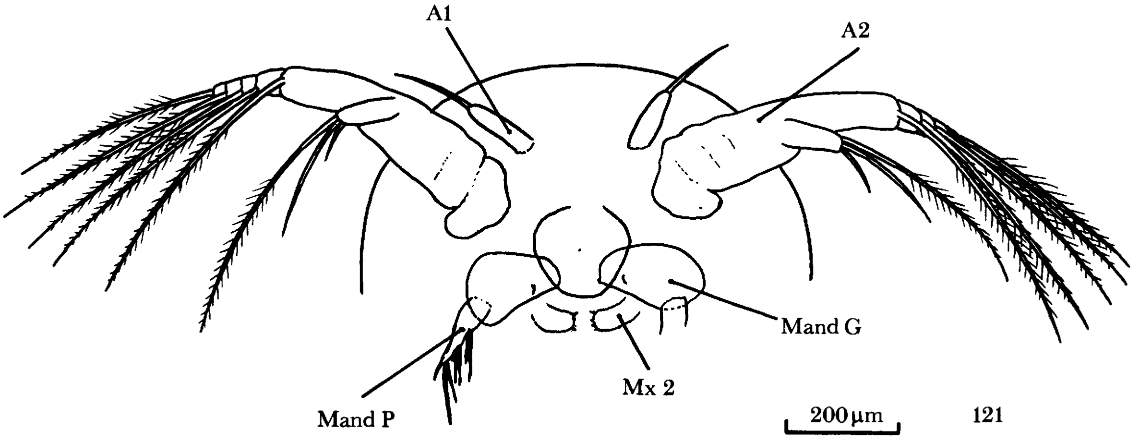
Although in general features the second instar of *L. arcticus* is much more advanced than is that of *Triops cancriformis*, the mandibular gnathobases are at essentially the same stage of development (cf. figures 122 and 105). The primitive anamorphic pattern of development, to some extent disrupted in *Triops*, is even more obscured in *L. arcticus* where the anterior trunk segments and their appendages show precocious development and throw the state of the mandibles, that retain their primitive, slower, rate of development, into sharp relief.

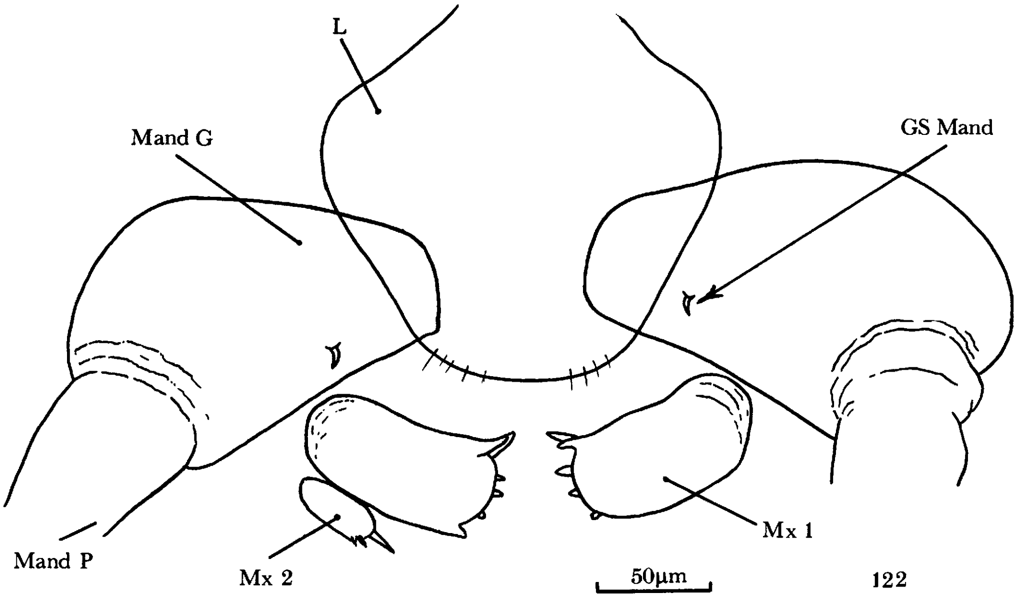
As in earlier stages, in stage 3 larvae, which are essentially miniature adults though the full complement of functional trunk limbs is still incomplete, the antennae are devoid of either proximal or distal masticatory spines. As the larva is now feeding by the adult mechanism, at no stage do the antennae play any part in the feeding mechanism. The mandibles have now developed a masticatory armature, can meet in the mid-line, and function in the adult manner. Their palps are now much reduced, remote from the scene of operations and non-functional, as are the minute gnathobasic spines. Thus at no stage do either the mandibular palps or the gnathobasic spines play any part in the feeding mechanism. The situation during the ontogeny of the feeding mechanism of *L. arcticus* is thus very different from that in *Triops* where antennae, mandibular palps and gnathobasic spines of the mandibles are all involved. In *L. arcticus* there is in fact no naupliar contribution to the feeding mechanism at any stage, though a true nauplius is retained as a transient stage of ontogeny. This is an interesting example of adaptive radiation in the larval stages of organisms that retain many similarities as adults and, as shown by the fossil record, have done so for a vast period of time.

The redundancy of the gnathobasic spines of the mandibles, although apparently trivial, is in fact of considerable interest. Larval *Triops* share the use of such a spine not only with those of the Anostraca but with those of the Devonian lipostracan *Lepidocaris*, so this is clearly a very ancient branchiopod character. In the functional, and well-nigh actual, loss of this character *L. arcticus* thus differs from its close relatives of the genus *Triops* more than do members of that genus from two very remotely related orders of branchiopods.

Stage 4 larvae display enhanced development of the trunk limbs and furcal rami but retain their antennae. The latter, however, appear often to be curved backwards more or less parallel to the margin of the carapace and remain still during locomotion, though they have been seen to beat at times.

These early stages display a very striking dorsal light reaction. Illuminated from above they forage ventral surface down. If they are illuminated from below they promptly turn over and swim inverted, to return to the normal posture as soon as the source of illumination is again reversed. It is in inverted larvae that beating of the antennae has been seen.





Figures 121 and 122. *Lepidurus arcticus.*

Figure 121. The 'naupliar' appendages of a stage 2 larva. Note the absence of any proximal or distal masticatory spines on the antennae, the minute gnathobasic spines of the mandibles (see figure 122 for details) that are clearly incapable of handling food, and the degenerate nature of the mandibular palps – directed somewhat towards the observer and therefore slightly foreshortened – (cf. *T. cancriformis*, figure 105).

Figure 122. The mandibular gnathobases and maxillules of a stage 2 larva. Note the precocious development of the latter and that the mandibles are clearly non-functional at this stage. The minute gnathobasic spines of the mandibles (GS Mand) contrast strikingly with their conspicuous homologues in *T. cancriformis* (figure 105).

A further example of larval adaptive radiation is displayed in the development of a hedgehog-like array of stout spines on the abdomen and of robust denticles in the sulcus region of the carapace of the early stages. Abdominal spines are evident in stage 2 and are very prominent by stage 3 (figure 123) whose furcal rami are also armed with spines. This formidable armature is probably related to life in habitats where enemies are to be

