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THE COMPARATIVE ANATOMY OF TWO COPEPODS, A PREDATORY CALANOID AND A PARTICLE-FEEDING MORMONILLOID

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[Plates 1–3]

CONTENTS

The skeletomusculature of a large predatory calanoid, *Euaugaptilus placitus*, is described and compared with that of a small, particle-feeding mormonilloid, *Mormonilla phasma*. The comparisons are extended to other copepod groups for which data are available, to identify any general patterns in copepod musculature. Anatomy has been related to presumed function wherever possible, and functional interpretations are offered of the feeding and swimming apparatus in both species.

The trunk muscles of *Euaugaptilus* and *Mormonilla* conform to the typical copepod pattern of paired dorsal and ventral bundles but *Euaugaptilus* lacks the oblique muscles that originate on the postmaxillary apodemes in *Mormonilla* and other copepods. The prosome–urosome joint has a similar structure in both genera but the joints are not homologous because *Euaugaptilus* is a gymnoplean in which the prosome–urosome division occurs between thoracic somites 6 and 7 whereas in *Mormonilla*, a podoplean, it occurs between somites 5 and 6. Differentiation of the prosome–urosome joint during ontogeny and the development of trunk tagmosis are described. The difference between Podoplea and Gymnoplea is merely that these processes are completed by the second copepodid stage in the former, by the third in the latter. It is concluded that the primary factor affecting trunk tagmosis is the evolution of an efficient metasome, specialized for rapid swimming movements. Differences in metasome composition between gymnopleans and podopleans may be related to behavioural differences. The former jump by using their swimming legs primarily as an escape reaction whereas normal swimming in the latter involves repeated jumping movements of the swimming legs.

The musculature of the cephalosomic limbs of *Euaugaptilus* is complex. Each limb, especially those involved in prey capture and manipulation, has the ability to perform several roles and it is this multiplicity of function that explains the relative complexity of the musculature. The ventral cephalic tendon system is correspondingly elaborate and additional apodemes, anterior to the mandibles and medial to the maxillae, are present in *Euaugaptilus*. *Mormonilla* has secondarily reduced musculature, especially in the cephalosome. It is a specialized particle-feeder but each limb performs relatively simple movements and has a restricted range of functions. The numbers of extrinsic limb muscles are reduced and the posterior ventral cephalic tendon is lost, resulting in a change in site of origin for some remaining muscles.

Interpretations of the segmental composition of the mouthparts are summarized. Lack of evidence has made these highly subjective. A common pattern of homologies is established based on their musculature, which allows the coxa–basis joint to be identified as a reference point. It is concluded that the protopod of the postmandibular limbs (maxillules, maxillae and maxillipeds) primitively comprised three segments but that in most extant copepods the praecoxa and coxa are partly or completely fused, forming a syncoxa. There is no evidence of a praecoxa in the antennae and mandibles, which both have a protopod comprising coxa and basis only. The copepod antennule is primitively uniramous and multisegmented. Reports of a vestigial second ramus in some siphonostomatoids are examined and reinterpreted.

Recent studies of planktonic feeding mechanisms and increased knowledge of the dominance of viscous forces in the environment experienced by copepods have led to the generation of a new model of copepod feeding. This is applied to the predatory behaviour of *Euaugaptilus* and to the feeding of *Mormonilla* on suspended particles. Fine scale adaptations of the feeding appendages, such as the button setae of *Euaugaptilus* and the interlocking setae of the filter basket walls of *Mormonilla*, are also described. The gross anatomy of the gut is described for both genera and compared with that of a range of other copepods.

The skeletomusculature of the swimming legs is described. Both *Euaugaptilus* and *Mormonilla* display the characteristic copepod patterns of extrinsic and intrinsic muscles. Fine scale adaptations of the legs are also examined. *Euaugaptilus* feathers its oar-like rami so that they form a median longitudinal keel during the recovery stroke.

Mormonilla closes up its rami and flexes its legs posteriorly during the recovery stroke, as does *Euaugaptilus* also, but is unable to feather its leg rami in the same way.

Data on the ontogeny of the musculature during the nauplius stages are summarized for representatives of the Harpacticoida, Cyclopoida and Calanoida. There is no clear indication as to which of these taxa is the most primitive but the Calanoida appears to exhibit the most regular anamorphic developmental sequence.

1. INTRODUCTION

Copepods are typically the dominant metazoan group in marine planktonic communities both in terms of numbers and biomass, and have been intensively studied because of their role as primary consumers of the phytoplankton. The feeding dynamics, life history statistics, distribution patterns and general biology of the common species are adequately known but little has been published on feeding mechanisms. Recent cinematographic work is improving this situation but progress is hampered by the lack of even basic knowledge of the skeletomusculature of the feeding apparatus. Published accounts are available on the trunk and extrinsic limb musculature of the calanoids *Calanus* (Lowe 1935; Perryman 1961), *Metridia* (Hessler 1964) and *Epilabidocera* (Park 1966), on the intrinsic limb muscles of *Cyclops* (Hartog 1888) and on aspects of the musculature of harpacticoids (Lang 1948) but the only full account of any copepod is that of the misophrioid *Benthomisophria* (Boxshall 1982). Comprehensive descriptions of the skeletomusculature of representatives of all copepod orders would greatly facilitate functional interpretation of their feeding apparatus.

The trunk and limb musculature of the calanoid *Euaugaptilus placitus* (Scott) and the mormonilloid *Mormonilla phasma* Giesbrecht is described here. These species represent the two main lineages of copepod evolution, the Gymnoplea and the Podoplea respectively. Unlike most calanoids, which feed on suspended particulate matter, *Euaugaptilus* is a predator but it can be regarded as representative of the Calanoida as a whole because, as recent studies have shown (for example, Price *et al.* 1983), calanoid feeding on suspended particles is a selective process and can involve similar raptorial movements of the mouthparts to those of predatory copepods. *E. placitus* is also a large species, up to 10 mm total body length: a considerable advantage in anatomical studies. *Mormonilla*, the only genus of the recently recognized order Mormonilloida (Boxshall 1979), is a small specialized particle-feeder. As a detailed account already exists of a misophrioid, one of the most primitive podoplean groups, it was considered that the specialized Mormonilloida would be suitable for comparative studies. Also, the mormonilloids are so poorly known that any new anatomical information will be of value in assessing their phylogenetic relationships.

2. MATERIALS AND METHODS

Material was obtained from RMT1 + 8M net samples taken in the North Atlantic at *Discovery* stations 10376 (female *E. placitus*), 7709 (male *E. placitus*) and 10378 (*M. phasma*). Stations 10376 and 10378 were in the vicinity of 32° N 29° W and 7709 was at 60° N 20° W. Most samples were fixed initially in 5% formalin in sea water and later transferred to a preserving fluid based on that of Steedman (1974). Some specimens of *Mormonilla* were fixed in Bouin's fluid, some in 70% (by volume) ethanol and some in 2.5% (by volume) glutaraldehyde.

Mormonilla was examined by scanning electron microscopy (s.e.m.) with an ISI 60A microscope. Specimens were prepared by dehydration through graded acetone, critical point dried, mounted on stubs and sputter coated with palladium. Sections of *Euaugaptilus* and *Mormonilla* were examined by light microscopy. Transverse and longitudinal serial sections were made of specimens embedded in paraffin wax and stained by using Masson's trichrome technique or haematoxylin and eosin. Specimens for dissection were cleared in lactophenol. Cleared exoskeletons were prepared by heating specimens in 10% (by mass) potassium hydroxide solution at 50 °C for 24 to 48 h. All drawings were made with the aid of a camera lucida.

3. TAXONOMY

Euaugaptilus placitus was described by Scott in 1909 (as *Augaptilus placitus*), from two females taken during the Siboga Expedition at about 0–1° S 127–129° E in the Halmahera Sea. Sewell (1947) placed it in the synonymy of *E. laticeps* (Sars, 1905) and also followed Farran (1929) in regarding *A. antarcticus* Wolfenden, 1911 as a synonym of *E. laticeps*. Sewell's material comprised three females and two juveniles from the northern and central Arabian Sea and his description agrees closely with that of Scott (1909) for *A. placitus* but differs from Sars' *E. laticeps* in the setation of the maxillule and mandibular palp. Matthews (1972) re-examined a syntype of *A. placitus* and found it 'to agree in all essential details with *E. laticeps*'. Tanaka & Omori (1974) described a new species, *E. perodiosus*, from Japanese waters and listed *E. laticeps* of Sewell (1947) as a synonym, together with *A. antarcticus* and material that Wolfenden (1911) described as *A. fungiferus* Steuer. *E. perodiosus* is distinguished from *E. laticeps* by the possession of four setae on the mandibular exopod and one seta on the second inner lobe of the maxillule compared with five and two, respectively.

The syntype female of *A. placitus* examined by Matthews (1972) has four setae on the mandibular exopod (as also figured by Scott 1909) and one on the second inner lobe of the maxillule. *E. placitus* (Scott, 1909) is the oldest available name for this taxon. *E. perodiosus* and *A. antarcticus* are junior synonyms of *E. placitus* and the specimens described by Sewell (1947) as *E. laticeps* and by Wolfenden (1911) as *A. fungiferus* also belong to this species. *E. placitus* occurs in Antarctic waters, in the Indo-Pacific from the Arabian Sea to Japan, and in the North Atlantic.

Two species of *Mormonilla*, *M. phasma* and *M. minor* Giesbrecht, comprise the entire order Mormonilloida (Boxshall 1979). Both are known only from females and no specimens have ever been reported as carrying either egg sacs or spermatophores. Larval development is unknown. In the North Atlantic *M. phasma* and *M. minor* are commonest between 400 and 700 m but both are known to occur down to 3000 m.

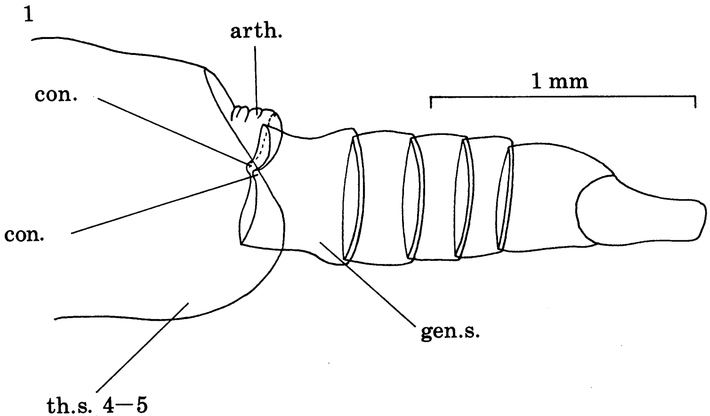
4. TRUNK SKELETOMUSCULATURE

(a) *Euaugaptilus*

(i) *Trunk exoskeleton*

The body of *Euaugaptilus* comprises a large anterior prosome and a small posterior urosome. The prosome is rigid anteriorly, all five cephalic somites and the first thoracic somite bearing the maxillipeds being fused to form the cephalosome which is covered by a continuous dorsal shield formed by the fusion of the tergites of its constituent somites. The posterior part of the prosome, the metasome, comprises five thoracic somites, each of which bears a pair of swimming legs ventrally. The first three pedigerous somites are free but the fourth and fifth are fused into a double somite bearing two pairs of legs. Traces of the original boundary between these somites are observable as intersomitic tendinous interruptions in the ventral longitudinal trunk muscles and in the presence of the transverse intersomitic ridge on the ventral body surface in the middle of the double somite (figure 2, i.s.r.$_5$).

The free pedigerous somites are separated dorsally and laterally by narrow strips of arthrodial membrane which permit some telescoping of each within the preceding one. A small amount of dorsoventral flexion of the prosome was observed by Perryman (1961) as part of the swimming process in *Calanus*. Ventrally the integument of the prosome comprises a number of sclerites of varying thickness (see §7*a*). The conspicuous articulation between prosome and urosome (figure 1) is a transverse pivot joint with the axis lying between two well developed condyles (figure 1, con.) that lie just dorsal to the mid-height level. The joint has extensive arthrodial membrane dorsally and ventrally (figure 2). Very little lateral flexion is possible.



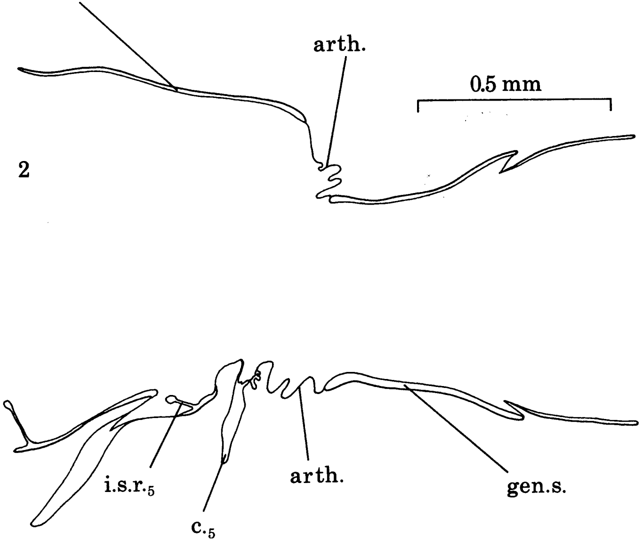


FIGURE 1. The urosome of an adult male *Euaugaptilus*, showing the axis of movement at the prosome–urosome joint.

FIGURE 2. Median longitudinal section through the prosome–urosome joint in *Euaugaptilus*, showing areas of extensive arthrodial membrane.

The female urosome (figure 4) comprises a large genital double somite, a small middle somite and the anal somite. The genital double somite bears the single genital opening ventrally. It consists of the seventh thoracic or genital somite and the first abdominal somite fused. The part of the double somite lying posterior to the genital opening represents the abdominal somite. There is a tendinous interruption in some of the dorsal longitudinal trunk muscles which marks the position of the lost intersomitic boundary. The second urosome somite is a simple hoop of integument that can be telescoped inside the genital double somite to some extent, as can the anal somite inside the middle somite. The anal somite bears the caudal rami posteriorly, one either side of the slit-like median anus.

The male urosome (figure 1) comprises a short genital somite with the single genital opening asymmetrically on the right side, and four other somites, the last of which is the anal. Narrow strips of arthrodial membrane allow some telescoping of each somite into the preceding one. The second, third and fourth somites are simple hoops of integument and the structure of the anal somite is the same as in the female.

(ii) *Trunk musculature*

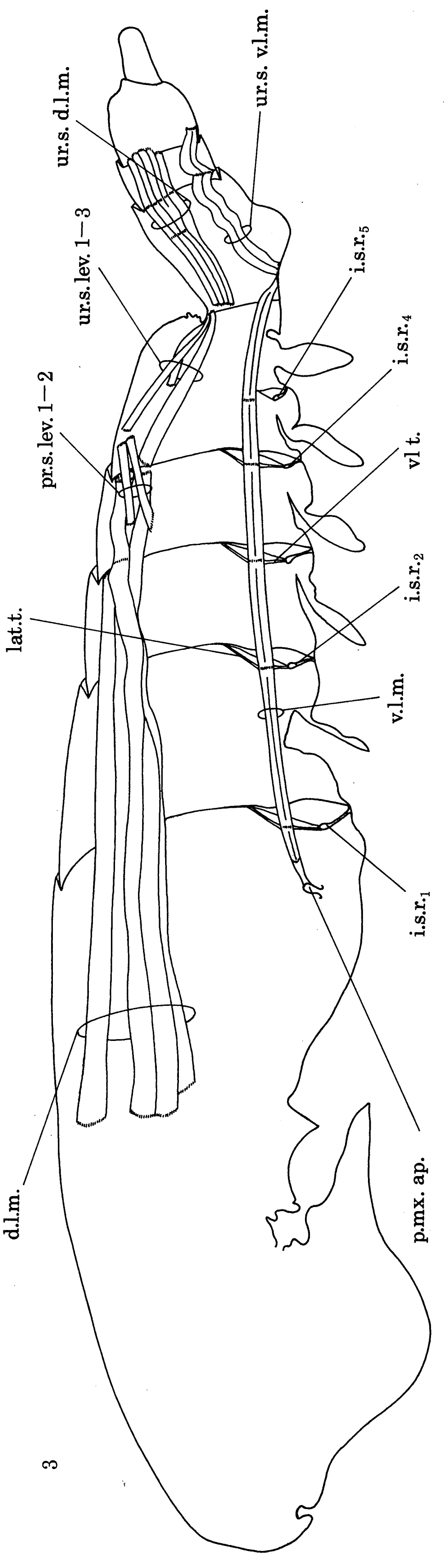
Euaugaptilus, like other copepods, has paired dorsal and ventral longitudinal muscles. Each dorsal muscle comprises four large blocks of fibres originating anteriorly on the dorsolateral wall of the cephalosome about at the level of the junction between mandibular and maxillulary somites. It passes posteriorly through the first and second pedigerous somites in the form of a broad band of fibres just beneath the dorsal body wall. Within the first pedigerous somite the two most lateral blocks subdivide and overlie each other to some extent, as can be seen in transverse section in figure 76. En route all the muscle fibres are attached, via tendinous inserts, to the anterior rim of the second pedigerous somite. Two of the muscle blocks insert on the anterior rim of the third pedigerous somite. Of the remaining two, one attaches at this level via a tendinous interruption and the other passes through into the third somite. Both insert on the anterior rim of the fourth somite.

Paired prosome levator muscles (figure 4, pr.s. lev. 1–2) originate dorsally in the anterior part of the third pedigerous somite and pass posteromedially into the double somite to insert on the dorsal wall just anterior to its mid-level. These can produce telescoping of the double somite within the third somite. Originating within the double somite are three pairs of urosome levators. One (ur.s. lev. 1) originates near its anterior rim and passes posteroventrally to insert on the anterior rim of the urosome just dorsal to the lateral condyle of the prosome–urosome articulation; the others (ur.s. lev. 2–3) dorsally near the mid-level and pass posteriorly to insert dorsolaterally around the anterior rim of the urosome.

A paired muscle (d.m.l.m.) originates near the dorsal midline at the posterior end of the cephalosome. This narrow strand passes posteriorly towards its insertion on the anterior rim of the urosome, attaching anteriorly in the second to fourth somites en route.

The dorsal longitudinal muscles within the urosome originate anteriorly on the dorsal wall of the genital double somite, pass posteriorly as a broad flat band, fanning out laterally to a broad dorsal to lateral insertion inside the anal somite. The more median fibres have tendinous interruptions in the posterior third of the genital double somite, but these are not attached to the body wall. All the strands are attached via a tendinous insert to the anterior rim of the second urosome somite.

Each ventral longitudinal muscle has a single origin on the postmaxillary apodeme. Each



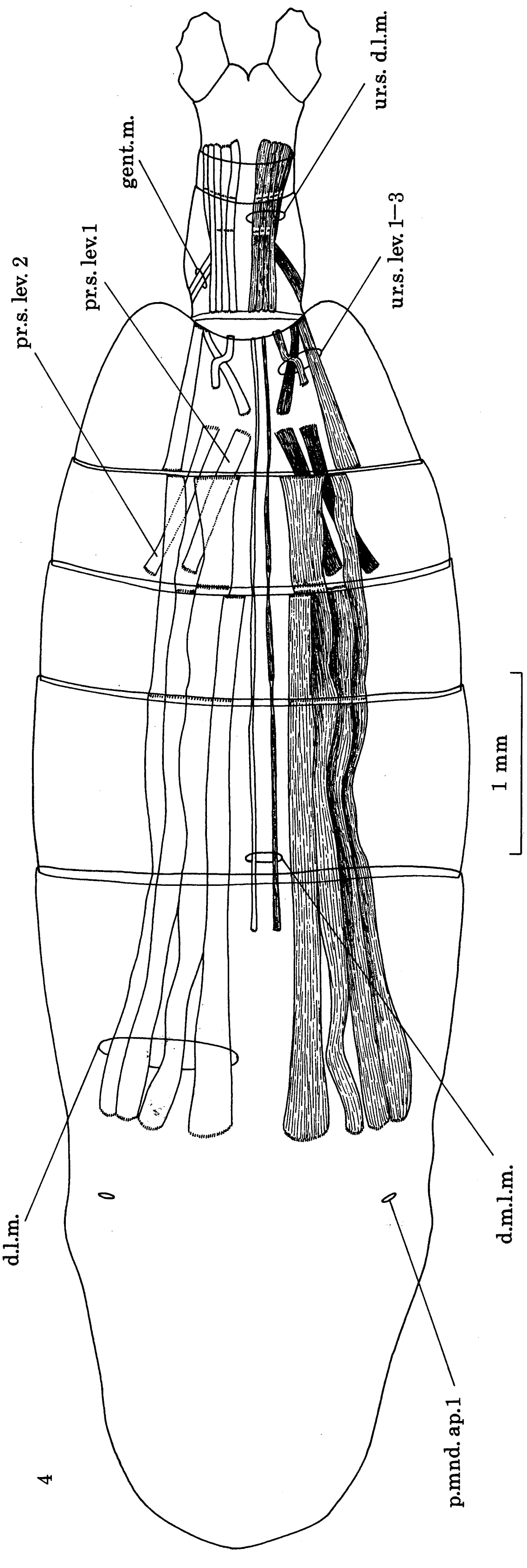


FIGURE 3. Median interal view of the longitudinal trunk muscles of an adult female *Euaugaptilus* of body length 9.9 mm.
FIGURE 4. Dorsal view of longitudinal trunk muscles of the same specimen as figure 3.

comprises a double strand and passes posteriorly towards its insertion on the ventral wall just inside the genital double somite. These muscles probably act as depressors flexing the urosome ventrally. At each intersomitic junction between prosomal somites the muscle is interrupted by a small section of tendon. These are attached to the body wall indirectly via short ventral and lateral tendons. The tendinous interruption marking the position of the boundary between the fused fourth and fifth pedigerous somites is free from the body wall. The lateral tendons (lat. t.) attach to the lateral body wall whereas the ventral tendons (vl t.) attach to the transverse intersomitic ridges which protrude into the body cavity (figure 3). In *Euaugaptilus* there is no oblique trunk muscle like that found in many other calanoids.

The ventral longitudinal muscles within the urosome originate anteriorly in the genital double somite, on the ventral wall immediately posterior to the insertion of the ventral prosomal muscles. They extend posteriorly to a ventral insertion inside the anal somite, attaching to the anterior rim of the second urosome somite in passing.

(*b*) *Mormonilla*

(i) *Trunk exoskeleton*

The elongate body of *Mormonilla* is divided into prosome and urosome by a pivot joint at the posterior margin of the fourth pedigerous somite. The prosome comprises a cephalosome of five fused cephalic somites plus the completely incorporated maxilliped-bearing first thoracic somite, and four pedigerous somites. The first pedigerous somite is elongate and about equal to the remaining three together. These three somites are similar in length but taper posteriorly so that, at its posterior extremity, the prosome is little wider than the urosome. There is no arthrodial membrane between the cephalosome and the first pedigerous somite and no telescopic flexion occurs there. At the articulations between first to fourth pedigerous somites narrow strips of arthrodial membrane permit slight dorsal telescoping of each somite into the preceding one.

The prosome–urosome joint allows considerable dorsoventral flexion of the urosome relative to the prosome. It has large amounts of arthrodial membrane both dorsal and ventral to the transverse dicondylar pivot joint. The condyles are not as well developed or as heavily sclerotized as those of *Euaugaptilus*.

Each urosome articulation is provided with a narrow hoop of arthrodial membrane which permits limited telescopic flexion in any direction. The first somite is the sixth thoracic which bears no trace of the fifth pair of swimming legs in the adult. The second bears the single genital opening midventrally and probably represents a double somite, as in many other copepods, though there is no trace of any lost articulation in the arrangement of the trunk muscles (figure 5). The third somite is a simple cylinder capable of slight flexion relative to the genital somite, as is the anal somite. The anus, a median dorsal slit, is not covered by an operculum. At its proximal articulation each caudal ramus has some arthrodial membrane medially. The caudal muscle (cd. m.) adducts the ramus about its lateral rim which forms the hinge line. Abduction is presumably by integumental elasticity so that the rami are slightly divergent in the resting position.

(ii) *Trunk musculature*

The trunk muscles are reduced by comparison with other copepods but follow the same basic pattern. The paired dorsal and ventral longitudinal muscles are the major groups but there are also paired oblique muscles passing between them from ventral to dorsal, within the prosome (figures 5 and 6).

Each dorsal muscle comprises three main strands originating on the dorsal wall within the posterior part of the cephalosome, from the level of the mandibular somite back. These pass posteriorly, uniting into a single block which attaches anteriorly in the fourth pedigerous somite via a tendinous section and inserts dorsally just inside the urosome. An additional strand originates anteriorly in the third pedigerous somite and passes posteromedially to a dorsal insertion inside the fourth pedigerous somite. A narrow dorsomedian muscle (figure 6, d.m.l.m.) originates posteriorly in the first pedigerous somite. It lies medial to the main dorsal bundle, extends posteriorly and inserts on the anterior rim of the urosome.

The dorsal muscles within the urosome are each double stranded. They originate near the insertion of the prosomal muscles and insert on the anterior rim of the anal somite. Along its course each has a tendinous attachment to the genital double somite and the third urosome somite.

The ventral longitudinal muscles originate on the postmaxillary apodeme. No fibres originate on the postmaxillulary apodeme although the two are linked by a narrow strand of tendon (figure 33, susp.t. 4). Each ventral muscle passes through the prosome without intermediate attachments and inserts ventrally just inside the urosome. Also originating on the postmaxillary apodemes are the paired oblique muscles (figure 5, ob. m.) Each is double stranded and passes posterodorsally around the dorsal muscle to insert dorsally in the posterior third of the second pedigerous somite.

The ventral muscles in the urosome form a broad band of fibres which originates near the insertion of the prosomal ventral muscles. Each attaches via tendinous inserts in the anterior part of the genital double somite and on the rim of the third urosome somite before inserting on the anal somite. The origin and insertion of the short caudal muscle are shown in figures 5 and 6. As in other copepods the dorsal and ventral muscles serve respectively to levate and depress the urosome at the prosome–urosome articulation. Contraction of the dorsal and oblique muscles in the prosome may also telescope one somite into the preceding one. The urosomal muscles produce flexion in various directions, of one somite against the next.

(*c*) *The prosome–urosome joint in copepods*

(i) *Morphology*

The position of the joint separating prosome from urosome was used by Giesbrecht (1892) as the primary systematic division within the Copepoda. It is located between thoracic somites five and six in the Podoplea, between somites six and seven in the Gymnoplea. All copepod orders other than the Calanoida share the former arrangement. This division into two lineages is still recognized in modern classifications (Kabata 1979). Although in a different position in the two groups the structure of the joint is more or less the same. It has a transverse pivot line with extensive arthrodial membrane dorsally and ventrally which permits considerable dorsoventral, but little lateral, flexion. The pivot line (figure 1) lies slightly above the mid-height level of the urosome allowing greater ventral than dorsal flexion.

Flexion is produced mainly by the antagonistic dorsal and ventral longitudinal trunk muscles. In *Euaugaptilus* the arrangement of the dorsal muscles is atypical as the main fibres do not continue through the last pedigerous somite to insert on the urosome. The dorsal muscles which raise the urosome all originate within the fourth double somite, although they are probably

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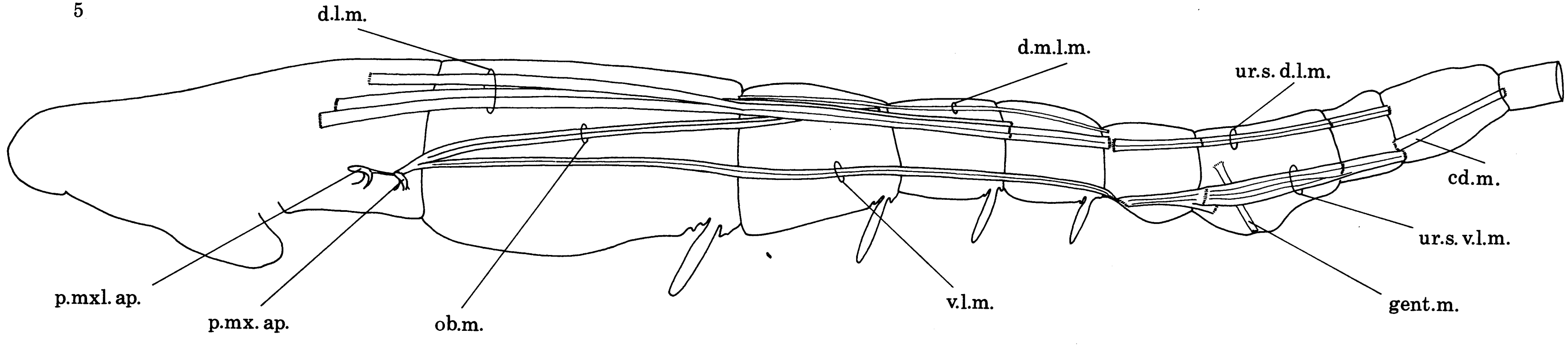

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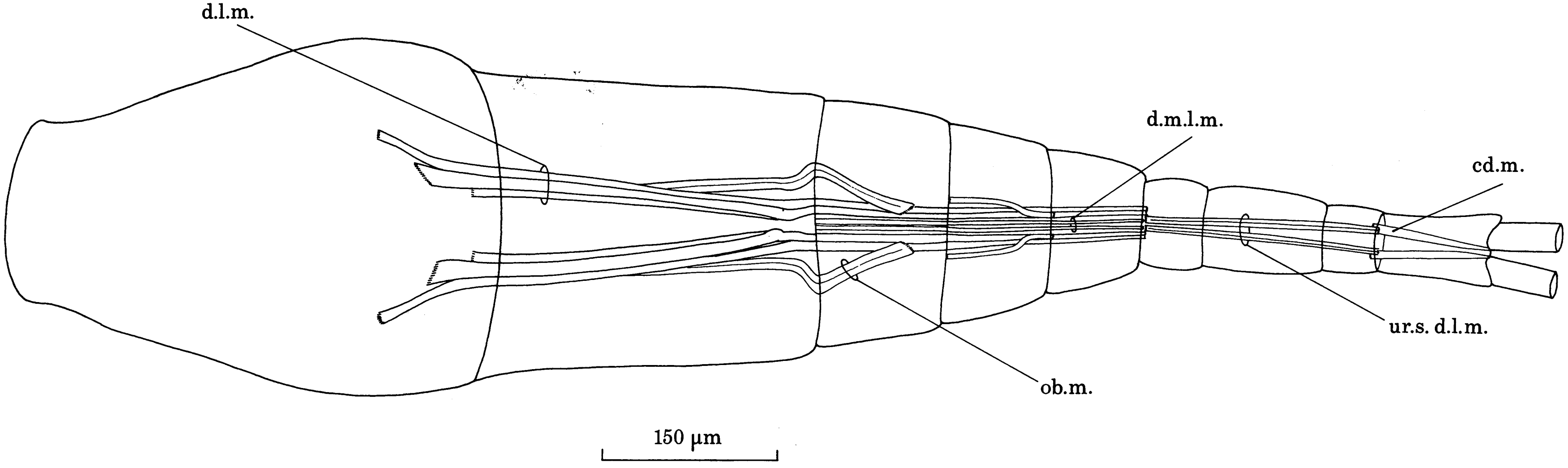

Figure 5. Median internal view of the longitudinal trunk muscles of an adult female *Mormonilla* of body length 1.35 mm.
Figure 6. Dorsal view of the longitudinal trunk muscle of the same specimen as figure 5.

derived from the main dorsal longitudinal muscles. In other calanoids, such as *Calanus* (Perryman 1961), *Metridia* (Hessler 1964) and *Epilabidocera* (Park 1966), the dorsal muscles may attach in the third and fourth pedigerous somites but some strands pass into the urosome to insert dorsally on its anterior rim. In all three of these genera a continuation of the oblique trunk muscle (as present in *Mormonilla*, figure 5, ob. m.) forms at least part of the muscle bundle that inserts on the urosome rim. Those fibres of the dorsal muscles which in some genera insert posteriorly on the dorsal wall of the last pedigerous somite may act indirectly to increase the dorsal flexion of the urosome by lowering the dorsal surface of the somite immediately adjacent to the prosome–urosome joint.

The ventral longitudinal muscles insert ventrally just inside the anterior rim of the urosome in all copepods investigated. In the calanoid genera mentioned above, in the misophrioid *Benthomisophria* (Boxshall 1982) and in *Mormonilla* both dorsal and ventral muscle groups in the prosome taper into a narrow tendinous insertion on the urosome. In the harpacticoid *Sunaristes paguri* Hesse they pass into the urosome as broad sheets and each has a broad insertion around the rim of the urosome (Lang 1948). If this arrangement were combined with the presence of lateral arthrodial membrane and less well developed condyles more lateral flexion would be possible at the prosome–urosome joint. Those harpacticoids with a vermiform body may have this ability though, like those with a more typical expression of the podoplean facies (a large broad prosome and narrow urosome) such as the Tisbidae, they still show predominantly dorsoventral flexion.

Although the prosome–urosome joints of gymnopleans and podopleans are very similar in morphology it is clear that they are not homologous. It is therefore relevant to consider whether the common ancestor of these two lineages possessed either of these arrangements or whether it lacked a well defined division into prosome and urosome. Examination of the formation of the prosome–urosome joint during ontogeny may provide clues as to its evolutionary origins.

(ii) *Ontogeny*

Copepods typically have a maximum of six naupliar and five copepodid stages. The first copepodid always comprises a cephalosome (cephalon plus first thoracic somite), four free somites and a telson (figures 7*a–d*). The telson has been referred to as the anal somite in the descriptive sections of the present account. In gymnopleans at this stage the functional division between prosome and urosome appears to lie between thoracic somites four and five (Corkett & McLaren 1978; Grice 1969; Shih & MacLellan 1977) giving a urosome of two somites. Some authorities have placed the dividing line one somite to the posterior leaving only a one-segmented urosome (Corkett 1967). In podopleans the functional division into prosome and urosome in the first copepodid is even less obvious and interpretation consequently more subjective. In harpacticoids some authors divide the trunk between thoracic somites four and five (Thia-Eng 1975; Vincx & Heip 1979), some behind the fifth somite (Rosenfield & Coull 1974) and others merely cite the total number of postcephalosomic somites (Carter & Bradford 1972; Itô 1971). In cyclopoids both Dudley (1966) and Hipeau-Jacquotte (1978) regarded the dividing line as falling between somites four and five whereas others place it behind somite five (Valderhaug & Kewalramani 1979) or give the total number of somites (Lescher-Moutoué 1973). The same difficulties have been experienced in the interpretation of tagmosis in other podoplean orders. The most likely explanation is that no highly differentiated joint is present at the first copepodid stage and that the joints between somites four and five and between five and the telson are

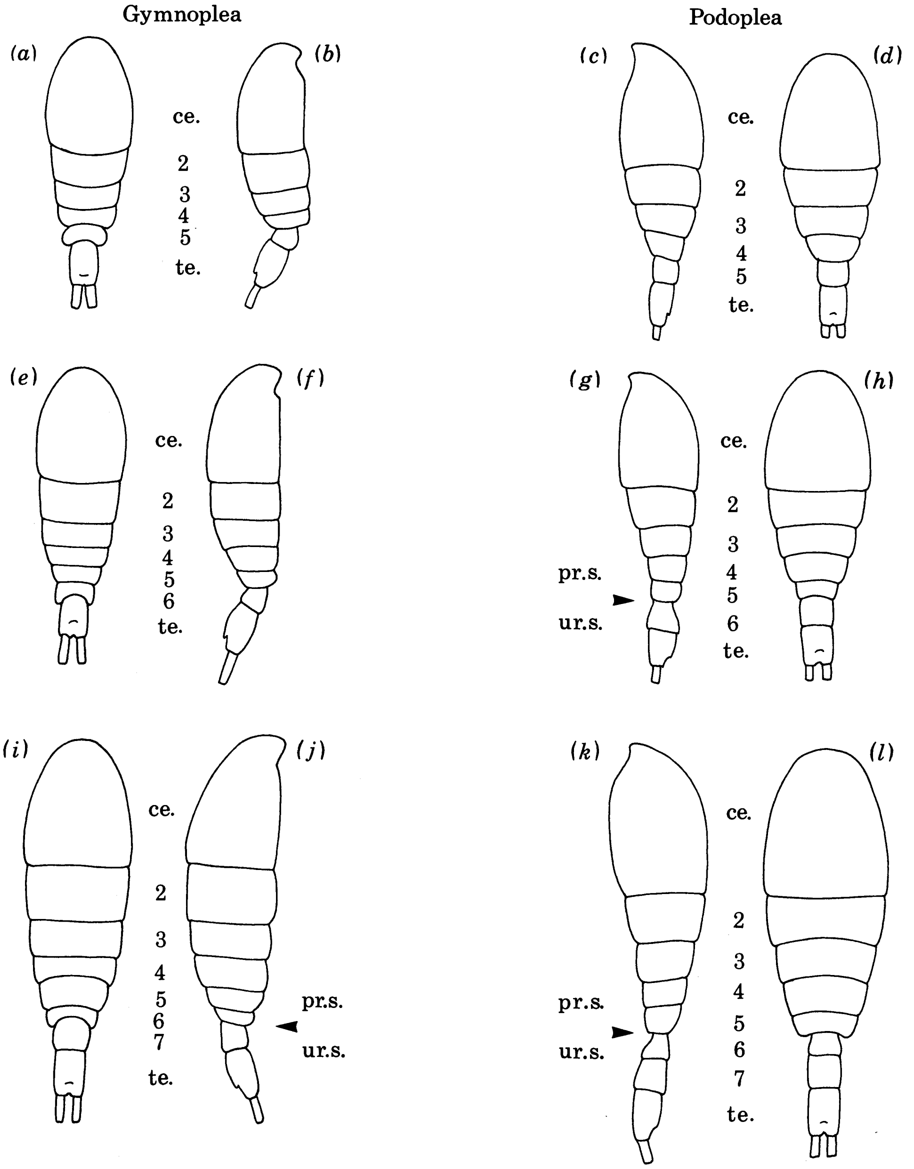

FIGURE 7. Comparison of body segmentation and tagmosis in the first three copepodid stages of gymnoplean and podoplean copepods.

basic telescopic joints provided with hoops of arthrodial membrane, as found between urosome somites in the adult.

