The Skeletomusculature of Siphonostomatoid Copepods, with an Analysis of Adaptive Radiation in Structure of the Oral Cone

G. A. Boxshall

Phil. Trans. R. Soc. Lond. B 1990 **328**, 167-212
doi: 10.1098/rstb.1990.0113

Phil. Trans. R. Soc. Lond. B **328**, 167–212 (1990) [167]
Printed in Great Britain

THE SKELETOMUSCULATURE OF SIPHONOSTOMATOID COPEPODS, WITH AN ANALYSIS OF ADAPTIVE RADIATION IN STRUCTURE OF THE ORAL CONE

By G. A. BOXSHALL
British Museum (Natural History), Cromwell Road, London SW7 5BD, U.K.

(*Communicated by G. Fryer, F.R.S. – Received* 18 *August* 1989 – *Revised* 7 *December* 1989)

[Plates 1–4]

CONTENTS

The skeletomusculature of a primitive siphonostomatoid copepod, *Hyalopontius typicus*, is described and compared with that of a relatively advanced siphonostomatoid, *Lepeophtheirus pectoralis*, an ectoparasite of flatfishes. The comparison is used to assess how adaptation to parasitism has affected the morphology and musculature of the appendages. Anatomy has been related to presumed function wherever possible, and functional interpretations are presented for the feeding apparatus of both species and for a range of other siphonostomatoids.

The longitudinal trunk muscles of *Hyalopontius* are arranged in paired dorsal and ventral bundles, as in free-living copepods, but are smaller and less powerful. A further reduction takes place in *Lepeophtheirus*, and is presumably correlated with a limited swimming ability. The tagmosis of *Hyalopontius* is typically podoplean, with the prosome–urosome junction between fourth and fifth pedigerous somites. *Hyalopontius* possesses a cephalothorax comprising the cephalosome plus the first pedigerous somite. The tagmosis of *Lepeophtheirus* is modified and the prosome–urosome junction is no longer functional. In adult females the fourth pedigerous somite forms a waist-like region separating anterior cephalothorax from posterior genital complex. The shield-like cephalothorax comprises the cephalosome plus the first three pedigerous somites. The fifth pedigerous, genital and probably the first abdominal somites are fused to form a genital complex. The eudactylinid genus *Bariaka* is identified as one of the only two siphonostomatoids that possess a free genital somite, not incorporating the first abdominal somite.

The structure and musculature of the sternal furca of *Lepeophtheirus* is described. It is concluded that the furca is an elaboration of the median intersomitic sclerite lying between the maxillipedal and first pedigerous somites. The musculature of the sternal furca is derived from the ventral longitudinal trunk muscles.

The musculature of the cephalosomic appendages of siphonostomatoids is reduced compared with that of free-living copepods. The mandibles and maxillules increasingly lose any adduction–abduction movements. In *Hyalopontius* some adduction of the mandible is possible and extrinsic adductor muscles originating on the anterior cephalic tendon are retained. These are absent from *Lepeophtheirus*. The maxillules have no ventral extrinsic muscles in *Hyalopontius* and few dorsal muscles. In *Lepeophtheirus* there are no maxillulary muscles. The antennae, maxillae and maxillipeds are all basically subchelate and their intrinsic muscles are arranged in antagonistic extensor and flexor groups. These commonly insert on an apophysis that extends proximally from the base of the subchela.

A pattern of homologies for the segmental composition of the limbs of the siphonostomatoids is established, based on evidence from their musculature. The inner lobe of the maxillule is homologous with the praecoxal arthrite of other copepods, the outer lobe with the rest of the palp. The proximal segment of the maxilla is the syncoxa. The distal claw represents the basis and its proximal endite, and there is no vestige of the endopod in any siphonostomatoid. The subchela of the maxilliped is derived from the endopod and the endopodal segments are often fused to each other and to the distal claw.

The oral cone in a range of siphonostomatoid families is described. Adaptive radiation in feeding mechanisms mainly involves modification of the oral cone and maxillules, rather than of the appendages used for attachment to the host. In *Hyalopontius*, *Pontoeciella* and *Entomopsyllus* the oral cone is specialized for fluid feeding. There are efficient seals both around the distal opening of the cone and along the labrum–labium boundary. Suction pressure is produced by labral muscles concentrated in the proximal part of the cone. In *Lepeophtheirus* the oral cone is specialized for surface grazing and it lacks efficient sealing mechanisms distally and along the labrum–labium boundary. Food material is transported up the oral cone by sequential contraction of labral muscles. In adult *Lernaeocera* the oral cone acts as an enlarged oral disc forming a feeding seal distally. Suction is generated by oesophageal peristalsis.

The musculature of the swimming legs of *Lepeophtheirus* is described. Several remotor muscles insert on the ventral body wall remote from the basal foramina of the swimming legs. These muscles probably function as a dorsoventral tensors, and assist in creating suction beneath the disc of the cephalothorax. The posterior sinuses on the rear margin of the cephalothorax function as outlet valves during swimming. They are opened and closed by sinus muscles derived from modified promotor muscles of the second swimming legs.

1. Introduction

The copepod order Siphonostomatoida comprises about 1500 described species characterized by possession of a tubular sucking mouth containing stylet-like mandibles. Most species parasitize fishes but various invertebrate groups are also used as hosts, including sponges, cnidarians, echinoderms and crustaceans. The appendages of siphonostomatoids are typically modified for grasping the host and for specialized feeding behaviour. Gross morphology is often highly transformed as an adaptation to parasitism. Little has been published on the skeletomusculature of siphonostomatoids, although the mouth tube has been studied in a number of species (Lemercier 1964; Heptner 1968; Kabata 1974; John & Nair 1974; Boxshall 1986; Chandran & Nair 1988). The skeletomusculature of representatives of the orders Misophrioida, Calanoida and Mormonilloida has been described and compared in detail (Boxshall 1982, 1985) and some general patterns of copepod musculature have been identified. The musculature of the mouthparts has also been used to establish a system of homologies of the limb segments in these free-living copepods (Boxshall 1985). This comparative study of siphonostome musculature was undertaken to establish whether these general patterns are detectable in derived parasitic forms and to identify homologies of limb segmentation between siphonostomatoids and other copepods.

The musculature of *Hyalopontius typicus* Sars is described in detail. This species is common in plankton hauls taken below 3000 m in the North Atlantic but its host is unknown (Boxshall 1979). *H. typicus* was chosen because of its large size and because it retains several primitive features. A detailed comparison is made with *Lepeophtheirus pectoralis* Müller, a highly modified parasite from flatfish hosts in British waters (see Boxshall (1974)). Additional observations are presented on: the structure of the oral cone in two sponge parasites, *Entomopsyllus adriae* (Eiselt) and an unnamed new species of *Asterocheres*; the planktonic *Pontoeciella abyssicola* Scott; two highly modified parasites, *Nicorhiza rockallensis* Lincoln & Boxshall from a crustacean host and *Lernaeocera branchialis* (L.) from a fish host; and *Stygiopontius hispidulus* Humes, an external associate of deep-sea polychaete worms.

2. Materials and methods

H. typicus was obtained from RMT1+8 net samples taken in the North Atlantic at *Discovery* stations 8509 and 9541 in the vicinity of 44° N 12° W and 20° N 21° W respectively. *P. abyssicola* was taken in the same nets at the latter station only. Samples were fixed initially in 5% formalin in sea water and later transferred to a preserving fluid based on that of Steedman (1974). *L. pectoralis* was collected from flounders (*Platichthys flesus* L.) caught in the North Sea off Whitby (Boxshall 1974). *E. adriae* was found in washings from a sponge collected at Banyuls-sur-Mer, France. The unnamed new species of *Asterocheres* was collected from the sponge *Agelas clathrodes* (Schmidt) taken in shallow water off Carrie Bow Cay, Belize. *N. rockallensis* was obtained from an isopod host (*Dendromunna compsa* Lincoln & Boxshall) caught in the Rockall Trough in the vicinity of 54° N 12° W (Lincoln & Boxshall 1983). *Stygiopontius hispidulus* was collected by the deep-sea submersible *Cyana* at 2635 m on the East Pacific Rise (12°49.1′ N 103°56.9′ W) (Humes 1987). Premetamorphic adults and larvae of *Lernaeocera branchialis* were collected from the gills of *Myxocephalus scorpius* (L.) taken off Greenland.

Transverse and longitudinal serial sections were made of specimens embedded in paraffin wax and stained by using Masson's trichrome technique. 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. Specimens examined by scanning electron microscopy (S.E.M.) were prepared by dehydration through graded acetone, critical-point dried and sputter-coated with palladium.

3. Trunk skeletomusculature

(a) *Hyalopontius*

(i) *Trunk skeleton*

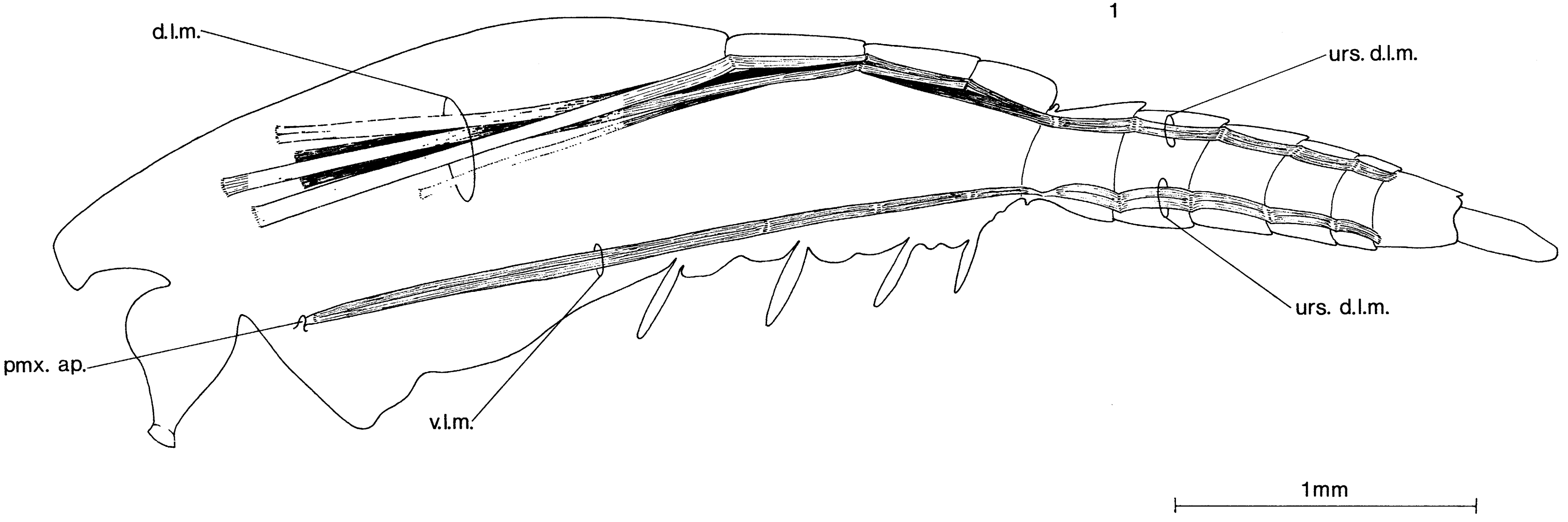
The body comprises a large anterior prosome and narrow posterior urosome (figure 1). The prosome comprises the cephalothorax, consisting of five cephalic and the first two thoracic somites, and three free thoracic somites, each of which bears a pair of swimming legs. The cephalothorax is covered by a continuous dorsal shield formed by the fusion of its constituent tergites. The free pedigerous somites are separated dorsally and laterally by narrow strips of arthrodial membrane which permit some telescoping of each somite within the preceding one. Ventrally the prosome wall comprises a number of sclerites of varying thickness.

The articulation between prosome and urosome is a transverse pivot joint with the axis lying just dorsal to the mid-height level. The joint is provided with extensive dorsal and ventral arthrodial membrane but allows little lateral flexion.

The female urosome (figure 2) comprises the fifth pedigerous somite, the large genital double somite, two abdominal somites and the anal somite. The genital double somite consists of the genital (seventh thoracic) somite and the first abdominal somite fused. It bears paired genital apertures anteriorly on its dorsolateral surface. The free abdominal somites are simple hoops of integument that can be telescoped inside the preceding somite to some extent, as can the anal somite. The anal somite bears the caudal rami posteriorly, on either side of the slit-like median anus.

The male urosome (figure 1) is similar to that of the female except that the genital and first abdominal somites are separate. Only a single testis and vas deferens are developed and the

1



2

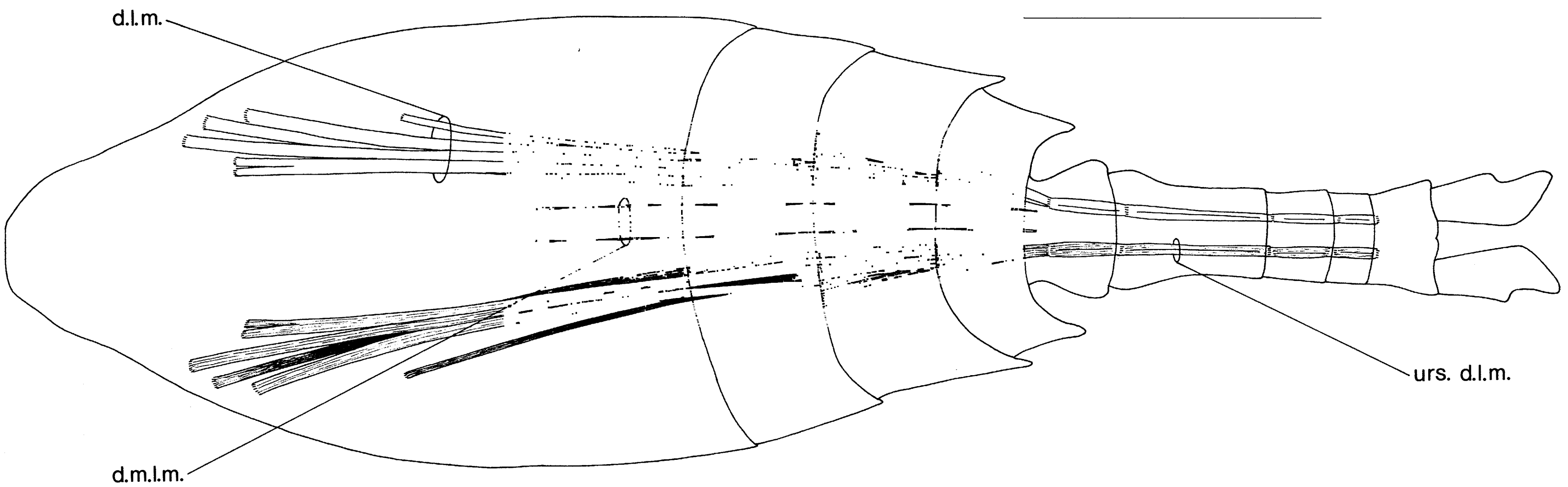


FIGURE 1. Median internal view of the longitudinal trunk muscles of male *Hyalopontius*.

FIGURE 2. Dorsal view of longitudinal trunk muscles of female *Hyalopontius*.

genital aperture is functional on the right side of the body only. It is located on the ventral surface at the posterior margin of the genital somite.

(ii) *Trunk musculature*

Hyalopontius has paired dorsal and ventral longitudinal muscles both of which are narrow and relatively poorly developed. The dorsal muscle (figure 2, d.l.m.) comprises four muscle blocks originating on the dorsolateral wall of the cephalosome in the mandibular and maxillulary somites, and a fifth block originating posterolaterally on the maxillipedal somite. The latter inserts on the anterior rim of the third pedigerous somite. One of the four main blocks attaches to the anterior rim of the second pedigerous somite, all attach to the rim of the third and insert on the rim of the fourth. A pair of urosome levator muscles originates anteriorly in the third pedigerous somite and inserts anteriorly on the dorsal surface of the first urosome somite. A paired dorsal muscle (d.m.l.m.) originates near the dorsal midline at a level marking the anterior extent of the fused first pedigerous somite. It passes posteriorly, attaching on the anterior rim of each somite, until its insertion on the first urosome somite. Within the urosome the dorsal longitudinal muscle extends to an anterior insertion on the anal somite, attaching via a tendinous interruption at each intersomitic boundary.

The ventral longitudinal muscle (figure 1, v.l.m.) consists of a triple strand that extends from its origin on the postmaxillary apodeme to a ventral insertion inside the first urosome somite. There are tendinous interruptions in the muscle, marking the boundaries between the pedigerous somites, but these are free from the body wall. The ventral muscle continues as a double strand within the urosome, attaching at each intersomitic boundary and inserting ventrally on the anal somite.

(*b*) *Lepeophtheirus*

(i) *Trunk skeleton*

The body is dorsoventrally flattened and comprises the anterior cephalothorax and the posterior genital complex (figures 3 and 5). The cephalothorax comprises five cephalic and the first four thoracic somites (bearing maxillipeds and legs 1 to 3). It is covered by a subcircular dorsal shield that is concave ventrally and convex dorsally. All cephalothoracic limbs are ventrally located. The anterior margin of the cephalothoracic shield is produced into two frontal plates, lying between the antennules. A broad strip of marginal membrane extends around the lateral margins of the shield and the anterior margins of the frontal plates. The entire cephalothorax acts as a sucker and this marginal membrane forms a seal that facilitates adhesion to the host. Posteriorly the cephalothorax has a pair of deep, lateral indentations, the posterior sinuses. These are provided with a strip of marginal membrane that acts as a valve, closing off the sinus. Dorsally the shield is marked with sutures forming an H-shape. The transverse suture is overlain by a membranous flap (h.f.) extending from the anterior section of the cephalothorax (figure 6). This suture represents the somitic boundary between the first and second pedigerous somites. Longitudinal sutures separate the lateral areas of the shield.

The urosome comprises three tagmata, according to Kabata (1979), the free thoracic somite, the genital complex and the abdomen. The somitic boundaries between these tagmata are well defined in the male (figure 5) but indistinct in the gravid female (figure 3). The articulation between cephalothorax and free thoracic somite is not telescopic and lacks arthrodial membrane. However, limited dorsoventral and lateral flexion of the genital complex relative

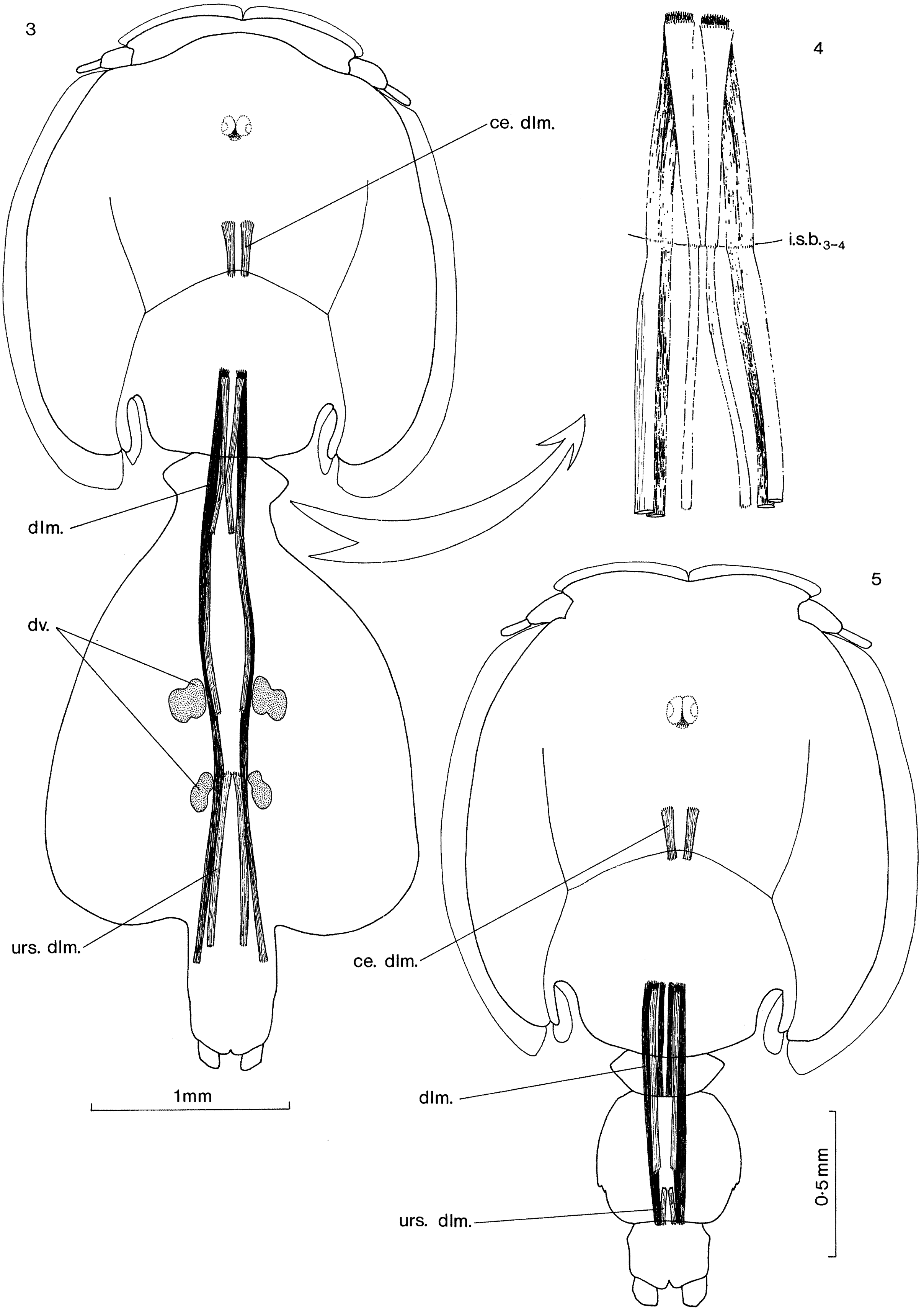


FIGURE 3. Dorsal view of female *Lepeophtheirus*, showing dorsal longitudinal trunk muscles.

FIGURE 4. Detail of dorsal musculature at prosome-urosome boundary.

FIGURE 5. Dorsal view of male *Lepeophtheirus*, showing dorsal longitudinal trunk muscles.

to the cephalothorax is possible by deformation of the relatively thin integument in this waist-like area.

The free thoracic somite bears the fourth legs ventrolaterally and is fused to the genital complex. In the female an incomplete suture is present ventrally (figure 6); in the male the suture is complete.

The genital complex comprises at least two fused somites, the sixth and seventh thoracic. The former bears reduced fifth legs. The seventh thoracic (= genital) somite bears the paired ventral genital apertures, which are closed off by plates representing the sixth legs. The structure of the genital complex appears to be the same in both sexes. It is possible that the first abdominal somite is completely incorporated into the genital complex (see §3*c*).

The abdomen is indistinctly two-segmented in *L. pectoralis* and bears the caudal rami either side of the slit-like anus.

(ii) *Trunk musculature*

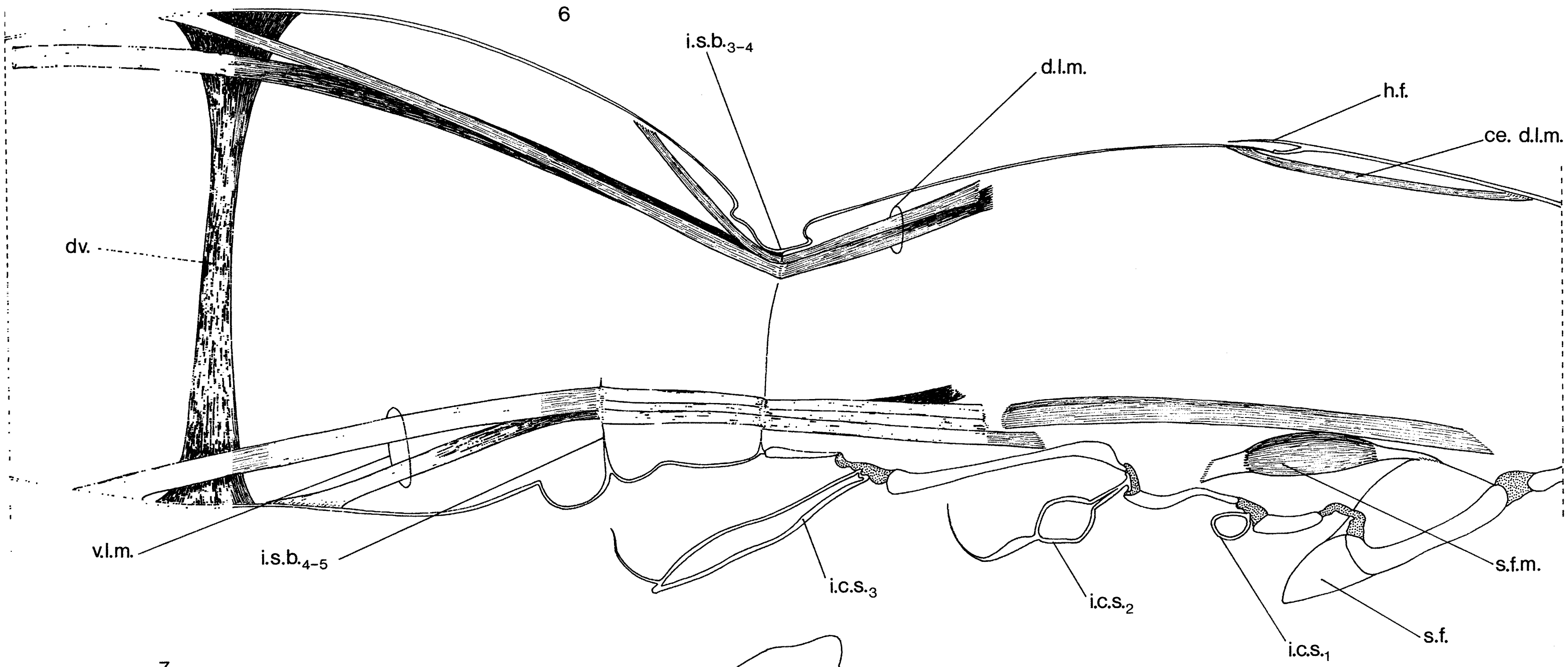
The longitudinal trunk muscles are narrow and relatively poorly developed. Despite the sexual dimorphism exhibited in the genital area, both sexes exhibit the same basic pattern of trunk muscles. The dorsal muscles are discontinuous (figures 3, 5 and 6). There is a short anterior section consisting of a single muscle pair (ce.d.l.m.) originating at the level marking the anterior boundary of the fused first pedigerous somite and extending posteriorly to insert just posterior to the suture between first and second pedigerous somites. This muscle may produce slight flexion between the two parts of the cephalothorax. The posterior section (d.l.m.) originates at about the level of the boundary between second and third pedigerous somites. It is triple-stranded and has an intermediate attachment at the anterior rim of the free thoracic somite (figure 4). The medial strand inserts dorsally at a level marking the anterior rim of the genital complex. The two more lateral muscles continue posteriorly into the genital complex. One inserts dorsally, midway along the genital complex the other passes through the genital complex to insert dorsally in the abdomen. A short muscle (urs.d.l.m.) originates dorsally in the posterior half of the genital complex and inserts inside the abdomen.

The ventral trunk muscles (figures 6 and 7) are also interrupted. The main origin is on the thickened ventral body wall to either side of the sternal furca. This thick muscle passes posteriorly, inserting ventrally at the boundary between second and third pedigerous somites. Originating at this level is a five-stranded continuation of the ventral muscle. It has an intermediate, tendinous attachment ventrally at the anterior rim of the free thoracic somite. At the partial suture representing the anterior rim of the genital complex two muscles insert and the others are attached via tendinous inserts. Three muscles pass posteriorly to insert ventrally well inside the genital complex.