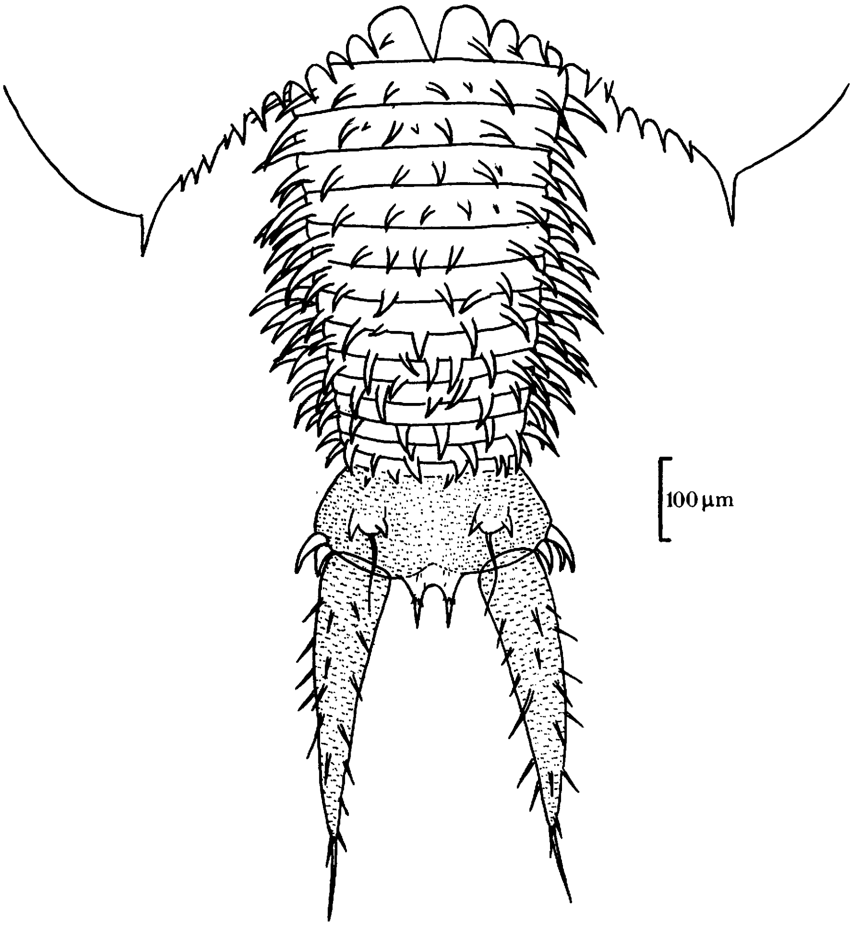


FIGURE 123. *Lepidurus arcticus*. Abdomen and sulcus region of carapace of a stage 3 larva, dorsal, to show the massive protective armature of spines present during the early stages of development (compare with the adult condition: figures 2 and 3).

encountered. Although such spines will be useless against fishes (small size and bottom grubbing habits probably being more helpful to early instars) they will clearly be protective in the face of attacks from such predators as insects and large cyclopoid copepods, which, by their abundance, are probably major enemies. Temporary-pool dwellers do not have to face such hazards. Swimming without the use of the antennae, whose beating takes them beyond the limits of the protective carapace thus rendering them vulnerable, is also a possible protective mechanism.

The problem remains as to whether in some populations of *L. arcticus* the eggs hatch at an advanced stage, omitting the nauplius. Johansen (1912) observed overwintering eggs and describes how 'a small *Apus* young, very like the adult, is formed inside', and refers to being able to distinguish such characters as the carapace, which appears to confirm what he says. Indeed he specifically emphasizes that when the eggs hatch as the ice melts 'the characteristic fry of the year are found' and that the larva in question is 'a kind of metanauplius' † and that 'the free-swimming nauplius is thus wanting in *Apus glacialis*' (= *L. arcticus*).

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† 'Metanauplius' is a vague term that has been mis-used in ways that lead to confusion. Borgstrøm & Larsson (1974) and Einarsson (1979) both use the term when nauplius is implied. The larva so named by Johansen is also ill-designated.

It is relevant, however, that in nauplii still within the egg membrane, seen from the side, the outline of the developing carapace can be made out beneath the naupliar cuticle, a point already noted by Borgstrøm & Larsson (1974) and seen also in *Lepidurus apus* by Brauer (1874), and it is conceivable that this is what was seen by Johansen.

Nevertheless, Johansen may have been correct and there may be different races or populations of *L. arcticus* with different patterns of development. The elimination of the transient nauplius by moulting within the egg would be a very small step. This would be in keeping with the existence of small morphological differences between larvae from Greenland described by Poulsen (1940) and from Norway studied by Borgstrøm & Larsson (1974) to which the latter authors draw attention.

Differences in the pattern of development in populations currently attributed to *L. apus* are indeed evident from the literature. The early development of this species was described with some care as long ago as 1874 by Brauer from German material, and more recently by Campan (1929) using animals from southwest France. In both cases the eggs hatched as a nauplius, but whereas the second stage of Brauer's population showed but a small advance on the first, that of Campan's population moulted into a much more advanced larva 'qui a déjà une forme d'Apus typique', which he illustrates, and which appears to be at the same stage of development as that at which some believe *L. arcticus* to hatch, and the equivalent of stage 2 in populations of that species in which a nauplius is present.

It is evident that the taxonomy of the Notostraca calls for further investigation and that, as Borgstrøm & Larsson (1974) remark, larval characters may prove important in this respect. What is already clear is that there has been considerable adaptive radiation in the larval stages and that, from a functional point of view, the larvae of, for example, *Lepidurus arcticus* and *Triops cancriformis*, differ from each other far more than do their respective adults.

13. THE MANDIBLES OF THE EARLY STAGES AND THEIR MUSCULATURE

Gross features of mandibular development are noted in §§11 and 12. An outstanding attribute of the adult mandibles of the Notostraca is the absence of 5c muscles. These muscles are present in adults of all other extant branchiopods investigated. Here, unlike the rest of the transverse series that originate on the transverse mandibular tendon, they unite the posterior margins of the mandibles and, in effect, comprise continuous bands of muscle between the two mandibles (e.g. see figs 18 and 19 in Fryer (1963)). In fact each originates on a tiny fibrous sheet in the mid-line and pulls against its partner, the rigidity of the insertion depending on mutual antagonism.

It would be tempting to correlate the lack of such muscles in adult notostracans with the ability of the mandibles to abduct widely, also a unique attribute of the group among the branchiopods. However, 5c muscles are present in the early stages of development (figures 125 and 129, and see below), and these stages are also capable of wide abduction of the mandibles. The presence of these muscles as part of a complement that already shows the adult arrangement (figures 124–129) is clearly not incompatible with wide abduction and the reason is easy to see. The 5c muscles are located dorsal to the rest of the transverse mandibular series. Thus, when the abductors contract, and the mandibles in effect pivot about the ends of the transverse mandibular tendon, the 5c muscles are no impediment to this movement. They possibly contract slightly during this process to obviate flaccidity. Their contraction towards