In the second copepodid an additional somite has separated off from the anterior end of the telson (figure 7*e*–*h*). The prosome–urosome boundary is now clearly located between thoracic somites five and six in both gymnopleans and podopleans and is the definitive condition for the latter group. The urosome is two-segmented in both lineages at this stage. A further somite separates off from the telson by the third copepodid (figure 7*i*–*l*), making the urosome three-segmented in the podopleans. In the Gymnoplea, however, the prosome–urosome boundary is located further back, between thoracic somites six and seven, in its definitive adult position. The urosome remains two-segmented at this stage.

The ontogeny of the musculature, especially the longitudinal trunk muscles, is an important aspect of the differentiation of the prosome–urosome joint. Information on trunk muscle ontogeny is sparse. Only Perryman's (1961) unpublished thesis on *Calanus* provides sufficient detail to be useful. She showed that the longitudinal trunk muscles appeared late in the second nauplius stage. In the third nauplius both dorsal and ventral longitudinal muscles originate mid-dorsally on the thick integument in the mandibular somite (figure 8). The dorsal muscle inserts dorsally on the anterior margin of the telson (the unsegmented postmandibular region). The ventral passes posteroventrally, attaching to the anterior edge of the telson via a tendinous projection, before passing into the telson to its ventral insertion near the posterior end of the body. As the thoracic somites begin to differentiate with successive moults to the sixth nauplius stage the dorsal muscles subdivide so that some fibres insert on the anterior rim of each somite as it separates from the telson (figure 9). In the fifth nauplius the rudiment of the postmaxillulary apodeme (p.mxl. ap.) appears, onto which some fibres of the ventral muscles attach.

The significant changes in trunk musculature that occur at the nauplius to copepodid moult are described by Perryman (1961) but not figured. Figure 10 is based on her description. The dorsal muscle becomes broader, extending its origin down the dorsolateral body wall. The ventral muscle loses the portion between its naupliar origin and the postmaxillulary apodeme. It also divides into an oblique portion which passes posterodorsally to insert dorsolaterally on the telson, and a ventral portion which attaches ventrally on the rim of the telson and inserts near the posterior end of the body (figure 10). It is possible to derive the basic trunk muscles of both gymnoplean and podoplean copepods from those of the first copepodid stage. Those of adult *Calanus* (figure 11) differ only in the addition of a strand inserting mid-dorsally on the fifth pedigerous somite and of the dorsal urosomal muscles. In adult podopleans the trunk muscle system is essentially the same as that of the first copepodid (figure 10), with the addition of the dorsal urosomal muscles.

A general ontogenetic pattern for the trunk muscles can be recognized in Perryman's data. The dorsal muscle begins as a simple block originating dorsolaterally in the mandibular somite and inserting on the anterior rim of the telson. The ventral muscle is a simple strand inserting posteriorly inside the telson. At each moult from the third nauplius onwards a new somite begins to separate off from the anterior end of the telson. As this occurs the ventral muscle simply lengthens but the dorsal subdivides so that part inserts on the anterior rim of each newly separated somite and part remains inserted on the rim of the telson. This process continues until the first copepodid in podopleans; the second in gymnopleans. Subsequently in each group prosomal organization and musculature remain more or less fixed even though a further urosome somite separates off from the telson at each moult through the copepodid series. These urosome somites derive their longitudinal muscles from the dorsal and ventral bundles, the former now incorporating the oblique muscles, both of which remain inserted in the telson but develop new intermediate attachments on each new somite as it separates. The development of the prosome and its muscles follows the same pattern in podopleans and gymnopleans but the process is completed at an earlier stage in the former group.

(iii) *Functional significance and evolution*

The differentiation of prosome and urosome in copepods can be related to the functional specialization of the regions. Boxshall (1983*a*) suggested that the primary factor affecting tagmosis is the evolution of an efficient thoracic tagma, the metasome, specialized for rapid

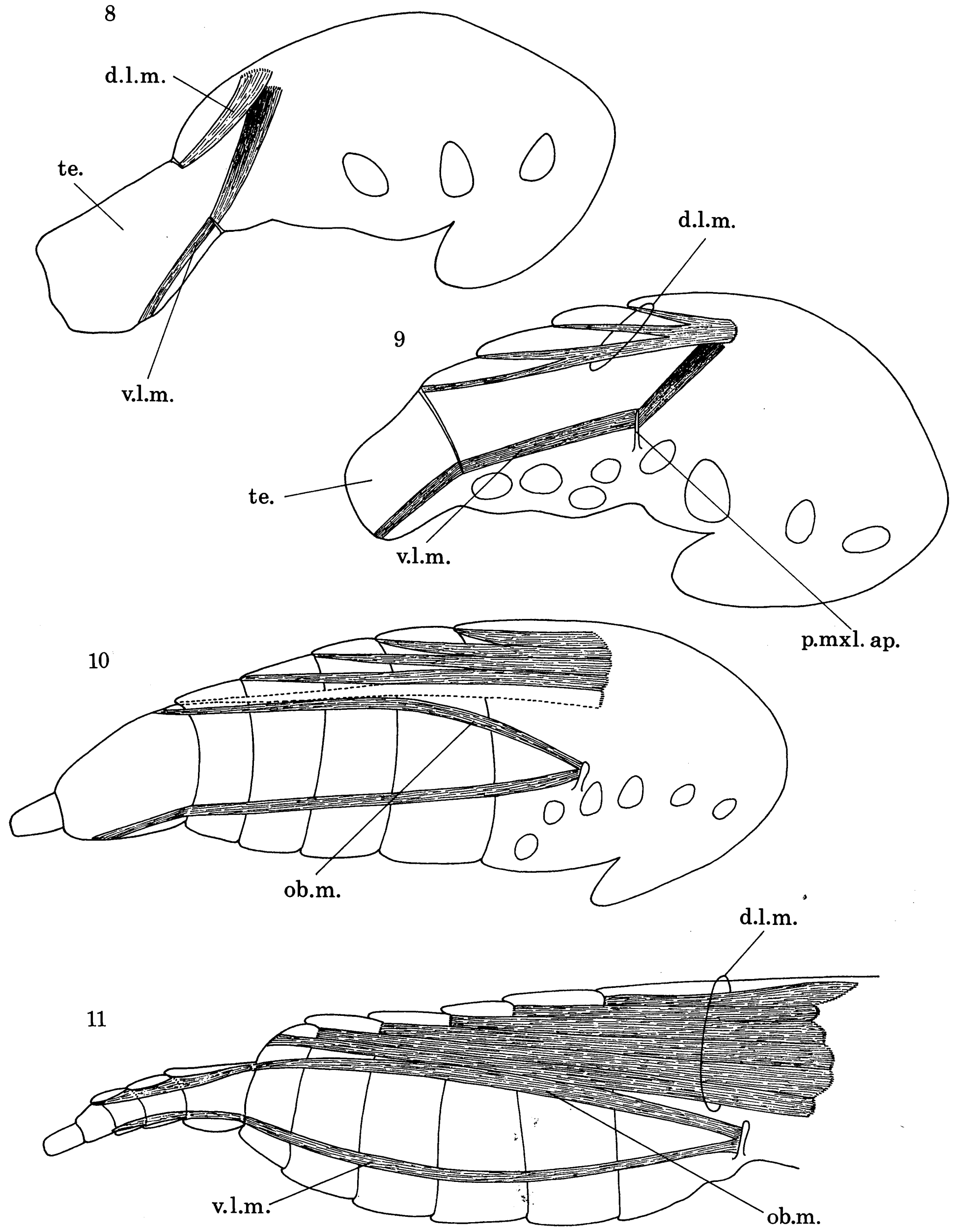

FIGURE 8. Median internal view of the trunk muscles of nauplius III of *Calanus*, adapted from Perryman (1961).

FIGURE 9. Median internal view of the trunk muscles of nauplius VI of *Calanus*, adapted from Perryman (1961).

FIGURE 10. Median internal view of the trunk muscles of copepodid I of *Calanus*, constructed semidiagrammatically from data given in Perryman (1961).

FIGURE 11. Median internal view of the trunk muscles of adult *Calanus*, adapted from Perryman (1961).

swimming movements. He regarded the evolution of a specialized limbless urosome as secondary although the urosome plays an important role in swimming and fulfils a number of other functions. The main difference between gymnoplean and podoplean organization is the presence of a larger prosome bearing five pairs of swimming legs in the former compared with four in the latter. This difference calls for a functional explanation.

As swimming legs are added during ontogeny their somites are incorporated into the prosome by loss of ventral intersomitic articulations. Manton (1977) stated that 'the whole skeletal system concerned with the copepod's jump is of such strength as to prevent unwanted flexure which might detract from the force of the jump'. This especially includes the ventral integument of the pedigerous somites and also explains why the pedigerous somites are capable only of dorsal telescopic movements. It is likely that in evolution, as in ontogeny, the formation of the prosome is linked to the development of the swimming legs. It is postulated that the ancestral stock of the Copepoda did not exhibit a major division of the body into prosome and urosome and that each postcephalosomic somite was separated from the preceding somite by a hoop of arthrodial membrane which allowed some telescoping. This ancestral copepod had six pairs of swimming legs, each with intercoxal sclerites (see Boxshall *et al.* 1984), which beat metachronally but were not modified to produce a strong jump. The sixth legs were probably already specialized as a reproductive structure at this stage. The evolution of the prosome with its complex ventral wall lacking articulation between somites appears to have been closely linked to the perfection of the jumping mode of locomotion. The mainly pelagic gymnopleans usually swim by vibration of the cephalic appendages and jumping is used primarily as an escape mechanism, whereas the mainly benthic podopleans normally swim by repeated jumping movements of the swimming legs. Such a difference in behaviour within the ancestral copepod stock could have led, by selection, to structural specialization; five pairs of legs would produce a stronger jump for the escape mechanism of gymnopleans whereas reduction to four pairs, as in podopleans, is one way of allowing more rapid repetition of the jump while retaining a basically metachronal rhythm. Despite these differences both escape reactions are highly efficient.

The precise role of the prosome is therefore the major determinant of the number of pedigerous somites it incorporates, and hence of the position of the prosome–urosome joint. The evolutionary differentiation of the joint itself from the original telescopic condition into a pivot joint with restricted movement is more likely to have been determined by the specialized functions of the urosome, in particular by its role in locomotion.

The limbless urosome serves several functions, including steering and stabilizing the body during swimming. A steering role has been attributed to it by a number of workers (Perryman 1961; Park 1966; Strickler 1974) but its morphology is not ideally suited to this role because, to maximize its turning effect, it should have the ability to flex laterally at one or more intersomitic joint, especially the proximal prosome–urosome joint, and also the caudal setae should form a vertical fan along the longitudinal axis. In pelagic copepods almost none of the characters predicted is present. There is little, if any, lateral flexion at the prosome–urosome joint. There is typically some fusion of urosome somites which are reduced to four in *Calanus*, *Metridia* and *Mormonilla*, and to three in *Euaugaptilus* and *Epilabidocera*. This trend toward reduced segmentation is widespread and carries with it a concomitant reduction in flexibility. Lastly, the caudal setae are arranged not as a vertical but as a horizontal fan. In pelagic copepods, at least, it would appear that some role other than steering determines the form of the urosome. Some degree of turning can be achieved by lateral flexion of the urosome but, as Strickler (1974) found in *Epischura* and *Cyclops*, the antennules are probably much more important in this role. Steering however, may be a major function of the urosome in vermiform interstitial harpacticoids which appear capable of some lateral flexion at the prosome–urosome joint as well as the urosomal joints.

Perryman (1961) found that when *Calanus* is at rest with its legs directed forwards or is swimming slowly by means of its cephalic appendages, the prosome is held horizontally and the urosome flexed dorsally at an angle of 30–40°. During the remotor swing the urosome is swung ventrally coming to rest almost vertically downwards. Strickler (1974) analysed the movement of the urosome in more detail in *Cyclops*. He found it was flapped dorsoventrally during swimming and, in addition, that the angle between the fan of caudal setae and urosome varied during the cycle of swimming movements. He identified the downwards flap as a power stroke the effect of which is enhanced by the setal fan. However, it is probable that urosomal flapping is more important in controlling the pitch or attitude of the copepod in the water. If the urosome is held ventrally across the anteroposterior current produced during the remoter swing the anterior end of the copepod would be lowered. Similarly if it is flexed dorsally this would raise the anterior end. Finally, the urosome may also act as a stabilizer with the horizontal fan of caudal setae assisting the laterally directed antennules in reducing roll about the longitudinal axis.

5. Skeletomusculature of the cephalosomic appendages

All the extrinsic and intrinsic muscles of the appendages are illustrated. They are named according to presumed function except when this is not clear, in which case names relate to position within the appendage. The courses of the major muscles are described but the complexity, in *Euaugaptilus* especially, is such that it was considered unnecessary to detail all sites of origin and insertion for minor muscles except when this is not clear from the figures.

(*a*) *Euaugaptilus*

(i) *Antennule*

The female antennule (figure 13) is 25-segmented. The first two segments are fused to form a functional unit, rigid distally, more flexible proximally. The angle at which they are fused directs the distal segments laterally rather than ventrally. The proximal articulation with the head (figure 12) allows primarily for a promotor–remotor swing of the whole limb about the oblique posterolateral to anteromedial pivot line. Segments 2–25 are separated from each other by telescopic joints, each provided with a narrow ring of arthrodial membrane allowing limited flexion in any direction. The joint between segments 14 and 15 shows some indication of specialization restricting flexion mainly to one plane; that between segments 8 and 9 is unmodified, as found by Bowman (1978) for other genera of the Augaptilidae.

The extrinsic antennulary muscles (figures 13 and 15) originate on the dorsolateral wall in the anterior part of the cephalosome, except for the long levator (atl. lev.) which originates dorsally in the mandibular somite. Two large (atl. rem. 1–2) and two small (atl. rem. 3–4) muscles insert around the posterior rim of segment 1 and produce remotion of the whole limb about the proximal pivot line (figure 12). These are opposed by a single promotor (atl. pr.m.) inserting anterolaterally. A short depressor (atl. dep.) inserts anterolaterally on segment 2. The long levator passes into the limb, attaching proximally in segment 4 before inserting on the proximal rim of segment 8.

The intrinsic muscles (figure 13) all originate on the rigid integument of segment 2. The three bundles of flexors are distributed evenly around the circumference of the cylindrical antennule.

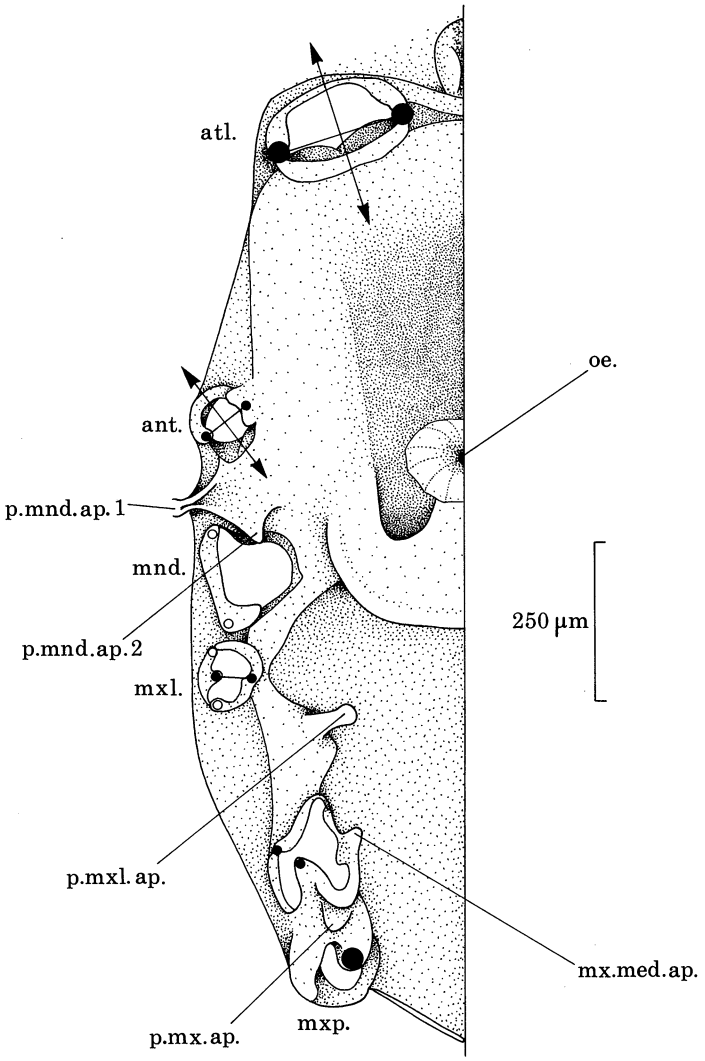

FIGURE 12. Internal view of the ventral surface of the cephalosome of *Euaugaptilus*, showing the basal foramina of the appendages. The positions of the main pivots, pivot lines and axes of movement are also marked.

All three attach to the proximal rim of each segment from segment 4 onwards. Flexor 3 inserts proximally on segment 19 whereas flexors 1 and 2 continue as an antagonistic pair to the apical segment.

The male antennules (figure 14) are asymmetrical. The right is unmodified and similar to that of the female. The left is geniculate and used for grasping the female during the spermatophore placement. Its proximal portion is similar to that of the female as far as segment 18, though the articulation between segments 6 and 7 is provided with more arthrodial membrane. Between segments 18 and 19 is a specialized joint which allows the distal portion to be flexed anteroventrally. Segment 19 represents three fused segments (19, 20 and 21) of the female. Segment 20 represents two fused segments (22 and 23). Segments 21 and 22 are simple segments homologous with segments 24 and 25 of the female.

The extrinsic musculature of both male antennules is the same as that of the female except that the long levator attaches to segments 5 and 6 and then inserts on segment 7. The intrinsic

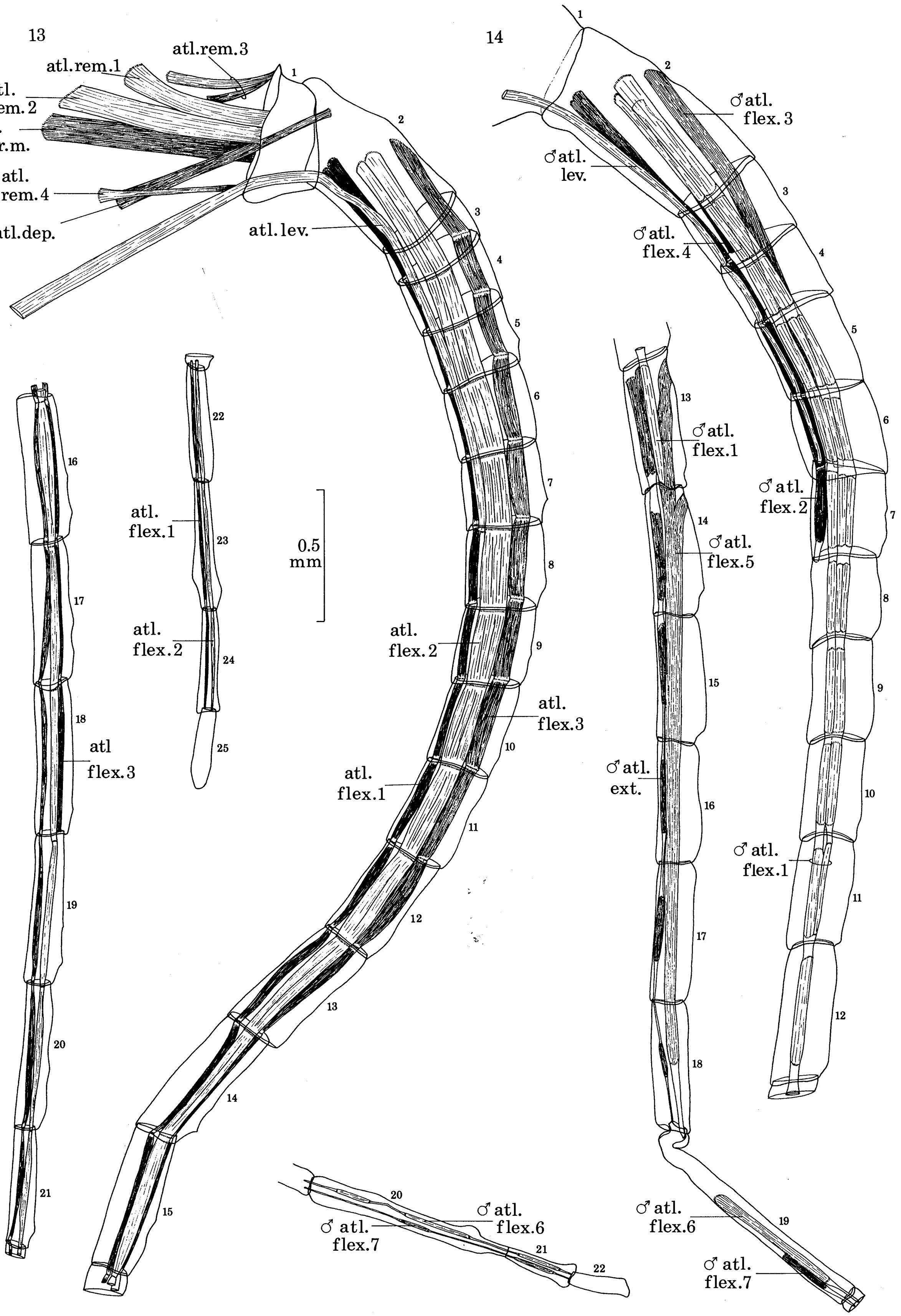

FIGURE 13. Posteroventral view of the left antennule of female *Euaugaptilus*, showing musculature. Segments 1–25 are numbered.

FIGURE 14. Posteroventral view of the geniculate left antennule of male *Euaugaptilus*, showing intrinsic musculature only. Segments 1–22 are numbered.

muscles (figure 14) are different, there being an additional muscle and some different insertion sites. The proximal flexors (♂atl. flex. 1–4) all originate in segment 2 as do the three of the female. Flexor 1 has a double origin and attaches proximally on every segment from segment 3 to its insertion on segment 14. Flexor 2 has a double origin but extends only to segment 8. Flexor 3 inserts proximally on segment 7. Flexor 4, absent from the female, extends only as far as the rim of segment 4. A pair of antagonistic muscles originates in segment 13, one of which (♂atl. flex. 5) also has some fibres originating in segment 14. This muscle inserts on the proximal rim of segment 19 at the geniculation without attaching in any intervening segment. It flexes the entire distal portion. The other (♂atl. ext.) attaches proximally in each segment from 14 to 18 and inserts on the rim of segment 19 at the geniculate joint. It extends the whole distal portion. A pair of opposing flexors originates in segment 19 and is responsible for flexing the remaining segments. Flexor 6 has an intermediate attachment point near the middle of segment 20 indicating this segment's derivation from two fused segments.

(ii) *Antenna*

The biramous antenna articulates with the head via a complex joint about whose anteromedial to posterolateral pivot line (figure 12) the promotor–remotor swing takes place but which also allows significant adduction and abduction. Arthrodial membrane is present all round this joint. The protopodal segments are fused but a suture line marks the position of the vestigial coxa–basis joint. The thickness of the coxal integument varies greatly. As some muscles insert on thickened areas the limb may be capable of some flexion by deformation of the coxal integument. The basis is elongate and bears the endopod distally. The endopod comprises two segments, each articulating with the segment proximal to it via an anterolateral hinge. The exopod is eight-segmented and is located laterally in the proximal third of the basis. It articulates with the basis via a pivot joint at which the pivot line lies parallel to the long axis of the basis. Movement here is primarily a promotor–remotor swing of the ventrolaterally directed ramus. Simple telescopic joints separate the cylindrical exopod segments.

Numerous extrinsic muscles (figure 16), which produce a range of whole limb movements, originate on the dorsal and lateral walls of the cephalosome and on the anterior ventral cephalic tendon. A large promotor (ant. pr.m. 1) inserts anteromedially on the proximal rim of the limb and two smaller promotors (ant. pr.m. 2–3) share a common anterolateral insertion. Three remotors (ant. rem. 1–3) share a common posterior insertion on a thickened area of integument about at the level of the coxa–basis suture. A long muscle (ant. rem. 4) originating high on the dorsal wall inserts on the thickened area of anterior coxal wall. Its contraction probably assists the remotor swing once the limb passes its midpoint. Also originating on the cephalosome wall but lower down are a short abductor (ant. abd.) which inserts laterally inside the limb and an exopod remotor (figure 17, ant. exp. rem. 1) which inserts posteriorly on the proximal rim of this ramus. Three muscles (ant. add. 1–3) originate close together on the ventral surface of suspensory tendon 5 near its attachment to the anterior ventral cephalic tendon (figure 32). Two of these insert on the posterior rim of the limb and produce adduction and some remotion of the whole limb. The third passes into the limb to insert anteriorly near the origin of exopod remotors 2–3. A fourth adductor (ant. add. 4) follows a similar course to adductors 1–2, inserting on the posterior rim, but its origin is on a small free tendon located ventral to the anterior cephalic tendon. This free tendon is held in position by suspensor muscles which pass up to the anterior cephalic tendon and down the ventral body wall, and by the antagonistic action of the paired adductors.

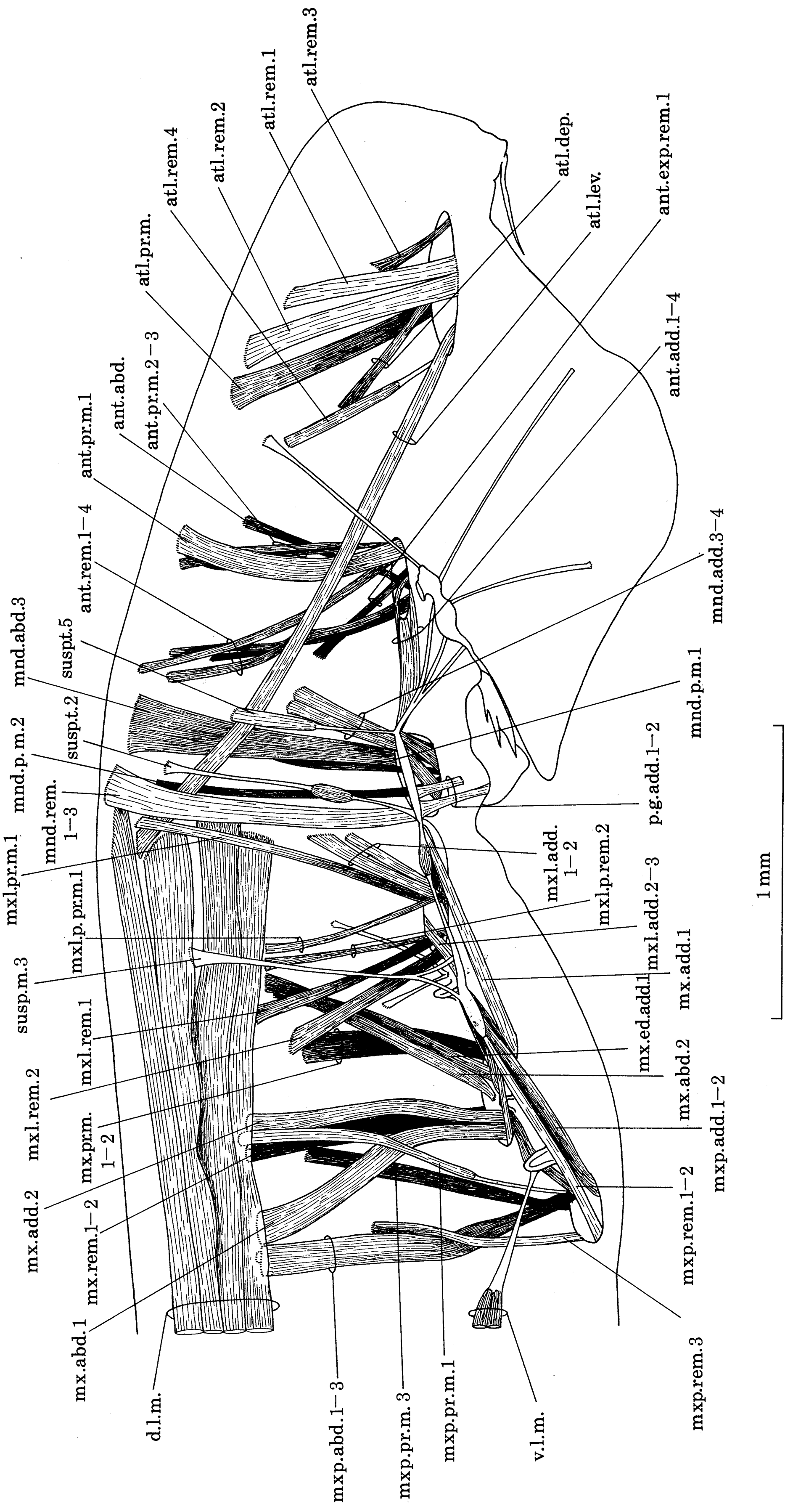

FIGURE 15. Median internal view of the musculature of the cephalosome. All other organs systems have been removed.

The intrinsic muscles are complex and difficult to interpret. Five of them (ant. at. 1–5) cannot be identified by their functional type. These are all situated around the anterior wall of the limb and all extend across the plane of the coxa–basis suture. Three endopod flexors (ant. end. flex. 1–3) originate posteriorly in both coxa and basis and insert in the endopod. As the basis is directed ventrally they act at the basis-endopod joint to flex the ramus laterally, and at the joint between segments 1 and 2, to direct the apex of the limb dorsally. When both of these joints are flexed the long apical setae of the endopod are directed up onto the dorsal shield covering the cephalosome. The setae are manipulated by apical muscles lying within the terminal segment of the ramus. The exopod (figure 17) is moved as a whole by the extrinsic remotor (ant. exp. rem. 1) and various intrinsic muscles. A flexor and two remotors originate close together on the anterior coxal wall. The former (ant. exp. flex. 1) inserts on exopod segment 2, the remotors (ant. exp. rem. 2–3) on the proximal rim of the ramus. The single promotor (ant. exp. pr.m.) originates in the basis and inserts on the rim. Another flexor (ant. exp. flex. 2) originates distally in the basis and inserts on the second segment. Within the exopod are two flexors and two apical muscles, the latter presumably manipulating the long apical setae.

(iii) *Labrum*

The labrum is a massive, posteriorly directed expansion of the ventral cephalic surface. It extends from behind the antennules, overlies the mouth, and continues as a free lobe forming the ventral wall of the preoral chamber . Its proximal portion represents a swelling of the cephalic surface but the true labrum is the free distal lobe containing all the musculature and the labral glands. There are three pairs of labral muscles (figure 71, lab. m. 1–3) and some oesophageal dilator muscles, all of which serve to dilate either the preoral chamber or the oesophagus.

(iv) *Mandible*

The mandible (figure 20) comprises a stout proximal segment (the coxa) and a biramous palp. The coxa bears a rigid gnathobase which extends medially, almost parallel to the ventral body surface, dorsal to the labrum. Its toothed margin is in close apposition to that of the other mandible. The coxa presents a wide foramen at its articulation with the head (figure 12). The small amounts of arthrodial membrane around this joint allow both promotion–remotion and adduction–abduction but seem insufficient to account for the high mobility of this limb observed in living copepods. The palp has a two-segmented endopod and a four-segmented exopod. Its basis is constricted proximally at its joint with the coxa. This joint has a well developed medial and a weak lateral pivot and ample arthrodial membrane. The main movement of the palp appears to be adduction about the medial pivot but a promotor–remotor swing about the weak transverse pivot line is also possible. The joints within the palp are all simple telescopic joints.