(iii) *Sternal furca*

Lepeophtheirus possesses a sternal furca located on the ventral midline between the maxillipeds and the first swimming legs. It has a hollow, conical basal part and a pair of distal tines. At rest it is directed posteroventrally (figure 6) but it can be erected to stand perpendicular to the body. The basal rim is surrounded with thin integument anteriorly and posteriorly (stippled in figure 8) but at its widest point it is in contact with two thickened ridges of integument. The tips of these ridges form the pivots (figure 8, pi.) about which the furca swings. The furca is erected by a pair of short, robust muscles (figure 9, s.f.m.) originating on the ventral body wall

6



7

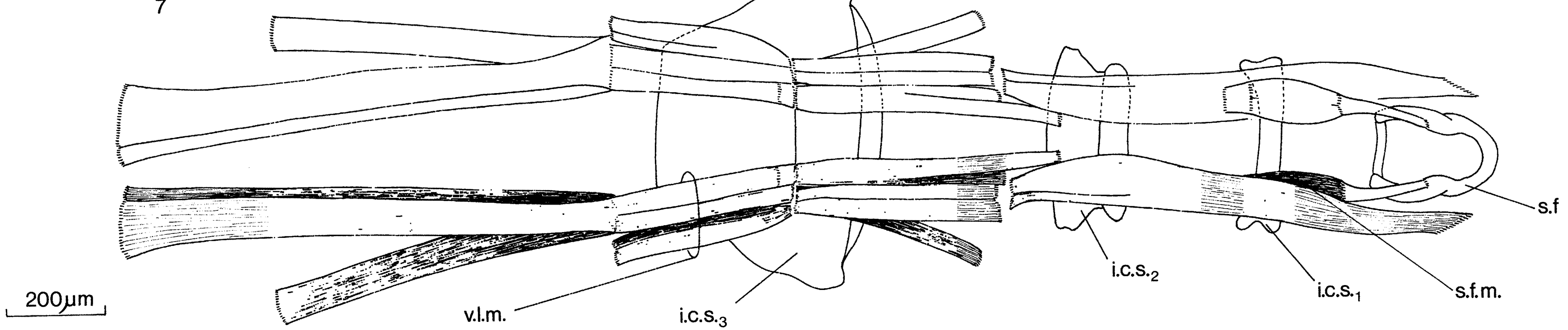
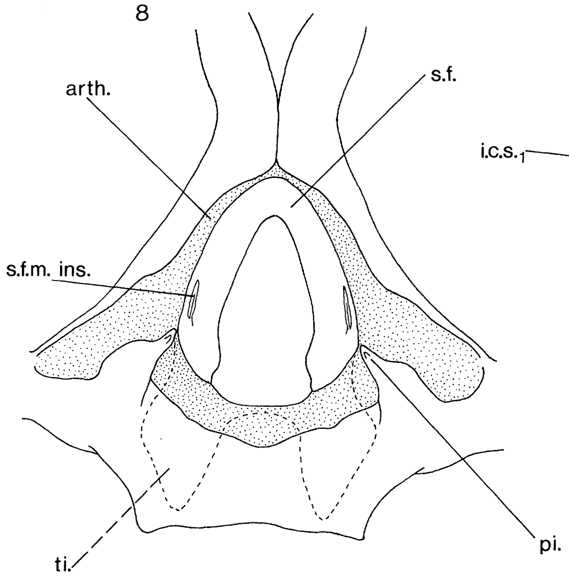


FIGURE 6. Median internal view of female *Lepeophtheirus*, showing longitudinal trunk muscles, sternal furca, and intercoxal sclerites of legs 1–3.

FIGURE 7. Ventral trunk muscles of same specimen as in figure 6, shown in dorsal view.



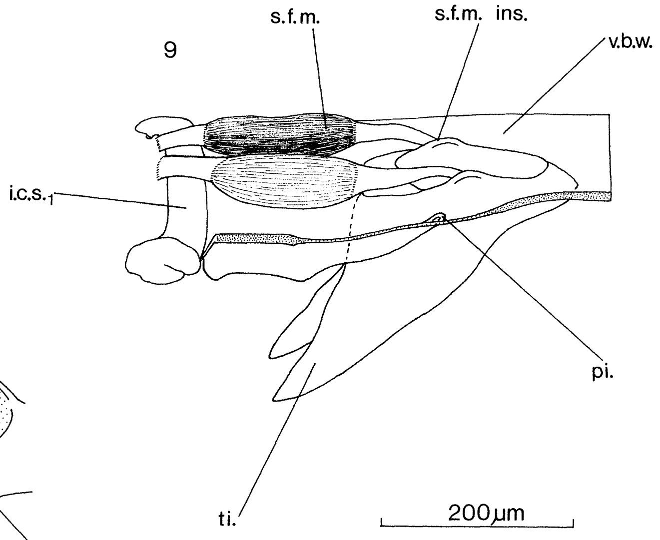


FIGURE 8. Dorsal internal view of base of sternal furca. The stippled area represents thin, flexible integument.

FIGURE 9. Lateral view of sternal furca, showing musculature and articulation with ventral body wall.

at the level of the boundary between the first and second pedigerous somites. These muscles insert via a long tendon on the rim of the furca, anterior to the pivots. There are no opposing muscles so the furca presumably returns to its resting position by cuticular elasticity.

The homology of the sternal furca of caligids has been the subject of much debate. Ferris & Henry (1949) considered that it represented a vestigial pair of appendages belonging to the ninth true body somite. Lang (1951) concluded that the sternal furca was derived from the intercoxal plate of the maxillipeds. He regarded the presence of muscles leading to the sternal furca as evidence of this derivation. Heegaard (1947) suggested that the sternal furca was derived from the cuticle of a sternite and later (Heegaard 1955) identified it as a secondary outgrowth from the sternal plate of the second maxillary segment. Lewis (1966) reviewed the debate and suggested that the furca was derived from one of a segmentally arranged series of sternites although he regarded the available evidence as inconclusive.

The skeletomusculature associated with the sternal furca of *Lepeophtheirus* reveals its homology. The ventral body wall of copepods typically consists of a series of median intersomitic sclerites interspersed with the legs and connected by areas of flexible integument and arthrodial membrane (Boxshall 1982, 1985). Ventral trunk muscles attach or insert on the median intersomitic sclerites, never on the intercoxal sclerites of the legs. The muscles of the sternal furca originate at the intersomitic boundary between first and second pedigerous somites and insert on the sternal furca, about at the intersomitic boundary between the maxilliped-bearing and first pedigerous somites. This strongly suggests that these muscles are derived by modification of the longitudinal trunk muscles and that the sternal furca represents an elaboration of the median intersomitic sclerite.

(*c*) *Patterns of somite fusion in siphonostomatoids*

The tagmosis of *Hyalopontius* and *Lepeophtheirus* is different. The former retains the primitive podoplean division into prosome and urosome, separated between fourth and fifth pedigerous somites by a specialized joint that allows only dorsoventral flexion of the urosome. In *Lepeophtheirus* the functional division into anterior and posterior tagmata lies between the third and fourth pedigerous somites. This is the most mobile intersomitic junction in the caligid body and separates the shield-like cephalothorax from the rest of the body. It is not a specialized pivot joint but has a waist-like zone of relatively thin integument that allows considerable flexion in all directions. The main podoplean joint, between fourth and fifth pedigerous somites, is non-functional in *L. pectoralis*.

All siphonostomatoids possess a cephalothorax comprising five cephalic and at least the first two thoracic somites. The cephalothorax of *Hyalopontius* comprises only these seven somites whereas that of *Lepeophtheirus* consists of five cephalic plus four thoracic somites. This extended cephalothorax of *Lepeophtheirus* represents the end of an evolutionary sequence within the caligiform group of families. In the primitive family Dissonidae the cephalothorax incorporates two thoracic somites, as in *Hyalopontius*. The cephalothorax incorporates three somites in the Trebiidae, and four in the Caligidae, including *Lepeophtheirus*. The transverse suture on the cephalothoracic shield of *Lepeophtheirus* marks the somite boundary homologous with the end of the cephalothorax in *Hyalopontius* and the family Dissonidae.

The genital double somite of female *Hyalopontius* is not homologous with the genital complex of female *Lepeophtheirus*. The former comprises the fused seventh thoracic (= genital) and first abdominal somites (figure 10). The genital complex of *Lepeophtheirus* comprises the fused sixth (= fifth pedigerous) and seventh thoracic (= genital) somites (figure 12), as indicated by the presence of fifth and sixth legs, and the first abdominal somite may also be incorporated (see below).

The genital double somite of the *Hyalopontius* type is found in primitive representatives of most siphonostomatoid families associated with invertebrate hosts, such as the Asterocheridae and Nicothoidae. No members of the families formerly grouped together as the Cyclopoida Siphonostoma have retained separate genital and first abdominal somites, although in some the genital double somite cannot be recognized because of further reduction or fusions between urosomal somites. Externally this type of genital double somite is characterized by the location of the genital apertures about in the middle of the double somite and by the presence of a maximum of three free abdominal somites (figure 10).

The caligiform group of families (Dissonidae, Trebiidae, Caligidae, Euryphoridae, Pandaridae and Cecropidae) all possess the kind of genital complex found in *Lepeophtheirus*, in which there is recognizable fusion between sixth thoracic and genital somites (figure 12). This genital complex may be common to a wider group of siphonostomatoids parasitic on fishes, including the Dichelesthiidae, Lernanthropidae, Kroyeriidae, Pseudocycnidae, and Hatschekiidae (Kabata 1979). It is possible that the *Lepeophtheirus* type genital complex also incorporates the fused first abdominal somite. The indirect evidence for this interpretation is the presence of a maximum of only three free postgenital abdominal somites in all of these families when four is the basic number for the Copepoda. [The five abdominal somites of *Caligus quinqueabdominalis* Heegaard (Heegaard 1962) are here interpreted as secondary annulations of the abdomen rather than as primary abdominal somites.] The location of the

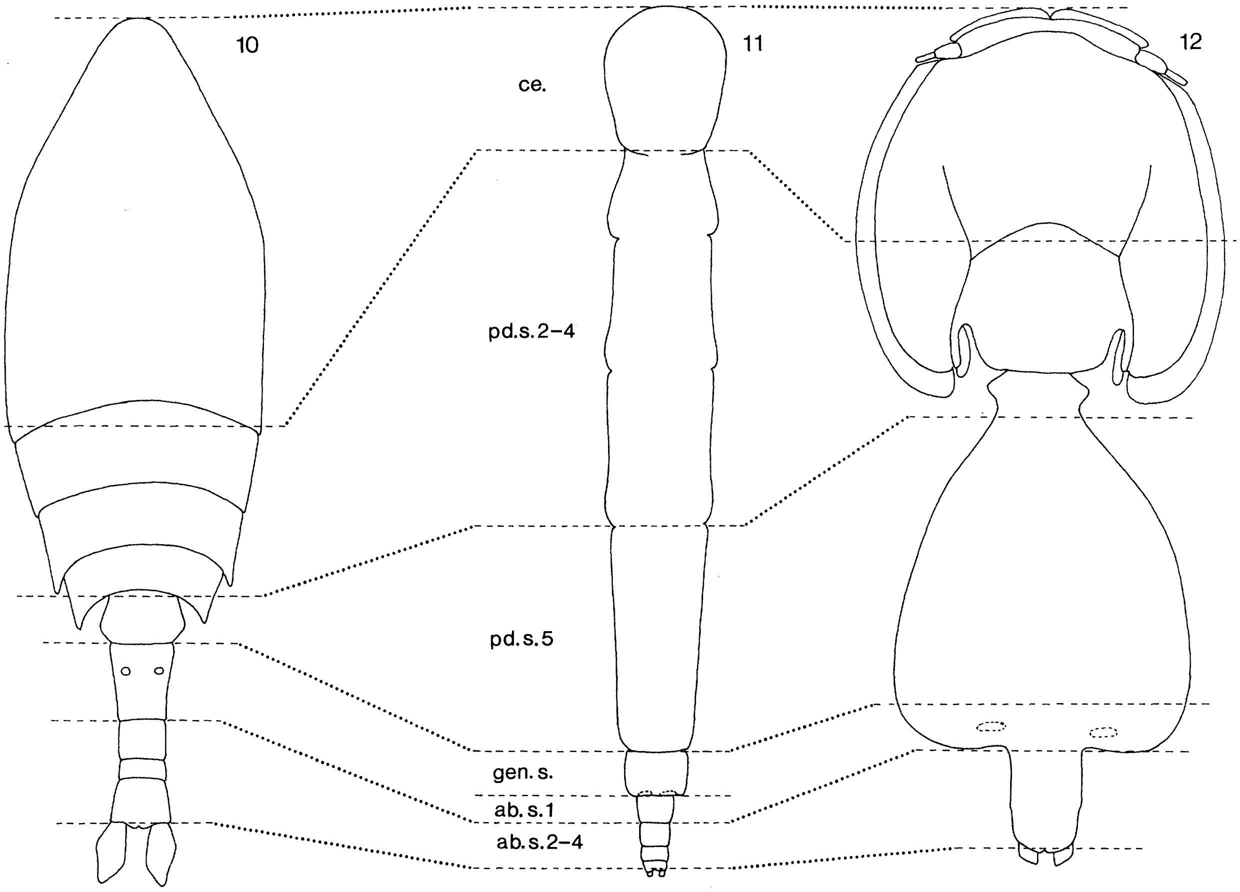


FIGURE 10. Dorsal view of female *Hyalopontius*, showing tagmosis.
FIGURE 11. Dorsal view of female *Bariaka*, showing tagmosis.
FIGURE 12. Dorsal view of female *Lepeophtheirus*, showing tagmosis.

female genital apertures near the posterior margin of the genital complex, rather than in the middle as in *Hyalopontius*, suggests that the first abdominal somite is not incorporated into the complex. Examination of the trunk musculature provides no direct evidence for either interpretation.

The *Lepeophtheirus* type of genital complex is not the primitive state within the family Eudactylinidae. This family includes the genera *Bariaka* Cressey and *Protodactylina* Laubier, the females of which have a free genital somite and four free abdominal somites (figure 11). The genital apertures are located ventrally at the posterior margin of the genital somite (Cressey 1966). These are the only genera of siphonostomatoids to exhibit a free genital somite. In other eudactylinid genera, such as *Nemesis* and *Eudactylina*, there is a maximum of three free abdominal somites and the female genital apertures are located more anteriorly, away from the posterior margin. This is interpreted here as evidence of the possession by these other genera of a genital double somite comprising the fused genital and first abdominal somites, as in *Hyalopontius*.

4. Skeletomusculature of the cephalosomic appendages

(a) *Hyalopontius*

(i) *Antennule*

The female antennule (figure 13) is 11-segmented. The first and last segments each represent several fused segments, as indicated by their setation. Each joint is provided with a hoop of arthrodial membrane, which allows limited flexion; those between segments 4 and 5, 7 and 8, and 10 and 11 have more extensive membrane anteriorly and posteriorly, permitting greater movement in this plane. The proximal articulation with the head allows primarily for raising and lowering the limb about the oblique anteromedial to posterolateral pivot line. Some movement in other directions is also possible. There is a prominent apodeme situated laterally on the rim of the limb.

The extrinsic antennulary muscles (figures 13 and 15) originate on the dorsolateral wall of the cephalothorax. Three muscles (atl. prm. 1–3) insert on the lateral rim and raise the limb so that the first segment is directed laterally. A fourth muscle (atl. prm. 4), which inserts posterolaterally, aids in this movement. These are opposed by two muscles (atl. rem. 1–2) which insert inside the first segment, medial to the pivot line. The double, long levator muscle (atl. lev.) originates dorsally about at the level of the maxillae and inserts just inside the posterior rim of the limb. It is opposed by a slender muscle (atl. rem. 3) that inserts anteriorly.

The intrinsic musculature of the female (figure 13) consists of eight muscles. A flexor (atl. fl. 6) originates at the insertion of the extrinsic levator, extends through segments 1 to 4 and inserts dorsally on the rim of segment 5. Two other flexors (atl. fl. 1–2) originate on the midlateral wall of the first segment and insert around the dorsal rim of segment 5. All three produce dorsal flexion of the distal part of the limb at the hinge joint between segments 4 and 5. A long muscle (atl. fl. 3) originates anteromedially on segment 1 and passes, without intermediate attachments, through to a dorsomedial insertion on the rim of segment 11. Two muscles originate on the lateral wall of segment 6. One (atl. fl. 4) inserts laterally on the rim of segment 8; the other (atl. fl. 5) on the rim of segment 11. A double-stranded muscle (atl. fl. 7–8) originates laterally in segment 8 and inserts on the lateral rim of segment 11.

(ii) *Antenna*

The antenna comprises a two-segmented protopod and two one-segmented rami (figure 14). Its articulation with the head has a well developed transverse pivot line about which the main promotor–remotor swing takes place. Arthrodial membrane around the joint permits movement in other directions. Coxa and basis are fused but a suture, without arthrodial membrane, marks the position of the original joint. The free endopodal segment is positioned distally on the elongate second segment. The latter is probably an allobasis (alb.), representing the fused basis and first endopodal segment. The plane of fusion is marked by the intermediate attachment of the large intrinsic, adductor muscle (see below). The articulation between allobasis and free endopod has a well developed pivot line which allows adduction of the ramus and its long terminal claw. The exopod is small, one-segmented, and located midway along the allobasis. There is no arthrodial membrane around its base.

The extrinsic muscles (figures 14 and 15) are in two groups, promotors and remotors. The former comprises a slender muscle (ant. prm. 3), which originates adjacent to the origin of antennulary remotor 4 and inserts anteromedially on the coxal rim, and two powerful muscles

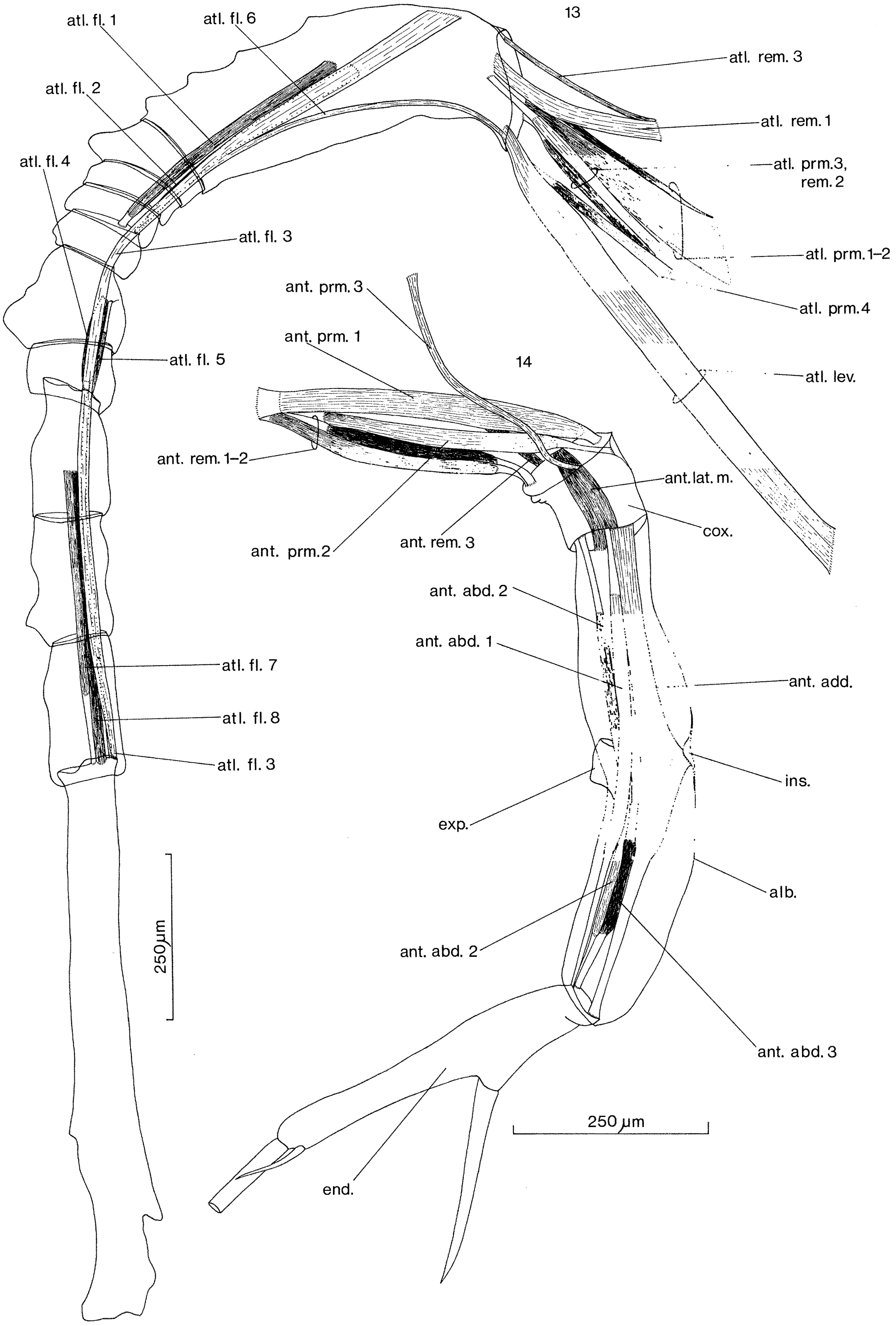


FIGURE 13. Dorsal view of antennule of *Hyalopontius*, showing musculature.
FIGURE 14. Median view of antenna of *Hyalopontius*, showing musculature.

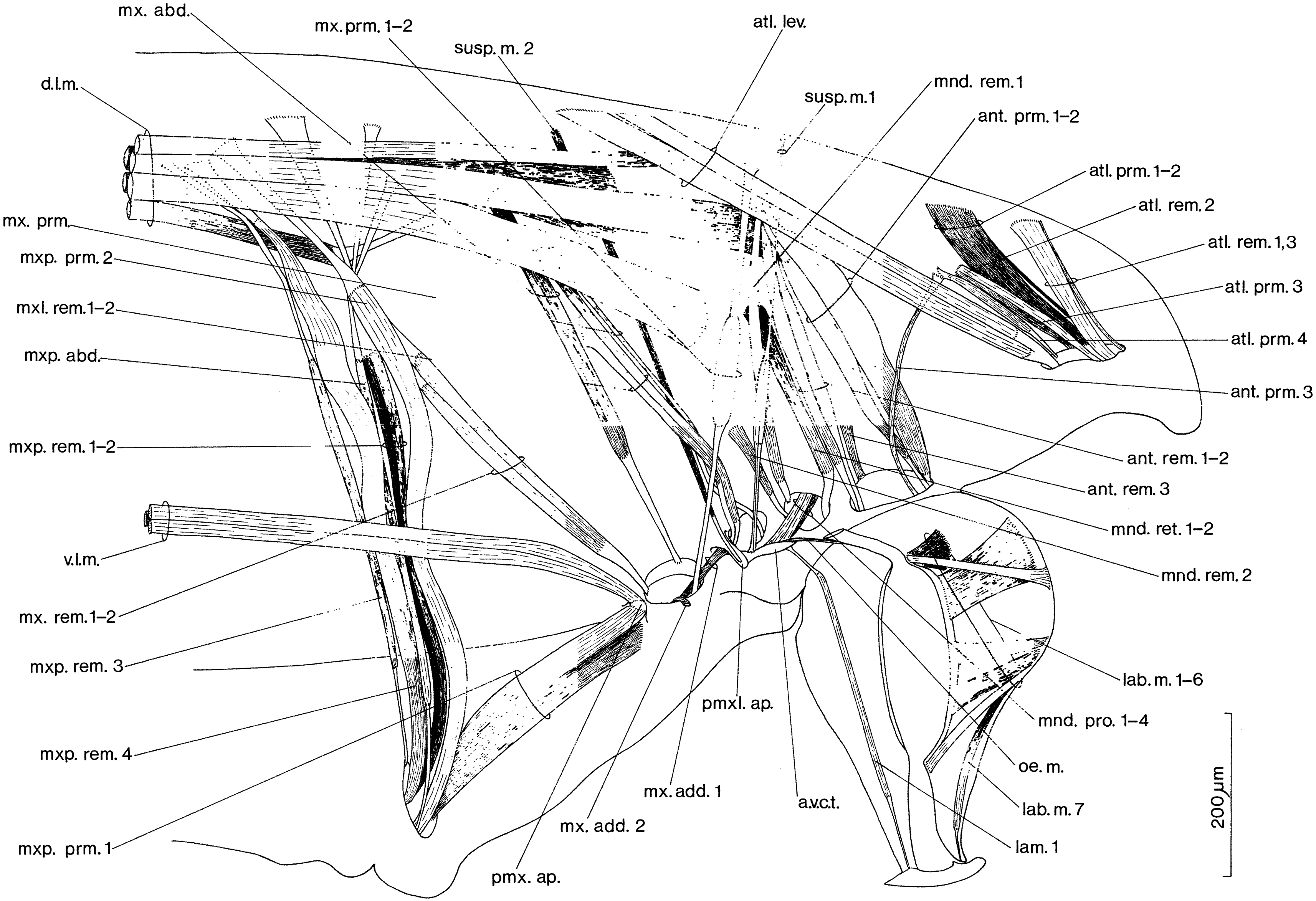


FIGURE 15. Median internal view of musculature of the cephalosome of *Hyalopontius*. All other organs have been removed.

(ant. prm. 1–2) originating high on the dorsolateral wall and inserting anteriorly on the thickened integument just inside the limb. The remotor group comprises two powerful muscles (ant. rem. 1–2), originating high on the dorsolateral wall and inserting posteriorly inside the coxal rim, and a third (ant. rem. 3), with a low lateral origin, inserting posterolaterally on the rim.

There is a broad intrinsic muscle (ant. lat. m.) passing from the lateral coxal rim to rim of the basis, spanning the vestigial articulation. All other intrinsic muscles insert on the proximal rim of the free endopodal segment. A powerful adductor (ant. add.) originates anteromedially at the coxa–basis suture and inserts anteromedially via a long tendinous section. It has an intermediate attachment to a thickened area midway along the anterior wall of the allobasis. This is opposed by three abductors. One (ant. abd. 1) originates next to the adductor and shares a posterolateral insertion with the second (ant. abd. 2), which originates posteromedially at the coxa–basis suture. This muscle has a tendinous middle section in addition to tendinous end sections. The third (ant. abd. 3) originates distally on the lateral wall of the allobasis and also inserts posterolaterally. No muscles insert on the exopod.

(iii) *Oral cone*

The oral cone is formed from the anterior labrum and posterior labium, which are produced together into a tapering tubular structure that opens distally. Anatomically the lumen of the oral cone is homologous with the preoral food chamber of other copepods (Boxshall 1982). The labrum and labium remain separate but are held together distally by a complex arrangement of overlapping ridges and grooves, which effectively seal the lateral slit between labrum and labium.

The labrum is robust and muscular. Six pairs of muscles (lab. m. 1–6) are concentrated in the swollen proximal part (figure 15). These increase the size of the lumen, producing suction that draws in material through the cone opening. Another pair (lab. m. 7) extends distally to insert at the tip of the labrum. The labral integument lining the lumen of the oral cone is folded and consists of thickened ridges and plates separated by thinner areas. The labrum does not contribute to the oral disc which is entirely labial in origin.

The labium is derived from the fused paragnaths (Boxshall 1986). At its tip it bears a flared membrane, the oral disc, encircling the opening of the cone. The labium contains a pair of lateral muscles (lam. 1) and a median unpaired muscle (lam. 2), all of which originate on the ventral surface of the cephalic tendon (figure 30, a.v.c.t.) and pass ventrally through channels in the suboesophageal ganglion. The paired muscle inserts on the apex of the labium and may be responsible for moving the oral disc. The short median muscle inserts proximally on a tendinous sheet that runs the length of the labium, dividing it along the ventral midline. This sheet may represent the plane of fusion of the paragnaths.

(iv) *Mandible*

The mandible is reduced to a single protopodal segment drawn out into a long slender stylet derived from the gnathobase (figure 16). There is no palp. The proximal rim of the mandible is thickened on three sides but not laterally, and arthrodial membrane is present all round the rim but is most extensive laterally. The stylet arises medially on the protopod. No arthrodial membrane is present at its base but the angle of the stylet may be altered by deformation of the protopodal integument.

There are no intrinsic muscles in the mandible. There are two groups of four extrinsic muscles (figures 15 and 16), one group arising on the lateral and dorsolateral body wall, the other on the cephalic tendon. The former comprises a double-stranded muscle (mnd. ret. 1–2) originating laterally and inserting on the narrow base of the stylet, a long muscle (mnd. rem. 1) originating dorsolaterally and inserting posterolaterally on the protopod, and a short muscle (mnd. rem. 2) originating low on the lateral wall and inserting posteriorly on the protopod. The four muscles (mnd. pro. 1–4) originating on the cephalic tendon pass ventrolaterally into the mandible, inserting together on its lateral wall. They appear to be protractors of the stylet, pulling on the lateral wall of the protopod and forcing the stylet further down into the oral cone so that its apex protrudes from the opening. They may be assisted by the two remotors but are opposed by the paired retractors (mnd. ret. 1–2), which withdraw the stylet dorsally into the cone and away from the opening. These movements of the stylet are small.

(v) *Maxillule*

The maxillule (figure 18) is reduced to a protopodal segment produced into an inner lobe and an outer, distal lobe. The proximal rim of the limb is thickened on three sides but not medially. A small amount of arthrodial membrane is present all round the limb base. The inner lobe arises from the anteromedial surface of the protopod. No arthrodial membrane is present at its base which is marked by a partial suture. The angle between the inner lobe and the protopod can be altered by deformation of the protopodal integument. The outer lobe arises distally on the protopod and is separated from it by a complete suture, lacking arthrodial membrane. The derivations of these lobes are discussed below (see §4*d*).

The musculature (figures 15 and 18) comprises one intrinsic muscle and three extrinsic muscles. The intrinsic muscle (i.g.b.m.) originates on the lateral wall of the protopod and passes transversely to its insertion on a thickened area of the medial wall just proximal to the base of the inner lobe. All three extrinsic muscles originate on the dorsolateral wall. Two (mxl. rem. 1–2) insert posteromedially inside the protopod, the other (mxl. prm.) on thickened integument at the base of the inner lobe.