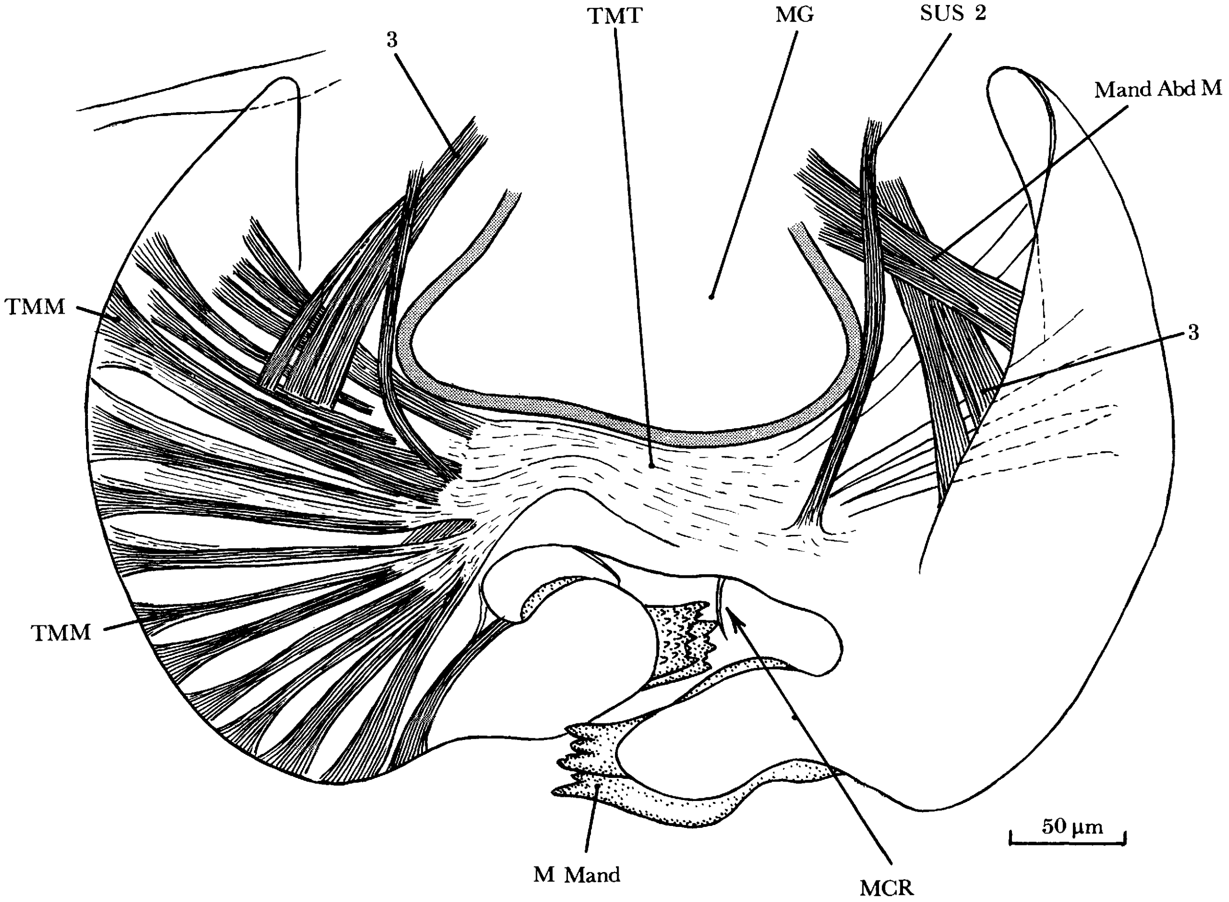
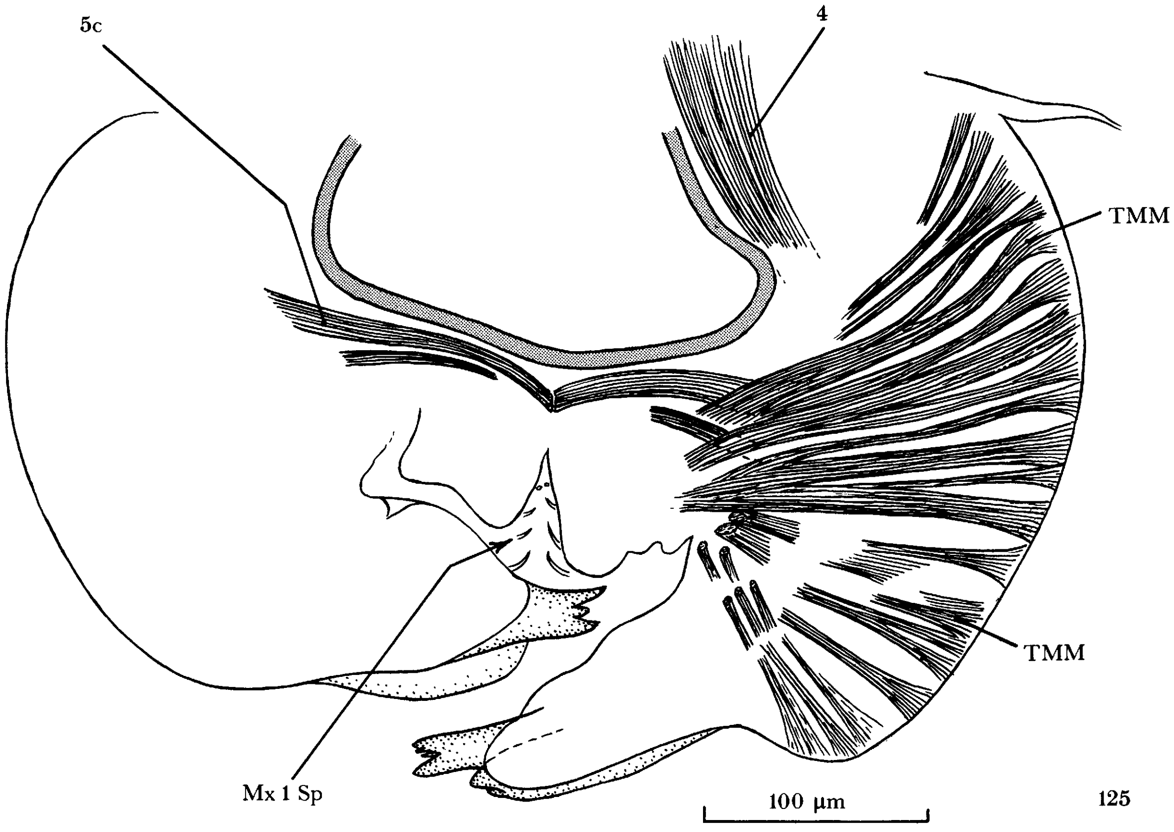


FIGURE 124. *Triops cancriformis*. Transverse slice through the anterior region of the mandibles of a young individual (about stage 8), showing the major muscles at this level. Note the well-developed abductor (Mand Abd M). The transverse mandibular tendon (TMT) has buckled during fixation, pulling the distal portion of the right mandible out of position. In life its armature faces that of the left mandible.

the end of the adduction phase will help to give an additional 'bite' to the posterior teeth of the mandibles.

No attempt has been made to study the muscles of the earliest naupliar stages that are much obscured by yolk. As skeletal features and mandibular action are the same in all early stages subsequent to that at which they become functional, this presumably applies also to the muscular system. Muscles of the 5c series are therefore almost certainly present from the outset and involved in mandibular movement from the time this begins. They are present in stage 3 larvae of *T. longicaudatus* and are seen in a stage 4 larva of that species in figure 116, and in later stages of *T. cancriformis* in figures 125 and 129. In *T. longicaudatus* the orientation of the mandibles is markedly oblique in the early stages. Although, in preparation for their subsequent function they are already coarsely toothed, the teeth are armed with needle-like spines (figure 117) that will inevitably help them to handle the minute particles that compose much of the diet at this stage, yet clearly do not prevent the uptake of larger, but still very small, items that have been seen in the gut. The oblique orientation of the mandibles may also improve their efficiency at passing minute particles forward. The mandibular armature is different from that of *T. cancriformis* at stages 3 and 4 (figures 106 and 107): an interesting example of divergence in a larval character.



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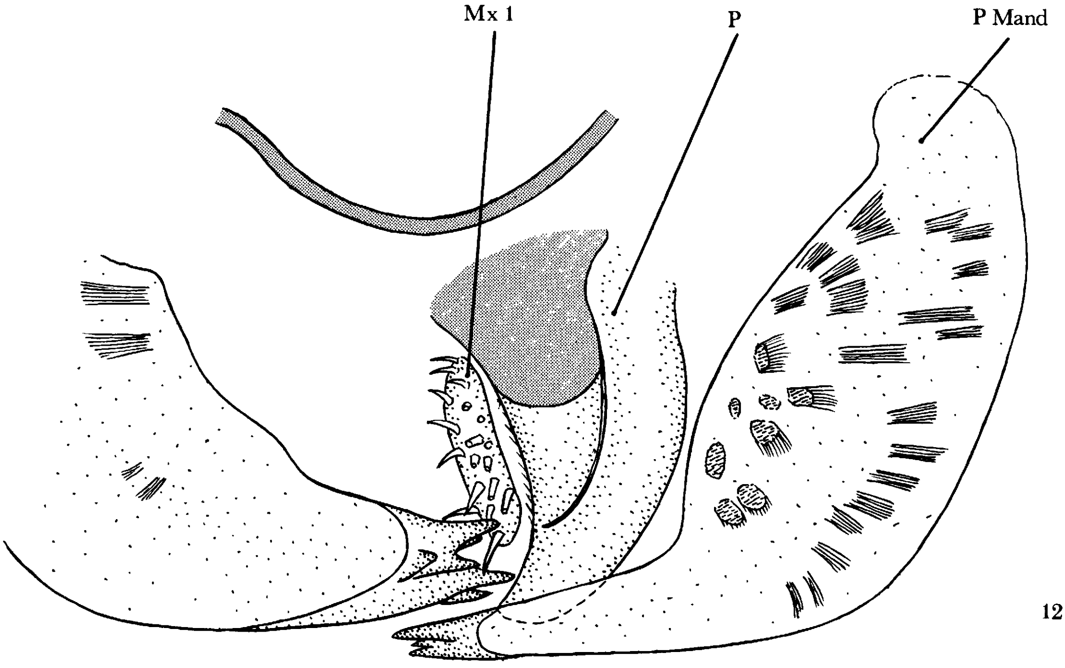

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FIGURES 125 AND 126. *Triops cancriformis.*

FIGURE 125. As figure 124; a slice towards the posterior margins of the mandibles to show especially the well-developed 5c muscles, present in the juvenile stages but not in the adult.

FIGURE 126. The same, at the level of the extreme posterior limits of the mandibles. Some ventral spines of the maxillule omitted for clarity. This and the two preceding figures reveal the biting nature of the juvenile mandibular armature.