The extrinsic muscles fall into three groups on the basis of their origins, on the dorsal body wall (figure 15), on a premandibular apodeme (figure 12, p.mnd. ap. 1) situated low on the lateral wall, and on the anterior cephalic tendon (figure 32). The foremost group comprises the well developed remotors, here regarded as consisting of three bundles (mnd. rem. 1–3) which insert posteriorly on the coxal rim, the large abductor 3 which inserts laterally on the rim, and two slender palp muscles (mnd.p. m. 1–2) which may act as an antagonistic pair producing

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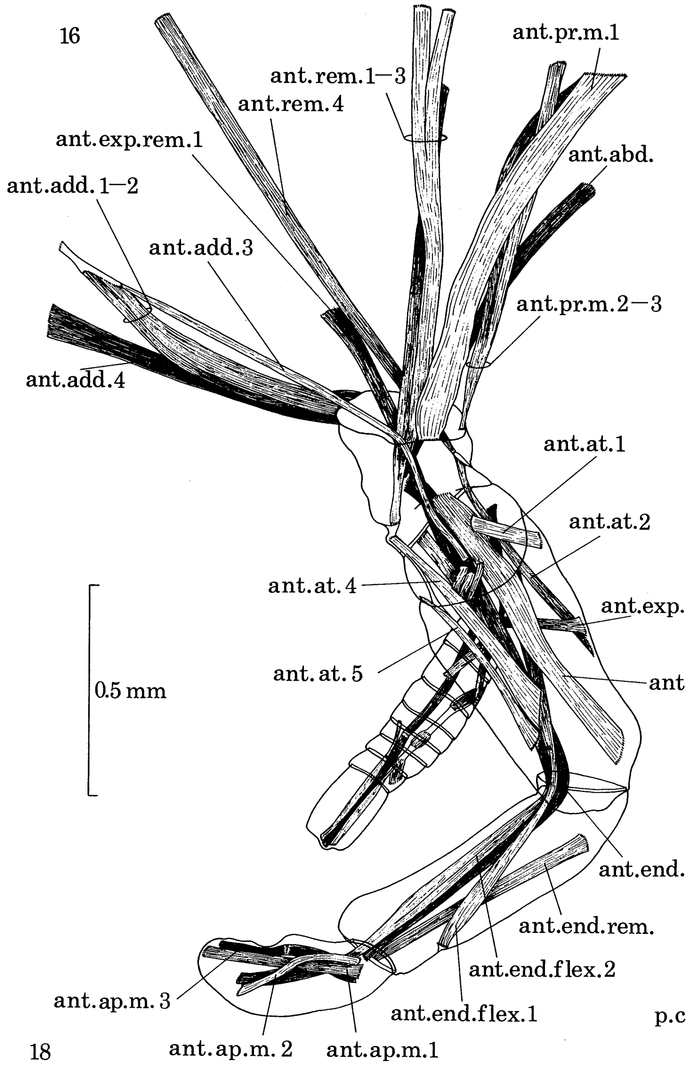

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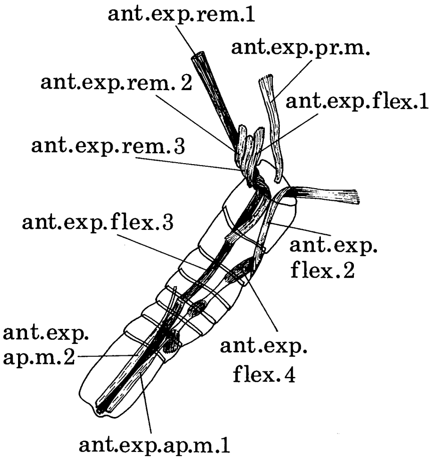

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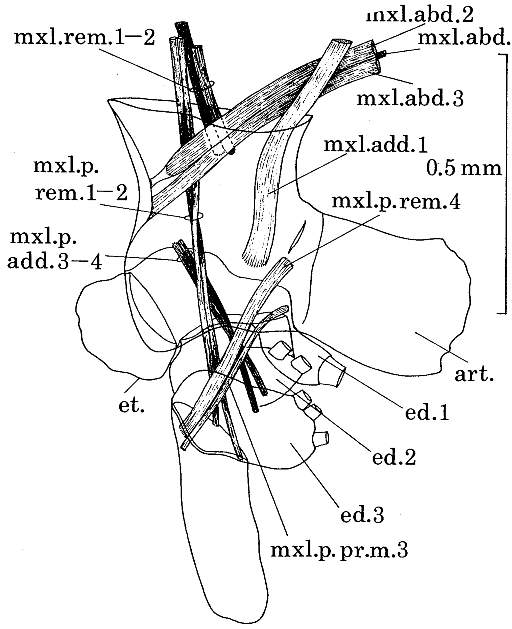

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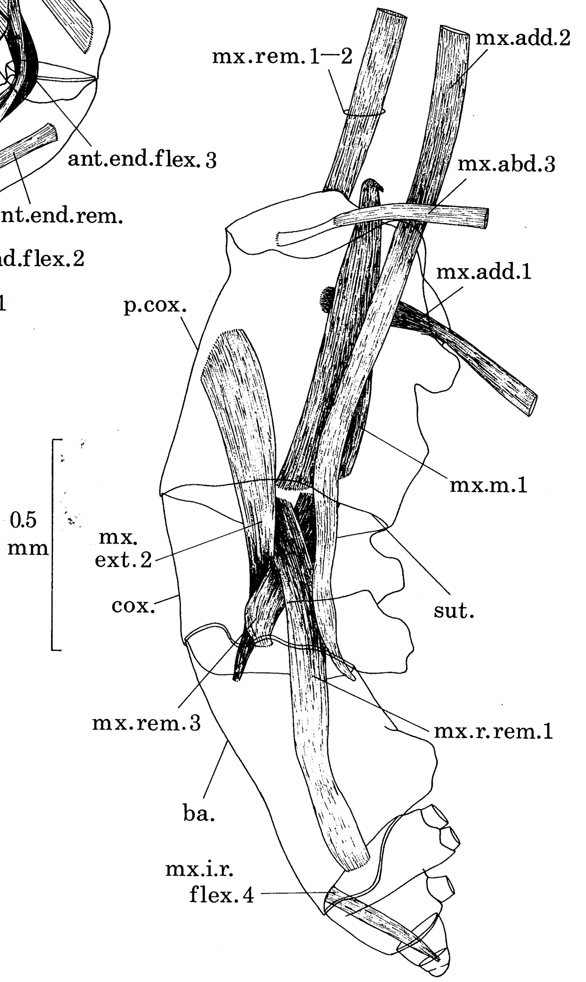

FIGURE 16. Anteromedial view of antenna, showing musculature.

FIGURE 17. Anterior view of antennary exopod and its musculature.

FIGURE 18. Anterior view of maxillule; most of the anterior muscles have been removed to reveal the posterior muscles.

FIGURE 19. Anterior view of maxilla; most of the anterior muscles have been removed to reveal the posterior muscles.

the promotor–remotor swing. The second group comprises a pair of short, powerful adductors (mnd. add. 3–4) inserting in the gnathobase, anteromedial to the palp articulation. The third group comprises five muscles; two adductors (mnd. add. 1–2) which insert on the posterodistal coxal wall, two abductor/promotor muscles (mnd. abd./pr.m. 1–2) which insert in the anterolateral angle and along the anterior wall of the coxa, and a palp flexor (mnd.p. end. flex. 1) which extends into the apical segment of the endopod. This flexor may assist in adducting the palp as a whole, acting together with a short intrinsic adductor (mnd.p. add. 1) which originates posteriorly in the coxa and inserts posteriorly in the basis. Another endopod flexor (mnd.p. end. flex. 2) originates on the lateral coxal wall and extends into the apical segment of the ramus. Movement of the exopod is produced by an antagonistic flexor and extensor pair. Both originate in the basis and insert on the fourth and first segments respectively.

(v) *Paragnath*

The paragnaths are short ridges which extend from the gap between the bases of the mandible and the maxillule, posteriorly at first, and then curve medially at the level of the apex of the labrum. They comprise most of the lateral walls of the preoral food chamber and also partly delimit the posterior extent of the chamber though there is a considerable gap in the midline between them. Their thick integument is continuous with the thickened dorsal wall of the preoral chamber. They are not capable of significant adduction.

The paragnaths have two pairs of muscles (figure 32, p.g. add. 1–2). Both arise from the ventral surface of the posterior hoop of the anterior ventral cephalic tendon (a.v.c.t.), pass ventrally through channels at the anterior end of the suboesophageal ganglion (see also figure 71), and insert posterodistally on the paragnaths. They may be able to move the paragnaths to a limited extent, by deformation of the basal integument as they have no basal articulation, but probably serve primarily as suspensors of the free cephalic tendons.

(vi) *Maxillule*

The copepod maxillule (figure 21) is here regarded as comprising a three-segmented protopod (praecoxa, coxa and basis), an endopod and an exopod (see §5*d*). In *Euaugaptilus* the praecoxa and coxa are fused but the line of fusion is marked by a suture, present on the posterior surface but not the anterior. The praecoxa has a large movable endite, the arthrite, proximally. The coxa has a slender endite (ed. 1) and a large flattened exite (et.), and the basis has two endites (ed. 2–3). There is a one-segmented exopod and no endopod. Movement at the articulation with the head occurs primarily about two pivot lines (figure 12), one transverse about which the promotor–remotor swing takes place, the other antero-posterior near the lateral margin of the limb, allowing adduction–abduction. The praecoxal arthrite is delimited posteriorly from the segment by a fold in the integument and is capable of some flexion relative to the segment. The coxal exite is also capable of movement but this must depend on deformation of the integument as no articulation is present. Posteriorly the plane of fusion between praecoxa and coxa is marked by a suture which extends to the margin of the endite. There is a true coxa–basis articulation (figures 18 and 21), with arthrodial membrane all round, which permits a range of relative movements. The basis has two medially directed endites and is marked on its anterior surface by an integumental fold continuous with the proximal margin of the distal endite. The distal endite may represent the vestigial endopod fused to the basis. The basis–exopod joint is also a true articulation, with arthrodial membrane, movement at which is mainly a promotor–remotor swing though some adduction is probably possible.

The extrinsic muscles originate high on the dorsal and lateral walls of the cephalosome (figure 15), on both anterior and posterior cephalic tendons and on the ventral wall of the cephalosome just anterior to the limb base. All muscles are illustrated in figure 21, only the posterior muscles in figure 18. Originating high on the dorsal shield is a promotor (mxl. pr.m. 1) which inserts via a long tendinous portion on the anterolateral praecoxal wall. This is opposed by two remotors (mxl. rem. 1–2) which originate posteriorly on the dorsolateral body wall and insert posteriorly on the praecoxa (figure 18). Two other remotors (mxl.p. rem. 1–2) originate nearby and insert posteriorly and medially on the proximal rim of the exopod. Two short muscles (mxl. add. 2–3) originate low on the lateral wall and pass obliquely into the limb to insert on the thickened area of integument on the anterior wall of the praecoxa near the base of the arthrite (figure 21). In addition to moving the arthrite these may produce some adduction and promotion of the whole limb. Five muscles originate on the anterior cephalic tendon (figure 32) and insert at several sites in the protopodal segments. That inserting on the posterior wall of the praecoxa (figure 18, mxl. add. 1) is probably an adductor. Two insert on the proximal rim of the basis, one posteromedially (mxl.p. rem. 5) which produces some remotion and adduction of the basis, the other anteromedially (mxl.p. pr.m. 1) producing promotion and adduction. Another muscle (mxl.p. pr.m. 2) inserts on the anterior wall of the basis at the level of its proximal endite, produces promotion of the basis and may also move the endite. The last of this bundle of muscles (mxl. abd. 1) appears to attach just inside the rim of the maxillule before extending into the coxal exite. This is the only muscle inserting in the exite and must be responsible for any flexion that occurs. Three muscles originate on the posterior cephalic tendon (mxl. abd. 2–4). They are all abductors inserting on the thickened lateral wall of the praecoxa. A single short muscle (mxl. add. 4) originates on the ventral wall of the cephalosome anterior to the limb base, passes into the limb and inserts medially on the proximal rim of the basis.

The intrinsic musculature is relatively simple because of the loss of the endopod. Three muscles originate on the thickened lateral wall of the praecoxa. One (mxl. i.g.b.m.) runs transversely to insert anteriorly on the thickened integument at the base of the arthrite, the others (mxl.p. pr.m. 4, mxl.p. abd. 2) insert anterolaterally on the rim of the basis and produce both promotion and abduction of the palp. One of a pair of slender muscles (mxl.p. add. 3–4) originating posteriorly in the praecoxa inserts on the proximal endite, the other on the distal endite of the basis. An antagonistic promotor and remotor originate medially in the praecoxa and coxa respectively (figure 18, mxl.p. pr.m. 3, rem. 4) and both insert around the lateral margin of the exopod. Also inserting on the proximal rim of the exopod is a short remotor (mxl.p. exp. rem.) which originates in the basis. Three exopod apical muscles originate anteriorly in the middle of the basis and pass to the apex of the ramus where they manipulate the apical setae by deforming the integument of the apex.

(vii) *Maxilla*

The basic copepod maxilla is here regarded as comprising a praecoxa and coxa each bearing two endites, a basis bearing one endite and an endopod of a variable number of segments (see §5*d*). In *Euaugaptilus* the praecoxa and coxa are partly fused, forming a syncoxa, but a suture line marks the boundary between them (figure 19). The endopod is treated as three-segmented although the apical segment almost certainly represents two fused segments. A wide range of movements is possible at the joint with the head as there is no strongly developed

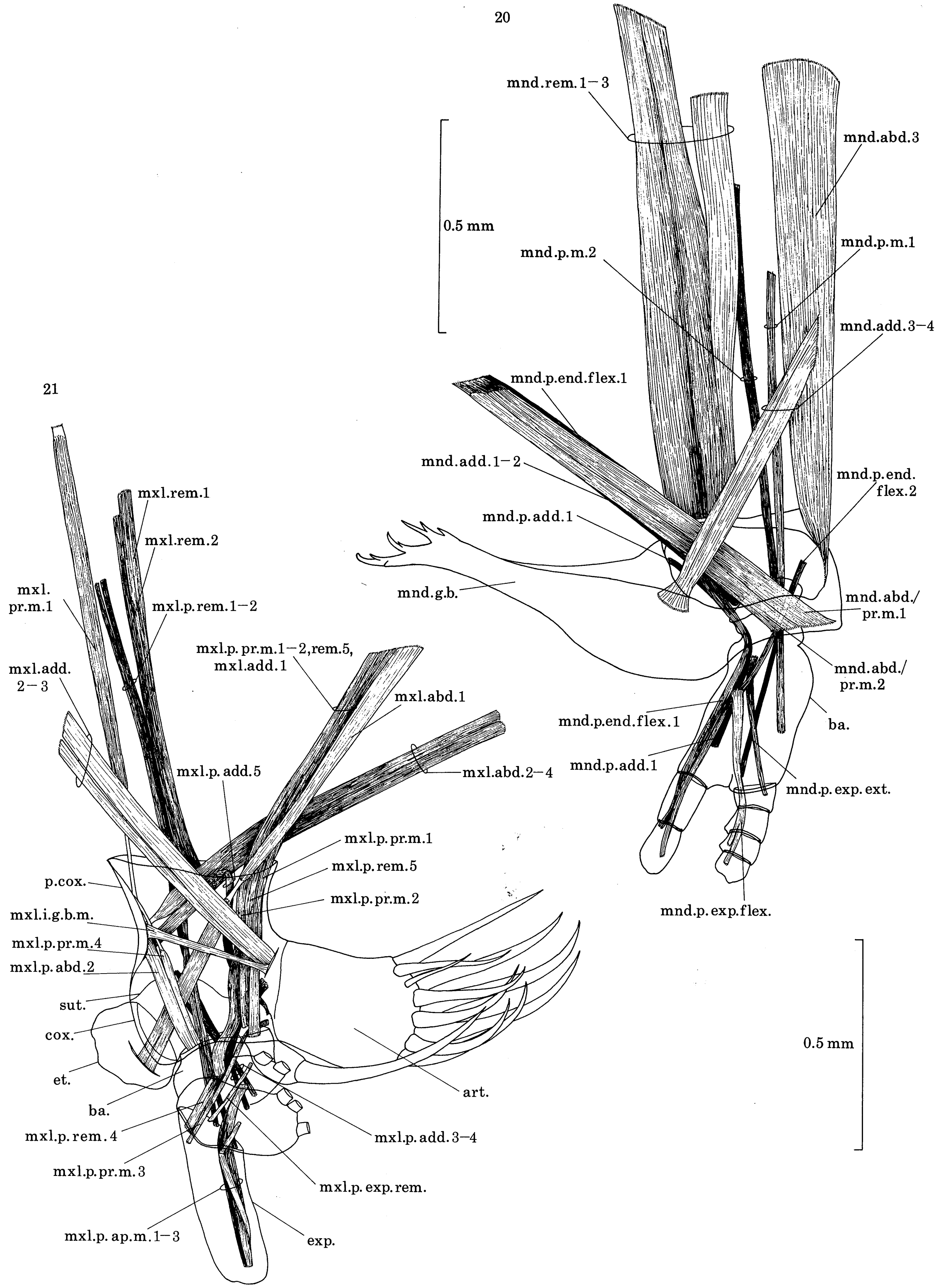

Figure 20. Anterior view of mandible, showing musculature.

Figure 21. Anterior view of maxillule, showing musculature.

pivot line to restrict it. The whole limb is capable of promotion–remotion and adduction–abduction. Within it no flexion is possible at the praecoxa–coxa joint. Movement at the coxa–basis and basis–endopod joints is primarily adduction and abduction about an axis parallel to the long axis of the body. The joints between the endopod segments permit adduction and abduction movements relative to each other.

The extrinsic muscles (figure 22) originate on both cephalic tendons, on the dorsolateral wall and on the postmaxillary apodeme. The dorsolateral muscles have their origins in the adjacent maxillulary and maxillipedal somites as well as in the maxillary somite (figure 15). Displacement of the sites of origin presumably occurs during ontogeny and provides each muscle with a better mechanical advantage than is available from within the somite. Two muscles originate in the maxillulary somite. One (mx. ed. add. 1) inserts proximally on the distal coxal endite, the other (mx. abd. 2) proximally on the lateral praecoxal wall and acts as an abductor of the whole limb. Two short promotors (mx. pr.m. 1–2) originate anteriorly in the maxillary somite and insert anteriorly within the limb. These are opposed by a pair of remotors (mx. rem. 1–2) originating posteriorly within the somite and inserting posteriorly on the rim of the praecoxa. A long adductor (mx. add. 2) originates adjacent to the remotors and inserts medially on the proximal rim of the basis. A long muscle (mx. abd. 1) originates in the maxillipedal somite, passes into the maxilla attaching to the praecoxal wall just inside the rim and again just inside the coxa, before inserting laterally on the proximal rim of the basis. Its function is abduction of the whole limb and of the basis relative to the coxa.

A single adductor originates posteriorly on the ventral surface of the anterior cephalic tendon (figure 32) and inserts posteromedially in the praecoxa (figure 19, mx. add. 1). Four major muscles originate on the posterior cephalic tendon. Two have a double origin but single insertions. The large mx. add. 3 originates mainly on the posterior cephalic tendon but a small strand arises from the posterior segment of suspensory tendon 1. These insert together on the anteromedial wall of the praecoxa. Muscle mx. ed. add. 3 passes over the rim of the limb into the coxa to insert at the proximal edge of the distal endite, presumably causing it to adduct. A large adductor (mx. add. 4) originates on the broad posterior portion of the posterior cephalic tendon, passes into the limb and inserts anteromedially on the proximal rim of the basis. The fourth muscle (mx. abd. 3) originates at the attachment of suspensory tendon 4 to the posterior cephalic tendon, passes posterolaterally around the medial maxillary apodeme (figure 32, med. mx. ap.) to a posterolateral insertion just inside the limb. It presumably produces abduction of the whole limb. Muscle mx. m. 1 originating on the postmaxillary apodeme curves over the rim of the limb and passes down to a broad, fan-like insertion on the distal part of the posterior wall of the praecoxa. Its function is difficult to ascertain.

Two intrinsic muscles originate on the anteromedial praecoxal wall near the insertion sites of promotors 1 and 2 (figure 22). They may represent continuations of the promotors, in which case the common origin and insertion site represents an intermediate tendinous attachment. One of them (mx. ed. flex.) is double stranded and inserts distal to the base of the first praecoxal endite, the other (mx. ed. add. 2) inserts at the base of the distal coxal endite. A broad extensor (mx. ext. 2) originates laterally in the praecoxa and inserts posterolaterally on the rim of the basis. A shorter remotor (figure 19, mx. rem. 3) originates posterodistally in the praecoxa and inserts posteriorly on the rim of the basis. This is opposed by a long promotor (mx. pr.m. 3) originating proximally on the medial praecoxal wall and inserting anteriorly on the rim of the basis. A single intrinsic muscle passes through the plane of the coxa–basis joint to insert directly

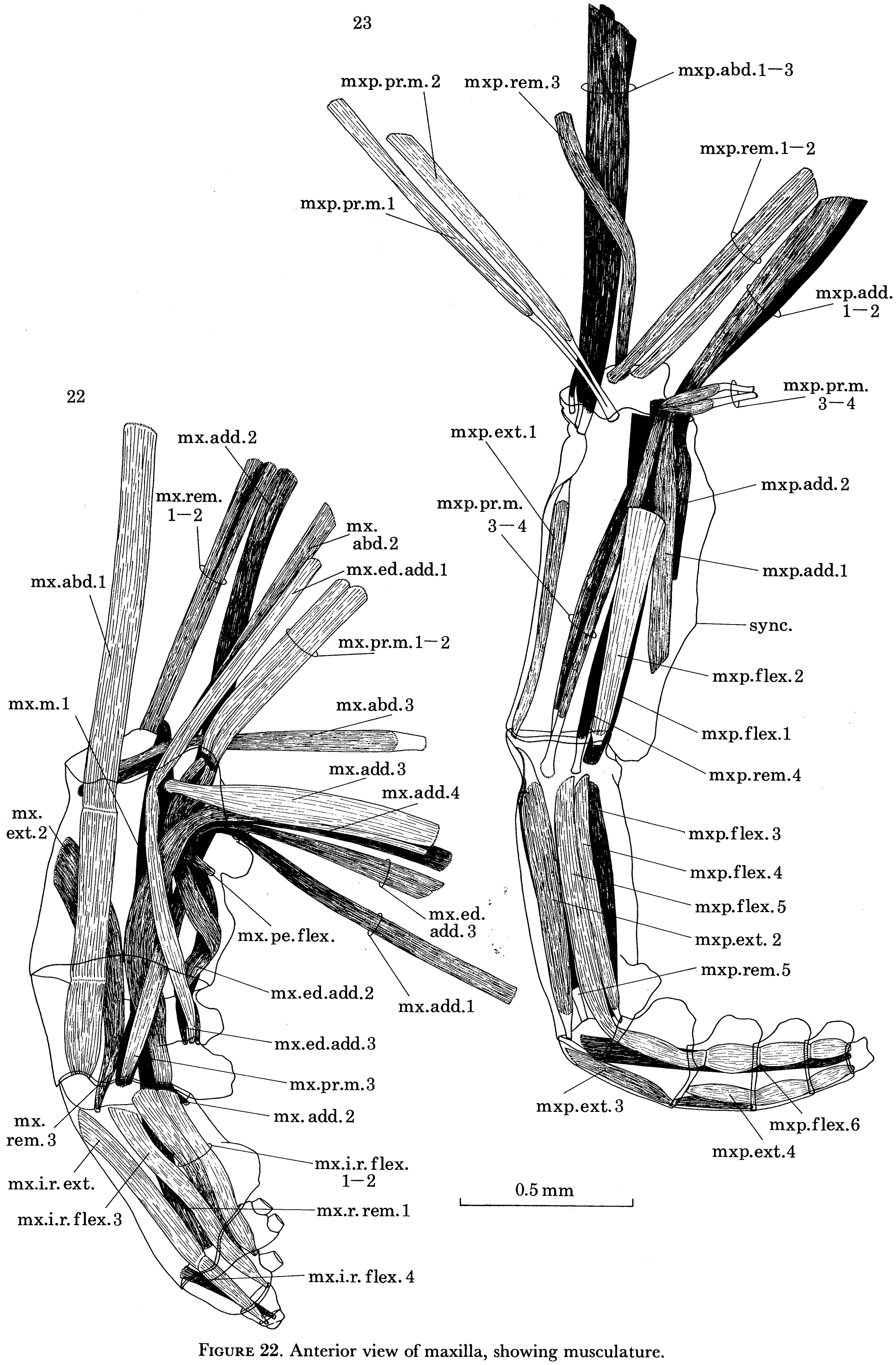

Figure 22. Anterior view of maxilla, showing musculature.

Figure 23. Anterior view of maxilliped, showing musculature.

on the endopod. This remotor (mx.r. rem. 1) originates in the praecoxa. Five muscles originate within the basis (figure 22) and flex and extend the endopod relative to the basis and the endopod segments relative to each other.

(viii) *Maxilliped*

The typical copepod maxilliped is here regarded as comprising a fused praecoxa and coxa, the syncoxa, a basis and one ramus of several segments, probably the endopod (see §5*d*). In *Euaugaptilus* the maxilliped has a five-segmented endopod (figure 23). A wide range of movements is possible at the head–limb joint, which has no dominant pivot line and is well supplied with arthrodial membrane. The whole limb is capable of promotion–remotion and adduction–abduction. Movement between the syncoxa and basis is primarily adduction–abduction but limited flexion in other planes may also be possible. Movement at the basis–endopod joint is restricted to adduction–abduction as there is a well developed dicondylar pivot line and arthrodial membrane only laterally and medially. Telescopic joints between the endopod segments allow mainly adduction–abduction movements.

Three groups of extrinsic muscles originate on the dorsolateral body wall (figure 15), on the posterior cephalic tendon (figure 32) or on the postmaxillary apodeme. A single promotor (mxp. pr.m. 1) originating on the wall of the maxillary somite and another (mxp. pr.m. 2) originating anteriorly within the maxillipedal somite insert together anteriorly just inside the proximal rim of the syncoxa (figure 23). They are opposed by three remotors (mxp. rem. 1–3) which insert posteriorly at the same level. One of these (rem. 3) originates on the body wall, the others on the posterior cephalic tendon. The three main abductors (mxp. abd. 1–3) originate on the body wall and insert on the thickened proximal area of the lateral wall of the syncoxa. The main adductors (mxp. add. 1–2) originate laterally on the posterior cephalic tendon, pass over the medial rim of the limb and insert separately on the medial wall of the syncoxa. The remaining pair of extrinsic muscles (mxp. pr.m. 3–4) originates on the postmaxillary apodeme. They pass over the rim of the syncoxa and down towards their common insertion on the anterior wall of the basis. They are probably promotors of the basis.

The syncoxa–basis articulation has four intrinsic muscles inserting around its proximal rim. An extensor (mxp. ext. 1) originating on the thickened lateral wall of the syncoxa inserts posterolaterally, a broad flexor (mxp. flex. 2) anteriorly, and two long remotor/adductors (mxp. rem. 4/flex. 1) posteromedially. No muscles pass through the coxa–basis joint without inserting there. Originating proximally within the basis are five muscles, four of which insert around the proximal rim of the first endopod segment. Two are flexors, two extensors. The fifth extends into the endopod, attaches proximally in segments 2–4 and inserts on segment 5. Two extensors and a flexor within the endopod move the segments relative to one another.

(*b*) *Mormonilla*

(i) *Antennule*

The antennule is three-segmented in *M. phasma*. Each segment is elongated but the first comprises over half the total length of the appendage. It articulates with the head via a dicondylar pivot joint in which the main pivot line lies horizontally in an oblique posterolateral to anteromedial direction (figure 24). Extensive arthrodial membrane on both sides of the pivot line permits a wide promotor–remotor swing. The proximal rim of the limb and its foramen lie in the horizontal plane but the first segment bends outwards through nearly a right angle

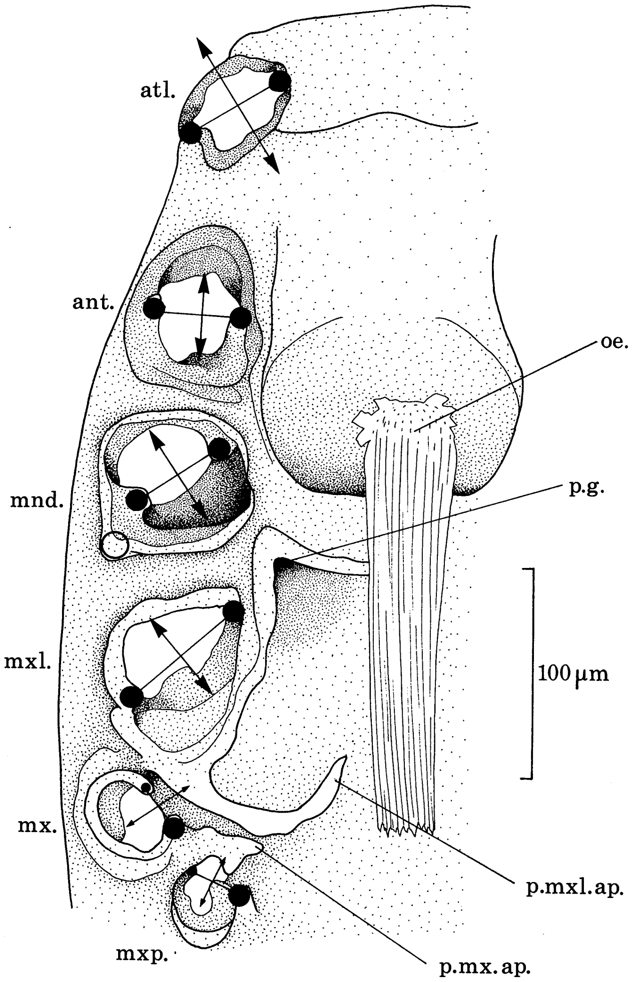

FIGURE 24. Internal view of the ventral surface of the cephalosome of *Mormonilla*, showing the basal foramina of the appendages. The positions of the pivots, pivot lines and axes of movement are also marked. Those of the mandibular palp and gnathobase are shown by filled and open circles respectively.

so that the distal part of the segment and the remainder of the limb are directed laterally and slightly ventrally. The promotor–remotor swing moves it from an anterolaterally directed to a posterolaterally directed position.

The musculature of the antennule is reduced to three extrinsic and an antagonistic pair of intrinsic muscles, and is illustrated in figures 25 and 28. One extrinsic (atl. lev.) originates on the anterior horn of the cephalic tendon.

(ii) *Antenna*

The antenna (figure 26) comprises a small undivided sympod, a long two-segmented endopod and a seven-segmented exopod. The joint with the head has a transverse pivot line with extensive arthrodial membrane either side allowing a promotor–remotor swing of the whole limb through a wide arc. This joint is rather loose and also has arthrodial membrane laterally and medially which may permit other rotational or adduction–abduction movements (figure 24). The sympod comprises fused coxa and basis and bears both rami distally. The joint

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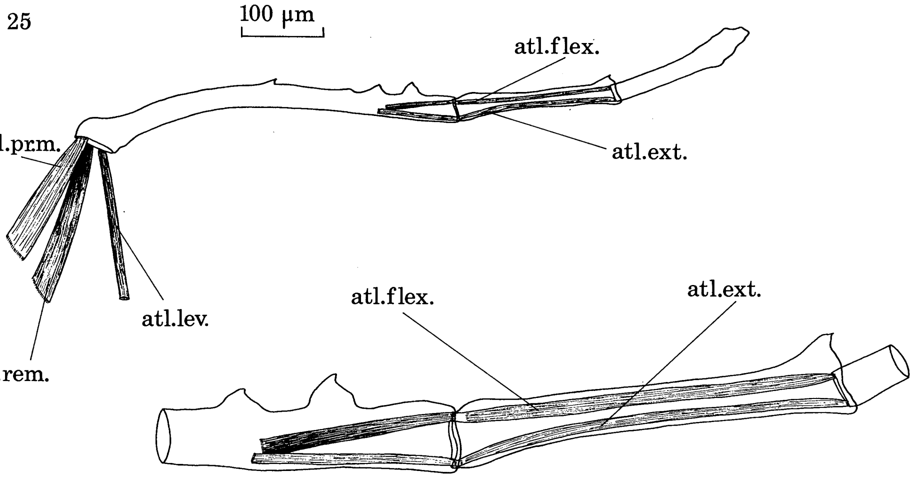

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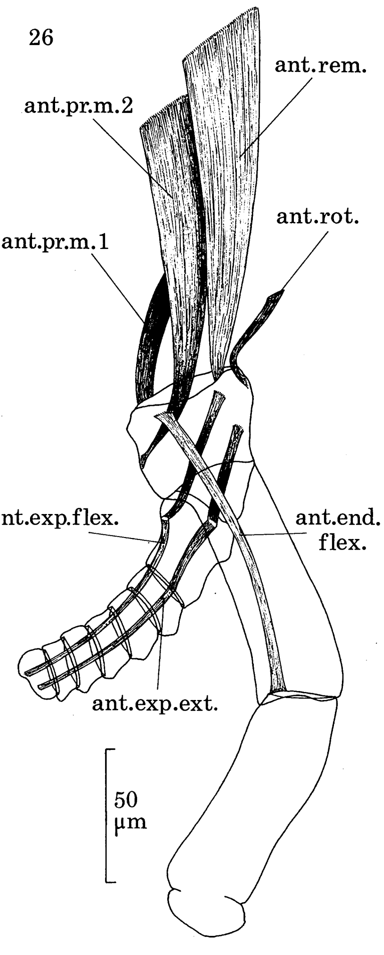

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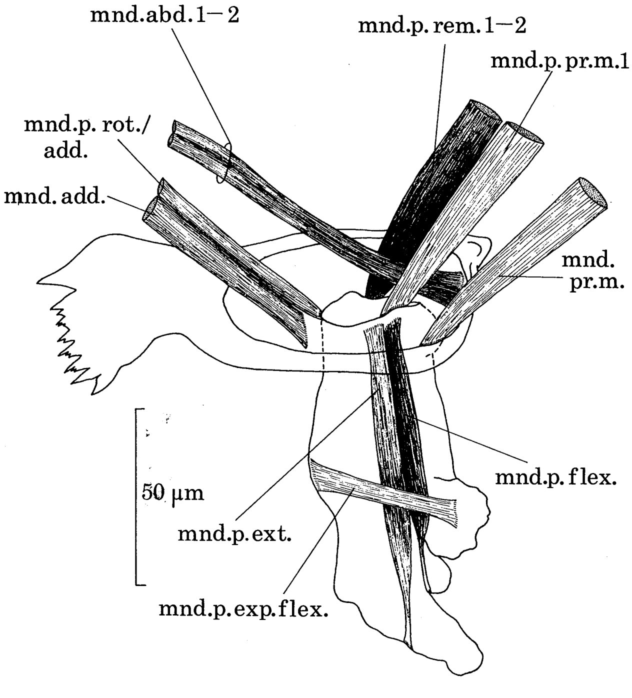

FIGURE 25. Posterior view of female antennule of *Mormonilla*, showing extrinsic musculature, with an inset showing intrinsic muscles.

FIGURE 26. Median view of antenna, showing musculature.

FIGURE 27. Anterior view of mandible, showing musculature.

between sympod and endopod is marked by a suture line but has no arthrodial membrane. The sympod and first endopod segment form a single, ventrally directed functional unit, the main movement of which is a promotor–remotor swing. The second segment flexes laterally about a medial hinge line. The exopod–sympod joint has a weakly developed anteroposterior pivot line lying in the horizontal plane, about which flexion and extension of the whole ramus takes place. Hoops of arthrodial membrane allow limited flexion between exopod segments.

Three extrinsic muscles (figures 26 and 28) originate on the dorsolateral wall, and a fourth (ant. rot.), identified as a rotator but which may act mostly as a remotor, originates on the anterior horn of the anterior cephalic tendon. The endopod has a single flexor which flexes laterally the second segment with its apical array of long setae, but it has no extensor. It is presumably exended by the elasticity of the integument in the lateral hinge. The exopod flexor (figure 26) raises the laterally directed exopod and the extensor lowers it. Contraction of the intraexopodal continuation of the flexor presumably spreads the fan of plumose setae on the inner ventral margin of the exopod thereby increasing its effective surface area. The intraexopodal continuation of the extensor would have the opposite effect.

(iii) *Labrum*

The labrum is an inflated, posteroventrally directed lobe which overlies the mouth and acts as the ventral wall of the preoral chamber. Its anterior limit is marked by a transverse furrow visible in ventral view. It appears to be formed as a ventral outgrowth of the antennary somite although the ventral cephalic wall in the antennulary somite is inflated where it meets the labrum (figure 28). All the labral muscles and labral glands lie within the antennary somite. The labral muscles (figure 28, lab. m.) dilate the preoral chamber and outermost part of the oesophagus.

(iv) *Mandible*

The mandible (figure 27) comprises a massive proximal segment bearing a well developed gnathobase and a distal palp. The proximal segment is regarded as the coxa (see §5*d*). The palp comprises the basis and two unsegmented distal lobes which probably represent the exopod and endopod. The head–mandible joint has a large opening and is provided with small amounts of arthrodial membrane all round. There is a well developed condyle at the posterolateral angle of the coxa about which most of the whole limb movements take place. The distal margin of the gnathobase carries several blades. A well developed dicondylar pivot joint (figure 24) with an oblique posterolateral to anteromedial pivot line separates the coxa and basis. Arthrodial membrane is present, allowing the promotor–remotor swing of the palp about this line. The rami have no true articulation with the basis.