(vi) *Maxilla*

The maxilla (figure 17) is subchelate, comprising a long segment, the syncoxa, bearing a slender distal claw representing the basis. Its articulation with the head is loose, allowing for movement in all directions, although there is a well-developed, almost transverse, pivot line. Posterior to this line the maxillary rim is thickened; anterior to it there is a slight depression in the body surface formed from flexible integument. Movement of the claw is restricted to flexion and extension in the anteroposterior plane about a pivot line between two well-developed condyles. Anteriorly the proximal rim of the claw is produced into a slender apophysis (apo.), which extends about 50 μm back into the syncoxa.

There are seven extrinsic muscles (figures 15 and 17), one of which (mx. add. 1) originates on the postmaxillulary apodeme and inserts on the anterior wall of the syncoxa. A second adductor (mx. add. 2) originates on the ventral body wall, passes over the medial rim of the limb, and also inserts on the anterior syncoxal wall. A double-stranded promotor (mx. prm. 1–2) originates high on the dorsal wall and passes ventrally to insert inside the anterior rim. It is muscular only for the middle third, having long tendinous sections at each end. A long abductor (mx. abd.) originates lateral to the dorsal trunk muscles and inserts on the lateral rim.

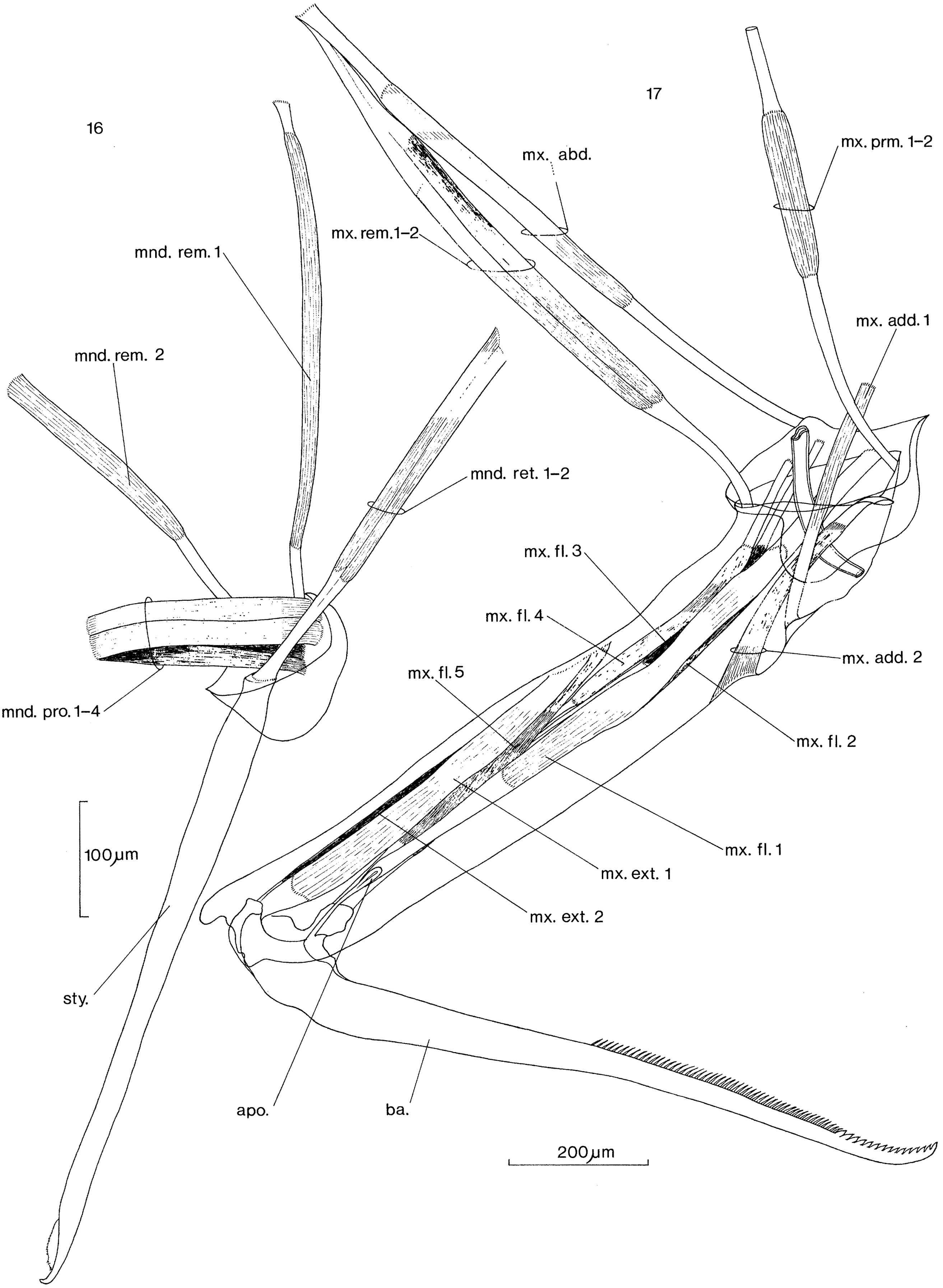


FIGURE 16. Anterior view of mandible of *Hyalopontius*, showing musculature.
FIGURE 17. Median view of maxilla of *Hyalopontius*, showing musculature.

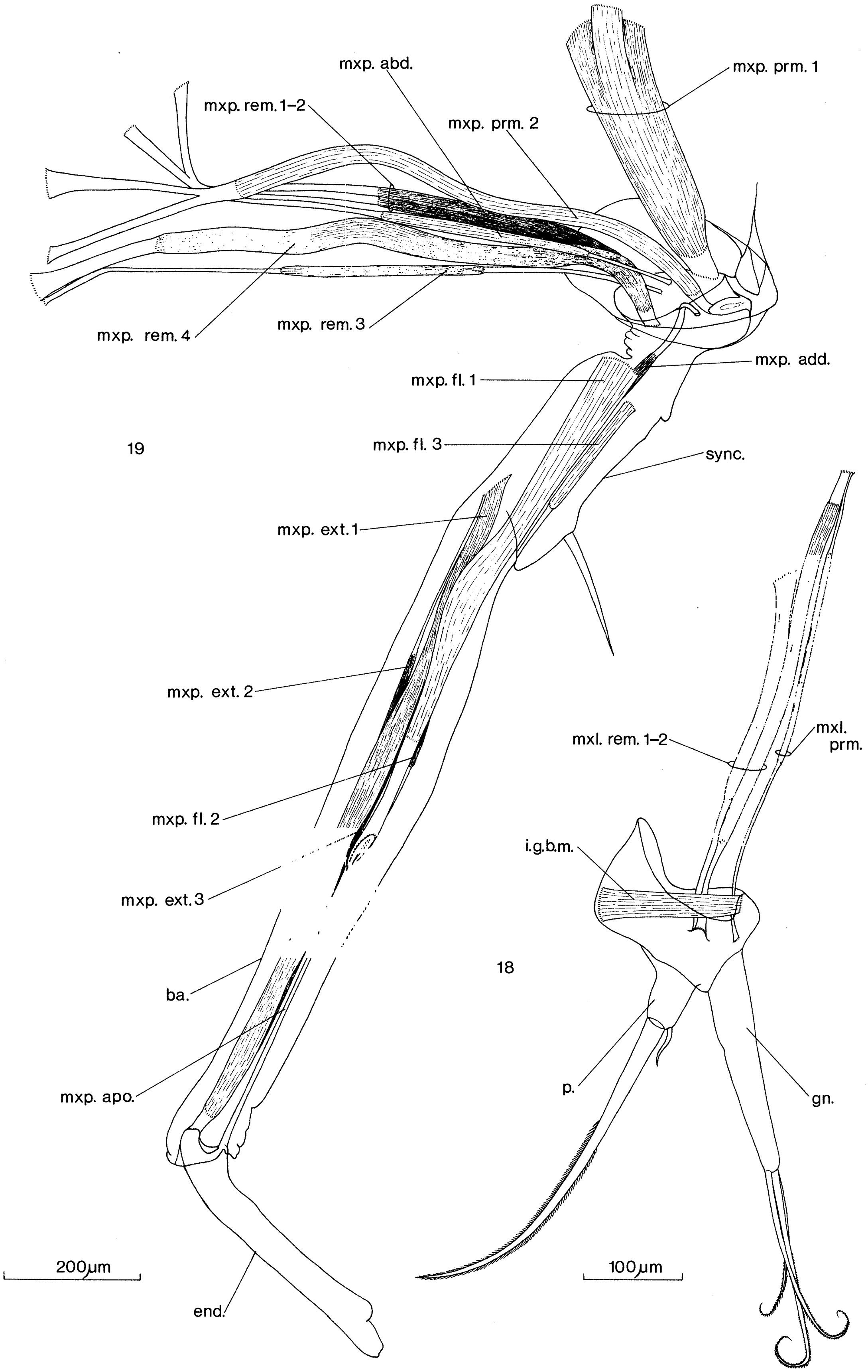


FIGURE 18. Anterior view of maxillule of *Hyalopontius*, showing musculature.

FIGURE 19. Median view of maxilliped of *Hyalopontius*, showing musculature. The terminal claw is not shown.

Two remotors (mx. rem. 1–2) share a complex tendinous origin with four maxillipedal and a dorsal longitudinal trunk muscle. Tendons from these seven muscles are joined together and attached to the dorsolateral wall of the maxillipedal somite by five suspensory tendons. This suspended origin presumably spreads the force of any one muscle contracting over a wide area of integument.

The intrinsic muscles (figure 17) are arranged in two opposing groups, flexors and extensors. Four of the five flexors originate near the proximal rim of the syncoxa and extend throughout the length of the segment. All four have tendinous sections at their origins. The largest (mx. fl. 1) is medially placed and has a tendinous part leading to its insertion on the apophysis of the basis (figure 17, mx. apo.). Following a similar course is a lateral flexor (mx. fl. 2) which inserts on the swollen rim of the claw. Two other flexors (mx. fl. 3–4) originate posterolaterally, and have long tendinous sections extending towards their common insertion with flexors 2 and 5. The fifth flexor (mx. fl. 5) originates on the posterior wall of the syncoxa. The two extensors (mx. ext. 1–2) originate on the posterior syncoxal wall and insert posteriorly on the rim of the claw. They each have a short tendinous section at their insertion. There are no muscles within the claw.

(vii) *Maxilliped*

The three-segmented maxilliped (figure 19) bears a long terminal claw. The first segment represents the syncoxa and is separated from the second, the basis, by an incomplete suture. The third segment, the endopod, probably represents a number of fused segments. The maxillipeds are located on a prominent ridge, the maxillipedal pedestal (mxp. ped.), which extends across the midline and their articulations are with the sloping posteroventral face of the ridge. The proximal articulation is relatively loose, allowing a wide range of whole limb movements. The syncoxa and basis are partly fused and the plane of fusion is marked by an incomplete suture. The basis–endopod joint restricts movement of the endopod plus claw to extension and flexion in the anteroposterior plane. The proximal rim of the endopod is produced into a long, rigid apophysis (figure 19, mxp. apo.) extending halfway down the basis.

The extrinsic muscles (figure 15 and 19) are well developed. A large, powerful promotor (mxp. prm. 1) passes from its broad origin on the postmaxillary apodeme and adjacent body wall, to insert on the anterolateral wall just inside the limb. The long muscle (mxp. prm. 2), sharing the common suspended origin described above, inserts on a small anteromedial apodeme on the rim of the limb and probably acts as a promotor–adductor. The three other maxillipedal muscles sharing this suspended origin pass ventrally into the limb. One (mxp. abd.) inserts laterally, the other two (mxp. rem. 1–2) posterolaterally. Two other muscles originate close together high on the dorsolateral wall and insert posteriorly (mxp. rem. 3) and posteromedially (mxp. rem. 4). A small muscle (mxp. add.) originates on a thickened area of the maxillipedal pedestal (figure 30, mxp. ped. ap.) and passes laterally over the rim and down to its insertion on the lateral wall of the syncoxa. The insertions of the extrinsic muscles are spread round the rim and can produce the complex whole limb movements necessary for grasping prey.

The arrangement of the intrinsic muscles (figure 19) is similar to that of the maxilla. The larger of the two main flexors (mxp. fl. 1) originates medially near the base of the syncoxa and inserts on the swollen tip of the endopodal apophysis. The smaller flexor (mxp. fl. 2) originates proximally on the lateral wall of the basis and also inserts on the apophysis. These are opposed by three extensors. Two (mxp. ext. 1–2) originate posteriorly at the level of the syncoxa–basis suture, the third laterally just distal to the swollen part of the median flexor. All three extensors insert posteriorly on the rim of the endopod. A small muscle (mxp. fl. 3) originates anteromedially on the syncoxa and inserts anteriorly on the proximal edge of the basis.

(*b*) *Lepeophtheirus*

(i) *Antennule*

The antennule is reduced to a robust basal segment and a cylindrical distal segment. It has an elongate articulation with the ventrolateral margin of the head and is capable of limited flexion in all directions. There is no distinct pivot line at the articulation. The joint between basal and apical segment is telescopic and is provided with arthrodial membrane all round.

The main extrinsic muscles (figures 20 and 23) originate on the dorsal cephalothoracic shield. Two muscles (atl. prm. 1–2) insert anteriorly on the rim and direct the whole limb more anteriorly. A powerful double-stranded muscle (atl. lev.) inserts dorsally and raises the limb off the substratum; it is opposed by a single muscle (atl. dep.) that inserts ventrally. A short, narrow muscle (atl. rem.) originates on the ventral body wall adjacent to the limb base. It passes over the posterior rim and inserts midway along the posterior wall of the basal segment.

Two intrinsic muscles (atl. fl. 1–2) originate on the ventral wall of the basal segment. They share a common tendinous insertion ventrally on the proximal rim of the apical segment and flex the apex ventrally to come into contact with the substratum, the host's surface. They are presumably opposed by the elasticity of the integument around the articulation.

(ii) *Antenna*

The uniramous antenna has a two-segmented protopod and a recurved, claw-like endopod (figure 22). All segments are heavily sclerotized. The articulation with the head allows considerable mobility and has no dominant pivot line. The coxa-basis joint lacks arthrodial membrane and is non-functional. The basis-endopod articulation has a well developed pivot line extending between anterior and posterior condyles. This allows adduction and abduction of the endopod only.

The extrinsic muscles (figures 22 and 23) all originate on the dorsal cephalothoracic shield. A pair of short muscles (ant. abd. 1–2) inserts on the lateral rim of the coxa. These abduct the whole limb and are opposed by a single adductor (ant. add.) inserting on the medial rim. The two largest muscles insert inside the limb, on the walls of the coxa. One (ant. prm.) inserts anterolaterally and both adducts the limb and swings it forwards; the other (ant. rem. 1) inserts posteromedially and abducts and swings the limb backwards. A short remotor (ant. rem. 2) inserts on the posterior rim of the coxa.

Three intrinsic muscles operate the endopodal claw. A powerful adductor (ant. end. add.) swings it medially until it engages with the surface of the host. This is opposed by two abductors, one originating in the coxa (ant. end. abd. 1), the other in the basis (ant. end. abd. 2).

(iii) *The oral cone*

The structure of the oral cone (figure 24) has been summarized by Boxshall (1986). It consists of an anterior lip, the labrum, and a posterior lip, the labium. Its basic structure is similar to that of *Hyalopontius* (see §4*a*iii) but differs in that both labrum and labium form the distal opening, each having an apical membrane that together form an incomplete border

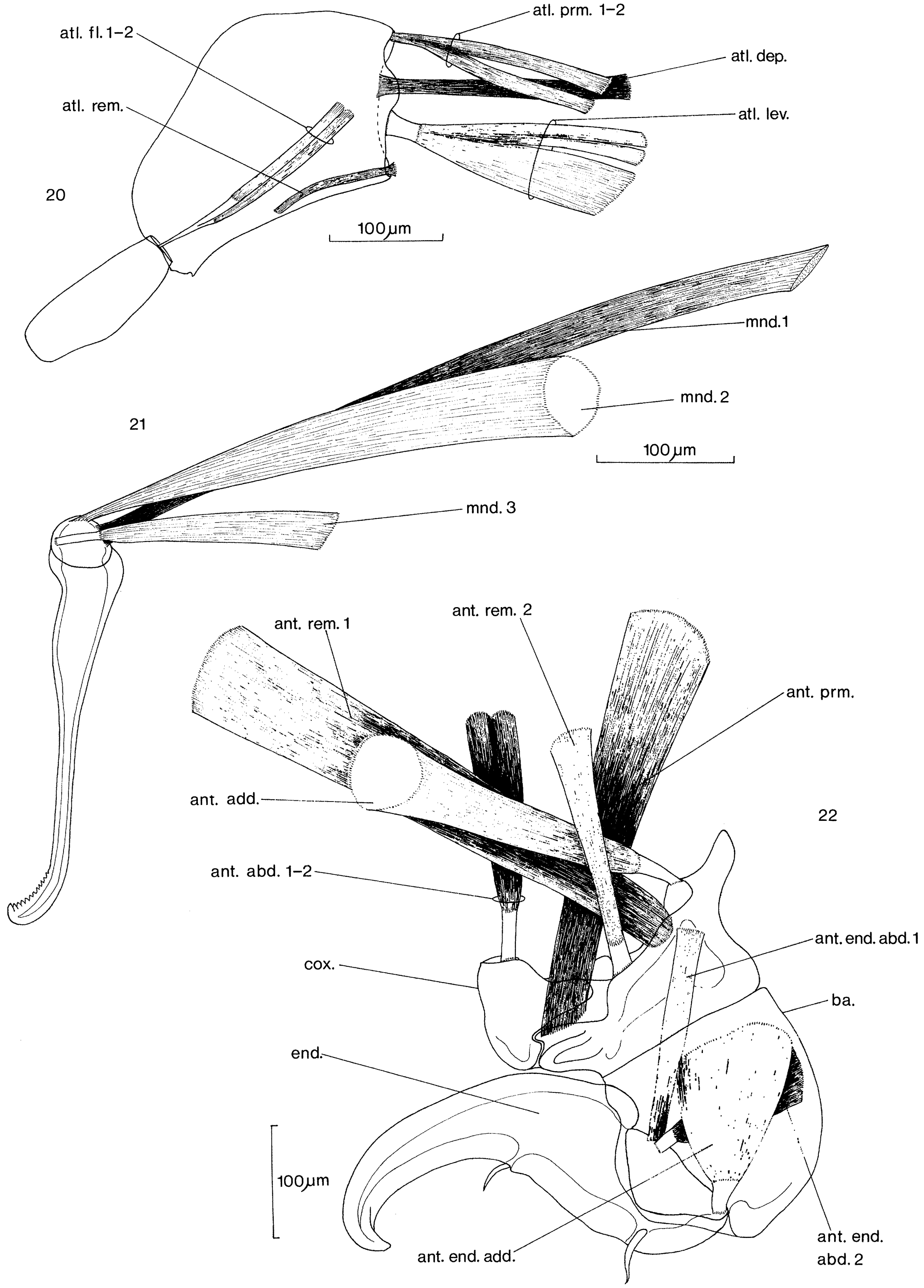


Figure 20. Dorsal view of antennule of *Lepeophtheirus*, showing musculature.
Figure 21. Anterior view of mandible of *Lepeophtheirus*, showing musculature.
Figure 22. Posterior view of antenna of *Lepeophtheirus*, showing musculature.

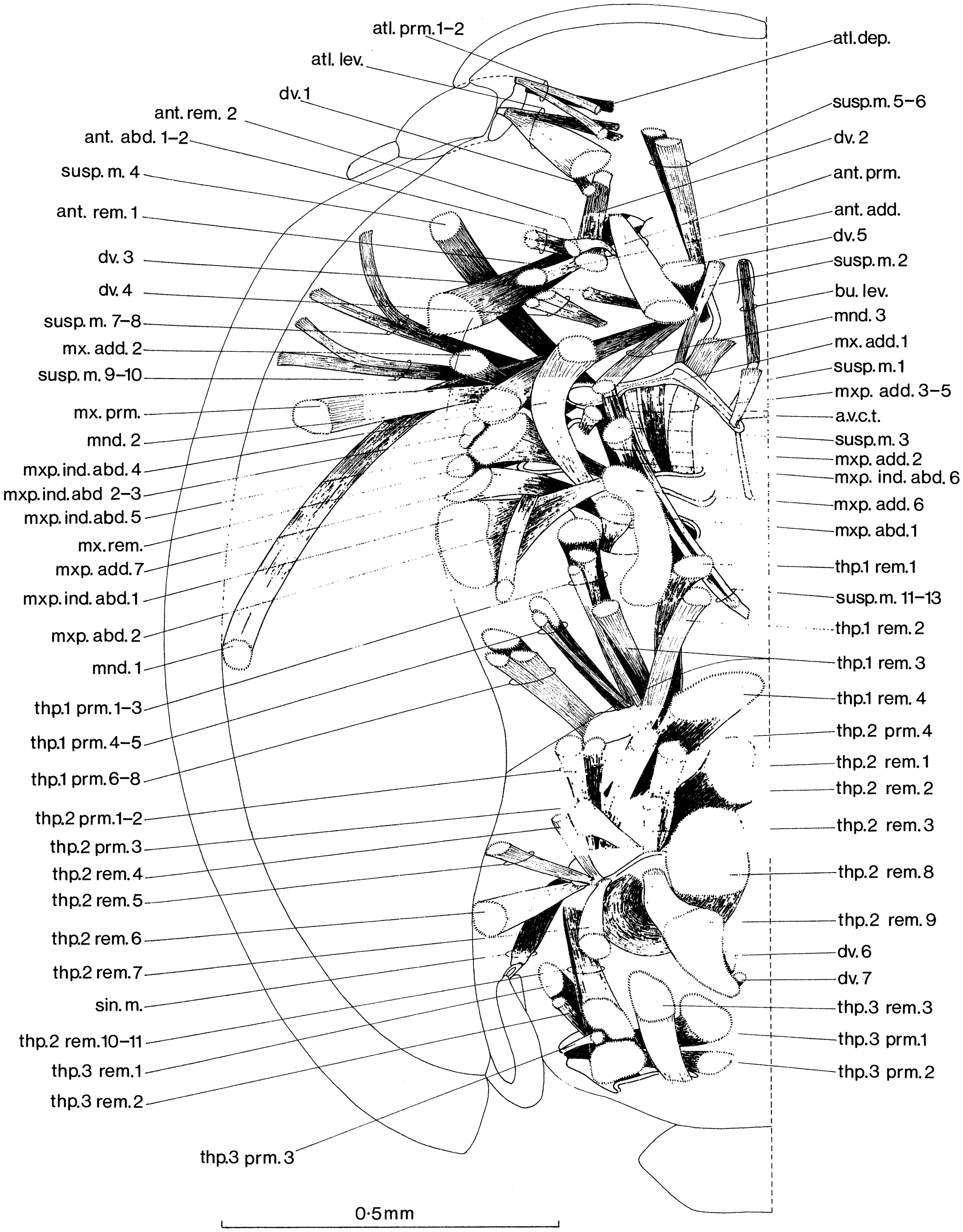


FIGURE 23. Dorsal view of left side of cephalothorax of *Lepeophtheirus*, showing musculature. All other organs have been removed.

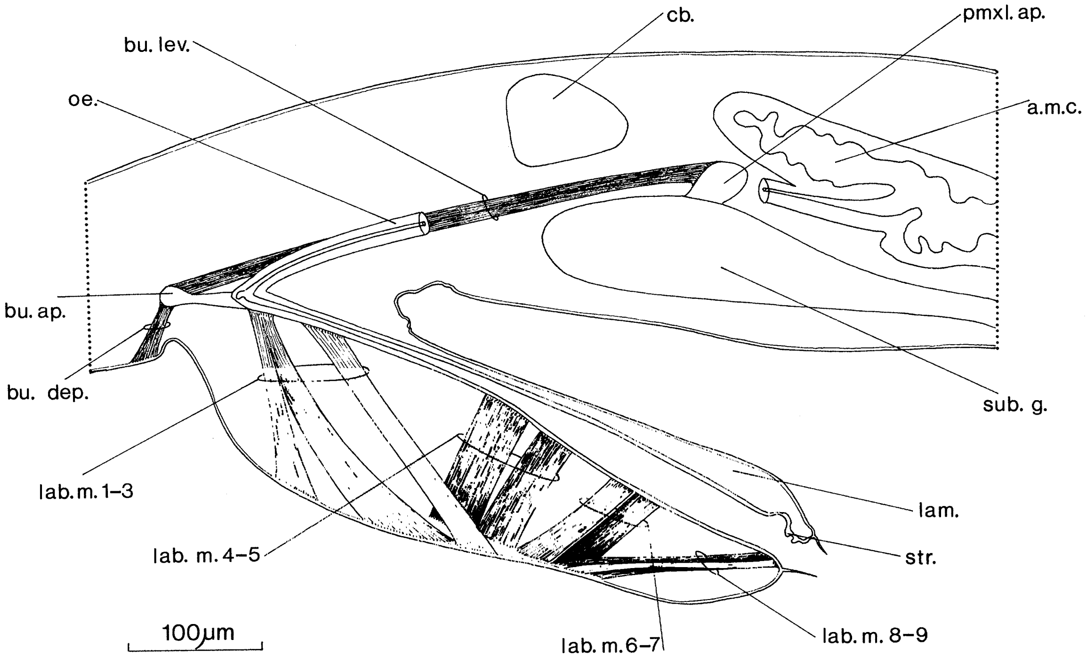


Figure 24. Median internal view of oral cone of *Lepeophtheirus*, showing associated musculature.

around the distal opening. During feeding the entire oral cone is erected to stand almost perpendicular to the ventral surface. At rest it is posteroventrally directed. The mandibular stylet passes obliquely into its lumen as in *Hyalopontius*. The maxillule is reduced and does not enter it.

The labrum is highly muscular (figure 24). The muscles (lab. m. 1–9) are arranged along its length and contract to enlarge the lumen of the oral cone and produce suction. The labium is slender and contains no muscles. The lining of the buccal cavity is uniform in thickness. The oesophagus passes posterodorsally from the base of the oral cone, through the nerve ring, to its junction with the midgut. At its junction with the oesophagus the buccal cavity is drawn out into a pair of buccal apodemes (figure 24), which act as the lever mechanism by which the oral cone is erected. Two pairs of levator muscles originate on the postmaxillulary apodemes, pass forwards through the nerve ring and insert on the buccal apodemes. These raise the oral cone into its feeding position. A single pair of depressor muscles originates on the ventral body wall anterior to the oral cone. Each inserts on a buccal apodeme and returns the oral cone to its resting position.

(iv) *Mandible*

The mandible (figure 21) is reduced to a slender stylet that passes medially into the lumen of the oral cone. There is no palp. The stylet is derived from the coxal gnathobase. It is slightly curved distally and bears 12 denticles along the concave margin. The basal articulation with the head lacks arthrodial membrane but a degree of mobility is possible by deformation of the surrounding integument. This allows for erection of the oral cone containing the mandible, and for movements of the mandibular stylet within it.

There are three extrinsic muscles inserting on the proximal rim of the mandibular stylet. One (mnd. 1) is extremely long, with its origin in the lateral area of the cephalothoracic shield (figure 23) about at the level of the first swimming legs, and inserts posteriorly. The other two are shorter and insert posterolaterally (mnd. 2) and anterolaterally (mnd. 3). These three muscles can produce a range of slight scraping and retraction movements of the stylet. There are no intrinsic muscles.

(v) *Maxillule*

The maxillule is reduced to a spinous lobe and a small papilla bearing three sensory setae. The spinous lobe is bifurcate in the female and trifurcate in the male. Neither part of the limb is mobile relative to the head and there are no maxillulary muscles.

(vi) *Maxilla*

The maxilla is uniramous and two-segmented. It comprises a syncoxa and an elongate basis drawn out into a claw-like process (figure 25). It is highly mobile and its main function appears to be grooming. There is no dominant pivot line at its articulation with the head and a range of whole limb movements is possible, facilitated by the presence of arthrodial membrane all round. The syncoxa–basis articulation has a well developed anteroposterior pivot line between two condyles (con.). This restricts movement to an adduction–abduction swing.

There are four extrinsic muscles, one (mx. add. 1) originating on the postmaxillulary apodeme, the other three on the dorsal cephalothoracic shield. The former inserts midway along the medial surface of the syncoxa and acts as an adductor of the whole limb. Another adductor (mx. add. 2) inserts on the proximal part of the medial wall. The remaining two muscles insert anterolaterally (mx. prm.) and posteriorly (mx. rem.) on the syncoxal rim and act as promotor–abductor and remotor respectively.

There are two antagonistic pairs of intrinsic muscles. One pair (mx. fl. 1–2) inserts on the medial rim of the claw-like basis and causes flexion of the claw. The other (mx. ext. 1–2) inserts on the lateral rim and extends the claw. There are no muscles within the basis and claw.