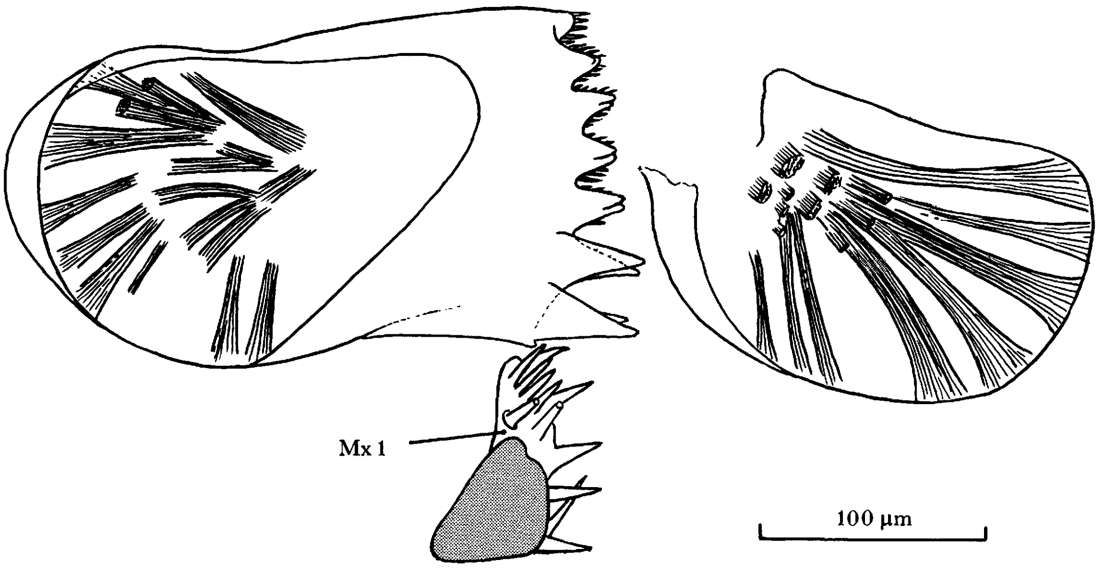
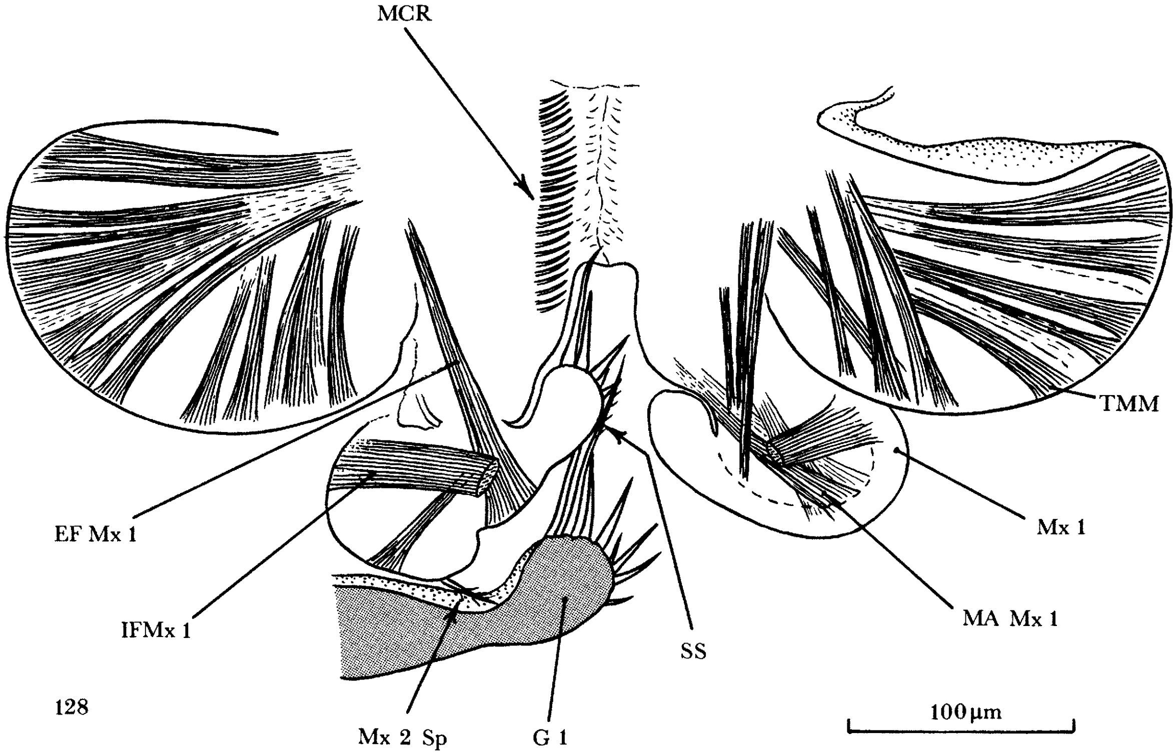


Figure 127. *Triops cancriformis*. Horizontal slice near the extreme ventral part of the mandibles of an individual at about the same stage as that shown in figures 124–126; ventral. The armature of the right mandible inclines dorsally (i.e. deeper into the plane of the paper) towards its anterior end (see figure 118). Note the powerful development of the two posteriormost toothed ridges. The distal portion of the right maxillule (Mx1) is seen. The denticles seen are those that perform biting actions.

The possession of 5c muscles is clearly an ancient branchiopod character, and their presence in larval notostracans, although it could not have been predicted from the adult condition, raises no phyletic difficulties. There remains, however, the problem why, if the possession of 5c muscles is not incompatible with mandibular abduction, they should be lost in the post-larval stages? Although they cannot be proved, two suggestions can be made. The most obvious is that, in adult notostracans, the demands of adduction–abduction biting are greater than those of mandibular swing, which can be coped with adequately by the obliquely directed muscles of the transverse mandibular series. The 5c muscles may indeed have become redundant yet persist almost as vestigial organs in the early stages of ontogeny.

A further possible factor is that the presence of 5c muscles, which are located dorsal to the transverse mandibular tendon, inevitably restricts the space available for the midgut. This is no problem in branchiopods feeding on fine particles in which there is no need for the midgut to be wide at this point. This can be seen, for example in *Eurycercus* (Anomopoda) (Fryer 1963, figure 18) which shows very nicely how the diameter of the midgut is often constrained by the 5c muscles in anomopods, and in a juvenile *Branchinecta* (Anostraca) (Fryer 1983, figures 51–53, plate 1) which shows that the available space is not fully occupied by the midgut. By contrast, in the Notostraca, that ingest large food items, the midgut is expansive in this region (figures 63, 87 and 88) and abuts against the transverse mandibular tendon. The situation is the same in *Triops* and in *Lepidurus*. Were 5c muscles to be present, the gut could not be so wide. The advantages of the space gained may therefore amply compensate for the loss of these muscles that may in any case have been rendered redundant after the assumption of feeding habits that involved biting rather than swinging mandibles. The restriction on space imposed by 5c muscles may be no impediment in the early stages that feed on finer particles.



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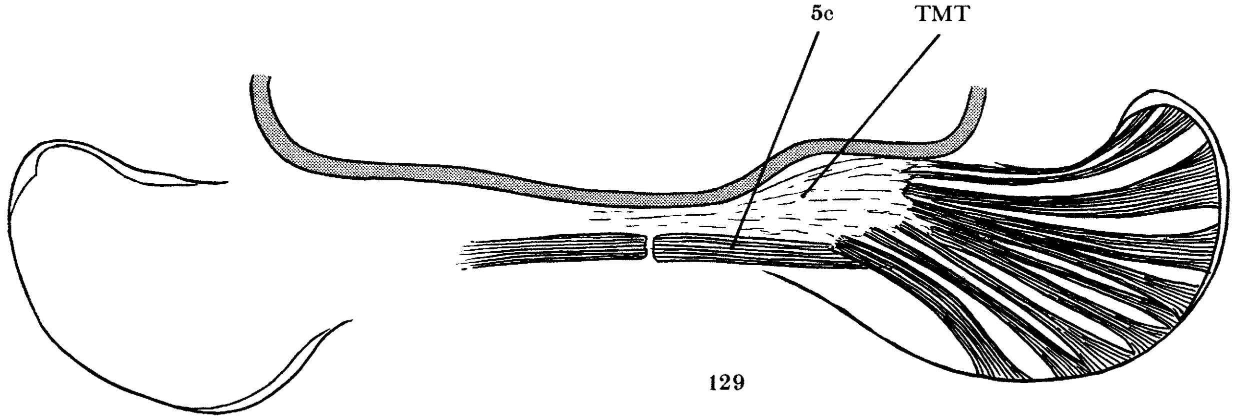

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FIGURES 128 AND 129. *Triops cancriformis.*

FIGURE 128. As figure 127, more dorsal. The roof of the atrium oris just posterior to the oesophagus is seen. Not all the muscles of the maxillules can be seen at this level.

FIGURE 129. The same, more dorsally, showing the well-developed 5c muscles.