The extrinsic muscles (figures 27 and 28) originate either on the dorsolateral wall or on the anterior cephalic tendon and its suspensory tendons. A large palp promotor (mnd.p. pr.m. 1) originates near the dorsal midline and inserts on the proximal rim of the basis anterior to the pivot line. This is opposed by a partly subdivided remotor (mnd.p. rem. 1–2) which follows a similar course but inserts posteriorly. The third dorsolateral muscle (mnd. pr.m.), a small promotor, inserts at the anterolateral angle of the coxa and swings the whole limb about the posterolateral condyle. Two of the remaining extrinsics (mnd. abd. 1–2) originate on the anterior cephalic tendon (figure 33). These are abductors that pass between the palp promotors and remotors before inserting on the lateral coxal wall. The last two extrinsic muscles originate

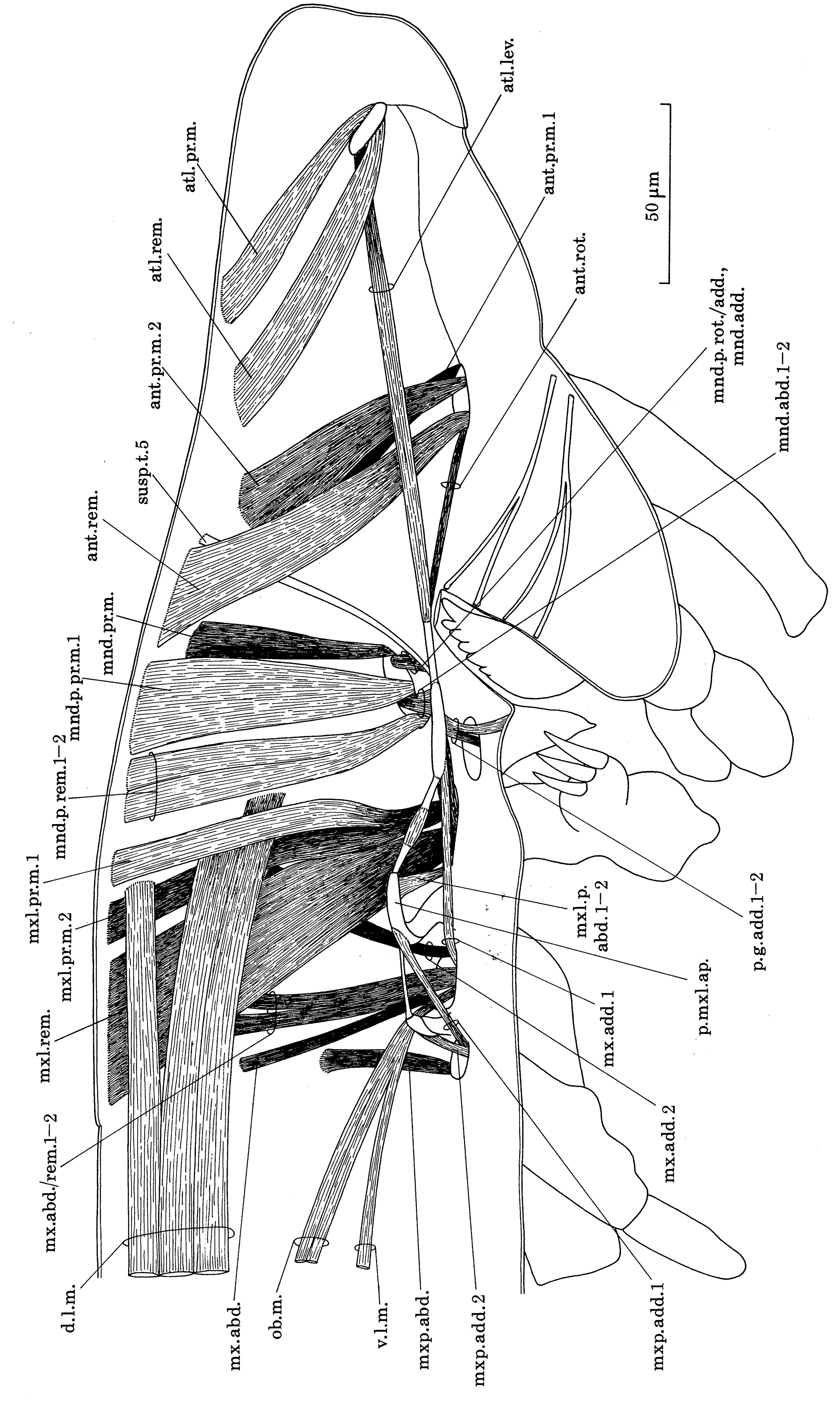

FIGURE 28. Median internal view of the musculature of the cephalosome of *Mormonilla*. All other organ systems have been removed.

on the proximal portion of suspensory tendon 5 (figure 33, susp.t. 5). One (mnd. add.) is the main adductor of the gnathobase inserting on its ventral wall medial to the palp foramen, the other (mnd.p. rot./add.) inserts medially on the rim of the basis and produces some adduction of the palp.

The intrinsic musculature is simple (figure 27). The extensor (mnd.p. ext.) and flexor (mnd.p. flex.) muscles are presumably involved in manipulating the fan of endopodal setae. The transverse flexor (mnd. exp. flex.) presumably moves the exopod by deforming its basal integument as there is no true articulation.

(v) *Paragnath*

The paragnaths are asymmetrical conical structures whose acute tips are directed anteriorly and broad bases, posteriorly (figure 69). They lie either side of the ventral midline and fill the gap between the mandibular gnathobase and the arthrite of the maxillule. Their tips have relatively thick integument. A pair of muscles is associated with each paragnath (figure 28). All arise from the ventral surface of the anterior cephalic tendon and pass dorsoventrally through canals in the suboesophageal ganglion. One muscle that passes into the paragnath and inserts posteriorly may move it by deformation of the integument around its base. The other inserts near the ventral midline and serves primarily as a suspensor of the cephalic tendon.

(vi) *Maxillule*

The maxillule (figure 29) is simplified and comprises a two-segmented protopod, an exopod and an endopod. The proximal part of the protopod is regarded as a syncoxa, representing the fused praecoxa and coxa (see § 5 *d*). It bears a large medial arthrite armed with several spines and setae around its distal margin. The syncoxa–basis joint is a true articulation. The basis telescopes slightly inside the syncoxa, and is provided with a small amount of arthrodial membrane all round. Both exopod and endopod are flattened and separated from the basis by a telescopic articulation with arthrodial membrane all round and no dominant pivot line. The maxillule–head articulation (figure 24) allows promotor–remotor movements about the oblique pivot line. There is a large amount of arthrodial membrane posteriorly and smaller amounts anteriorly and medially, the latter allowing adduction of the whole limb about the lateral margin which acts as the hinge line.

The extrinsic musculature is well developed (figures 28 and 29). A powerful remotor (mxl. rem.) with a broad origin high on the dorsal cephalic wall inserts posteriorly on the proximal rim of the syncoxa. It is opposed by two promotors (mxl. pr.m. 1–2) which originate anterior to it. One of these passes lateral to the dorsal longitudinal trunk muscles, the other medial, and they insert together on the anterior rim of the syncoxa. Two shorter muscles originate on the lateral cephalic wall, one (mxl. pr.m. 3) inserts on the anterior syncoxal wall near the base of the arthrite, the other (mxl.p. pr.m.) anteromedially on the proximal rim of the basis. Three muscles originate on the mid portion of the cephalic tendon. One (mxl.p. add.) passes through the syncoxa and inserts medially on the proximal rim of the basis. This produces adduction of the basis relative to the syncoxa. Another (mxl. add. 1) inserts medially inside the syncoxa, proximal to the arthrite and acts as the main adductor of the whole limb. The third (mxl. add. 2) follows a similar course but inserts medially just at the base of the arthrite. A pair of palp abductors (mxl.p. abd. 1–2) originates on the anterior surface of the postmaxillulary apodeme and inserts posteriorly on the proximal rim of the basis.

The three intrinsic muscles are shown in figure 29. The intragnathobasic muscle (mxl. i.g.b.m.) probably moves the arthrite. Each ramus has one flexor, that of the exopod producing remotion relative to the basis.

(vii) *Maxilla*

The uniramous maxilla (figure 30) is five-segmented. The first segment representing the syncoxa comprises over half the total length of the limb (see §5*d*). The second is the basis and the remaining three represent the endopod. The maxilla–head joint has a relatively small opening (figure 24) and is well supplied with arthrodial membrane. There is a well developed posteromedial pivot point about which much of the whole limb movement takes place, and a weaker anteromedial pivot. The line between them marks the axis about which the main adduction–abduction movement occurs. The syncoxa bears a short proximal endite and two long distal endites, and the basis a single proximal endite. The syncoxa–basis joint allows a predominantly adduction–abduction movement. The joints between basis and endopod, and between endopod segments are telescopic, each having a small amount of arthrodial membrane.

The extrinsic muscles (figures 28 and 30) originate variously on the cephalic tendon, the dorsolateral and lateral cephalic walls and the postmaxillary apodeme. The main adductor (mx. add. 1) originates posteriorly on the cephalic tendon (figure 33), passes obliquely back into the limb and inserts on the anteromedial syncoxal wall. A second adductor (mx. add. 2) originates on the lateral wall in the maxillulary somite and inserts in a similar position. Three muscles originate on the wall of the maxillary somite. One is an abductor (mx. abd.) which inserts on the posterolateral rim of the syncoxa, the others (mx. abd./rem. 1–2) are abductor/remotors which share a common insertion just inside the syncoxa on the posterior wall. Two muscles (mx. flex. 1–2) originate on the postmaxillary apodeme. One inserts proximal to the base of the distal syncoxal endite, the other on the medial rim of the basis. The former flexes the endite, the latter adducts the basis.

Figure 30 shows the three intrinsic muscles. That originating proximally in the syncoxa acts as an extensor opposing flexor 1. The other two act as a flexor–extensor pair for the endopod segments. The extensor will effectively spread the long distal setae of the endopod into an open fan, the flexor closes them again.

(viii) *Maxilliped*

The uniramous maxilliped (figure 31) consists of a long syncoxa and either the basis or, more likely, the fused basis and endopod. The syncoxa has three groups of setae along its medial margin, interpreted here as representing the three endites typically found on the syncoxae of copepod maxillipeds (see §5*d*). The head–maxilliped articulation (figure 24) is similar to that of the maxilla. The syncoxa–basis joint is a simple telescopic joint with most arthrodial membrane medially and laterally located to accommodate the flexor and extensor movements.

The main adductor muscle (mxp. add. 1) originates on the posterior surface of the postmaxillulary apodeme, passes over the rim of the maxilliped and inserts medially near the proximal group of enditic setae (figures 28 and 31). A single abductor (mxp. abd.) originates on the lateral body wall and inserts posterolaterally just inside the limb. A short muscle (mxp. add. 2) originates on the postmaxillary apodeme and inserts on a thickened intucking of the lateral wall of the syncoxa. This is primarily an adductor but may also produce some rotation of the limb. The disposition of the four intrinsic muscles is shown in figure 31.

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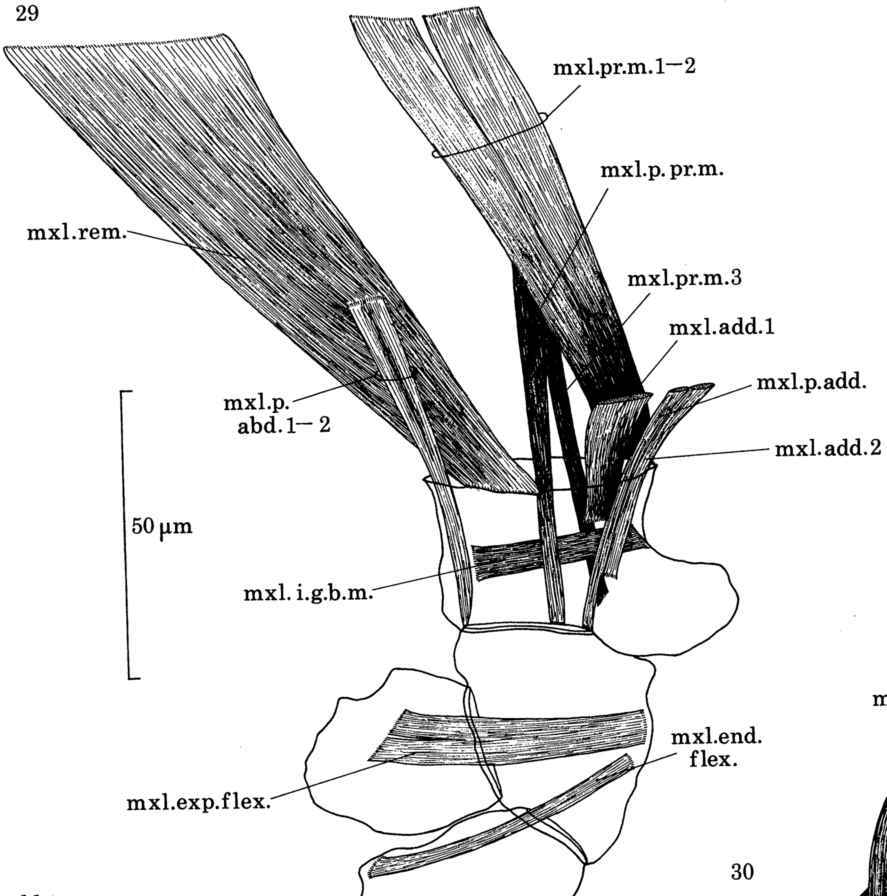

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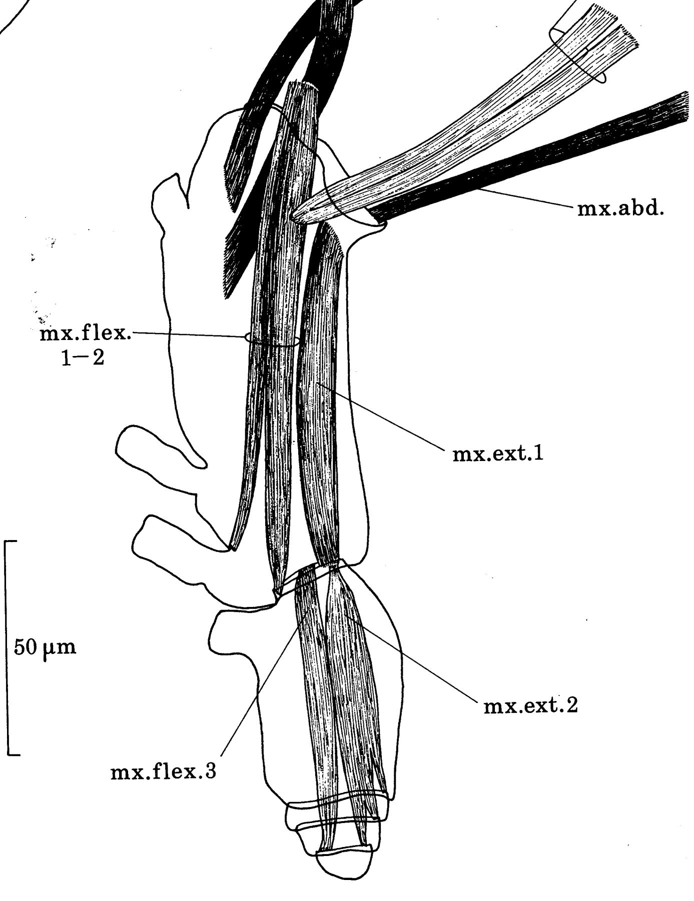

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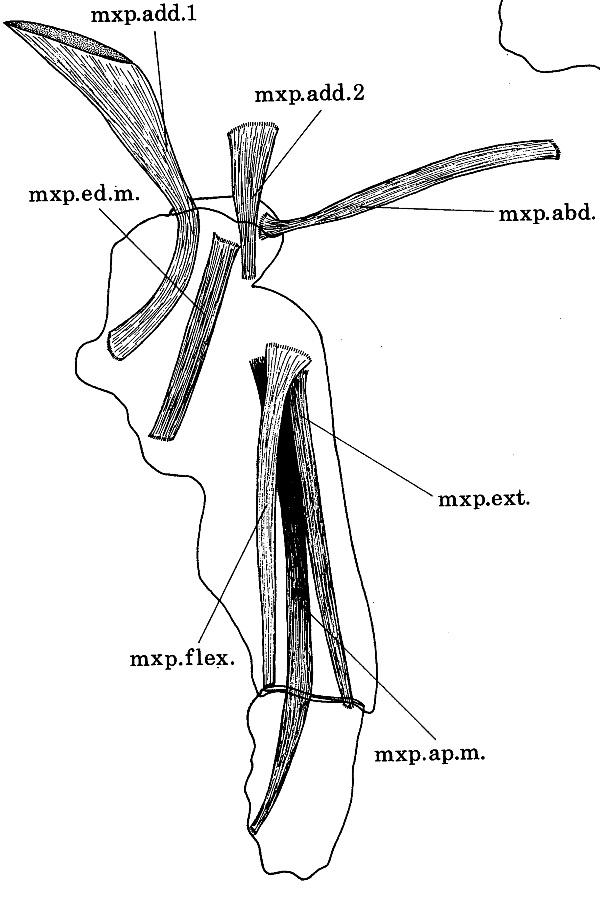


Figure 29. Posteromedial view of maxillule, showing musculature.

Figure 30. Posterior view of maxilla, showing musculature.

Figure 31. Anterior view of maxilliped, showing musculature.

(c) *The ventral cephalic tendons*

(i) *Euaugaptilus*

The system of ventral cephalic tendons, or free endosternites, is much more complex in *Euaugaptilus* than in *Benthomisophria* (Boxshall 1982) and *Mormonilla*. As in *Benthomisophria* and *Calanus* (Lowe 1935; Perryman 1961) there are two tendons suspended between the midgut and the suboesophageal ganglion by a system of suspensory tendons and muscles. The cephalic tendon system (figure 32) provides the sites of origin for all the ventral extrinsic muscles of the appendages from the antennae to the maxillipeds, and for some of the oesophageal dilator muscles.

The anterior tendon is held anteriorly by two suspensory tendons (susp.t. 5) which pass dorsolaterally to their origins on the body wall in the mandibular somite. They have a muscular portion near their origin but are tendinous distally near their attachment to the cephalic tendon. At the same level a pair of suspensory muscles (susp. m. 1) passes from a ventrolateral origin on premandibular apodeme 2 (p.mnd. ap. 2) to a ventral insertion on the anterior tendon. This tendon has two foramina, the anterior of which (figure 32, at. for.) is diamond-shaped. The posterior foramen (post. for.) is large and a branch of suspensory tendon 6, which originates high on the dorsolateral body wall (figure 15), passes through it and inserts on the ventral wall of the head. The other branch of this tendon inserts on the connective of the anterior cephalic tendon that lies lateral to the foramen. At the posterolateral angles of the anterior tendon two suspensory tendons are attached. One (susp.t. 2) passes laterally towards its origin on the ventrolateral body wall anterior to the base of the maxillule, the other (susp.t. 1) posteriorly to act as a longitudinal connective between the two cephalic tendons. Both have muscular insets, presumably to maintain tension. The anterior cephalic tendon is also attached ventrally via the paired paragnath muscles and three dorsoventral suspensory tendons (figure 71, susp.t. 7–9).

The posterior tendon (p.v.c.t.) lies in a slightly lower plane than the anterior. It is attached to suspensory tendon 1 by two short transverse connectives which enclose a foramen (figure 32, lat. for.) on each side of the midline. Anteriorly it is attached by paired dorsoventral suspensory muscles (susp. m. 2) which originate on the ventral body wall. Suspensory muscle 3, with its origin between the fibres of the dorsal longitudinal trunk muscles high on the body wall (figure 15), has a double insertion on suspensory tendon 1. At its midlevel the posterior cephalic tendon is attached by a pair of ventrolateral suspensory tendons (susp.t. 3), each of which originates on the postmaxillulary apodeme. The posterolateral angles of the posterior tendon are attached by suspensory tendons (susp.t. 4) which have their origins on the medial maxillary apodemes (mx. med. ap.). The posterior tendon is not directly attached to the postmaxillary apodeme, as it is in *Benthomisophria*.

The muscles that have their origins on the cephalic tendons are shown in figure 32. The ventral muscles of the antenna and mandible originate on the anterior cephalic tendon. Muscles of the maxillule originate on both. The maxillary muscles originate mainly on the posterior tendon, with the exception of adductor 1 (mx. add. 1) which originates on the anterior tendon and one other muscle (mx. m. 1) which originates on the postmaxillary apodeme. Maxilliped muscles originate on the posterior cephalic tendon and postmaxillary apodeme.

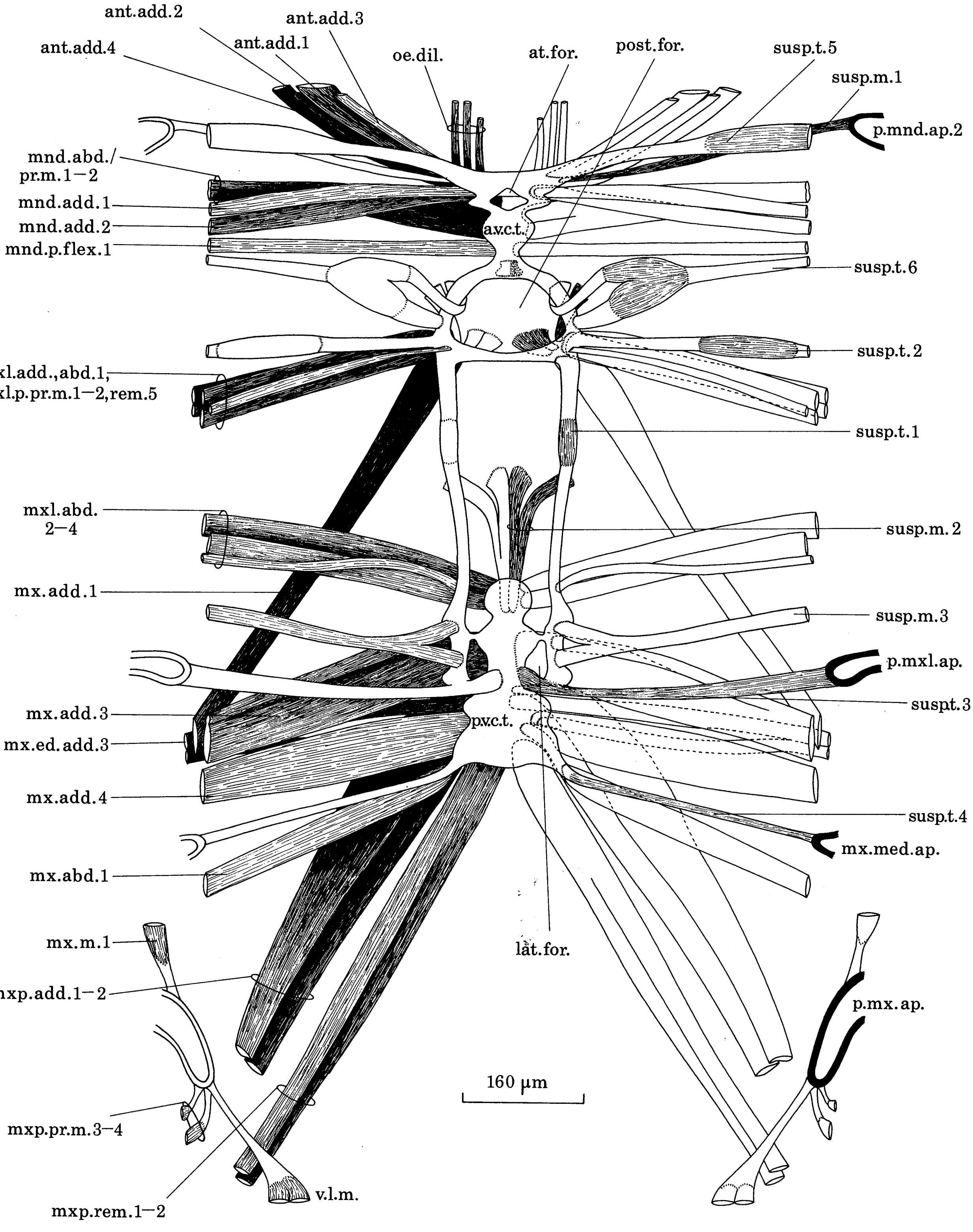


FIGURE 32. Semidiagrammatic dorsal view of ventral cephalic tendon system of *Euaugaptilus*, reconstructed from serial transverse sections and from dissections. The sites of origin of the ventral extrinsic muscles to the appendages are shown.

(ii) *Mormonilla*

The ventral cephalic tendon system of *Mormonilla* is much reduced (figure 33). Only an anterior tendon is present. In the place of the posterior tendon is a narrow tendinous strand (figure 33, susp.t. 3/p.v.c.t.) extending transversely between the tips of the postmaxillulary apodemes. This tendinous strand probably represents both the paired suspensory tendons which attach the posterior tendon to these apodemes in other copepods, and some vestige of the posterior tendon itself. The loss of the posterior tendon has markedly affected the pattern of muscle origins for the posterior cephalosomic appendages. Some muscles have been lost, the musculature of these appendages being generally reduced, but others have a different site of origin from that in *Euaugaptilus* and *Benthomisophria*. Maxilliped adductor 1, for example, originates on the posterior cephalic tendon in both the latter but on the much enlarged postmaxillulary apodeme in *Mormonilla*. This shift is almost certainly related to loss of the posterior tendon. The maxillulary abductor muscles originate on the postmaxillulary apodeme in *Mormonilla* and *Benthomisophria*; on the posterior tendon in *Euaugaptilus*. This difference cannot be attributed to loss of the posterior tendon in *Mormonilla*, as *Benthomisophria* which has a similar site, possesses both tendons.

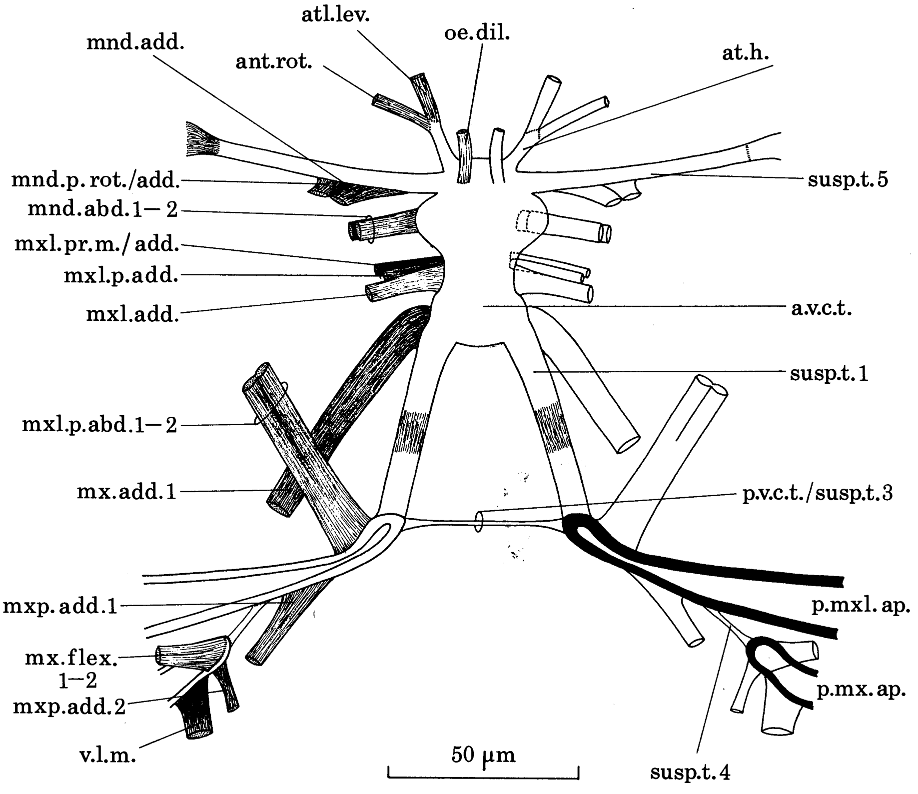


FIGURE 33. Semidiagrammatic dorsal view of the ventral cephalic tendon system of *Mormonilla*, reconstructed from serial transverse and longitudinal sections. The sites of origin of the ventral extrinsic muscles to the appendages are shown.

The anterior cephalic tendon (figure 33, a.v.c.t.) lies medially between the anterior midgut and the suboesophageal ganglion (figure 73), suspended by only two pairs of tendons. Anteriorly it is held to the body wall by paired suspensory tendons (susp.t. 5), posteriorly to the apex of each postmaxillulary apodeme by suspensory tendon 1. As in other copepods suspensory tendon 1 has a muscular inset. The anterior tendon has anterior horns (figure 33, at. h.) directed anterolaterally, either side of the midline, on which some muscles originate. The maximum width of the tendon is about at the level that the paragnath muscles originate on the ventral surface. The latter, particularly the medial pair, are primarily suspensory muscles of the cephalic tendon. The postmaxillulary and postmaxillary apodemes are connected on either side of the body by an oblique tendinous strand (figure 33, susp.t. 4).

The muscles originating on the cephalic tendon system, including the postmaxillulary and postmaxillary apodemes, are shown in figure 33 and require no description. The origin of the antennulary levator muscles on the cephalic tendon system is a feature not found in any other adult copepods although in the sixth nauplius of *Calanus* a similar muscle is found (Perryman 1961).

(*d*) *Homologies of the appendage segments*

(i) *The postmandibular limbs*

All the postmandibular cephalosomic limbs of copepods have been the subject of controversy and several systems of nomenclature for the constituent parts of each are in use today. The main interpretive works are Giesbrecht (1892), Hansen (1925), Borradaile (1926), Gurney (1931), Heegaard (1947) and Lang (1948). Opinions differ concerning: the number of protopodal segments; the distribution of endites and exites between these segments; the position of the articulation between protopod and ramus; and which ramus or rami are present. These are summarized in table 1. Each scheme was arrived at mainly from comparative studies of external morphology either in various copepods, or in copepods and other crustaceans. Little new evidence relating to the composition of these limbs has been presented since the start of this debate and, as they are rather variable in external morphology, interpretation has been largely subjective.

The present study of limb skeletomusculature in calanoids and mormonilloids and similar work on misophrioids (Boxshall 1982) reveals a common pattern in all three limbs in all three groups. The homologies of their constituent parts can now be established with confidence by reference to their musculature.

Comparison shows that in *Euaugaptilus* the articulation between segments 1 and 2 of the maxilliped has almost the same musculature as that between segments 2 and 3 of the maxilla (figures 22 and 23). At this articulation there is a hiatus in the musculature. All the extrinsic, and all except one of the proximal intrinsic muscles, of both appendages insert there, on the proximal rim of the distal segment. Only one maxillary muscle passes right through the plane of this joint without inserting there. Otherwise, all muscles responsible for moving segments distal to this joint originate distal to it. The same hiatus in musculature is found between coxa and basis in copepod swimming legs (see §7*a* and *b*). The extrinsic muscles insert either within the coxa or at the proximal rim of the basis, and muscles moving the rami all originate within the basis. By using the position of the hiatus, the joint between segments 2 and 3 of the maxilla and 1 and 2 of the maxilliped in *Euaugaptilus* can be identified as the coxa–basis joint. Thus identified this joint can be used as a reference point in the maxilla and maxilliped of all copepods to establish homologies. The joint between the first and second segments of the maxilla and maxilliped in *Mormonilla* (figures 30 and 31) can be identified as the coxa–basis joint by its musculature. The second maxilliped segment in *Mormonilla* may represent the fused basis and endopod but this does not affect the interpretation of its proximal articulation as the coxa–basis

TABLE 1. SEGMENTAL COMPOSITION OF THE POSTMANDIBULAR APPENDAGES

maxillule

	praecoxa	coxa	basis	protopod segment 4	exopod	endopod
Giesbrecht (1892)	–	2 endites 1 exite	+	–	+	+
Hansen (1925)	2 endites 1 exite	1 endite	+	–	+	+
Gurney (1931) Borradaile (1926)	1 endite	1 endite 1 exite	1 endite	+	+	+
Lang (1948) present account	1 arthrite	1 endite 1 exite	1 endite	–	+	+

maxilla

	praecoxa	coxa	basis	exopod	endopod
Giesbrecht (1892)	–	4 endites	1 endite	–	+
Hansen (1925) Gurney (1931)	+	2 endites	2 endites	vestigial†	1 endite
Heegaard (1947)	–	2 endites	2 endites	1 endite	vestigial‡
Lang (1948) present account	2 endites	2 endites	1 endite	–	+

maxilliped

	praecoxa	coxa	basis	exopod	endopod
Giesbrecht (1892)	–	3 endites	+	–	+
Hansen (1925) Lang (1948)	+	3 endites	+	–	+
Heegaard (1947)	–	3 endites	+	+	vestigial§
present account	2 endites	2 endites	+	–	+
	syncoxa				

† Represented by single outer seta.

‡ Represented by fourth endite.

§ Possibly represented by distal endite on basis.

joint. Similarly in *Benthomisophria* the joints between maxilla segments 2 and 3 (Boxshall 1982; figure 18) and between maxilliped segments 1 and 2 (Boxshall 1982; figure 12) are homologous with the coxa–basis joint.

The identification of this as the coxa–basis joint shows that Heegaard's (1947) interpretation of the fourth endite on the maxilla as the endopod is wrong. The ramus begins at the next articulation. It is not possible to determine unequivocally, from its musculature, whether the single ramus is the exopod or endopod. The single external seta present on the outer margin of the proximal segment of the maxilla of some calanoids was regarded as representing the exopod by Hansen (1925). This interpretation must also be wrong as the seta is located on a segment proximal to that identified as the basis by its musculature. The remaining ramus of the maxilla and maxilliped in copepods is here regarded as the endopod.

It is now necessary to consider the composition of that part of these limbs proximal to the coxa–basis articulation. In the maxilla of *Benthomisophria* are two discrete segments proximal to the basis, each bearing two endites. These are regarded as praecoxa and coxa. The joint between them is shown by Boxshall (1982) as a telescopic joint although the presence of arthrodial membrane was not recorded. In most copepods this joint is non-functional: in many only a suture line marks its position (*Euaugaptilus*) or there is no trace of it (*Mormonilla*). In the latter forms the first segment should be regarded as a syncoxa. The maxillary segments often appear to be subdivided but these markings are surface folds in the integument, not true articulations provided with arthrodial membrane. These folds are typically continuations of the endite margins and probably enhance the range of movement possible for each endite, many of which are supplied with muscles.

The composition of the copepod maxilliped proximal to the coxa–basis joint is less clear. Sometimes the proximal segment appears to be subdivided into a small basal praecoxa and a larger coxa. Usually, however, there is only one segment proximal to the basis and this should be regarded as a syncoxa. This typically bears three groups of setae on its medial margin representing rudimentary endites. By comparison with the maxilla it is suggested that the proximal group represents a praecoxal endite, the distal groups two coxal endites. This interpretation is confirmed by the maxilliped of the primitive misophrioid *Archimisophria discoveryi* Boxshall which is apparently eight-segmented and has a subdivided syncoxa. Boxshall (1983*b*) was misled by the presence of integumental folds on the female maxilliped in his interpretation of the segmentation of the proximal part of this limb. The muscles of this appendage in a freshly dissected paratype of *A. discoveryi* reveal its true segmentation (figure 34). The protopod is three-segmented and the ramus five-segmented. The praecoxa has two endites and is separated from the coxa, which also has two endites, by a complete suture line lacking arthrodial membrane. The coxa–basis joint can be identified by its musculature. The lateral margins of both coxa and basis have fringes of long setules. Loss of the proximal seta and complete fusion of praecoxa and coxa would result in a typical syncoxa with three endites as found in many copepods.

Analysis of homologies can be extended to the maxillule by using the musculature to identify the coxa–basis joint as a reference point. The maxillule of *Mormonilla* (figure 29) displays the

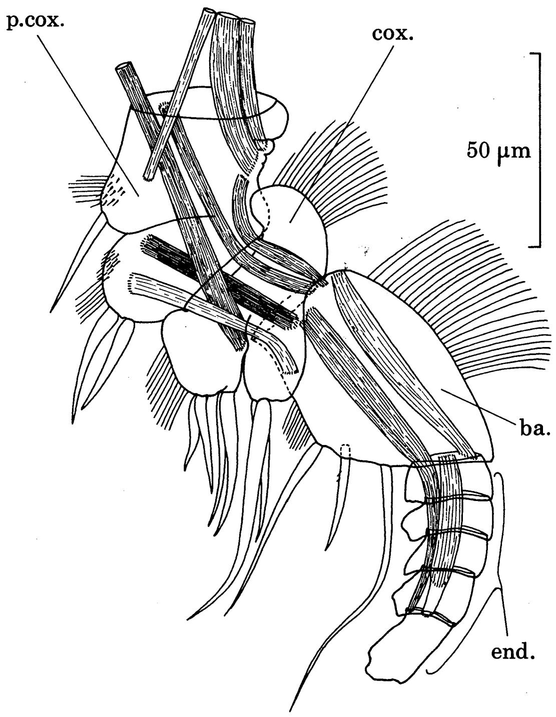


FIGURE 34. Anterior view of the maxilliped of a female *Archimisophria discoveryi*, showing segmentation and intrinsic musculature.

main components of the limb because it is somewhat simplified by reduction. It comprises a two-segmented protopod and two one-segmented rami. The extrinsic muscles insert on the proximal rim of the second protopodal segment indicating that the first joint is homologous with the coxa–basis joint of the maxilla. The first segment is then interpreted as a syncoxa, the second as the basis. Both rami have muscles originating in the basis, as in copepod swimming legs. The maxillule of *Euaugaptilus* (figure 21) has more elements and is more difficult to interpret. The coxa–basis joint is identifiable by its musculature. It is provided with arthrodial membrane and divides the protopod into a proximal syncoxa and distal basis. The syncoxa has a transverse suture line posteriorly but no markings on its anterior surface. This incomplete suture probably marks the level of a former joint separating the praecoxa, with its large arthrite, from the coxa which bears one endite and a foliaceous exite. The apparent subdivision of the basis is a superficial integumental fold which allows its endites some independent movement. A true articulation separates basis and exopod. The difference between anterior and posterior views of the calanoid maxillule has in the past increased the problems of interpretation, as noted by Gurney (1931).