(vii) *Maxilliped*

The maxilliped is a powerful, subchelate limb. It is uniramous, comprising a robust proximal segment, derived from the fused protopodal segments, and a curved, distal claw derived from the fused endopodal segments (figure 27). Its proximal articulation with the head is extremely complex as there are two large apodemes (mxp. ap. 1–2) extending transversely over the basal foramen of the limb (figure 28). The limb is set into a concavity in the ventral body surface and its basal foramen is vertically orientated. There is more arthrodial membrane round the ventral part of this foramen, than dorsally. The whole basal articulation can be forced ventrally and tilted away from the midline by mechanisms involving the long apodemes. The articulation at the base of the claw has a distinct pivot line between anterior and posterior condyles, restricting movement to extension and flexion in a single transverse plane.

There are two groups of extrinsic muscles, those inserting on the maxillipedal apodemes 1 and 2 and acting indirectly, and those inserting directly on the limb. A powerful muscle (mxp. ind. abd. 1) originates on the dorsal shield and inserts dorsally on the tip of apodeme 1. Five muscles insert on apodeme 2. Two (mxp. ind. abd. 2–3) originate laterally on the dorsal shield and insert on the dorsal surface of the apodeme near its tip. Two others (mxp. ind. abd. 4–5) originate anteriorly and insert dorsally in the middle of the apodeme. The fifth (mxp. ind. abd. 6) inserts on the proximal part of the apodeme. These muscles may serve as tensors, giving

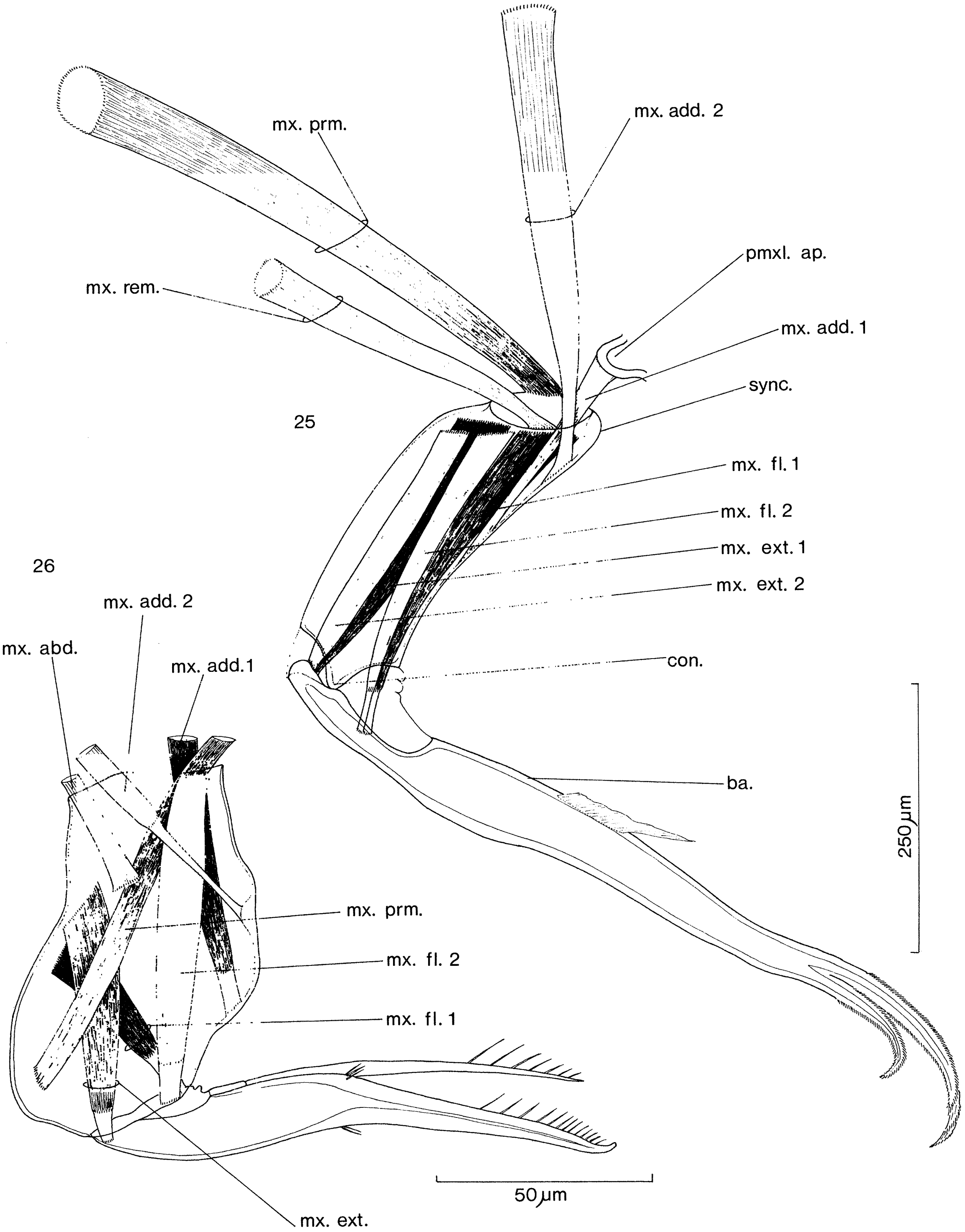
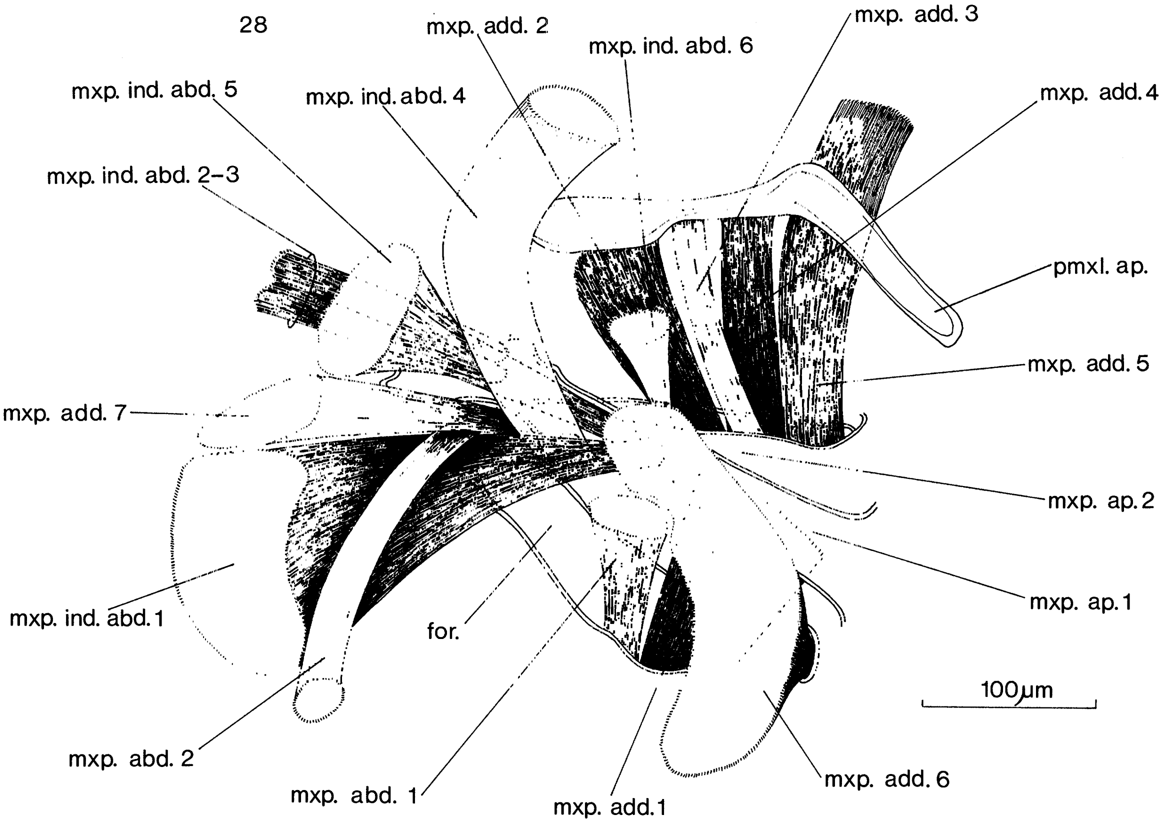


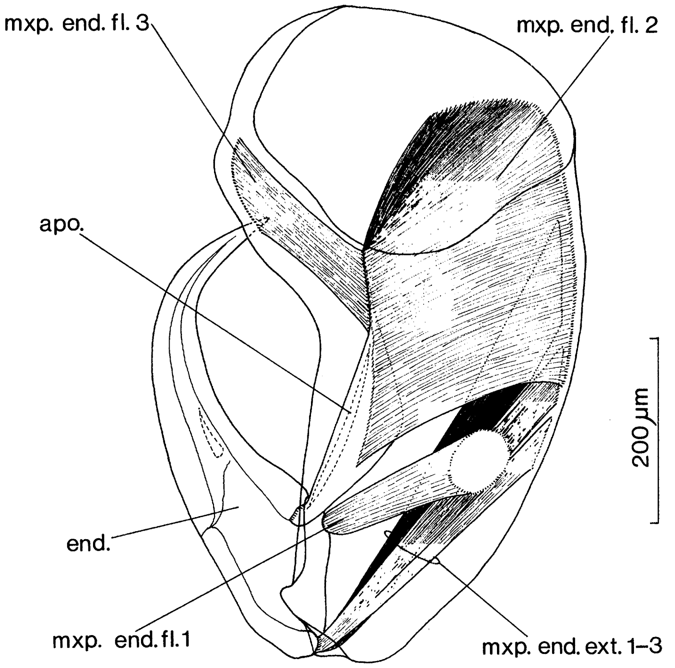
FIGURE 25. Posterior view of maxilla of *Lepeophtheirus*, showing musculature.

FIGURE 26. Posterior view of maxilla of *Stygiopontius*, showing intrinsic musculature.

28



27



29

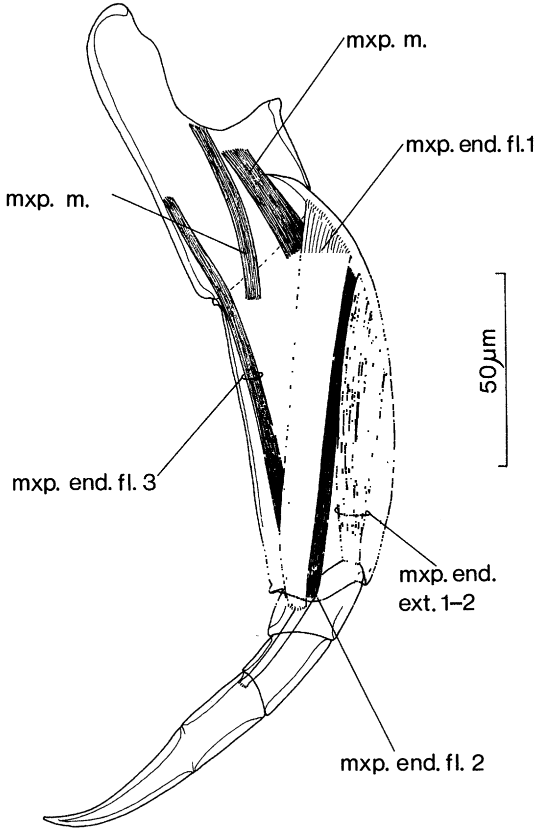


Figure 27. Anterior view of maxilliped of *Lepeophtheirus*, showing intrinsic musculature.

Figure 28. Dorsal view of extrinsic musculature of maxilliped of *Lepeophtheirus*.

Figure 29. Anterior view of maxilliped of *Entomopsyllus*, showing intrinsic musculature extending into endopod.

rigidity to the joint, and may also act as indirect abductors producing a downward force at the base of this apodeme which tends to tilt the basal articulation of the limb away from the midline.

The nine direct extrinsic muscles originate on apodeme 1, on the elongate postmaxillulary apodeme (pmxl. ap.), and on the dorsal cephalothoracic shield. A large adductor (mxp. add. 1) originates on the ventral surface of apodeme 1 and passes into the limb, inserting on the posteromedial wall. This probably acts as a remotor as well as adductor. Three adductors (mxp. add. 2–4) originate on the posteroventral surface of the elongate postmaxillulary apodeme and pass into the limb, inserting on the anteromedial wall. These probably have a promotor as well as adductor role. A fourth muscle (mxp. add. 5) inserts adjacent to these. It originates on the dorsal shield, passes beneath the postmaxillulary apodeme and into the limb. A massive adductor (mxp. add. 6) has a crescent-shaped origin on the dorsal shield immediately above the limb. It passes vertically to insert on the medial rim. A seventh adductor (mxp. add. 7) originates laterally and passes obliquely into the limb, to insert deep on the medial wall. A smaller muscle (mxp. abd. 1) has an adjacent origin and inserts posterolaterally, just inside the proximal rim. A second abductor (mxp. abd. 2) inserts anterolaterally on the rim.

The intrinsic muscles (figure 27) move the maxillipedal claw. There are three extensors (mxp. end. ext. 1–3), all inserting distally on the rim of the claw. These originate on the lateral wall of the basal segment. These are opposed by three flexors. One (mxp. end. fl. 1) originates on the anterior wall and inserts directly on the proximal rim of the claw. The other two insert on a hollow apophysis that extends proximally from the rim of the claw. One flexor (mxp. end. fl. 2) is massive and occupies much of the free space within the protopod. Its fibres run obliquely to insert on the apophysis. The fibres of the third flexor (mxp. end. fl. 3) also insert obliquely, on the other side of the apophysis, giving a pinnate arrangement of fibres.

(*c*) *Ventral cephalic tendon system*

(i) *Hyalopontius*

The cephalic tendon system (figure 30) consists of a single tendon (a.v.c.t.), homologous with the anterior tendon of misophrioid and calanoid copepods. This is attached at each side to the anteromedial surfaces of the postmaxillulary apodemes. Two paired suspensory muscles pass from their dorsal origins on the body wall to insert on the dorsal surface of the tendon near these attachments (susp.m. 1) or on the tip of the apodeme (susp.m. 2). The postmaxillulary apodemes (pmxl. ap.) are elongate and project medially almost to the ventral midline. The postmaxillary apodemes (pmx. ap.) are short and dorsally directed.

The muscles that originate on the cephalic tendon are shown in figure 30. There is a pair of short oesophageal muscles (oe. m.) originating dorsally and three labial muscles ventrally. The oesophageal muscles pass anteroventrally through the nerve ring before inserting on the ventral side of the oesophagus. The labial muscles pass through channels in the suboesophageal ganglion. The median, unpaired muscle (lam. 2) is tendinous until it emerges from the ganglion. It inserts proximally on a tendinous sheet that runs the length of the labium. The paired labial muscles (lam. 1) extend to the tip of the labium, and are probably responsible for moving the flared oral disc. The four mandibular protractors (mnd. pro. 1–4) originate anterolaterally. There are no ventral muscles to the maxillule. One maxillary adductor (mx. add. 1) originates on the mid posterior surface of the postmaxillulary apodeme; the other (mx.

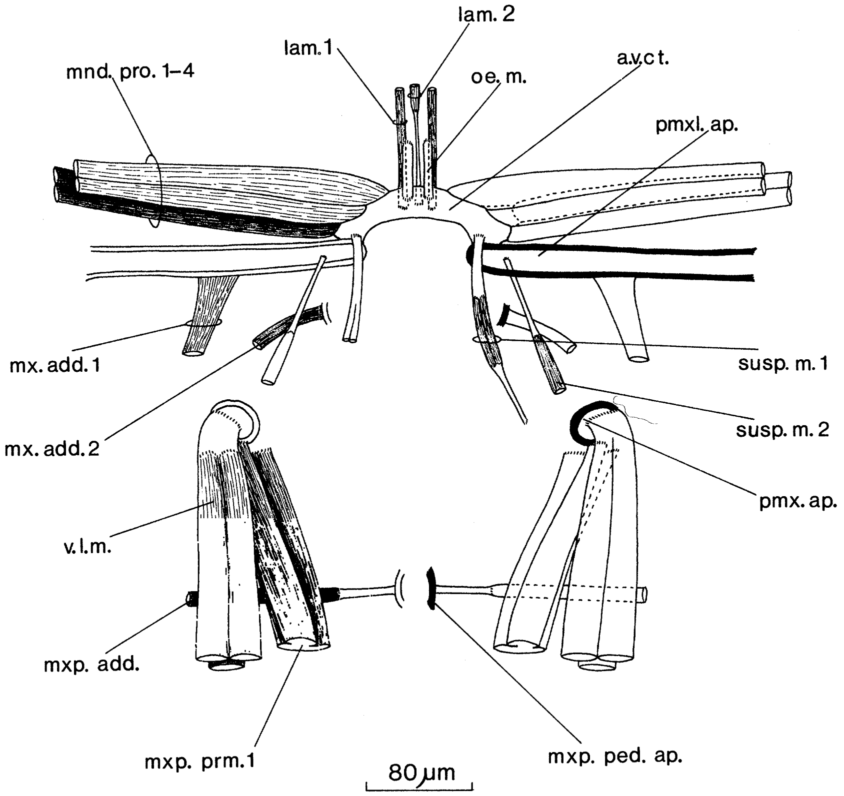


FIGURE 30. Semidiagrammatic dorsal view of ventral cephalic tendon system of *Hyalopontius* reconstructed from serial transverse and longitudinal sections. The sites of origin of the ventral extrinsic muscles to the appendages are shown.

add. 2) originates on the ventral body wall medial to the basal foramen of the limb. The triple-stranded ventral longitudinal trunk muscle (v.l.m.) originates on the tip of the postmaxillary apodeme and the powerful maxillipedal promotor (mxp. prm. 1) originates on its posterior surface and the adjacent ventral body wall. The slender maxilliped adductor (mxp. add.) originates on a median thickening of the wall of the maxillipedal pedestal.

(ii) *Lepeophtheirus*

The ventral cephalic tendon system is greatly reduced in *Lepeophtheirus* (figure 31). The single remaining tendon (a.v.c.t.) is reduced to a narrow strand connecting the tips of the postmaxillulary apodemes. The postmaxillulary apodemes (pmxl. ap.) comprise a transverse lateral part and an oblique medial part. A short suspensory muscle (susp.m. 1) passes down from its origin on the cephalothoracic shield to insert at the medial tip of the postmaxillulary apodeme. Suspensory tendons (susp.t. 1) pass posteroventrally from the tip of the postmaxillulary apodeme to the ventral body wall. The oral cone levator muscles share a common tendinous origin on each postmaxillulary apodeme. Two muscles (bu. lev.) on each side pass anteroventrally through the nerve ring to insert on the tip of the buccal apodemes (bu. ap.). Another suspensory muscle (susp.m. 2) inserts dorsally on the apodeme at the angle between lateral and medial sections. Also inserting anteriorly at the same position is the common tendon of the two long suspensory muscles (susp.m. 5–6) that originate on the dorsal shield about at the level of the antennules. The common tendon of these muscles passes around

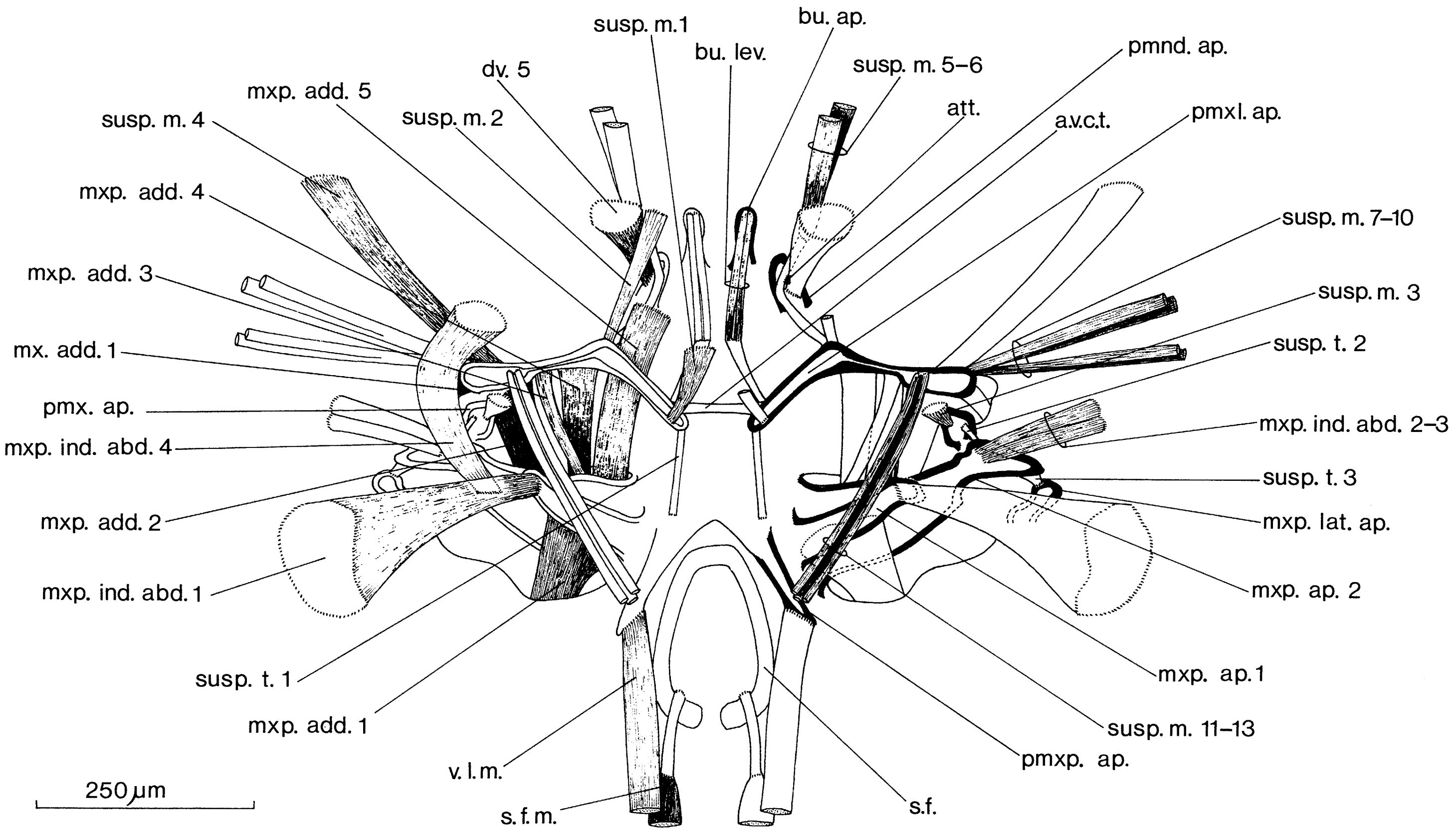


FIGURE 31. Semidiagrammatic dorsal view of ventral cephalic tendon system of *Lepeophtheirus* reconstructed from serial transverse and longitudinal sections. The sites of origin of the extrinsic muscles to the appendages are shown.

a dorsoventral muscle (dv. 5) that inserts on the small postmandibular apodeme (pmnd. ap.). The tendon is attached superficially to this muscle at the point of contact. The lateral extension of the postmaxillulary apodeme is well provided with suspensory muscles. Three slender muscles (susp.m. 11–13) originate near the dorsal midline, at the level of the sternal furca. They pass anterolaterally to insert on the dorsal surface of the apodeme. Five other suspensory muscles insert around the lateral tip of the apodeme. One muscle (susp.m. 4) originates dorsally and has an anterior insertion. Two long, double-stranded muscles (susp.m. 7–10) insert laterally. They originate near the lateral margin of the cephalothoracic shield.

There is a small postmaxillary apodeme (pmx. ap.) located just behind the postmaxillulary apodeme. It has a single vertical suspensory muscle (susp.m. 3), with a dorsal origin. It is connected by a short tendon (susp.t. 2) to the apex of maxillipedal apodeme 2 (mxp. ap. 2). The two large maxillipedal apodemes and their associated musculature have already been described (see §4*b*vii). There is a small apodeme (mxp. lat. ap.) located lateral to the basal foramen of the maxilliped. This is connected to the apex of maxillipedal apodeme 2 by a short tendon (susp.t. 3).

No muscles originate on the vestige of the anterior ventral cephalic tendon. Ventral muscles to the appendages all originate on the apodemes. There are no ventral muscles to the mandible and no muscles at all to the maxillule. A single maxillary muscle (mx. add. 1) originates on the ventral surface of the lateral extension of the postmaxillulary apodeme. Two maxillipedal adductors (mxp. add. 3–4) originate on the posterior surface of the postmaxillulary apodeme, and a third (mxp. add. 2) has its origin extending from the postmaxillulary apodeme and onto the adjacent postmaxillary apodeme. A large adductor (mxp. add. 1) originates on the ventral surface of maxillipedal apodeme 1. The ventral longitudinal trunk muscles originate on the thickening of the ventral body wall (pmxp. ap.) between the base of the maxilliped and the sternal furca. The muscles of the sternal furca are described in §3*b*iii.

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

Until recently, several different systems of nomenclature for the various parts of copepod cephalosomic limbs were widely used (see Boxshall (1985) for summary). Each system was based mainly on comparative studies of external morphology. New evidence, derived from study of the musculature, enabled Boxshall (1985) to establish the homologies of the limb segments in free-living copepods. A similar problem exists with the nomenclature of the limbs of parasitic copepods (see table 1). The use of such different systems causes confusion and conceals the homologies that must be identified prior to any analysis of phylogenetic relationships. The present study of limb skeletomusculature confirms that the system of homologies established by Boxshall (1985) can be applied to the parasitic siphonostomatoid copepods.

The antenna of *Lepeophtheirus* is uniramous. The exopod is lacking, as in all of the siphonostomatoid families parasitic on fishes except the Lernaeopodidae and Sphyriidae in which a 1-segmented exopod is retained. The endopod of *Lepeophtheirus* is claw-like and derived by fusion of the three ancestral segments. The position of the setae on the proximal part indicates the plane of fusion in many cases. There is a single free endopodal segment in *Hyalopontius*. This probably represents the fused second and third segments of the ancestral endopod, with the marginal seta marking the plane of fusion. The first endopodal segment is fused to the basis, forming an allobasis. The intermediate attachment of antennary adductor (figure 14, ant. add.) marks the original basis–endopod joint.

TABLE 1. SEGMENTAL COMPOSITION OF THE POSTMANDIBULAR APPENDAGES

	maxillule		
present account	praecoxal endite		palp
Giesbrecht (1899)	gnathobase		palp
Deets & Ho (1988) Kabata (1979)	endopod		exopod
Humes (1987)	inner lobe		outer lobe
Kabata (1979)	dentiform process		basal papilla
	maxilla		
present account	syncoxa		basis + endite
Kabata (1979)	lacertus		brachium
Giesbrecht (1899)	basipod 1		basipod 2 + claw
	maxilliped		
present account	syncoxa	basis	endopod segments 1–3
Humes (1987)	segment 1	segment 2	segments 3–5
Giesbrecht (1899)	basipod 1	basipod 2	endopod segments 1–3
present account	protopod		fused endopod + claw
Kabata (1979)	corpus		subchela

The mandibular stylet of caligids is often illustrated as comprising three or four segments. These are not true segments because the stylet represents the coxal gnathobase of the mandible. There is no mandibular palp in members of the caligiform families and none in *Hyalopontius* but in some families, such as the Asterocheridae, a 2-segmented palp is present. This presumably represents the basis plus a 1-segmented ramus. There is no evidence to indicate which ramus is retained.

The basic siphonostomatoid maxillule is bilobed, as in *Hyalopontius*. Giesbrecht (1899) regarded the inner and outer lobes as representing the gnathobase and palp respectively. They are, however, usually referred to as inner and outer lobes or as endopod and exopod (Deets & Ho 1988). Examination of the maxillulary musculature in *Hyalopontius* provides evidence supporting Giesbrecht's interpretation. The probable homologue of the intrinsic muscle running transversely from a lateral origin to a medial insertion at the base of the inner lobe (figure 18, i.g.b.m.) is the intragnathobasic muscle present in calanoids (Boxshall 1985) and misophrioids (Boxshall 1982). This confirms that the inner lobe is derived from the praecoxal endite. The outer lobe is separated from the inner by a non-functional suture line and represents the rest of the palp. In *Lepeophtheirus* the basal part of the maxillule is incorporated into the ventral body wall so that the two lobes of the maxillule appear to be independent. They are orientated along the long axis of the body. The anterior lobe is papillate and probably represents the palp. The posterior lobe is a spinous process and probably represents the praecoxal endite.