A possible argument against the need for space in this region by the gut of notostracans is that large adults of the anostracan *Branchinecta ferox* are carnivores but retain massive 5c muscles. Their mandibles, however, are of the crushing and rolling type whose effective swing is highly dependent on the 5c muscles, that could scarcely be sacrificed without serious loss of efficiency. Here too the much crushed food is probably restricted to relatively soft-bodied prey (Fryer 1983).

To ascertain the stage at which the 5c muscles are lost would involve much section cutting for a trivial reward and has not been attempted. The timing of the event is of no great significance and is perhaps contemporary with the disappearance of the antennae.

14. A NOTE ON LARVAL ANTENNAL SETAE

The antennae of larval *Triops cancriformis* have five natatory setae on the exopodite, three on the endopodite, a number that never increases as development proceeds. At no stage do these setae have a hinge or articulation about half way along their length, and they lack setules. All examined larval stages of *T. longicaudatus* and *Lepidurus arcticus* also have antennal setae that lack a hinge, and the illustrations of Campan (1929) show that this is so also in *L. apus*. A hinge on the antennal setae was noted by Sanders (1963) as characteristic of branchiopod nauplii, setting them apart from those of non-branchiopods. The difference is, however, clearly not diagnostic (though it does not nullify the distinction drawn by Sanders between the two categories of nauplii) for unjointed setae occur also in the nauplius of the anostracan *Branchinecta ferox* (Fryer 1983).

Like those of *T. cancriformis*, each antennal exopodite of *L. apus* and *L. arcticus* (figure 121) bears five setae. In at least the population examined, those of larval *T. longicaudatus* bore seven setae. Moreover, although in *T. cancriformis* the setae lack setules, their homologues in the other three species are setose, though sparsely so in *T. longicaudatus*. There has clearly been some radiation here in the larval stages. At a practical level this supports the suggestion of Borgstrøm & Larsson (1974) that larval characters may prove useful in taxonomy.

As the antennal setae are natatory in function, the absence of setules in *T. cancriformis* is perhaps surprising. Such setules are lacking on the natatory setae of the antennae of the nauplius of the anostracan *Branchinecta ferox* (Fryer 1983) but are of extremely wide distribution on natatory setae throughout the Crustacea.

15. LARVAL SWIMMING IN *TRIOPS*

Because of their small size the naupliar and early post-naupliar larvae of the Notostraca live in a viscous medium (a low Reynolds number environment) through which they lever themselves using viscous forces. They acquire scarcely any momentum and inertia is scarcely relevant. The consequences of such physical constraints on the movements of anostracan nauplii are described elsewhere (Fryer 1983). Similar constraints are operative in the lives of the early larval stages of the Notostraca, whose nauplii and, in *Triops*, several succeeding stages, like those of the Anostraca, row themselves through the water by a single pair of appendages, the antennae. In *Lepidurus* precocious development of the trunk limbs leads to early adoption of the adult means of locomotion, supplemented initially by a contribution from the antennae. Locomotion of the naupliar, and more specifically the early post-naupliar, stages of *Triops* is considered here.

Progression in these early stages is achieved entirely by swimming. The process is basically the same as that described for larval Anostraca (Fryer 1983) but certain differences call for comment. The early development of a carapace and, in relation to the Anostraca, the precocious development of the trunk limbs, quickly change the shape of the early instars. In *T. longicaudatus* feeble movements of the anteriormost of the rudimentary trunk limbs are evident in stage 3 larvae but probably make no contribution to propulsion. By stage 4 in this species, by which stage the animal has a length of *ca.* 1.2 mm, more positive movements of the trunk limbs take place and, although these appendages are still very minor contributors to propulsion, their activity is synchronized in a functional manner with the beating antennae that continue to serve as the major organs of propulsion. At room temperature the antennae of stage 4 larvae beat at about 5.5–6.0 cycles s^{-1} during steady swimming but the rate varies according to circumstances (see below).

A cycle of movement in a stage 4 larva whose antennae are beating at *ca.* 5.6 cycles s^{-1} is shown in figure 130. The outlines are based on projected individual frames from a cine film but do not purport to reveal trunk limb movements in detail. As the animal swims ventral surface down the trunk limbs can only be seen through the carapace. Also, to film swimming over a reasonable distance while the animal was in the field of view, low magnifications had to be employed. Projected individual frames therefore reveal only indistinct outlines of the limbs, though such movements as they make are readily seen when the film is run, and some side views of trunk limb movements were also recorded. In the diagrams therefore only the general outlines of the anterior trunk limb rudiments are shown. Posterior limb rudiments, which are immobile at this stage, are indicated schematically.

At *a* the antennae are just beginning their backward swing, the power stroke, which, in straight swimming, they do in perfect synchronization. At this stage the trunk limb rudiments are bunched together posteriorly. As the antennae swing posteriorly they are extended ('straighten out') and rotate (*b*) so as to allow the armature of setae of both exopodite and endopodite to present a large area in a plane more or less vertical to the long axis of the body. The swing of the antennae propels the larva forward, the distance covered between positions *a* and *b* being indicated by the length of the arrow adjacent to *b*. The time interval between *a* and *b* is 40 ms, (see also figure 131). As the antennae continue to swing posteriorly (*c–e*) propelling the animal forward, the anterior trunk limbs, especially the first pair, to a less extent the second, and to a minor extent the third pair, swing forward. At this stage the limbs are rudimentary and their forward swing probably detracts but little from the propulsive power developed by the antennae, but it is significant that they move forward during that phase of the antennal cycle of movement during which maximum power is developed. Notwithstanding any retarding influence of the forward swing of the trunk limb rudiments, the distance moved between *b* and *e* in 30 ms is appreciably greater than that moved between *a* and *b* in 40 ms. By the time the antennae are approaching their posterior limits of swing (*f*) their angle of attack has changed to one that gives less effective thrust, and this is reflected by a slowing down of forward movement (see arrows and also figure 131). Shortly thereafter (*g*) the antennae have more or less reached their posterior limits of swing and forward motion has virtually ceased. At this stage the exopodites have begun to flex into a distinct arc, whose convex surface is to the outside. The trunk limbs are now approaching the limits of what will eventually constitute their recovery stroke.

The antennae then begin their recovery stroke (*h*). Notwithstanding the fact that during this phase of the cycle the exopodites remain curved with the leading margin convex, thus reducing drag (exactly as in the Anostraca), and although the trunk limbs begin their posterior swing – the working stroke – the larva not only ceases to move forward but actually moves backward to a slight extent. This is the result of the force exerted by the recovering antennae. The power stroke of the rudimentary trunk limbs is clearly negligible at this stage but must inevitably reduce the backward component of motion to a slight extent.

