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THE LIFE CYCLE OF THE TANTULOCARIDA (CRUSTACEA)

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[Plates 1–7]

CONTENTS

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Four new species of parasitic crustaceans belonging to the class Tantulocarida are described, two of which are placed in a new genus, *Onceroxenus*. Three of them parasitize deep-sea tanaids, the other, a deep sea asellote. *Microdajus langi*, originally classified as an epicaridean isopod, is recognized as a tantulocaridan. It is reported from Scottish waters for the first time and from new host species. These records include the shallowest depth, 22 m, known for a tantulocaridan. *Cumoniscus kruppi*, a parasite of cumaceans, is also recognized as a tantulocaridan. The Tantulocarida now comprises eleven species and five genera, here assigned to the Basipodellidae and two new families, the Deoterthridae and Microdajidae.

Several life cycle stages are described and arranged in two developmental sequences. Evidence for a possible third sequence was found. Male development involves a unique type of metamorphosis in which the free-living adult differentiates from a dedifferentiated mass of tissue contained within the expanded trunk of the tantulus larva. Throughout this metamorphosis the male is supplied with nutrients from the host via a tissue connection, the umbilical cord, and the permanently attached larval head. The non-feeding adult male lacks cephalic appendages but possesses two clusters of aesthetascs on its anterior margin. It is free swimming and has six pairs of large thoracopods without endites. The first two thoracic somites are incorporated into the cephalothorax. The abdomen bears a posteriorly directed, median stylet, interpreted as the intromittent organ. It originates on the first abdominal somite.

The adult female has a large sac-like trunk attached by the larval head. The larval trunk is sloughed leaving a scar but no complete moult occurs. Eggs develop within the trunk sac and hatch directly at the infective tantulus larval stage. This extreme condensation of early ontogeny is compared with that of other crustaceans and is interpreted as an adaptation to parasitism in situations where a high dispersal ability is not advantageous.

In some females the trunk sac forms behind the head but the larval trunk is retained. Small and large females of this type are described, the largest being 737 μm in length. These probably represent females in which sloughing of the larval trunk has failed but it is possible that each may have contained a free-living adult female of comparable size to the adult male.

The tantulus larva is described in detail. Scanning electron microscopy reveals that the thoracopodal endites have a complex apical armature, including coupling spines which serve to link the members of a leg pair.

Tantulocaridans are permanently attached to their host by the oral disc, presumably by means of an adhesive. In the centre of the disc they make a minute puncture (between 0.5 and 2.0 μm in diameter) through the host integument, probably with the aid of their cephalic stylet. This constitutes their only access to the body fluids of the host.

The phylogenetic relationships of the Tantulocarida are discussed. They appear to be related to the barnacles (Thecostraca), both groups possessing a median penis derived from the seventh trunk limb. Their possession of a thorax of six somites and the location of the male gonopores on trunk somite seven suggests an affinity with a larger group containing the Thecostraca and the Copepoda.

1. INTRODUCTION

The class Tantulocarida was established in 1983 by Boxshall & Lincoln to accommodate two genera of minute parasitic crustaceans, *Basipodella* Becker, 1975 and *Deoterthron* Bradford & Hewitt, 1980. The two species of the former genus are known to parasitize harpacticoid copepods, two of the latter genus parasitize asellote isopods and the other, ostracods. Greve (1965) reported a new ectoparasitic crustacean found on tanaid hosts in Norwegian waters. This parasite, *Microdajus langi* Greve, 1965, was originally placed in the isopod family Dajidae but is now recognized as a tantulocaridan. *M. langi* was found at depths from 120–130 m in Raunefjorden and was the shallowest recorded tantulocaridan, other records ranging from depths of 384 m (Bradford & Hewitt 1980) to 5000 m (Becker 1975). *Cumoniscus kruppi*, described by Bonnier (1903) as an epicaridean, also appears to belong in the Tantulocarida. It parasitizes a cumacean and is known from an adult female only. Before this study the genus *Deoterthron* was known only from its larval stage, *Basipodella* from both larval and postlarval stages and *Microdajus* from larvae and adult females.

The present account reports the discovery of a new species of *Deoterthron* parasitizing a species of asellote isopod from the Rockall Trough, off the west coast of Scotland. Several stages of the life cycle have been found and are described. They provide new information on the biology and phylogenetic relationships of the Tantulocarida. Their life cycle involves a unique kind of metamorphic reorganization which serves to emphasize their isolation from other crustacean classes. A new genus of tantulocaridan is described based on larval and adult material recovered from a tanaid host collected on the lower continental slope and abyssal plain off the southwest of the English Channel. Only adult females of a second species of the new genus were found on a tanaid host taken in the Rockall Trough region. Also reported is the discovery of two more parasite species in Scottish waters, also from tanaid hosts. Females of *Microdajus langi* in the process of metamorphosis were found off Millport in the Firth of Clyde and in the Lynn of Lorne. These records of *M. langi* include the shallowest depth, 22 m, known for any tantulocaridan. Abundant material of *M. langi*, including three males, was collected from Raunefjorden, Norway. A new species of *Microdajus* was found on a tubicolous tanaid taken in deep water in the Rockall Trough.

2. METHODS

Isopod and tanaid hosts were inspected under a dissecting microscope for the presence of tantulocaridan parasites, and their site of attachment and stage of development noted. Parasites were examined as temporary mounts in lactophenol or as permanent mounts in polyvinyl lactophenol using magnifications of up to 1200 times. All light microscope drawings were made using a camera lucida. Specimens were prepared for scanning electron microscopy (SEM) by critical point drying and sputter coating with palladium.

3. *DEOTERTHRON HARRISONI* SP.NOV.

(*a*) *Description*

(i) *Tantulus larva*

The length is about 130 μm, from tip of rostrum to posterior margin of abdomen, and comprises the head, six-segmented thorax and two-segmented abdomen (figures 2 and 3, plate 1). The head tapers anteriorly towards the rostrum and has a straight posterior margin, although the posterolateral angles are deflected ventrally. The rostrum (figure 5, plate 1) has a broad base and was not observed in the reflexed position seen in *D. megacephala* (Lincoln & Boxshall 1983). The dorsal cephalic shield is ornamented with fine longitudinal lamellae, two of which extend onto the rostrum (figures 3–5, plate 1). The surface is ornamented with fine striations. There are two pores and two sensory setules posteriorly on the head, and two pores midway along the side of the head. Anteriorly near the base of the rostrum are a simple pore and a complex slit-like pore from which one long and three short setules emerge. This pore–setule pattern, shown diagrammatically in figures 6 and 7, is very similar to that reported for *D. megacephala*.

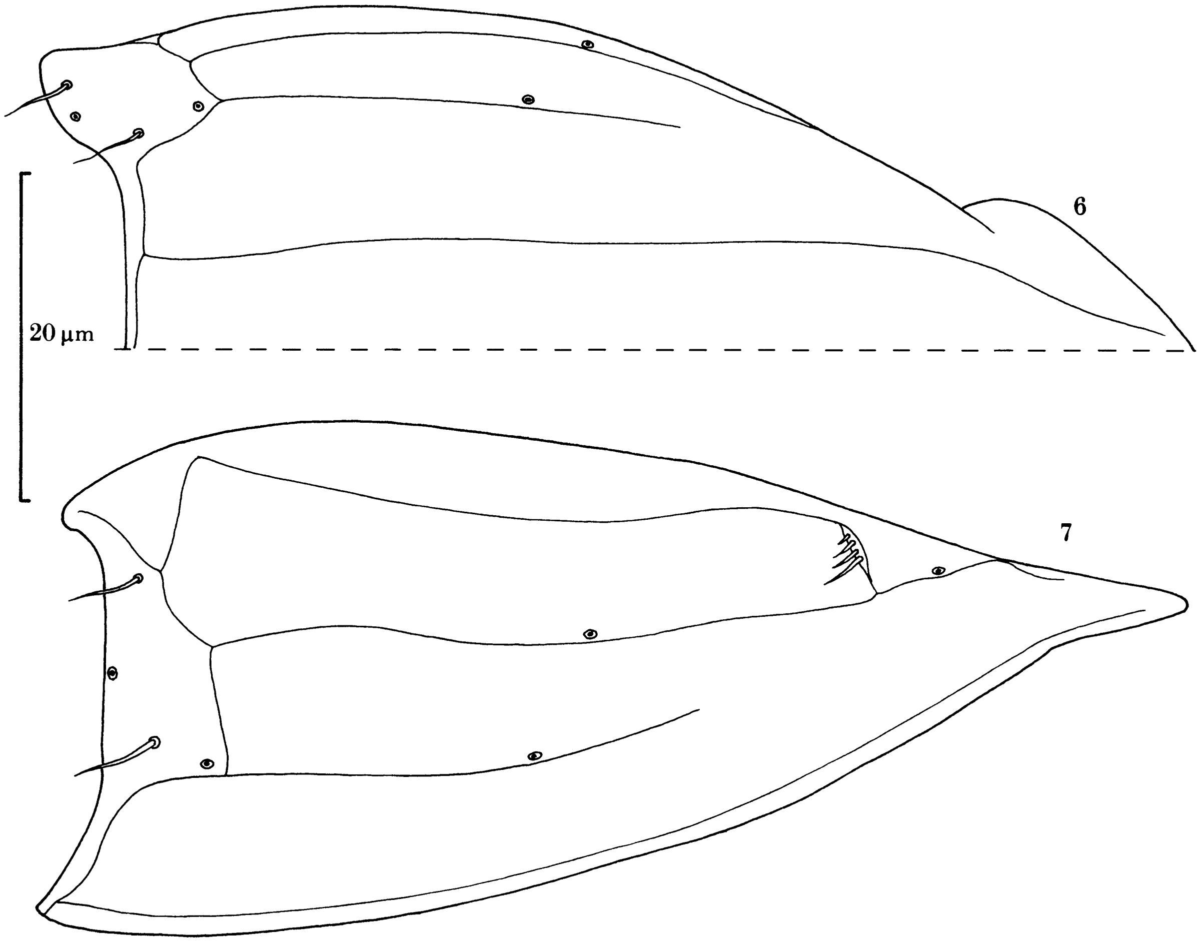

Figure 6. Dorsal view of left half of cephalic shield of *D. harrisoni* tantulus, showing pores and main lamellae.
Figure 7. Lateral view of the same, ventral surface uppermost.

Several cephalic structures are visible through the integument. The cephalic stylet (figure 8, c.sty.) is weakly curved and about 37 µm in length. Its orientation varies and it may curve in from either side or curve ventrally and appear straight in dorsal view (figure 47). It is hollow proximally but appears solid distally. Other internal organs include a long striated organ, a dense collar-like zone near the oral disc and two thickened linear structures directed towards the oral disc, as in *D. aselloticola* (Boxshall & Lincoln 1983).

The thorax comprises six free somites, loosely articulated and possessing distinct tergites (figure 8). The first thoracic somite is often partially overlain by the cephalic shield (figure 3, plate 1). All tergites are ornamented with a more or less hexagonal pattern of fine lamellae. Laterally each is separated from the pleura by a deep tergopleural groove (arrowed in figure 14, plate 2). Each thoracic somite bears a pair of thoracopods behind which the sternite protrudes ventrally. This swelling is especially marked behind the fifth leg pair (figure 12, s.s.) and is the structure referred to as the genital papilla in *D. aselloticola* (Boxshall & Lincoln 1983).

The abdomen is about 25 μm long and comprises a short first and an elongate second somite (figure 9). The articulation separating thorax and abdomen is very narrow and the abdomen is often detached at this position (figure 16, plate 2). The first abdominal somite has acute posterolateral angles but little ornamentation. The second is ornamented with short sections of longitudinal lamellae (figure 15, plate 2) dorsally and laterally. Anteriorly this somite carries a transverse ridge which may mark the position of a line of fusion between two original abdominal somites. The posterior margin of the abdomen is scalloped and the posterior surface is markedly indented. The paired caudal rami are located in the concave end of the abdomen. Each consists of a short lateral seta and two long setae borne on a short ramus.

The thorax bears six pairs of thoracopods ventrally (figure 20, plate 3). The first five pairs are biramous, the sixth uniramous. The setal armature of the thoracopods is an important taxonomic character at the specific level and figures 10–13 are provided for comparison with other *Deoterthron* species. The two-segmented exopods of thoracopods 1–5 each bear two long and two medium length setae on the distal segment. The endopod of thoracopod 1 (figure 10) bears a single seta midway along its outer margin, those of thoracopods 2–5 (figures 11 and 12) bear two setae at the same position. The endopods of the first five pairs appear to be divided into two segments by a suture distal to the origin of the endopod setae. At its apex each endopod bears a spatulate spine and a spiniform process, only one of which is often visible at a particular orientation. Thoracopods 1–5 each possess a lobate endite, the armature of which cannot be correctly ascertained without SEM. Thoracopod 6 (figure 13) bears two spines distally on the inner protopod margin and the ramus bears two long setae. It lacks an endite.

The complex structure of the thoracopods and their endites has been revealed by SEM. Figures 18 and 19 are composites drawn from numerous scanning electron micrographs and represent a typical thoracopod 2 of the new species. The protopod (prp.) bears rows of small denticles mainly on its anterior surface and the rami lie in a concavity on its distal margin. The exopod (exp.) comprises a small unarmed proximal segment and a large distal segment bearing four setae. The distal segment has transverse and longitudinal folds in its surface, the latter being extensions of setal bases perhaps allowing the setae to be spread apart to some extent. The two long exopod setae have swollen and possibly articulated bases, and all four setae are ornamented with two or more rows of tiny denticle-like setules. The elongate endopod (end.) bears, midway along its outer margin, two setae which appear to arise from a common base. The outer is armed with a curved setule and barb at about a third of its length, which together form an interlocking mechanism. The distal part of this seta and the inner seta are armed with two rows of tiny setules. Distal to the origin of these setae the endopod is divided by a complete transverse suture line (arrowed in figure 17, plate 2). Its apex bears a spiniform process and a spatulate spine set in a socket. The latter appears movable and is armed with a line of about five flap-like denticles which are directed proximally. This apical armature forms a gripping or attachment device and figure 17 (plate 2) shows a seta held between the spine and the process by the denticles.

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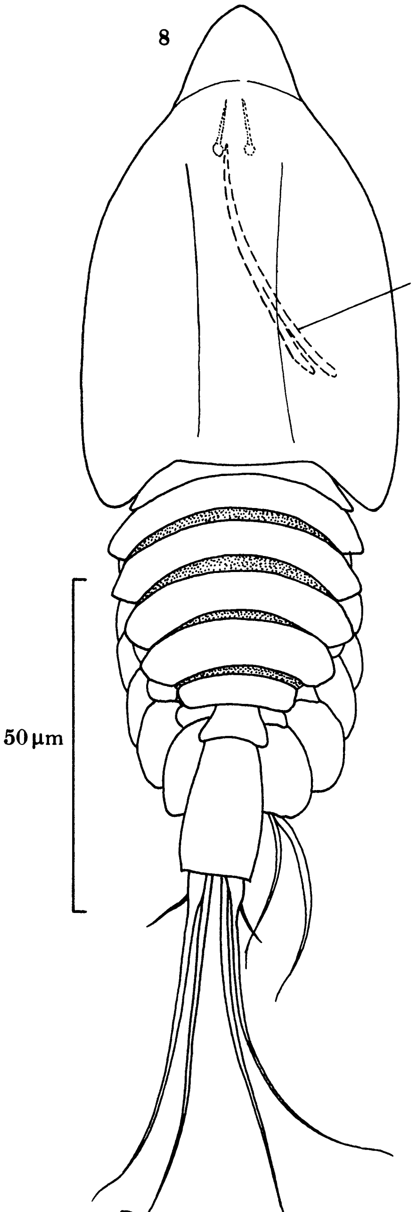

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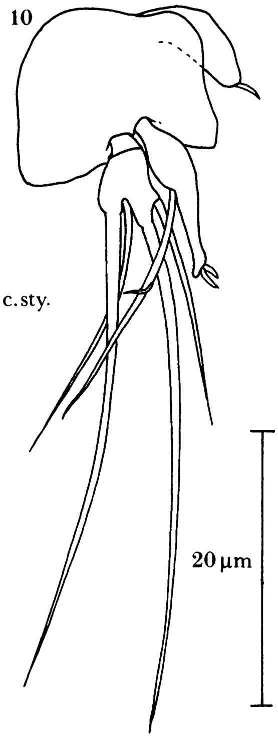

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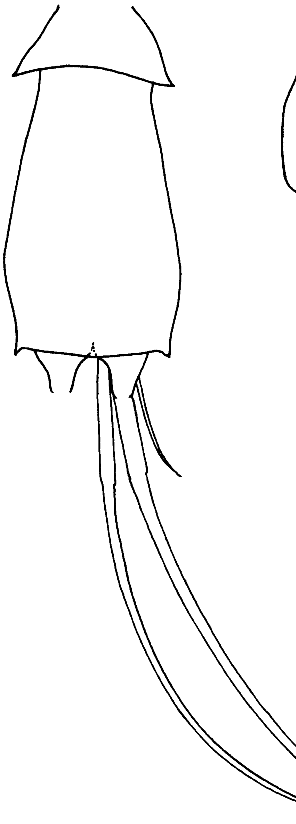

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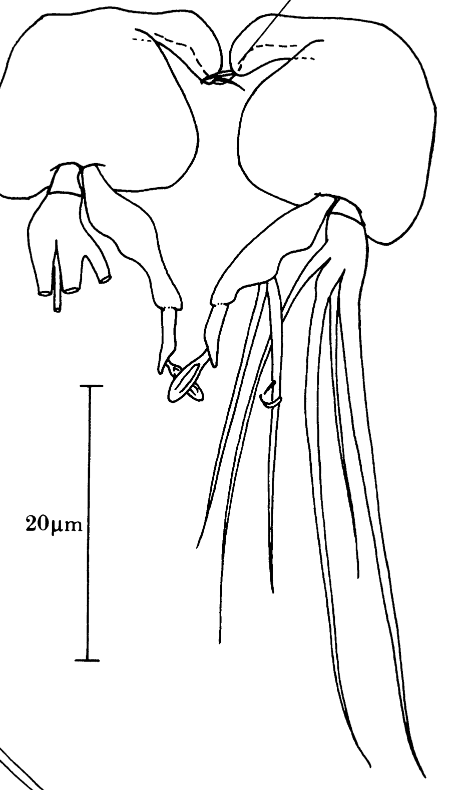

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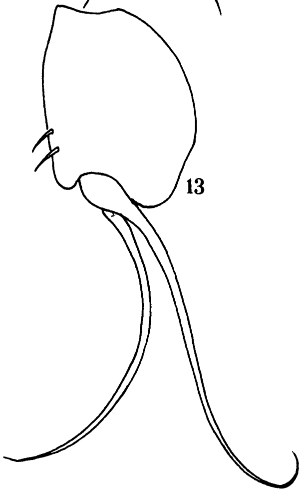

Figure 8. Dorsal view of *D. harrisoni* tantulus.

Figure 9. Abdomen, dorsal view.

Figure 10. First thoracopod, anterior view.

Figure 11. Second thoracopods, anterior view.

Figure 12. Anterior view of fifth thoracopods, hatched line shows median protrusion on sclerite posterior to leg bases.

Figure 13. Sixth thoracopod, anterior view.

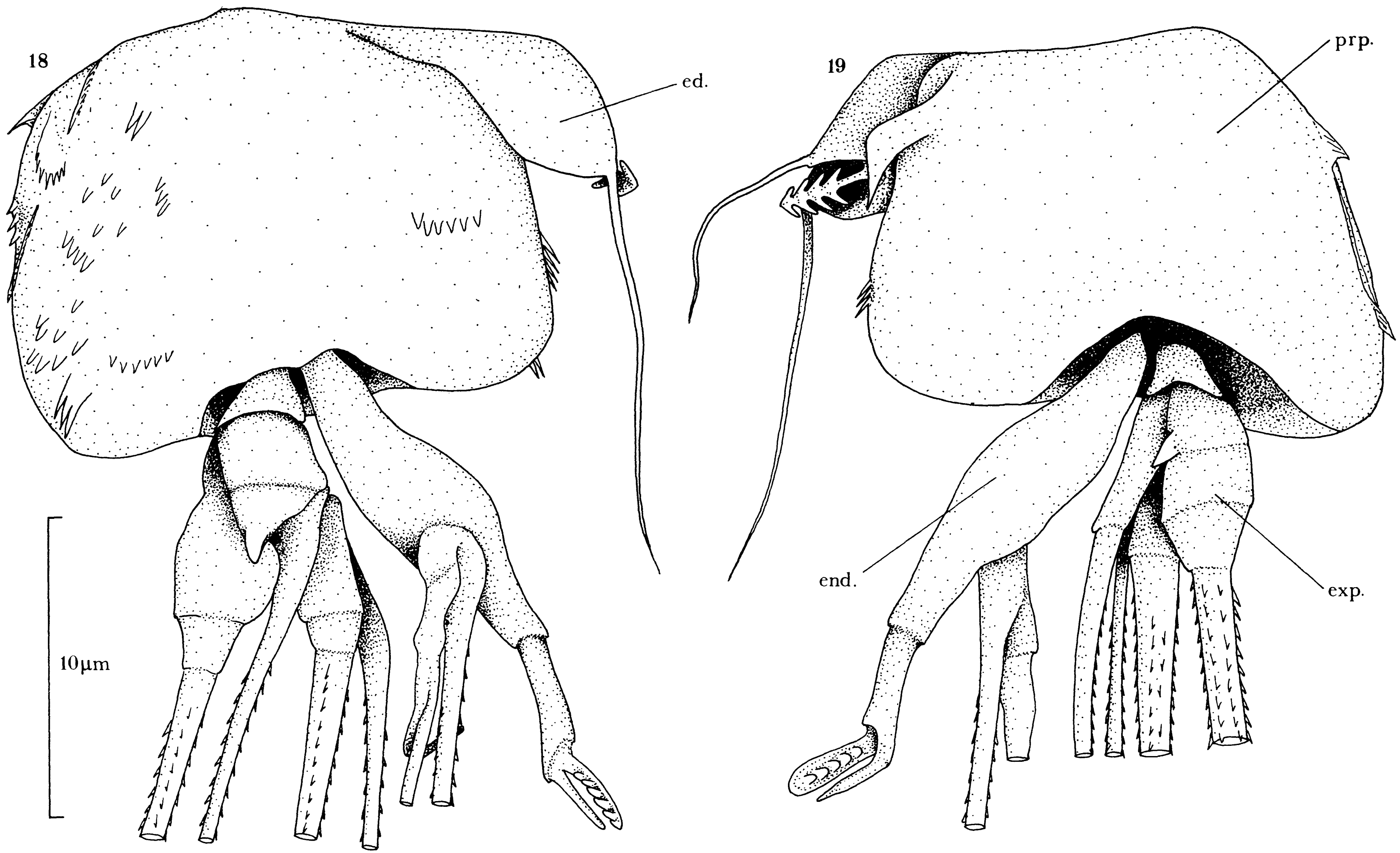

FIGURE 18. Anterior view of second thoracopod of *D. harrisoni*, compiled from scanning electron micrographs.

FIGURE 19. Posterior view of the same.

The endites (figure 18, ed.) are difficult to observe with light microscopy and their structure is more complex than hitherto realised. Each is a fleshy lobe arising from the extreme proximal rim of the protopod and extending medially to the ventral midline. The swollen distal part is slightly indented at its apex. Arising in the indentation is a complex barbed spine bearing three pairs of proximally directed barbs. These spines appear to function as grappling hooks securing the two members of a leg pair together (figure 21, plate 3). In addition, each endite bears two long setae situated at its apex, anterior and posterior to the apical indentation. These typically lie on the surface of the protopod and can be seen only as short spines with light microscopy. In posterior view the endites are often obscured by integumental flaps on the medial margin of the protopod.

Thoracopod 6 lacks an endite but the distal spines on the medial margin of the protopod are barbed like those on the endites (figures 22, plate 3). They presumably serve a similar coupling function.

(ii) *Male development*

A sequence of stages of *D. harrisoni* was found which illustrates the remarkable transformation that occurs during the life cycle (figures 23–27). The tantulus larva (figure 23) begins to swell posterodorsally at the rear of the thorax resulting in the separation of the thoracic tergites (figure 28, t1–t5). Expansion continues between tergites 5 and 6 causing the downward deflection of somite six and the abdomen (figure 25) until a huge sac-like swelling is produced at the rear of the thorax (figures 26 and 27). The head and rest of the thorax and abdomen remain unchanged from the larval condition. Internally during this process a total reorganization has taken place. At the stage illustrated in figure 25 the sac contains an undifferentiated cellular mass but this soon becomes organized so that the body form of the developing male can be recognized. The cephalothorax, thorax and abdomen are distinguishable and the thoracopod limb buds are present (figure 26). This 'embryo' undergoes considerable development within the sac, differentiating and increasing in size until it is ready to escape from the integument of the preceding stage (figure 27). Throughout this reorganization the parasite is dependent upon the host for its food supply which is carried to the rapidly growing 'embryo' by a strand of tissue referred to as the umbilical cord (figure 26, umb.). By the time development is complete the umbilical cord has degenerated and is no longer functional.

(iii) *Adult male*

The adult male develops within the sac-like swollen thorax of the preceding stage where it lies with its thoracopods and abdomen flexed under the cephalothorax (figure 27). Removed from its sac, the slender body unfolds to about 460 μm in length and comprises a cephalothorax, four free thoracic somites each bearing a pair of thoracopods, and an unsegmented abdomen

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DESCRIPTION OF PLATE 1

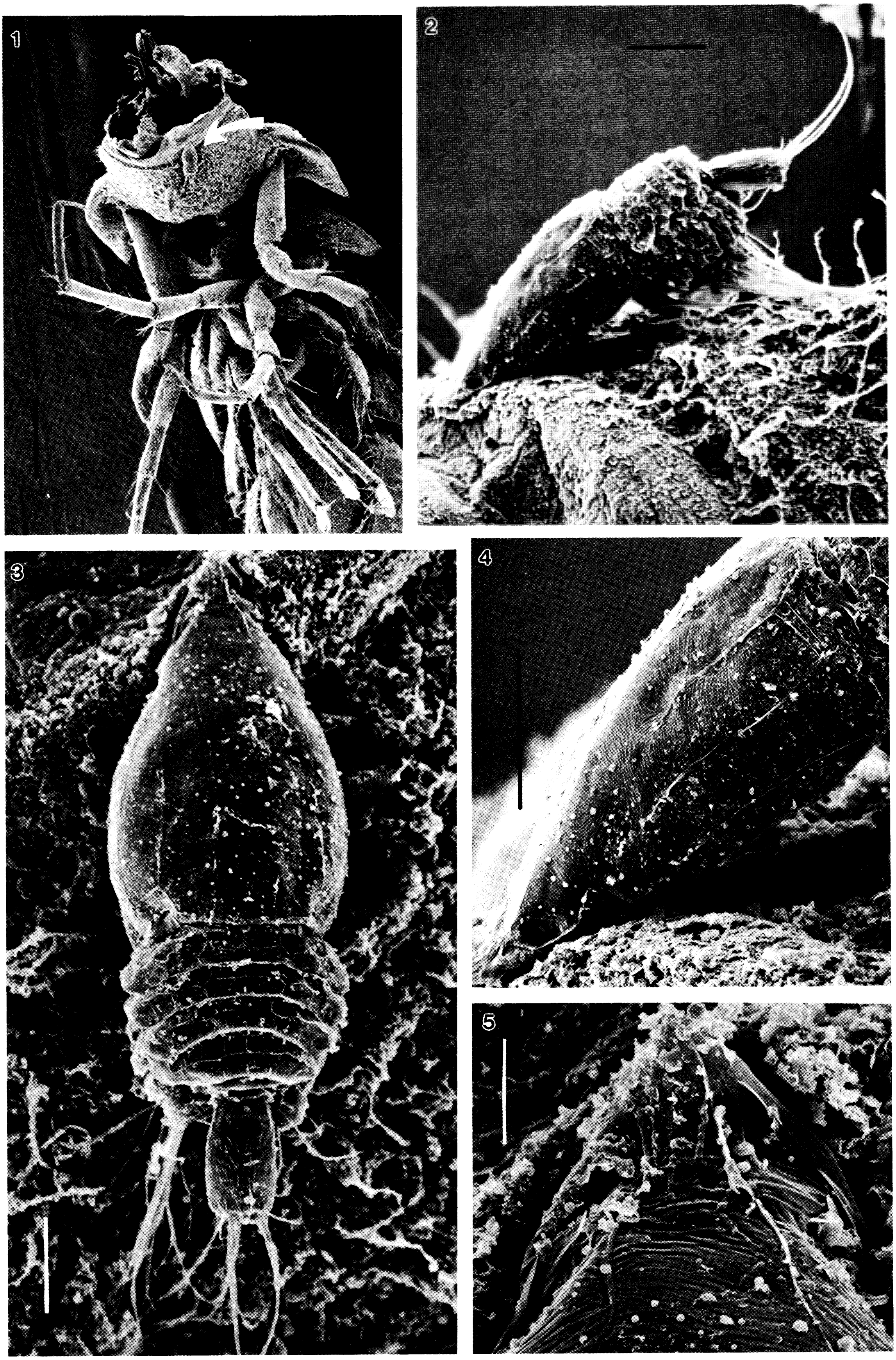
FIGURE 1. *D. harrisoni* tantulus attached to sternite of host. Scale bar 200 μm.