The maxilla is 3-segmented in the fossil *Kabatarina* Cressey & Boxshall and the first and second segments presumably represent praecoxa and coxa. The maxilla is 2-segmented in *Hyalopontius* and *Lepeophtheirus* and the proximal segment is a syncoxa. The distal segment is the basis drawn out into a long process, or recurved claw homologous with the proximal basal endite of misophrioids. The basis may be armed distally but it is never segmented. There is no vestige of the endopod. In some genera of the Dirivultidae there is a strong seta in the axil between maxillary syncoxa and claw (for example, in *Stygiopontius*) (figure 26). The origin of this seta is uncertain. According to Humes (1987) it originates on the syncoxa, in which case it would represent a vestige of the distal coxal endite and would be a unique plesiomorphy for the Siphonostomatoida. In *Stygiopontius hispidulus* this seta lies on a small process delineated on either side by integumental folds (figure 26), but it appears to be more firmly attached to the claw and come off with the claw when the latter is removed in dissection. It is probable that the seta is an element of the basal endite that forms the claw and is homologous with the short seta present on the claw in some members of the Asterocheridae, for example (see Ho (1984)).

In some siphonostomatoid families, such as the Entomolepidae and Asterocheridae, the distal part of the maxilliped is 3-segmented and represents the endopod (for example, in *Entomopsyllus*) (figure 29). In *Hyalopontius* the endopodal segments are fused into a single segment bearing the terminal claw. In *Lepeophtheirus* the endopodal segments fuse to form a heavily sclerotized, unitary claw. No muscles extend into the claw in either genus, although in *Entomopsyllus* one muscle (mxp. end. fl. 2) extends into the endopod to insert on the proximal rim of the third segment (figure 29). In copepod maxillipeds most endopodal muscles originate in the basis (Boxshall 1985). Most of the muscles operating the endopod in *Hyalopontius* originate proximally in the long second segment. This segment is interpreted as the basis. The first segment is, therefore, a much reduced syncoxa. The robust, proximal segment of the maxilliped in *Lepeophtheirus* is derived by fusion of all the protopodal segments.

5. Feeding mechanisms

(*a*) *Hyalopontius*

H. typicus has powerful raptorial limbs and a well developed oral cone. This species occurs only in deep water and presumably feeds on other deep-sea animals, either in the manner of a micropredator, attaching temporarily to its prey, or as a parasite, remaining attached to or associated with the host even when not feeding. Its food is referred to as prey in this account. The gut contents of several individuals included no solid matter, indicating perhaps that only fluids are ingested. The likely feeding mechanism can be suggested on the basis of the anatomy and range of possible movements of the mouthparts.

The prey is grasped by the long and highly mobile maxillipeds and drawn in towards the ventral surface of the head. The antennae, with their long terminal claws, may assist in holding and positioning the prey. While retaining hold of its prey *H. typicus* must manoeuvre itself so that the distal opening of the oral cone comes into contact with the prey. This is probably achieved by fine movements of antennae and maxillipeds. The subchelate maxillae may assist in maintaining the correct distance between the copepod and its prey during feeding. Contact between the oral cone and prey is monitored by the three sensory setae on the apex of the inner maxillulary lobe. Distally, these lie in a lateral channel within the longitudinal groove separating the labrum from the labium (figure 36, plate 1) but emerge around the tip of the oral cone. The stylet-like mandibles are used to puncture the prey. Once the puncture is made and a seal established around it by the flared oral disc, body fluids can be sucked out. The numerous labral muscles dilate the basal part of the lumen of the cone and provide the suction. After feeding the seal can be broken by the labial (lam. 1) and labral (lab.m. 7) muscles drawing the tip of the cone away from the prey.

(*b*) *Lepeophtheirus*

Feeding in caligid copepods has been studied by Kabata (1974) and some details of feeding in *L. pectoralis* were published by Boxshall (1976, 1986). In brief, the oral cone is erected almost perpendicular to the body so that the distal opening comes into contact with the surface of the host. Fish tissue is scraped off by movements of the strigil, a dentiferous bar on the labium, and then drawn back into the lumen of the oral cone by action of the mandibles (Kabata 1974). The only significant difference between the present study and that of Kabata (1974) is the site of origin of the oral cone levator muscles. These originate on the postmaxillulary apodemes (see §4*c*ii), not on the ventral wall of the cephalothorax as shown by Kabata.

(*c*) *Digestive tract*

(i) *Hyalopontius*

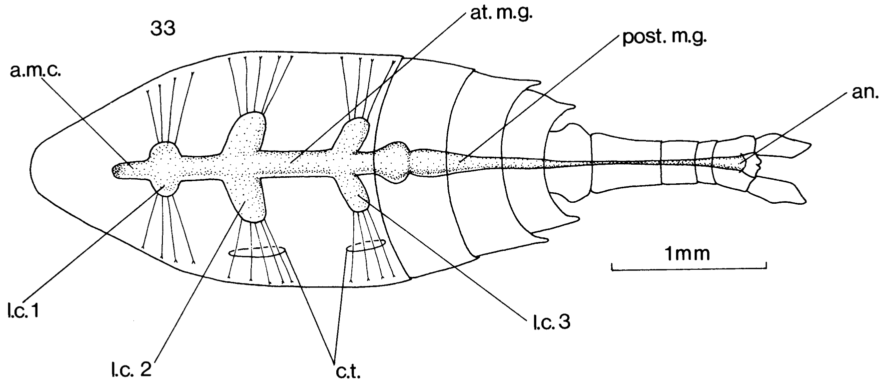
The oesophagus (figure 32) is provided with bands of circular (circ. m.) and longitudinal muscles. Several dilators (oe. dil.) originate on an intucking of the integument anterior to the labrum and on the cephalic tendon. All these muscles draw the food along the oesophagus and into the midgut (m.g.). Before it joins the midgut the oesophagus passes posterodorsally through the nerve ring formed from the cerebrum (cb.) and suboesophageal ganglia (sub.g.) and the circumoesophageal commissures. The small diameter of the nerve ring restricts the dilation of the oesophagus thereby allowing the passage of fluids or finely macerated food only.

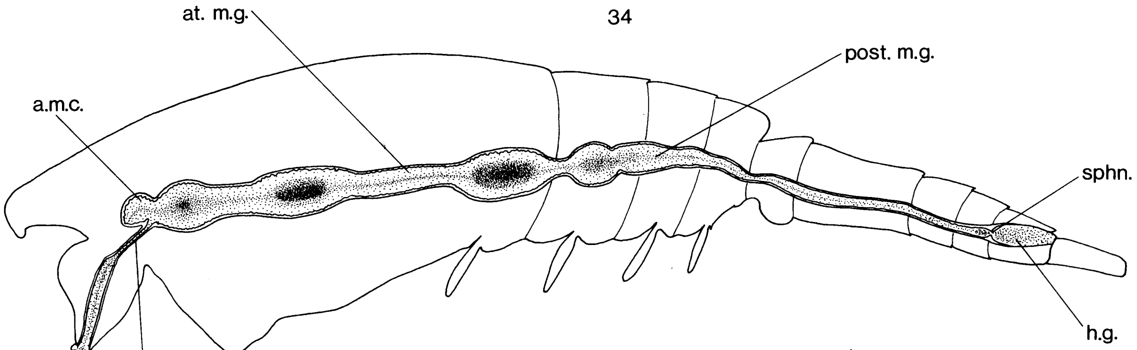
The midgut is divided into anterior and posterior sections by a constriction in the middle of the second pedigerous somite (figure 34). The oesophagus enters the midgut just posterior to the small anterior midgut caecum (figures 32 and 34, a.m.c.) which acts as a storage area for the build up of digestive enzymes, which can then be rapidly released during feeding to mix with the food. The anterior section of the midgut has three pairs of lateral caeca (figures 33 and 34, l.c.), which provide a large storage capacity. The presence of lateral caeca is interpreted as evidence of an intermittent, micropredatory feeding strategy as a large storage capacity is unnecessary in parasites that remain permanently attached to their hosts (Boxshall 1986). The lateral caeca are suspended from the lateral body wall by strands of connective tissue (figure 34, c.t.). The posterior section of the midgut is tubular and extends from the second pedigerous somite to the anterior rim of the anal somite. The short hindgut (h.g.) is separated from the midgut by a valve and opens via the slit-like anus between the caudal rami.

(ii) *Lepeophtheirus*

The gross morphology of the digestive tract of *L. pectoralis* is well documented (Scott 1901; Boxshall 1986). A supplementary description of the hindgut is presented.

The hindgut extends through the posterior part of the abdomen. Its junction with the end of the midgut is marked by well-developed, circular sphincter muscles (figure 35, sphn. m.). Numerous dilator muscles originate around the walls of the anal somite. These dilate the lumen of the hindgut for elimination of faecal pellets. They are also used for taking in water through the anus. It is then drawn up into the posterior part of the midgut by reverse peristalsis. This behaviour is referred to in the literature as anal respiration and has been reported in *L. pectoralis* previously (Scott 1901). It has been assumed that gaseous exchange takes place through the walls of the midgut but no detailed studies have been made to support this interpretation. Fox (1952) suggested that the role of anal water intake might be to assist defaecation but Fryer (1970) found that, in certain cladocerans, it appeared to prevent loss of digestion products and increase the efficiency of food utilization.





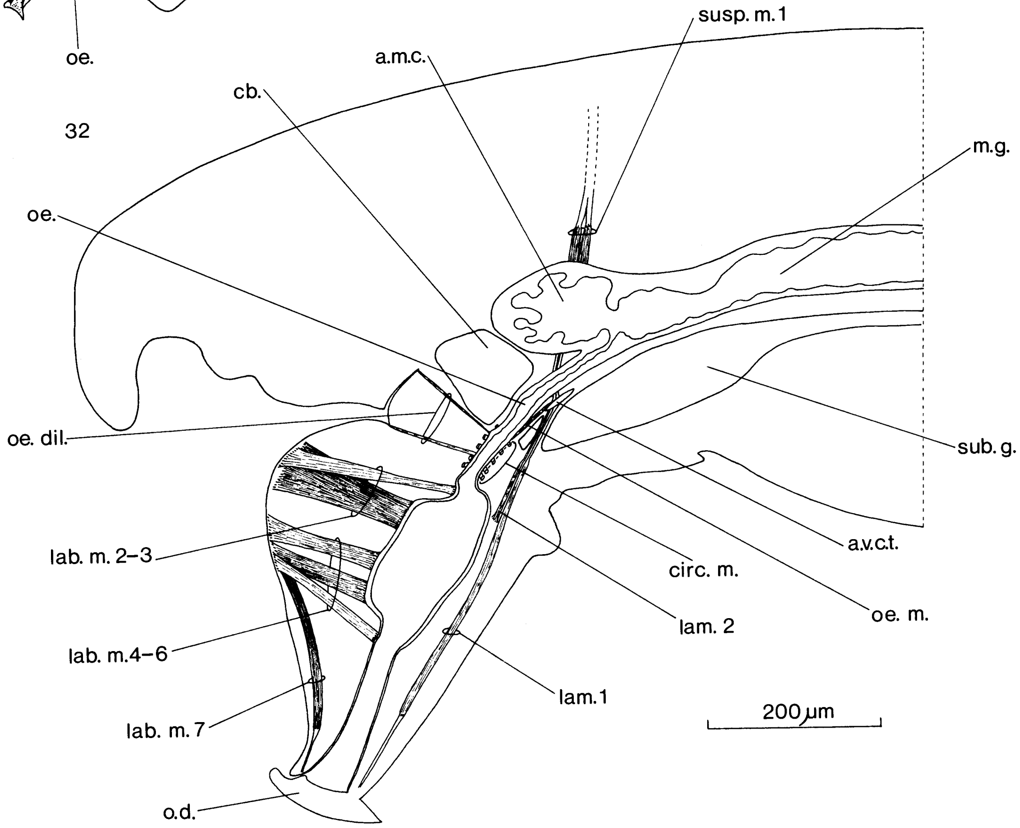


FIGURE 32. Thick median longitudinal section through oral region of *Hyalopontius*, drawn from a composite of several adjacent sections. The musculature of the oral cone is shown.

FIGURE 33. Dorsal view of *Hyalopontius*, showing lateral midgut caeca.

FIGURE 34. Median internal view of *Hyalopontius*, showing gross gut morphology.

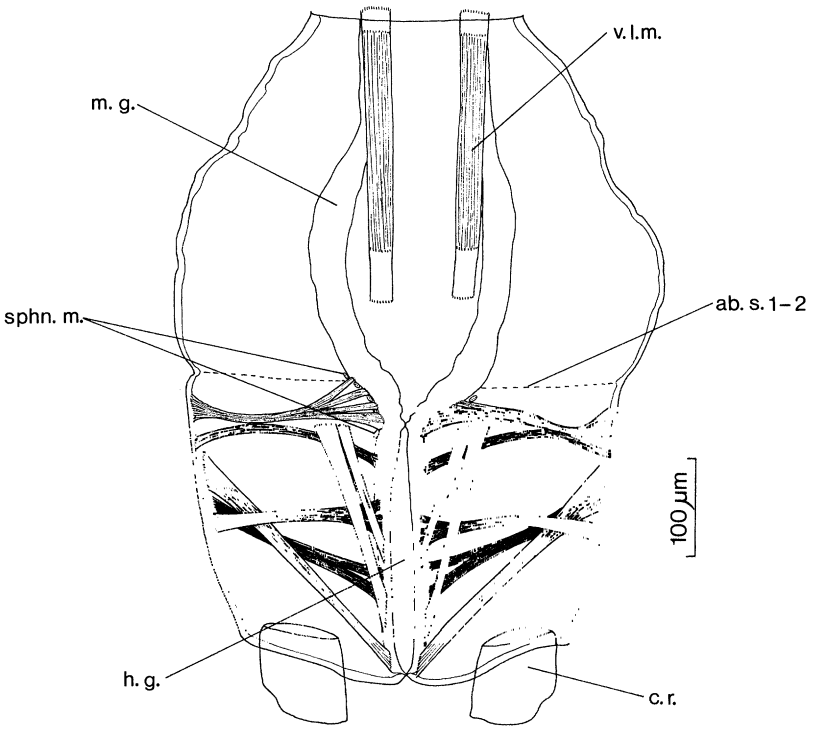


FIGURE 35. Ventral view of free abdomen of *Lepeophtheirus*, showing musculature associated with hindgut.

6. ADAPTIVE RADIATION IN ORAL CONE STRUCTURE

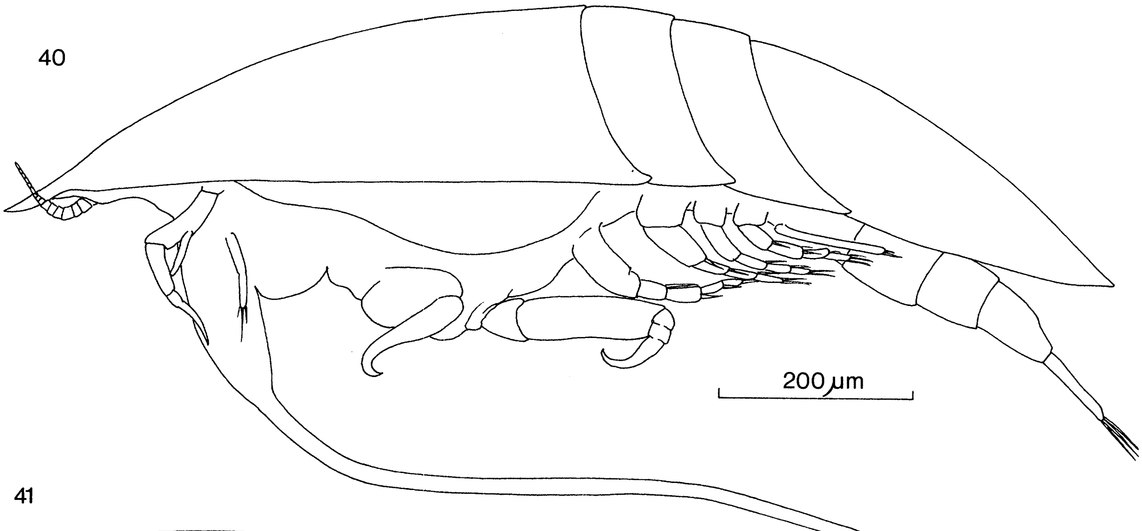
(*a*) *Asterocheres*

Asterocheres is a primitive representative of the Siphonostomatoida, and its species are sometimes abundant associates of sponges and other invertebrate hosts. The oral cone (figure 37, plate 1) differs considerably in length in different species. When short the cone comprises a broad labrum, which may have a distinct apical process fringed with a row of setules (figure 39, plate 1), and a smaller labium. The mandibles have a two-segmented palp and a slender stylet, which enters the oral cone laterally via the slits between labrum and labium. The palp is laterally directed and may have a sensory role. The inner lobe of the maxillule lies closely adpressed to the side of the oral cone, effectively sealing any gap around the mandibular stylet. A close fit is ensured by the presence of a longitudinal groove on the medial surface of the inner lobe (figure 38, plate 1). The four apical setae of this lobe extend to the tip of the oral cone and probably have a sensory function, as in *Hyalopontius*.

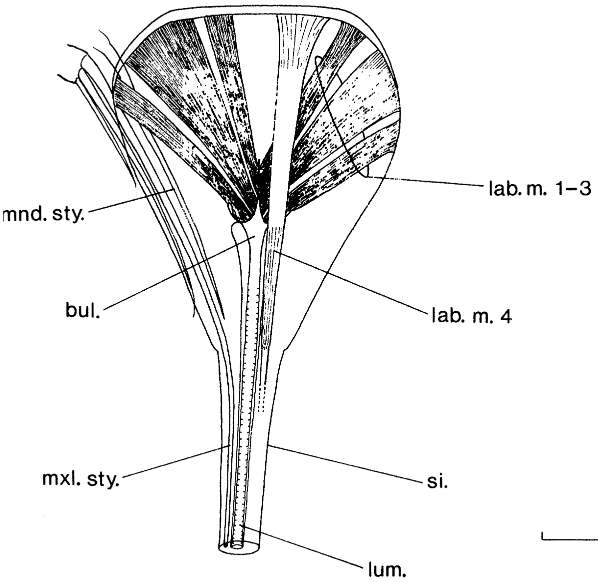
(*b*) *Entomopsyllus adriae*

Entomopsyllus is a small shield-shaped copepod that lives and feeds on sponges. It has an extremely well-developed oral cone, comprising a short, broad proximal part and an elongate disal part, the siphon (si.), which may be almost as long as the body (figure 40). The siphon is formed by extensions of both labrum and labium for its entire length (figure 45, plate 2). There is no oral disc at the apex of the siphon. The mandible has a well-developed two-segmented palp and a fine, stylet-like gnathobase, which enters the oral cone via the slit between labrum and labium (figure 44, plate 2). The inner lobe of the maxillule lies immediately adjacent to the mandibular stylet and its three apical setae also pass into the oral

40



41



42

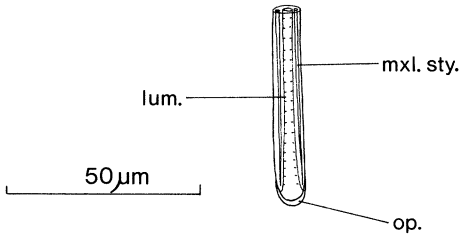


Figure 40. Lateral view of *Entomopsyllus*, showing oral cone and its long distal siphon.
Figure 41. Anterior view of oral cone of *Entomopsyllus*, showing labral musculature.
Figure 42. Apex of oral siphon.

cone via the same slit (figures **43** and **44**, plate 2). The mandibular stylet is short and only just reaches the base of the distal siphon. Two of the maxillulary setae are also short but the third is extremely long and extends to the tip of the siphon. This maxillulary seta does not enter the lumen of the siphon but lies in a separate channel, the maxillulary channel (arrowed in figure **47**, plate 2), contained within the oral cone, one on each side.

The musculature of the oral cone is largely confined to the proximal part of the labrum (figure 41). Most of these labral muscles (lab. m. 1–3) insert close together on folds in the wall of the oral cone lumen. The integument in this proximal part is relatively thin. Contraction of these dilator muscles greatly dilates the proximal internal bulb (bul.) of the oral cone providing powerful suction to drawn material into the siphon. Immediately distal to this internal bulb the lumen wall is much thicker but it tapers rapidly so that for most of its length the walls are thin and marked with minute internal annulations (figure **47**). One pair of labral muscles (lab. m.

4) originates either side of the midline at the base of the labrum and each has a muscular proximal part and tendinous distal part. They lie immediately beneath the anterior surface and extend into the siphon. The precise site of insertion could not be identified but it is probable that the tendinous sections extend to the apex of the labrum.

Feeding in *Entomopsyllus* is poorly understood. It presumably feeds on the contents of individual cells of its sponge host, punctured by the maxillulary setae which appear to extend to the distal opening of the siphon. The oral siphon is only 5 μm in diameter at its tip (figure 42); this small size may facilitate penetration deep into the matrix of the sponge. It can suck up fluids by the dilation of the internal bulb of the oral cone. The comb of tiny denticles around the distal opening of the siphon (figure 46, plate 2) may prevent larger particles being drawn into the siphon. In preserved specimens the siphon may be fixed in a wide variety of configurations and it appears to be very flexible. The arrangement of circular strengthening ridges on internal wall of the siphon (figure 47) prevents the lumen from collapsing when the siphon bends. However, it is not known how flexion is produced or how the siphon is used to penetrate the host.

(*c*) *Pontoeciella abyssicola*

Pontoeciella is a planktonic siphonostomatoid in which the oral cone is sexually dimorphic (Boxshall 1979). In the female (figure 48, plate 3) it is well developed, with a flared oral disc on the labium (figure 49, plate 3) and is erected by paired levator muscles (Boxshall 1986). The male oral cone is small, and lacks an oral disc. The adult male probably does not feed.

The muscles associated with the oral cone and mouthparts are shown in figure 52. As in *Lepeophtheirus*, the ventral cephalic tendon system is vestigial, reduced to a tendinous strand (a.v.c.t.) connecting the tips of the postmaxillulary apodemes (pmxl. ap.). No muscles originate on this tendon. The postmaxillulary apodemes are long, extending backwards beyond the origin of the ventral trunk muscles on the postmaxillipedal apodeme. The apodemes are held in position by suspensory muscles, four of which originate on the dorsal or lateral body wall.

DESCRIPTION OF PLATE 1

FIGURE 36. Lateral view of oral cone of *Hyalopontius*, showing mandibular stylet (open arrow) and inner lobe of maxillule (solid arrow) both entering slit between labrum and labium. Scale bar, 50 μm.

FIGURE 37. Anteroventral view of oral cone of *Asterocheres*, showing longitudinal groove (arrowed) in medial surface of inner maxillulary lobe. Scale bar, 20 μm.

FIGURE 38. Lateral view of oral cone of *Asterocheres*, showing mandibular stylet (arrowed) entering slit between labrum and labium. Scale bar, 20 μm.

FIGURE 39. Anterior view of apex of labrum of *Asterocheres*. Scale bar, 4 μm.

DESCRIPTION OF PLATE 2

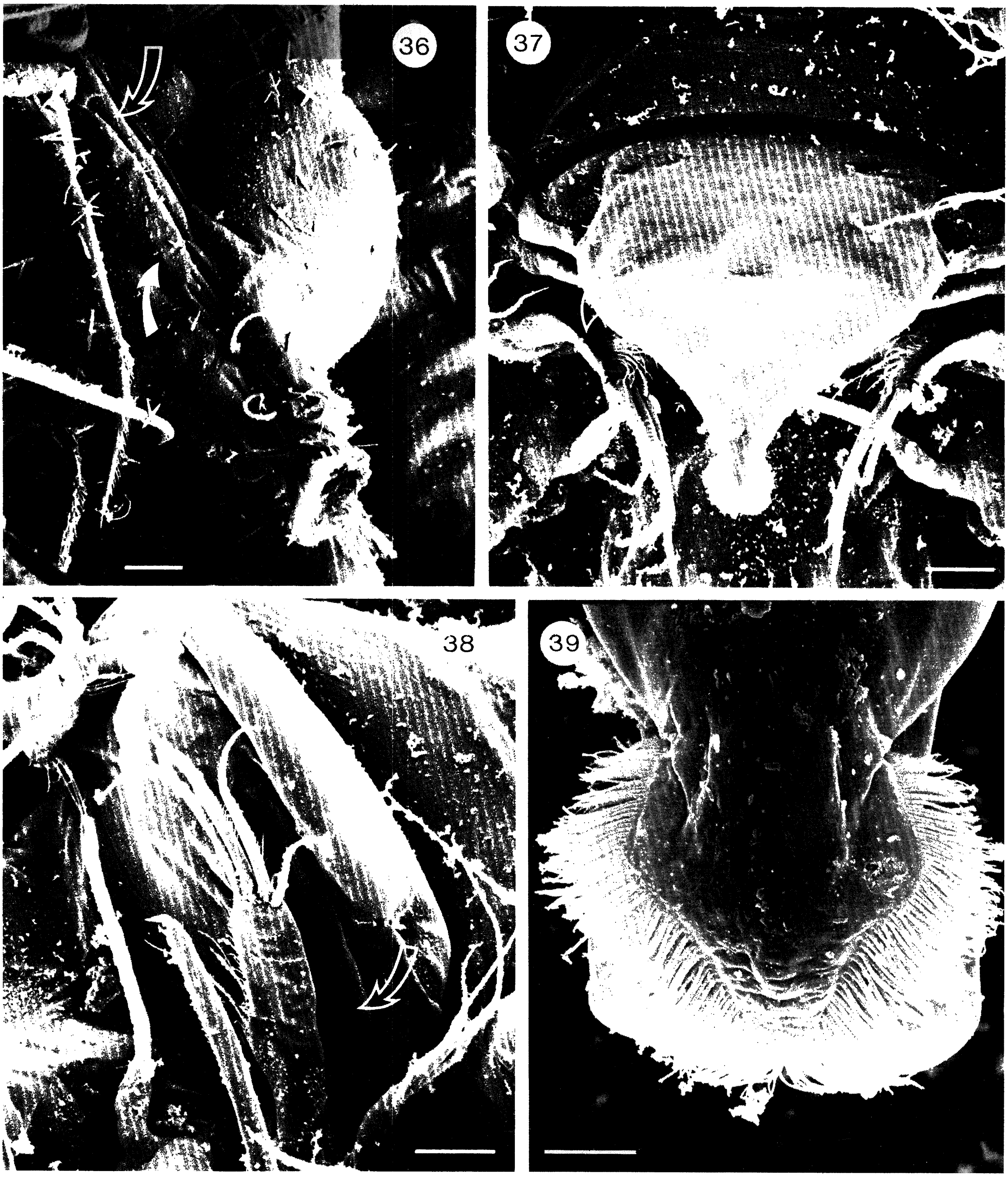
FIGURE 43. Ventral view of base of oral cone of *Entomopsyllus*, showing external annulations at base of distal siphon. Scale bar, 20 μm.

FIGURE 44. Lateral view of same, showing mandibular stylet (open arrow) and maxillulary setae (solid arrow) entering slit between labrum and labium. Scale bar, 10 μm.

FIGURE 45. Lateral view of midsection of siphon, showing labrum and labium. Scale bar, 2 μm.

FIGURE 46. Distal opening of oral siphon, showing comb of denticles on labrum. Scale bar, 1 μm.

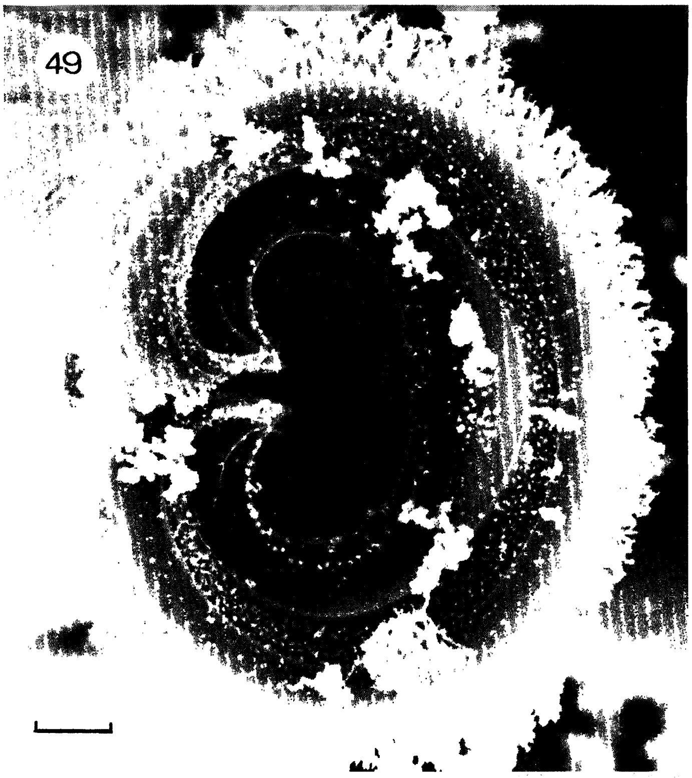
FIGURE 47. Transverse sectional view of oral siphon broken midway along its length, showing central lumen and lateral maxillulary channels (arrowed). Scale bar, 1 μm.



FIGURES 36–39. For description see opposite.

(*Facing p.* 204)

FIGURES 43–47. For description see p. 204.