The evolutionary trend towards reduction in both segmentation and armature of copepod appendages is clear and, whether occurring by fusion or loss of elements, can cause problems in interpretation. Homologies can be established, however, if reference points such as the coxa–basis joint can be recognized. Study of muscle patterns permits this.

(ii) *The naupliar limbs*

The limbs present in the nauplius, antennules, antennae and mandibles, are referred to here as the naupliar limbs. The homologies between their component segments have not been the subject of extensive discussion. Their basic organization differs significantly from that of the postmandibular limbs. Excluding the uniramous antennules, the naupliar limbs are biramous with few endopod and many exopod segments whereas postmandibular limbs have many endopod and few exopod segments. This fundamental difference in limb organization between naupliar and postmandibular limbs is probably a characteristic of the Crustacea as a whole and is clearly exhibited by the remarkably preserved Upper Cambrian crustaceans described by Müller (1983). Only the Phosphatocopida of Müller (1964 and 1979) do not conform to this pattern, exhibiting up to seven pairs of limbs with few endopod and many exopod segments, including postmandibular limbs.

To account for this reversal in pattern of organization von Vaupel Klein (1982) suggested that the rami of the postmandibular limbs in copepods have been rotated so that the multisegmented exopod of the naupliar limb is homologous with the multisegmented endopod of the postmandibular limb, to which he refers as 'ramus 1'. The naupliar endopod and the postmandibular exopod he designates as 'ramus 2'. There is no anatomical or ontogenetic evidence of such rotation either in Crustacea in general or in the Copepoda in particular. The suggestion that rami should be referred to by numbers is potentially confusing and should be strongly opposed.

Another attribute of the naupliar limb is that, in copepods at least, there is no evidence of a praecoxa. The mandibular musculature of *Benthomisophria*, *Mormonilla* (figure 27) and *Euaugaptilus* (figure 20) exhibits a similar hiatus at the base of the palp to that found at the coxa–basis joint of the postmandibular limbs. The palp is therefore regarded as consisting of the basis and rami when present. The mandibular gnathobase is regarded as coxal. Hansen

(1893) considered the annulations at the base of the palp to represent a third protopodal segment but they occur distal to the coxa–basis articulation. Gurney (1931) and Lang (1948) correctly suggest that these annulations are merely folds in the integument which enhance the mobility of the palp.

The antenna comprises a two-segmented protopod, exopod and endopod. The protopodal segments are presumably coxa and basis. Often, as in *Mormonilla* and *Benthomisophria*, coxa and basis are completely fused; sometimes, as in *Euaugaptilus*, a suture line without arthrodial membrane marks the line of fusion. No movement is possible here but several short muscles spanning the suture line indicate that it has been a functional articulation in recent evolutionary history.

The copepod antennule is uniramous. A second ramus has been reported in two unrelated species of siphonostomatoid, *Paranicothoe cladocera* (Carton 1970) and *Spongiocnizon vermiformis* (Stock 1967). The male of *P. cladocera* has a small articulated lobe at the base of the distal seta on the second segment which Carton (1970) regarded as the vestigial exopod. The structure and armature of the second segment indicate that it is derived by fusion of at least six original segments and a true exopod would not be located on a seven-segmented protopod. It can equally well be interpreted as the swollen base of an articulated seta. In both sexes of *S. vermiformis* the antennules are highly modified. Each comprises a small basal segment, a large second segment produced into a tapering asymmetrical lobe, and a conical apical segment which bears near its base an unsegmented cylindrical lobe armed with a single apical seta. This lobe arising proximally from the third segment was interpreted by Stock (1967) as a vestigial exopod. If, however, the third segment can be regarded as being produced into an asymmetrical tapering lobe like the second, the cylindrical lobe can be reinterpreted as the fourth and terminal segment of a uniramous limb. The antennule is uniramous at all stages of ontogeny in copepods for which the life history is known and is regarded here as primitively uniramous. It is further assumed that the main axis represents the exopod because its multisegmented condition is similar to that of the exopod of other naupliar limbs.

The segmentation of the copepod antennule has been closely studied and the application of Giesbrecht's (1892) trithek scheme in the analysis of the armature elements has enabled homologies between segments to be established in detail. Boxshall (1983*b*) described a female misophrioid, *A. discoveryi*, with 27 antennulary segments and Fosshagen (1970) described the same number in the calanoid *Exumella polyarthra* Fosshagen. These forms belong to different evolutionary lineages but their antennules have diverged little from the ancestral pattern of segmentation and armature given by Boxshall (1983*b*). The armature of the apical segment in extant copepods gives some indication that it is derived from two segments (von Vaupel Klein 1982), but the hypothetical ancestral pattern can easily be modified to incorporate an additional subapical segment.

The main antennulary flexor muscles of female *Euaugaptilus* (figure 13) attach in every segment from the fourth to the tip, and each segment from the third onwards is capable of flexion. This is interpreted as evidence that they represent true primary segments, not secondary annulations, and that the antennule of the ancestral copepod had many rather than few segments.

6. FEEDING MECHANISMS

(a) *Feeding in planktonic copepods*

The classical work on calanoid feeding currents is that of Cannon (1928). He described feeding and swimming currents created by *Calanus* by observing live copepods in small drops of water. According to Cannon a large swimming vortex is established by vibrations of the antennae, mandibular palps and distal parts of the maxillules. The feeding vortex is produced as a direct consequence of the swimming vortex and passes through the stationary maxillae which act like a sieve, filtering out food particles. This account has been accepted by most workers until recently. It has led to the establishment of a simplistic two-way classification of feeding in planktonic copepods, either filter feeding on particulate matter, or raptorial feeding by capture of individual larger particles, such as prey by predatory species.

The use of modern techniques, particularly high speed cinematography, and an increasing awareness of the dominance of viscous forces in the low Reynolds number environment of a copepod, has resulted in a complete reassessment of copepod filter feeding in the last decade. Cannon's feeding vortex has been shown to be an artefact resulting from the confinement of the copepod in a limited volume of water (Alcaraz *et al.* 1980; Yule & Crisp 1983). High speed cinematography has shown that the filtering limbs do not function like a sieve collecting particles on the grid of fine setules as they are swept through the water. The existence of a boundary layer around a feeding limb as it moves is determined by its low Reynolds number and means that suspended particles are moved backwards and forwards by the oscillations of the limb without actually coming into direct contact with it and without becoming trapped on its setae (Price *et al.* 1983). The new model of calanoid particle feeding is summarized below as a necessary prerequisite to understanding the feeding mechanisms of *Euaugaptilus* and *Mormonilla*. It is based largely on the work of Koehl & Strickler (1981), Cowles & Strickler (1983) and Price *et al.* (1983).

Calanoids capture algal cells by three methods, two for large, another for small cells. During slow swimming the antennae, maxillules, maxillipeds and probably the mandibular palps beat slowly. Once a large food particle has been detected, fluid motions generated by these appendages move it closer to the stationary maxillae. Actual capture is accomplished through suction created by an outwards flap of the maxillae combined with the rapid extension of its setae, and by the remotor swing of the swimming legs. A 'packet' of water containing the food particle is then captured as the maxillae close. Water is squeezed out through the feeding basket of maxillary setae as the maxillae come together and the food particle is retained. Water does not escape anteriorly because the antennae and maxillules continue to beat and push water posteriorly towards the maxillae while they are closing. Individually captured cells are combed off the maxillary setae by the setae on the maxillulary arthrite and passed to the mandible. Raptorial capture of a food particle does not necessarily interrupt slow swimming movements. In *Acartia* the swimming legs are also involved in generating feeding currents.

Small algal cells are captured by a different method in which the maxillae exhibit continuous low amplitude movement, interrupted periodically by combing movements. Commonly this involves the maxillary setae being drawn through the setae of the maxillulary arthrite, but long duration combing involving other limbs is also shown. The antennules are drawn through the angles between the flexed coxa–basis joint of the maxilliped, the antennae are scraped against the maxillulary arthrites and maxillae, and the maxillipeds scraped against the maxillae.

Throughout this period the maxillary setae are repeatedly drawn through the comb of maxillulary arthrite setae. These combing movements presumably remove small algal cells and pass them towards the mandibles but the actual mechanism of cell capture is unknown with this mode of feeding. It is possible that the continuous low amplitude movement of the appendages serves to reduce the boundary layer around the setae allowing small cells to be caught on the setules.

The calanoids studied by Price *et al.* (1983) fed by both methods. *Eucalanus pileatus* can switch rapidly between methods, the size threshold for the switch lying between 6 and 12 μm. The size threshold may vary from species to species, for example Price *et al.* (1983) inferred from the data of Frost (1977) that it occurred between 13 and 15 μm in *Calanus pacificus*.

The third method of feeding is practised by raptorial predators which grasp their prey directly with the tips of the maxillary and maxillipedal setae. Algal feeders may also occasionally grasp large cells in this way (the 'chopsticks' method of Alcaraz *et al.* 1980). This raptorial mechanism is common among predatory calanoids and is essentially the same as that described for predatory cyclopoids by Fryer (1957) though in these the large maxillules are also used for grasping prey. Many parasitic copepods have subchelate maxillae and maxillipeds that are used similarly, to grasp the host.

(*b*) *Feeding in Euaugaptilus*

(i) *Fine structure*

E. placitus (figure 35) is a large, powerful predator. Such species of *Euaugaptilus* whose gut contents have been examined had preyed primarily on other copepods (Harding 1974). Only

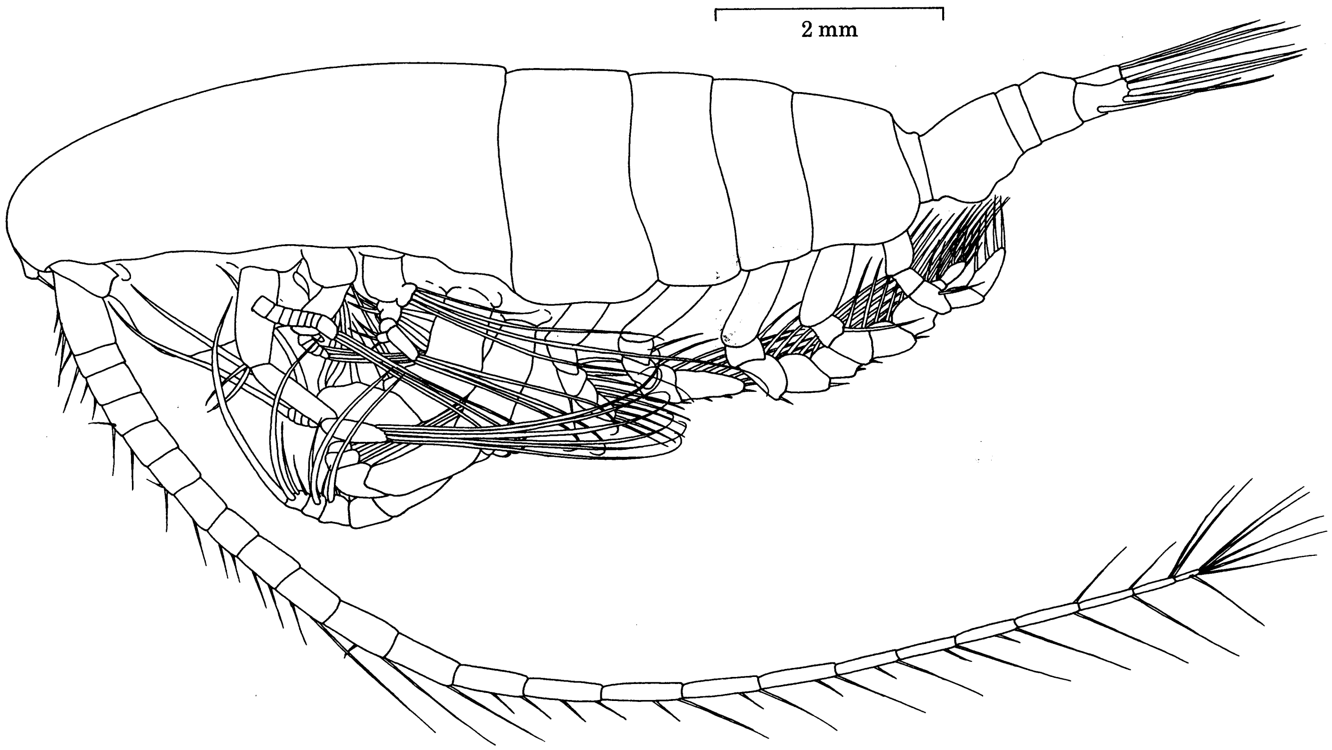


FIGURE 35. Adult female *Euaugaptilus placitus*, lateral view.

the maxillae and maxillipeds appear to be adapted for grasping prey. The other limbs serve a wide range of functions. The long antennules are primarily sensory and locomotory (steering and stabilizing) and their role in feeding is probably only in the remote detection of prey. Both rami of the antennae and mandibular palps are armed with long plumose setae apically and subapically. These setae have bilaterally arranged rows of closely set setules which, by analogy with the similarly armed setae on copepod swimming legs, are adapted for producing currents. The antennae and mandibular palps are mainly involved in making the slow swimming movements that draw the copepod closer to its prey. The elongate mandibular gnathobase (figure 20), provided with several slender teeth along its distal portion, is specialized for piercing and cutting, and probably tears prey into fragments small enough to be ingested.

The maxillule (figure 36) serves at least two roles. The plumose setae on its coxal exite and exopod could be used to assist the limbs producing slow swimming movements. The single plumose seta on the distal part of the basis may represent an endopodal element. Its armature links it functionally with the setae of the exopod and exite. The setae of the praecoxal, coxal and basal endites are of two types (table 2). The single seta on the coxal endite (figure 38) and most of the setae on the praecoxal arthrite are stout and armed with short irregularly arranged setules proximally and small stud-like denticles distally, and are probably involved in manipulating and transferring the prey from the maxillae to the mandibles. The stud-like denticles may increase friction between seta and prey and improve the grasp. The other three praecoxal setae and the setae on the basal endites are slender and armed as in figure 39. These setae may be involved in grooming the setae of the other feeding appendages.

Adduction of the distal ramus relative to the basis enables both the maxillae (figure 40) and maxillipeds (figure 44) to grasp items and pull them towards the other mouthparts. These limbs have a varied armature (table 2). Most prominent is the 'button' seta (figure 43). The other setae of the maxillae (figures 41 and 42) and of the maxillipeds (figures 45 and 46) are mostly of medium length and provided with irregularly arranged setules proximally and rows of short setules distally. These may be involved in grooming and also in the transfer of food particles from one appendage to another. Some may be sensory.

In the button setae the setules on the distal portion are replaced by integumental outgrowths variously termed buttons (Krishnaswamy *et al.* 1967), cup-shaped appendages (Matthews 1972) and disques pédicellés (Sars 1925). The degree of development of the stalked buttons varies considerably within the genus *Euaugaptilus* and within the family Augaptilidae as a whole. Development in *E. placitus* is moderate but in *Centraugaptilus horridus* (Farran) they are well developed. This species was the subject of a t.e.m. study by Krishnaswamy *et al.* (1967) who found the buttons to be integumental structures with no cellular component. No nerve endings were associated with them. The buttons on the maxillary setae of *C. horridus* are shown in figures 47–49, plate 1. The transition from normal setule to stalked button occurs over a short distance (figure 47) and shows that the buttons are modified setules. Their paired arrangement and stalks are also shown (figures 48 and 49).

It is widely assumed that the button setae are involved in prey capture and holding. Their position on the distal portions of the raptorial limbs also suggests a role in the grasping action. There are 11 button setae on the maxillae, only four on the maxilliped (table 2), here interpreted as evidence of the dominant role of the maxillae in prey capture. The role of the buttons themselves is unclear. It is probably to increase the surface area of the seta that comes into contact with the prey and to protect these primary feeding setae from damage. The stalked

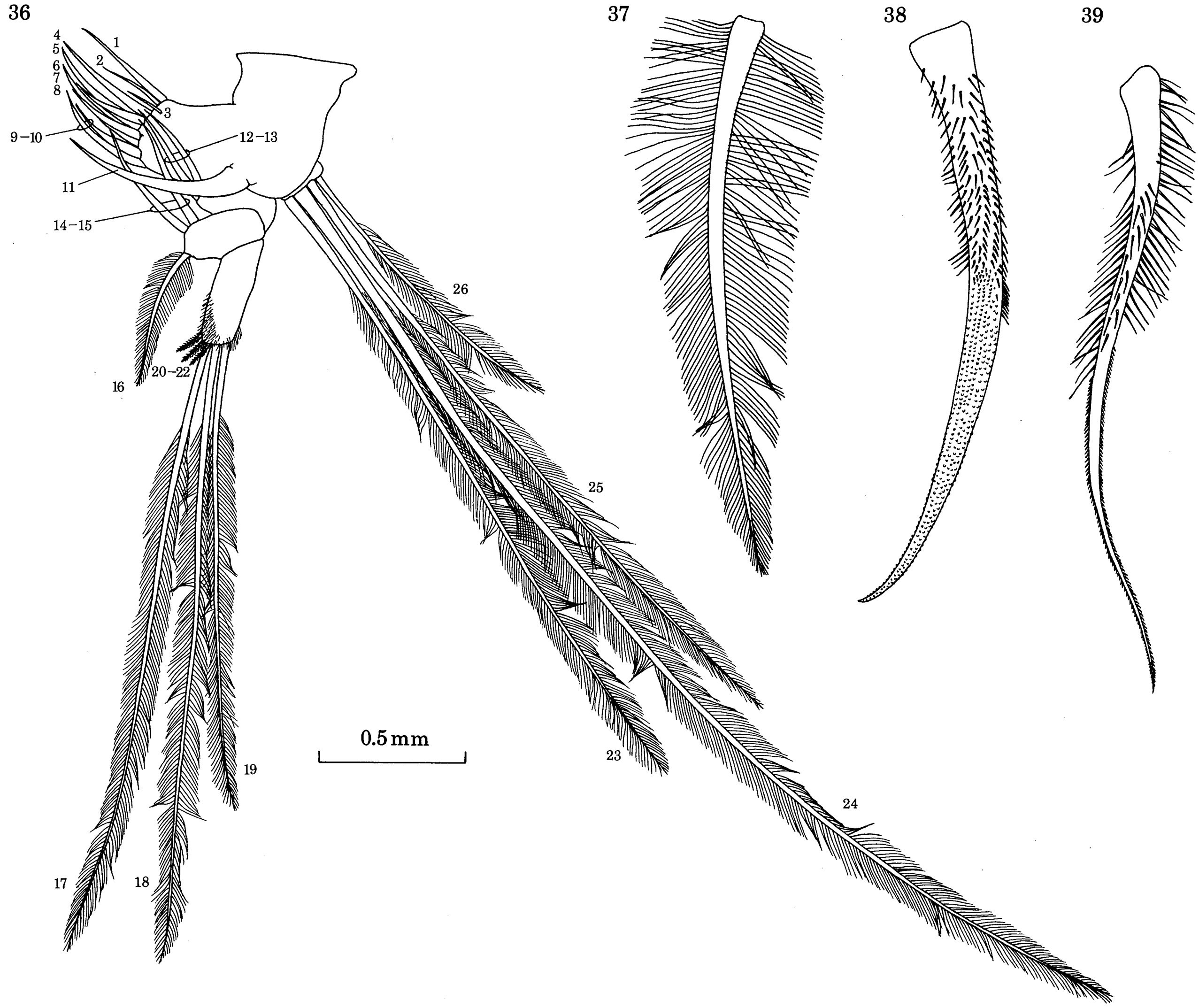


Figure 36. Anterior view of maxillule of *Euaugaptilus*, showing armature of palp and coxal exite numbered as in table 2.

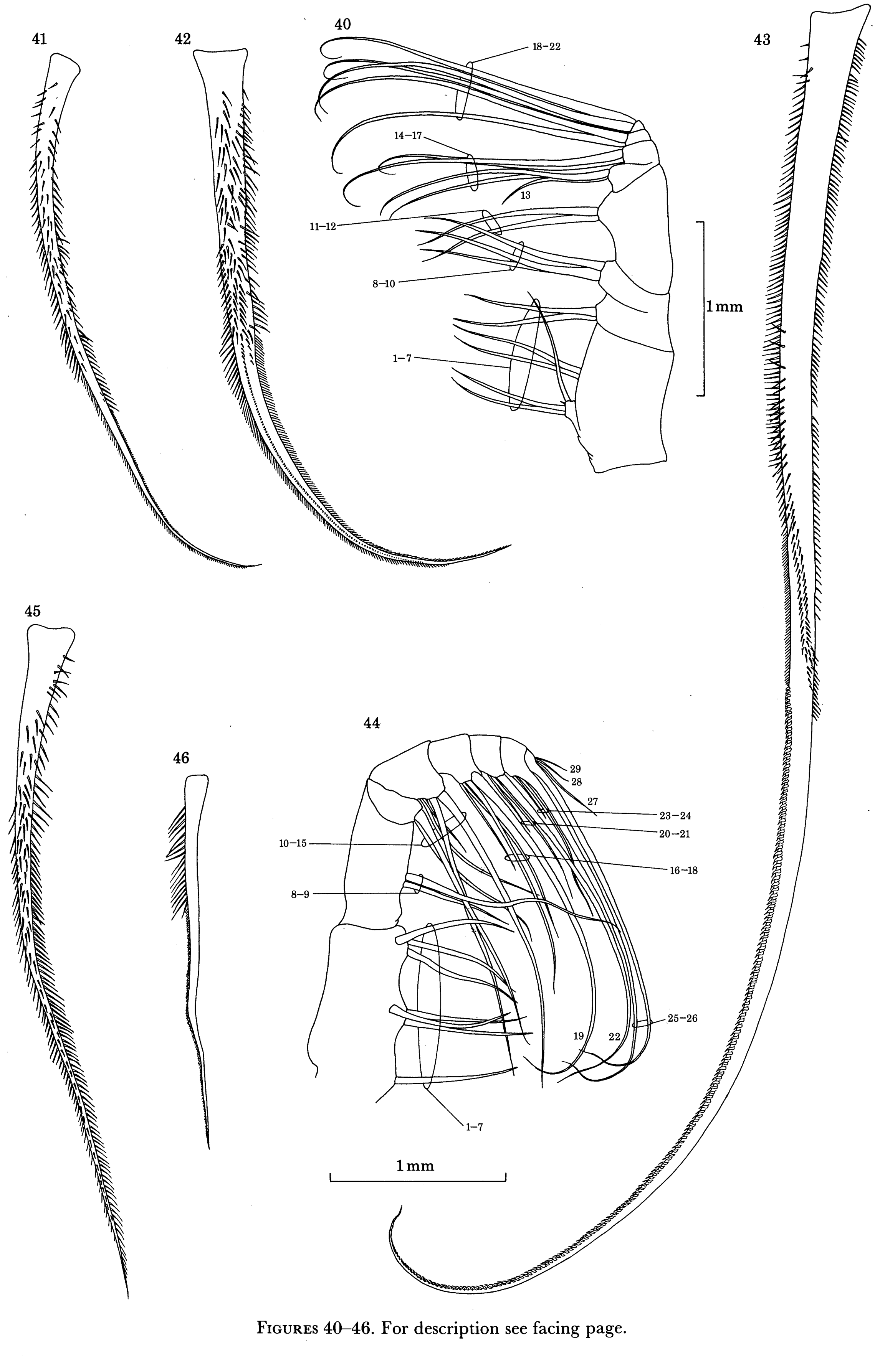
Figure 37. Distal seta on distal endite of basis.

Figure 38. Single seta on coxal endite.

Figure 39. Proximal seta on praecoxal arthrite.

Table 2. Armature elements of the postmandibular feeding appendages of *Euaugaptilus*

	plumose seta	stud seta	composite seta	button seta	hirsute seta
maxillulary seta number	16–19, 23–26 (figure 37)	4–11 (figure 38)	1–3, 12–15 (figure 39)	—	20–22
maxillary seta number	—	—	1–10, 13 (figures 41–42)	11–12, 14–22 (figure 43)	—
maxillipedal seta number	—	—	8–18, 20–21, 23–24, 27–29 (figure 46)	19, 22, 25–26	1–7 (figure 45)



FIGURES 40–46. For description see facing page.

buttons may act as buffers, absorbing some of the energy generated by the struggling prey, thereby protecting the seta, which cannot be replaced once damaged as adult copepods do not moult.

(ii) *The feeding mechanism*

Prey capture in *Euaugaptilus* is probably as follows. Approaching prey is detected as it enters the sensory field, or active space, around the copepod. Detection may involve both chemosensory and mechanosensory cues. The copepod advances by slow swimming movements of the antennae, mandibular palps and maxillules. When the prey is within reach of the maxillae they are abducted and extended by contraction of the extrinsic abductors and intrinsic extensors. This swings the whole limb laterally and straightens it, thereby spreading its setae. Contraction of the extrinsic adductors and intrinsic flexors swings the whole limb medially and pulls the setae through an arc towards the midline. The prey is grasped directly by the button setae of the maxilla. The maxillipeds may assist the maxillae in the initial capture of prey or, more likely, help to secure it once caught.

(*c*) *Feeding in Mormonilla*

(i) *Fine structure*

The model of calanoid particle-feeding behaviour outlined above (see §6*a*) is equally appropriate for podopleans which share the same ancestral type of gnathostomatous mouthparts. The mouthparts of *Mormonilla* are of this type and the mechanism proposed here is based on knowledge of its skeletomusculature and on recent insights into copepod feeding mechanisms gained from high speed cinematography. The basic structure and musculature of the feeding appendages has been described (§5*b*) but it is necessary to know the fine structure of their armature before the feeding mechanism can be fully understood.

The most striking external feature of *Mormonilla* is the relatively enormous filter basket, shown in lateral view in figures 50 and 51, plate 2. Its main ventrolateral components are the mandibular and maxillulary palps which are overlain by the antennae. The first pair of swimming legs forms the posterior wall (figure 52). The maxillae and maxillipeds lie laterally within it. The antennules probably play no part in the feeding process. They may be kept extended as a means of slowing the rate of sinking, except during the power stroke of the swimming legs when they are doubtless retracted.

The mandibular and maxillulary palps are similar in structure and only the latter is figured (figure 53). The exopodal setae of both palps are long and each is provided with two rows of closely set setules, oriented more or less in the same plane. The spacing between the setules increases distally along each seta but decreases again near the apex where the setules become shorter. These setae present the maximum possible surface area and generate maximum water

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FIGURE 40. Anterior view of maxilla, showing armature elements numbered as in table 2.

FIGURE 41. Seta on praecoxal endite of maxilla.

FIGURE 42. Seta on coxal endite of maxilla.

FIGURE 43. Button seta from endopod of maxilla.

FIGURE 44. Anterior view of maxilliped, showing armature elements numbered as in table 2.

FIGURE 45. Proximal seta on medial margin of syncoxa of maxilliped, representing a praecoxal endite.

FIGURE 46. Proximal seta on maxilliped endopod segment 2.

movement. Their close set setules prevent water being forced through the intersetule spaces and are set at an acute angle to the setal shaft so that each crosses over several setules of the adjacent seta. The row of setules from one seta lies on top of the nearside row of the adjacent seta and is supported by it. Each seta along the exopod margin supports the seta on one side and is supported by that on the other side. This allows the whole exopod fan to act as a broad flexible paddle. The endopodal setae of both palps are each armed with two rows of coarser, more widely spaced setules. The rows are oriented at an angle of 120–130° to each other and at an angle of 80–90° to the setal shaft (figures 52 and 53). These setae are adapted to allow water to be forced through the wide intersetule spaces while preventing the passage of any particulate matter. Their long setules are so distributed along the seta that they correspond precisely in position with those of the nearside row on the adjacent seta. The tips of corresponding setules interdigitate to provide mutual support and help to prevent them from being displaced by water pressure. This arrangement produces a large area of relatively robust open mesh which retains a high degree of flexibility. The larger setae on the basis of both appendages are similarly armed to those on the endopod.

The mandibular gnathobase is armed with seven strongly sclerotized teeth occupying the truncate distal margin, and a single seta (figure 60*a*, *b*). The arthrite of the maxillule bears six small spinous processes distributed over its surface (figure 54, spin.). It also carries seven spines or setae (figures 55–59) around its medial and dorsal surfaces.

The filter basket is closed lateral to the bases of the mandible and maxillule by setae of the posteriorly directed antennary exopod. These are bilaterally plumose and armed with two rows of setules oriented in the same plane. The basket is closed midventrally by the long apical setae of the antennary endopod that are armed with a row of long, relatively close set setules on one side, a row of peg-like setules on the other and, on some setae only, an additional row of peg setules.

The long plumose setae of both rami of the first swimming legs (figure 61) are typical natatory setae armed with bilateral rows of long, close-set setules, but those of the endopod become shorter and stouter distally. The medial surfaces of coxa, basis and both endopod segments have long spinous processes projecting into the interlimb midline space. The endopod also has an unusually armed sigmoid seta subapically on its inner margin. This seta carries a comb of long setules proximally and a row of large denticles distally. The anterior surfaces of both coxa and basis are provided with patches of slender setules up to 30 μm in length. The second swimming leg (figure 62) exhibits no unusual armature along its medial margin and probably plays no part in feeding.

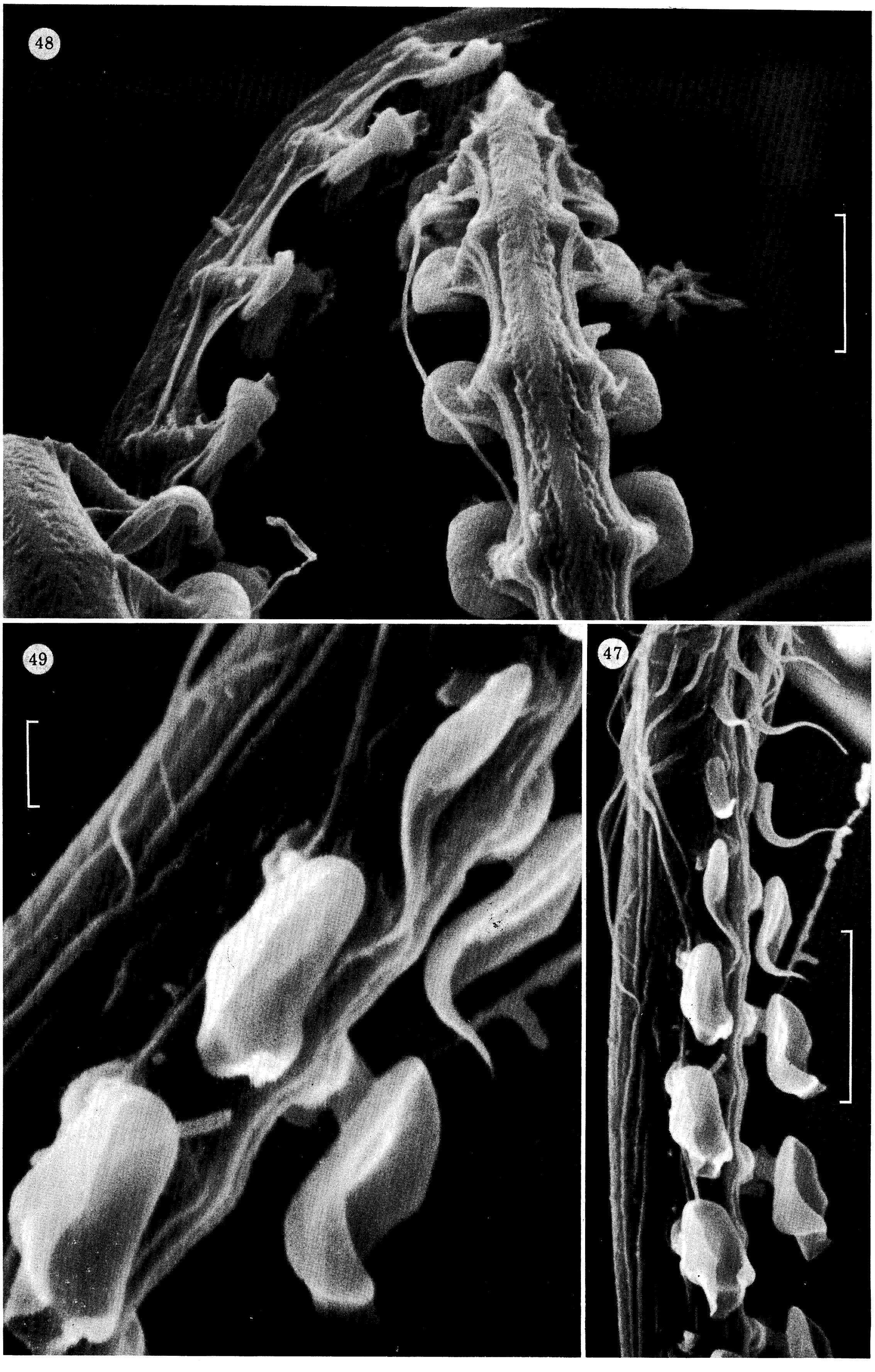
The maxilla and maxilliped lie within the filter basket. The maxillary setae are of three types; A as found on the proximal endite (figure 63), B as found on the distal endites and including the apical seta, and C as found on the distal segments comprising the ramus. Type A setae are relatively short and armed with two rows of stout setules proximally and three distally.

DESCRIPTION OF PLATE 1

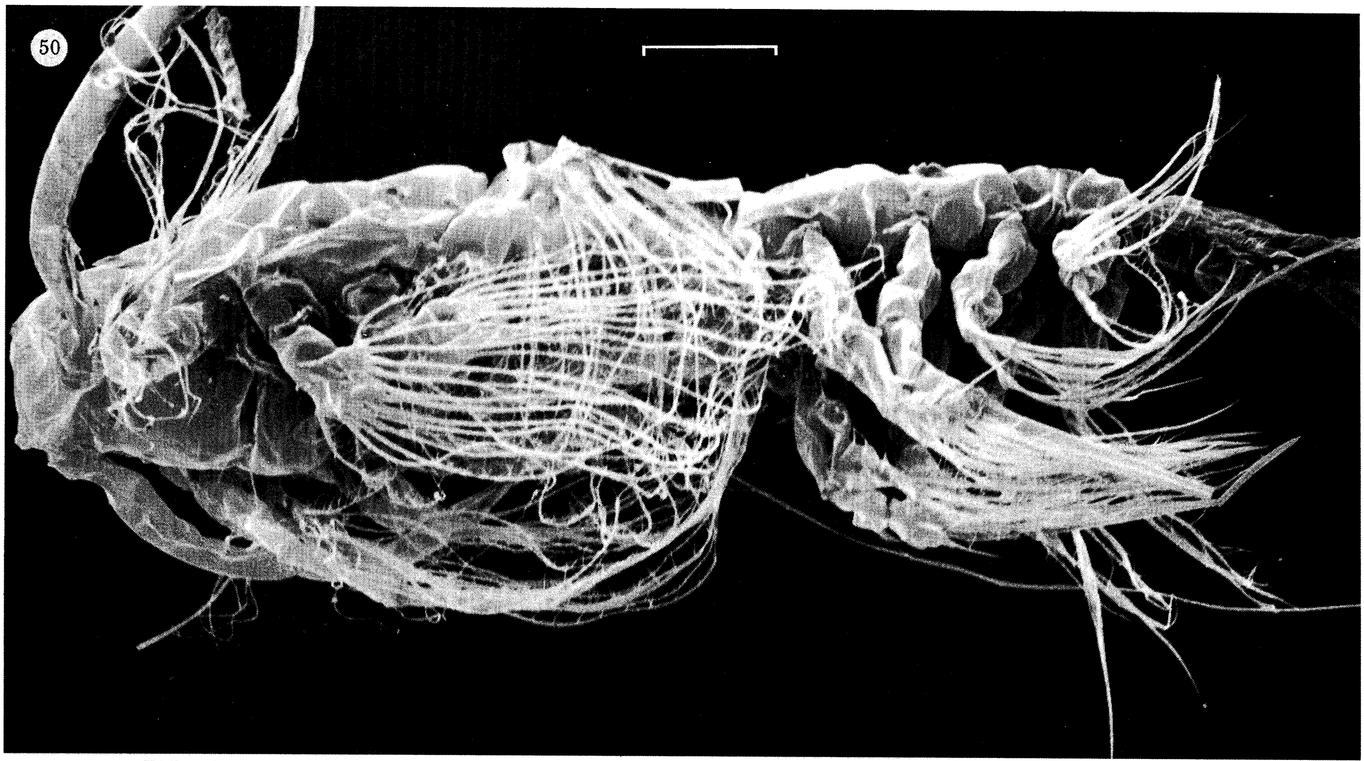
FIGURE 47. Button seta on maxilla of *Centraugaptilus horridus*, showing zone of transition between normal setule and button. Scale bar 10 μm.