Coordination of the movements of the appendages continues as the antennae, their

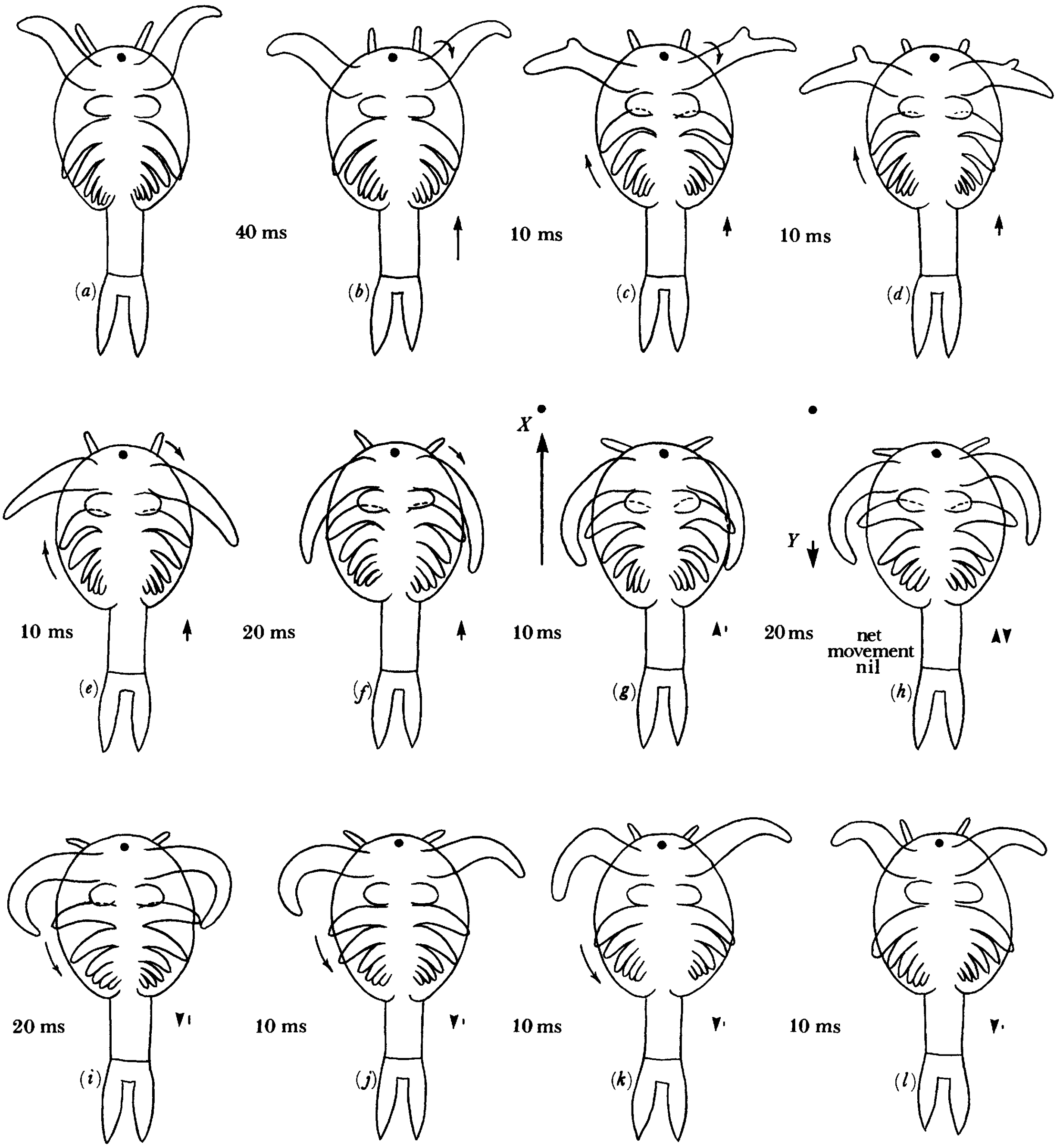
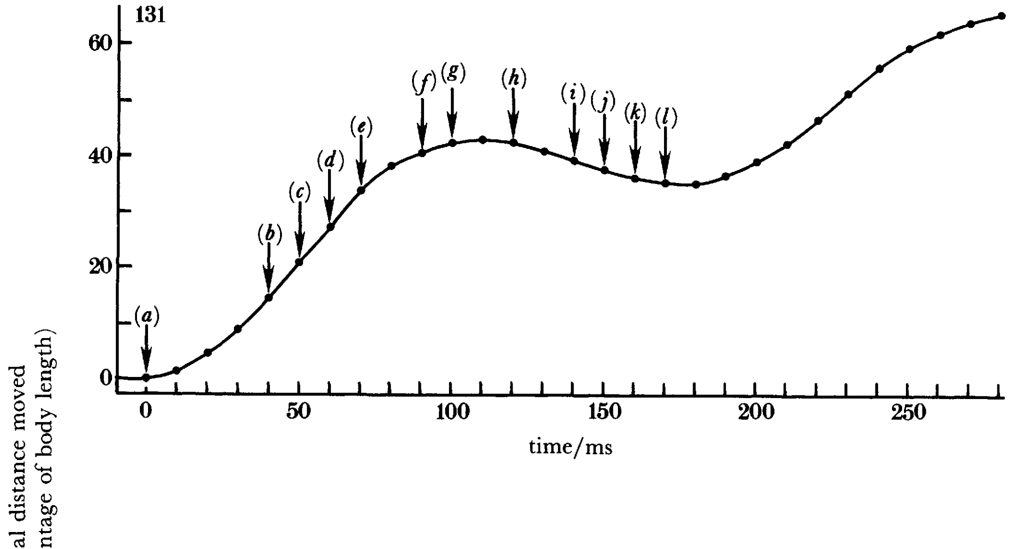


FIGURE 130. *Triops longicaudatus*. Swimming in a stage 4 larva (length *ca.* 1.2 mm). The figures are simplified outlines, made from cine film, of a complete cycle of locomotory activity in a larva swimming horizontally, ventral surface down. The carapace, which overlies the appendages, is shown as if transparent except in the case of the antennules of which, for convenience and simplicity, only the distal portion is shown. The natatory setae and distal 'masticatory' spines of the antennae are omitted. Vertical arrows indicate the distance and direction moved from the previous position. When the distance is less than the length of the arrow head used, direction is shown by the arrow head, distance by the adjacent line. Time intervals between positions (not the same in each case) are also shown. The arrowed line *X* (at *g*) shows the total forward movement: the adjacent spot reproduces the position of the antennal tip at the beginning of the cycle (position *a*). Arrowed line *Y* (at *h*) shows the total posterior movement of the larva during the recovery stroke of the antennae: the spot indicates the point to which the antennae have to reach during the recovery stroke (equivalent to that shown at *a*). For details see text. See figure 131 for a graphical representation of this cycle.



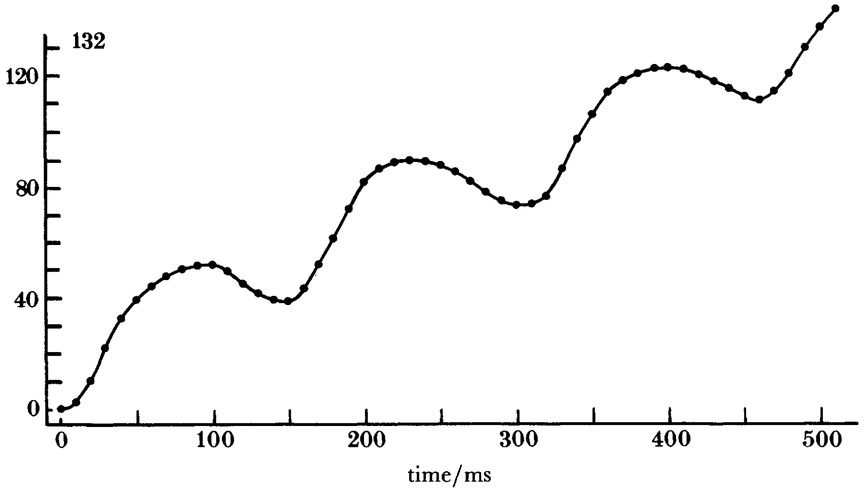


Figure 131. *Triops longicaudatus*. Progression in a stage 4 larva swimming horizontally, ventral surface down, at room temperature, throughout the same cycle of movement of the antennae, as illustrated in figure 130. Rate of antennal beat about 5.6 cycles s^{-1}. The points on the curve were obtained by plotting at intervals of one frame the location of the anteriormost point of the body from greatly enlarged images cast by a film made at 100 frames s^{-1}. Lettering of the arrows corresponds with that used in figure 130.

Figure 132. *T. longicaudatus*. Progression in a stage 4 larva (conditions as in figure 131) throughout three consecutive cycles of antennal beating at about 6.5 cycles s^{-1}.

exopodites markedly flexed into arcs, (*i,j*) continue the recovery stroke. During this phase of the cycle the trunk limb rudiments continue their working stroke and are approaching their posterior limits of swing as the antenna approach their anterior limits (*k*). As the cycle nears completion (*l*), the antennal exopodites are extended as the trunk limbs 'pile up' posteriorly. Throughout the recovery phase of antennal movement the larva moves steadily backward (figure 131), ceasing to do so as the antennae reach full extension before the backward swing.

In straight swimming the antennae move in near perfect unison. In the cycle illustrated there is a slight degree of asymmetry (not asynchrony), perhaps in response to some stimulus, which is instructive. It illustrates that the mechanism is not rigidly stereotyped but can be adjusted according to need, as is essential for changing direction.

The antennules are directed anteriorly during forward movement. This is the most advantageous position for sensing the environment and one that can be afforded in such a small organism where streamlining is relatively unimportant. As the antennae approach the end of their propulsive stroke the antennules begin to swing posteriorly. This is a positive, not a passive, swing though the contribution to propulsion must be negligible. They return to an anteriorly directed position as the antennae make their recovery stroke.

In the cycle illustrated the rate of antennal beat was about 5.6 cycles s^{-1}. Gross forward movement was about 42 % of the body length, the backward movement during the recovery stroke of the antennae about 8.5 % and net forward progression about 34 %. The next cycle was virtually identical. At other times the same larva moved more quickly. Over three consistently paced consecutive cycles (figure 132) the rate of antennal beat was *ca.* 6.5 cycles s^{-1}. Both forward and backward components of movement were greater (*ca.* 52, 51 and 49 %, and *ca.* 14, 16 and 12 % of body length respectively in the three cycles) and net forward progression was slightly greater (*ca.* 38, 35 and 37 %) than at the slower rate of antennal beat. Net forward progression was at a speed slightly below 3 body lengths s^{-1}. In nature, unimpeded swimming is probably sometimes at speeds slightly faster than this at similar temperatures.