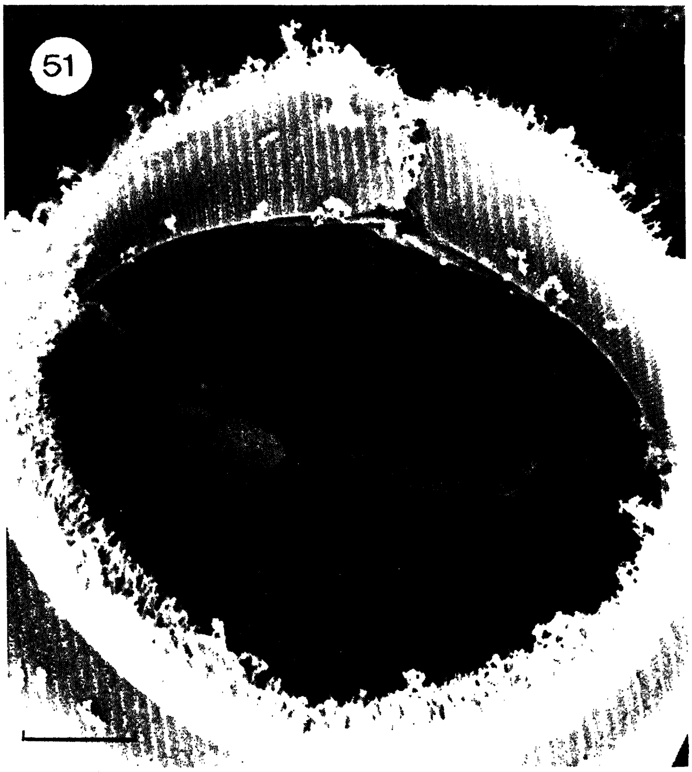


FIGURE 48. Lateral view of oral cone of female *Pontoeciella*, showing mandibular stylet (arrowed) entering slit between labrum and labium, and inner lobe of maxillule. Scale bar, 20 μm.

FIGURE 49. Oral disc at apex of oral cone of *Pontoeciella*. Scale bar, 2 μm.

FIGURE 50. Posterior view of oral cone of premetamorphic adult female of *Lernaeocera*, showing large opening. Scale bar, 20 μm.

FIGURE 51. View into distal opening of oral cone of *Lernaeocera*, showing buccal stylets on internal wall of labrum. Scale bar, 10 μm.

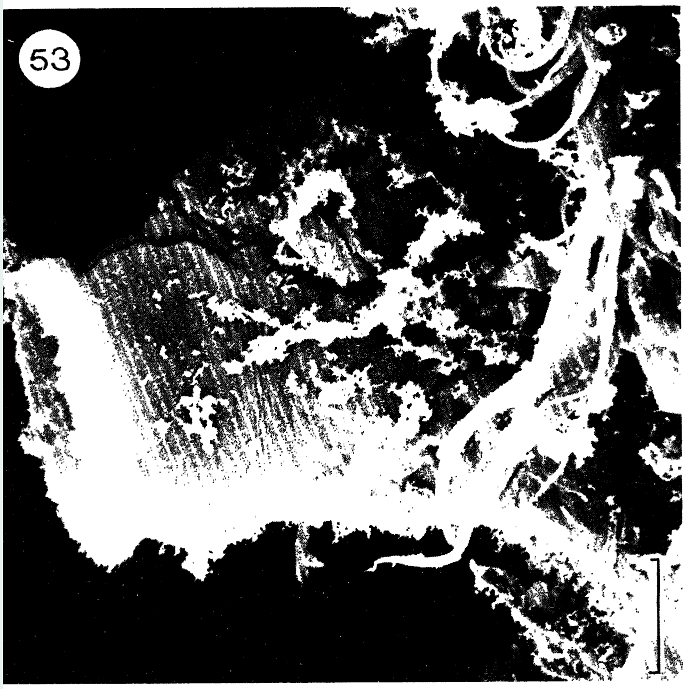


FIGURE 53. Lateral view of oral cone of premetamorphic adult female of *Lernaeocera*, showing short labrum and oral disc present on labium only. Scale bar, 25 μm.

FIGURE 54. Lateral view of oral cone of early copepodid stage of *Lernaeocera*, showing labrum and labium of equal length, each bearing part of oral disc. Mandibular stylet (arrowed) displaced out of oral cone. Scale bar, 20 μm.

FIGURE 55. Lateral view of oral cone of *Stygiopontius*, showing mandibular stylet (arrowed) entering large gap between labrum and labium. Scale bar, 20 μm.

FIGURE 56. Apical view of oral cone of *Stygiopontius*, showing setose setae forming labial section of oral disc, and dentate apices of mandibular stylets (arrowed). Scale bar, 2 μm.

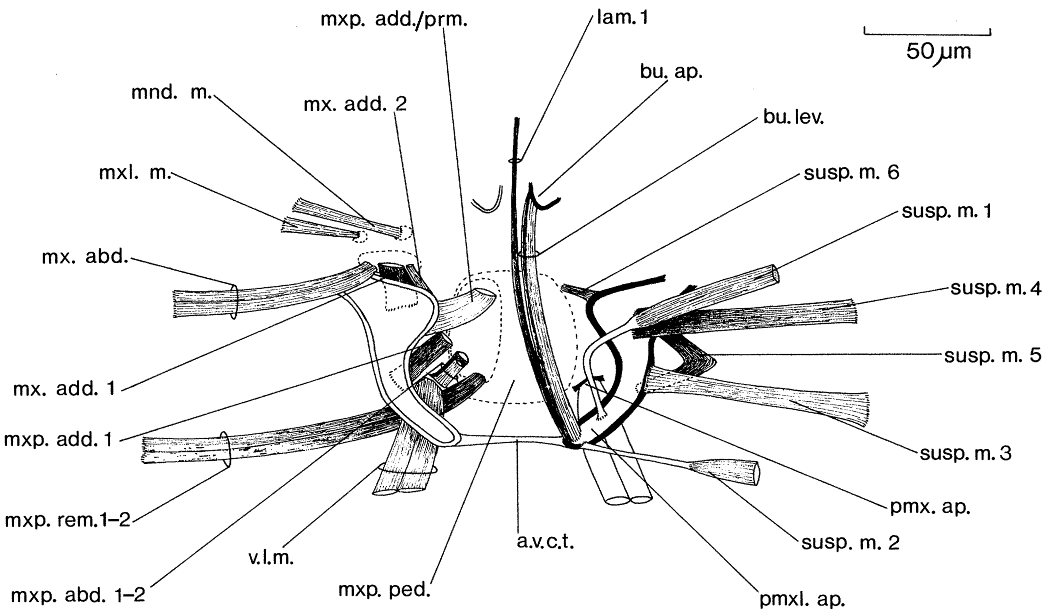


FIGURE 52. Semidiagrammatic dorsal view of the ventral cephalic tendon system of *Pontoeciella* reconstructed from transverse serial sections. The dorsal extrinsic muscles are also shown.

Two (susp.m. 1–2) have long tendinous sections and insert dorsally at and near the tip of the apodeme. One (susp.m. 3) originates laterally and inserts midway along the lateral surface, and another (susp.m. 4) inserts more proximally on the dorsal surface. Two suspensory muscles originate on the ventral wall of the cephalothorax and insert ventrally midway along the apodeme (susp.m. 5), or ventrally on its anteromedial angle (susp.m. 6).

The oral cone levator muscles originate at the apex of the postmaxillulary apodemes. Two muscles on each side pass anteroventrally, alongside the oesophagus, through the nerve ring to insert on the buccal apodemes (bu. ap.). Also originating at the apex of the apodemes is a pair of slender labial muscles (lam. 1). These are tendinous as they pass anteroventrally through channels in the suboesophageal ganglion, but are muscular as they enter the labium. They extend to the tip of the labium and are probably responsible for movement of the oral disc.

The mandibles and maxillules each have a single extrinsic muscle, originating low on the lateral wall of the cephalothorax. There are three extrinsic muscles, two (mx. add. 1–2) originating on the postmaxillulary apodeme and the third (mx. abd.) on the dorsolateral cephalothoracic wall. Two maxillipedal muscles (mxp. add.–prm.; mxp. add. 1) originate on the postmaxillulary apodeme and two (mxp. abd. 1–2) on the postmaxillipedal apodeme. A double-stranded extrinsic muscle (mxp. rem. 1–2) originates on the dorsolateral cephalothoracic wall. The double-stranded ventral longitudinal trunk muscles (v.l.m.) originate on the postmaxillipedal apodeme.

(*d*) *Lernaeocera branchialis*

Postmetamorphic adult females of the pennellid *L. branchialis* live with the cephalothorax deeply embedded into the tissues of the host fish. Premetamorphic adults and larvae are found on the gills of flatfishes and other intermediate host fishes. The oral cone of the premetamorphic female is cylindrical (figure 50, plate 3) and has a large apical opening encircled by a marginal membrane. Only the labium contributes to the apical opening (figure 53, plate 4). The labrum forms the anterior wall of the oral cone but does not reach the opening. Internally the labrum carries a pair of buccal stylets (figure 51, bu. sty. (plate 3)), which lie in the lumen of the cone. The dentate mandibular stylets lie free within the lumen of the cone. There is no mandibular palp. The maxillule is bilobed and both lobes lie lateral to the cone and do not enter the slits between labrum and labium. When seen in transmitted light the oral cone appears to consist of three chitinous rings (Kabata 1962). The rings are broad bands of thicker integument that alternate with bands of thinner integument. This allows the oral cone to shorten like a concertina, when pressed against the host. In earlier developmental stages the oral cone is less well developed. Both labrum and labium extend to the apex of the cone and both have marginal membranes contributing to the oral disc (figure 54, plate 4).

(*e*) *Stygiopontius hispidulus*

S. hispidulus lives in association with polychaete worms in deep-sea hydrothermal vent communities (Humes 1987). The oral cone is well developed but labrum and labium are loosely associated (figure 55, plate 4) rather than held tightly together by overlapping ridges. Both labrum and labium contribute to the distal opening of the cone, and both bear a fringe of heavily setose setae (figure 56, plate 4) that form the oral disc. The mandibular stylet passes medially into the gap between labrum and labium and its dentate apex extends to the distal opening of the cone (figure 56). There is no mandibular palp. The labium carries additional dentate structures on its anterior (inner) surface; these structures may function like the strigil of *Lepeophtheirus* in dislodging host epithelial tissues.

(*f*) *Nicorhiza rockallensis*

The feeding mechanism of *Nicorhiza* is highly specialized. The adult female comprises an inflated, heart-shaped prosome and a 4-segmented urosome. The parasite is attached by four root-like processes, which penetrate the isopod host. According to Lincoln & Boxshall (1983) the presence of a pair of stylet-like mandibles between the two anterior and the two posterior processes indicates that the processes are derived from the oral cone. In relatively unmodified members of the family Nicothoidae, as in other siphonostomatoids, the mandibles lie between labrum and labium (Lemercier 1964). In *Nicorhiza* the anterior pair of processes represents the labrum and the posterior pair, the labium. These processes are embedded in the host and function as an absorptive system as well as an attachment mechanism.

(*g*) *Discussion*

The primary role of the oral cone is to transport food from the host or prey up into the oesophagus. Primitively this is achieved by the action of the labral musculature. A feature common to most cyclopiform siphonostomatoids, such as *Hyalopontius* and *Pontoeciella*, is the concentration of the labral muscles in the basal part of the oral cone. These muscles generate powerful suction capable of drawing fluids up into the oesophagus. Comparison between *Hyalopontius*, *Pontoeciella* and *Entomopsyllus* reveals an evolutionary trend towards elongation of the distal part of the oral cone. The increased length of the distal siphon must be correlated with the ability to generate increased suction. The musculature around the basal bulb of *Entomopsyllus* provides a mechanism by which the lumen, with its thin, folded walls, can be greatly dilated to create suction. These suction systems will only work efficiently if the distal opening of the cone is sealed onto the surface of the host, and if the junction between labrum and labium is also tightly sealed. In *Hyalopontius* and *Pontoeciella* the seal around the distal opening is formed by the oral disc. In *Entomopsyllus* the long, tapering siphon is used to penetrate deep inside the host and extract the contents of cells. The host tissues effectively create the seal around the distal opening. The junction between labrum and labium in all these fluid feeding species is formed by a complex system of interlocking ridges and grooves.

In *Lepeophtheirus*, transport of material up the oral cone is achieved by sequential contraction of muscles distributed along the labrum. This mechanism is effective for moving pieces of host epidermal tissue up towards the oesophagus. The membranes at the tip of the labrum and labium form an incomplete border around the distal opening of the cone and would be ineffective at maintaining a seal. Their function is probably to prevent loss of pieces of host tissue detached by action of the strigil. The slit between labrum and labium is also poorly sealed, permitting considerable movement of the mandibular stylets inside the lumen. This type of oral cone is also found in other surface-feeding forms, including the dichelesthiiform families (John & Nair 1974; Kabata 1979) and the Lernaeopodidae (Chandran & Nair 1988).

The ontogenetic data available for *Lernaeocera* reveal that the structure of the oral cone changes between early copepodid and adult. The distal opening is formed by both labrum and labium in the early copepodid stages but the labrum decreases in size during development until it no longer reaches the distal margin of the cone. The broad opening of the cone in the adult is labial in origin. The construction of the adult cone allows it to shorten like a concertina and the entire cone acts as an enlarged oral disc, forming a tight seal when pressed against the host. This efficient seal is typical of other fluid feeders but in *Lernaeocera* the labrum is so reduced that the suction required for feeding must be generated by oesophageal peristalsis.

The most extreme development of the oral cone is found in highly derived nicothoids, such as *Nicorhiza*. The oral cone permanently penetrates the tissues of the crustacean host and forms absorptive rootlets. Nutrient transport is internal, occurring after absorption through the specialized integument of the oral rootlets.

Siphonostomatoids utilize a great variety of host taxa and exhibit a wide range of feeding methods. This diversity is reflected primarily in modifications of the oral cone rather than of the cephalosomic appendages. The antennae, maxillae and maxillipeds are typically raptorial and are responsible for grasping and holding onto the host irrespective of the feeding technique employed. These three pairs of appendages may vary in size and orientation but all retain a basically subchelate construction. The grasping appendages are lost in adult *Nicorhiza*, which is attached by means of the oral rootlets.

The mandibular stylet lies within the lumen of the oral cone. In fluid-feeding species, such as *Hyalopontius* and *Pontoeciella*, the stylet is used to puncture the host. In surface-grazing forms, such as *Lepeophtheirus*, the mandibles assist in detaching pieces of host tissue and drawing them into the oral cone. This type of mandible is characterized by the row of teeth on one side of the stylet near its apex.

The extent to which inner lobe of the maxillule is functionally involved with the oral cone differs. In the Nicothoidae, *Lernaeocera*, *Lepeophtheirus* and the Dirivultidae it lies to the side of the oral cone and is entirely separate from it. In *Asterocheres* the inner lobe is closely adpressed to the side of the oral cone and has a longitudinal groove medially (figure 37) that ensures a close fit to the mandibular stylet. In *Hyalopontius* and *Entomopsyllus* the apical setae of the inner lobe pass into the oral cone via the slits between labrum and labium (cf. figures 36 and 44) and lie in lateral maxillulary channels within the oral cone but separate from its lumen (figure 47).

In the former genus the maxillulary seta emerge from the oral cone at the base of the oral disc and have a sensory function. In *Entomopsyllus* a maxillulary seta extends to the distal opening of the siphon and may be involved in feeding, having taken over the role of puncturing the host that is typically performed by the mandibular stylet, as in *Hyalopontius*. Unlike a true mandibular stylet, this maxillulary stylet never enters the central lumen of the oral siphon.

7. Swimming legs

The skeletomusculature of the swimming legs of *Hyalopontius* is similar to that of *Benthomisophria* and *Euaugaptilus* (Boxshall 1982, 1985) and will not be described here. *Lepeophtheirus* has a modified morphology, adapted to an ectoparasitic habit. The swimming legs and locomotory mechanism enable adult *Lepeophtheirus* to move freely over the surface of the host without becoming detached (Kabata & Hewitt 1971).

The musculature of the first three pairs of swimming legs is shown in dorsal view in figure 23. The members of each leg pair are joined by intercoxal sclerites (often called interpodal bars) as in other copepods. The presence of intercoxal sclerites determines that the primary movement of these legs is a promotor–remotor swing. The extrinsic muscles of the first leg can be divided into two groups, promotors and remotors, both of which originate on the dorsal cephalothoracic shield anterior to the limb foramen. There are eight promotors (thp1. prm. 1–8) inserting anteriorly and anterolaterally along the rim of the coxa. They are opposed by three remotors (thp1. rem. 1–3) inserting posteriorly on the coxal rim. A fourth remotor (thp1. rem. 4) inserts on the ventral cephalothoracic wall midway between the foramina of legs 1 and 2. This muscle may act as a dorsoventral tensor and be involved in generating cephalothoracic suction (see §8*c*).

The extrinsic muscles of the second and third legs all originate dorsally on the double somite that makes up the posterior part of the cephalothoracic shield. There are four promotors (thp2, prm. 1–4) inserting anteriorly on the coxal rim of the second leg. There are eleven remotors. Of these, three (thp2. rem. 1–3) insert posteromedially and four (thp2. rem. 4–7) posterolaterally on the coxal rim. Two large muscles (thp2. rem. 8–9) insert just posterior to the basal foramen of the limb, on a process that extends anteriorly over the foramen. These muscles probably act as remotors via the apodeme and may also raise the ventral wall of the cephalothorax. The larger of these muscles (thp2. rem. 8) follows a sinuous course, passing from its origin medial to that of remotor 9 to its insertion, which lies lateral to that of remotor 9. Two other remotors (thp2. rem. 10–11) insert midway between the foramina of legs 2 and 3. They may function as tensors in a similar manner to thp1. rem. 4. A powerful muscle (sin. m.) extends between the posterolateral corner of the coxa of the second leg and the apex of the posterior sinus. Contraction of this muscle probably serves to close down the posterior sinus.

The third leg has three promotors (thp3. prm. 1–3) inserting anterolaterally on the coxal rim. These are opposed by three remotors, one (thp3. rem. 3) inserting posteromedially and the others (thp3. rem. 1–2) posterolaterally on a broad process that extends over the foramen.

The swimming mechanism of adult caligids was studied by Kabata & Hewitt (1971). Rapid swimming is produced by the antagonistic beating of the first and second legs. The present work supplements their study in describing the musculature responsible for the promotor–remotor swing of the legs. The powerful musculature of the second leg supports their view that it is the most important locomotory appendage. The membranous flap closing the posterior cephalothoracic sinus was identified by Kabata & Hewitt (1971) as a one-way valve. The powerful muscle extending to the sinus suggests that it is actively, rather than passively, closed during the recovery (promotor) stroke of the second legs. This prevents water from being sucked in through the sinus into the space behind the second legs and allows the first legs to force water backwards, beneath the second legs, into that space. Closure of the posterior sinus must be coordinated with leg movements, particularly those of the second legs. The origin of the sinus muscle on the rim of the second leg suggests that it represents a modified promotor of the second leg, and may share a common nervous control with the other promotors.

The third legs have promotor and remotor muscles but do not appear to be involved in locomotion, at least when the copepod is on its host. According to Kabata & Hewitt (1971) the third legs play an important role in attachment to the host. They can raise the cephalothorax slightly by pushing down onto the host's surface. This enlarges the space beneath the cephalothorax and enhances the suction holding the parasite to the host.

8. Musculature patterns

(*a*) *Trunk musculature*

The trunk musculature of *Hyalopontius* is reduced compared with that of free-swimming copepods such as calanoids and misophrioids (Boxshall 1982, 1985). In calanoids the well-developed trunk musculature is associated with body flexion during swimming (Perryman 1961). The reduced musculature is correlated with the reduced amount of swimming in *Hyalopontius*, which spends part of its time temporarily attached to the prey (see §5*a*). The trunk musculature of *Lepeophtheirus* is further reduced in comparison with that of *Hyalopontius*. This reduction is correlated with a restricted swimming ability.

(*b*) *Appendage musculature*

The musculature of the cephalosomic appendages is reduced in siphonostomatoids compared with that of a predatory calanoid such as *Euaugaptilus* (Boxshall 1985). The reduction is mainly in the mandibles and maxillules, which increasingly lose any abduction–adduction movement. The mandibular palp is reduced or absent, and the gnathobase has a restricted range of movements. In *Hyalopontius* some adduction of the mandible is possible and the limb retains extrinsic adductor muscles originating on the anterior ventral cephalic tendon. In *Lepeophtheirus* the mandible is capable of only limited protraction–retraction movements within the oral cone, and there are no ventral extrinsic muscles. The maxillule also has restricted movement, and in *Hyalopontius* is primarily a sensory appendage. It has no ventral muscles, few dorsal extrinsic muscles and a single intrinsic muscle. In contrast, the extrinsic musculature of the antennae and maxillipeds is well developed. These subchelate limbs are raptorial and are used to catch and manipulate prey in *Hyalopontius*, and to attach to the host in *Lepeophtheirus*. The maxillae are also subchelate in *Hyalopontius*. All three limbs flex the distal part relative to the proximal in one plane only, and the intrinsic musculature is correspondingly simplified. The extrinsic musculature of the long antennules of *Hyalopontius* is similar to that of free-living copepods such as *Benthomisophria* (Boxshall 1982). The two-segmented antennules of *Lepeophtheirus* have reduced musculature, lacking the long levator muscles that originate in the maxillary somite of *Hyalopontius*.

The reduction in importance of the ventral cephalic tendon system is obvious in siphonostomatoids. In all genera studied only the anterior tendon remains; it serves as an origin for extrinsic limb muscles only in *Hyalopontius*. The ventral musculature is generally reduced and the enlarged postmaxillulary apodemes are the site of origin of the remaining extrinsic muscles.

(*c*) *Cephalothoracic suction*

The evolution of a flattened body has resulted in modification of the musculature of *Lepeophtheirus*. Dorsal and ventral body surfaces are separated by a small distance and most extrinsic muscles are shorter than in untransformed body types. The lateral areas of the cephalothoracic shield appear to be cephalic in origin, as they contain extrinsic muscles only from the mandibles and maxillae, not from the maxillipeds or swimming legs. The posterolateral areas of the shield also contain large numbers of fine muscle fibres passing vertically between dorsal and ventral surfaces. These presumably function as tensors, helping to maintain the shape of the shield.

It has long been known that the cephalothorax of caligids forms an effective sucking cup provided with a strip of marginal membrane around its rim. The mechanism by which suction is produced is poorly understood, although Kabata & Hewitt (1971) suggested that the third legs were involved. There are several muscles within the cephalothorax that insert ventrally in positions remote from the base of any appendage. These are shown in figure 23 and are referred to as dorsoventral muscles (dv. 1–7). They appear to be extrinsic limb muscles, the insertions of which have migrated onto the ventral cephalothoracic wall. Together with the large remotors (thp1. rem. 4 and thp2. rem. 10–11) that insert on the ventral wall of the cephalothorax remote from the foramina of the legs these muscles presumably raise the ventral wall of the cephalothorax and increase the suction between parasite and host. The mechanism by which the shift in insertion sites of these muscles occurred is of interest, as this is a rare phenomenon in copepods. It is probable that the dorsoventral muscles and the large remotors originally inserted on a separate praecoxal segment, which has since become incorporated into the ventral cephalothoracic wall.

I am very grateful to Geoffrey Fryer, F.R.S., for his detailed comments on the manuscript; to D. W. Cooper for preparing serial sections for light microscopy; and to Alan Warren, Don Claugher and the staff of the Electron Microscopy unit for assistance with scanning electron microscopy. Thanks are also due to Arthur G. Humes (Boston University) for sending me the *Stygiopontius hispidulus*, to Howard Roe (Institute of Oceanographic Sciences) for arranging the original donation of the *Hyalopontius* and *Pontoeciella*, to Greg Deets (University of California, Long Beach) for sending the *Bariaka*, and to Klaus Ruetzler (Smithsonian Institution) for identifying the sponge from Belize. The *Asterocheres* from Belize was collected under the auspices of the Caribbean Coral Reef Ecosystems (CCRE) Program, Smithsonian Institution.

REFERENCES

Boxshall, G. A. 1974 The population dynamics of *Lepeophtheirus pectoralis* (Müller, 1776): seasonal variation in abundance and age structure. *Parasitology* **69**, 361–371.

Boxshall, G. A. 1976 The histopathology of infection by *Lepeophtheirus pectoralis* (Müller, 1776) (Copepoda: Caligidae). *J. Fish. Biol.* **10**, 411–415.

Boxshall, G. A. 1979 The planktonic copepods of the northeastern Atlantic Ocean: Harpacticoida, Siphonostomatoida and Mormonilloida. *Bull. Br. Mus. nat. Hist.* D **35**, 201–264.

Boxshall, G. A. 1982 On the anatomy of the misophrioid copepods, with special reference to *Benthomisophria palliata* Sars. *Phil. Trans. R. Soc. Lond.* B **297**, 125–181.

Boxshall, G. A. 1985 The comparative anatomy of two copepods, a predatory calanoid and a particle-feeding mormonilloid. *Phil. Trans. R. Soc. Lond.* B **311**, 303–377.

Boxshall, G. A. 1985 The comparative anatomy of two copepods, a predatory calanoid and a particle-feeding copepods. *Syllogeus* **58**, 158–169.

Chandran, A. & Nair, N. B. 1988 Functional morphology of the mouth tube of a lernaeopodid *Pseudocharopinus narcinae* (Pillai, 1962) (Copepoda: Siphonostomatoida). *Hydrobiologia* **167/168**, 629–634.

Cressey, R. F. 1966 *Bariaka alopiae* n.gen., n.sp. (Copepoda: Caligoida), a parasite on the gills of a thresher shark. *Bull. mar. Sci.* **16**, 324–329.

Deets, G. & Ho, J.-S. 1988 Phylogenetic analysis of the Eudactylinidae (Crustacea: Copepoda: Siphonostomatoida), with descriptions of two new genera. *Proc. biol. Soc. Wash.* **101**, 317–339.

Ferris, G. F. & Henry, J. M. 1949 The nervous system and a problem of homology in certain Crustacea (Crustacea: Copepoda: Caligidae). *Microentomology* **14**, 114–120.

Fox, H. M. 1952 Anal and oral water intake by Crustacea. *J. exp. Biol.* **169**, 1051.

Fryer, G. 1970 Defaecation in some macrothricid and chydorid cladocerans, and some problems of water intake and digestion in the Anomopoda. *Zool. J. Linn. Soc.* **49**, 255–270.

Giesbrecht, W. 1899 Die Asterocheriden des Golfes von Neapel und der angrenzenden Meeresabschnitte. *Fauna Flora Golf. Neapel* **25**, 1–217.

Heegaard, P. 1947 Contribution to the phylogeny of the arthropods. *Spolia zool. Mus. haun.* **8**, 1–229.

Heegaard, P. 1955 Parasitic copepods from tropical West Africa. *Atlantide Rep.* **3**, 41–56.

Heegaard, P. 1962 Parasitic Copepoda from Australian waters. *Rec. Aust. Mus.* **25**, 149–233.

Heptner, M. V. 1968 Description and functional morphology of *Megapontius pleurospinosus* sp.n. from the Pacific with some remarks on the status of the genus *Megapontius* within the system of families of the Siphonostoma group (Copepoda, Cyclopoida). *Zool. Zh.* **11**, 1628–1638.

Ho, J.-S. 1984 Copepoda associated with sponges, cnidarians, and tunicates of the Sea of Japan. *Rep. Sado mar. Biol. Stat., Niigata Univ.* **14**, 23–61.

Humes, A. G. 1987 Copepoda from deep-sea hydrothermal vents. *Bull. mar. Sci.* **41**, 645–788.

John, S. E. & Nair, N. B. 1974 Functional morphology of the mouth tube of *Hermilius longicornis* Bassett-Smith, a parasitic copepod on *Ariodes dussumieri* Valenciennes. *Monit. zool. Ital.* **8**, 133–140.

Kabata, Z. 1962 The mouth and mouth-parts of *Lernaeocera branchialis* (L.), a parasitic copepod. *Crustaceana* **1**, 342–352.

Kabata, Z. 1974 Mouth and mode of feeding of Caligidae (Copepoda), parasites of fishes, as determined by light and scanning electron microscopy. *J. Fish. Res. Bd Can.* **31**, 1583–1588.

Kabata, Z. 1979 *Parasitic Copepoda of British fishes.* London: Ray Society.

Kabata, Z. & Hewitt, G. C. 1971 Locomotory mechanisms in Caligidae (Crustacea: Copepoda). *J. Fish. Res. Bd Can.* **28**, 1143–1151.

Lang, K. 1951 On the nature of the so-called sternal furca in the Caligidae. *Arkiv zool.* **1**, 499–502.