FIGURE 2. Lateral view of tantulus on host. Scale bar 20 μm.

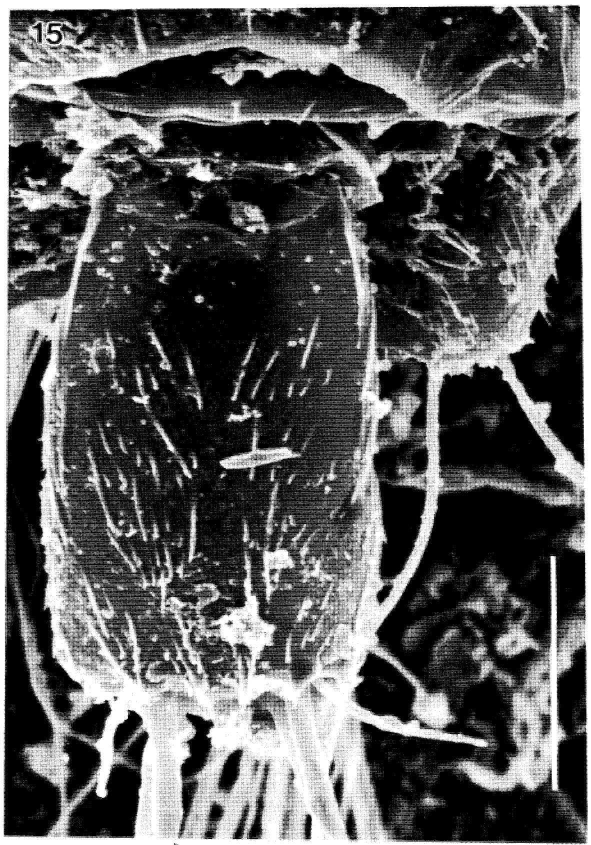
FIGURE 3. Dorsal view of tantulus on host. Scale bar 25 μm.

FIGURE 4. Lateral view of cephalic shield. Scale bar 20 μm.

FIGURE 5. Dorsal view of rostrum. Scale bar 5 μm.



FIGURES 1–5. For description see opposite.



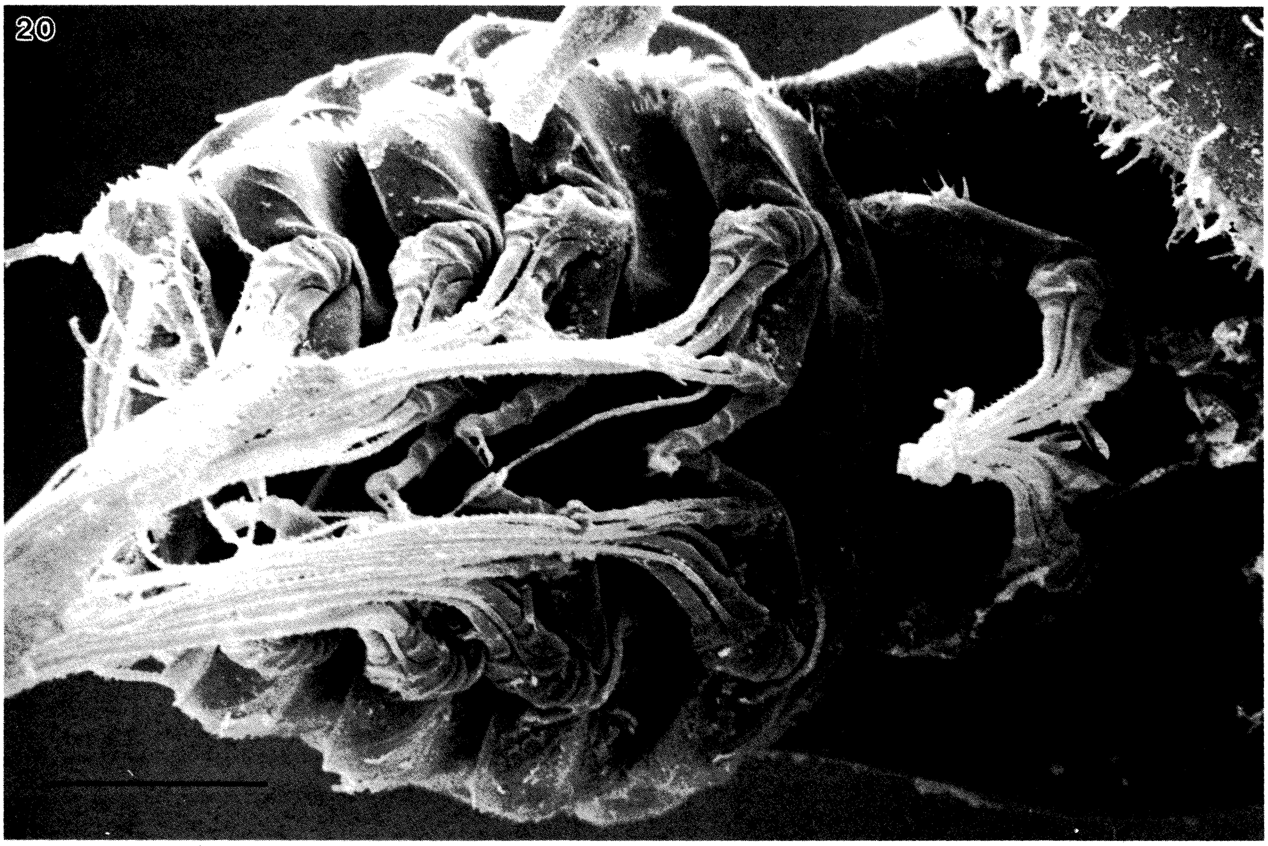
DESCRIPTION OF PLATE 2

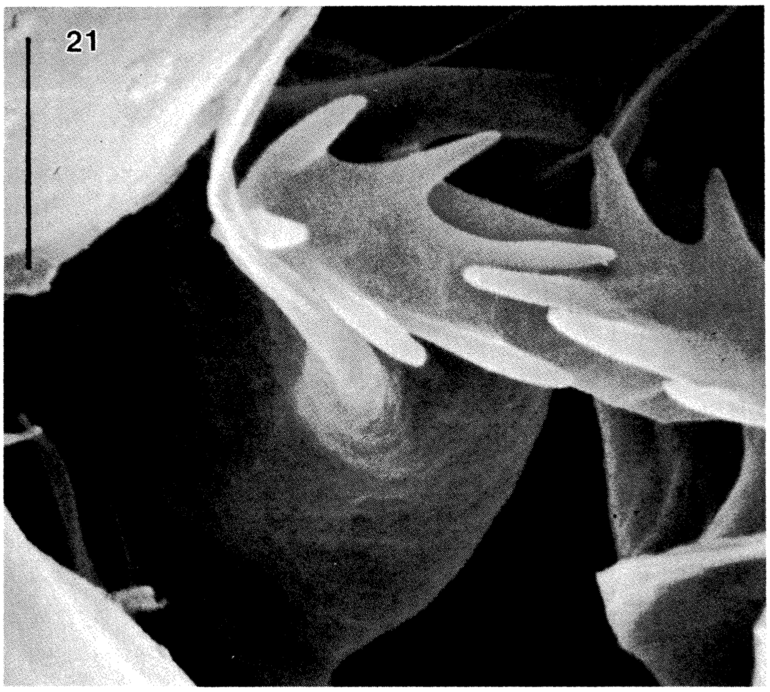
FIGURE 14. Lateral view of thorax of *D. harrisoni* tantulus, showing tergopleural grooves. Scale bar 5 μm.

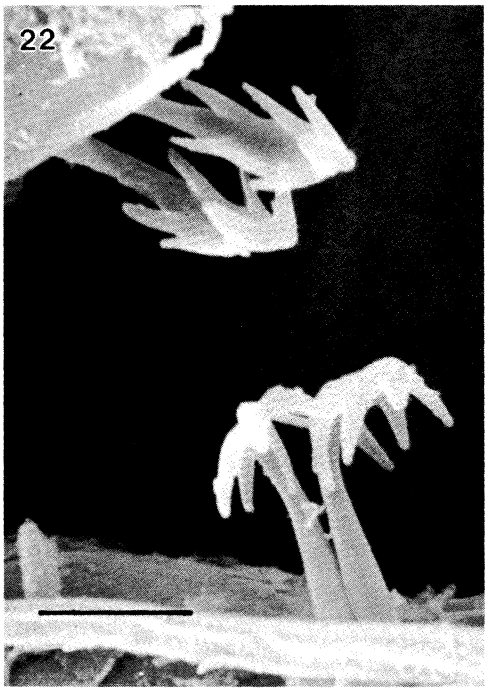
FIGURE 15. Tantulus abdomen, dorsal view. Scale bar 10 μm.

FIGURE 16. Posterior view of thorax, showing attachment site of detached abdomen. Scale bar 10 μm.

FIGURE 17. Apex of endopod of third thoracopod. Scale bar 1 μm.





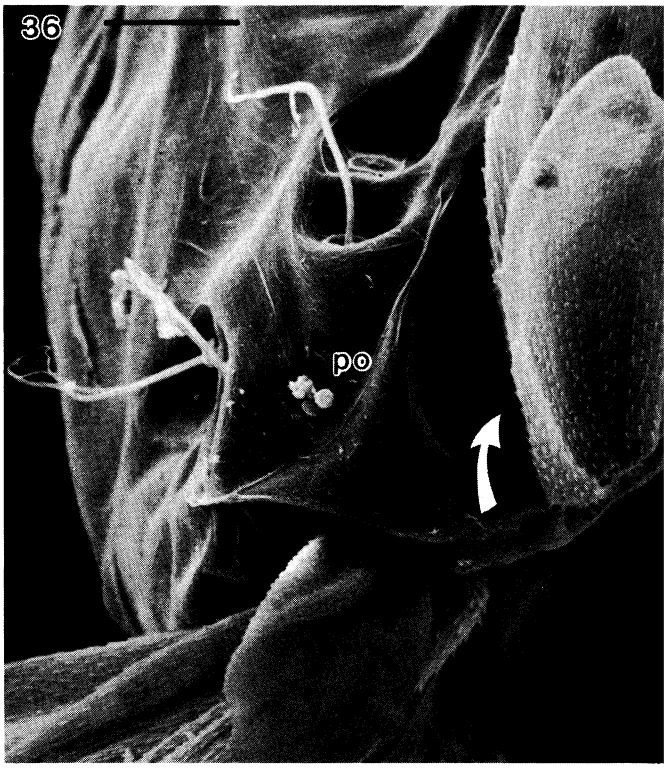


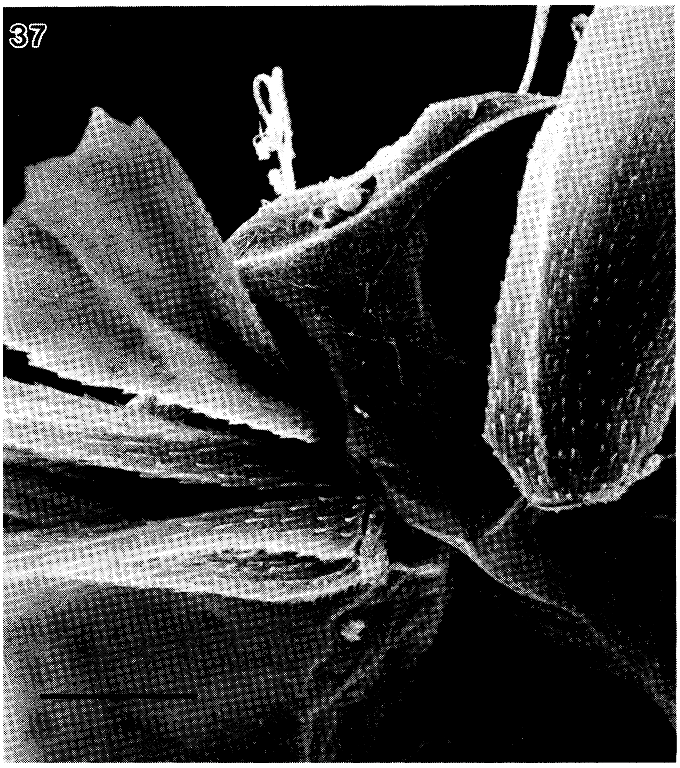
DESCRIPTION OF PLATE 3

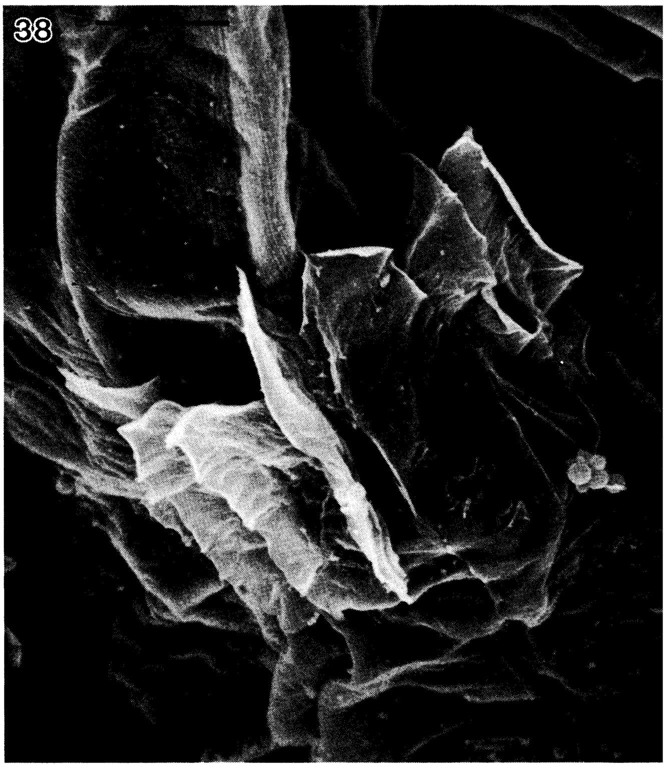
FIGURE 20. Ventral view of thoracopods of *D. harrisoni in situ*. Scale bar 10 μm.

FIGURE 21. Anterolateral view of interlocking spines on endites of third thoracopod. Scale bar 1 μm.

FIGURE 22. Posterior view of coupling spines on protopods of sixth thoracopods. Scale bar 1 μm.







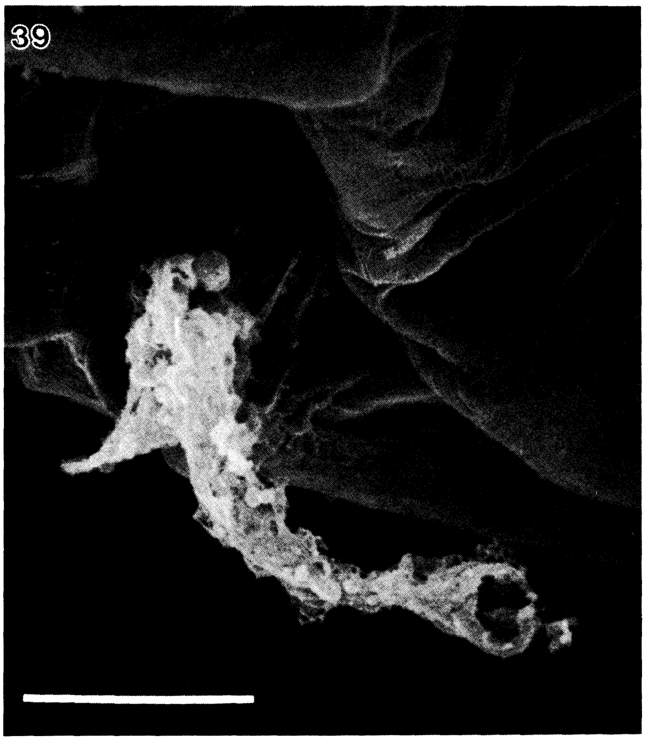
DESCRIPTION OF PLATE 4

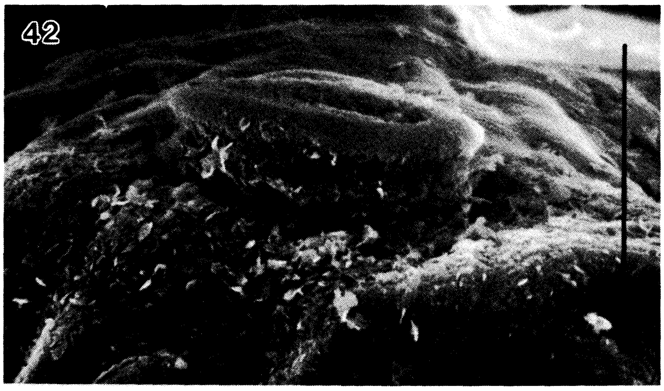
FIGURE 35. Frontolateral process on cephalothoracic shield of male *D. harrisoni*, showing setules. Scale bar 5 μm.

FIGURE 36. Anterolateral view of rostrum and associated sensory setules. Scale bar 5 μm.

FIGURE 37. Bases of aesthetascs on anterior margin of cephalothorax. Scale bar 10 μm.

FIGURE 38. Detail of lamellate structure on ventral surface, anterolateral. Scale bar 5 μm.





DESCRIPTION OF PLATE 5

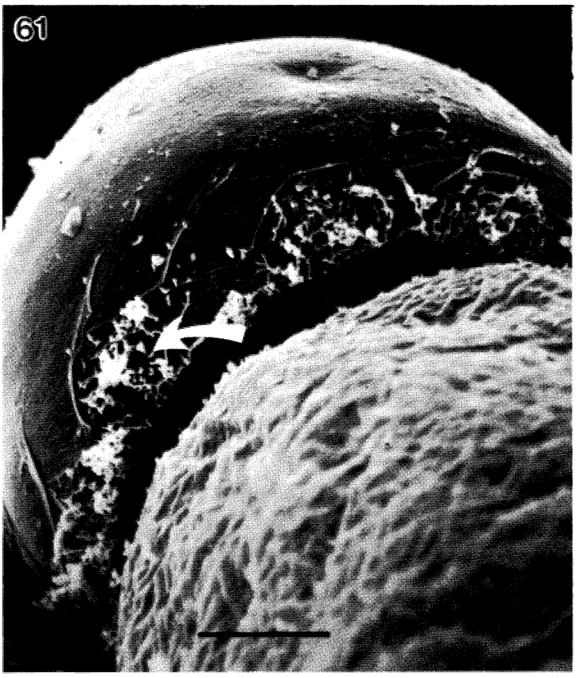
FIGURE 39. Shrivelled tubular structure emerging from pore on ventral surface of the cephalothorax of a male *D. harrisoni*. Scale bar 5 μm.

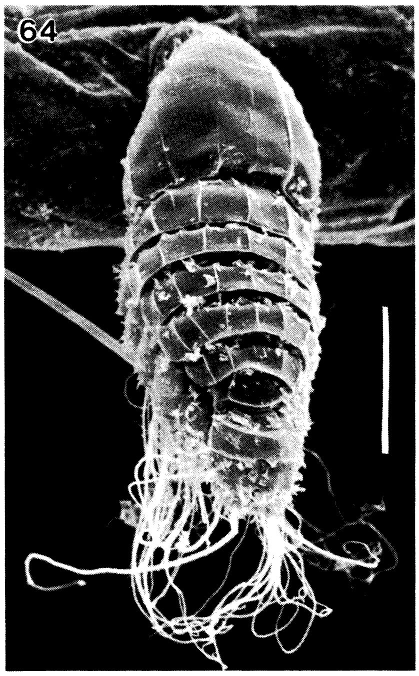
FIGURE 40. Apex of brush setae of male thoracopods. Scale bar 5 μm.

FIGURE 41. Early female *D. harrisoni* showing folded integument of trunk sac. Scale bar 50 μm.

FIGURE 42. Same specimen, showing detail of raised ventral scar left by sloughed larval trunk. Scale bar 5 μm.

FIGURE 43. Same specimen, showing scar in lateral view. Scale bar 5 μm.





DESCRIPTION OF PLATE 6

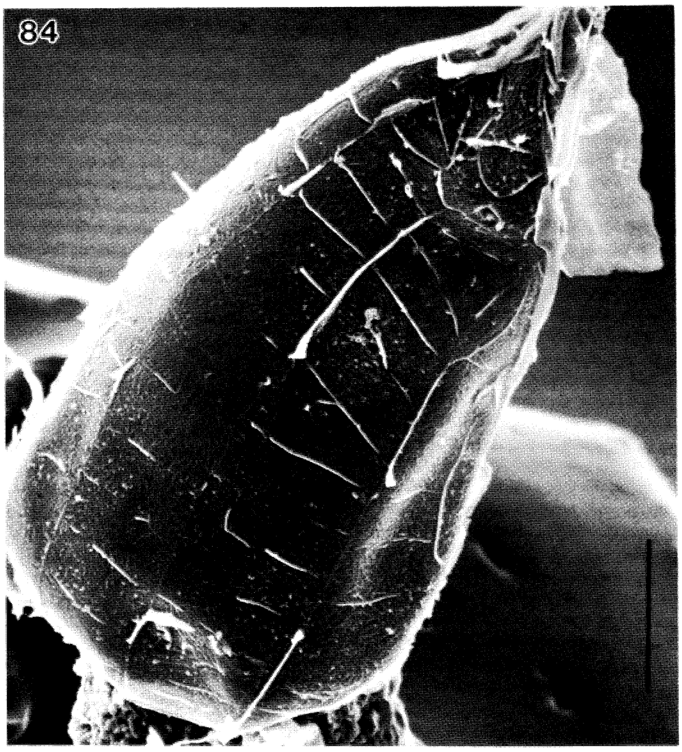
FIGURE 60. Dorsal view of early female *M. langi* showing wrinkled integument of trunk sac. Scale bar 40 μm.

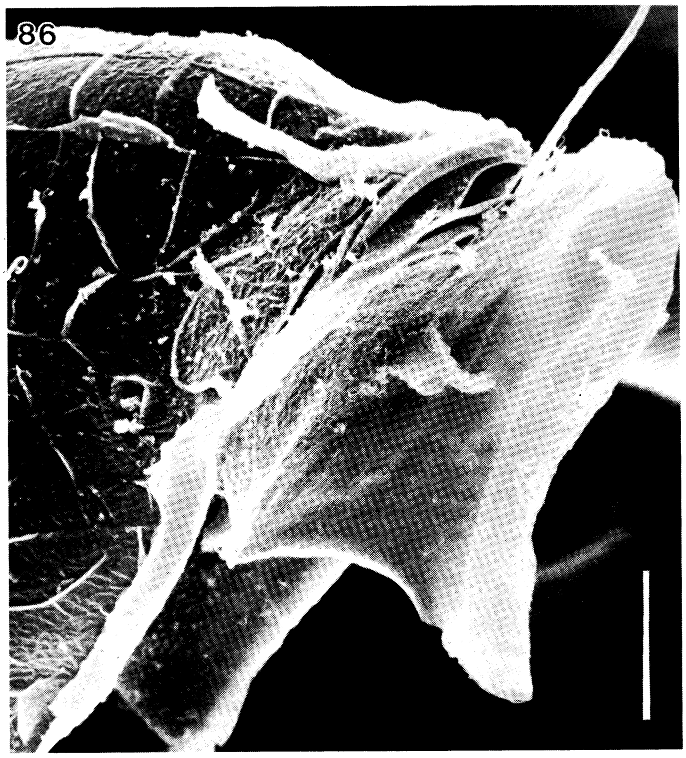
FIGURE 61. Posterior view of early stage female *M. langi* showing posterior rim of cephalic shield. Scale bar 5 μm.

FIGURE 62. Lateral view of head showing ornamentation and associated pores. Scale bar 12 μm.

FIGURE 63. Dorsal view of rostral area of *M. langi* female. Scale bar 2 μm.

FIGURE 64. Dorsal view of *O. birdi* tantulus attached to pereopod of its host tanaid. Scale bar 25 μm.





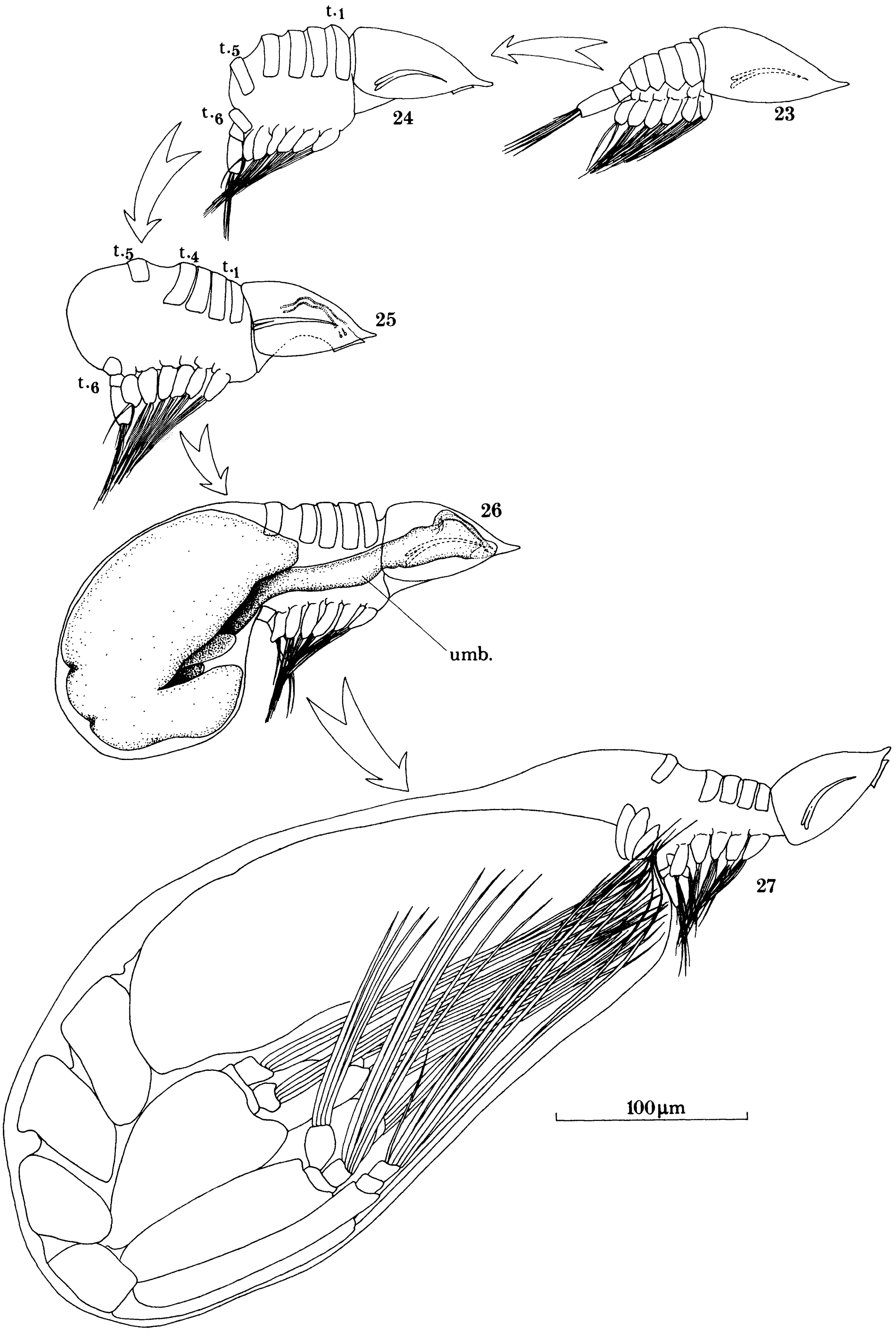
DESCRIPTION OF PLATE 7

FIGURE 83. Dorsal view of abdomen of tantulus of *O. birdi*. Scale bar 5 μm.

FIGURE 84. Lateral view of head shield of female *O. curtus* showing ornamentation and pore pattern. Scale bar 10 μm.

FIGURE 85. Highly folded, convoluted integument of trunk sac of adult female *O. curtus*. Scale bar 10 μm.

FIGURE 86. Head of *O. curtus* still attached to a torn fragment of host integument, showing puncture point at centre of oral disc and the tubular structure penetrating the host's integument. Scale bar 2 μm.



Figures 23–27. Developmental sequence of *D. harrisoni* from tantulus (figure 23) to adult male, showing the formation of the trunk sac within which the adult male grows.

(figure 28). The first two pedigerous thoracic somites are fused to the cephalon and this cephalothorax constitutes over half the body length.

The cephalothorax is covered by a dorsal shield which extends anteriorly to form a small rostrum, has sinuous lateral margins and a straight posterior margin extending ventrally round the sides of the cephalothorax. Its entire surface is ornamented with fine lamellae. A pair of conspicuous dorsal processes is present near its anterolateral angles (figure 28, f.p.). Each bears two double setules arising from a smooth pocket of integument (figure 35, plate 4). Two pairs of similar setules are present just behind the rostrum (figure 36, plate 5) and two further pairs are spaced out along the mid dorsal surface of the shield (figure 28, se. 3–se. 4). A single large pore (po.) is present near the anterior rim of the rostrum (figure 36, plate 4).