These speeds are a little slower than those of stage 4 larvae of the anostracan *Branchinecta ferox* which achieves between *ca.* 3.6 and 4.4 body lengths s^{-1} (Fryer 1983) and both are much slower in relation to body length than adult chydorid cladocerans of many species that also use a single pair of antennae as oars (Fryer 1968), though these animals are somewhat smaller (usually less than 1 mm in length). The presence of a carapace may be an impediment to *Triops* not suffered by anostracan larvae, but in such small animals streamlining is less important than in large.

As in anostracan nauplii, the dimensions of these small notostracan larvae are such that water effectively constitutes a viscous medium through which the antennae lever rather than propel. Absolute backward movement by the antennae during a cycle of movement is therefore small. This was shown in a graph for *Branchinecta ferox* (Fryer 1983) and can be appreciated in respect of *Triops* from information given in figure 130. Subtraction of the distance moved by the larva from one position to the next (shown by arrows) from the axial distance moved by the antennal tip in the same time, shows how little is the latter.

Summation of the total distance moved forward is indicated by the arrow *X* at position *g*. Its posterior end is aligned with the level of the antennal tip. Comparison of the level of the point of this arrow with the level of the antennal tip at position *a* (also indicated by a spot at *g*) shows how short is the axial distance travelled by the antenna on its backward swing. Contrariwise the long forward reach of the antennae during their return stroke in relation to the axial distance moved posteriorly is readily appreciated by comparing the length of arrow *Y*, representing a summation of posterior movement, with the distance that the antennae have to reach forward from about the position shown at *h* to that depicted at *a*, (also indicated by a spot at *h*).

An important distinction between the naupliar and early post-naupliar stages of the Anostraca and Notostraca is that whereas in the former the antennae serve not only as organs of locomotion but as collectors of food (Fryer 1983), in the latter they serve for locomotion only. Here food collection is either the responsibility of the mandibular palps (*Triops*) (§11), or does not begin until the precursor of the adult mechanism becomes operative (*Lepidurus*) (§12).

16. FUNCTIONAL AND ONTOGENETIC DIFFERENCES AND SIMILARITIES IN THE EARLY STAGES OF THE NOTOSTRACA AND ANOSTRACA

It is now possible to compare the early developmental stages of the branchiopod orders Notostraca and Anostraca more precisely than hitherto. As the differences are of phyletic interest, a brief summary is presented.

Although there are deviations in some notostracans (*Lepidurus*), these are clearly secondary and the basic developmental sequence of both orders is anamorphic: eggs hatch as nauplii that gradually change in form by the addition of segments at each moult. Certain anostracans display this undoubtedly primitive sequence at its simplest level. Thus *Branchinecta ferox* develops over a long series of moults, adding segments and appendage rudiments very gradually. Even at instar 11 only the three naupliar appendages are functional and after each subsequent moult usually only one pair of trunk limbs becomes functional per moult (Fryer 1983). Although some anostracans make greater advances than this at each moult, even these are less than is usual in the Notostraca, as exemplified for example by *Triops cancriformis*. In this respect therefore, the Anostraca is to be regarded as retaining a more primitive pattern than the Notostraca.

Moreover, at least one notostracan, *Lepidurus arcticus*, departs from this pattern, as apparently do some populations of *L. apus*. In adequately studied populations of *L. arcticus* or the species complex to which it belongs, the nauplius is retained as a transient stage that quickly moults into a much more advanced larva, a step involving the condensation of several stages of the more primitive sequence (§12). (In other populations it is possible that the nauplius may have been eliminated and that even further telescoping of development has taken place but confirmation is desirable.) Such a series of developmental pathways in closely related animals of similar adult morphology shows with almost diagrammatic clarity how metamorphosis can be introduced into an originally anamorphic life cycle.

The accelerated development of the Notostraca *vis-à-vis* the Anostraca is shown particularly in the transient nature of the naupliar stages as collectors of food (when they do so at all), by the early development of biting modifications of the mandibles, the early incorporation of functional maxillules into the food handling apparatus, and the rapid takeover by the adult trunk-limb food-collecting device. The assumption first of predominant, then of complete, responsibility for locomotion by the trunk limbs also takes place at a much earlier stage of development, and in larger increments, than in the Anostraca: as early as stage 2 in adequately studied populations of *L. arcticus*.

Except in *L. arcticus* (and probably some races of the *L. apus* complex) both orders have feeding nauplii, though the first nauplius does not feed. The feeding mechanism utilized by each is, however, very different. In the Anostraca food particles are collected by distal masticatory spines of the antennae; in the Notostraca by the mandibular palps. In this respect the Anostraca are similar to the conchostracan orders Spinicaudata and Laevicaudata and to the extinct Lipostraca, and differ markedly from the Notostraca.

A shared similarity of the nauplii of the Anostraca, Lipostraca and conchostracan orders is the possession by each of a large fleshy labrum. In the Notostraca the labrum is small and plate-like.

Notwithstanding these striking differences there are certain similarities between the early stages of anostracan and notostracan development that can only be regarded as deep-seated and indicative of remote common ancestry. The employment by both (except when secondarily lost) of a proximal masticatory spine on the antenna may be one, but copepods and barnacles employ such, which means that this structural feature is of little precise phyletic significance, though (unless independently acquired several times) it suggests that it is an ancient attribute of the crustacean nauplius. The bifid nature of the proximal masticatory spine, displayed to varying degrees by at least some representatives of both orders, is perhaps also an ancient similarity but could have been convergently acquired by homologous structures. The possession of a gnathobasic spine on each mandible is an important shared attribute: a synapomorphy in the language of the cladist. Particularly informative is the way in which, in the Anostraca and at least some notostracans, for the duration of a single instar, the mandibular gnathobases lack masticatory armature and sweep food forward by means of the gnathobasic spines alone.

Another shared feature is the pattern of armature of the mandibular palp of the nauplius. This, shared also with the Lipostraca, is an extremely conservative character whose proven persistence for at least 300 Ma is, at this level of morphology, perhaps unparalleled in the entire animal kingdom. Although it indicates the persistence of long-established ontogenetic processes, subtle differences in morphological detail in the different orders reveal how such an ancient attribute has been adapted to different ways of life and different feeding mechanisms during the course of branchiopod evolution.

These indications of a probable ancient common ancestry are in keeping with the demonstration by Dahl (1959) that, in spite of great topographical differences, the ontogeny of the protocerebral sense organs in many respects follows the same pattern in the two orders. In some cases, so far as comparative data are available, these similarities are not shared with, for example, the Malacostraca. The origin of the cells that make up the distal part of the ganglion opticum of the compound eye are a case in point. They originate largely or entirely from the proliferation zone in both the Anostraca and Notostraca; from the brain in the Malacostraca.

17. The position of the Notostraca among the Branchiopoda

The relationships of the Notostraca to other branchiopods have been interpreted in different ways by different workers. Most have recognized the group as a well-defined order, but this has been challenged by Preuss (1951) whose classification was followed, and apparently in part supported, by the work of Elofsson (1966) on the nature of the nauplius eye and frontal organs. As a revised classification of the branchiopod orders has recently been proposed (Fryer 1988), and as it is hoped eventually to discuss their affinities, the only point that is made here is that the present study has emphasized the isolated nature of the Notostraca. Contrary to the proposal of Preuss (1951), it does not support its close association with the so-called Diplostraca (= Onychura), a taxon that I believe to have no phyletic standing. According to Preuss, the Anostraca is the most isolated order of the Branchiopoda. Indeed, in setting the Notostraca apart from what he regarded as constituting the Anostraca, he relegated it to a suborder of what he designated as the order Phyllopoda, comprising the Notostraca and Onychura (= Diplostraca).