Lemercier, A. 1964 Comparaison du complexe buccal de trois copépodes parasites: *Sphaeronella* sp., *Choniosphaera maenadis* (Bloch & Gallien) (Choniostomatidae) et *Nicothoe astaci* Audouin et Milne-Edwards. *Bull. Soc. Linn. Normandie* **4**, 119–139.

Lewis, A. G. 1966 The sternal furca of caligoid copepods. *Crustaceana* **10**, 7–14.

Lincoln, R. J. & Boxshall, G. A. 1983 Deep-sea asellote isopods of the N.E. Atlantic: the family Dendrotionidae and some new ectoparasitic copepods. *Zool. J. Linn. Soc.* **79**, 297–318.

Perryman, J. C. 1961 The functional morphology of the skeletomusculature system of the larval and adult stages of the copepod *Calanus*, together with an account of the changes undergone by this system during larval development. Ph.D. thesis, University of London.

Scott, A. 1901 *Lepeophtheirus and Lernaea.* L.M.B.C. Memoirs on Typical British Marine Plants and Animals, vol. 6, pp. 1–54.

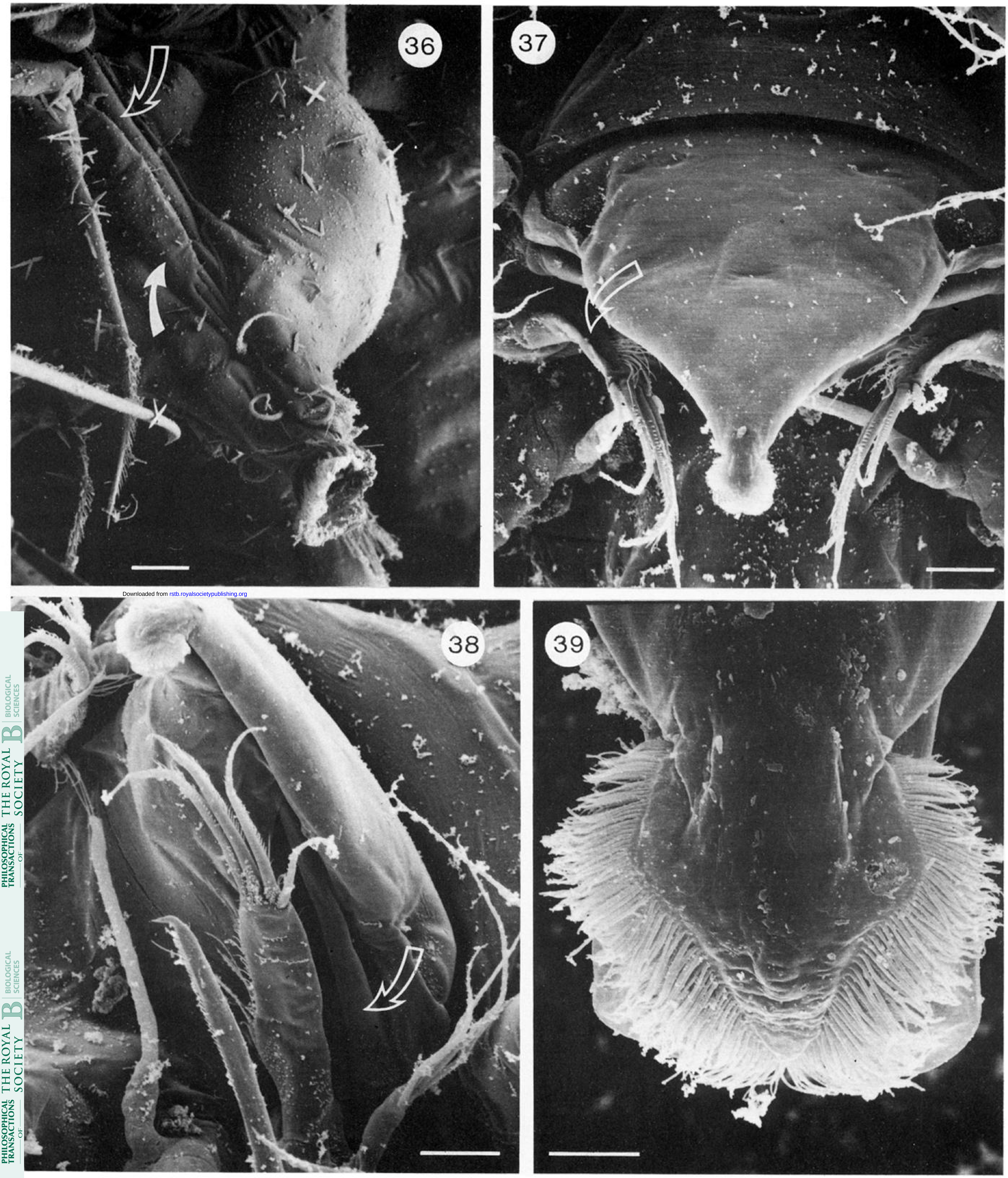
Steedman, H. F. 1974 Laboratory methods in the study of marine zooplankton. *J. Cons. perm. int. Explor. Mer.* **35**, 351–358.

ABBREVIATIONS USED IN FIGURES

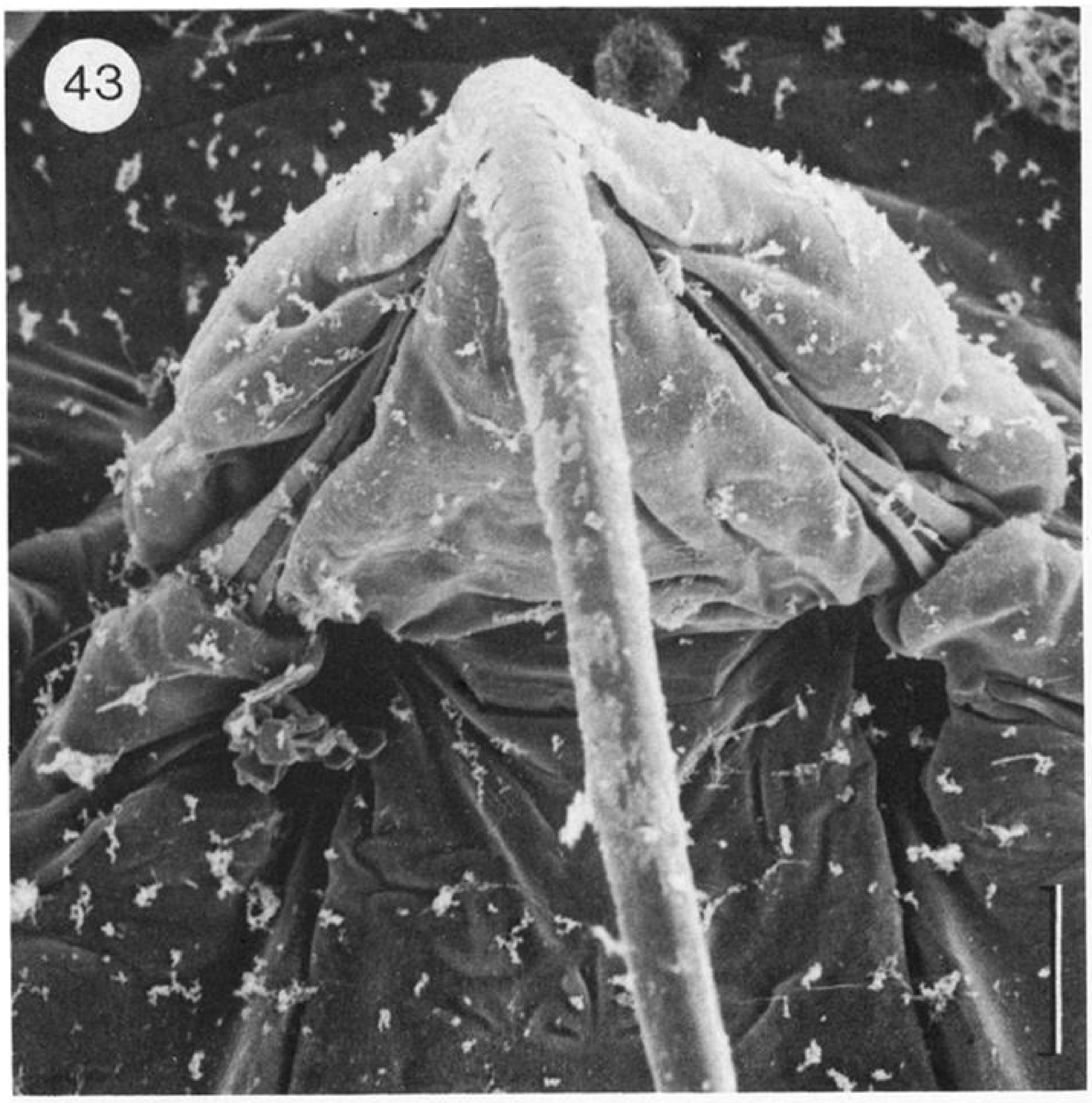
ab.s.	abdominal somite	ant.	antenna, antennary
abd.	abductor muscle	ap.	apodeme
add.	adductor muscle	apo.	apophysis
alb.	allobasis	arth.	arthrodial membrane
a.m.c.	anterior midgut caecum	at.	anterior
an.	anus	atl.	antennule, antennulary

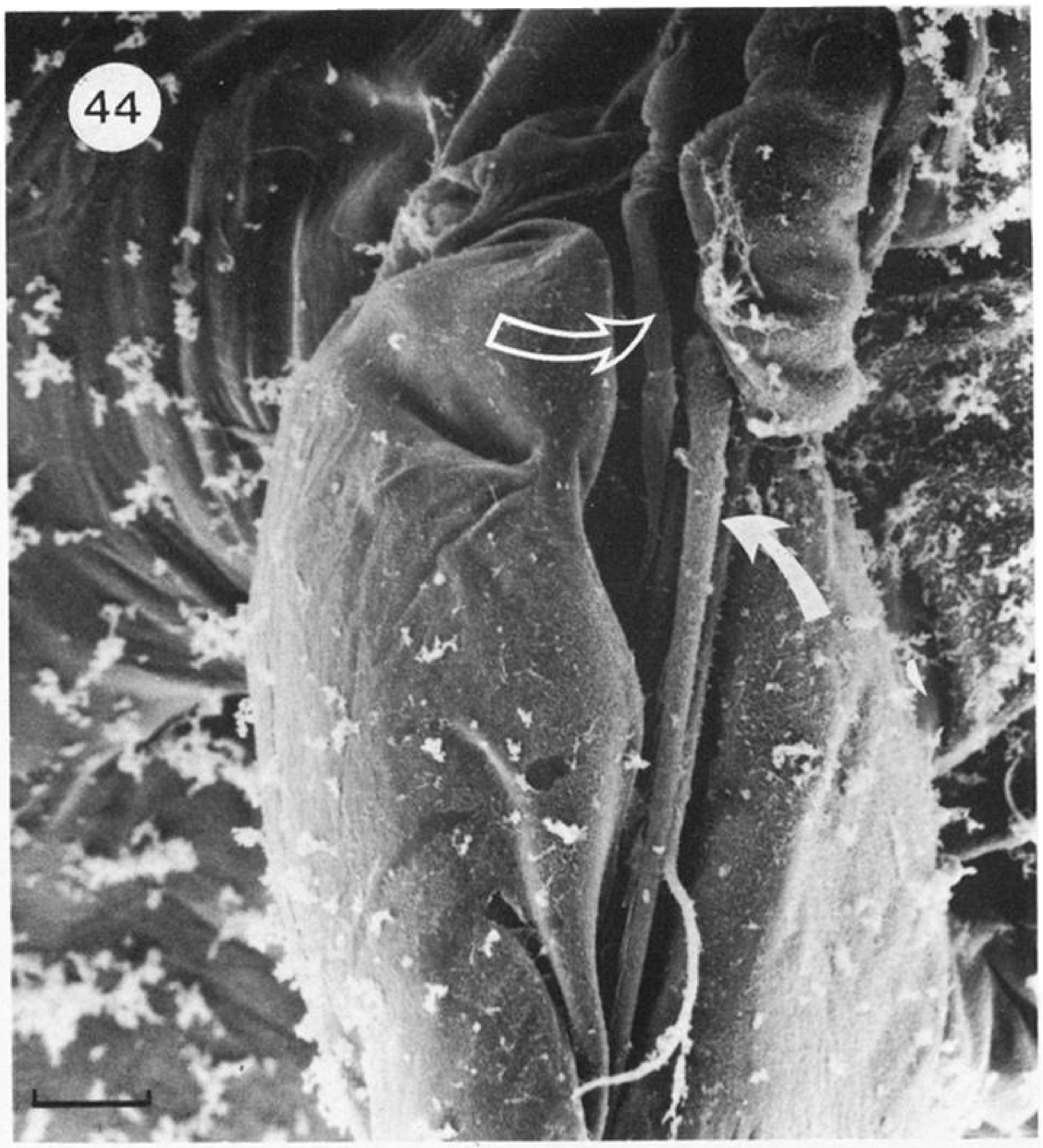
att.	attachment
a.v.c.t.	anterior ventral cephalic tendon
ba.	basis
bu.	buccal
bul.	internal bulb of oral cone
cb.	cerebrum
ce.	cephalosome, cephalosomic
circ.	circular
con.	condyle
cox.	coxa
c.r.	caudal ramus
c.t.	connective tissue
dep.	depressor muscle
dil.	dilator muscle
d.l.m.	dorsal longitudinal trunk muscle
d.m.l.m.	dorsomedian longitudinal trunk muscle
dv.	dorsoventral muscle
ed.	endite
end.	endopod
exp.	exopod
ext.	extensor muscle
fl.	flexor muscle
for.	foramen
gen.s.	genital somite
gn.	gnathobase
h.f.	hyaline frill
h.g.	hindgut
i.c.s.	intercoxal sclerite
i.g.b.m.	intragnathobasic muscle
ind.	indirect
ins.	insertion
i.s.b.	intersomitic boundary
lab.	labrum, labral
lam.	labium, labial
lat.	lateral
lev.	levator muscle
l.c.	lateral midgut caecum
lum.	lumen
m.	muscle
m.g.	midgut
mnd.	mandible, mandibular
mx.	maxilla, maxillary
mxl.	maxillule, maxillulary
mxp.	maxilliped, maxillipedal
o.d.	oral disc
oe.	oesophagus, oesophageal
op.	opening of oral cone
p.	palp
pd.s.	pedigerous somite
ped.	pedestal
pi.	pivot
pmnd.	postmandibular
pmx.	postmaxillary
pmxl.	postmaxillulary
pmxp.	postmaxillipedal
post.	posterior
prm.	promotor muscle
pro.	protractor muscle
rem.	remotor muscle
ret.	retractor muscle
s.f.	sternal furca
si.	siphon
sin.	sinus
sphn.	sphincter
str.	strigil
sty.	stylet
sub.g.	suboesophageal ganglion
susp.	suspensory
sync.	syncoxa
t.	tendon
thp.	thoracopod (swimming leg)
ti.	tine
urs.	urosome, urosomal
v.b.w.	ventral body wall
v.l.m.	ventral longitudinal trunk muscle

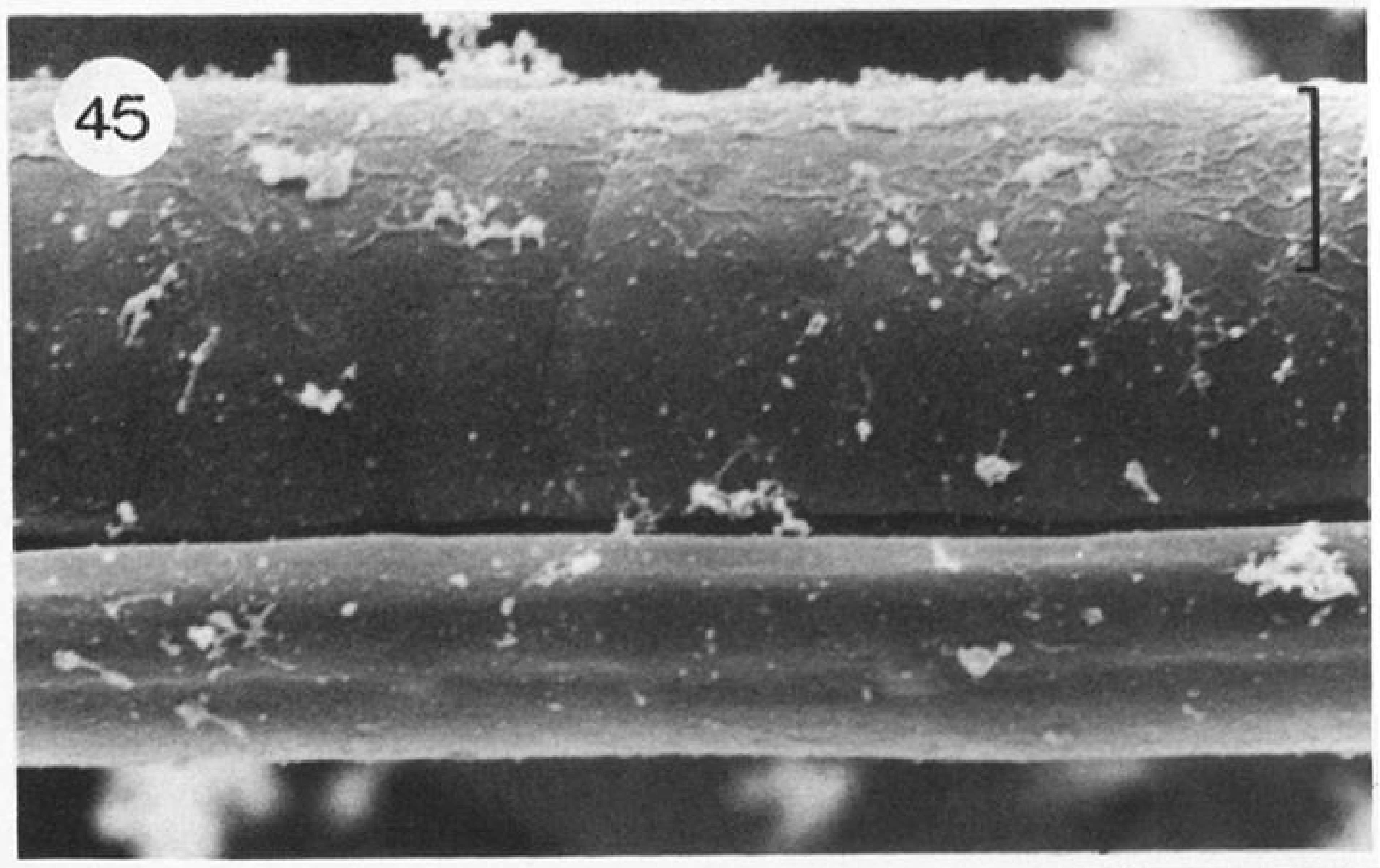
BIOLOGICAL SCIENCES B THE ROYAL SOCIETY PHILOSOPHICAL TRANSACTIONS OF

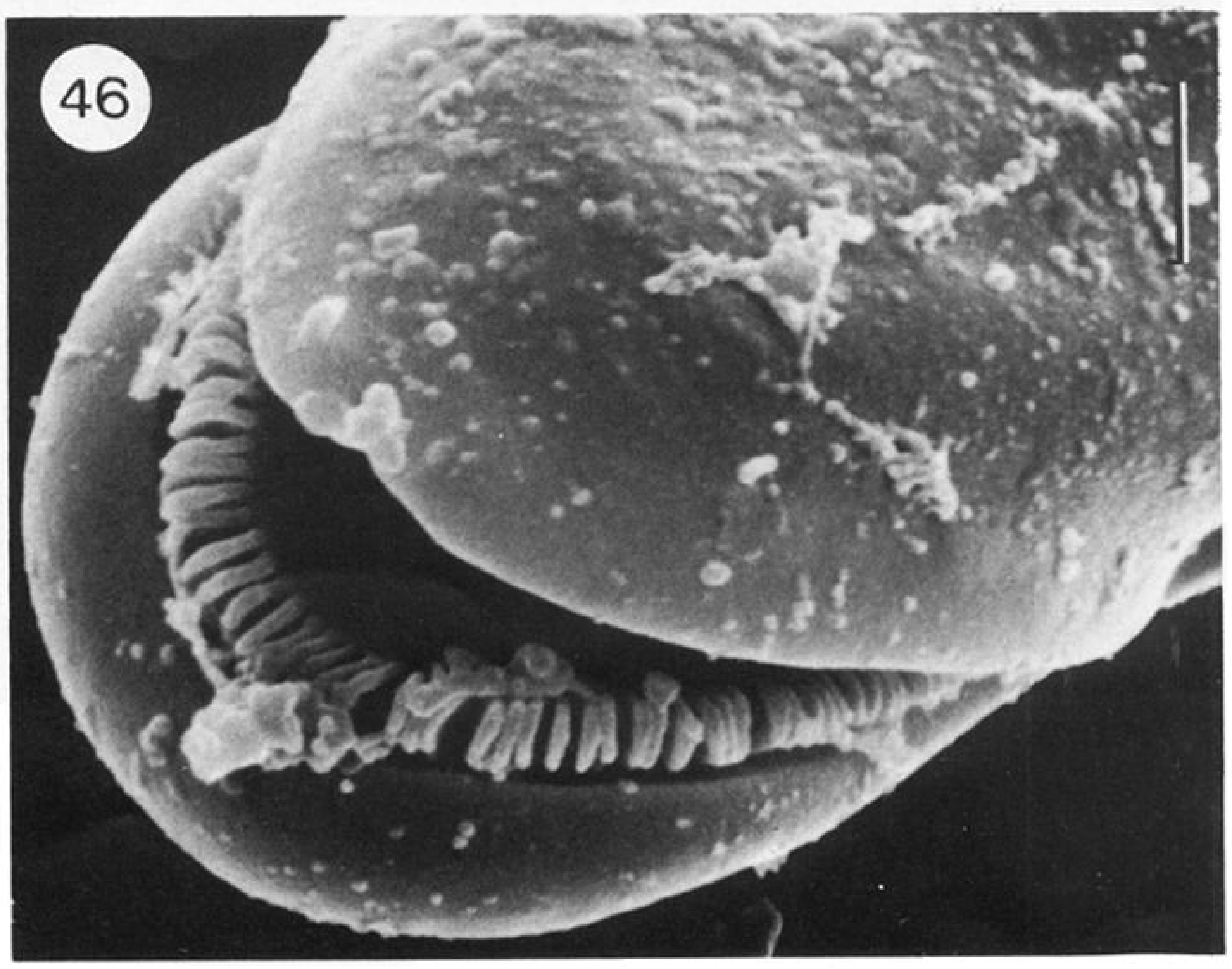


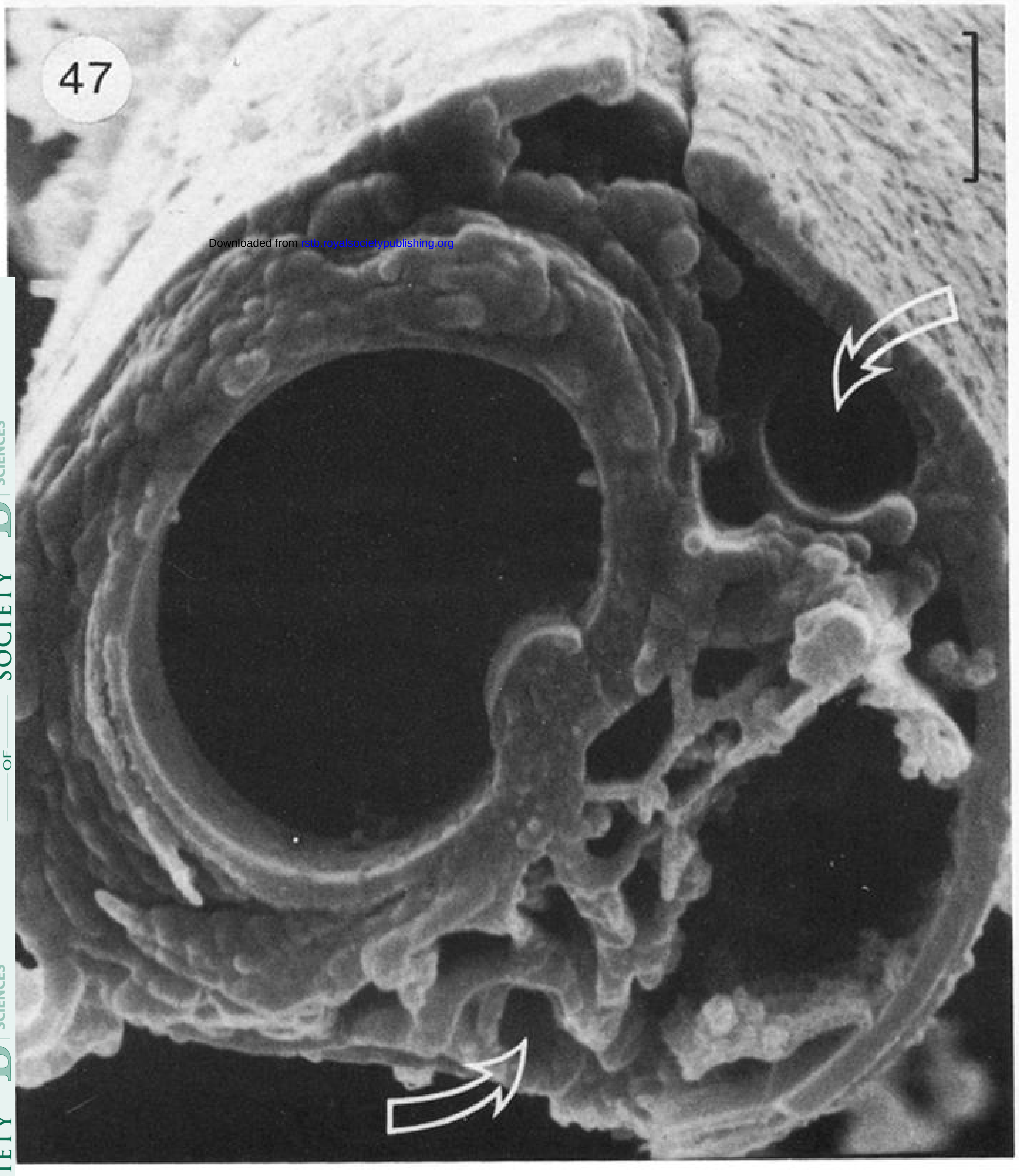
FIGURES 36–39. For description see opposite.