The first two thoracic somites are incorporated in the cephalothorax and no external suture lines mark the lines of fusion. Each of the four free thoracic somites has produced posterolateral angles and each is narrower than the preceding one so the body tapers markedly from cephalothorax to abdomen.

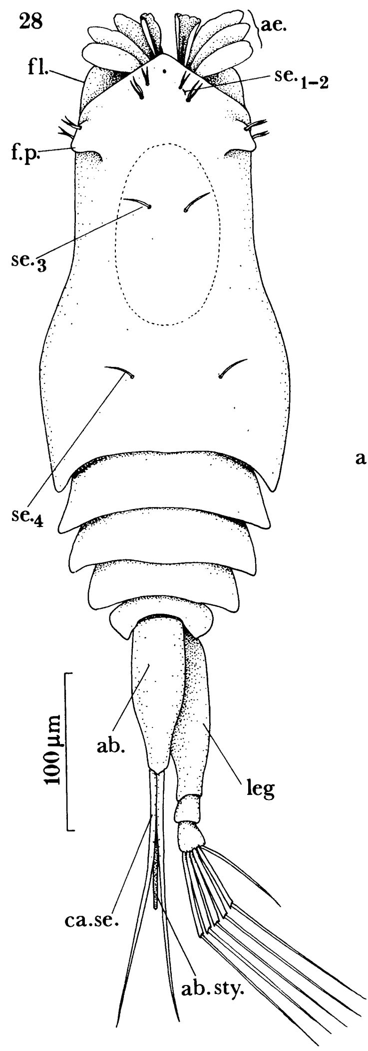
The abdomen narrows posteriorly and bears a pair of long caudal setae (ca.se.). It is raised and lowered by contraction of the dorsal (d.l.m.) and ventral longitudinal trunk muscles (v.l.m.) respectively (figure 29). Arising from the ventral surface is a long, posteriorly directed stylet (figure 29, ab.sty.) with a rigid central axis and an expanded tip surrounded by a pair of sheathing structures (figure 30). The stylet originates on the abdomen distal to its midlevel. No articulation is present at its base and it appears to be immobile. There are two pairs of longitudinal trunk muscles in the abdomen (figure 29, ab.l.m.) but these lie dorsal to the stylet, passing towards their insertions at the base of the caudal setae. They are not associated with the stylet and nor were any other internal organs visible in the unstained preparation. The stylet is interpreted as the intromittent organ.

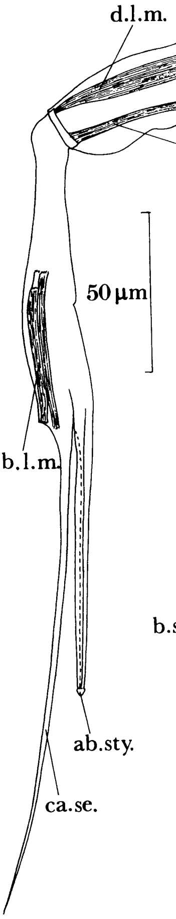
Anteriorly the cephalothorax bears four pairs of aesthetascs (figure 28, ae.) which originate in depressions lying either side of the rostrum (figure 37, plate 4). Posteroventral to the aesthetasc group the lateral cephalothoracic margin is expanded into a conspicuous rounded flange (figure 28, fl.). Each cluster of four aesthetascs appears to arise directly from the surface of the cephalothorax. The site of attachment of a broken off aesthetasc is arrowed in figure 36 (plate 4). No obvious vestige of any limb is associated with the aesthetascs, which are foliaceous and have sparsely serrated margins but lack any terminal pore. The entire surface of each is ornamented with a reticulum of fine ridges and denticles.

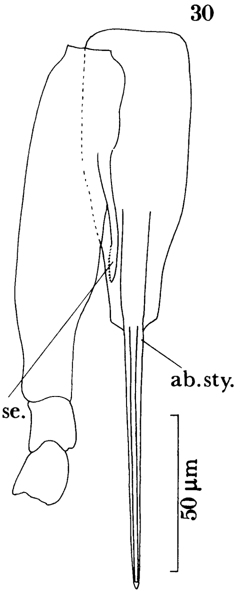
No well developed mouthparts are present. The ventral surface of the cephalic portion of the cephalothorax bears two structures on the midline (figure 31, lam., tu.). The anterior (lam.) consists of four pairs of overlapping plates which lack ornamentation or armature. These are free from the body surface anteriorly (figure 38, plate 4). The ridged ventral body surface extends beneath them but no pores or other openings were observed (see §9). The posterior structure (tu.) is a short strand of material looking like a collapsed tube (figure 39, plate 5). It issues from a relatively large opening in the body surface and may represent the degenerated umbilical cord.

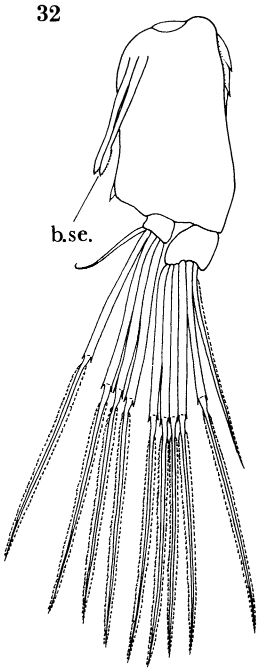
Little internal structure is discernible except for a dense oval shaped mass in the middle of the cephalothorax. There is no cephalic stylet and no nauplius eye. The large extrinsic muscles of the thoracopods are visible through the body wall.

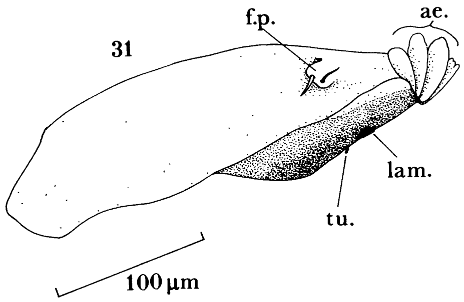
There are six pairs of thoracopods, two on the cephalothorax and one on each free somite. Thoracopods 1–3 are biramous with a one-segmented protopod (figure 32), 4 and 5 biramous

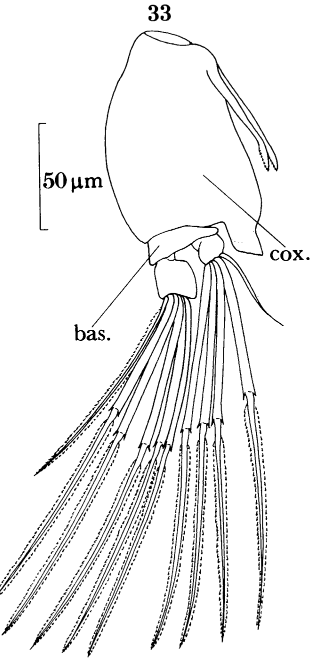












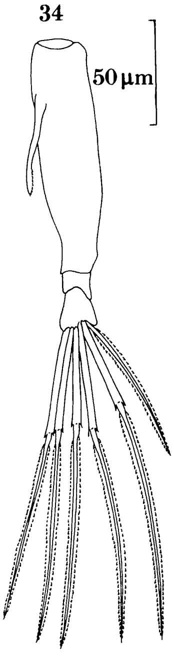


FIGURE 28. Adult male of *D. harrisoni*, dorsal view.

FIGURE 29. Last thoracic somite and abdomen of male, lateral view showing trunk musculature visible through integument.

FIGURE 30. Ventral view of abdomen with caudal setae removed, showing abdominal stylet and relative position of the sixth thoracopod.

FIGURE 31. Lateral view of cephalothorax of male.

FIGURE 32. Second thoracopod.

FIGURE 33. Fifth thoracopod.

FIGURE 34. Sixth thoracopod.

with a two-segmented protopod (figure 33); the sixth is uniramous (figure 34). Thoracopods 1 to 3 each have a massive muscular protopod. This bears two brush setae, proximally on its medial surface (figures 32–34, b.se.), that arise from an indentation in the medial protopod margin and appear to be fused proximally. They may be movable relative to the limb as they are joined to it by a region of finely ridged integument. The tip of each is armed with a brush of fine setules (figure 40, plate 5). The foramen between limb and somite is relatively small and cross-shaped, with the transverse arms of the cross longer than the longitudinal. The rami are one-segmented. On its distal margin the exopod bears one short seta laterally and five long setae. The former bears strips of serrated membrane bilaterally, the latter are hinged just proximal to their midpoint and armed with strips of serrated membrane distal to the hinge. On its distal margin the endopod bears four similar hinged setae and a short, naked inner seta.

Thoracopods 4 and 5 have a massive, muscular coxa and a small basis which bears the one-segmented rami (figure 33, cox., bas.). There are brush setae on the coxa and the rami are armed as for thoracopods 1–3 so that the division of the protopod into coxa and basis is the only major difference. The basis is separated from the coxa by a telescopic articulation. The rami, especially the exopod, are capable of some lateral flexion, spreading the serrate setae into a broad fan.

Thoracopod 6 (figure 34) is three-segmented, comprising a long muscular coxa, a short basis, and a one-segmented exopod. The coxa bears a single brush seta proximally on its medial margin. The basis is unarmed and the exopod bears the same armature as the other thoracopods.

(iv) *Female development*

A complete sequence of developmental stages is not available for the female. Commencing at the tantulus larval stage development proceeds in one of two directions. In both, the parasite remains attached by its head but its trunk starts to swell posterodorsally immediately behind the cephalic shield. Typically (figures 44–48) the entire trunk is then lost leaving a raised circular scar on the ventral body surface (figure 45, sc., and figures 42 and 43, plate 5). The surface of the trunk is highly folded and wrinkled (figure 41, plate 5) allowing for expansion from a small globular shape (figure 45) to a large sac (figure 48). The head remains unchanged during this process and the stylet, longitudinal organ and other internal structures are clearly visible (figure 47). The largest specimen of this type has a total length of about 310 μm but the trunk tissues remained undifferentiated other than into an outer layer and a central, cellular mass (figure 48). The scar marking the position of the sloughed thorax and abdomen is raised off the body surface and has a thickened lip (figures 42 and 43, plate 5).

A small number of specimens (figures 49 and 50) swell posterodorsally behind the cephalic shield but the larval thorax and abdomen are retained. They are deflected ventrally by the growth of the trunk sac. The largest specimen on this pathway (figure 50) had a body length of 737 μm but the enormous trunk sac was empty.

(*b*) *Material examined*

D. harrisoni was obtained from dredge and epibenthic sledge samples collected at depths of about 2000–3000 m in the vicinity of the Rockall Trough between 1973 and 1983 (see table 1). All specimens were found on an asellote isopod, *Macrostylis magnifica* Wolff, whose state of maturity was noted. The holotype male of *D. harrisoni* was contained within the trunk sac of

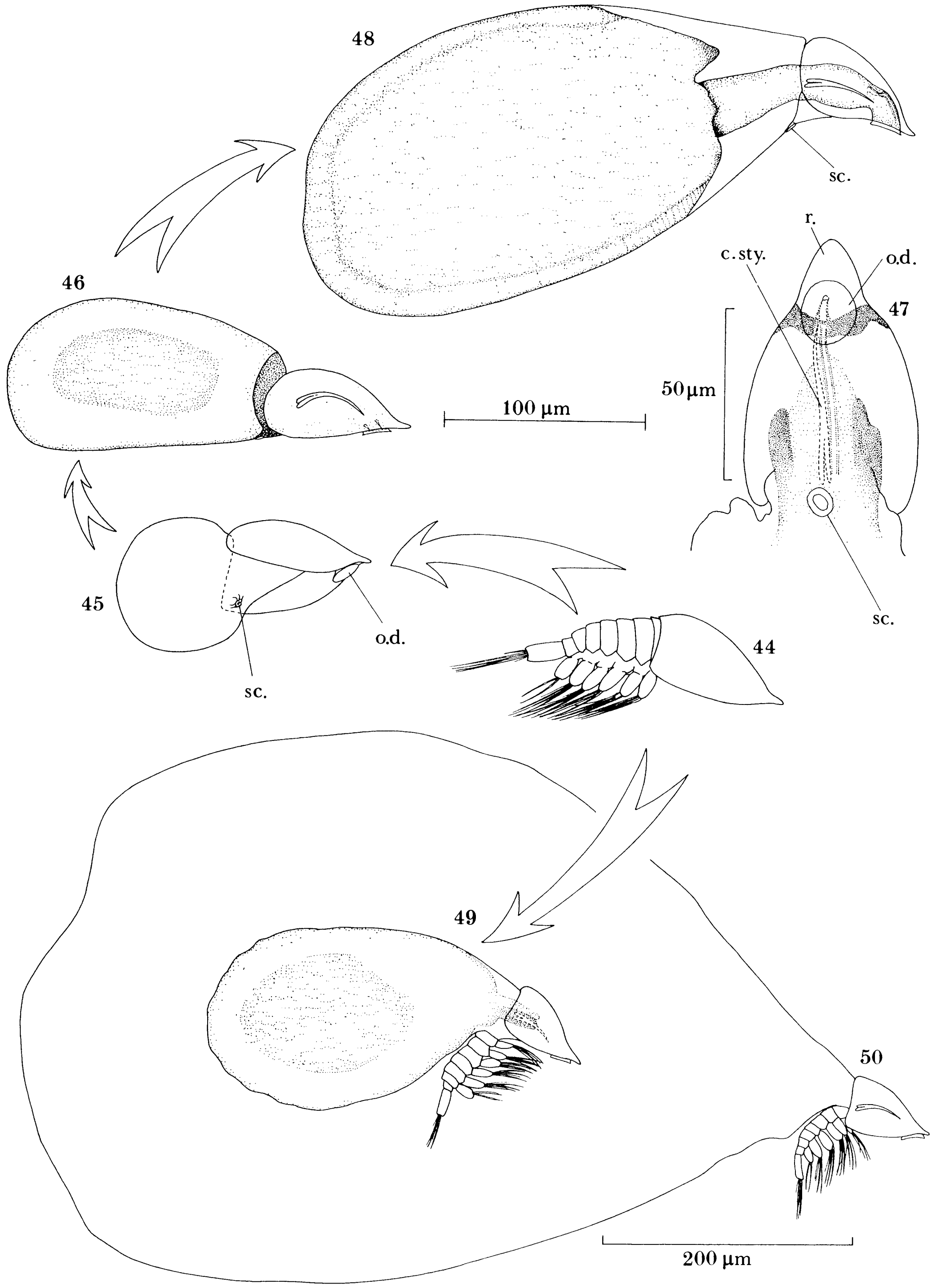


Figure 44. Tantulus larva of *D. harrisoni*.

Figure 45. Early stage female *D. harrisoni* showing newly formed trunk sac immediately behind the head and the ventral scar left by the sloughed larval trunk.

Figure 46. Later female in which trunk sac is larger.

Figure 47. Ventral view of head of same specimen.

Figure 48. Large female *D. harrisoni* without attached larval trunk, showing sac contents differentiated into an outer layer of columnar cells and an inner cellular mass.

Figure 49. Early stage female *D. harrisoni* in which the newly formed trunk sac is causing the ventral deflection of the retained larval trunk.

Figure 50. Largest specimen of *D. harrisoni* found, showing retained larval trunk and enormous but empty trunk sac.

TABLE 1. STATION DATA FOR *MACROSTYLIS MAGNIFICA* COLLECTIONS

station	position	date	depth/m
4	56° 52′ N, 10° 01′ W	5 June 1973	1993
6	55° 03′ N, 12° 29′ W	2 July 1973	*ca.* 2900
12	56° 49′ N, 10° 15′ W	20 Sep. 1973	2076
27	54° 40′ N, 12° 16′ W	3 Nov. 1973	*ca.* 2800
55	54° 40′ N, 12° 16′ W	17 Nov. 1975	2878
111	54° 40′ N, 12° 16′ W	22 Oct. 1976	2886
137	54° 34′ N, 12° 19′ W	22 Feb. 1978	2900
143	54° 41′ N, 12° 14′ W	14 Apr. 1978	2892
180	54° 42′ N, 12° 12′ W	15 Sep. 1980	2886
185	54° 44′ N, 12° 15′ W	10 Apr. 1981	2907
197	57° 21′ N, 10° 29′ W	19 Aug. 1981	2200
232	57° 17′ N, 10° 16′ W	19 May 1983	2195
244	57° 23′ N, 10° 20′ W	25 July 1985	2150

preceding stage, BM(NH) registration number 1985.400. The paratype series consists of two head fragments, twenty-one tantulus larvae, four males undergoing reorganization, one adult male, three females each with a ventral scar, and three females with trunks; paratype registration numbers 1985.401–421.

Etymology. This species is named after Dr K. Harrison, who found the first specimens and the first adult male.

(*c*) *Taxonomic remarks*

This new species closely resembles the other three species of *Deoterthron* in the gross morphology of the tantulus larva. Other life cycle stages are known only for *D. harrisoni*, so taxonomic comparisons can only be made between tantulus stages. *D. dentatum* possesses only two setae on the exopod of thoracopod 1 whereas all other species have four. *D. aselloticola* lacks any setae on the endopod of thoracopod 1 whereas *D. megacephala* and the new species both have a single long seta on the outer margin. The last two species have the same thoracopod armature, and the cephalic shield composes just over half the total body length in both. However, *D. megacephala* is much the larger, with a maximum length of 177 μm and width of 55 μm compared with about 130 μm and 48 μm in the new species. The rostrum of the new species is broader than in *D. megacephala*, which also lacks the fine surface ornamentation on the cephalic shield present in the new species. *D. harrisoni* also differs in the apparent division of the exopod into two segments, but this feature may have been overlooked in other species described only by light microscopy.

4. *MICRODAJUS LANGI* GREVE, 1965

(*a*) *Description*

(i) *Tantulus larva*

The length is about 110–120 μm, from anterior margin of cephalic shield to posterior margin of abdomen, and comprises the head, six-segmented thorax and two-segmented abdomen (figure 51). The head is about as long as it is wide, with a small amount of ornamentation posteriorly (see §4a, ii). There is no rostrum and the oral attachment disc is located near the extreme anterior margin. A weakly curved cephalic stylet (c.sty.), about 14 μm in length, is visible through the integument.

The six free thoracic somites are loosely articulated and possess distinct tergites. The first is often partly overlain by the cephalic shield. Each bears a pair of thoracopods. The abdomen is about 20 μm long and consists of two subequal somites, the second bearing one long and one short caudal seta on each side.

The thoracopods are reduced in segmentation and armature compared with those of *Deoterthron*. Thoracopods 1–5 each comprise a broad flattened plate indented distally. Lateral to the distal indentation are two apical setae (figures 52 and 53). Thoracopod 6 (figure 54) is uniramous and bears two apical setae. None of the thoracopods has a medial endite and thoracopod 6 lacks coupling spines on the protopod.

(ii) *Female development*

The female stages of *M. langi* can be arranged in a single series (figures 55–59). The trunk swells immediately behind the cephalic shield, and the larval thorax and abdomen are lost, leaving a raised circular scar (sc.) on the ventral body surface to mark their former position. The trunk becomes sac-like (figure 56) but the parasite remains attached by its head which is unmodified. The integument of the trunk is at this stage wrinkled but not highly folded (figure 60, plate 6). It is more highly folded in a narrow region immediately behind the head and it is likely that new integument is produced here and drawn down into the trunk as it swells and as the long 'neck' region is formed. The posterior margin of the cephalic shield overhangs the trunk slightly (figure 61, plate 6). All the larval thoracic tergites are lost.

The head remains unchanged. It is mostly smooth apart from a narrow region near the posterior margin of the cephalic shield (figure 61, plate 6). The ornamentation comprises a series of oblique lamellae between which the surface is finely ridged. The shield, near its posterior margin, bears six pores (arrowed in figure 61) each of which is surrounded by a fringe of minute hairs set within a larger patch. The posterior margin is also armed with a fringe of tiny setules and at least two pairs of longer sensory setules (arrowed in figure 62, plate 6). The head also has a pair of large pits anterolaterally within which are sensory setules (figure 62, po.). The anterior margin of the head is rounded (figure 63, plate 6). The small crescentic flap (r.) lying dorsal to the oral disc may represent a vestige of the rostrum. The oral attachment disc is well developed close to the front of the head. It adheres firmly to the host surface (figure 63, plate 6) and the parasites are difficult to detach.

The trunk continues to swell and the neck to elongate (figure 57). The body now comprises the larval head, a long, often twisted neck, and an ovoid trunk full of eggs. As the eggs develop the sac continues to swell reaching a total body length of over 1 mm. At this stage (figure 58) the eggs are almost fully developed. Each egg membrane contains a tantulus (figure 59) which is indistinguishable from the larva found attached to the host (see §4a, i). Each larval head contains a stylet and the larvae are presumably capable of infecting a host soon after hatching.

(iii) *Adult male*

Three sac-like specimens of *M. langi* were found, each of which contained a male at an advanced stage of development. The tantulus swells posterior to the sixth thoracic tergite to form the sac (figure 65). The abdomen is deflected by the expanding sac. The male is visible through the sac wall. All three males were still connected by the umbilical cord (umb.) to the larval cephalic tissues and were, therefore, not ready to hatch.

Removed from its sac and unfolded, the male is about 200 μm long. It comprises a

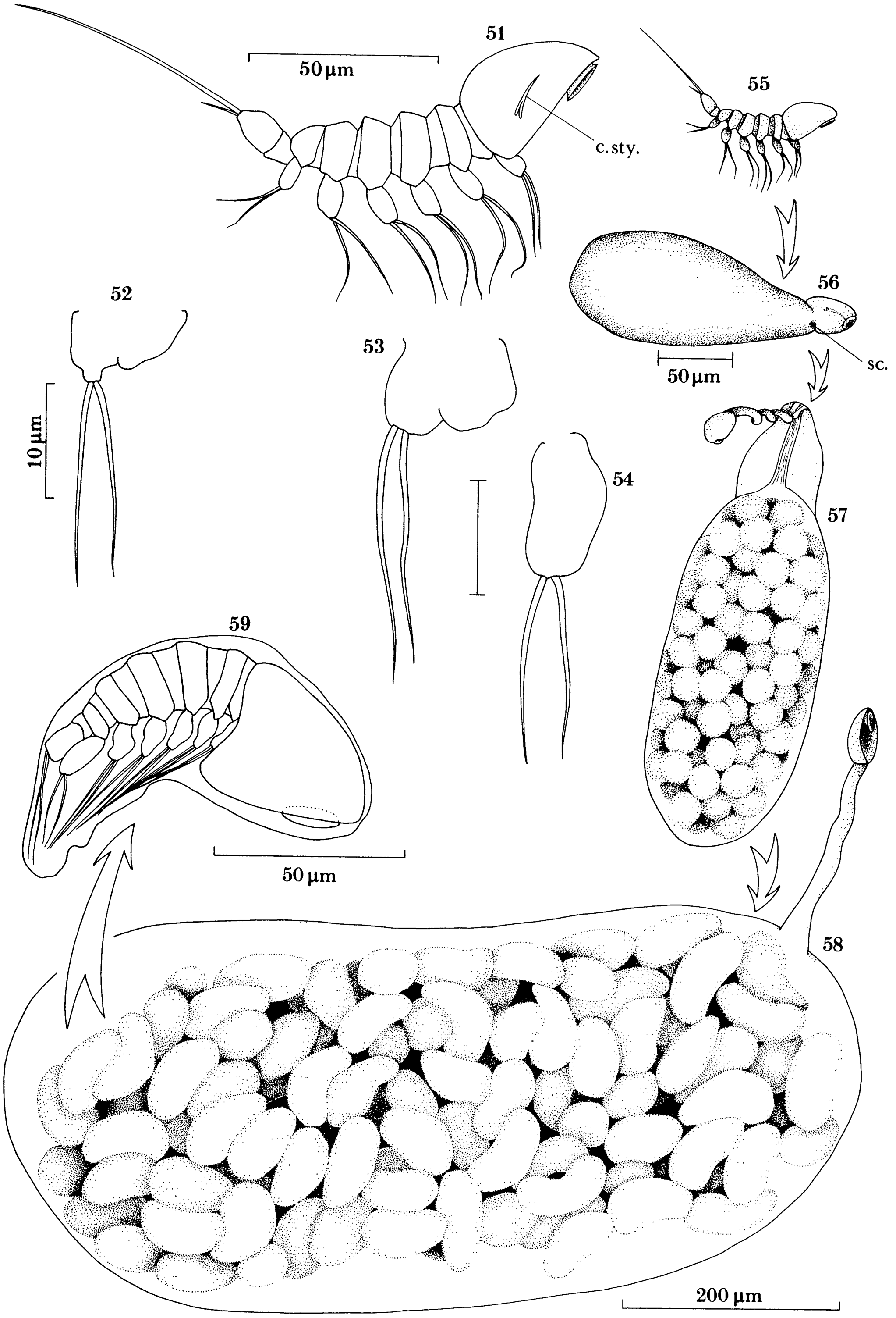


FIGURE 51. Tantulus of *M. langi*, lateral view.
FIGURE 52. First thoracopod of tantulus.
FIGURE 53. Fifth thoracopod of tantulus.
FIGURE 54. Sixth thoracopod of tantulus.
FIGURE 55. Tantulus of *M. langi*.
FIGURE 56. Early stage female from Firth of Clyde showing trunk sac and ventral trunk scar.
FIGURE 57. Gravid female *M. langi* from the Lynn of Lorne, showing twisted neck and containing 80–90 eggs.
FIGURE 58. Adult female from Norway, containing tantulus larvae ready to hatch.
FIGURE 59. Tantulus contained within egg membrane removed from trunk sac of same specimen.

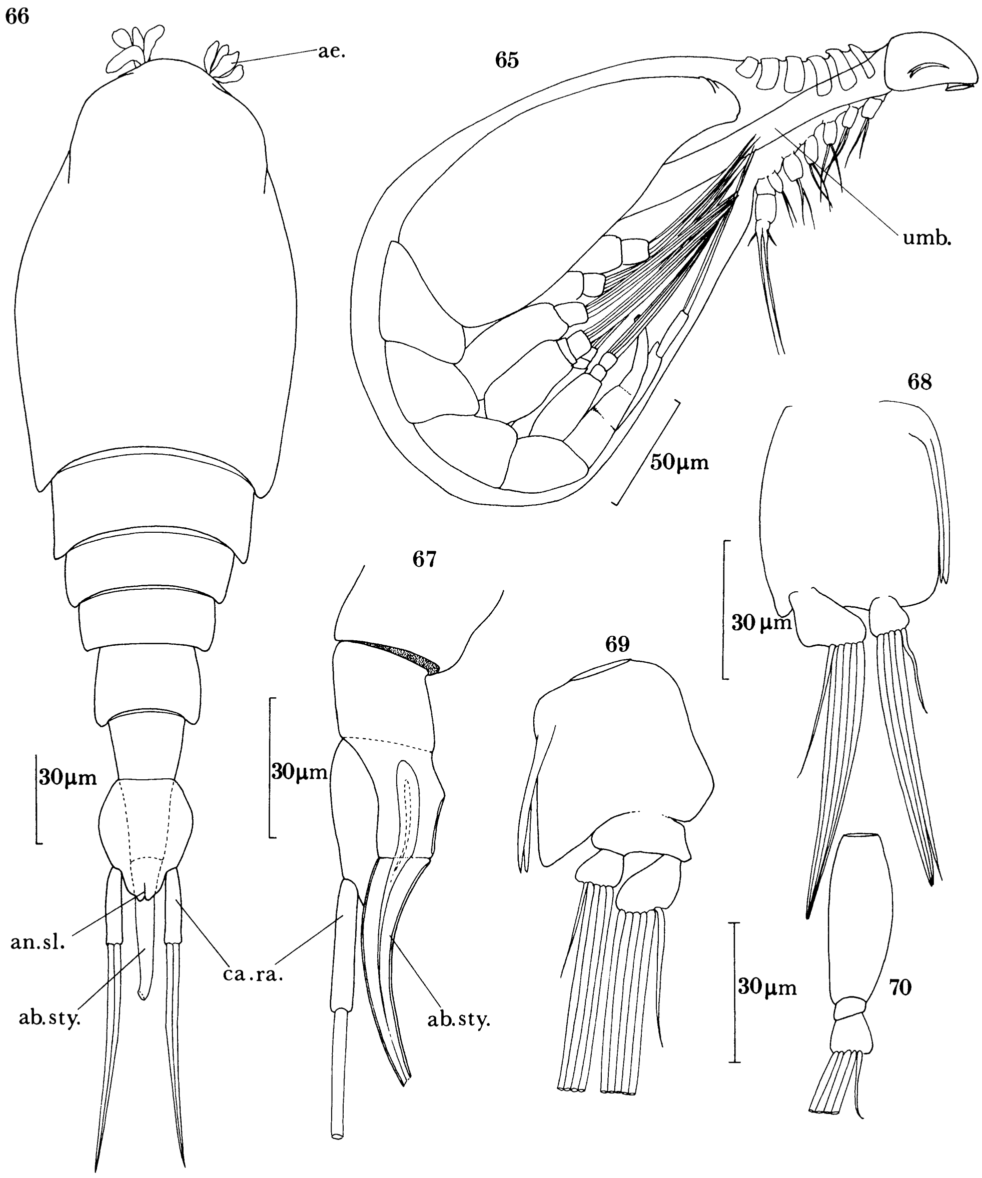


Figure 65. Adult male of *M. langi* contained within trunk sac formed by the preceding tantulus stage.