There are in fact profound differences between the Notostraca and all the component groups of the so-called Diplostraca, which is in fact a polyphyletic assemblage of great heterogeneity. These, which involve very different functional complexes (e.g. locomotion of adult notostracans is exclusively by means of the trunk limbs and does not involve the antennae) greatly outweigh the similarities between them and, for example, the conchostracan orders to which Elofsson (1966) drew attention. Members of the latter in fact differ among themselves in the nature of the attributes discussed by Elofsson, and in ways that cut across the relationships of its component groups. In considering single systems, such as the naupliar eye and frontal organs studied by Elofsson, with whom Anadón & Anadón (1980) are in disagreement on certain points, one may be concerned with attributes that, like the pattern of setal armature on the naupliar mandibular palp or, apparently, the form of the spermatozoa (Wingstrand 1978), may have persisted for a vast period of time in organisms that have diverged in other ways. Alternatively, such systems may have diverged at an early stage of their evolution. Some systems may have followed one of these evolutionary pathways; others the other. Thus the evidence provided by the naupliar eyes of the Anostraca and Notostraca, taken alone, would point to a different conclusion from that provided by their naupliar mandibular palp. Further, systems such as these, where scope for divergence and radiation is limited, are probably less useful guides to affinity than are functional complexes that involve a whole series of organs. Here, however, the only point made is that the Notostraca is a well-defined group, separated by many trenchant characters from other groups of branchiopods, and probably has stronger claims than the Anostraca to be regarded as the most isolated of the extant, and adequately known extinct, branchiopod orders. Its distinctive features include not only gross form, including the dorsal carapace, and a telson and caudal rami unlike those of any other extant branchiopod, but distinctive, paired, sessile eyes; mandibles, maxillules and maxillae different from those of other branchiopods (where a common pattern is widespread), and trunk limbs that are equally diagnostic and more numerous than in any other order. They extend also to such minutiae as the nature of sensillae. It is worth noting that both Cannon (1933) and Eriksson (1934), who studied branchiopods from comparative and functional standpoints, also independently concluded that the Notostraca occupies an isolated position within the group.

Notostracans, although primitive, may be less so than anostracans. Structurally they display greater elaboration. For example the differentiation of the trunk limbs along the series contrasts with the serial uniformity of anostracan trunk limbs; the mouthparts are more elaborate, both the mandibles and maxillules being able to bite in ways not paralleled in other branchiopods and involving the development of unique muscles, and there is employment of apodemes that are unknown in the Anostraca. The development of sensillae on the trunk limbs also far outstrips in complexity that of anostracans. In their feeding mechanisms they are more versatile than the Anostraca. In addition, in development they depart, often markedly, from the primitive anamorphic pattern that is shown almost to perfection by certain anostracans.

Only the kind collaboration of colleagues and friends enabled the material for this study to be obtained. Preserved specimens of *Lepidurus apus* from Israel and Australia were provided by

Dr C. Dimentman and Dr P. S. Lake respectively, and of *Triops granarius* from South Africa by Mrs N. R. Rayner and Dr Elaine Robson. I am particularly grateful to Dr Maria Miracle for sending to me dried mud from Spain and Dr D. Belk for sending similar material from the U.S.A. from which I hatched *Triops cancriformis* and *T. longicaudatus* respectively. Neither mud nor eggs sent from the F.R.G. by Professor N. Rieder and Dr R. Foster yielded notostracans but Professor Rieder's mud produced other primitive branchiopods. Dr Gisli Gislason kindly arranged for Mr Olafur Einarsson to collect adults of *Lepidurus arcticus* in an upland pool that I was able to bring back to England alive after a visit to Iceland.

I thank Dr Coral Hogben and Mrs Olive Jolly for practical help at various times, Dr J. P. Harding for the gift of a compressorium of his own design and construction that proved ideal for holding living larval stages for examination, Dr Ida Talling for kindly translating a paper from Icelandic, and Mrs Julie Waterhouse for her care and patience with the typing. Last, but not least, I thank Dr G. A. Boxshall for his meticulous reading of the text.

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Abbreviations used on the figures

A	adhesive material investing egg shell	AS	anterior spines of gnathobase
A1	antennule	AT	anteriormost tooth of right mandible
A2	antenna	AVBT	anteroventral bracing tendon
AA	anterior apodeme	AVF	anteroventral flange
Abd Mx 1	abductor muscle of maxillule	AVLM	anchorage of ventral longitudinal muscle
AF	anchoring fibres of cephalic bracing tendon		
AML	anchorage of transverse muscle fibres of labrum	B	boss
		BA M	basal mound of spine
ANT	anterior	BT	button

BF	bracing fibres (of ventral head cuticle)
BM 1, 2, 3, 4	bracing muscles 1, 2, 3, 4
BM Mx 1	bracing muscles of maxillule
BP	base of paragnath
C	corm of trunk limb
CAM	cuticular cup in which adductor muscle inserts
Cav	cavity of posterior mandibular apodeme
CB	cleaning bristles at margin of food groove
CBT	cephalic bracing tendon
CC	cephalic cuticle
CD	cutting denticles of maxillule
CE Mand	cut edge of mandible
CG	cerebral ganglion
CT	'core' of transverse mandibular tendon
CVM	cuticular vaulting muscle
D	denticles of mandibular teeth
DA	dorsal anchorage of fibrous sheet
DD	digestive diverticulum
DF Mx 1	distal flange of maxillule
DLM	dorsal longitudinal muscle
D Oe DM	dorsal oesophageal dilator muscles
DVM	dorsoventral muscles of trunk
E	eye
EF Mx 1	extrinsic flexor muscle of maxillule
EFS	cut edge of fibrous sheet
EN	endopodite
End 1, 2...	endite(s) 1, 2...
Endo	endoskeleton
EP	epipodite
ES	end sac of antennary gland
ET Mx 2	excretory tubule of maxilla
EX	exopodite
EXTL 2	exopodite of trunk limb 2
F	fibres
FE	fibrous anterior extension of transverse mandibular tendon
FG	food groove
F1G	flexor muscle of gnathobase
FM	fibrous mass
FS	fibrous sheet
G (1, 2...)	Gnathobase (1, 2...)
GS Mand	gnathobasic spine of mandible
GSp 1	spines of gnathobase 1
HSC	head shield cuticle
HSC′	inner face of head shield cuticle
Ht	heart
IBM	inner face of basal mound
IFMx 1	intrinsic flexor muscle of maxillule
IGC	inner face of trunk limb gnathobasic cuticle
IGW	intucking of midgut wall
I Mand C	inner face of mandibular cuticle
IM	inner membrane of egg
IT	intersegmental tendon
L	labrum
LA Mx 1	lateral adductor muscle of maxillule
LHJ	lateral hinge joint
LMH	lateral margin of head
MA Mx 1	median adductor muscle of maxillule
Mand	mandible
Mand Abd M	Mandibular abductor muscle
Mand C	mandibular cuticle
Mand G	mandibular gnathobase
Mand M	mandibular margin
Mand P	mandibular palp
MCR	mandible-cleaning rakes
MCR′	mandible-cleaning rake precursors
MG	midgut
MGW	midgut wall
M Mand	masticatory region of mandible
MS	meshwork spines
Mx 1	maxillule
Mx 1 Sp	spines of maxillule
Mx 2	maxilla
Mx 2 Sp	spines of maxilla
N	nerve
NC	nerve cord
NCo	nerve commissure
Oe	oesophagus
OeDM	oesophageal dilator muscles
OM	outer membrane of egg
ON	optic nerve
OTMT	outline of transverse mandibular tendon
P	paragnath
PAC	anterior prolongation of alimentary canal
PGS	proximal gnathobasic spine(s)
PMA	postmandibular apodeme
PMA/Mx 1	articulation between postmandibular apodeme and maxillule
P Mand	inner face of posterior wall of mandible
PMS	proximal masticatory spine
P Mx 1	inner face of posterior wall of maxillule
POST	posterior
PTL	posterior trunk limbs
PWP	posterior wall of paragnath
R	roof of atrium oris
RPMA	rudiment of post mandibular apodeme

S	'shell' of egg
SEN	sensilla(e)
SMG	suspensor of midgut
SMS	sub-marginal spines
SP	sensory pad
SS (G1, 2...)	sweeping spines (of gnathobase 1, 2...)
SUS 1, 2, 3	suspensors 1, 2, 3 of transverse mandibular tendon
SUS 1M, 2M, 3M	muscular basal region of suspensors 1, 2, 3
T1, 2...	trunk segments 1, 2...
TAG	tubule of antennary gland
TCR	thickened cuticular ridge
TDG	tubules of digestive gland
TL 1, 2...	trunk limbs 1, 2...
TLR	trunk limb rudiments
TMM	transverse mandibular muscles
TMM′	transverse mandibular muscles converging on transverse mandibular tendon
TMT	transverse mandibular tendon
VA	ventral anchorage of fibrous sheet
VHC	ventral head cuticle
VLM	ventral longitudinal muscles
3	mandibular promotor (or promotor roller) muscle
4	mandibular remotor (or remotor roller) muscle
5c	a transverse mandibular muscle
5e	levator muscle