FIGURE 48. Back and side views of button setae. Scale bar 10 μm.

FIGURE 49. Detail of buttons. Scale bar 2 μm.



FIGURES 47–49. For description see opposite.



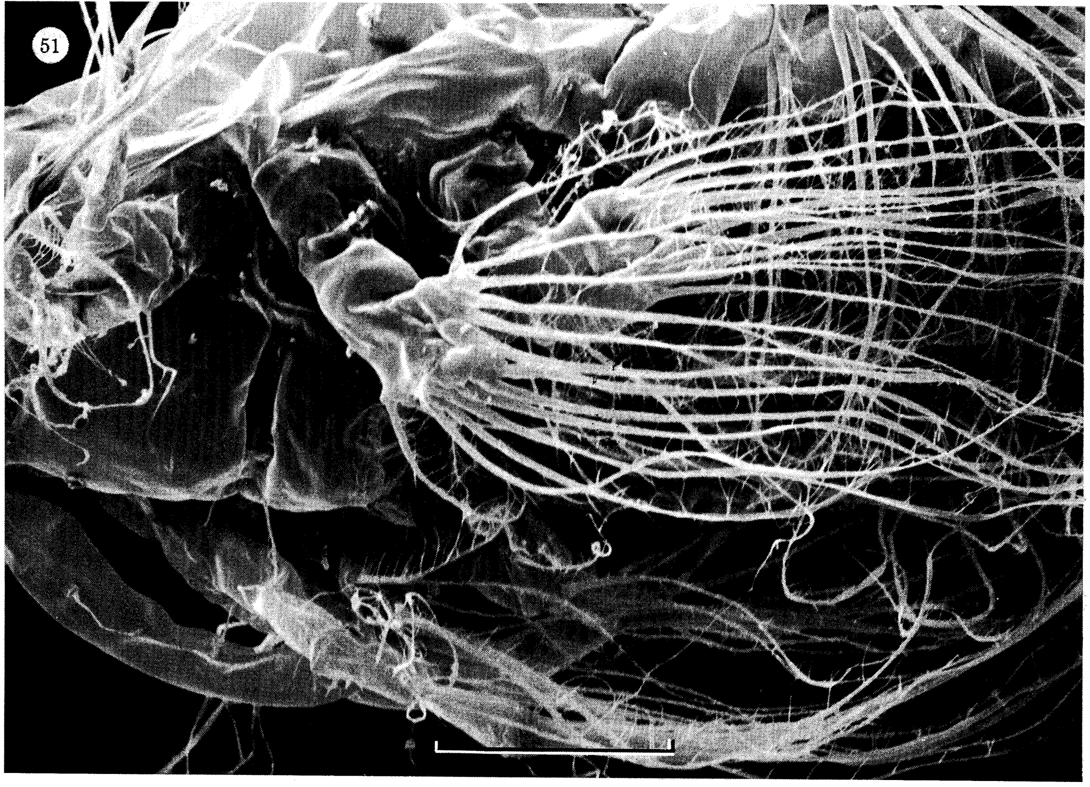


FIGURE 50. Lateral view of female *Mormonilla*, showing filter basket. Scale bar 100 μm.
FIGURE 51. Detail of filter basket wall. Scale bar 100 μm.

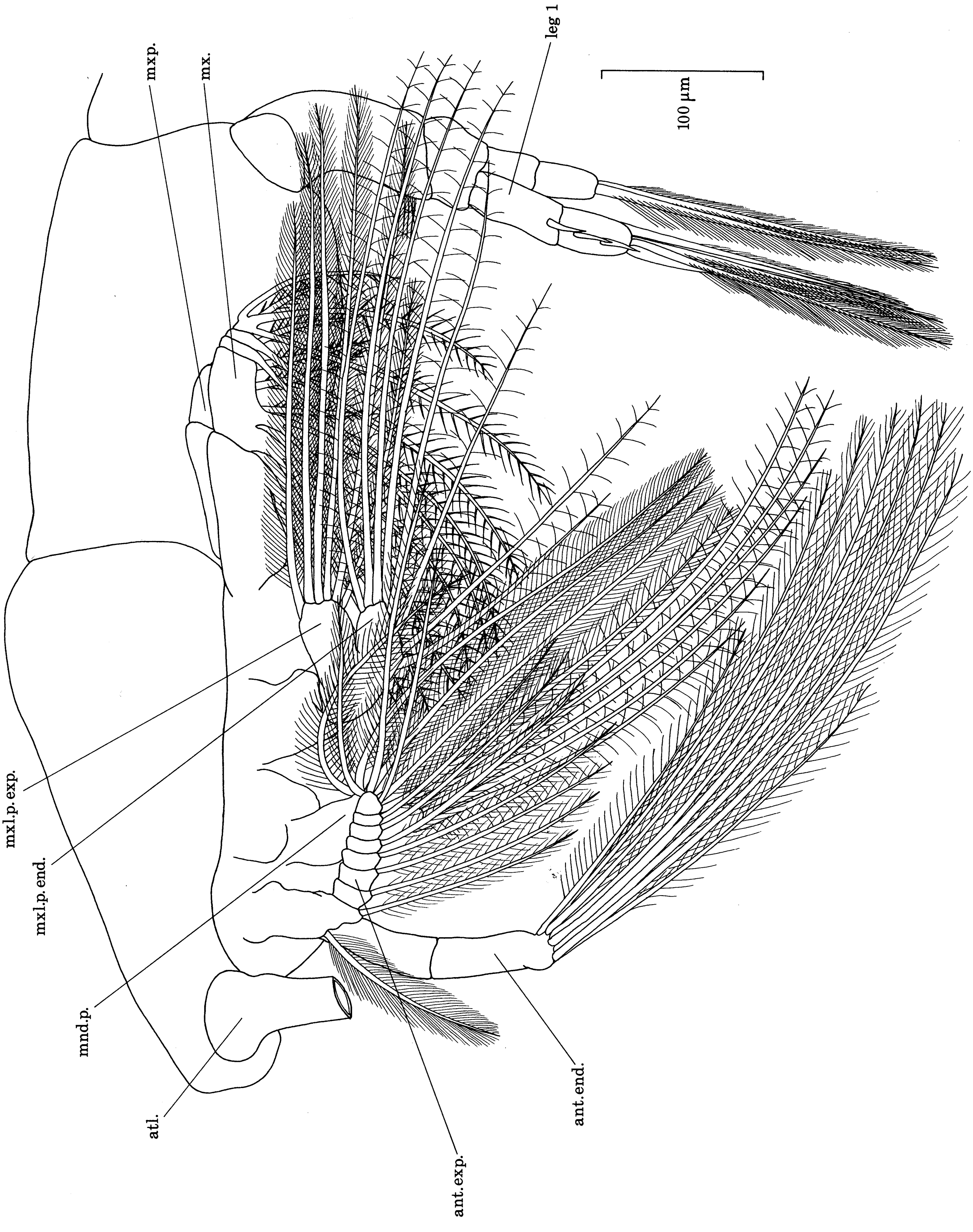
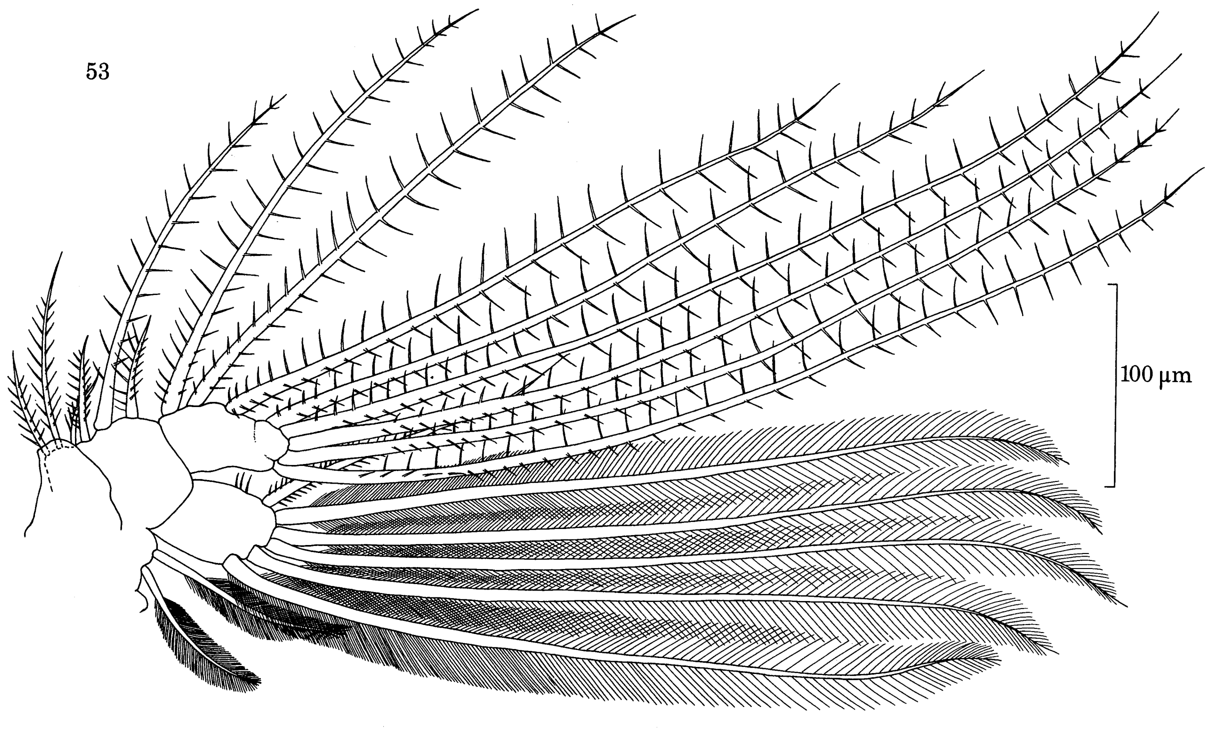
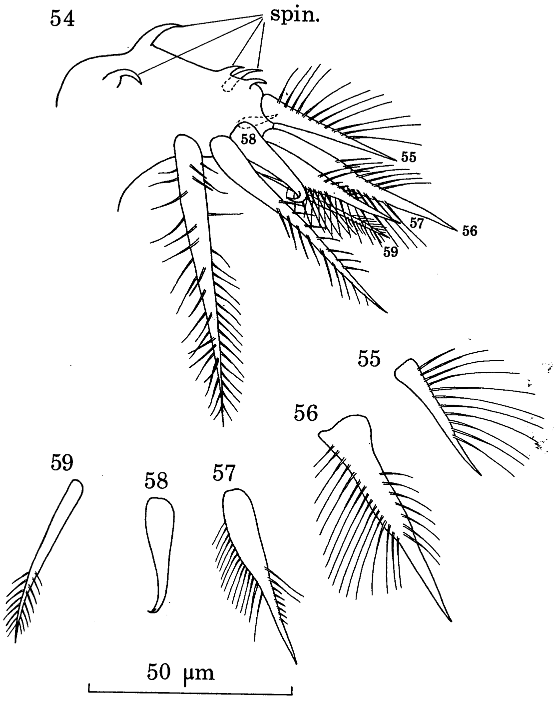


FIGURE 52. Lateral view of head of *Mormonilla*, showing filter basket.





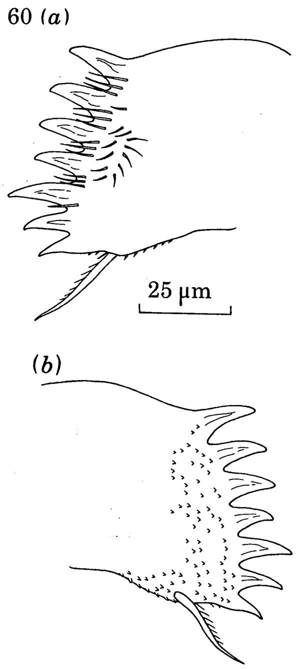


Figure 53. Anterior view of maxillulary palp of *Mormonilla*, showing armature elements.

Figure 54. Anterior view of maxillulary arthrite.

Figures 55–59. Arthrite armature elements.

Figure 60. Distal margin of mandibular gnathobase; (*a*) anterior; (*b*) posterior.

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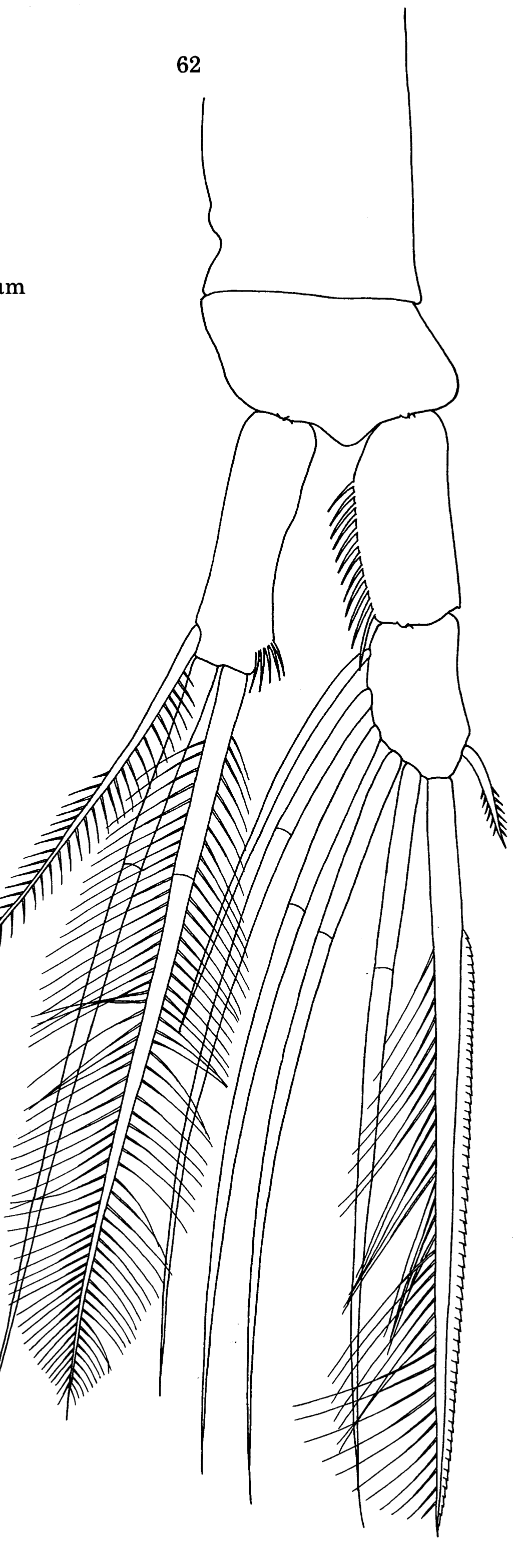

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Figure 61. Anterior view of first swimming leg.
Figure 62. Anterior view of second swimming leg.

Type B setae have two rows of widely spaced, slender setules oriented almost at right angles to the shaft. These do not lie in the same plane, but are separated by an angle of about 120–130°. As the setae on the distal endites diverge only slightly their setules interdigitate (figure 63) and presumably support each other in this way. Type C setae are similarly adapted but have three rows of setules (figure 64). The long and medium length setules are oriented along the shaft at an angle of about 90° to each other. The spacing of setules in the rows is the same. Further round the seta at an angle of about 130–140° to the long setules there is distally a row of short close set peg setules. The long setule of one seta interdigitates with the peg setules of the adjacent seta (figure 65). Type C setae diverge more than the B setae and can be spread apart or closed up by the intrinsic extensor and flexors inserting in the distal segments. During these movements their distal parts will separate more than the proximal and may therefore be more prone to being displaced. The larger number and closer spacing of the peg setules may increase the chance of a long setule interlocking with a peg setule even if slightly displaced.

The maxilliped setae (figure 66) are all armed with long setules, closer set than on the maxillary setae. The proximal three setae have three rows of setules, the seven main distal setae only two, set at an angle of 140–150° to each other. The setules are also set more acutely to the shaft than on the maxillary setae.

(ii) *The feeding mechanism*

Mormonilla feeds by extracting relatively small particles from the water. Despite the reduced and somewhat simplified musculature of the cephalosomic appendages it appears that the feeding mechanism is complex. This is deduced from the armature of the appendages. For example, the setae of the maxillulary exopod are specialized for generating water movement whereas those of the endopod prevent the loss of food particles as water is forced between their interdigitating setules. These rami, though similar in structure and musculature, have very different roles.

The antennae and the mandibular and maxillulary palps all have well developed basal pivot lines about which the promotor–remotor swing takes place (figure 24). That of the antenna is transverse, those of the two palps oblique so the limbs beat forwards and slightly away from the midline, and backward and towards the midline. At the end of the back stroke the mandibular exopod and both maxillulary rami are flexed so their setae come to be posteriorly directed (figure 51). During the promotor swing of all three limbs water will be drawn towards the midventral body surface from around the sides of the limbs both ventrally and anteriorly through the midventral space between their bases. If, at the same time, the swimming legs beat backwards and the maxillae and maxillipeds are abducted about their oblique pivot lines (figure 24) the process of drawing water in will be enhanced.

The large volume of water drawn towards the body is then enclosed by the filter basket. The remotor swing of antennae and mandibular and maxillulary palps closes the walls of the basket anteriorly, laterally and ventrally, and the promotor swing of the swimming legs closes the posterior wall. Pressing these limbs in towards the body will force some water through the intersetule spaces of the filter basket but loss of food particles will be prevented by the mesh of setules on the setae and by the spinous processes on the first legs. Adduction of the maxillae will sweep the outspread maxillary setae through this enclosed volume of water. Food particles will be captured by these setae despite the effect of boundary layers in the highly viscous

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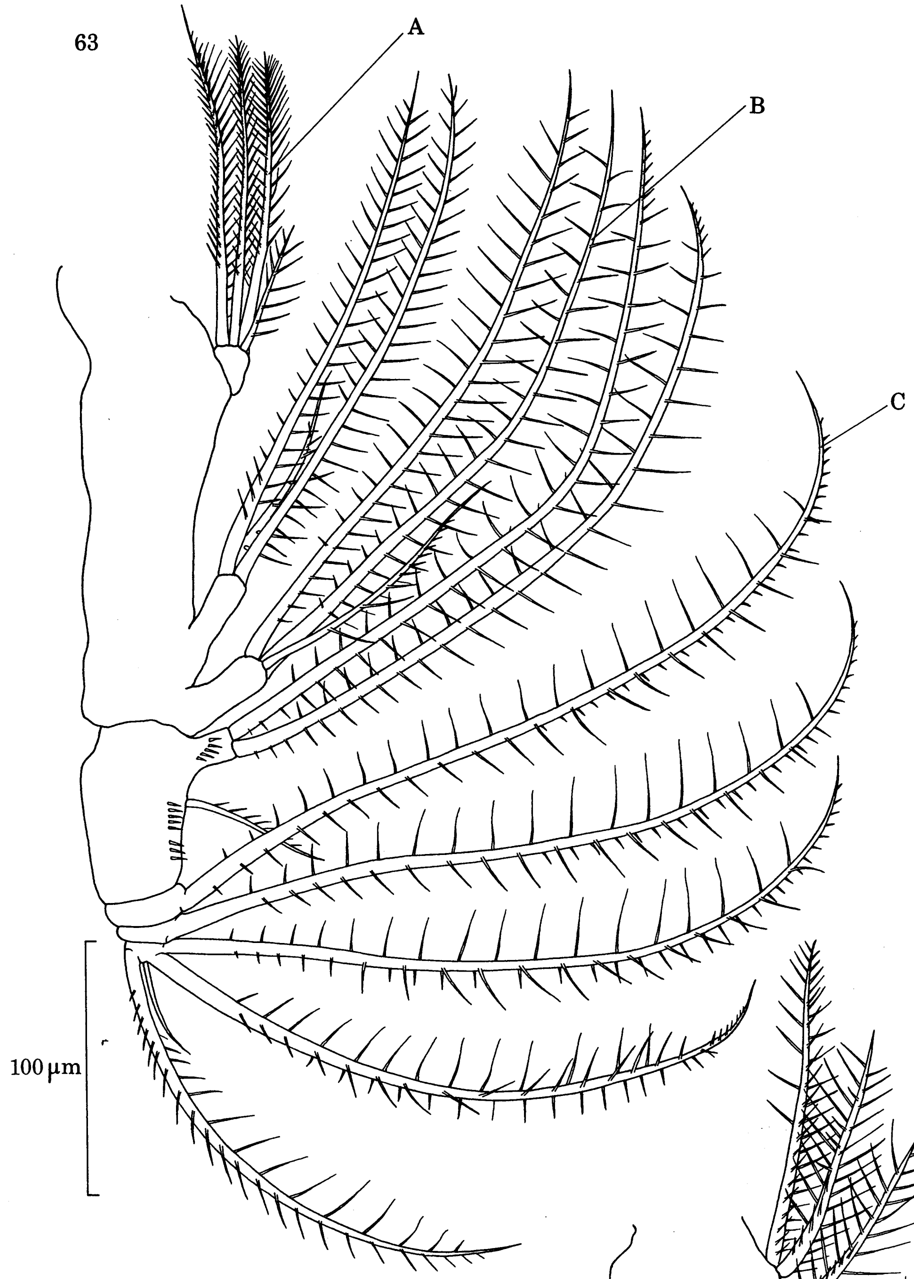

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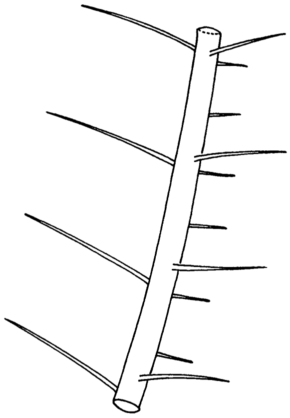

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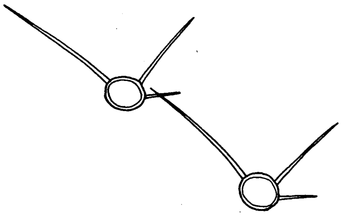

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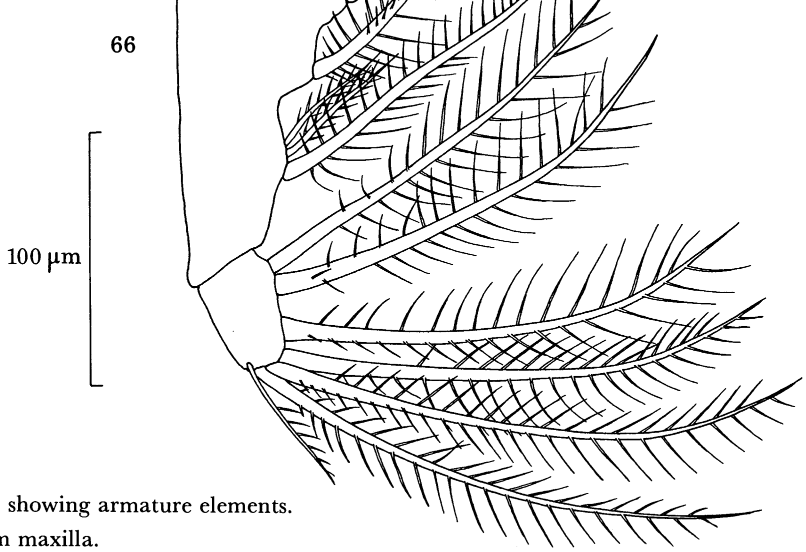

FIGURE 63. Anterior view of maxilla, showing armature elements.

FIGURE 64. Detail of type C seta from maxilla.

FIGURE 65. Transverse section through adjacent type C setae, showing interlocking long and peg setules.

FIGURE 66. Anterior view of maxilliped, showing armature elements.

environment experienced by the copepod because water can be forced between the setules in the confined space within the closed filter basket. The double construction of the basket wall reduces leakage but the posterior wall is only a single layer of setae, and is probably more leaky. Leakage here would be reduced if the adductor sweep of the maxillae included a promotor component so these limbs sweep forwards and together forcing water through their setae by creating pressure against the anterior and lateral walls. The maxillipeds are similarly oriented and can be adducted like the maxillae but they differ in armature and presumably have a different role from the maxillae. They may remove particles from the maxillary setae and pass them anteriorly onto the setae of the maxillulary arthrite. The setae of the maxilliped extend as far as the tip of the labrum (figure 67, plate 3) where their tips could be groomed by the mobile maxillulary arthrite (figure 68).

This postulated sequence of events could be varied. The maxillae may adduct before the filter basket closes if a particularly large particle has been detected: a sequence observed in calanoids (Price *et al.* 1983) when they capture large particles individually.

Once a food particle has been retained on the maxillary setae its passage to the mouth is presumably achieved by passing it from one appendage to another. The distal maxillary setae may be combed by the maxilliped setae. The proximal maxillary setae extend virtually to the mouth (figures 67 and 68) as do the maxilliped setae. The complex armature on the maxillulary arthrite (figure 69) can comb off particles from both maxillary and maxilliped setae. The mobility of the arthrite increases its effectiveness at this task. The setae of the maxillulary arthrite pass food mechanically on to the mandibular gnathobase, which can push it into the oesophagus. The toothed distal margin of the gnathobase (figure 60) is generalized. It is typical of particle feeders and differs markedly from the cutting gnathobase of the predatory *Euaugaptilus*.

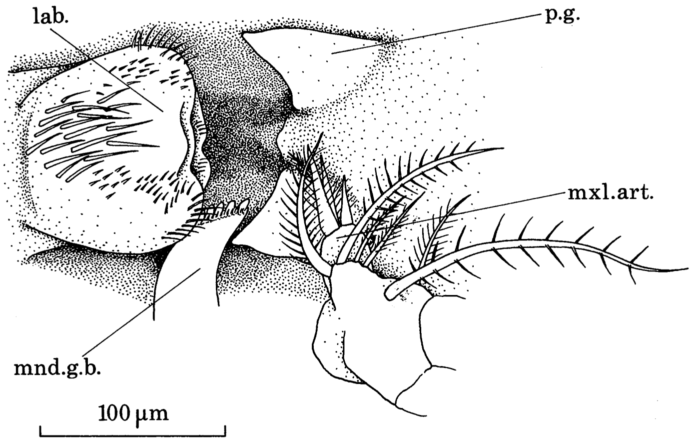

FIGURE 69. Ventral view of oral area of *Mormonilla*, showing spatial relationships between labrum, mandibular gnathobase, paragnaths and maxillulary arthrite.

DESCRIPTION OF PLATE 3

FIGURE 67. Ventral view of partially open filter basket of *Mormonilla*, showing adducted maxilliped *in situ*. Scale bar 50 μm.

FIGURE 68. Ventral view of oral area showing tips of maxillipedal setae (mxp.s.), maxillulary arthrite and some of the labral armature. Scale bar 10 μm.

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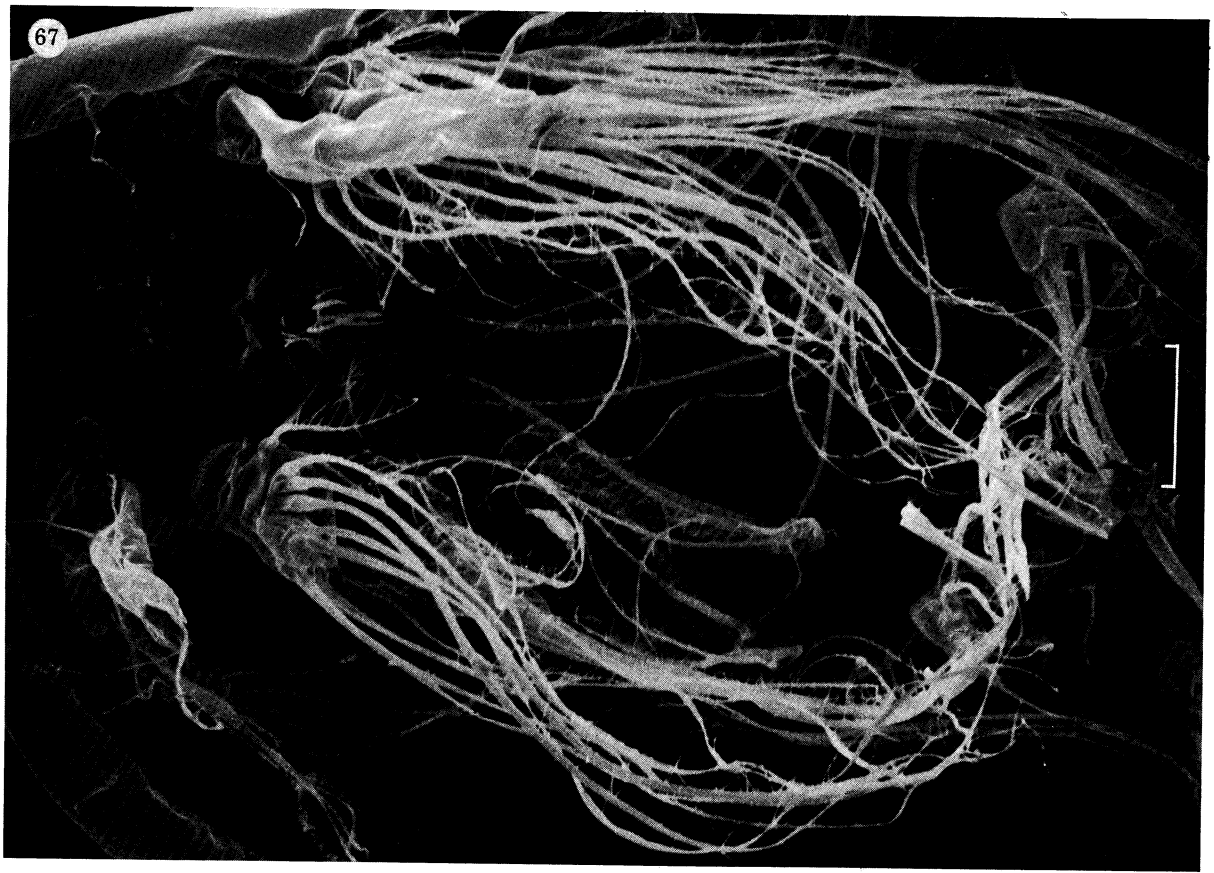

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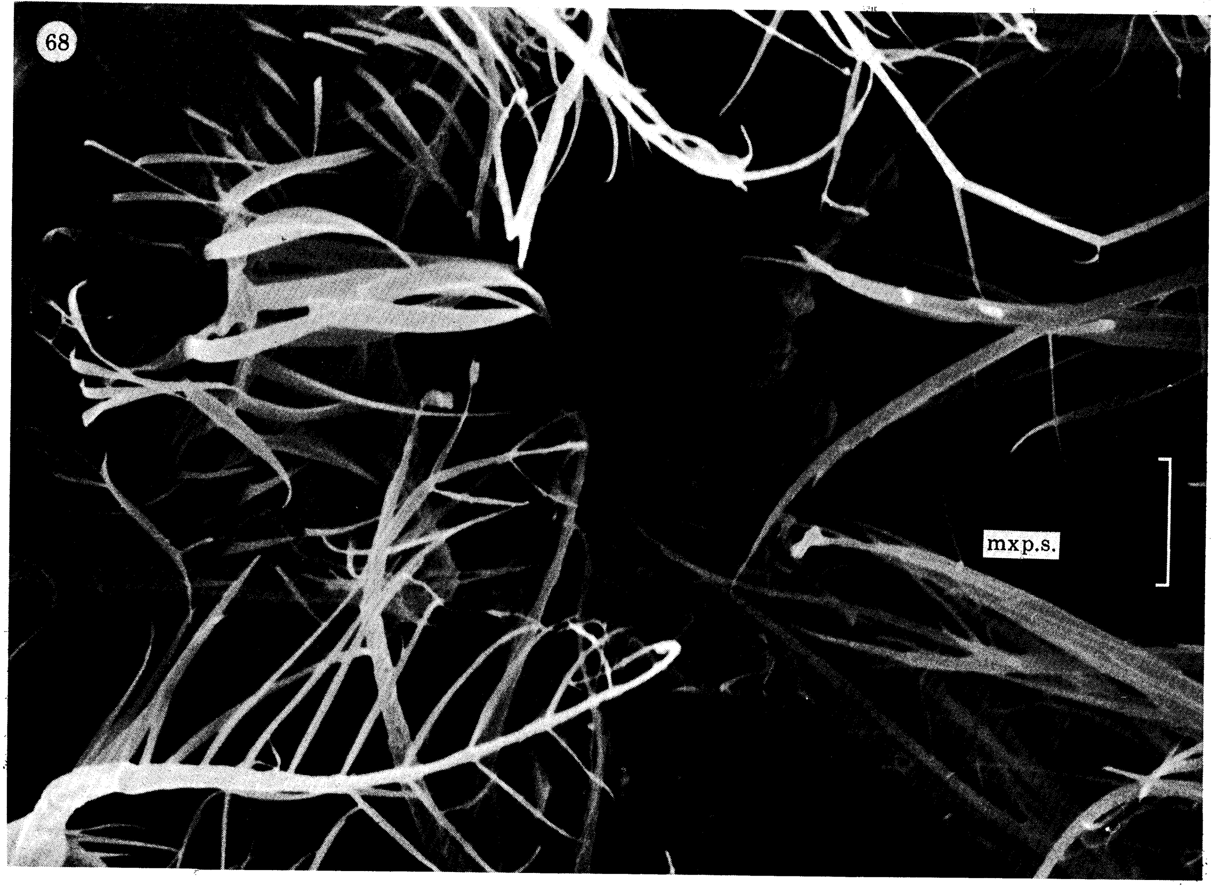
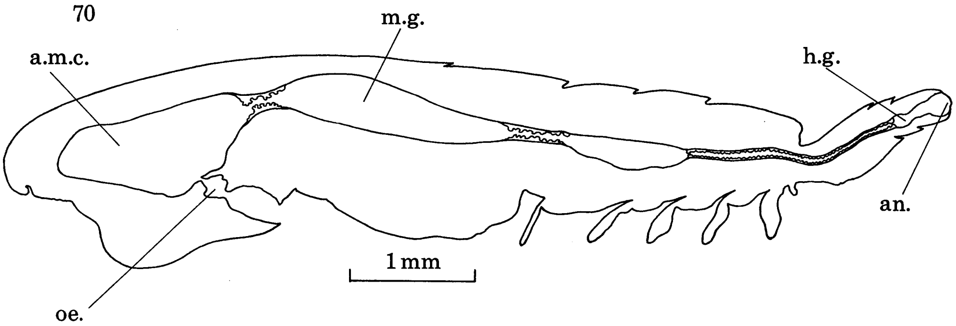


FIGURES 67 AND 68. For description see opposite.