Figure 66. Dorsal view of adult male, dissected out of trunk sac.

Figure 67. Lateral view of abdomen of male, showing curved abdominal stylet originating on the proximal abdominal somite.

Figure 68. Second thoracopod.

Figure 69. Fifth thoracopod.

Figure 70. Sixth thoracopod.

cephalothorax incorporating two pedigerous thoracic somites, four free thoracic somites and a two-segmented abdomen (figure 66). The cephalothorax is covered by a dorsal shield and is expanded anterolaterally into broad lobes. It bears the first two pairs of thoracopods but no cephalic appendages. The two clusters of aesthetascs (ae.) present on the anterior surface may represent vestigial antennules. Each free thoracic somite has produced posterolateral angles and each is narrower than the preceding one.

The abdomen consists of two somites, the first tapering posteriorly, the second with convex lateral margins and a posterior anal slit (an.sl.) in the midline. The first somite bears the stylet, the broad base of which continues as a posteroventral extension of the somite. The stylet is divided by a surface furrow into a rectangular proximal portion and a curved, robust distal portion (figure 67). It is hollow and has a large terminal opening but little internal structure is evident. The second somite bears a pair of slender caudal rami (ca.ra.), each armed with two setae.

The thoracopods are similar in segmentation and armature to those of male *D. harrisoni*. Thoracopods 1–3 (figure 68) have an unsegmented protopod bearing two one-segmented rami, thoracopods 4 and 5 (figure 69) a two-segmented protopod bearing them. Thoracopod 6 (figure 70) is uniramous and three-segmented. The armature elements were not fully developed.

(*b*) *Material examined*

Two early stage females from an unidentified juvenile tanaid host collected by D-net fished at a depth of 113 m at Cumbrae Elbow in the Firth of Clyde (53° 44′ N, 4° 59′ W) on 8 August 1984, BM(NH) registration number 1985.422. One late stage female was found on a specimen of *Leptognathiopsis attenuata* Holdich & Bird collected by Day grab at 22 m in the Lynn of Lorne, off the west coast of Scotland (56° 31′ N, 5° 26′ W) on 4 April 1984. BM(NH) registration number 1985.423. The latter specimen was collected by Dr D. Holdich (Nottingham University). Five tanaids infected with *M. langi* were examined on loan from Bergen Museum. Four specimens of *Leptognathia breviremis* (Lilljeborg) (registration numbers 64105, 64110, 64111 and 64113) were infected with two swollen females and a tantulus larva (registration numbers 64120*a–c*), a swollen female (registration number 64126), a head fragment (registration number 64134) and a swollen female (registration number 64129) respectively. The single *Typhlotanais aequiremis* (Lilljeborg) (registration number 64117) carried two swollen females (registration numbers 64128*a*, *b*). All these tanaids were collected by Ockleman dredge off a muddy bottom at 120–130 m in Raunefjorden, off Sletten, Norway. Several hundred specimens, including three developing males, were caught by Beyer net at 120 m in Raunefjorden in September 1985; the first ten specimens have been allocated BM(NH) registration numbers 1985.424–433.

(*c*) *Taxonomic remarks*

Microdajus was originally regarded as an epicaridean isopod and referred to the family Dajidae by Greve (1965). The larval stage exhibits the same tagmosis as the tantulus of *Deoterthron* and the similarities in cephalic anatomy indicate a close relationship between these genera. *Microdajus* lacks recognizable cephalic appendages but possesses the single cephalic stylet and the oral disc characteristic of the Tantulocarida. It possess six pairs of thoracopods, but without the endites on the first five pairs and with much reduced segmentation. Despite these differences *Microdajus* is herein placed in the Tantulocarida on the basis of its larval tagmosis and cephalic anatomy.

The adult male of *M. langi* differs significantly from that of *D. harrisoni* in having a two-segmented abdomen and paired caudal rami. The robust abdominal stylet is curved and originates from the first somite whereas the slender stylet of *D. harrisoni* originates distally on the slender, unsegmented abdomen. Finally the caudal rami are more primitive compared with those of *D. harrisoni* which are probably represented by the paired caudal setae.

5. *MICRODAJUS GAELICUS* SP.NOV.

(*a*) *Description*

(i) *Tantulus larva*

The body is about 120 µm long (figure 71) and has the same tagmosis as that of *M. langi*. The head is longer than it is wide and, using light microscopy, lacks surface ornamentation except near its posterior margin where a line of pores and a pair of lateral setules are present. Internally a pair of chitinous bars (figure 72, ch.) lead towards the central pore of the oral disc (o.d.), and a thick walled tubular structure (g.), possibly the gut, extends posteriorly from the bases of these bars. The stylet (c.sty.) is slightly curved and about 30 µm long. A cylindrical structure (cy.) was observed extending into the host from the puncture point (p.p.) in its integument. The thoracic tergites are not conspicuously ornamented. The two-segmented abdomen is short and bears one long and two short pairs of caudal setae.

The thoracopods (figure 71) are reduced as in *M. langi*. They lack endites and appear to lack distinct rami. The protopods are not bilobed as they are in *M. langi*, but have a slightly concave distal margin bearing two long curved setae except in the sixth pair. It is difficult to determine which ramus these setae represent. Thoracopod 6 bears a single, straight seta.

(ii) *Female development*

Many early stage females (figure 74) were found in which the larval trunk had been sloughed leaving a scar on the ventral surface behind the head. At this stage the trunk sac is small, appears to be drawn out from a narrow region just behind the head, and contains an undifferentiated mass of tissue. It continues to swell, attaining lengths up to 560 µm (figure 75), prior to developing a distinct neck. Further increase in size accompanies the drawing out of a long neck region (figure 76). Eggs at the eight-celled stage were present within the trunk sac which has a wrinkled integument, presumably to allow further swelling.

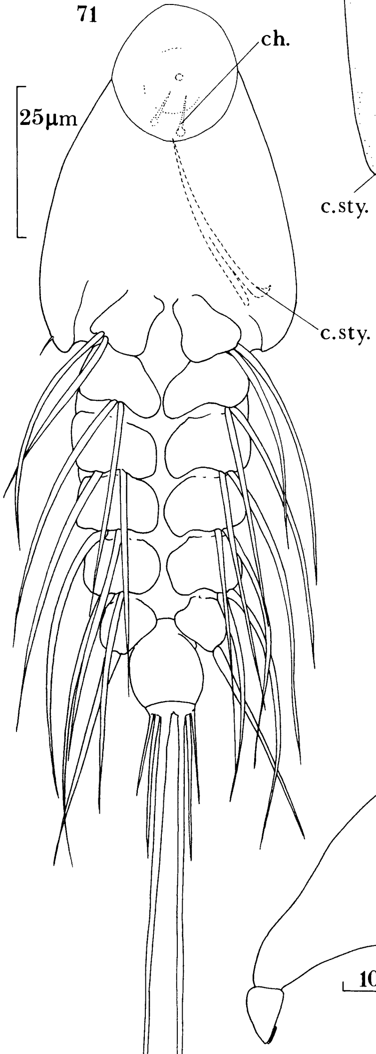
A single specimen was found in which trunk sac formation had commenced but the larval trunk was still present in a ventrally deflected position (figure 73). The larval trunk was accidently knocked off, leaving a raised circular scar (sc.) as in the other early stage females.

(*b*) *Material examined*

Holotype tantulus larva attached to the head of a *Typhlotanais pulcher* Hansen collected by epibenthic sledge at a depth of 2897 m at 55° 08′ N, 12° 53′ W (station 1.8) on 20 July 1976. Paratypes: ten developing females and one female with larval trunk from five host individuals in the same sample; one female from a *T. pulcher* caught by beam trawl in 2893 m at 55° 02′ N, 12° 41′ W on 4 July 1976; two females from two *T. pulcher* caught by beam trawl in 2895 m at 55° 04′ N, 12° 46′ W on 20 July 1976; one tantulus and seven females from three *T. pulcher* caught by beam trawl in 2884 m at 55° 00′ N, 12° 31′ W on 19 July 1976. All material was collected during INCAL cruises and the tantulocaridans were found by Dr G. Bird (University of Nottingham) during examination of the tanaids sorted by the Centre National de Tri d'Océanographie Biologique, Brest (CENTOB). Holotype and 11 paratypes stored in the Muséum National d'Histoire Naturelle in Paris, numbers Tt04–05; 11 paratypes stored in the BM(NH), registration numbers 1985.434–443.

Etymology. The specific name refers to the Gaelic speaking area off the west coast of Scotland, near which the material was collected.

71



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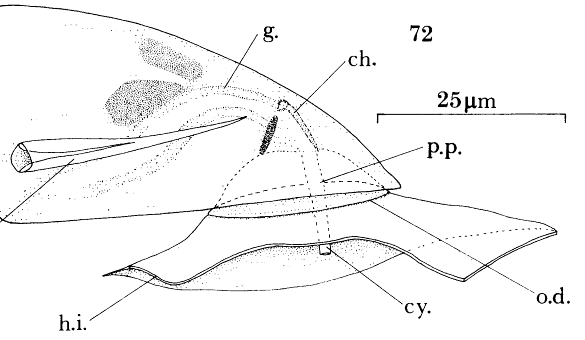

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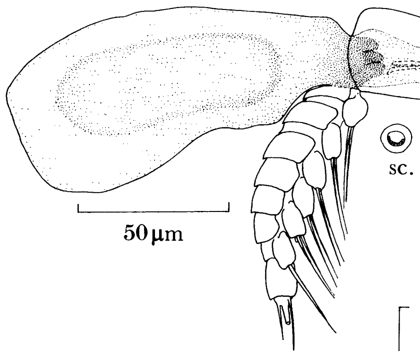

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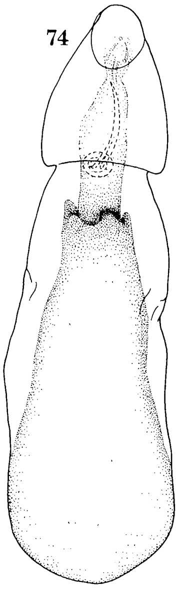

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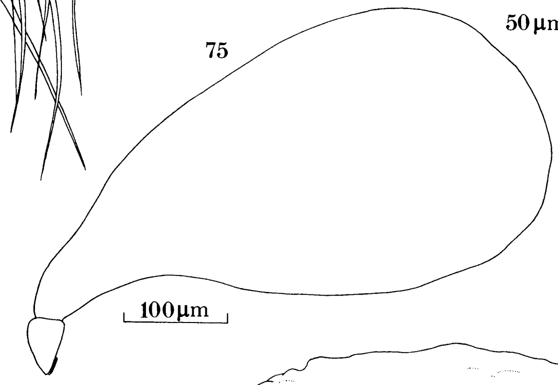

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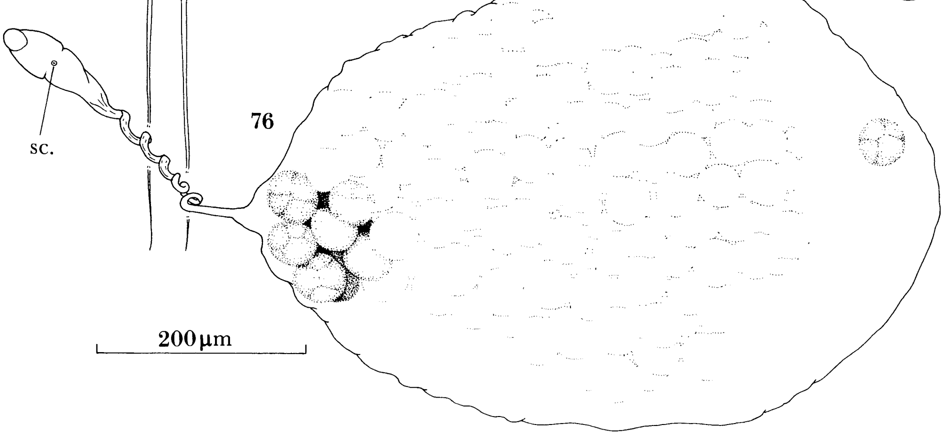


Figure 71. Ventral view of tantulus of *M. gaelicus* sp.nov., showing armature of thoracopods and abdomen.

Figure 72. Lateral view of head of *M. gaelicus* tantulus attached to host integument, showing internal anatomy.

Figure 73. Early stage female of *M. gaelicus*, showing small trunk sac forming behind head and deflected larval trunk. Inset shows ventral scar left when larval trunk was accidently knocked off.

Figure 74. Dorsal view of early stage female, showing contents of trunk sac.

Figure 75. Large empty female *M. gaelicus* with swollen trunk sac but no neck region.

Figure 76. Gravid female of *M. gaelicus* containing developing eggs and possessing a long twisted neck.

(*c*) *Taxonomic remarks*

The new species is placed in *Microdajus* because of its reduced thoracopods, two-segmented abdomen and ornamentation of the head shield, all of which are shared with *M. langi*. It differs from *M. langi* in its narrower head shield and in the sixth thoracopod which has a single straight seta whereas in *M. langi* it has two curved setae.

6. *ONCEROXENUS* GEN.NOV.

Diagnosis: Basipodellidae; tantulus larva with first thoracic tergite concealed beneath posterior margin of dorsal cephalic shield; thoracopods 1–5 of tantulus with well developed rami and endites, uniramous thoracopod 6 with paired coupling spines on protopod; abdomen of tantulus three-segmented; adult male formed within trunk sac formed posterior to sixth thoracic tergite of preceding stage.

Type species: *Onceroxenus birdi* gen. et sp.nov.

Etymology. The generic name is derived from the Greek *onkeros*, meaning swollen, and *xenos*, meaning stranger.

(*a*) *Onceroxenus birdi* gen. et sp.nov.

(i) *Tantulus larva*

The length is about 100 μm from the tip of the rostrum to the posterior margin of the abdomen (figure 77). The body consists of head, six segmented thorax and three segmented abdomen. The head tapers anteriorly towards a broad based rostrum. It is ornamented with a system of fine longitudinal and transverse lamellae and associated pores which are mapped in figures 78 and 79, compiled from scanning electron micrographs. The cephalic stylet is only slightly curved and is about 25 μm long. The first thoracic somite is almost completely overlain by the cephalic shield (figure 77). The tergites of all six thoracic somites are ornamented with longitudinal lamellae (figure 64, plate 6). The abdomen is about 18 μm long and comprises a narrow first somite and a swollen posterior portion which consists of at least two somites separated by a highly ornamented suture line (figure 83, plate 7). It bears conspicuous caudal rami posteriorly, which are directed somewhat dorsally. These appear segmented and bear an apical armature as well as elements arising to the side of the ramus base. The middle segment of the abdomen has surface ornamentation which suggests that it may have been derived by the fusion of two original somites (figure 83, plate 7).

The thoracopods have the structure typical for the group. In the first five pairs a large protopod bears the endite and two rami. Thoracopod 1 (figure 80) has a short endopod lacking any long setae, but with an apical spine. The exopod is two-segmented and bears two distal setae. Thoracopods 2–5 (figure 81) each have an elongate endopod bearing two outer margin setae and an apical spatulate spine which is opposed by a long spiniform process originating at the tip of the ramus. The exopod is two-segmented and armed with four setae. Thoracopods 1–5 each possess an endite, whose armature could not be ascertained by light microscopy. Thoracopod 6 is uniramous, lacks an endite and bears two setae on its one-segmented ramus (figure 82). It bears a pair of coupling spines (cop.) on the medial margin of the protopod.

(ii) *Male development*

Two specimens were found which belong in the male developmental sequence. One has just commenced swelling at the rear of the thorax, posterior to the sixth thoracic tergite but in front

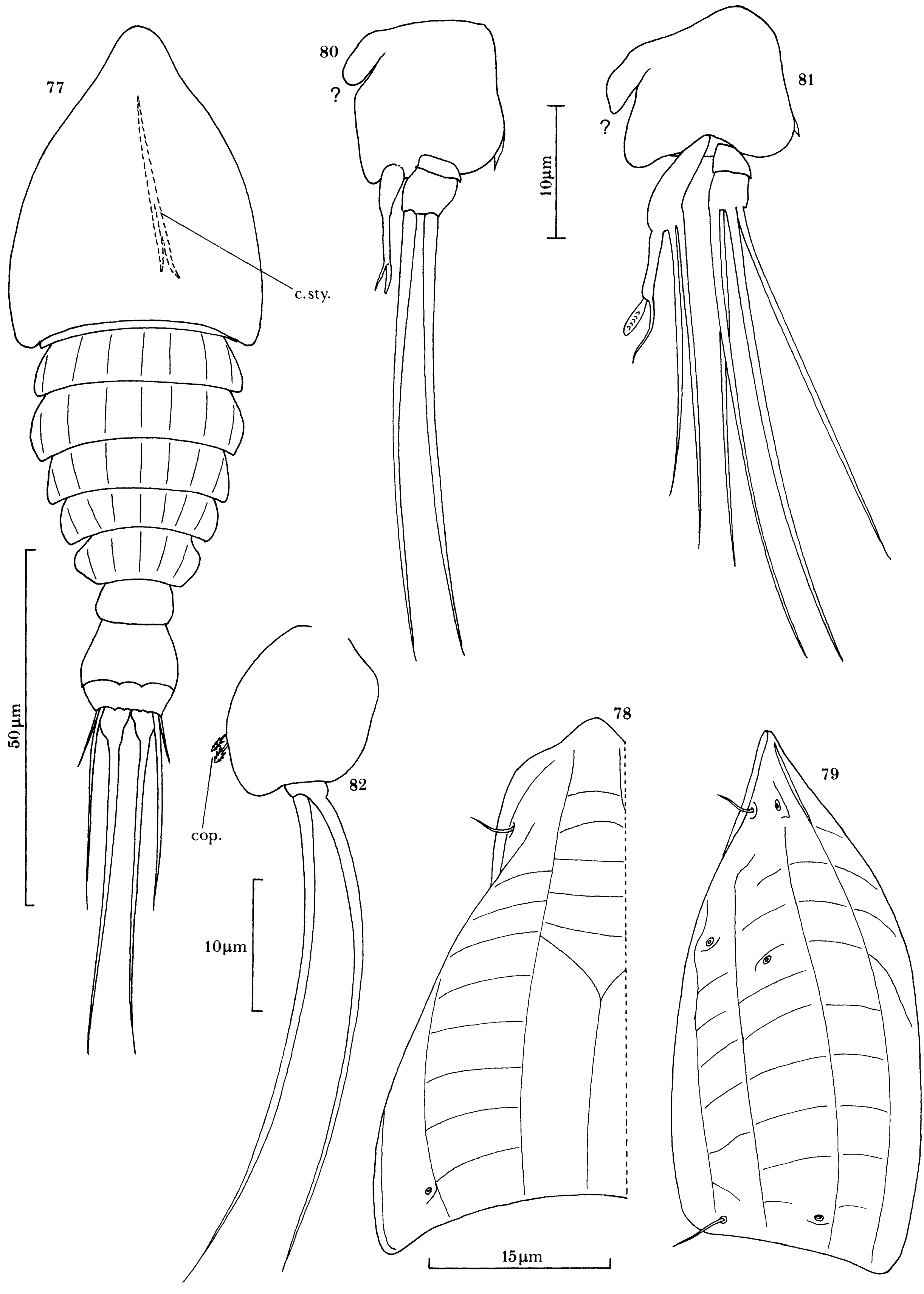


FIGURE 77. Dorsal view of tantulus of *O. birdi* gen. et sp.nov.

FIGURE 78. Dorsal view of left side of head shield, showing ornamentation and pore distribution, compiled from scanning electron micrographs.

FIGURE 79. Lateral view of the same, compiled from scanning electron micrographs.

FIGURE 80. First thoracopod of tantulus.

FIGURE 81. Second thoracopod of tantulus.

FIGURE 82. Sixth thoracopod of tantulus.

of the abdomen (figure 88). The head shield is unchanged from the larval condition (figure 87) and the abdomen is deflected ventrally by the sac. The other specimen is at an advanced stage of development contained within the sac of the preceding stage (figure 89). The tagmosis is similar to that of adult male *D. harrisoni* and limb buds with developing setae are present. The developing male derives its nutritional requirements via an umbilical cord which, in this specimen, has a distinct tubular appearance (figure 89, umb.). The male was slightly damaged and was not dissected from its enclosing sac but other features, such as the aesthetascs (ae.) on the front margin of the head, were observed.

(iii) *Female development*

Only females early in transformation were found (figure 90). The sac-like trunk had just commenced expansion but was still covered with highly folded integument. None had the thorax or abdomen attached and each had a circular scar (sc.) on the ventral surface behind the head, marking the site at which they were sloughed.

(iv) *Material examined*

Holotype male contained within trunk sac of preceding stage attached to pereopod 6 of male *Paranarthrura insignis* Hansen collected by Usnel corer at a depth of 2187 m at 47° 34′ N, 8° 39′ W (station KG 155) during the BIOGAS VIII cruise on 5 June 1979. Paratypes: two tantulus larvae and one tantulus and an early male obtained from a neuter and a male *P. insignis* respectively collected by epibenthic sledge at 4104 m at 47° 32′ N, 9° 36′ W (station DS 42) during the BIOGAS III cruise on 27 August 1973; two tantulus larvae, three head shields and three early females obtained from a neuter *P. insignis* collected by Usnel corer at 2798 m at 47° 32′ N, 9° 05′ W (station KG 168) during the BIOGAS IX cruise on 16 May 1980; one head shield attached to a manca stage of *P. insignis* collected by epibenthic sledge at 4190 m at 47° 32′ N, 9° 41′ W (station DS 21) during the POLYGAS cruise on 24 October 1972. All material was found by Dr G. Bird during examination of the host tanaids sorted by CENTOB. Holotype and eight paratypes stored in collections of Muséum National d'Histoire Naturelle in Paris, numbers Tt01–03; five paratypes stored in BM(NH) numbers 1985.444–448.

Etymology. The species is named after its discoverer, Dr G. Bird.

(v) *Taxonomic remarks*

The new genus differs from other genera in the possession of a three-segmented abdomen in the tantulus larva. *Basipodella* has six abdominal somites and both *Microdajus* and *Deoterthron* have two. There is also an indication in the surface ornamentation of the middle somite that the abdomen may be derived by the fusion of more somites. The new genus is placed in the Basipodellidae on the basis of its abdominal segmentation and because it shares with *Basipodella* the site of formation of the trunk sac in the male tantulus. The sac forms immediately posterior to the sixth thoracic tergite in *B. harpacticola* and the new genus, whereas in *Deoterthron* it forms between the fifth and sixth tergites. It forms behind the sixth tergite in *Microdajus* but this genus differs in larval thoracopod structure.

(*b*) *Onceroxenus curtus* sp.nov.

(i) *Female development*

The only stages collected belong to the female sequence. Two specimens are at an early stage, comprising the head and a small trunk sac. Neither possesses the larval thorax and abdomen,

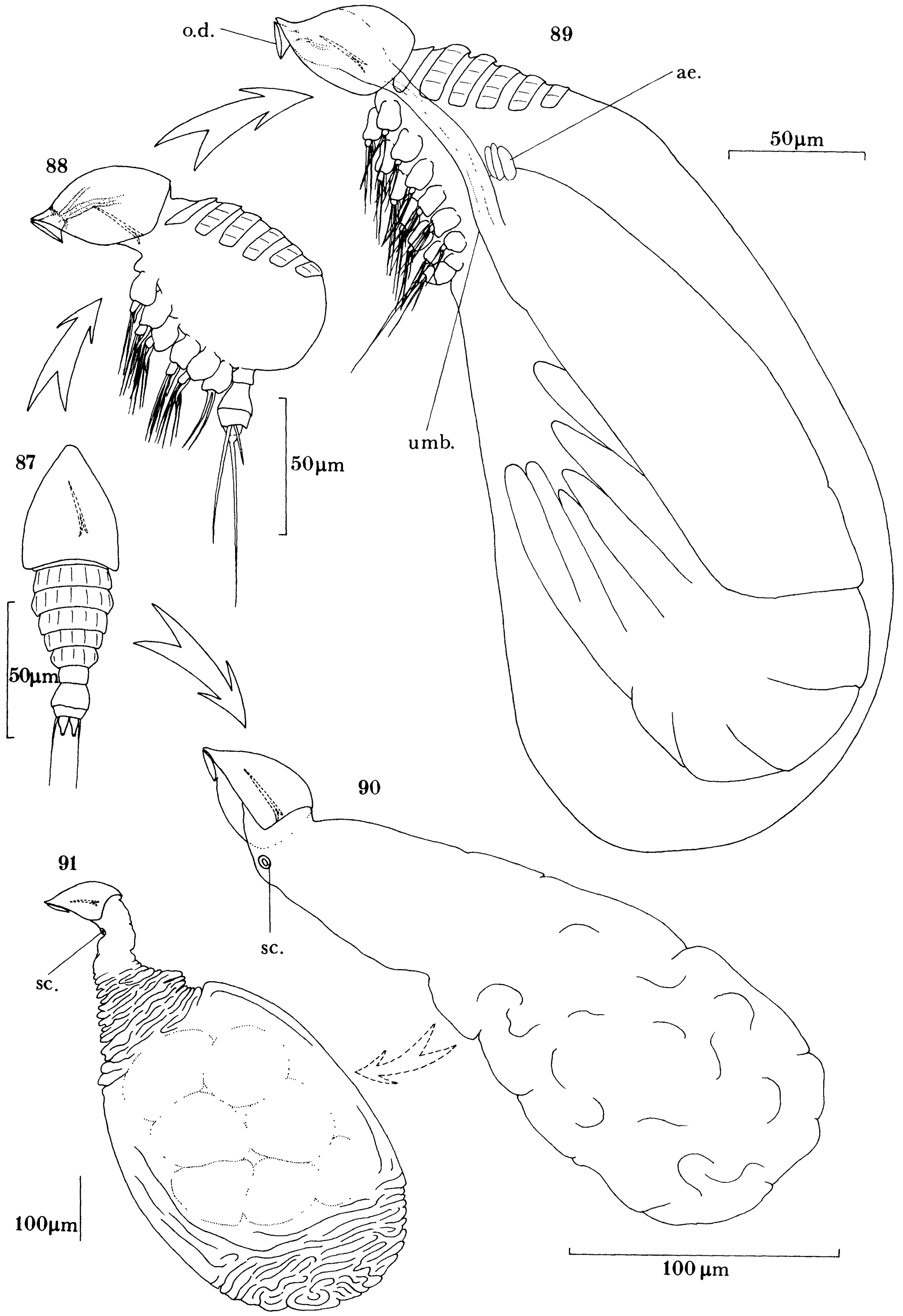


FIGURE 87. Tantulus of *O. birdi*.

FIGURE 88. Early stage male of *O. birdi* showing site of formation of trunk sac posterior to sixth thoracic tergite.

FIGURE 89. Adult male of *O. birdi* contained within trunk sac of preceding stage, showing tagmosis and limb buds of male and the umbilical cord.

FIGURE 90. Early stage adult female of *O. birdi* showing ventral scar and small trunk sac with wrinkled integument.

FIGURE 91. Adult female of *O. curtus* showing short neck region and swollen trunk sac covered with highly folded integument.

the position of which is marked by a small raised scar (sc.) on the ventral surface immediately behind the head. The head shield is slightly longer than wide and the oral disc is near the anterior margin. There is no rostrum. The surface ornamentation consists of a system of transverse and longitudinal lamellae extending over the entire shield.

Three specimens were at a more advanced stage (figure 91). The trunk sac is 340 μm in length, but its surface is highly folded and convoluted (figure 85, plate 7). The cephalic shield bears a system of transverse and longitudinal lamellae similar to that of *O. birdi* and the distribution of pores is also similar but they could not all be mapped from the single specimen available for SEM study (figure 84, plate 7). One specimen contained many differentiated eggs with a diameter of about 37 μm, another a small number of larger eggs (figure 91) and the third an undifferentiated cellular mass. All displayed the same circular scar (sc.) behind the head marking the site of sloughing of the thorax and abdomen.

(ii) *Material examined*

Holotype adult female containing eggs taken from a tanaid tentatively identified as *Leptognathia zezinae* Kudinova-Pasternak collected at a depth of 2907 m at 54° 44′ N, 12° 15′ W on 10 April 1981; BM(NH) registration number 1985.449. Paratypes: one adult female from the same host individual; one adult female from another individual of the same host collected at 2540 m at 56° 37′ N, 11° 04′ W on 4 July 1973; two early stage females from another specimen of the same host collected by beam trawl at 2513 m at 56° 32′ N, 11° 12′ W on 17 July 1976; BM(NH) registration numbers 1985.450–453. All material of *O. curtus* was found by Dr G. Bird in the collections of the Scottish Marine Biological Association.