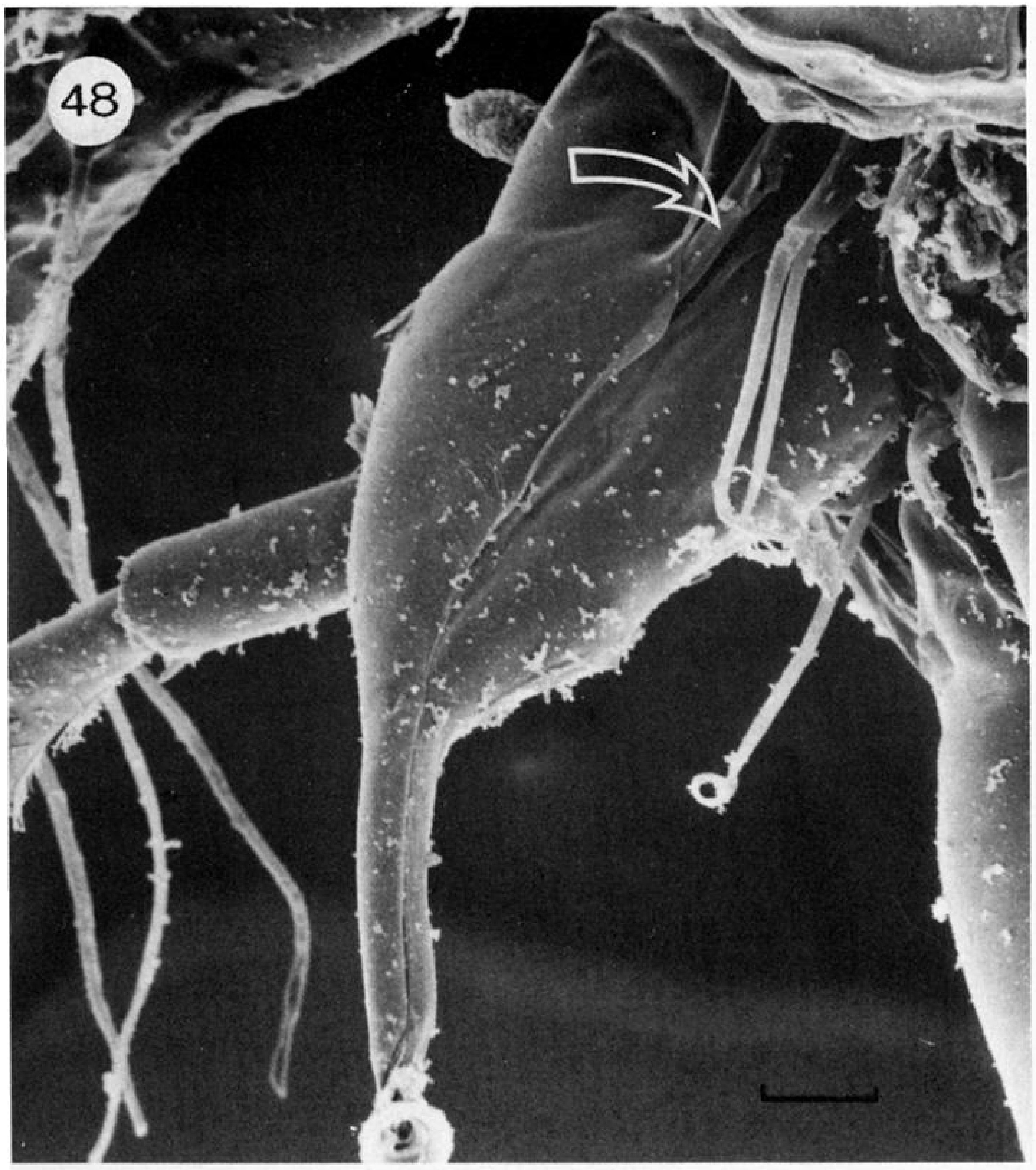


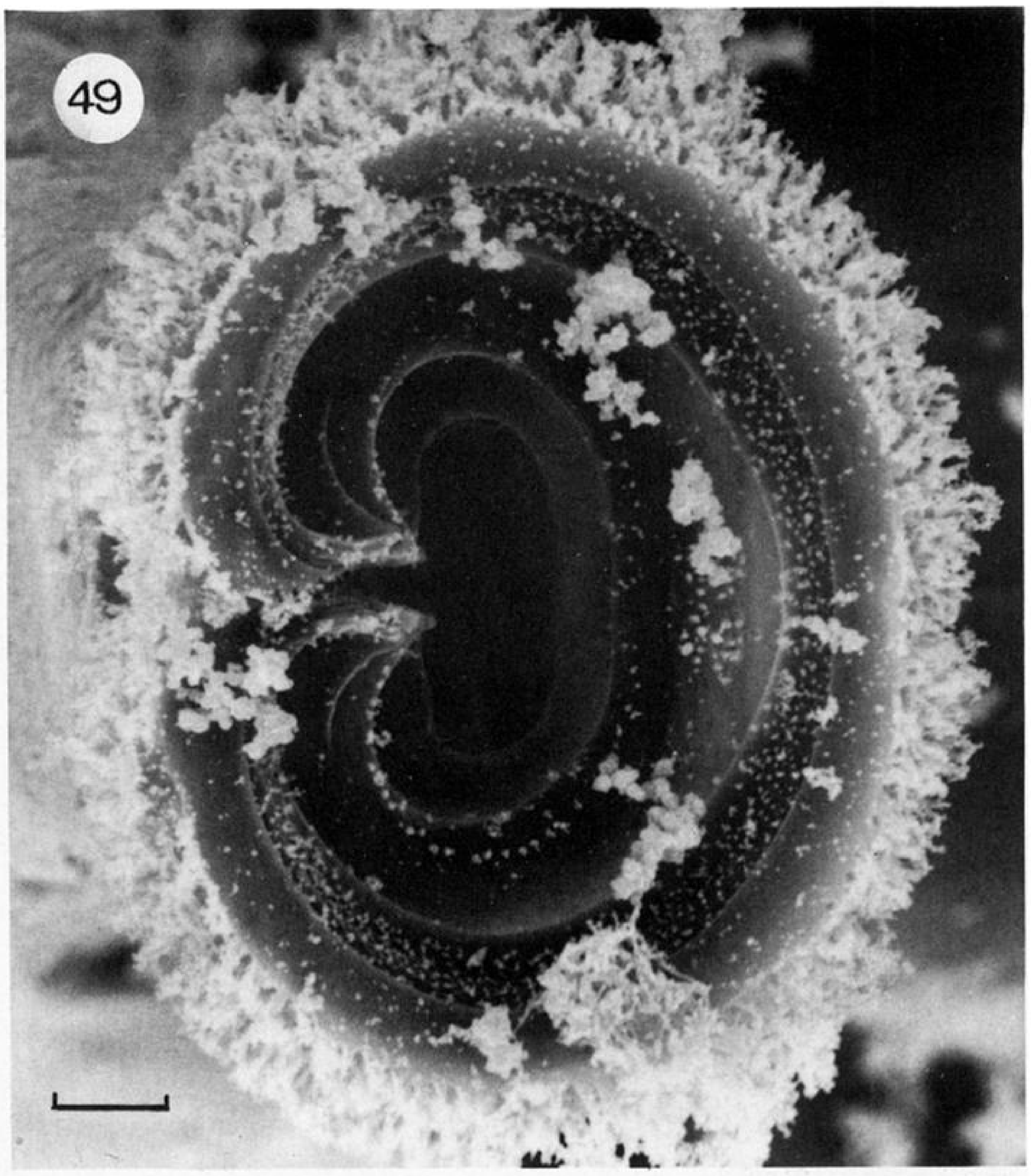


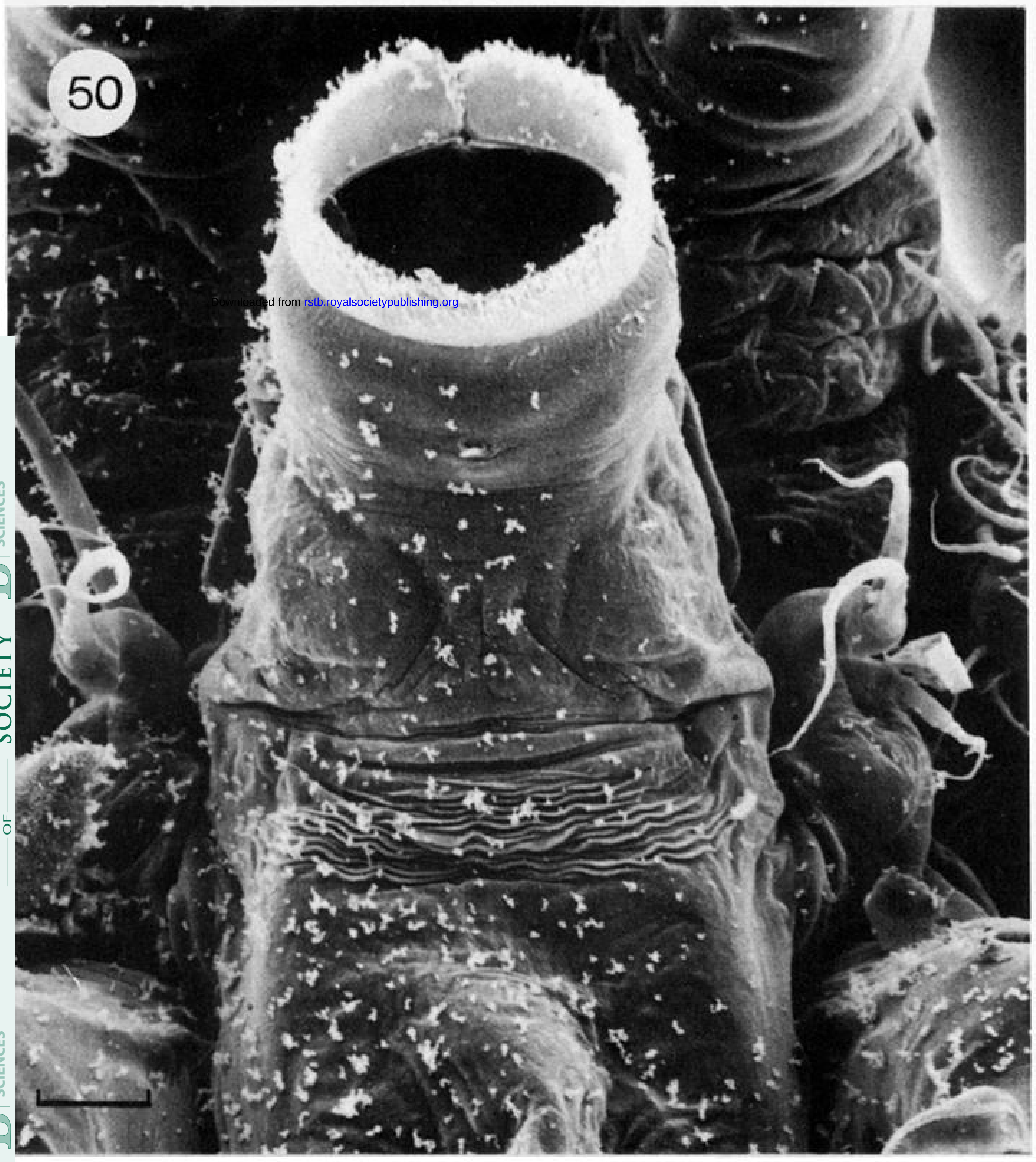




FIGURES 43–47. For description see p. 204.







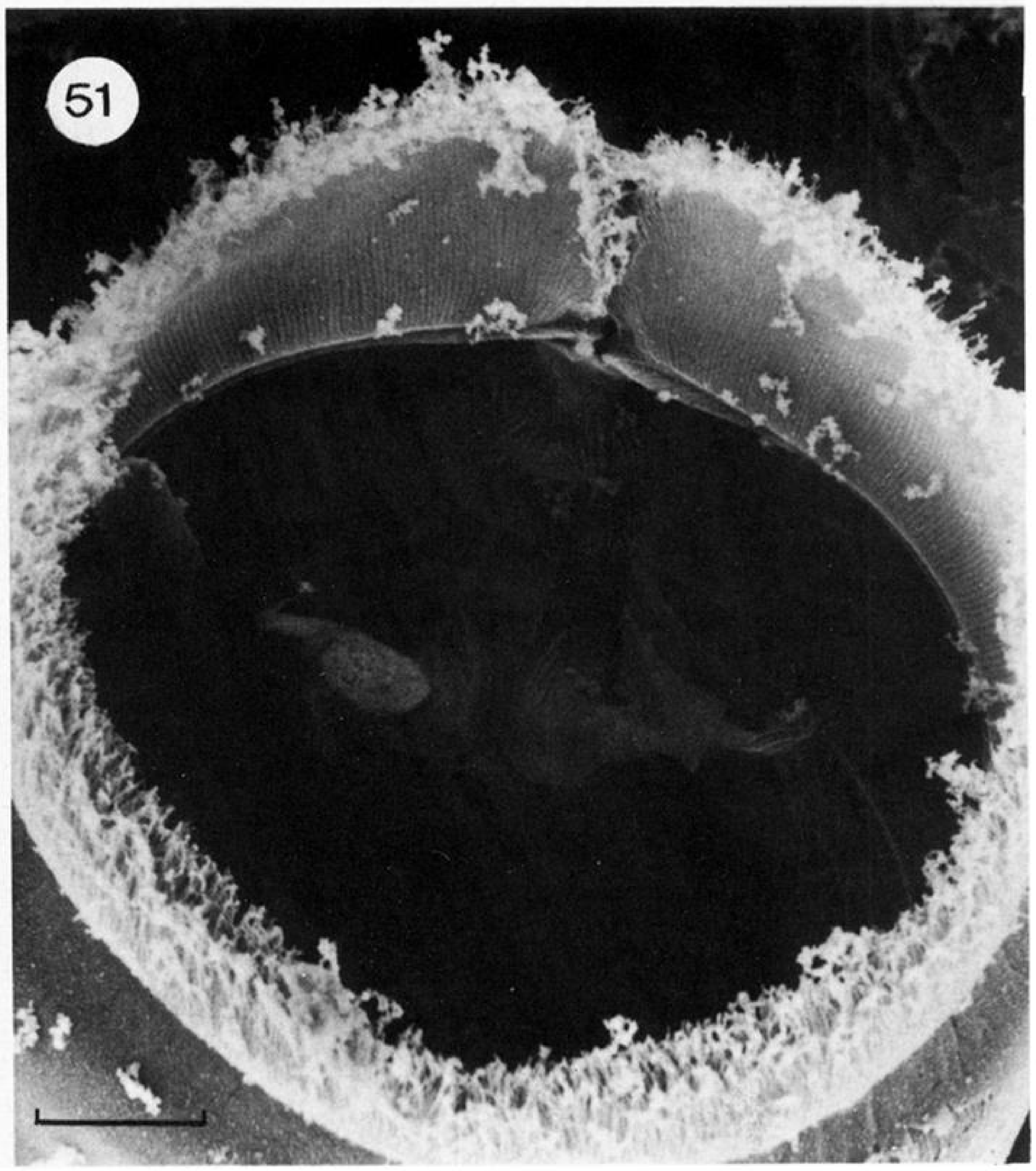
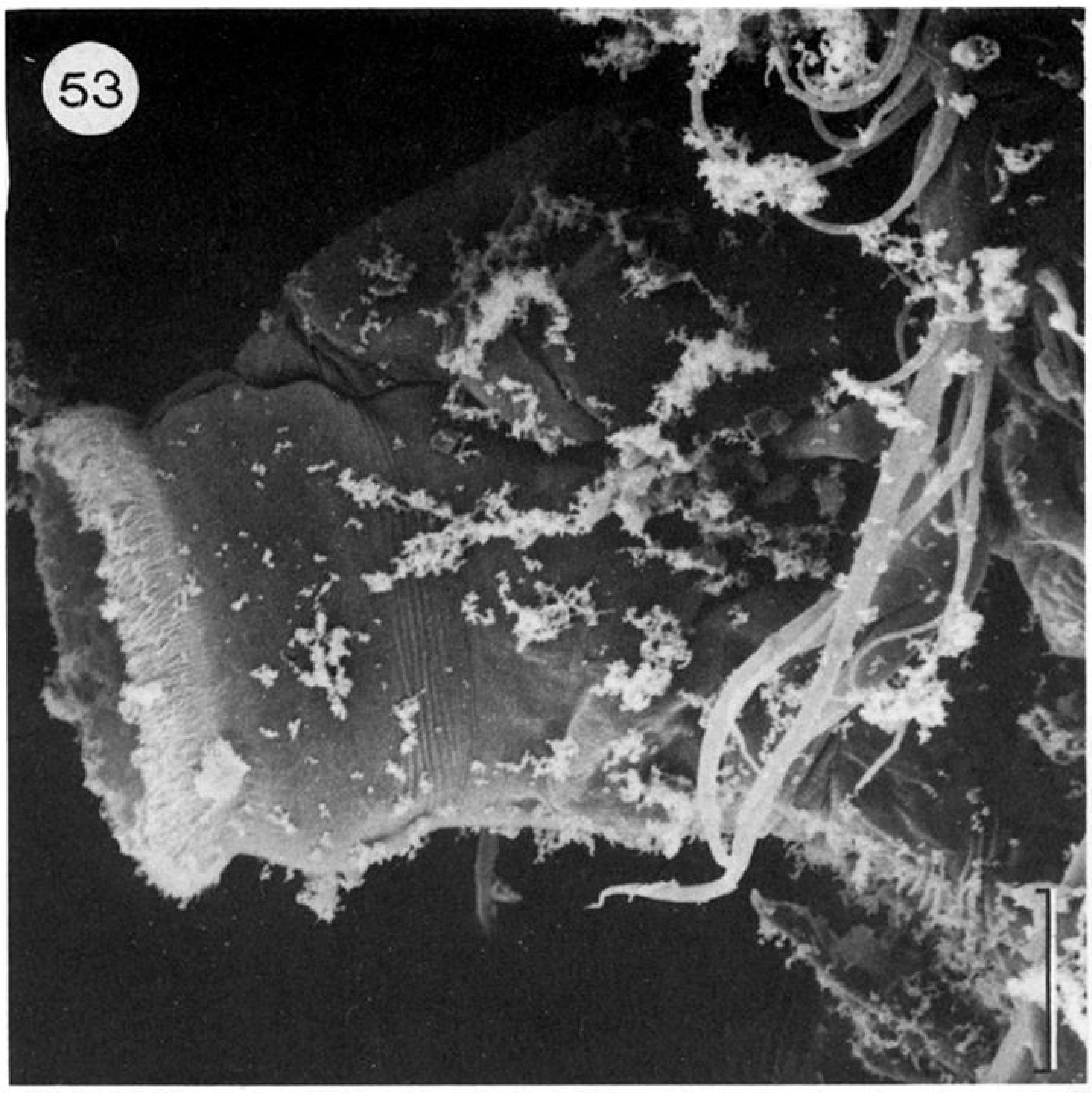


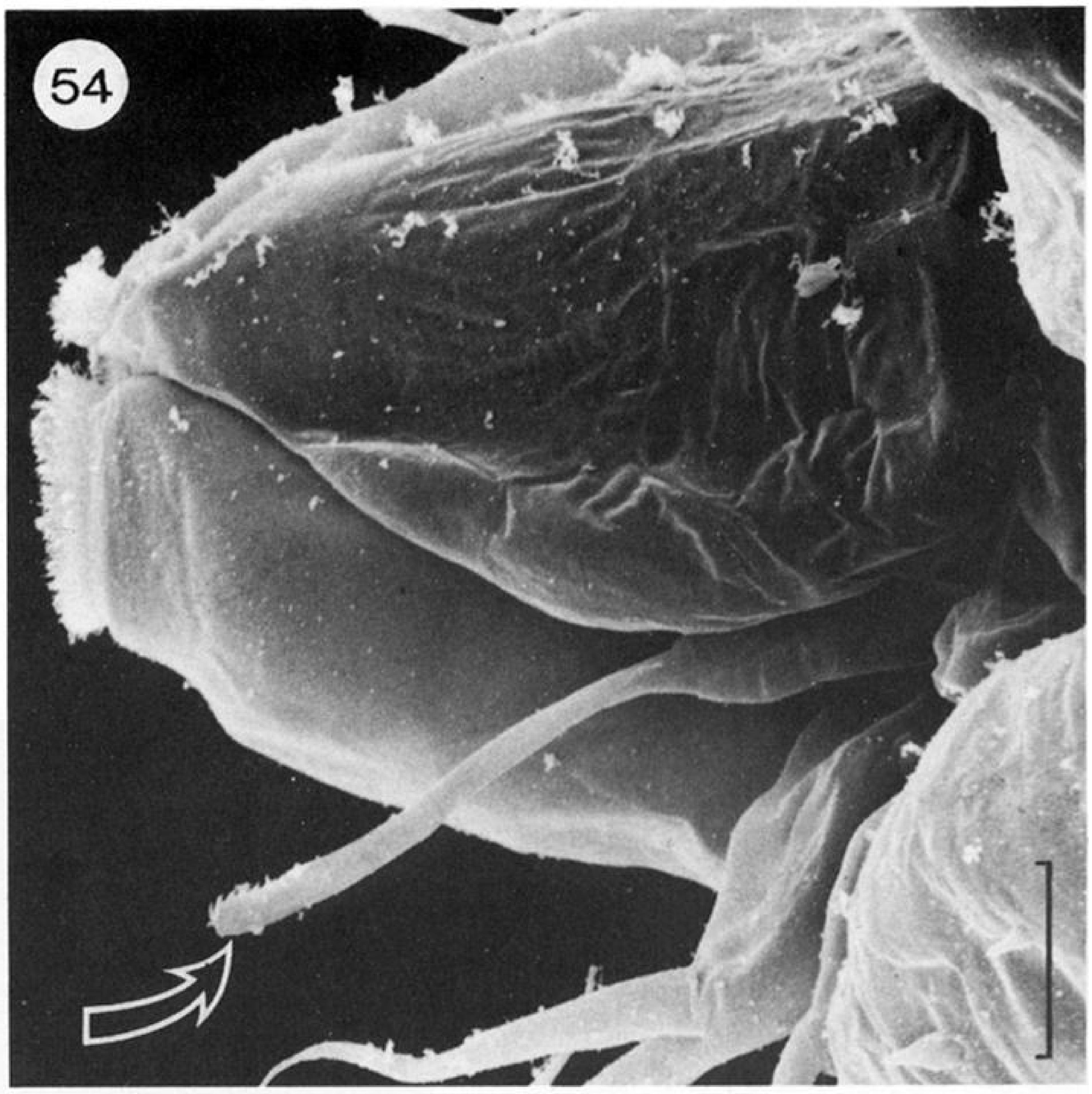
FIGURE 48. Lateral view of oral cone of female *Pontoeciella*, showing mandibular stylet (arrowed) entering slit between labrum and labium, and inner lobe of maxillule. Scale bar, 20 μm.

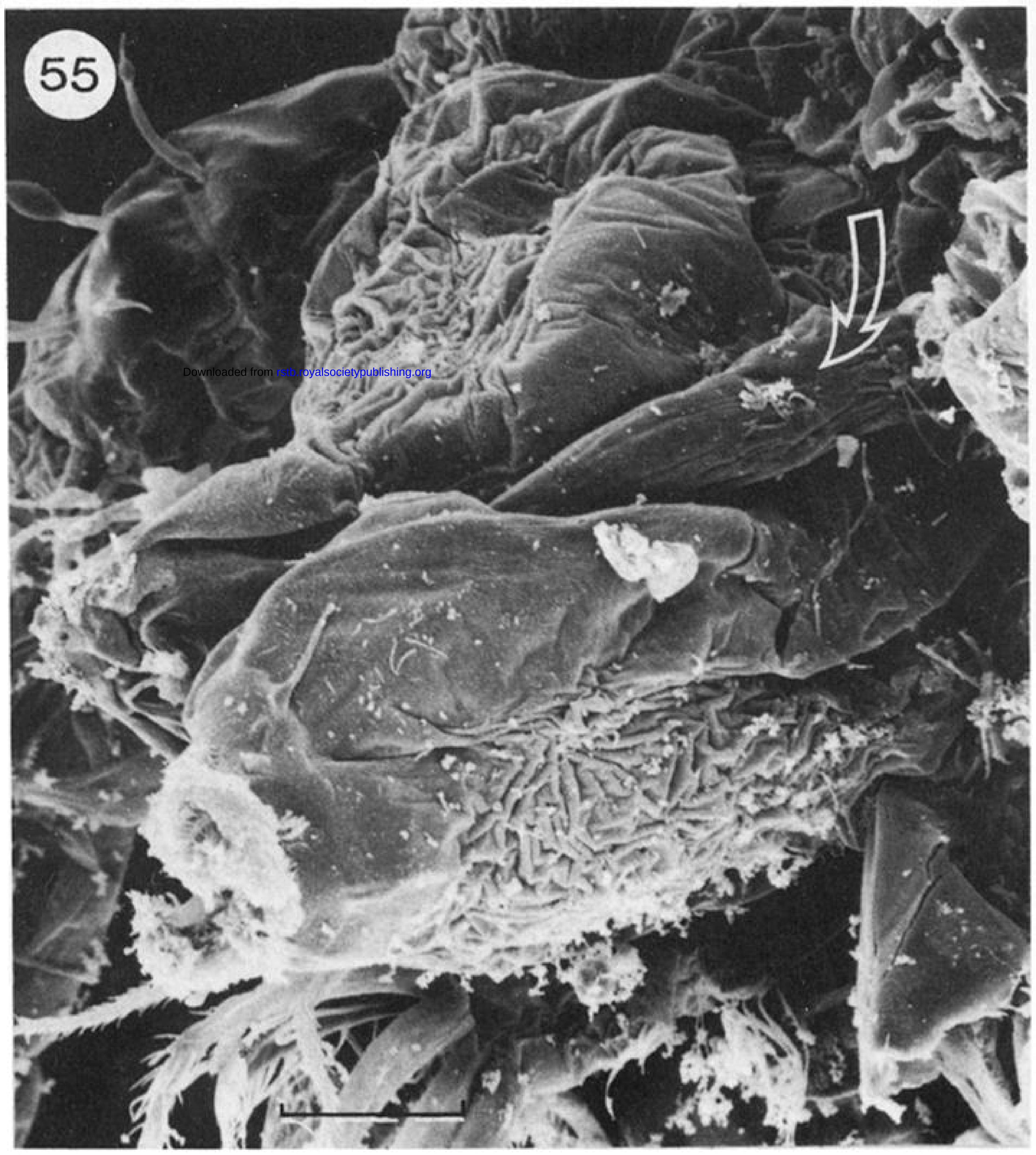
FIGURE 49. Oral disc at apex of oral cone of *Pontoeciella*. Scale bar, 2 μm.

FIGURE 50. Posterior view of oral cone of premetamorphic adult female of *Lernaeocera*, showing large opening. Scale bar, 20 μm.

FIGURE 51. View into distal opening of oral cone of *Lernaeocera*, showing buccal stylets on internal wall of labrum. Scale bar, 10 μm.







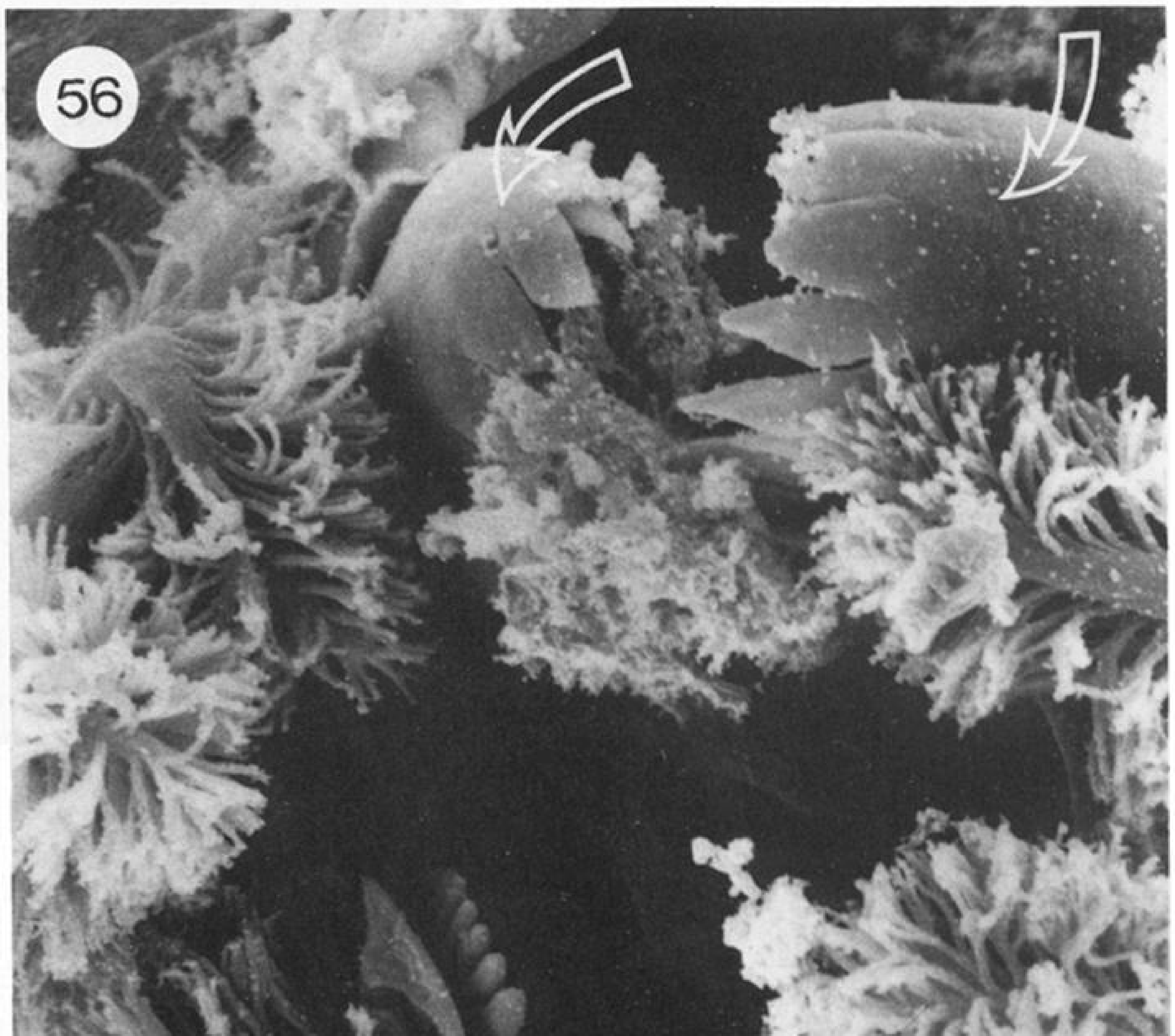


Figure 53. Lateral view of oral cone of premetamorphic adult female of *Lernaeocera*, showing short labrum and oral disc present on labium only. Scale bar, 25 μm.

Figure 54. Lateral view of oral cone of early copepodid stage of *Lernaeocera*, showing labrum and labium of equal length, each bearing part of oral disc. Mandibular stylet (arrowed) displaced out of oral cone. Scale bar, 20 μm.

Figure 55. Lateral view of oral cone of *Stygiopontius*, showing mandibular stylet (arrowed) entering large gap between labrum and labium. Scale bar, 20 μm.

Figure 56. Apical view of oral cone of *Stygiopontius*, showing setose setae forming labial section of oral disc, and dentate apices of mandibular stylets (arrowed). Scale bar, 2 μm.