(*d*) *The digestive tract*

(i) *Euaugaptilus*

E. placitus is a large predatory copepod whose extensive anterior midgut region can receive a large volume of food. The ventral surface of the head is swollen just anterior to the labrum but the labrum itself is small and muscular. The paragnaths are heavily sclerotized structures and may act as guides between which the prey is forced. The oesophagus (figure 71) is dilated by numerous dilator muscles originating on the ventral (anterior) wall of the labrum and on the anterior cephalic tendon. The dorsal wall of the labrum can be lowered to increase the volume of the preoral cavity by the three labral muscles (figure 71, lab. m. 1–3). Interspersed between the insertions of the dilators are circular oesophageal constrictors. Four of these occur



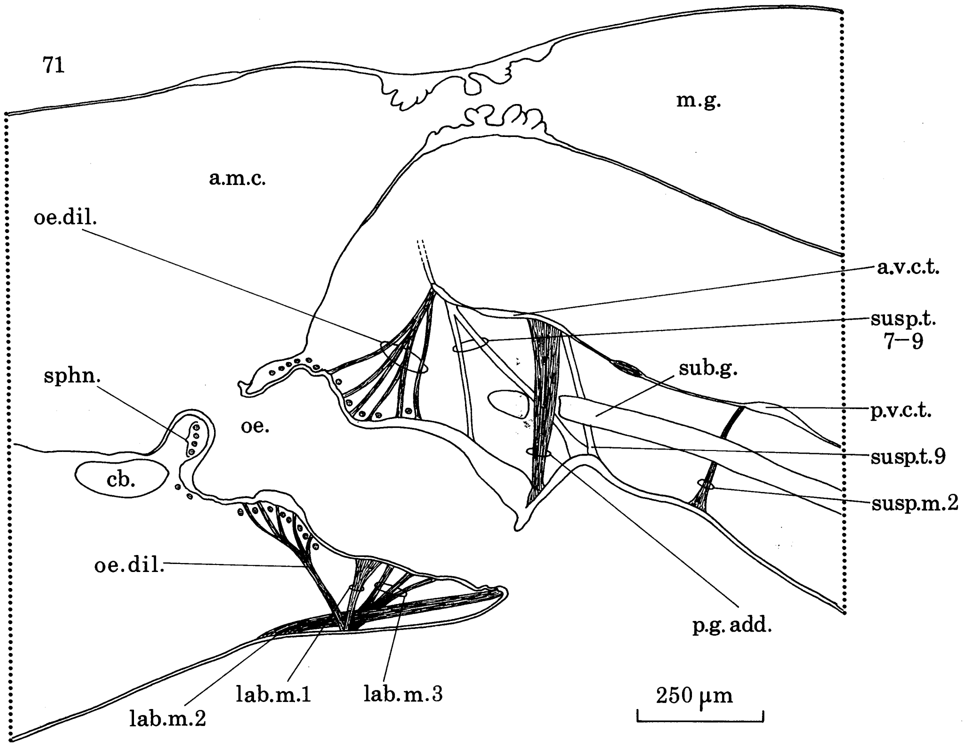


FIGURE 70. Median internal view of female *Euaugaptilus*, showing gross morphology of gut and subdivisions of midgut.

FIGURE 71. Thick median longitudinal section through oral region, drawn as a composite from several adjacent serial sections. The medial elements of the musculature of the oesophagus, labrum and paragnaths are shown.

in close proximity to the oesophageal opening into the midgut and probably act as a sphincter. The diameter of the nerve ring formed by the circumoesophageal commissures allows considerable dilation of the oesophagus and ingestion of large food items.

The midgut (figure 70) is subdivided into four regions, the first three of which are termed anterior, mid and posterior chambers. The anterior chamber is sac-like and probably incorporates the anterior midgut caecum. It presumably acts as a storage region in which digestion commences. Its walls are composed of thin columnar epithelial cells and are capable of limited distension. Isolated swollen areas of wall are scattered over the anterior chamber and are visible through the body integument. The anterior and middle chambers are separated by a constriction whose lumen is partly occluded by tall columnar cells with balloon-like distal extrusions (figure 71). The middle chamber has thin walls of flattened columnar epithelium and tapers as it extends into the first pedigerous somite. The middle and posterior chambers are separated at the boundary between first and second pedigerous somites by another constriction whose lumen is again occluded by tall columnar cells with distal extrusions. The posterior chamber extends through the second and third pedigerous somites. The fourth region is a narrow tube extending through the urosome to join the hind gut in the preanal somite. Its wall is thick and the lumen narrow. It appears to be closed off at both ends by valves formed by enlarged cells projecting into the lumen.

The short hind gut opens via the anus onto the dorsoposterior surface of the anal somite between the caudal rami. Its thin wall consists of a layer of flattened epithelial cells on a basement membrane. Its musculature has not been investigated in detail but it is basically similar to that of *Benthomisophria* (Boxshall 1982).

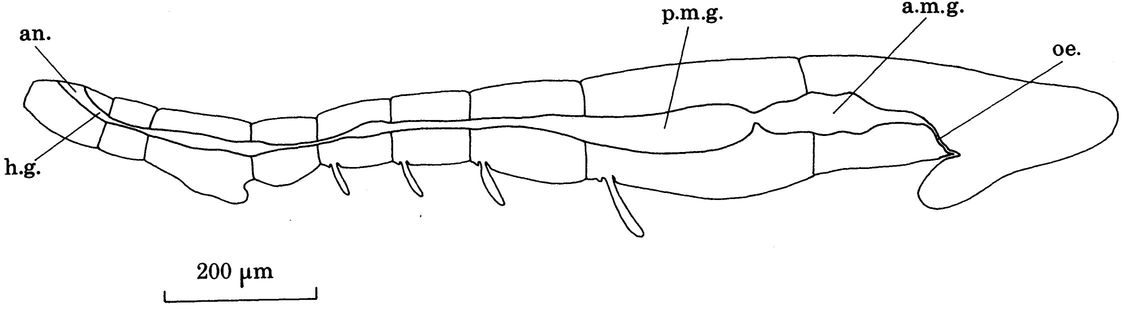
(ii) *Mormonilla*

It is difficult to obtain specimens of *Mormonilla* in which the digestive tract is complete. Even in material fixed as soon as it is recovered from the nets some decomposition has usually taken place.

Mormonilla has a short oesophagus and the diameter of the nerve ring indicates that only limited dilation can take place. It has a massive labrum containing well developed labral glands which secrete into the preoral cavity via a pore in the posterior surface of the labrum (figure 73, lab.p.). The preoral cavity is dilated by two pairs of labral muscles. The oesophagus is dilated by numerous dilator muscles (figure 73, oe. dil.). There are only two bands of circular muscles, the larger probably acting as a sphincter at the opening into the midgut.

The midgut is divided into three regions and has no anterior caecum (figure 72). The anterior chamber extends from the oesophageal sphincter into the first pedigerous somite where it is separated from the middle chamber by a marked constriction. Its wall comprises a simple columnar epithelium. The junction between anterior and middle chambers can probably be closed as it is provided with three well developed bands of sphincter-like circular muscles. In the specimens sectioned the middle chamber always appeared full of vacuolated material, the nature of which was not ascertained. This chamber tapers as it reaches the third pedigerous somite where the posterior region starts. The posterior midgut also has walls of columnar epithelium. It extends to the third urosome somite where it is separated from the short hind gut by a marked constriction.

72



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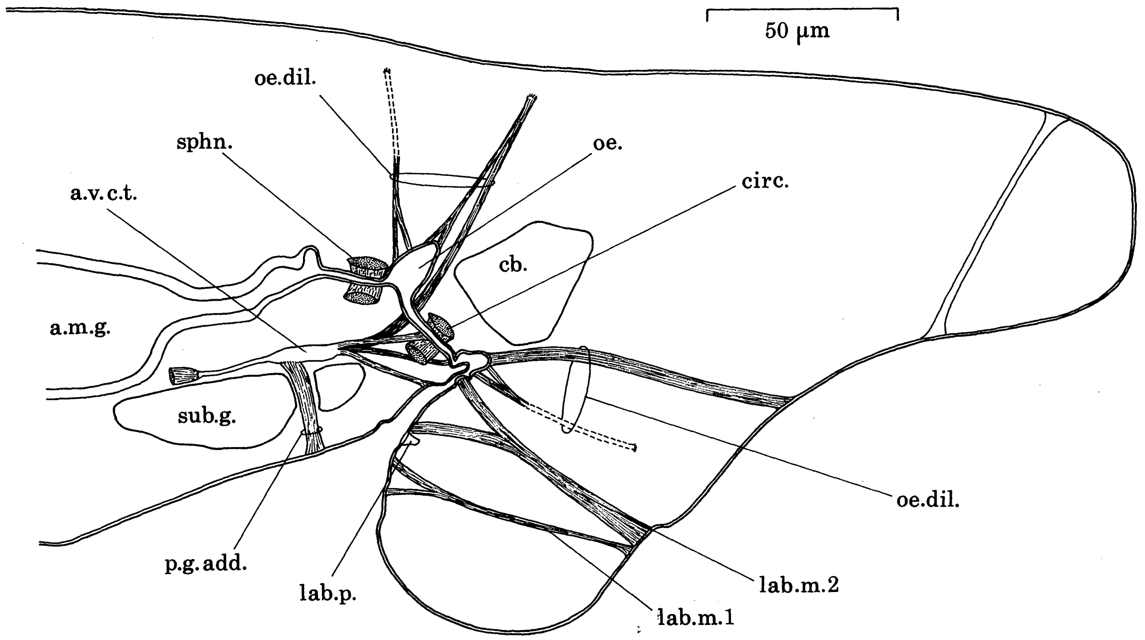

FIGURE 72. Median internal view of female *Mormonilla*, showing gross morphology of gut.

FIGURE 73. Thick median longitudinal section through the anterior end of the cephalosome, drawn as a composite from several adjacent serial sections. The medial elements of the musculature of the oesophagus, labrum and paragnaths are shown.

(iii) *Comparative morphology of the copepod digestive tract*

The gross morphology of the digestive tract has been described for representatives of most copepod orders. However, few comparative accounts have been published and no attempt has been made to identify general patterns for the whole group. Almost always the alimentary canal comprises an ectodermal integument-lined foregut or oesophagus, an endodermal midgut and an ectodermal integument-lined hind gut. The oesophagus is typically highly muscular and passes between circumoesophageal commissures to open, usually via a sphincter, into the midgut. The foregut of *Paranthessius anemoniae* Claus, a parasitic poecilostomatoid, is highly specialized. It comprises a short narrow oesophagus and an expanded sac-like distal expansion also lined with integument which Briggs (1977) suggested may act as a food storage region. This is separated from the midgut by a valve.

The midgut is variable in gross morphology but is typically divided into anterior and posterior sections about at the level of the third or fourth pedigerous somites. This division may be marked by a muscular constriction or sphincter as in some calanoids (Marshall & Orr 1955), harpacticoids (Fahrenbach 1961) and misophrioids (Boxshall 1982). It can also be detected by a change in cell type in the epithelial lining, as recorded for harpacticoids (Fahrenbach 1961; Sullivan & Bisalputra 1980), calanoids (Park 1966; Arnaud *et al.* 1978), misophrioids (Boxshall 1982), mormonilloids (present account), cyclopoids (Hartog 1888) and siphonostomatoids (John & Nair 1975). In his description of *P. anemoniae* Briggs (1977) wrongly identified the posterior region of the midgut (extending from the third pedigerous somite to the urosome) as the hind gut, as indicated by its lack of an integumental lining. In their review of harpacticoid gut morphology Sullivan & Bisalputra (1980) concluded that the midgut is absorptive, that its anterior part functions in merocrine and exocrine secretion, and that its posterior part contributes some holocrine secretion.

The midgut, especially the anterior region, may be further subdivided or possess other elaborations. Most copepods have an anterior midgut caecum which probably serves both as a storage area and as the region in which digestion commences. This feature is known in calanoids, harpacticoids, misophrioids, siphonostomatoids and cyclopoids. *Paranthessius* lacks an anterior caecum: storage is performed by the spacious foregut. The opening of the anterior caecum into the midgut may be constricted (Sullivan & Bisalputra 1980) and in *Benthomisophria* it can be entirely closed off by bands of circular muscles (Boxshall 1982). Sullivan & Bisalputra (1980) concluded that the anterior caecum in harpacticoids absorbs some digested nutrients and also has a secretory function. Its absence in some groups, such as the mormonilloids, is regarded as an advanced feature.

Many siphonostomatoids have large branching lateral midgut caeca. Only one pair of lateral caeca is usually present (Giesbrecht 1899) although each caecum may be multibranched or multilobed and occupy a large volume within the prosome. The presence of caeca appears to be associated with the intermittent feeding of some parasites and associates, and similar adaptations can be found in the parasitic Branchiura and ascothoracican Cirripedia. *Benthomisophria* has adopted gorging as a feeding strategy and the anterior midgut is capable of gross distension (Boxshall & Roe 1980). The presence of lateral midgut caeca appears to correlate with feeding specialization and is here regarded as a derived feature.

Euaugaptilus and two other calanoids, *Epilabidocera amphitrites* McMurrich and *Centropages typicus* Krøyer, all have the anterior midgut region subdivided near the level of the maxillae. This subdivision is marked by a change in epithelial cell type in *Epilabidocera*. The ultrastructural and histochemical studies of Arnaud *et al.* (1978) on *C. typicus* provide some evidence of functional specialization between the two parts.

The short hind gut is typically separated from the midgut by a valve and opens posteriorly via the anus. Dwarf parasitic males of the family Chondracanthidae lack an anus (Rousset & Raibaut 1983) as do the highly transformed females of the parasitic *Melinnacheres steenstrupi* (Bresciani & Lutzen 1961).

7. THE THORACIC LEGS AND SWIMMING

(*a*) *Euaugaptilus*

(i) *Skeletal structure*

E. placitus has five pairs of similar swimming legs in the female and the description given below for the first leg is applicable to all. The two members of each leg pair are united into a single functional unit by a hollow flattened structure, a coupler or interpodal bar, whose basic components are the same as in *Benthomisophria* (Boxshall 1982); two transversely flattened half cylinders of integument fused distally and joined laterally to the proximal part of the medial coxal margins. In *Euaugaptilus* the anterior half cylinder comprises thick integument and projects well into the body cavity. The posterior half cylinder is thinner and does not. It joins posteriorly into the adjacent median flexible integument (figure 75). The anterior half cylinder is attached anteriorly to the semirigid median intersomitic sclerite (figure 75, m.i.s.) which is thickest anteriorly at the intersomitic boundary where the transverse intersomitic ridge (i.s.r.) is located. The intersomitic ridge is the structure referred to by Perryman (1961) as the vertical intersegmental plate in *Calanus*. Intersomitic ridges are present on the median intersomitic sclerites between the maxilliped-bearing somite and the first pedigerous somite, and between all the pedigerous somites including 4 and 5 which are fused into a double somite. These ridges play a significant part in the promotor–remotor swing of the legs in *Calanus*, by increasing the angle through which they are able to swing.

The ventral body wall (figure 74) consists of median intersomitic sclerites, coupler openings and the median flexible integument along its midline. The paired leg bases occur in the middle of each somite, either side of the midline. Each is surrounded by lateral sclerites of only moderate thickness but has a system of reinforcing sclerotized ridges. At the lateral extremes of the ventral thoracic wall the border between the sternal area and the tergopleural area is marked by longitudinal ridges. Thoracic somites 1–4 are separated dorsally and laterally by slightly telescopic joints.

Heavily sclerotized ridges are associated with the leg bases although the system is more complex and difficult to interpret in functional terms than in either *Calanus* or *Benthomisophria*. Adjacent to each leg base save leg 1, is a sclerotized ridge of ventral body wall forming a lateral rim. There is no well developed lateral pivot about which the leg can swing. The basal articulation of the leg is very loose laterally but the fusion of the legs medially to the coupler provides a firm medial articulation. The lack of a distinct outer pivot is unusual for copepod swimming legs which have only one axis of movement and typically have a well developed transverse pivot line. The sclerotized ridge lateral to legs 2–4 extends both laterally and medially from its posterior end. Medially it extends to the anteriorly directed remotor process, which is present at each leg, though much reduced on leg 5. It extends laterally then curves anteriorly, delimiting a concavity in the body wall. The concavity is poorly developed lateral to leg 5.

Each swimming leg (figures 76 and 78) has a coxa, basis and two three-segmented rami. All the segments are flattened, though the coxa is more cylindrical proximally. The coxae, united by fusion to the coupler, articulate with the somite via a transverse pivot joint. The two well developed pivots lie at the medial angles of the coxae where they meet the coupler and the line between them marks the axis about which the promotor–remotor swing takes place. This axis is ill defined laterally and there is a pouch of flexible integument lying lateral to the limb base. The coxa–basis joint possesses arthrodial membrane posteriorly but not anteriorly.

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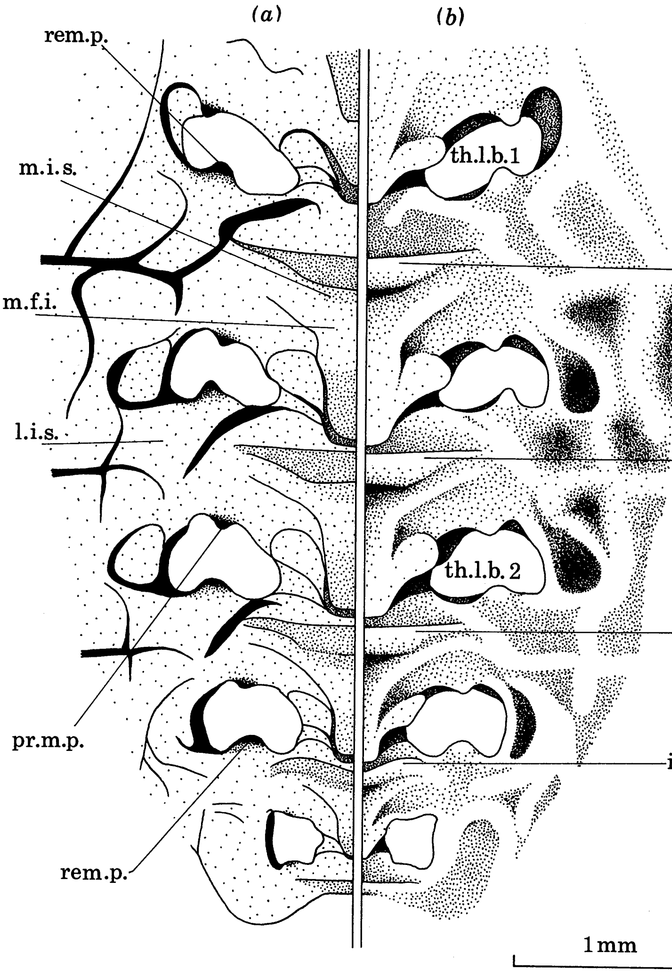

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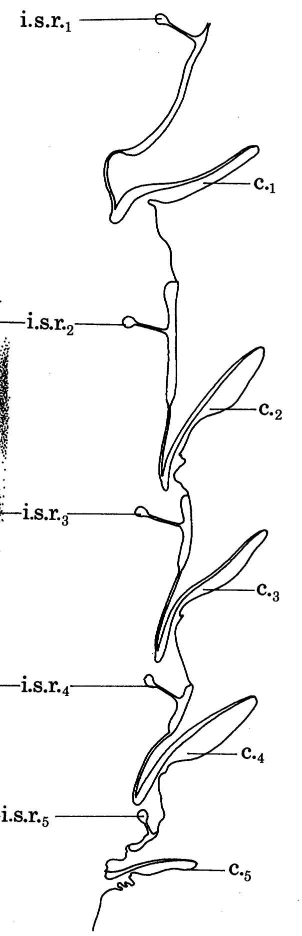

Figure 74. Internal view of ventral body surface of the pedigerous somites of *Euaugaptilus* with the swimming legs protracted as in figure 75, showing (*a*) the degree of sclerotization of the integument, as indicated by the intensity of shading, and (*b*) the topography of the ventral body wall.

Figure 75. Median longitudinal section through the ventral wall of the pedigerous somites, showing the differences in thickness of its components and the positions of the couplers and intersomitic ridges.

This allows posterior flexion of the basis about the anterior margin which acts as a transverse hinge line. The first endopod segment is telescoped inside the basis and is provided with a narrow ring of arthrodial membrane. This joint allows some bilateral and posterior flexion, and some rotation. The intraendopodal joints are the same. The first exopod segment is similarly telescoped into the basis and this joint is provided with arthrodial membrane all round. Movement at the basis–exopod joint is mainly medial flexion, with some posterior flexion and rotation. The intraexopodal joints are the same.

(ii) *Musculature*

The extrinsic limb muscles originate dorsolaterally (figure 76). There are three main groups, a promotor group of four and two remotor groups of two muscles each. Promotor muscles

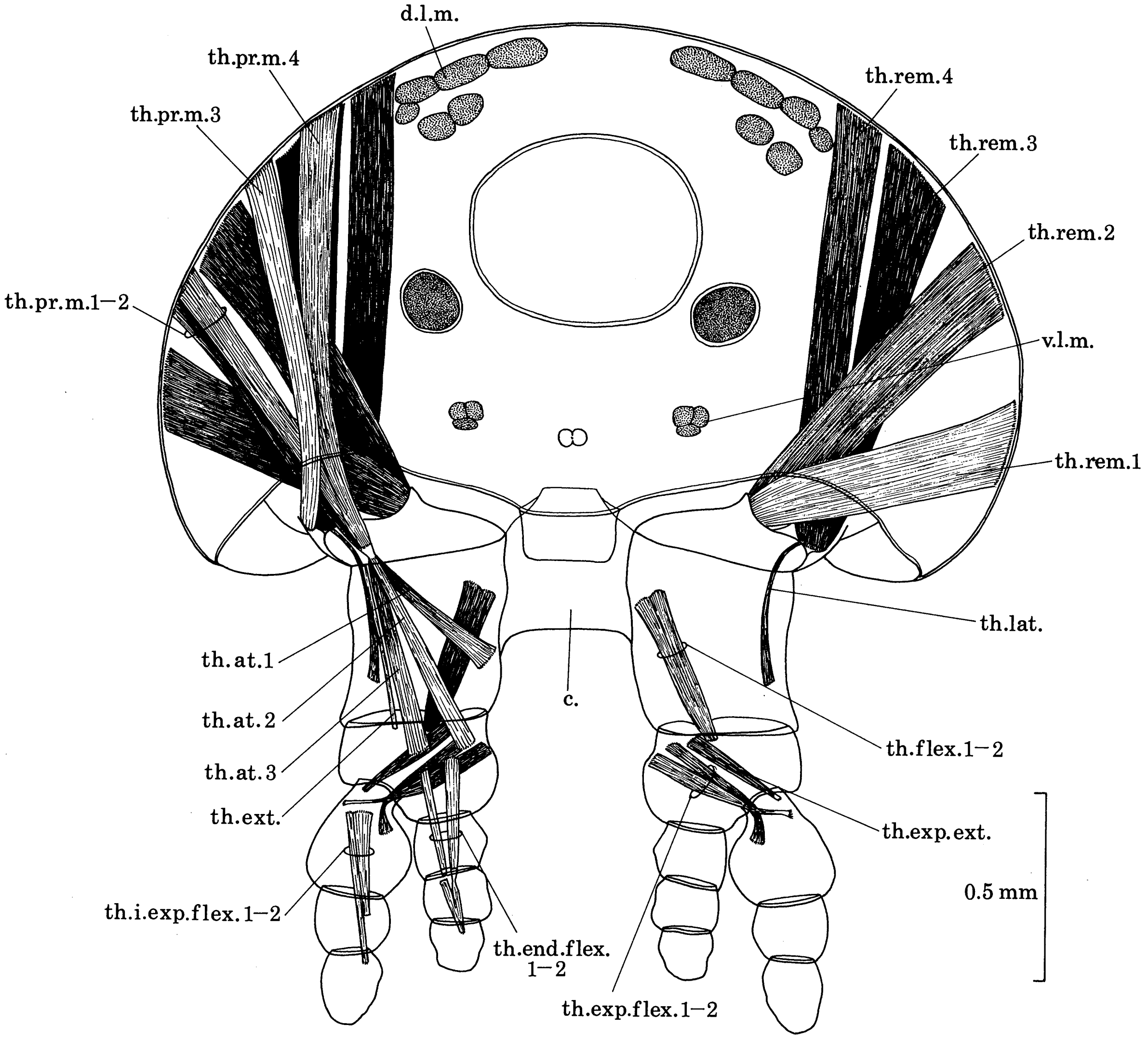

FIGURE 76. Anterior view of the first pedigerous somite with its pair of legs, showing the musculature. The anterior muscles are omitted from one side.

(th. pr.m. 1–2, 4) originate on the mid-dorsolateral wall and have a common insertion which extends from the promotor process (figure 74, pr.m.p.) of the ventral body wall to the anterior rim of the coxa. These muscles swing the leg forwards. Their action is partly direct as the insertion extends onto the coxal rim, partly indirect as the insertion on the promotor process will raise the whole anterior part of the coxa–somite articulation. In *Euaugaptilus* there is a fourth promotor (th. pr.m. 3) which inserts anterolaterally to the thickened rim of the leg base, on the area of flexible integument. This muscle acts indirectly by raising the body wall anterolateral to the limb. The anterior remotors (th. rem. 1–2) are well developed, with large cross-sectional areas and have broad origins on the lateral to mid-dorsolateral body wall. They share a common insertion along the lateral surface of the remotor process (figure 74, rem.p.), along the thickened ridge of integument adjacent to the limb base, and on the thinner integument posterior to it. The muscles pull the body wall and remotor process upwards thereby swinging the leg backward. The posteriorly located remotors 3–4 originate high on the dorsal body wall and insert together on the posterolateral hoop of thickened integument and the flexible integument adjacent to it. Their action is also indirect, swinging the leg back by pulling upwards on the posterolateral hoop and integument posterolateral to the limb base. None of the remotors inserts on the leg itself. The swimming power stroke is produced indirectly and the system of sclerotized ridges and processes increases its efficiency.

Several minor extrinsic muscles originate on the ventral body wall immediately adjacent to the limb base. Three (th. at. 1–3) originate at the common insertion site of the main promotors and pass into the limb to insert anteriorly on the coxa or basis. Those inserting in the basis flex it posteriorly relative to the coxa, during the recovery stroke. A narrow muscle (th. lat.) originates on the ventral body wall near the insertion of remotors 3–4. It passes over the rim of the limb to a posterior insertion on the coxal wall. Its function is unknown.

Two intrinsic muscles (th. flex. 1–2) originate posteromedially in the coxa and insert together on the midposterior wall of the basis which they flex posteriorly. They are opposed by the narrow extensor which runs beneath the anterior wall of the coxa to insert just inside the basis. The exopod is moved by a pair of opposing muscles lying transversely within the basis. The proximal extensor moves the ramus laterally, the flexor, medially. An additional flexor runs parallel but posterior to exopod flexor 1. There are two flexors within the exopod which, because of their asymmetrical insertions (figure 78), produce posteromedial flexion and some rotation. They control the feathering of the exopod during the recovery stroke. The endopod as a whole is moved by two flexors originating anteriorly in the basis. They insert separately on the proximal rim of segment 2 and terminate in a common insertion in segment 3. There is no endopod extensor.

(iii) *Swimming*

The swimming mechanism of *Calanus* was described in detail by Perryman (1961) and Manton (1977), using Perryman's results, commented on the unusual features of copepod locomotion. The skeletomusculature of the swimming legs of *Benthomisophria* is similar to that of *Calanus* and Boxshall (1982) postulated that the swimming mechanism would also be basically the same. These studies concentrated on interpretation of anatomical aspects of the swimming mechanism and, as *Euaugaptilus* shares the same anatomy, no new interpretations of the primary swimming mechanism are presented here. Studies on the energetics of copepod swimming (Vlymen 1970, 1977; Enright 1977; Lehman 1977; Strickler 1974, 1977) and studies on copepod feeding (see §6*a*) have emphasized the viscous nature of the environment experienced by a small slowly moving copepod. The dominance of viscous rather than inertial forces at this scale has important consequences for the swimming of all small crustaceans. They gain little momentum from the swimming power stroke so that as it ends they undergo rapid deceleration. During the recovery stroke the limbs are often flexed and oriented so as to reduce resistance but the drag from an immediate recovery stroke still contributes to deceleration after the power stroke is completed. In some larval crustaceans, such as the early nauplii of *Branchinecta ferox* (Milne–Edwards), the recovery stroke actually causes backward movement (Fryer 1983).

The swimming legs of *E. placitus* exhibit a number of fine scale adaptations which enhance the effectiveness of the power stroke and help to minimize drag during the recovery stroke. Most significant is the rotation, or feathering, of the oar-like rami during the recovery stroke. During the power stroke the rami are held flat in a transverse plane and are slightly spread so that, with their armature of long plumose setae, they present a large planar surface. The plumose setae are distributed along the inner margin of the endopod, around its apex, and along the inner margin of the exopod. Those on the endopod effectively close the median space between members of a limb pair, those on the exopod, the space between the rami. Each natatory seta is armed with two rows of long, close-set setules which increase its effective surface area and close the gaps between adjacent setae (figure 78). The length of the setules increases distally along each seta to compensate for the increasing gap between the distal portions of the diverging setae. The increasing length of distal setules is a feature only of the main natatory setae. The isolated inner coxal seta is also provided with close set setules bilaterally but these decrease in length distally. The setules of a natatory seta may gain some support or protection from those of the nearside rows of the adjacent setae. The setules are not hinged at their bases and do not fold during the recovery stroke.

Euaugaptilus uses a feathering mechanism to reduce the effective surface area of the swimming legs during recovery. Figure 77 shows the swimming legs in the middle of the recovery phase: legs 1 and 2 have completed their recovery stroke, leg 3 is at the midpoint of its swing, leg 4 is closing up and beginning to rotate its rami before the promotor swing and leg 5 still has its rami spread as at the end of the power stroke. Recovery thus appears to begin with leg 1 and proceeds as a metachronal wave back towards leg 5. The main promotors produce the recovery swing of the leg. During recovery the basis is flexed posteromedially relative to the coxa. There is also some rotation as the flattened basis lies in a somewhat oblique plane. Each ramus is flexed medially and rotated slightly so that it comes to lie in a near vertical longitudinal plane. The endopod setae lie in the same plane in the median space between the protopods of the following pair of legs, with their setules orientated dorsoventrally (figure 79). In the middle of the recovery stroke the exopod setae also lie in a near vertical plane along the midline. The rami and their setae form a median keel, seen in ventral view in figure 77 and in lateral view in figure 35, that may serve as a stabiliser in the period of deceleration during the recovery stroke.

(*b*) *Mormonilla*

(i) *Skeletal structure*

The swimming legs of *Mormonilla* have the typical biramous copepod pattern. The protopod comprises a long coxa and a shorter basis. A coupler is present, as in *Euaugaptilus*. Both species of *Mormonilla* have only four pairs of swimming legs but the segmentation of their rami is different. *M. phasma* is described here. Legs 1–4 have a two-segmented exopod. The endopod is two-segmented in leg 1, only one-segmented in legs 2–4. Movement of the whole limb is limited by the presence of the coupler to a promotor–remotor swing.

The anterior half cylinder of the coupler projects further into the body cavity than the posterior (figure 80). Both are attached to the ventral body wall via areas of thin arthrodial membrane. The ventral body wall between each successive pair of legs is composed primarily of a thickened median intersomitic sclerite which has a slight transverse thickening just anterior to its midpoint corresponding to the transverse intersomitic ridge of *Euaugaptilus*. The portions anterior and posterior to the thickening are homologous with the areas referred to as the median flexible integument and median intersegmental sclerite respectively in *Benthomisophria*.

Areas of arthrodial membrane (indicated by a light stipple in figure 81) extend across the body anterior and posterior to the leg bases. The main features of the body wall associated with the limbs are large hoops of heavily sclerotized integument (figure 81, hoop) located lateral

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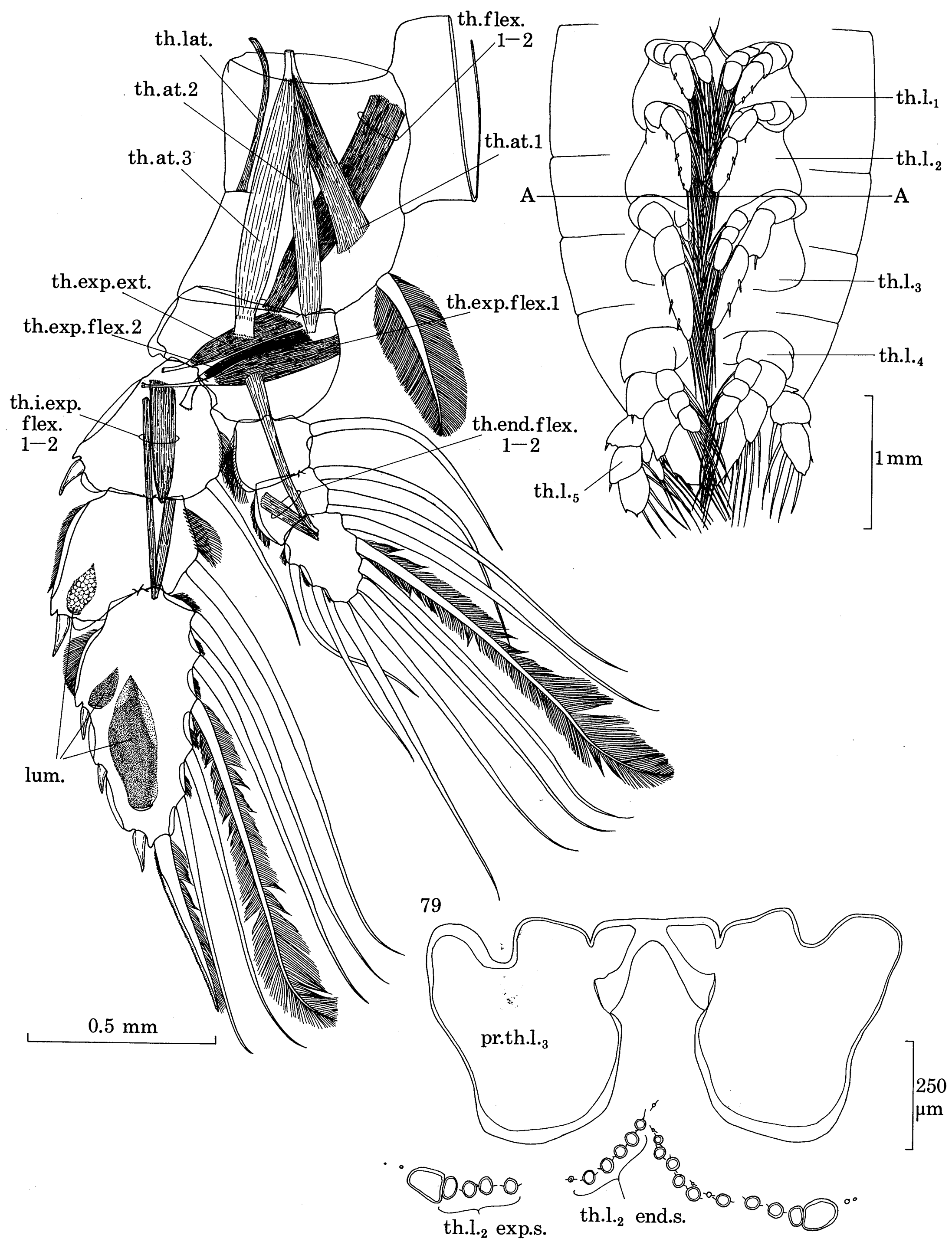

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FIGURE 77. Ventral view of pedigerous somites of *Euaugaptilus*, showing the positions of the swimming legs about at the mid point of the recovery (promotor) stroke.

FIGURE 78. Third swimming leg of female *Euaugaptilus*, showing intrinsic muscles and armature elements in detail. Bioluminescent organs (lum.) are present in the second and third exopod segments.

FIGURE 79. Transverse section approximately through the plane A–A in figure 77, showing the natatory setae on the rami of the second legs being held partly feathered in the median space between the protopods of the third pair of legs.