Etymology. The specific name refers to the short neck of the adult female.

(iii) *Taxonomic remarks*

This species is placed in the genus *Onceroxenus* on the basis of its head shield ornamentation, which is very similar to that of *O. birdi*. Detailed taxonomic comparisons cannot be made because its tantulus larva is unknown. However, this species differs from *O. birdi* in the precise arrangement of transverse lamellae on the head shield (cf. figures 79 and 84).

7. Systematics of the Tantulocarida

The Tantulocarida now comprises five genera and eleven species, all parasitic on other crustaceans. The discovery of tantulocaridans at several separate localities in the northeast Atlantic over a depth range of over 4000 m to only 22 m is an indication that these parasites are probably common but have previously been overlooked. Although variation within the largest genus, *Deoterthron*, is mostly limited to relatively small features of shape or thoracopod armature there are major differences between the known genera. To reflect these differences and to provide a framework for the incorporation of further new taxa it is proposed to establish two new families.

Class Tantulocarida Boxshall & Lincoln, 1983

Family Basipodellidae Boxshall & Lincoln, 1983

Diagnosis: Tantulocarida with three to six abdominal somites and with thoracopodal endites in the tantulus larva; trunk sac containing adult male formed posterior to sixth thoracic tergite.

Type genus: *Basipodella* Becker, 1975
  Type species: *Basipodella harpacticola* Becker, 1975
  Other species: *B. atlantica* Boxshall & Lincoln, 1983
 Other genera: *Onceroxenus* gen.nov.
  Type species: *Onceroxenus birdi* gen. et sp.nov.
  Other species: *O. curtus* gen. et sp.nov.

Family Deoterthridae nov.

Diagnosis: Tantulocarida with a two-segmented abdomen and thoracopodal endites in the tantulus larva; trunk sac containing adult male formed between thoracic tergites five and six; paired caudal setae present on the unsegmented abdomen of the adult male, caudal rami lacking.

Type genus: *Deoterthron* Bradford & Hewitt, 1981
  Type species: *Deoterthron dentatum* Bradford & Hewitt, 1980
  Other species: *D. aselloticola* Boxshall & Lincoln, 1983
    D. megacephala Lincoln & Boxshall, 1983
    D. harrisoni sp.nov.

Family Microdajidae nov.

Diagnosis: Tantulocarida with a two-segmented abdomen but lacking thoracopodal endites in the tantulus larva; trunk sac containing adult male formed posterior to sixth thoracic tergite: adult male with two-segmented abdomen, bearing distinct caudal rami.

Type genus: *Microdajus* Greve, 1965
  Type species: *Microdajus langi* Greve, 1965
  Other species: *M. gaelicus* sp.nov.

Incertae sedis

Genus: *Cumoniscus* Bonnier, 1903
  Type species: *Cumoniscus kruppi* Bonnier, 1903

This genus is known from a single adult female and cannot be placed in a family. It is sac-like and firmly attached to its host by a minute adhesive disc at its anterior end. These characters indicate that *Cumoniscus* probably belongs in the Tantulocarida.

8. Host–parasite relationships

(*a*) *Location on host*

Tantulocaridans can be found all over the body and appendages of their hosts. The positions of *D. harrisoni* on the isopod *Macrostylis magnifica*, are shown in figure 92. There appears to be a predilection for the propodus of the first pereopods which may be related to the way in which hosts encounter infective larvae but too little is known about the behaviour of both parasite and host to offer any explanation. No specimens were found on the host's pleopods.

O. birdi is found all over its host, *Paranarthrura insignis*, including the pleon and pleopods which

92

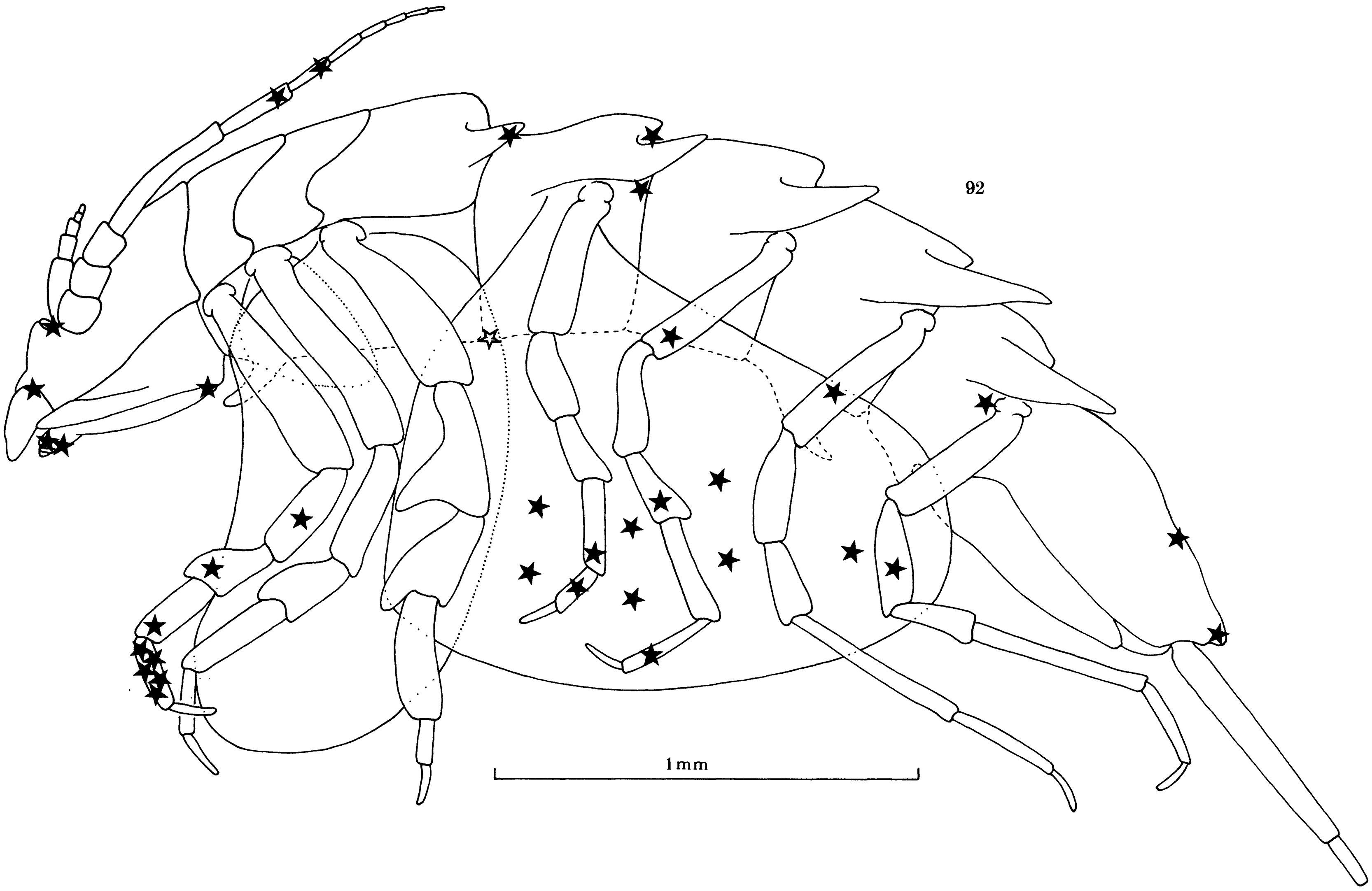


Figure 92. Lateral view of isopod *Macrostylis magnifica* with oostegites folded out, stars showing attachment sites of *D. harrisoni*.

are exposed in tanaids. *O. curtus* and *M. langi* are similarly distributed over the body and appendages of their hosts. The presence of such relatively large, inflated parasites (figures 93 and 94) will almost certainly interfere with the normal behaviour of the host. *M. gaelicus* was found on a tubicolous tanaid, *Typhlotanais pulcher*, especially on the head and anterior thoracic somites, and their appendages (figure 95). These are the parts of the body which will be extended from the opening of the tanaid's burrow during feeding and are thus the most easily available sites for the tantulus larvae.

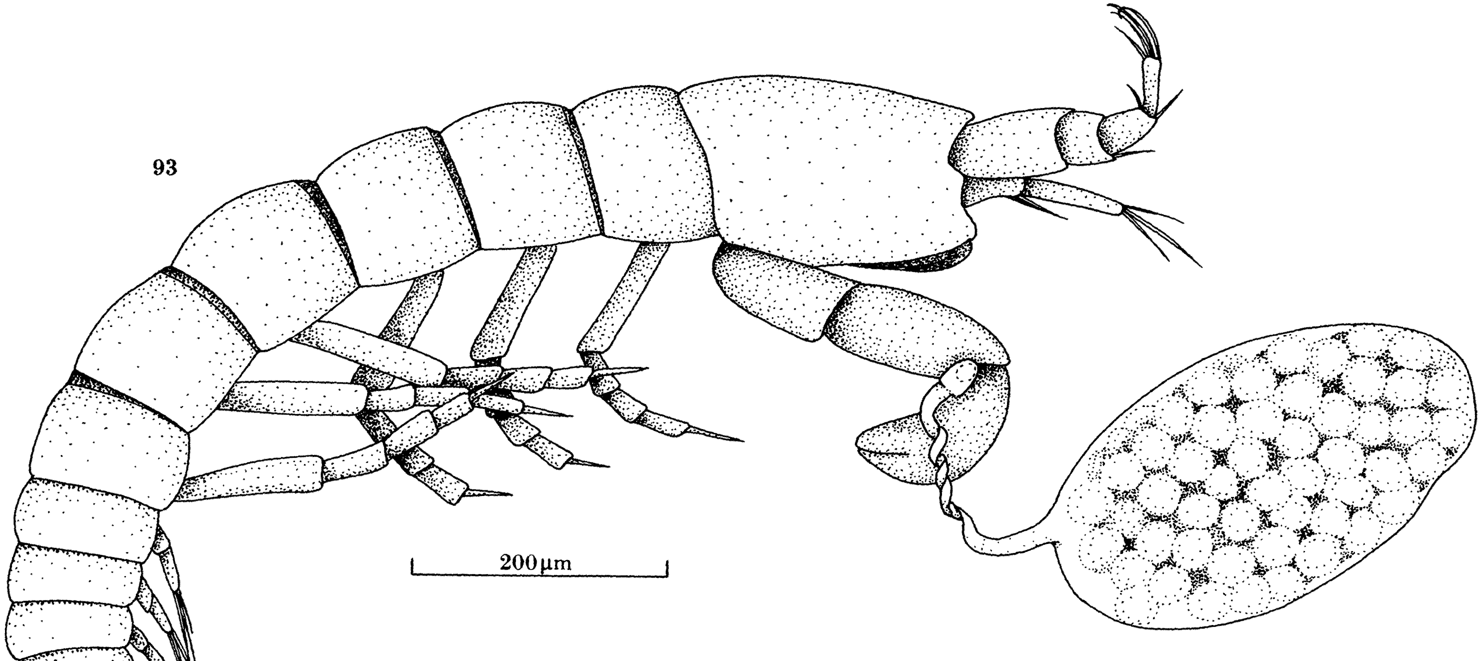
(*b*) *Population dynamics*

The availability of a series of samples taken at different seasons (table 1) permits some assessment of the interrelationship between *M. magnifica* and its infestation by *D. harrisoni*. The population of *M. magnifica* was centred at a depth of about 2000–2200 m though isolated specimens were collected down to 2900 m. *D. harrisoni* occurred only between 2076 and 2200 m at stations 12, 197, 232 and 244. The last three stations provide evidence of marked seasonal changes in the reproductive status of the host population (table 2). At station 197 in August 1981 the *M. magnifica* population comprised mainly preparatory females lacking oostegites (72 %), adult males (16.5 %) and mancae (11 %), with very few ovigerous females (< 0.5 %). In May 1983 there were about equal numbers of adult males (31 %), ovigerous females (24 %) and females lacking oostegites (31 %). Just two months later, in July 1983, the population resembled that of August 1981, with few ovigerous females (2 %). These changes in the population of *M. magnifica* are consistent with a reproductive cycle in which breeding takes place mainly in the late spring, followed by a moult of oostegite-bearing females that then revert to the preparatory condition. Moulting of a substantial proportion of the host population within a short period will have a profound effect on the ectoparasitic *D. harrisoni* population. The parasites will be shed along with the exuvium to which they are permanently attached. This effect can be seen in the July 1983 sample in which most preparatory females, having presumably just passed through a post-reproductive moult, have a clean integument devoid both of tantulocaridans and of the usually conspicuous load of epizoic microorganisms. Tantulocaridans do not appear to have the ability to suppress moulting in the hosts, as do some rhizocephalans (Veillet 1945).

(*c*) *Attachment and feeding*

Tantulocaridans lack cephalic appendages at all stages of their life cycle. Attachment to the host is effected by means of the oral disc which is closely applied to the host integument and is probably held there permanently by means of an adhesive secretion. The attachment can be permanent because the parasite completes its development on the host without moulting. Attempts to remove a parasite from its host result in tearing off the integument of the host in the area beneath the oral disc revealing the underlying tissue and a puncture point, the position of which coincides with the centre of the disc. In *D. harrisoni* the puncture diameter is about 2 μm and it presumably marks the point of penetration of the tubular structure observed in *D. aselloticola* (Boxshall & Lincoln 1983). Similarly, when a specimen of *M. langi* was removed, part of the host's integument was torn away. Viewed from inside a circular puncture of 0.5 μm diameter was seen, in a position corresponding to the centre of the oral attachment disc. The puncture is the only access the parasite has to the body fluids of the host so all nutrients required by the metamorphosing adults must pass through it.

93



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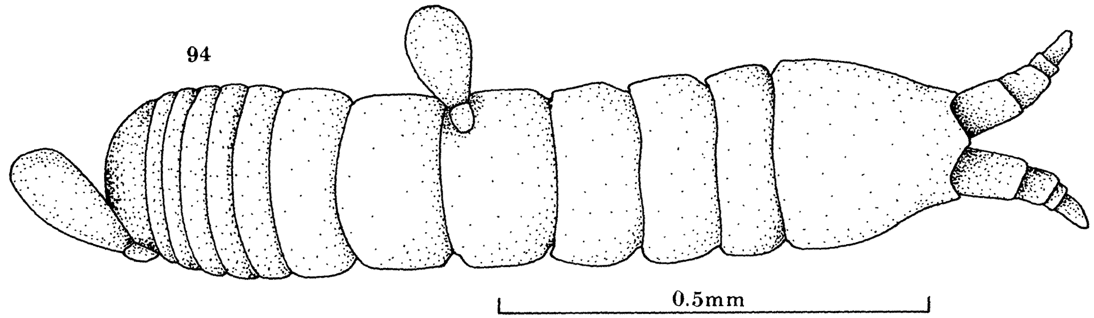

FIGURE 93. *Leptognathia breviremis* from Raunefjorden, Norway, with attached female *M. langi*.

FIGURE 94. Unidentified juvenile tanaid from Firth of Clyde, with two early stage female *M. langi* attached.

95

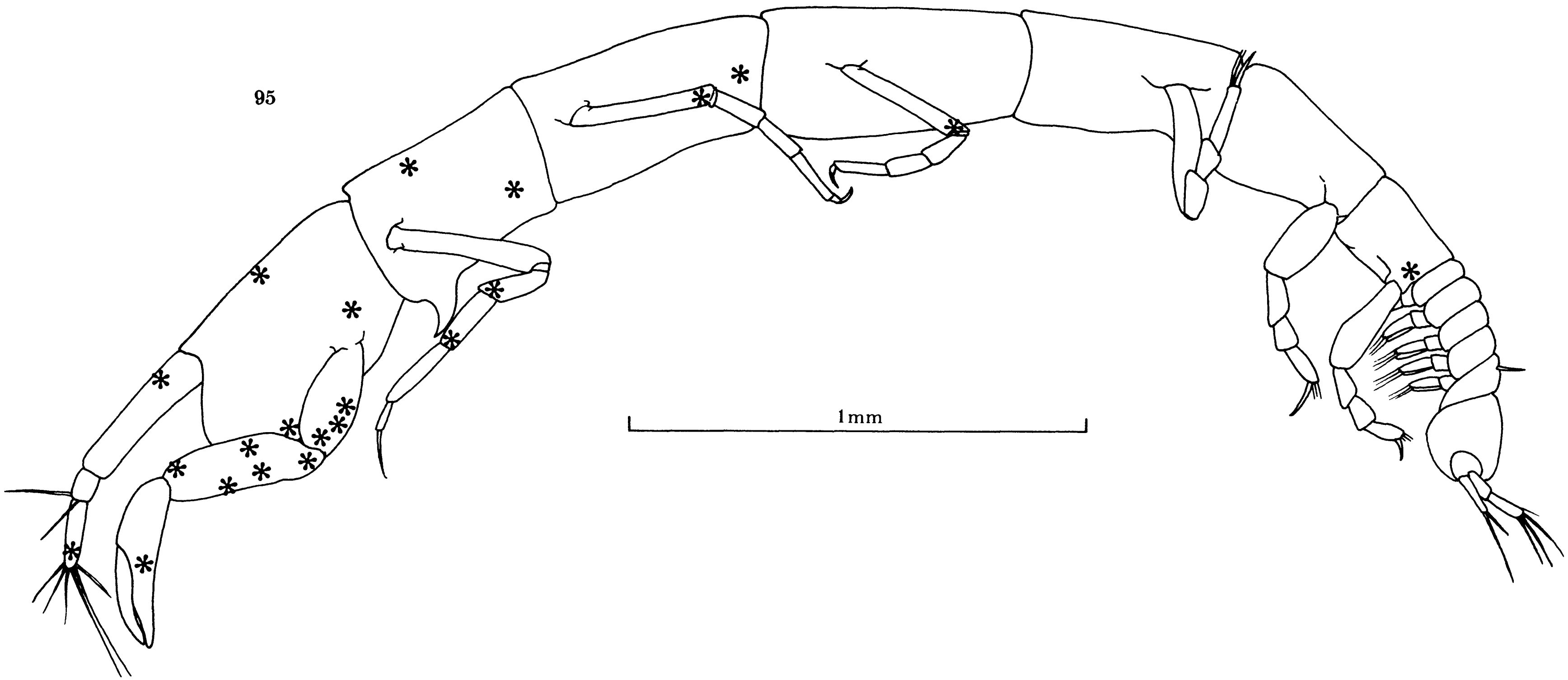

FIGURE 95. The tubicolous tanaid *Typhlotanais pulcher* from the Rockall Trough, asterisks showing attachment sites of *M. gaelicus*.

TABLE 2. *MACROSTYLIS MAGNIFICA* POPULATION AGE STRUCTURE

station	adult males	immature males	ovigerous females	preparatory females	mancae	fragmented specimens
4	19	—	19	15	3	2
6	2	—	6	7	—	1
12	16	—	—	59	68	6
27	—	—	2	1	—	—
55	—	—	1	—	—	—
111	—	—	1	—	—	—
137	1	—	1	2	—	—
143	—	—	—	—	1	—
180	1	—	—	1	—	—
185	—	—	—	1	—	—
197	191	—	4	827	130	7
232	27	2	21	27	10	—
244	142	1	12	400	27	16

An adult female *O. curtus* was also removed, still attached to a piece of torn integument. Viewed from the inside a raised cylindrical structure can be seen (figure 86, plate 7) in a position corresponding to the middle of the oral disc. This appears to be the puncture point, lined in some way, as it passes into the tissues of the host. A small strand protrudes from the internal end of this puncture and may be a remnant of a parasite organ which normally extends into the host. The diameter of the puncture is about 1.3 μm.

In all these species there is evidence that a puncture is made through the host integument approximately in the middle of the oral attachment disc, probably by the cephalic stylet of the tantulus, the tip of which is often located close to the central pore of the oral disc. The holes vary in diameter but are all minute. Clearly the parasite can take in only fluids, either host body fluids or predigested tissues.

(*d*) *Host specificity*

The two species of *Basipodella* parasitize harpacticoid copepods but none of the host species has been identified. *Cumoniscus* parasitizes a cumacean of the family Leuconidae. The type species of *Deoterthron*, *D. dentatum*, is found on the myodocopid ostracod *Metavargula mazeri* Kornicker (Kornicker 1979). The three other known species of the genus are found on deep-sea asellote isopods, each on one host species only. Two species occur on hosts belonging to the family Haploniscidae: *D. aselloticola* on *Hydroniscus lobocephalus* Lincoln and *D. megacephala* on *Haploniscus tangaroae* Lincoln. *D. harrisoni* occurs only on *Macrostylis magnifica* in the family Macrostylidae. The other two tantulocaridan genera are found on tanaid hosts. *M. langi* was found on *Haplocope angusta* Sars, *Leptognathia breviremis* (Lilljeborg) and *Typhlotanais aequiremis* (Lilljeborg) by Greve (1965). Specimens parasitizing *Leptognathia gracilis* (Krøyer) are present in the collections of Bergen Museum. Here we record *M. langi* on *Leptognathiopsis attenuata* Holdich & Bird and on an unidentified juvenile tanaid. The new species, *M. gaelicus* was found only on *Typhlotanais pulcher* Hansen. Hansen (1913) figures an attached tantulus on *Typhlotanais variabilis* Hansen and refers to it as a minute parasitic copepod. All records of the genus *Microdajus* involve hosts belonging to the family Leptognathiidae. *Onceroxenus curtus* also parasitizes a member of the Leptognathiidae whereas *O. birdi* is found on *Paranarthrura insignis* Hansen, belonging to the tanaid family Anarthruridae.

Tantulocaridans occur on copepod, ostracod, cumacean, isopod and tanaid hosts and exhibit varying levels of host specificity. Some species occur on hosts of more than one family (*Basipodella harpacticola*), others on a single host species. They may well be more common than hitherto expected as they are difficult to see when attached to the host. This may introduce a bias into the collecting process because later developmental stages are more readily observed than the tantulus larvae. Also, all stages are easier to observe on tanaids than on heavily calcified deep-sea asellotes (figure 1, plate 1).

9. The life cycle

Tantulocaridans hatch as a tantulus larva. The tantulus contained within the egg membrane is identical to that found on the host, possessing cephalic stylet, oral disc and a complete set of thoracopods. It is probably infective immediately on hatching. The course of development after it attaches to a host can now be postulated, based on the different stages described above. In *D. harrisoni* the tantulus develops in one of three ways: it can begin to swell immediately posterior to the cephalic shield, causing the ventral deflection of the retained larval thorax and abdomen, it can swell in the same position but slough the larval trunk leaving a raised circular scar to mark the site, or it can swell between thoracic somites five and six. The most complete sequence of stages is available for the latter pathway (figures 23–27) and this leads to the production of an adult male by a remarkable reorganization process. A complete sequence of stages is not available for the females in *D. harrisoni* but is in *M. langi* (figures 55–58). Here swelling commences behind the cephalic shield and the larval trunk is sloughed, leaving a circular scar on the ventral body surface. The trunk continues to swell forming an enormous sac containing eggs which develop into fully formed tantulus larvae before hatching. This is clearly a female pathway. Evidence of a possible third pathway comes from *D. harrisoni* in which a few specimens are swollen behind the cephalic shield but retain the larval trunk (figures 49 and 50). The largest specimen of this sort (figure 50) is larger than that containing the adult male but is empty. A single specimen with this configuration was also found in *M. gaelicus* (figure 73) but during attempts to reposition it after drawing, the larval trunk was detached leaving a raised circular scar typical of the female pathway in which the trunk is sloughed (figures 74–76). This suggests that the third pathway merely represents females in which sloughing of the larval trunk has failed.

Tantulocaridans have a female developmental pathway characterized by the development of a trunk sac behind the cephalic shield and by the sloughing of the larval trunk. Swollen forms with a ventral, raised, circular scar are known in four tantulocaridan genera. The structure referred to as the gonopore in adult female *B. atlantica* (Boxshall & Lincoln 1983, fig. 3*b*, *c*) is clearly the ventral scar. The larval trunk is sloughed very early in the swelling process (figure 45). There is no evidence of a moult and the tenfold increase in length is achieved by stretching and filling out of the highly folded integument of the trunk sac. This female pathway culminates in the production of infective tantulus larve.

Male development is characterized by the site of trunk sac formation near or at the back of the thorax. The larval trunk is retained. A profound reorganization of the body occurs within the trunk sac of the swollen tantulus. The male sequence is known for *Deoterthron*, *Microdajus* and *Onceroxenus* and these genera differ in the position of the trunk sac, formed between thoracic tergites 5 and 6 in the foremost, behind tergite 6 in the others.

The male is free-living and may serve as a dispersal phase. It is non-feeding, as it lacks a mouth, a cephalic stylet, functional mouthparts and any means of attachment, and is evidently a powerful swimmer, with large muscular thoracopods. Its sensory apparatus which includes two clusters of aesthetascs on the anterior margin of the head, a pair of dorsolateral processes bearing long setules and other scattered setules on the surface of the cephalothorax, is much more elaborate than that of the tantulus which must be able to locate a suitable host. However, the non-feeding, free-living male has to find a mate and presumably does so by use of the chemosensory aesthetascs.

How the male obtains its food as it grows inside the trunk sac of the tantulus is of interest. Food must be derived from the host via the only point of contact, the tantulus head and oral disc. Developing males have a tissue connection with the tantulus head in the form of an apparently tubular structure referred to above as the umbilical cord (figure 89, umb.). Nutriment must pass along this tube, the only available pathway. The tissue in the anterior part of the tantulus head is unchanged from the tantulus condition, in the posterior part it is separated from the integument by a space and is continuous with the umbilical cord. This is a remarkable situation, the tantulus head is supplying the nutritional requirements of the male as it redifferentiates and grows. The umbilical cord may contain the larval gut. If the larval gut is blind ending (no anus has been observed in the tantulus) the male may be organized around it, from the dedifferentiated cellular mass that fills the early trunk sac. As development is completed the umbilical cord degenerates so the male lies free within the sac. This may leave a trace on the ventral surface of the male head, such as the short strand of tissue emerging from an opening found in *D. harrisoni* (figure 39, plate 5).

The abdomen of the male bears a median stylet which is interpreted as an intromittent organ, and the identification of this stage as the adult male is based primarily on its possession of the stylet. It is extremely unlikely that the stylet is an ovipositor because tantulocaridans do not lay eggs. Although the stylet cannot be flexed relative to the abdomen, the whole abdomen can be flexed and extended by the longitudinal trunk muscles (figure 29). The posteriorly directed stylet of *D. harrisoni* can therefore, be directed ventrally or even anteriorly, beneath the cephalothorax. That of *M. langi* is curved, with its apex posteroventrally directed. The stylet is about 100 μm long, relatively enormous compared to the tantulus larva (130 μm in length). This disparity in size suggests that mating could not occur between an adult male and a tantulus. It is probable that the male mates with partially swollen female stages, fertilizing by injection of sperm or spermatogonia through the body wall, as in some rhizocephalans (Høeg 1982). It is also possible that there exists a large, free-swimming and non-feeding female stage which has not yet been discovered. There is some evidence of a third developmental pathway in which the trunk sac is formed immediately behind the head and the larval trunk is retained in a ventrally deflected position (figures 49, 50 and 73). This pathway may just represent a series of specimens in which the usual sloughing of the larval trunk has failed to take place or it may represent a sexual female cycle, in which a large free-swimming female develops inside the trunk sac. Mating would then be between the free-swimming sexual stages.

10. Phylogenetic relationships

(*a*) *Life cycle pattern*

(i) *Condensation*

The development of tantulocaridans is extremely condensed compared with the primitive anamorphic pattern of crustaceans in which somites and limbs are added sequentially at each moult. They hatch at an advanced, infective stage which does not appear to moult, though the female cycle involves sloughing of the larval trunk. Male development involves a metamorphic reorganization within the integument of the preceding stage which presumably represents a moult. The primitive type of regular anamorphic development, commencing at the nauplius stage, is exhibited by the Cephalocarida (Sanders 1963) and Anostraca (Fryer 1983). Most other crustaceans have a modified pattern; that of the Remipedia is unknown.

Condensation of early developmental stages is common amongst other parasitic crustaceans. The life cycle of akentrogonid rhizocephalans, which have no nauplii and which hatch as infective cyprid larvae (Bocquet-Védrine & Bourdon 1984), has an abbreviated pattern similar to that of tantulocaridans. The loss of the typical nauplius dispersal phase may help to ensure that the infective larvae are released in the vicinity of suitable hosts.

(ii) *Metamorphosis and male development*

Metamorphoses are common in the Crustacea, in both free-living and parasitic forms. In such parasitic copepods as the Pennellidae, metamorphosis occurs in the adult female stage, after mating, and represents a terminal addition to the ancestral anamorphic ontogeny (Boxshall 1986). These changes in form occur without moulting, by allometric growth, and are comparable with those of female tantulocaridans (see figures 56–58). Other metamorphoses represent a condensation in which changes brought about by two or more moults in the ancestral anamorphic sequences are concentrated into a single moult, for example, between zoea and megalopa in decapods, between nauplius and copepodid in copepods, between metanauplius and calyptopis in euphausiaceans, and between metanauplius and cyprid in cirripedes. None of these metamorphoses is comparable with the transformation that occurs during the development of a male tantulocaridan within the trunk sac of the tantulus as no moulting occurs. Such a transformation is otherwise unknown in the Crustacea (Snodgrass 1956). It is more analogous to the pupal metamorphosis of some insects in the dedifferentiation and reorganization processes that occur but differs as the male continues to obtain nourishment from the host via the larval cephalic tissues throughout its development. If the umbilical cord represents, at least in part, the larval tissue then the male is produced at the posterior end of the tantulus, by a process equivalent to budding.

(*b*) *Affinities with other Crustacea*

When the Tantulocarida was established (Boxshall & Lincoln 1983) it was suggested that discovery of the adult male and larval stages would provide information valuable in interpreting phylogenetic affinities. Unfortunately the condensed early development provides little additional information. In the absence of a larval stage possessing cephalic appendages it is not even possible to confirm the crustacean affinity of the group. Itô (1985) illustrated a possible derivation of the larval tantulocaridan thoracopod from the postantennular limbs of copepod and cirripede nauplii. Based on comparison between these limbs, it is invalid because of fundamental differences in construction between thoracopods and those limbs present in the nauplius (see Boxshall 1985).

The adult male provides more phylogenetic information despite the absence of cephalic limbs. The two clusters of aesthetascs are probably antennulary in origin, as the antennules are the primary sensory appendages, but no trace of an appendage was found at the site of attachment of the aesthetascs. The cephalon of the tantulus larva was presumed to comprise the basic five somites of the crustacean head (Boxshall & Lincoln 1983) so the incorporation of the first two thoracic somites produces a cephalothorax of seven somites. Such a cephalothorax is found in some advanced harpacticoid copepods and within some malacostracan groups but none of the nine currently recognized classes of Crustacea primitively exhibits this condition. Copepods and remipedes both primitively possess a cephalothorax of six somites.

The male of *D. harrisoni* bears a pair of frontolateral processes on the dorsal shield. These lack any articulation or musculature and do not appear to represent either vestigial limbs or eye stalks. They resemble the paired frontolateral horns on the dorsal shield of cirripede nauplii which are secretory and are retained in the cyprid larva as frontal horn gland pores (Walker 1973). There are no frontolateral horns in ascothoracid nauplii (Wagin 1976) and Grygier (1983*a*) concluded that the anteroventral carapace pores of the ascothoracid *Waginella* Grygier are not homologous with the gland pores of cirripede cyprids. The frontolateral processes of male *Deoterthron* lack pores and carry two sensory setules. They are not secretory and are probably not homologous with cirripede frontolateral horns. The male of *M. langi* lacks well developed frontolateral processes, which possibly represent a generic feature of *Deoterthron* only.

The position of the gonopore is important in crustacean systematics. It is not situated on the fifth thoracic somite in tantulocaridans as indicated by Boxshall & Lincoln (1983). The structures identified as a genital papilla in the tantulus and as a gonopore in the adult female are reinterpreted here as a median protrusion on the sternite marking the end of the row of thoracopodal endites, and as the raised circular scar marking the position of the sloughed larval trunk, respectively. The gonopore of male tantulocaridans is on the seventh trunk somite and the abdominal stylet probably represents an appendage modified as an intromittent organ. It is positioned distally on the unsegmented abdomen of *D. harrisoni* but in *M. langi* it clearly originates on the first abdominal somite (trunk somite seven). Ascothoracids and cirripedes, classified together as the Thecostraca (Grygier 1984), are the only other crustaceans with a single median penis carried on the seventh trunk somite. Copepods have their gonopores on this somite in both sexes but, primitively, the seventh trunk limbs are not modified as an intromittent organ in the male, instead acting as opercula closing the genital openings of both sexes.

Larval tantulocaridans possess twelve trunk somites (including the telson), a character shared only with the recently established Skaracarida, an Upper Cambrian fossil group (Müller & Walossek 1985). Thecostracans and copepods possess eleven, as do mystacocarids and possibly ostracods (Schulz 1976). This number has been widely used as diagnostic of the Maxillopoda (Newman 1982, 1983; Grygier 1983*b*) though it incorporates taxa with less, such as the Branchiura. If the Tantulocarida and Skaracarida are related to the Maxillopoda then twelve trunk somites rather than eleven may represent the basic maxillopodan state (Müller & Walossek 1985). The affinities of the Skaracarida, which lack thoracopods other than a pair of maxillipeds, are difficult to assess. Those of the Tantulocarida appear to lie with the Copepoda and Thecostraca, with which they share a thorax of six somites each bearing a pair of thoracopods, and the position of the male gonopores on trunk somite seven, and in particular with the Thecostraca, with which they also share a median penis derived from the seventh thoracopod. This scheme of relationships suggests that possession of eleven trunk somites may have arisen independently in copepods and thecostracans and casts further doubt on the usefulness of trunk somite number as a character in a group like the Crustacea in which reduction in somite numbers is such a widespread phenomenon (Boxshall 1983).

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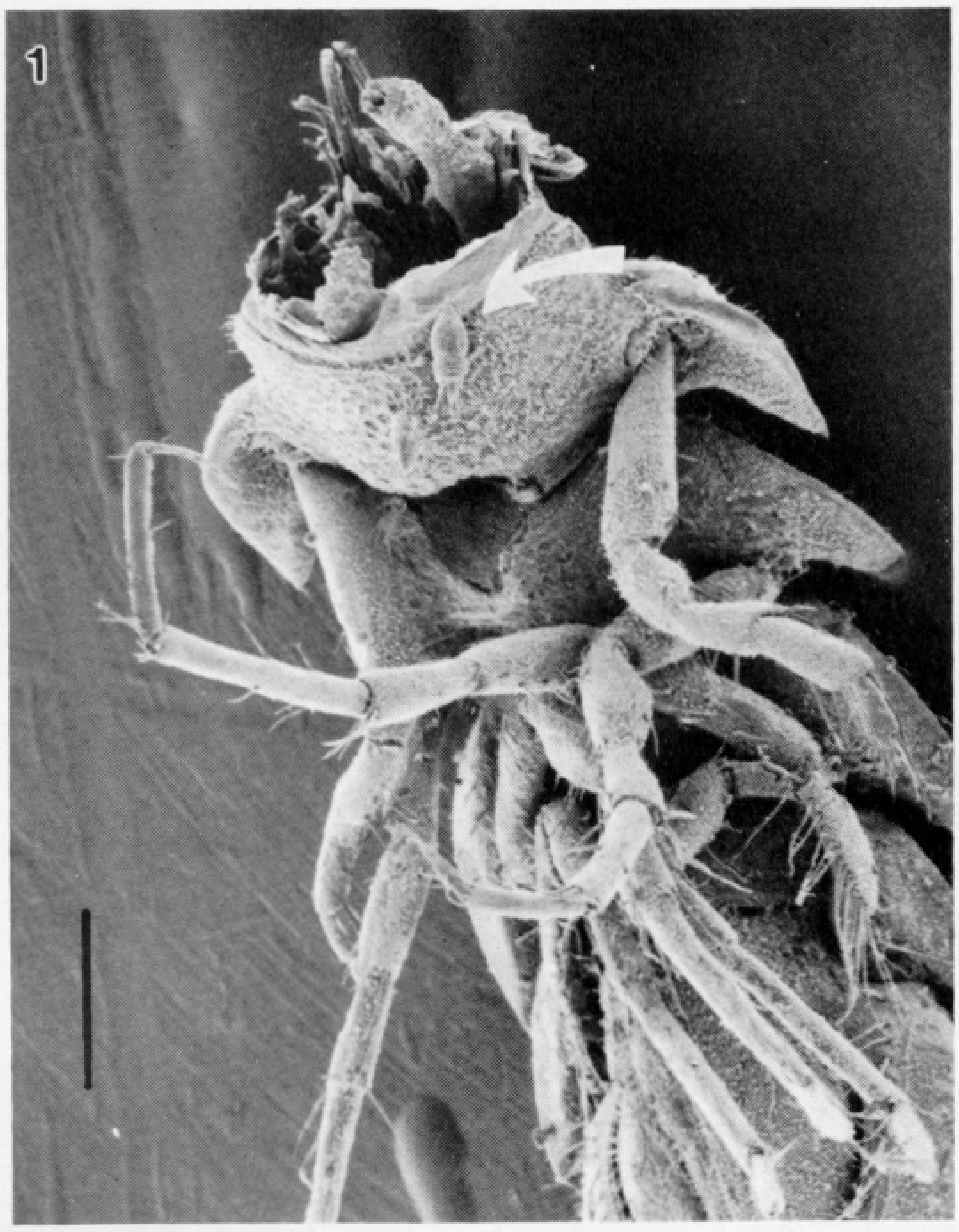
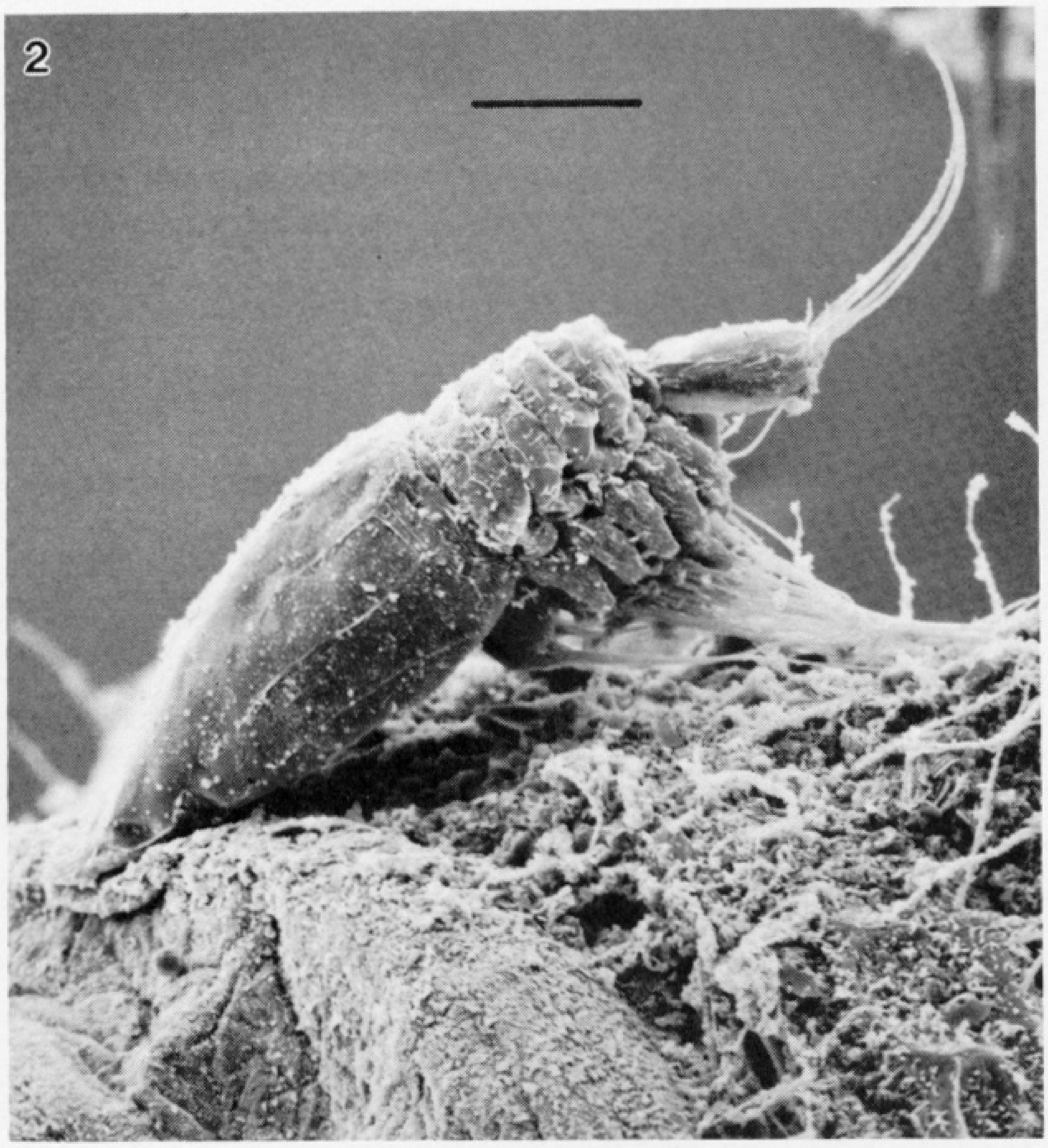
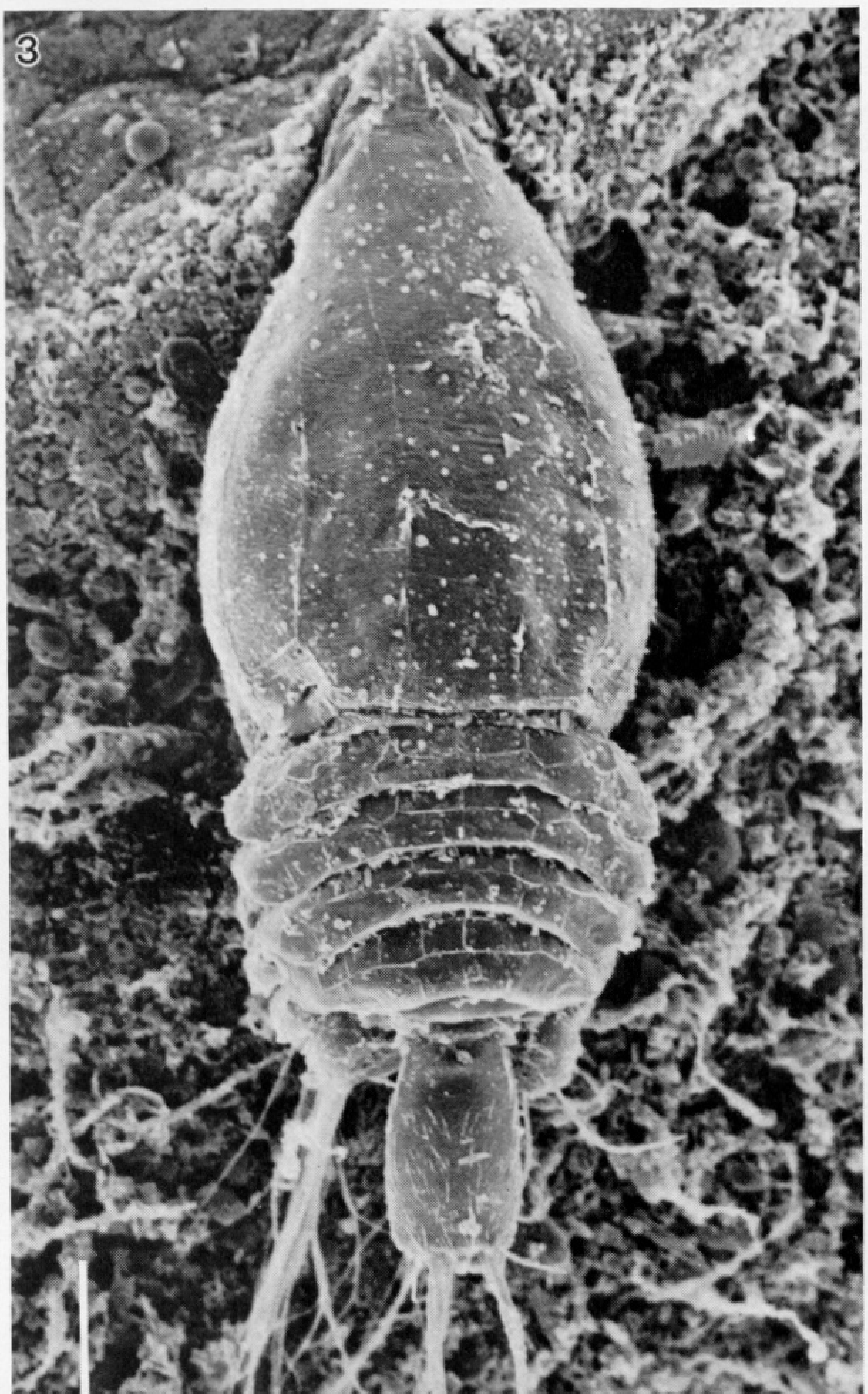
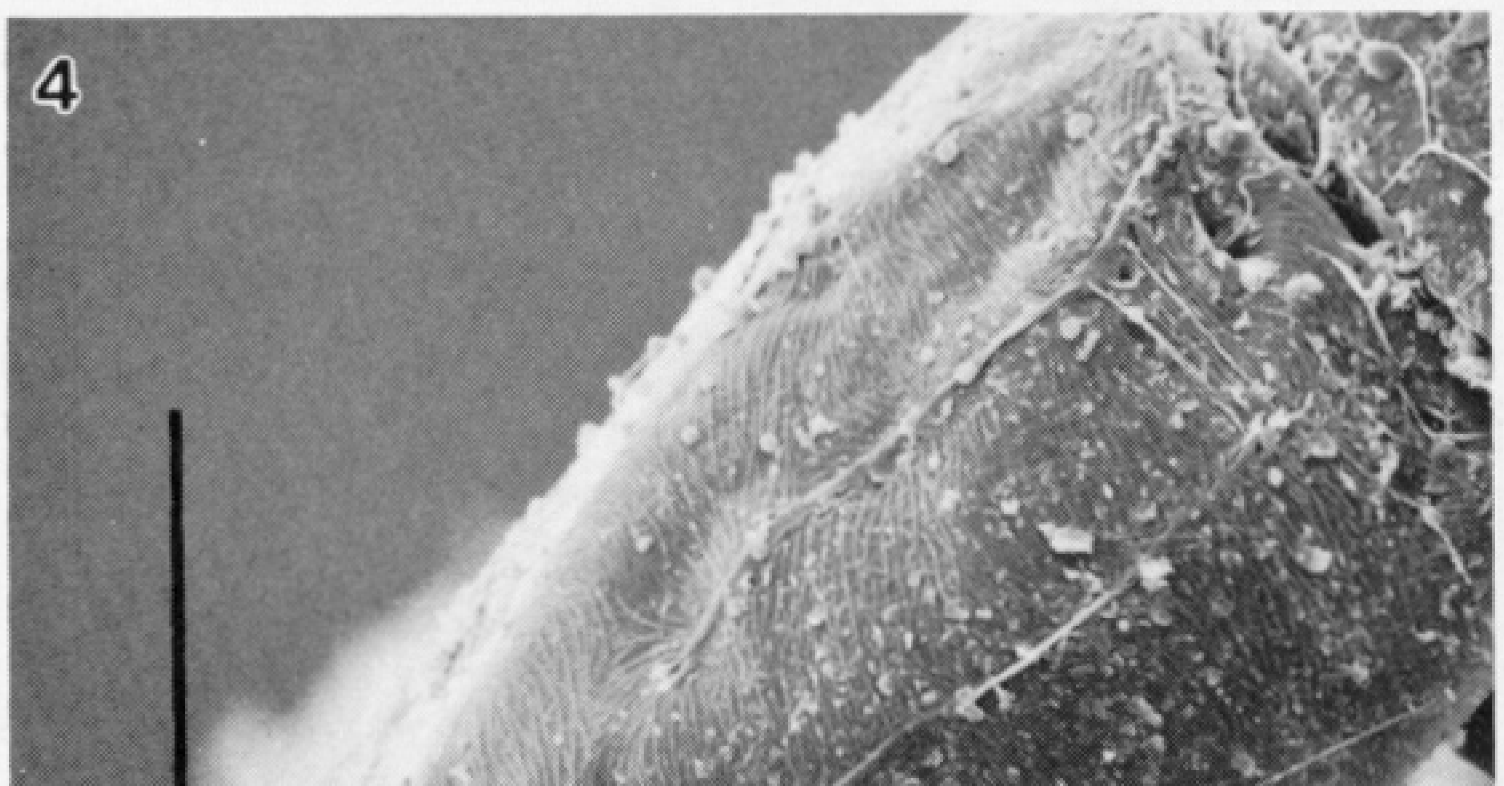
ABBREVIATIONS USED ON FIGURES

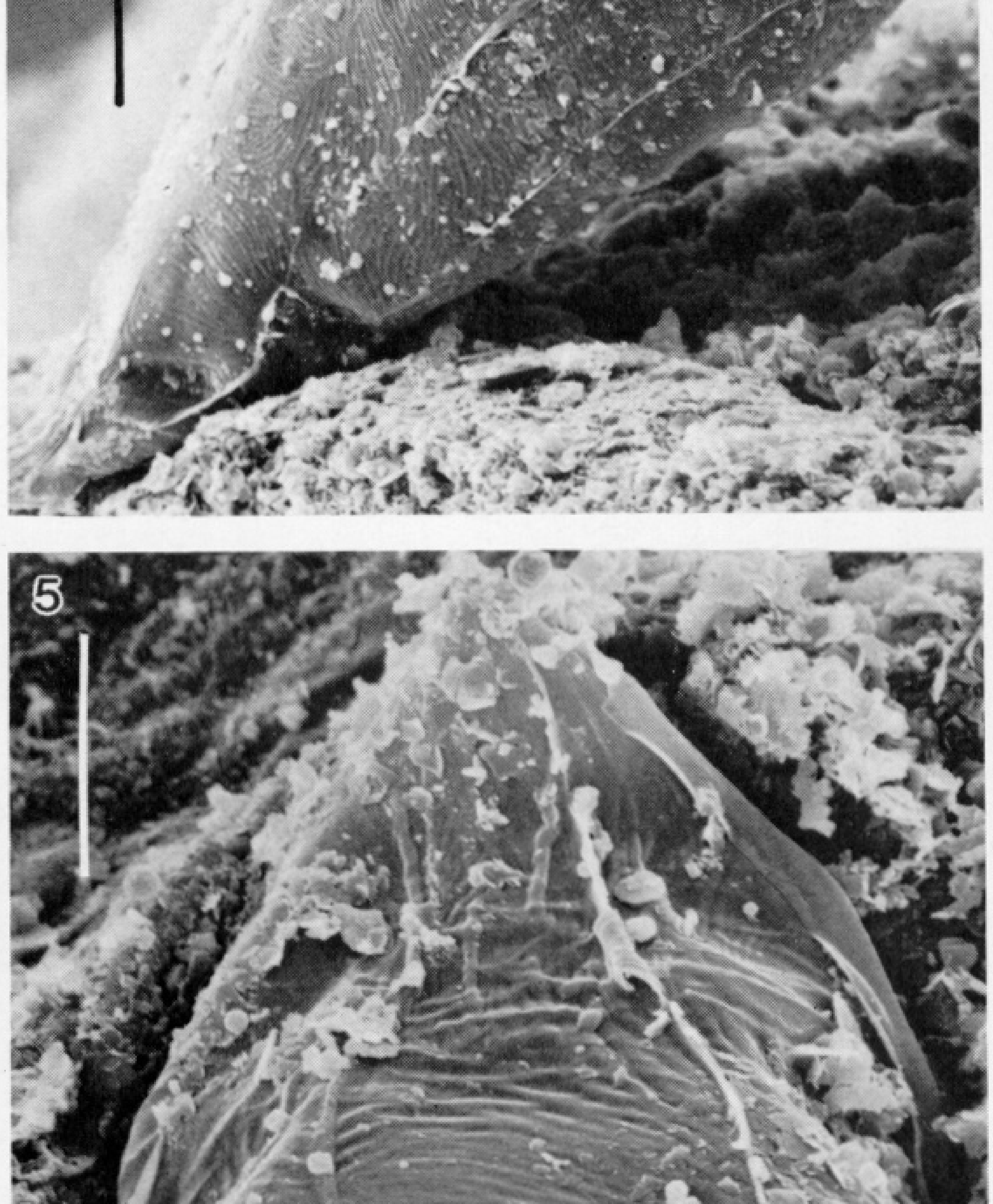
ab.	abdomen, abdominal	fl.	flange
ab.l.m.	abdominal longitudinal muscle	f.p.	frontolateral process
ab.sty.	abdominal stylet	g.	thick walled tubular structure
ae.	aesthetasc	h.i.	host integument
an.sl.	anal slit	lam.	lamellate structure on male head
b.se.	brush seta	o.d.	oral disc
bas.	basis	p.p.	puncture point
c.sty.	cephalic stylet	po.	pore
ca.ra.	caudal rami	prp.	protopod
ca.se.	caudal seta	r.	rostrum
ch.	chitinous bar	s.s.	sternal swelling
cop.	coupling spine	sc.	scar
cox.	coxa	se.	setule
cy.	cylindrical structure penetrating host	sty.	stylet
d.l.m.	dorsal longitudinal trunk muscle	t.	tergite
ed.	endite	tu.	tubular vestige on male head
end.	endopod	umb.	umbilical cord
exp.	exopod	v.l.m.	ventral longitudinal trunk muscle