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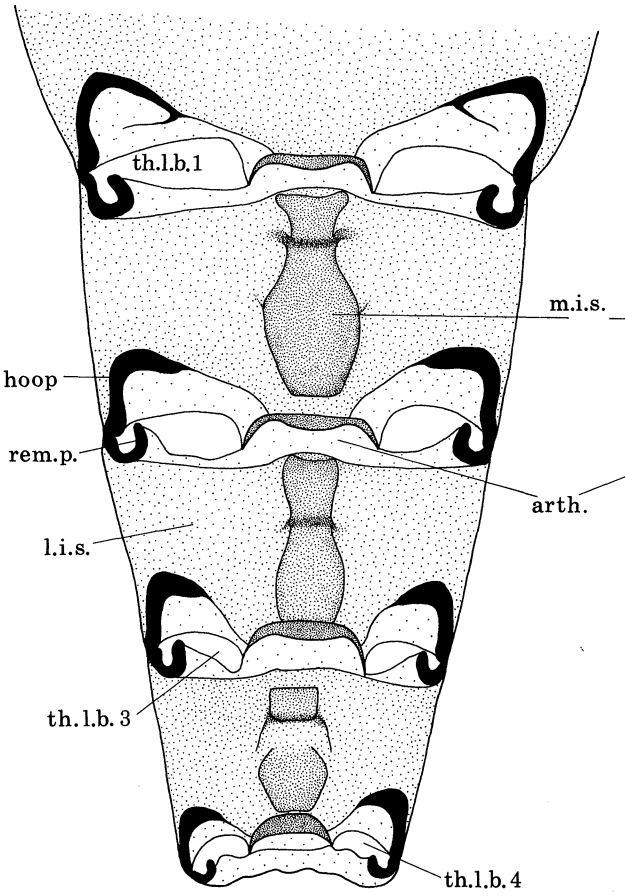

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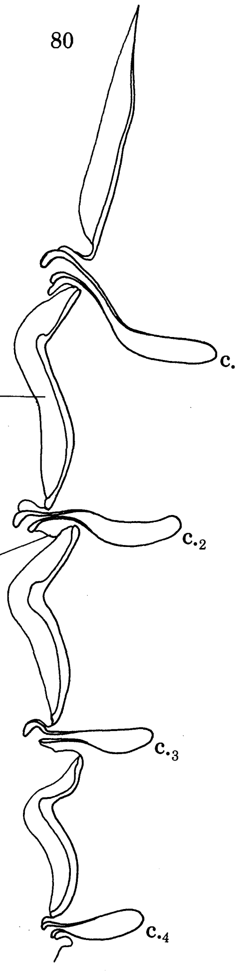

FIGURE 80. Median longitudinal section through the ventral wall of the pedigerous somites of *Mormonilla*, showing the positions of couplers and sclerites.

FIGURE 81. Internal view of the ventral body surface of *Mormonilla* with the swimming legs retracted as in figure 80. The intensity of shading indicates the degree of sclerotization of the integument.

to each leg base. Each curves medially through about 90° at its anterior end and through a semicircle at its posterior end, where it forms the remotor process extending over the limb base. The process is smaller in the more posterior legs. The area of body wall delimited by these hoops comprises arthrodial membrane which bulges ventrally to form a swollen base to which the proximal rim of the limb coxa is attached. This arrangement produces a weaker, less rigid articulation of the swimming legs but increases the arc through which they can swing. The lateral intersomitic sclerites, between successive leg bases, are of moderate thickness.

Legs 2–4 are located about two thirds of the distance along the somite from its anterior margin, as in most copepods. The first leg, however, is situated relatively much further back, due to the marked elongation of the anterior part of this somite (figure 82). The first pedigerous somite is over three quarters the length of the cephalosome and the process of elongation has affected the musculature of the first leg. Elongation appears to be linked to the enlargement of the filter basket as the first legs form its posterior wall.

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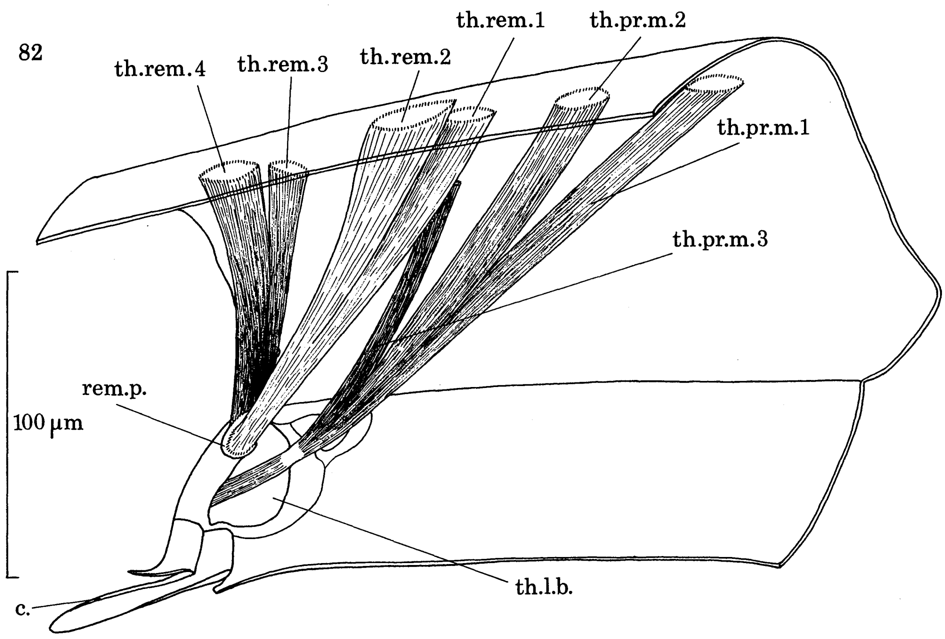

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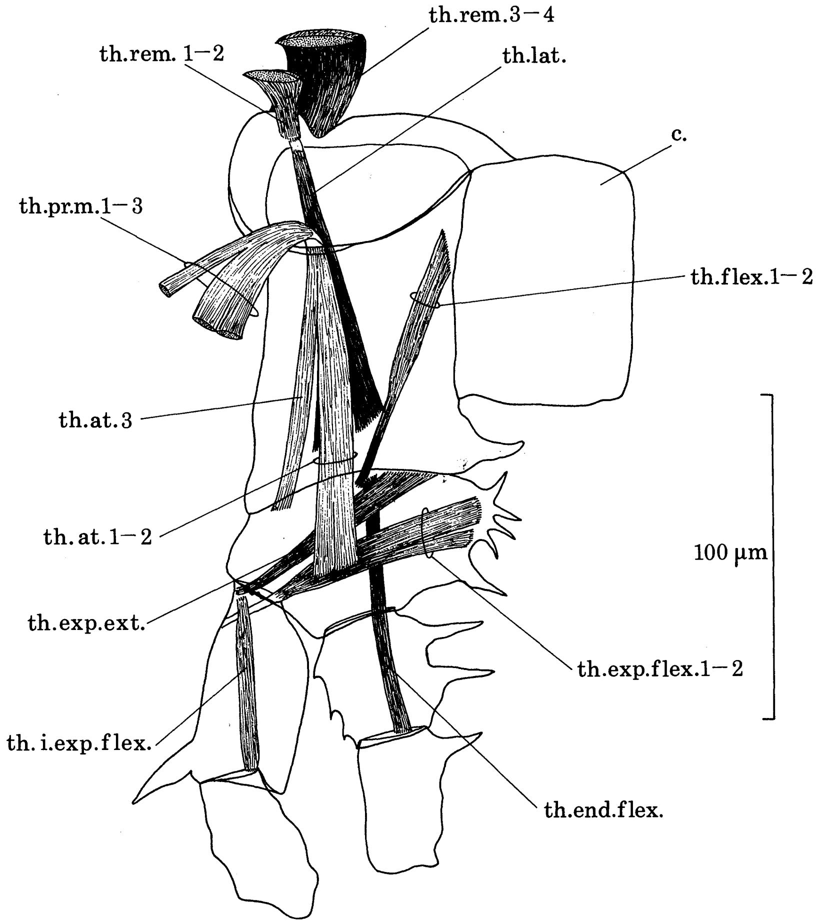

FIGURE 82. Oblique internal view of first pedigerous somite of *Mormonilla*, showing the extrinsic limb muscles.
FIGURE 83. Anterior view of first swimming leg of *Mormonilla*, showing intrinsic muscles.

(ii) *Musculature*

Three blocks of extrinsic muscles are responsible for the promotor–remotor swing (figure 82). The promotor block comprises three strands which originate dorsolaterally and laterally in the anterior half of the somite and converge on a common insertion on the proximal rim of the coxa and on the bulging ventral body wall just anterior to the rim. This muscle appears to continue from this insertion into the protopod, subdividing within the coxa before inserting on the anterior wall of the basis. The intrinsic continuation may represent discrete intrinsic muscles whose origins are continuous with the insertions of the extrinsic promotors. The two remotor blocks each comprise two strands which originate dorsolaterally. Remotors 1 and 2 insert together on the lateral surface of the remotor process. Remotors 3 and 4 share a common insertion spread around the posteromedial part of the remotor process. The lateral muscle (th. lat.) inserts distally on the posterior coxal wall and originates out of the limb adjacent to remotors 1 and 2 (figure 83).

The intrinsic muscles follow the common pattern for copepod swimming legs (Boxshall 1982; table 2). Movement of the exopod is produced by an extensor (th. exp. ext.) and a pair of flexors (th. exp. flex. 1–2) originating within the basis and passing obliquely into the exopod. A single intraexopodal flexor inserts medially on the rim of segment 2. The endopod has a single flexor (th. end. flex.) which moves the whole endopod medially.

(iii) *Swimming*

M. phasma is a weak swimmer. Live specimens, brought up from depths of 400–500 m off the Azores made irregular, single swimming movements, not bursts of rapidly repeated jumps as did some of the other copepods from the same samples. The swimming movements observed frequently involved only legs 4 and 3, or legs 4, 3 and 2, rather than all four pairs.

Reductions in the segmentation and musculature of the rami of the swimming legs and in the longitudinal trunk muscles can be interpreted as evidence of relatively weak swimming ability. Also the elongate, slender body and long setose antennules and caudal rami are adaptations that can decrease the rate of sinking and are suggestive of a passive floating habit. Forward swimming may well be produced by the regular feeding movements of the antennae, and the mandibular and maxillulary palps which probably pull the copepod through the water at slow speed. Jumping produced by the beat of the swimming legs may be primarily an escape reaction as in calanoids.

The long plumose setae of the leg rami (figures 61 and 62) increase the effective area of the leg during the power stroke. The legs are fully extended during the power stroke but are flexed posteriorly at the coxa–basis joint during recovery. The muscles that spread the rami are probably relaxed during the recovery phase so that the rami and their natatory setae close up, but there is no indication that the rami are feathered, as in *Euaugaptilus*.

8. General observations on copepod musculature

Sufficient information has now been published to permit some generalizations concerning copepod musculature. Most available accounts relate to calanoids (Lowe 1935; Perryman 1961; Park 1966; Hessler 1964) but some information is also available on cyclopoids (Hartog 1888), harpacticoids (Lang 1948; Fahrenbach 1964), misophrioids (Boxshall 1982) and mormonilloids (present account). Some of the most important homologies have been identified between the copepod orders but detailed homologies of the complex musculature of the cephalosomic appendages will not be presented here. Trunk musculature has been discussed above (see §4*c*).

There are marked differences between the extrinsic muscles of the cephalosomic limbs of *Euaugaptilus* (figure 15), *Mormonilla* (figure 28) and *Benthomisophria* (Boxshall 1982: figure 13). In *Euaugaptilus* they are extremely complex. This is a rapidly swimming predator, each of whose cephalosomic limbs, other than the antennules, appears capable of a wide range of movements. The antennules are involved in steering and in the detection of prey and approaching predators. The antennae are probably involved in grooming, prey detection, and the production of water currents as part of the feeding mechanism. The mandibles and maxillules are involved in producing currents and movement of food while the maxillae and maxillipeds must perform several raptorial and manipulative movements during prey capture and handling. The ability of any given limb to perform several roles, especially those relating to manipulation of prey, is dependent upon the possession of complex musculature and articulation systems as well as sophisticated sensory systems. It is this functional multiplicity that explains the complexity of the musculature in *Euaugaptilus*. No single functional role is dominant and, while the muscles exhibit a range of sizes (in terms of cross-sectional area) there is none that is grossly better developed than the others. The cephalosomic musculature of the omnivorous calanoid *Epilabidocera amphitrites* is similar in overall complexity (Park 1966).

The pattern of extrinsic musculature in *Benthomisophria* is basically similar to that of *Euaugaptilus* although slightly fewer muscles are present. Both genera are predatory and the shared requirement for manipulative movements during prey capture and handling determines the similarities in postmandibular limb musculature. Differences between them are related to the increased importance of the reflexed mandibular palps and antennae in *Benthomisophria*. These appendages are involved in grooming the carapace-like outgrowth covering the first pedigerous somite and their muscles are among the most powerfully developed in the head.

Calanus has hitherto been regarded as a good example of copepod filter feeding and the work of Cannon (1928) on feeding currents was based on observations of living specimens. The newly emerging model of calanoid feeding behaviour (see §6*a*) suggests that feeding on suspended particulate matter and raptorial predation can involve similar grasping movements of the mouthparts, although very small particles are treated in a different way. The limb muscles of *Calanus*, as described by Perryman (1961), are therefore similar in complexity to those of *Euaugaptilus*. The extrinsic maxillary and maxilliped muscles of *Euaugaptilus* are more powerfully developed than those of *Calanus* because it has to grasp relatively large prey with these appendages.

The basic gnathostomatous type of mouthparts, as found in *Calanus*, *Benthomisophria* and representatives of other orders, can be used for both particle feeding and predation and it has been suggested that the ancestral copepod was a generalist possessing this type of mouthparts (Boxshall *et al.* 1984). The relatively complex musculature of these appendages is probably also a shared ancestral character. The comparatively simple musculature of *Mormonilla* is therefore an advanced or derived condition. *Mormonilla* is a highly specialized particle-feeder and has fewer muscles than either *Euaugaptilus* or *Benthomisophria*. The main movement of its antennules, antennae, and mandibular and maxillulary palps is the promotor–remotor swing about basal pivot lines. Accordingly each has relatively simple extrinsic muscles arranged antagonistically. The mandibles and maxillules also have adductors and abductors for their gnathobases. Only the maxillae and maxillipeds have the capacity for more complex twisting movements, executed as they move within the filter basket. Even for these limbs the range of possible movements is small and the reduction in numbers of extrinsic muscles has resulted in the loss of the posterior ventral cephalic tendon, and in changes in the site of origin of the remaining ventral extrinsic muscles. The secondary reduction in numbers of muscles was probably achieved by loss of some muscles as well as by the failure of some of the larger muscle blocks to subdivide during ontogeny.

Little information is available on the ontogeny of copepod musculature. Appendage morphology and musculature in the copepodid stages is very much like that of the adult. The most interesting information is provided by the developing musculature during the sequence of naupliar stages. The most comprehensive accounts of naupliar anatomy are those of Fanta (1972, 1976) on the harpacticoid *Euterpina acutifrons* (Dana) and the cyclopoid *Oithona ovalis* Herbst, and Perryman (1961) on *Calanus*. The sequence of appearance of the muscles of the cephalic appendages given by these authors is summarized in table 3. The data from Fanta refer only to the dorsal extrinsic muscles so Perryman's data have been subdivided into dorsal and ventral components to facilitate comparison.

TABLE 3. NAUPLIAR MUSCULATURE: NUMBERS OF DORSAL EXTRINSIC LIMB MUSCLES, WITH NUMBERS OF ADDITIONAL VENTRAL MUSCLES GIVEN IN PARENTHESES WHEN KNOWN

	atl.			ant.			mnd.			mxl.			mx.		
stage	O	E	C	O	E	C	O	E	C	O	E	C	O	E	C
N I	2	2	2 (+1)	2	2	4 (+1)	2	2	4 (+4)	—	—	—	—	—	—
N II	2	2	3 (+1)	2	2	4 (+1)	2	2	4 (+4)	—	—	—	—	—	—
N III	3	2	3 (+1)	3	2	5 (+1)	2	2	4 (+4)	—	—	—	—	—	—
N IV	3	2	3 (+1)	3	3	5 (+1)	3	3	4 (+5)	2	—	2 or 3	—	—	?
N V	3	3	3 (+1)	4	3	5 (+1)	3	3	4 (+5)	2	—	2 or 3	—	—	?
N VI	3	4	4 (+1)	4	7	6 (+1)	3	4	6 (+6)	2	—	3	—	—	2

O, *Oithona ovalis* (data from Fanta 1976); E, *Euterpina acutifrons* (data from Fanta 1972); C, *Calanus finmarchicus* (data from Perryman 1961); N I–VI, nauplius 1–6.

The minimum set of dorsal extrinsic muscles necessary to move a limb is one antagonistic pair, precisely as present at the first nauplius stage for the antennules, antennae and mandibles of *Euterpina* and *Oithona*, and for the antennules of *Calanus*. In the antennae and mandibles of *Calanus* either one or both of the muscles are subdivided. Muscle numbers increase gradually during the sequence of six naupliar stages. There is probably little significance in differences between the genera in the absolute numbers of muscles present, though more are present in *Calanus* at most stages. Muscles for the rudimentary maxillules appear at nauplius IV in *Oithona* and *Calanus*, and between nauplius IV and VI for the maxillae of *Calanus*. There are no postmandibular limb muscles in *Euterpina* at any stage of naupliar development and no naupliar maxilliped muscles in any of the three genera. These comparisons are superficial because of the paucity of published information. Comparison of numbers of muscles present gives no indication of their precise homologies. The long antennulary levator/promotor muscle in the adults of most copepod groups (see Boxshall 1982) can be identified from its origin in the mandibular somite as one of the two present in nauplius I of *Euterpina* but it is not one of the two present in nauplius I of *Calanus* as it does not appear until nauplius VI in this genus. It is not identifiable in any of the naupliar stages of *Oithona*.

There is no clear indication that any one of these genera represents a more advanced group than the others. The most gradual build up to large numbers of muscles is that of *Calanus*, and it is only *Calanus* that develops maxillary muscles during the naupliar stages. While it might be inferred that *Calanus* exhibits the most regular anamorphic development many more data are required for these and other groups before this can be confirmed.

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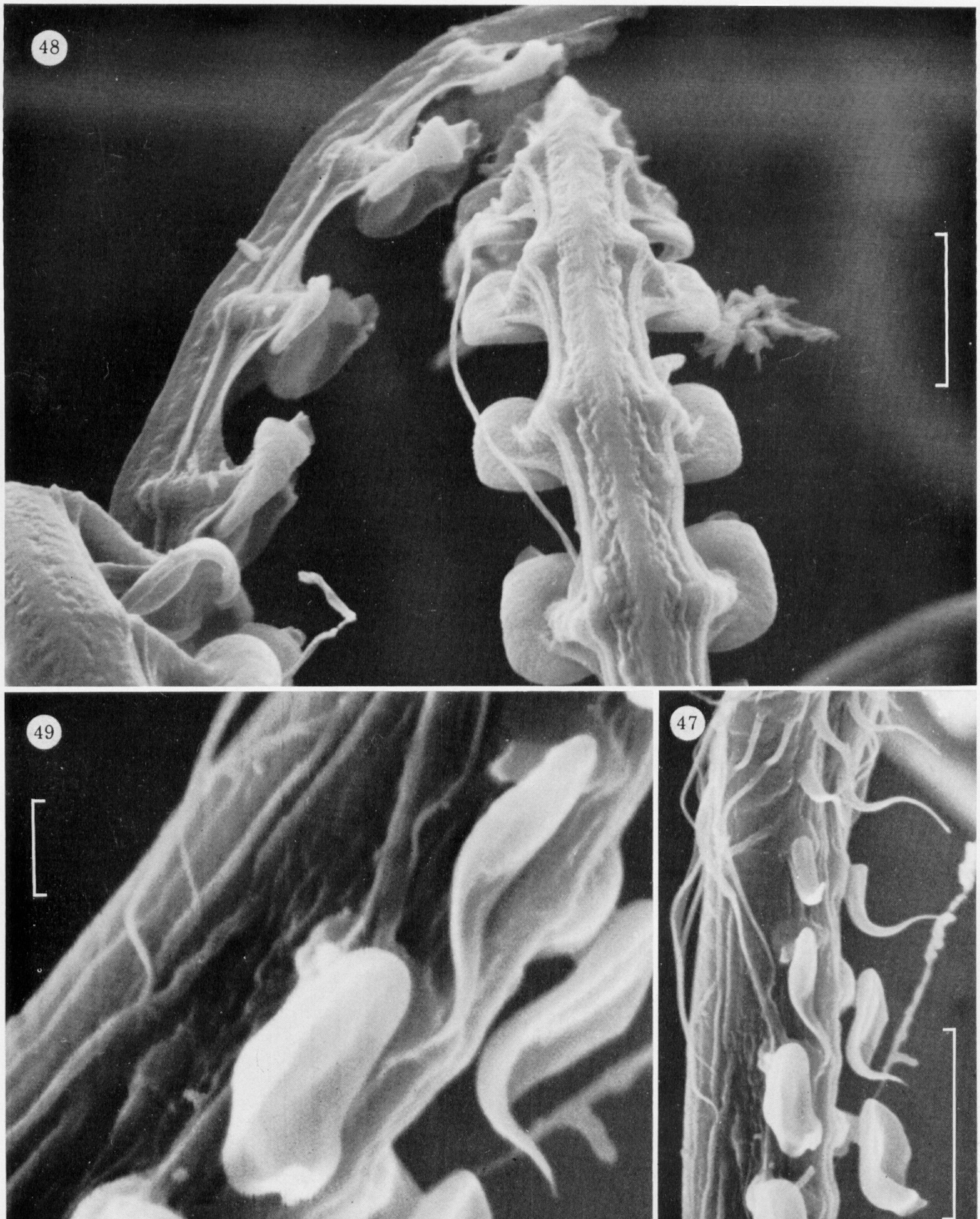
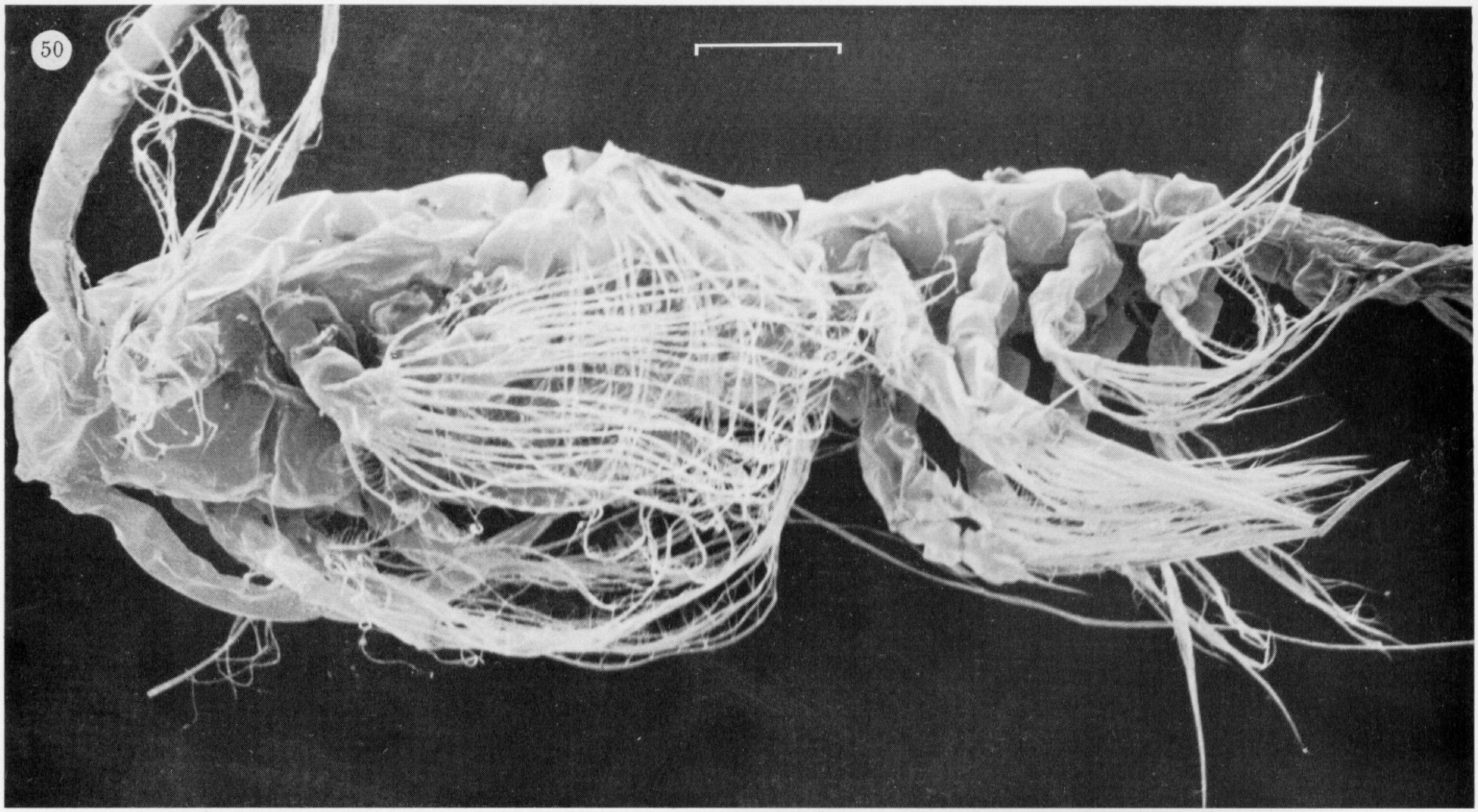
LIST OF ABBREVIATIONS USED ON FIGURES

abd.	abductor muscle
add.	adductor muscle
a.m.c.	anterior midgut caecum
an.	anus
ant.	antenna, antennary
ap.	apodeme
ap.m.	apical muscle
art.	arthrite
arth.	arthrodial membrane
at.	anterior
atl.	antennule, antennulary
a.v.c.t.	anterior ventral cephalic tendon
ba.	basis
c.	coupler
cb.	cerebrum
cd.	caudal
ce.	cephalosome
circ.	circular
con.	condyle
cox.	coxa
dep.	depressor muscle
dil.	dilator muscle
d.l.m.	dorsal longitudinal trunk muscle
d.m.l.m.	dorsomedian longitudinal trunk muscle
ed.	endite
end.	endopod
end.s.	endopodal setae
et.	exite
exp.	exopod
exp.s.	exopodal setae
ext.	extensor muscle
flex.	flexor muscle
for.	foramen
gen.s.	genital somite
gent.	genital
h.	horn
h.g.	hind gut
hoop	skeletal hoop

i.exp.	intraexopodal
i.g.b.m.	intragnathobasic muscle
i.s.r.	intersomitic ridge
lab.	labrum
lab.p.	labral pore
lat.	lateral
l.b.	leg base
lev.	levator muscle
l.i.s.	lateral intersomitic sclerite
lum.	bioluminescent organ
m.	muscle
med.	median
m.f.i.	median flexible integument
m.g.	midgut
m.i.s.	median intersomitic sclerite
mnd.	mandible, mandibular
mnd.g.b.	mandibular gnathobase
mnd.p.	mandibular palp
mx.	maxilla, maxillary
mx.i.r.	maxillary intraramal
mxl.	maxillule, maxillulary
mxl.p.	maxillulary palp
mxp.	maxilliped
mxp.s.	maxillipedal setae
ob.	oblique
oe.	oesophagus, oesophageal
p.cox.	praecoxa
p.e.	proximal endite
p.g.	paragnath
p.m.g.	posterior midgut
p.mnd.	premandibular
p.mx.	postmaxillary
p.mxl.	postmaxillulary
post.	posterior
pr.	protopod
pr.m.	promotor muscle
pr.m.p.	promotor process
pr.s.	prosome
p.v.c.t.	posterior ventral cephalic tendon
rem.	remotor muscle
rem.p.	remotor process
rot.	rotator muscle
sphn.	sphincter
spin.	spinous process
sub.g.	suboesophageal ganglion
susp.m.	suspensory muscle
susp.t.	suspensory tendon
sut.	suture
sync.	syncoxa
t.	tendon
te.	telson
th.	thoracic
th.l.	thoracic leg
th.s.	thoracic somite
ur.s.	urosome
vl	ventral
v.l.m.	ventral longitudinal trunk muscle



FIGURES 47–49. For description see opposite.



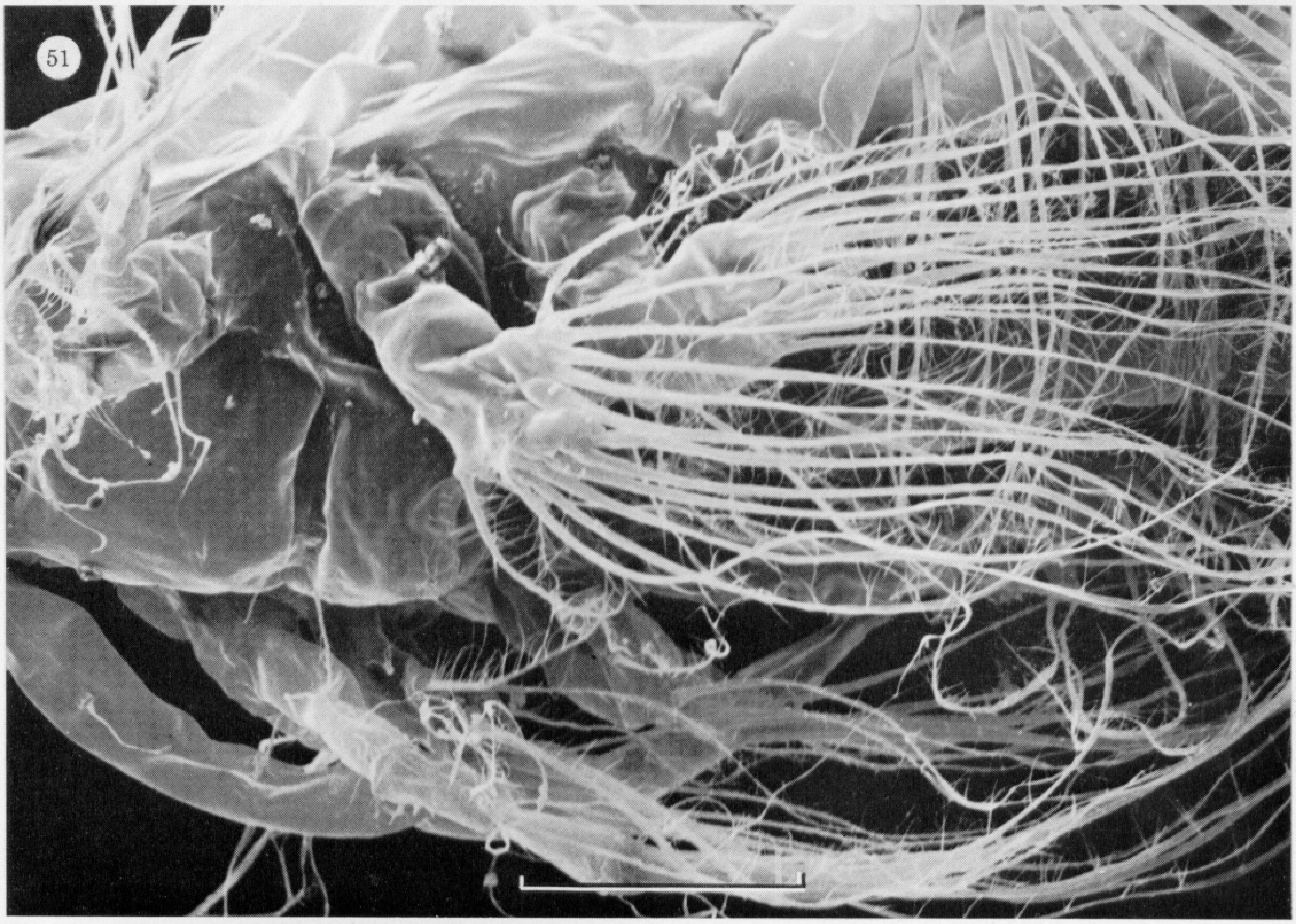
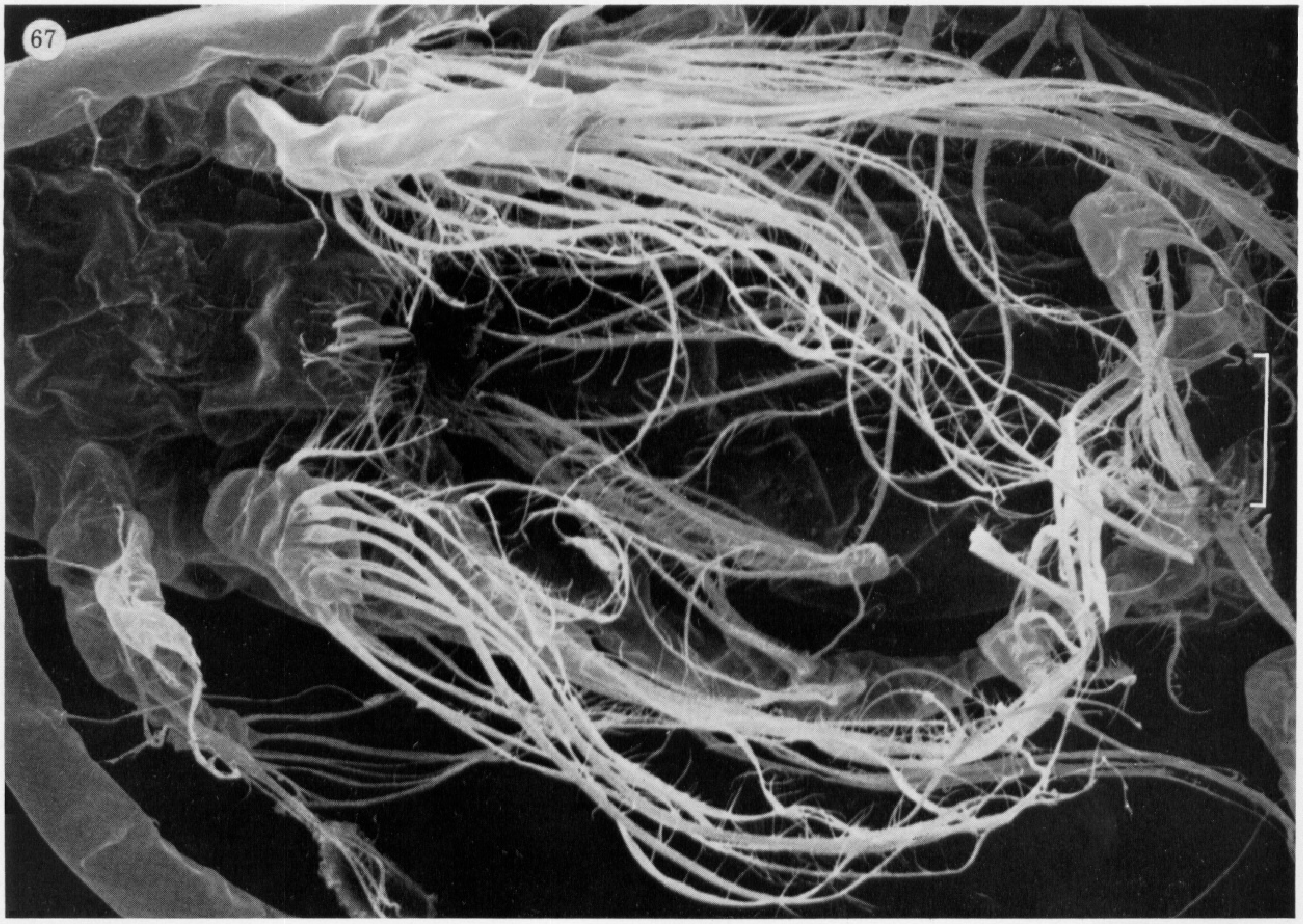


FIGURE 50. Lateral view of female *Mormonilla*, showing filter basket. Scale bar 100 μm.

FIGURE 51. Detail of filter basket wall. Scale bar 100 μm.



FIGURES 67 AND 68. For description see opposite.