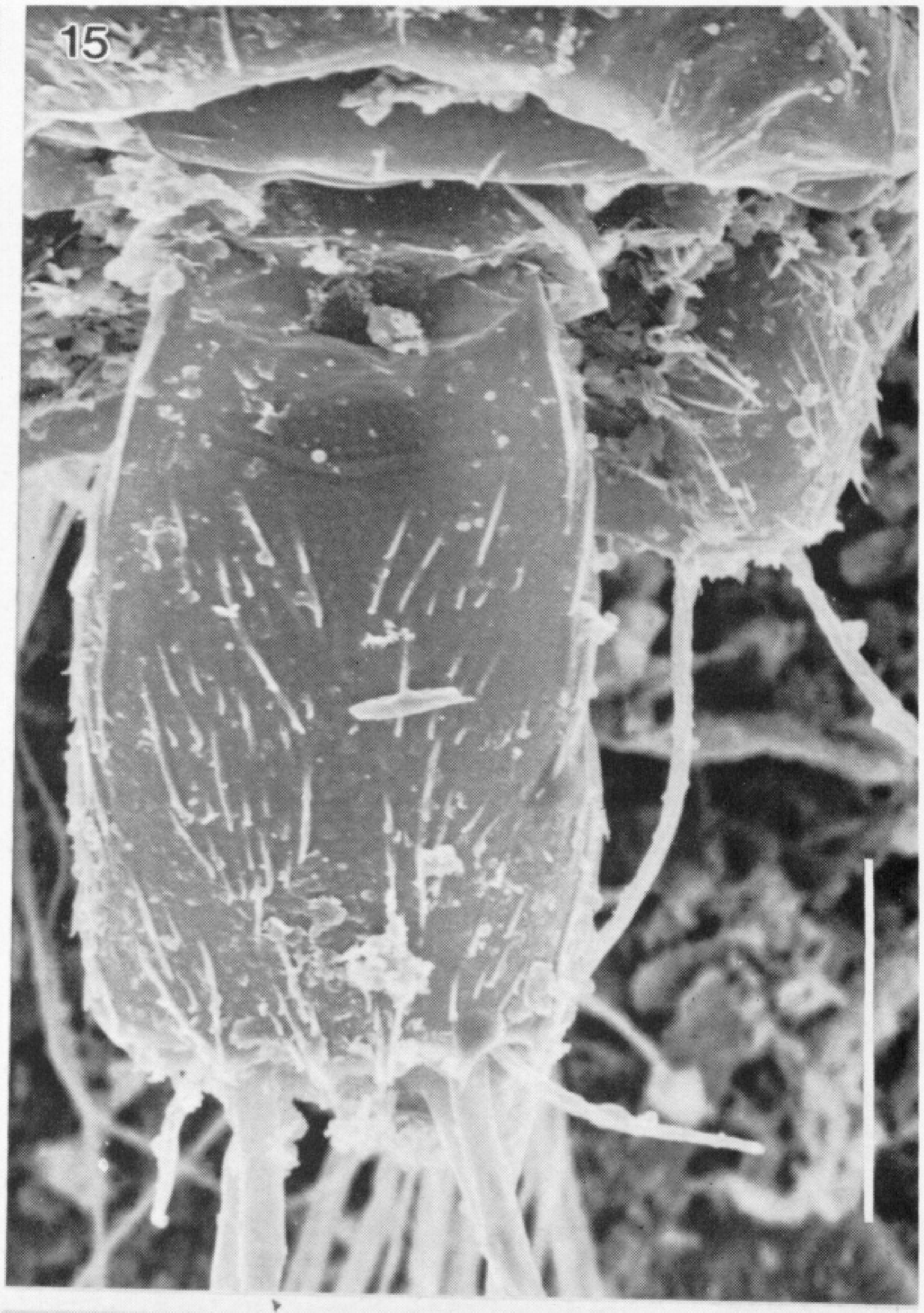


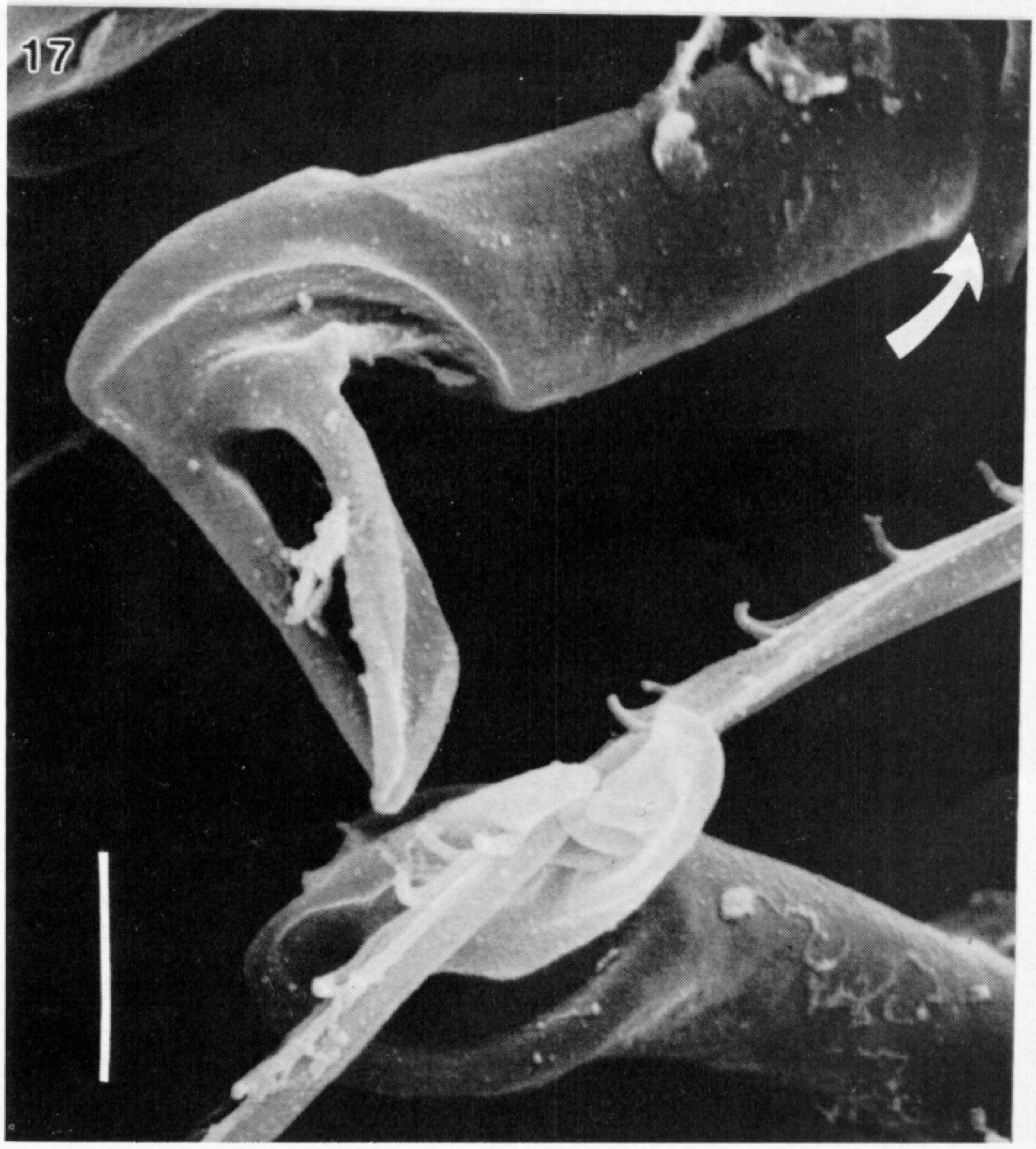


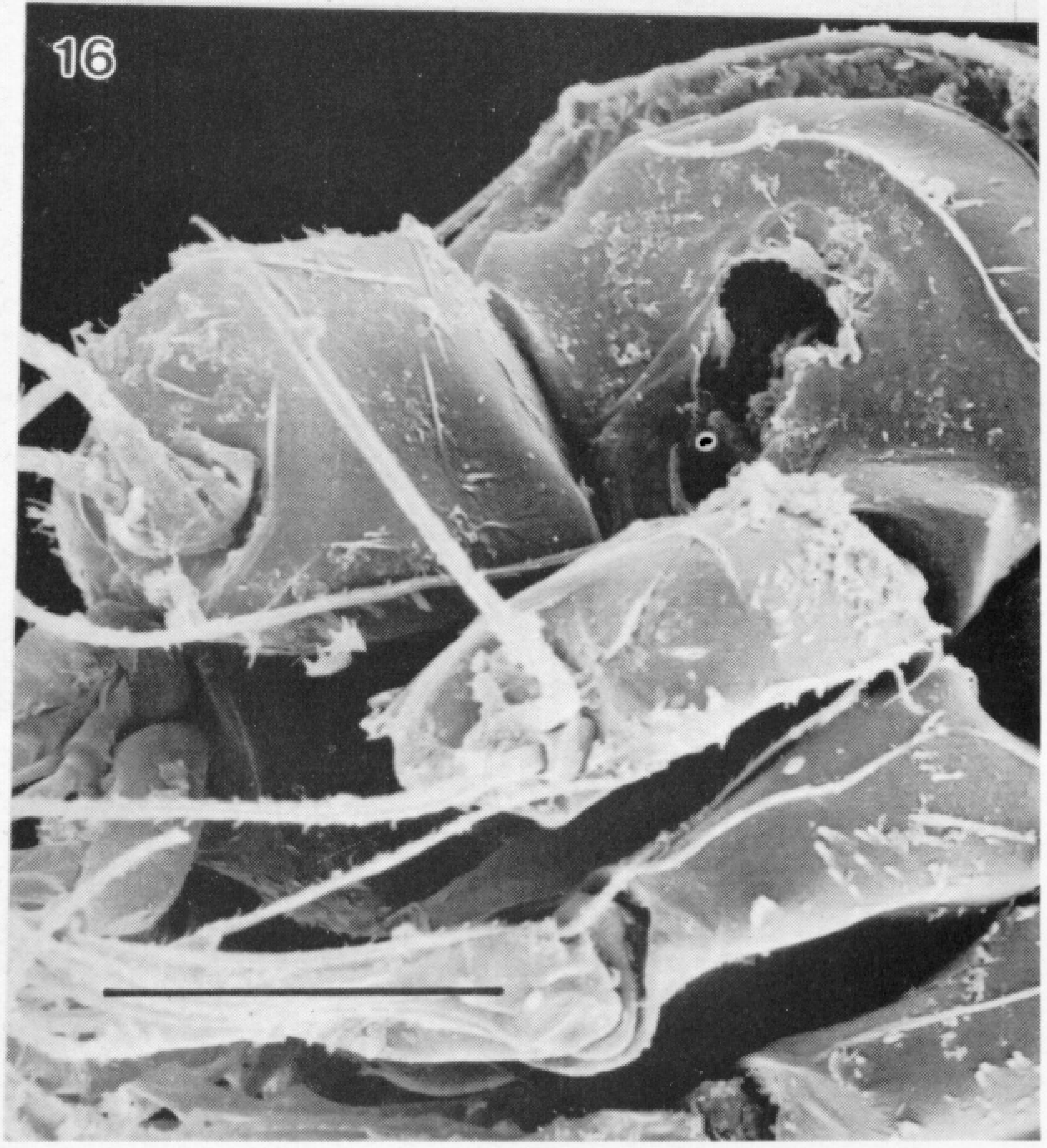




Figures 1–5. For description see opposite.







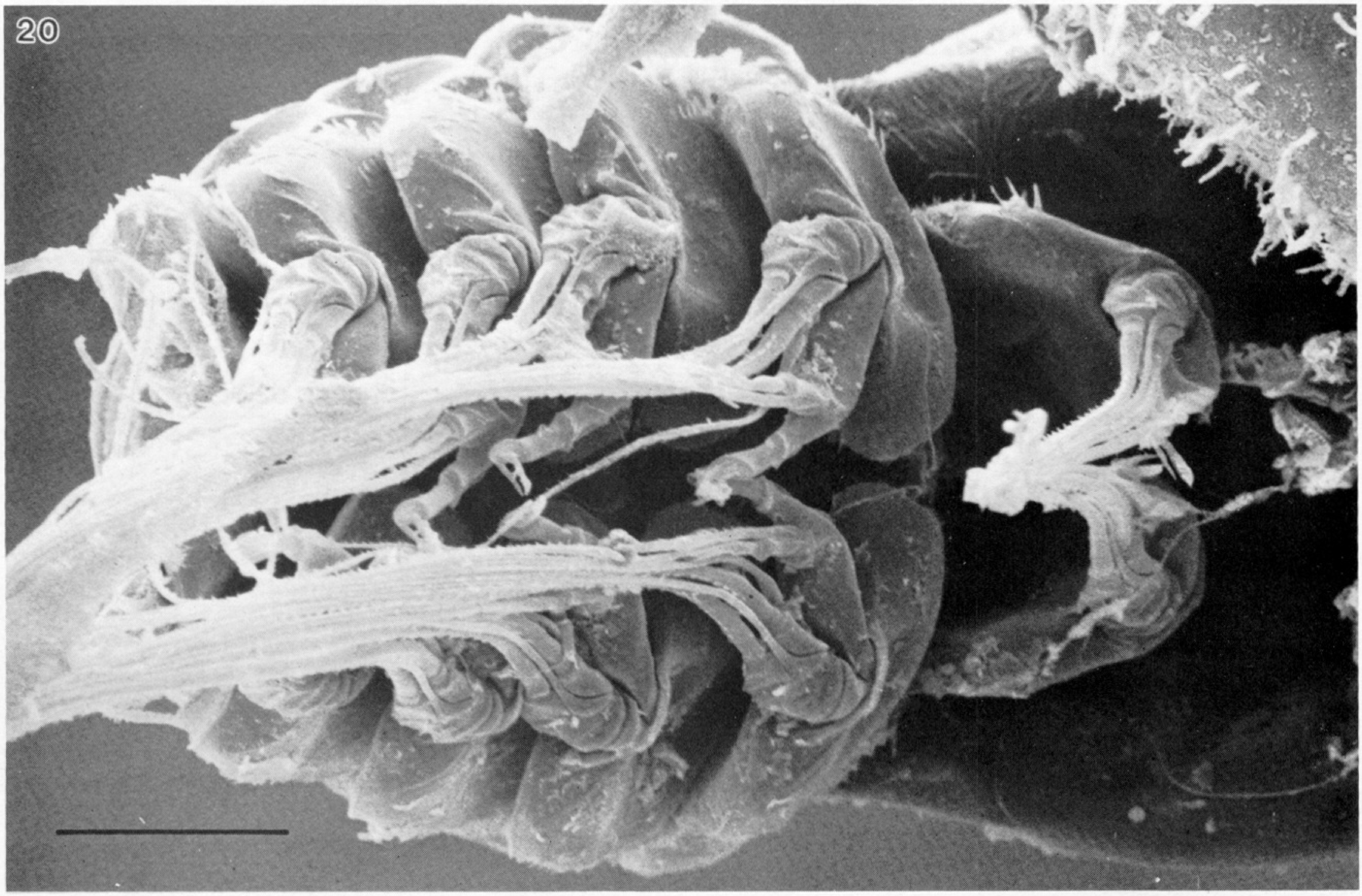
Description of plate 2

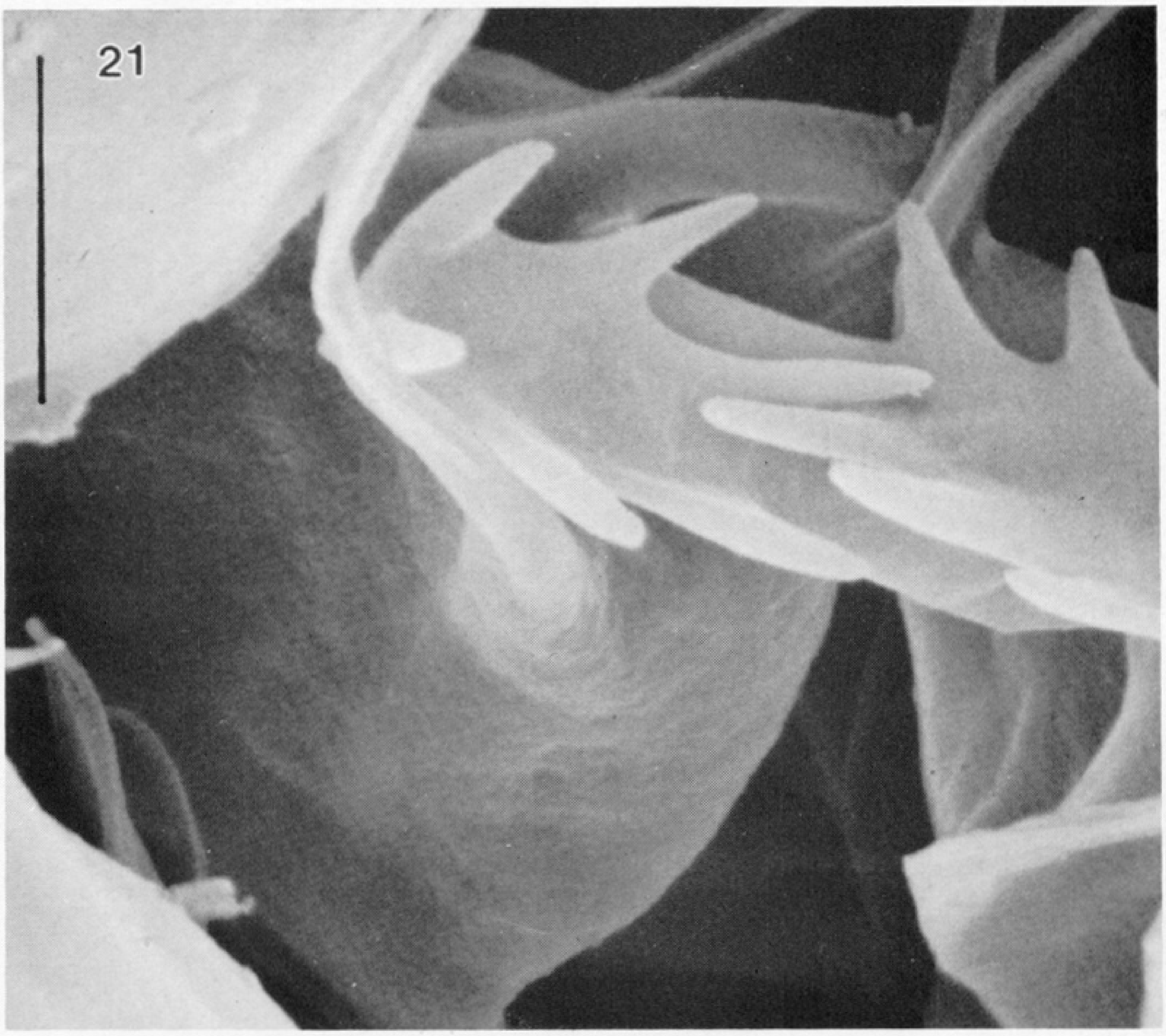
Figure 14. Lateral view of thorax of *D. harrisoni* tantulus, showing tergopleural grooves. Scale bar 5 μm.

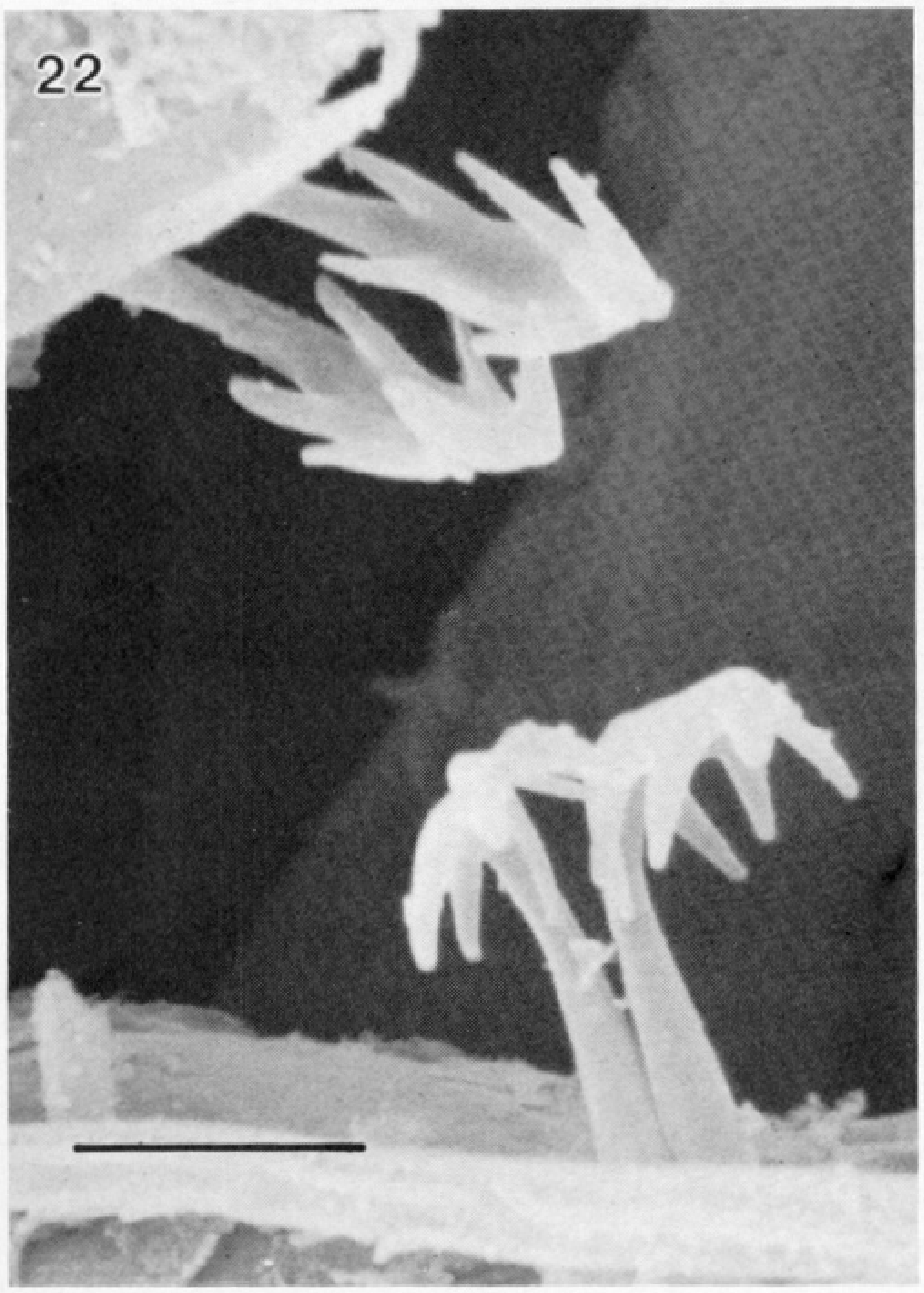
Figure 15. Tantulus abdomen, dorsal view. Scale bar 10 μm.

Figure 16. Posterior view of thorax, showing attachment site of detached abdomen. Scale bar 10 μm.

Figure 17. Apex of endopod of third thoracopod. Scale bar 1 μm.





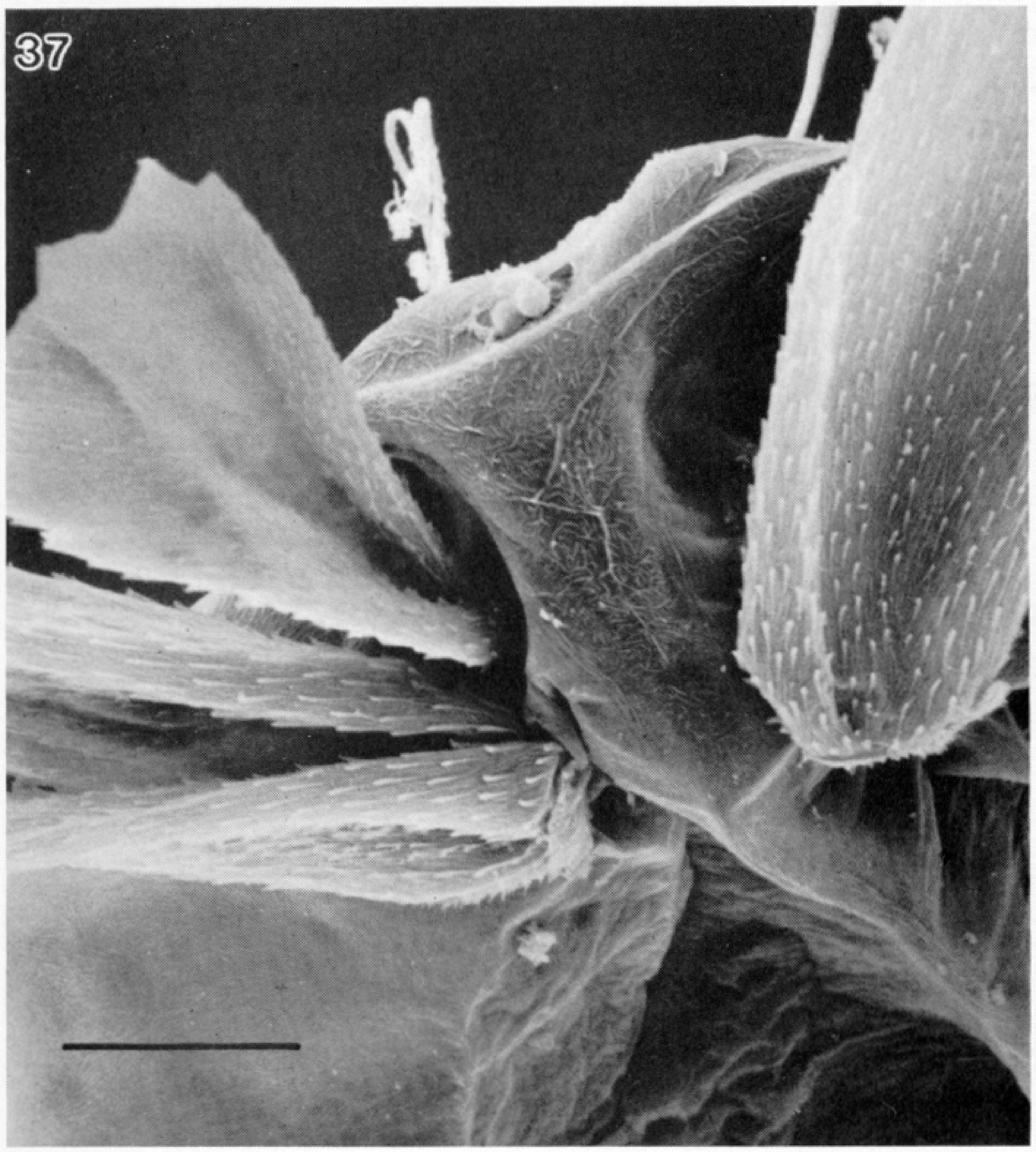


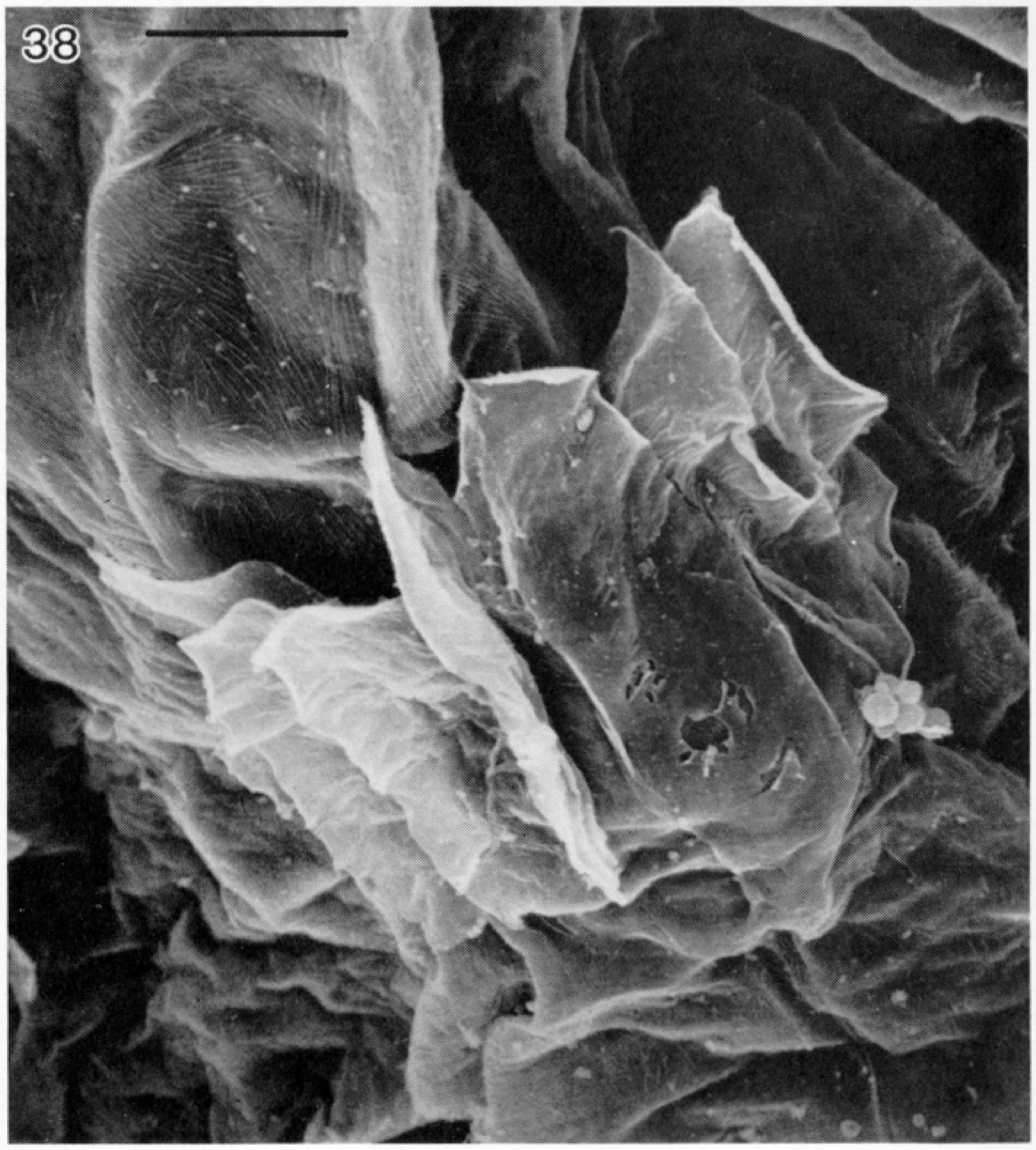
Description of plate 3

Figure 20. Ventral view of thoracopods of *D. harrisoni in situ*. Scale bar 10 μm.

Figure 21. Anterolateral view of interlocking spines on endites of third thoracopod. Scale bar 1 μm.

Figure 22. Posterior view of coupling spines on protopods of sixth thoracopods. Scale bar 1 μm.





DESCRIPTION OF PLATE 4

FIGURE 35. Frontolateral process on cephalothoracic shield of male *D. harrisoni*, showing setules. Scale bar 5 μm.

FIGURE 36. Anterolateral view of rostrum and associated sensory setules. Scale bar 5 μm.

FIGURE 37. Bases of aesthetascs on anterior margin of cephalothorax. Scale bar 10 μm.

FIGURE 38. Detail of lamellate structure on ventral surface, anterolateral. Scale bar 5 μm.

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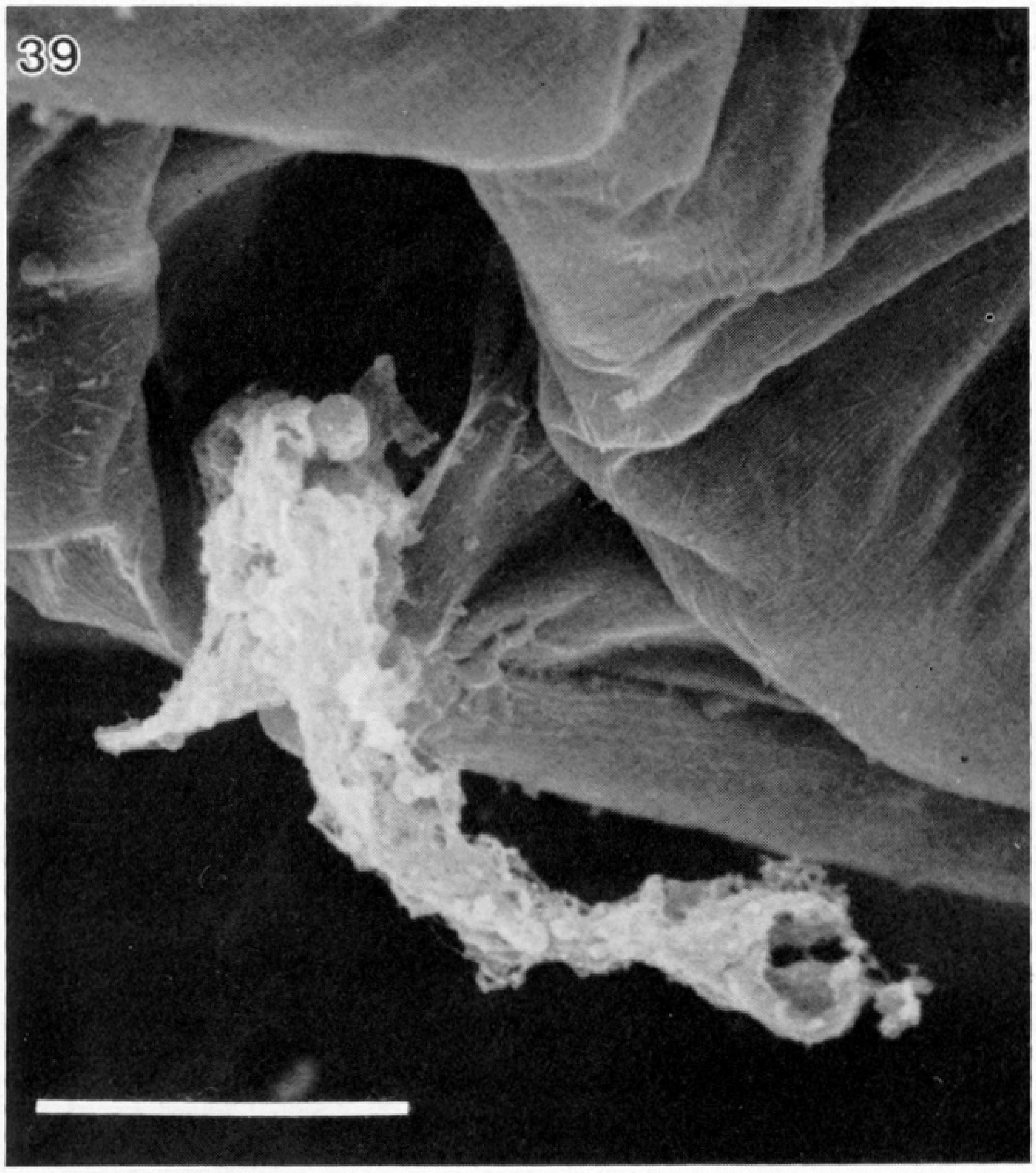

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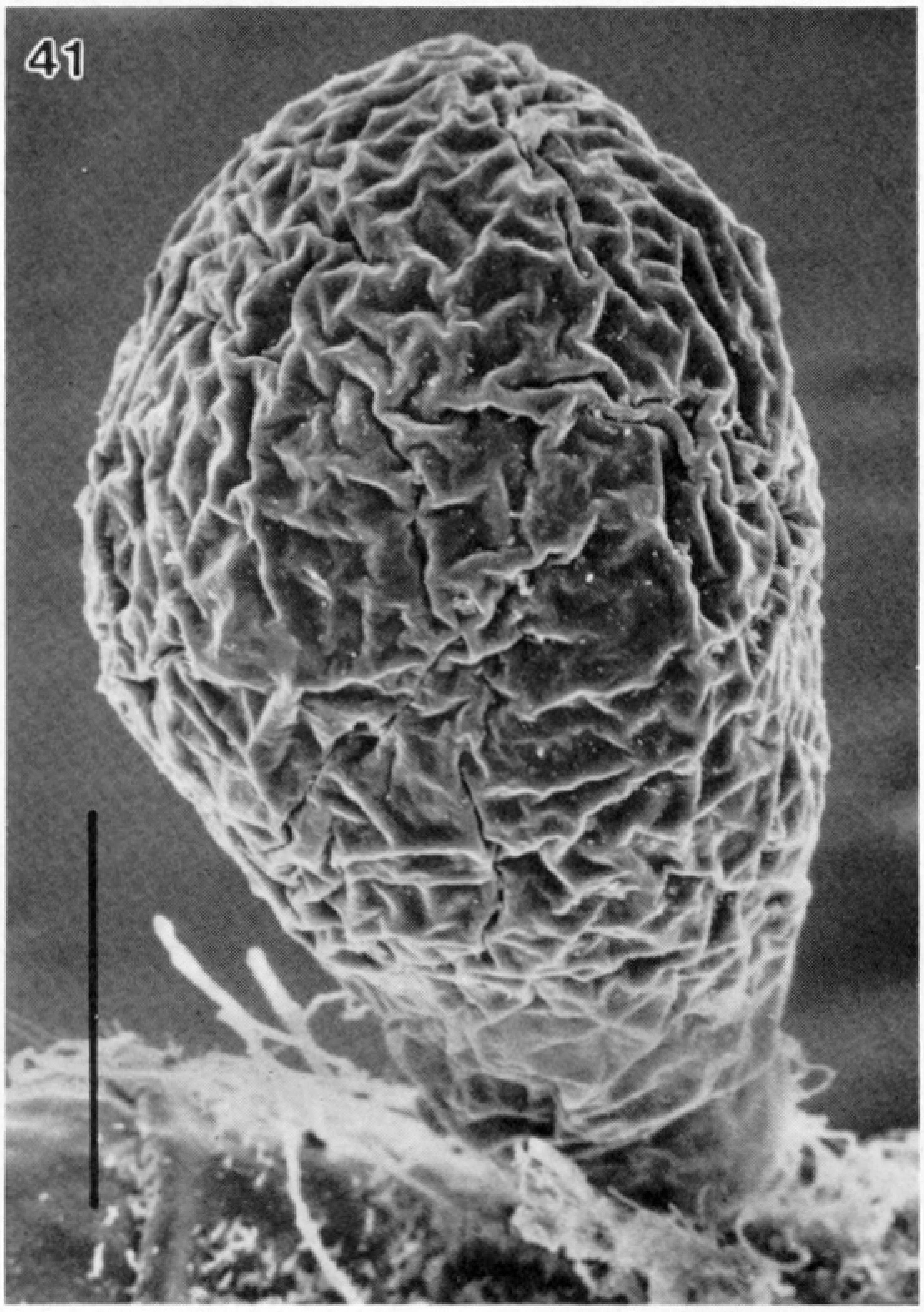

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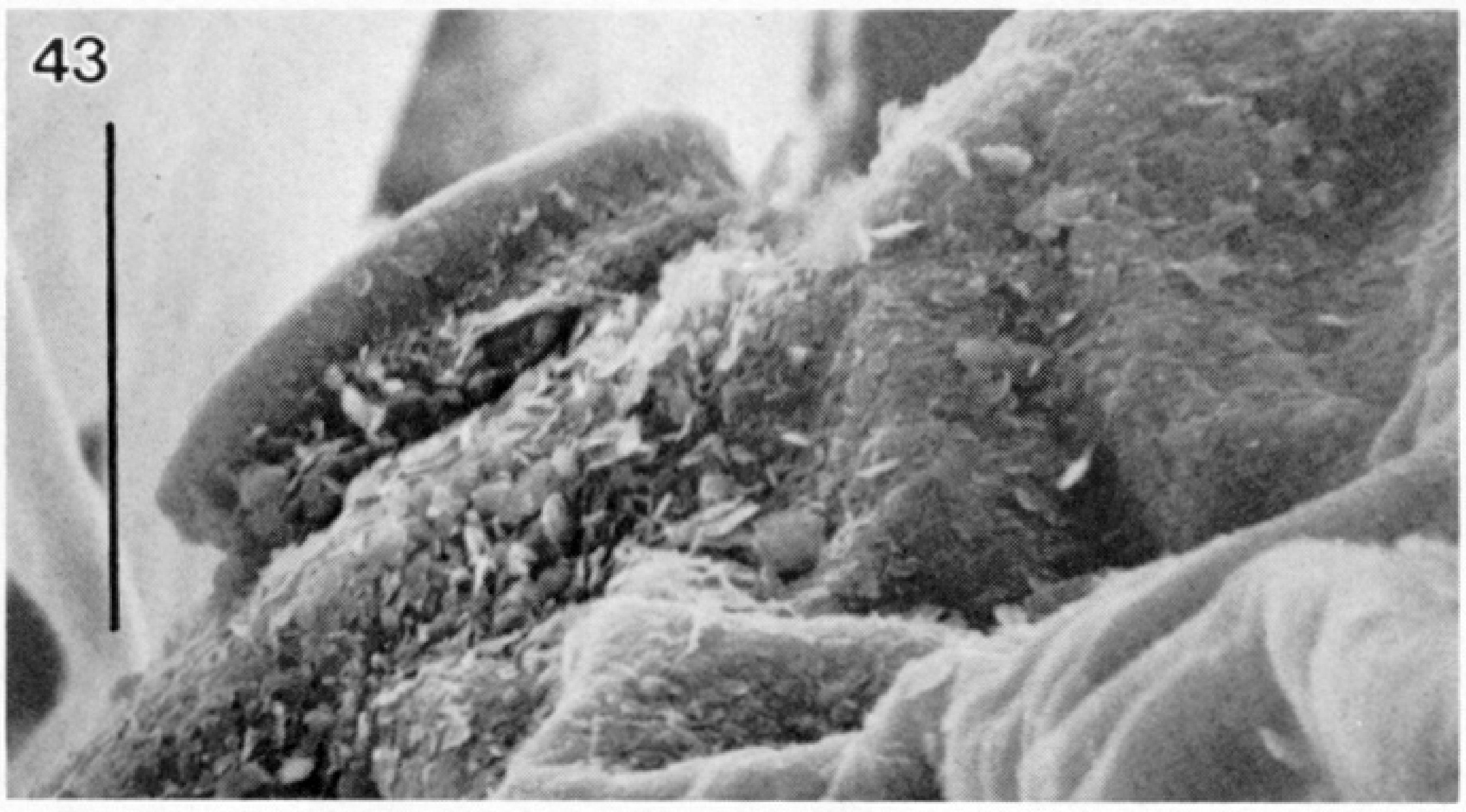


DESCRIPTION OF PLATE 5

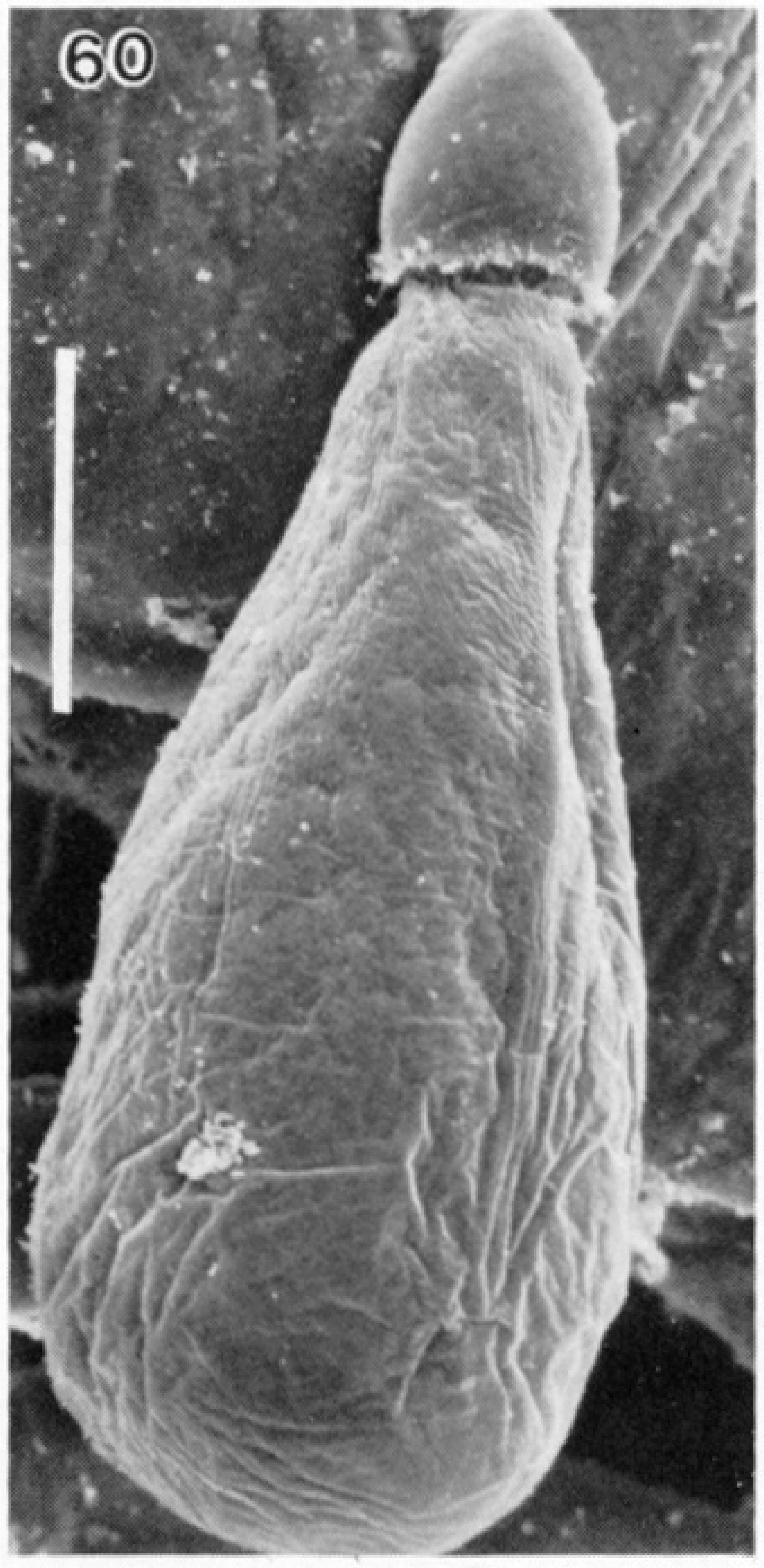
FIGURE 39. Shrivelled tubular structure emerging from pore on ventral surface of the cephalothorax of a male *D. harrisoni*. Scale bar 5 µm.

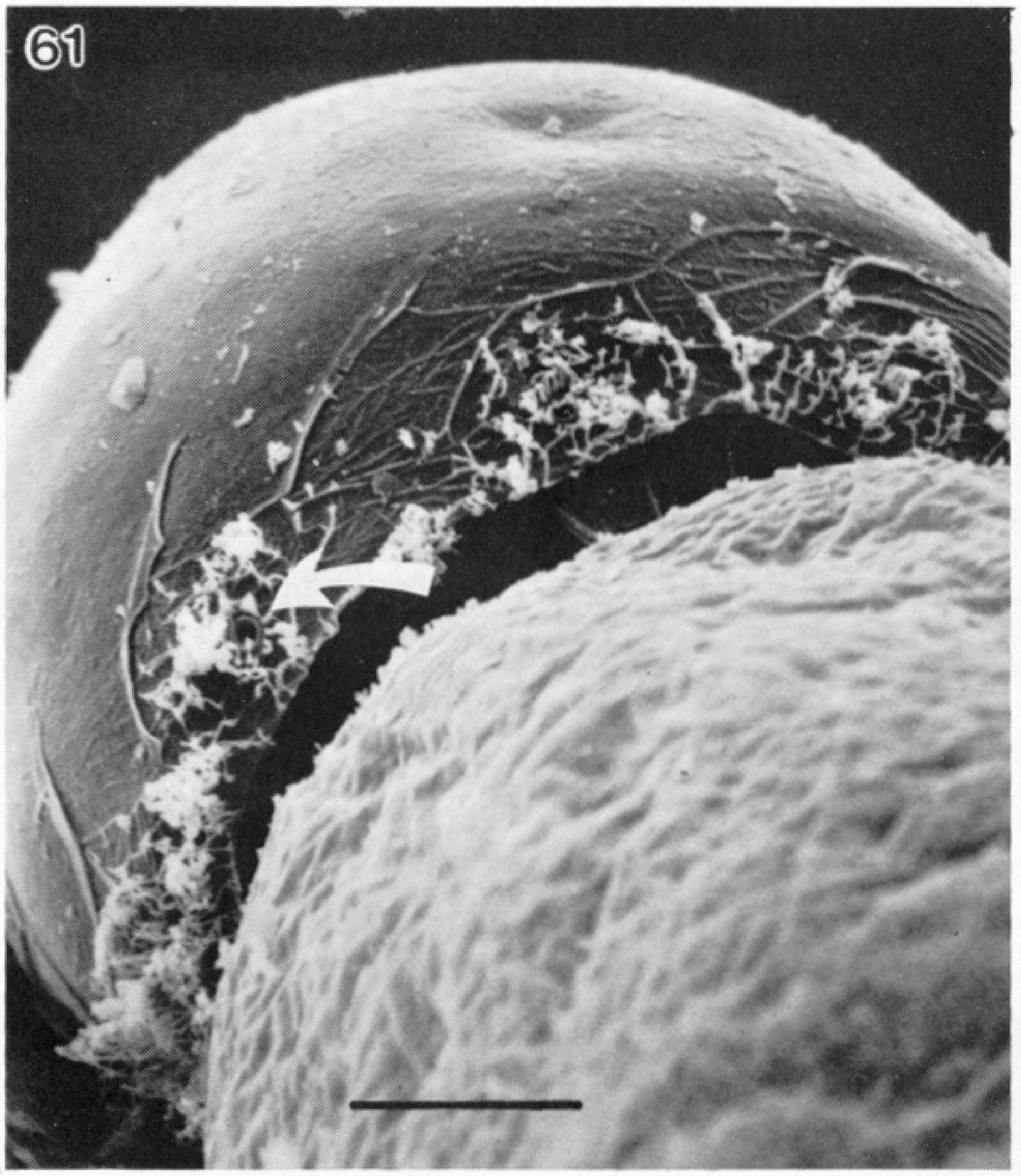
FIGURE 40. Apex of brush setae of male thoracopods. Scale bar 5 µm.

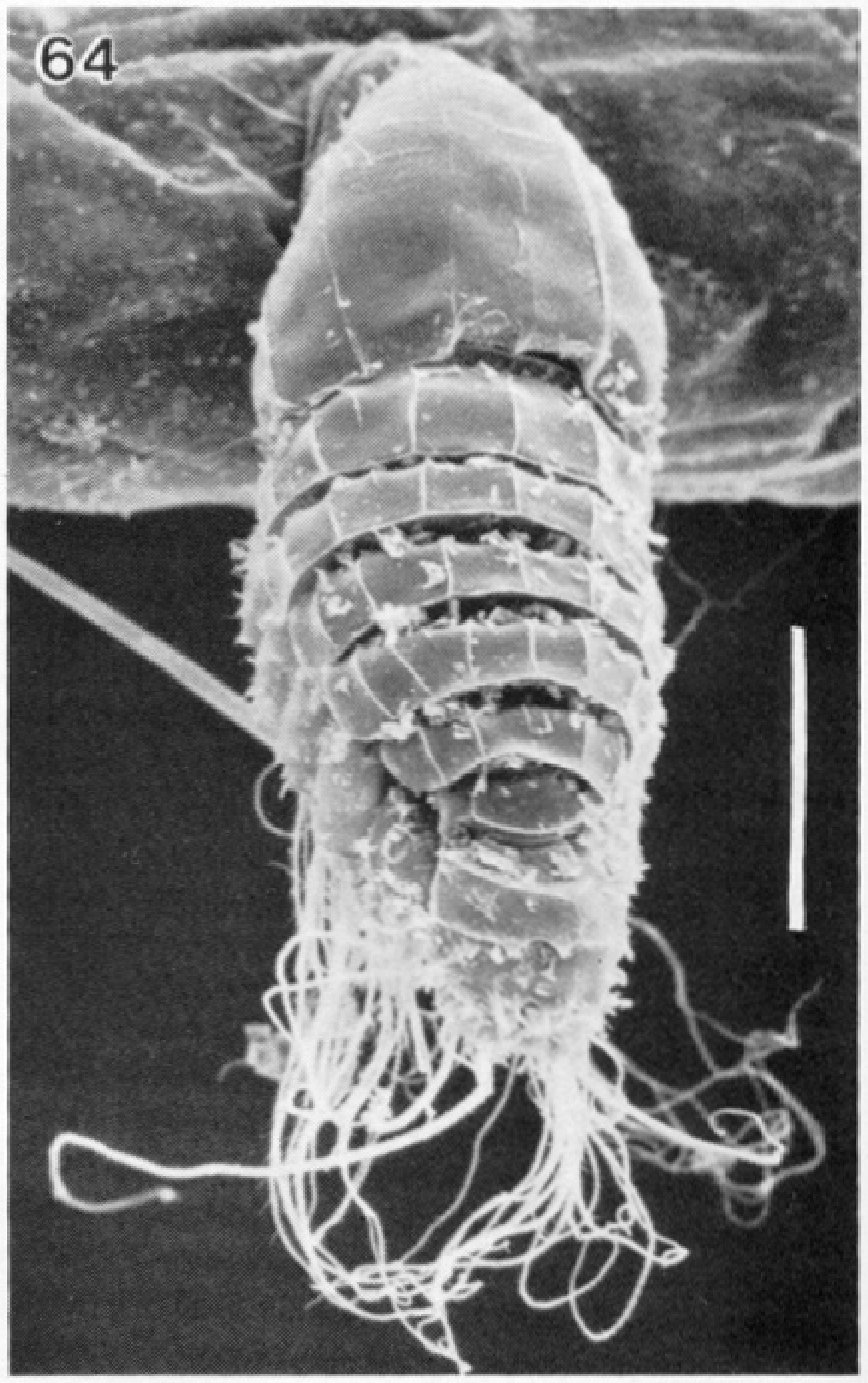
FIGURE 41. Early female *D. harrisoni* showing folded integument of trunk sac. Scale bar 50 µm.

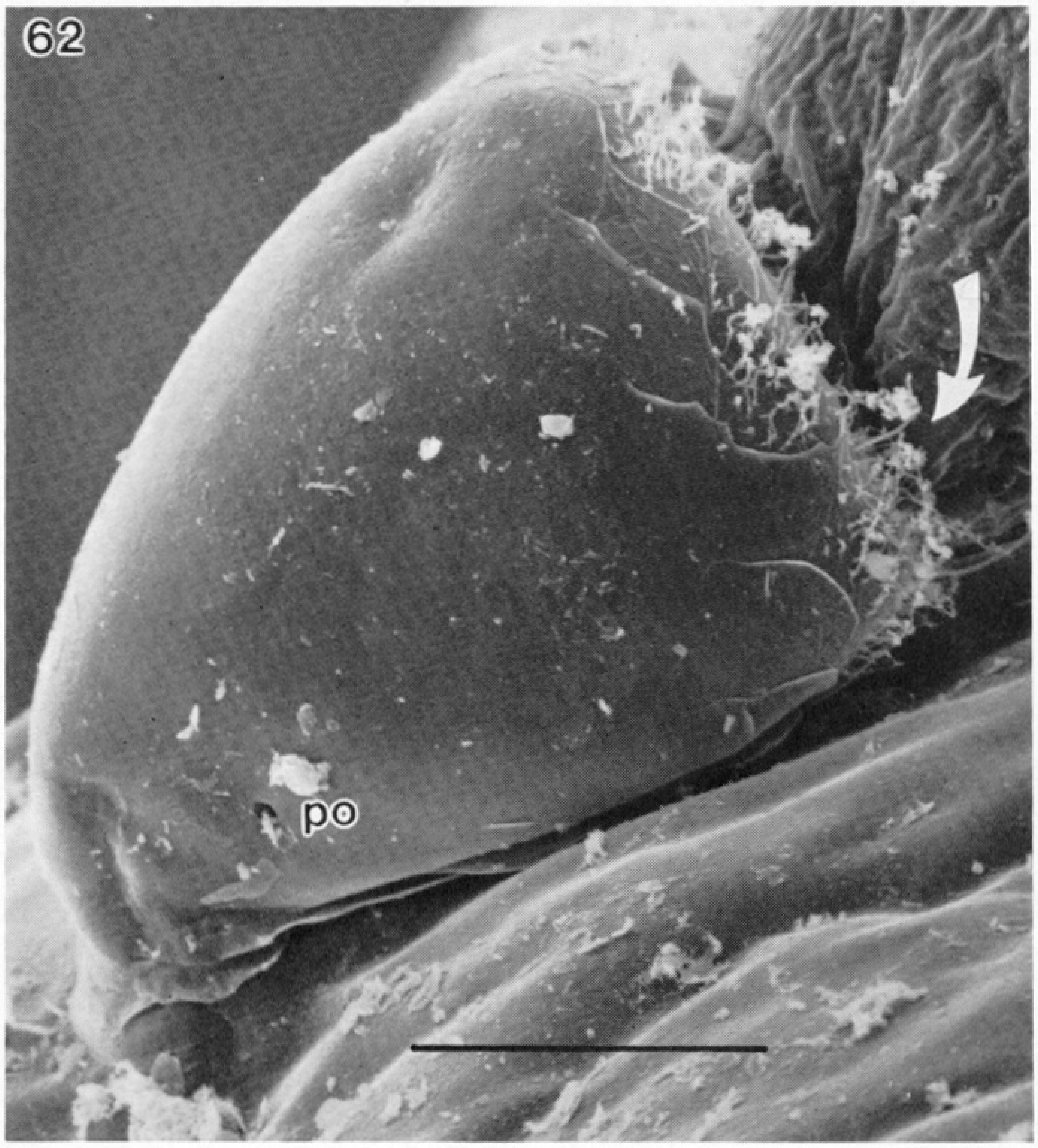
FIGURE 42. Same specimen, showing detail of raised ventral scar left by sloughed larval trunk. Scale bar 5 µm.

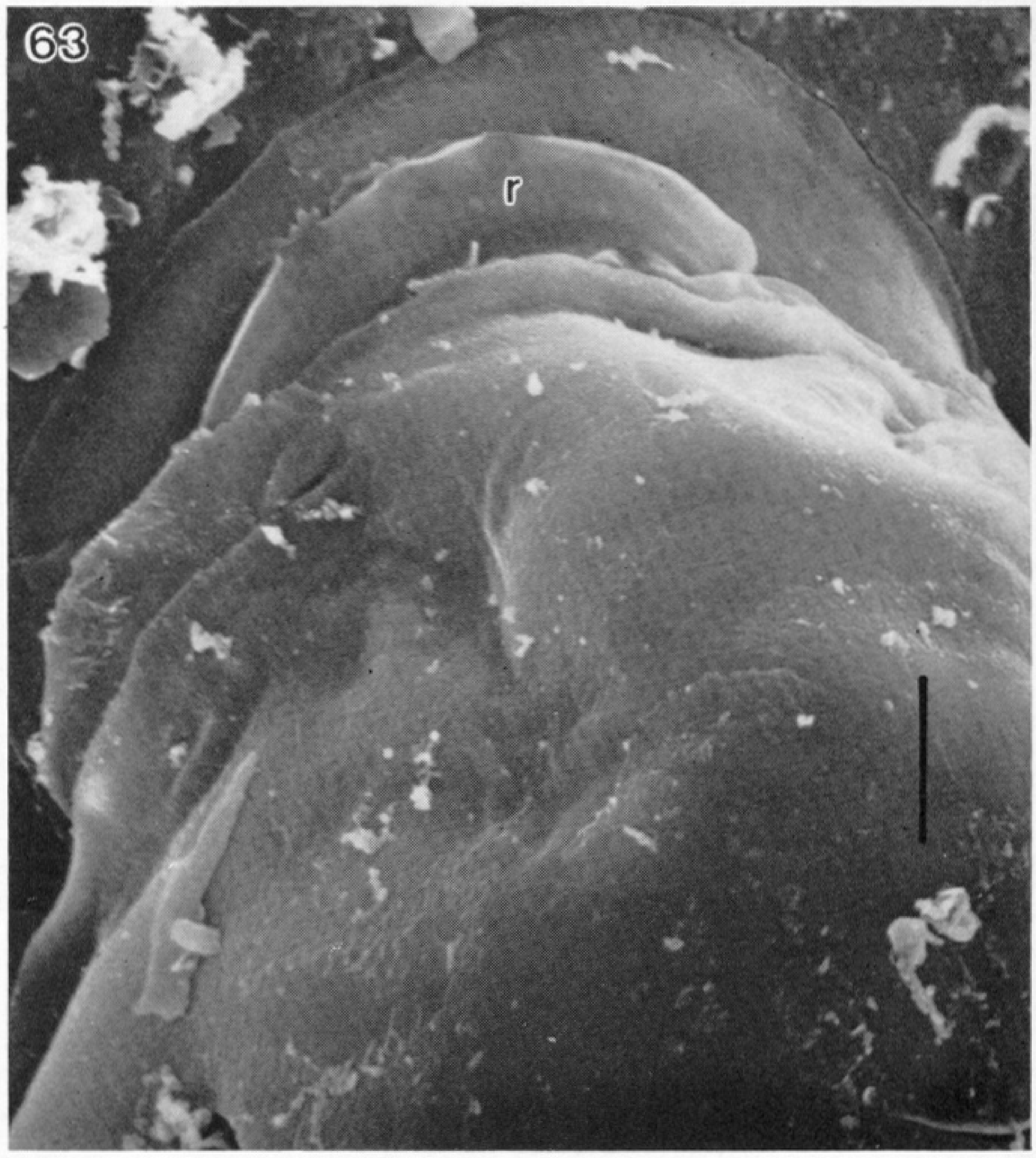
FIGURE 43. Same specimen, showing scar in lateral view. Scale bar 5 µm.











Description of plate 6

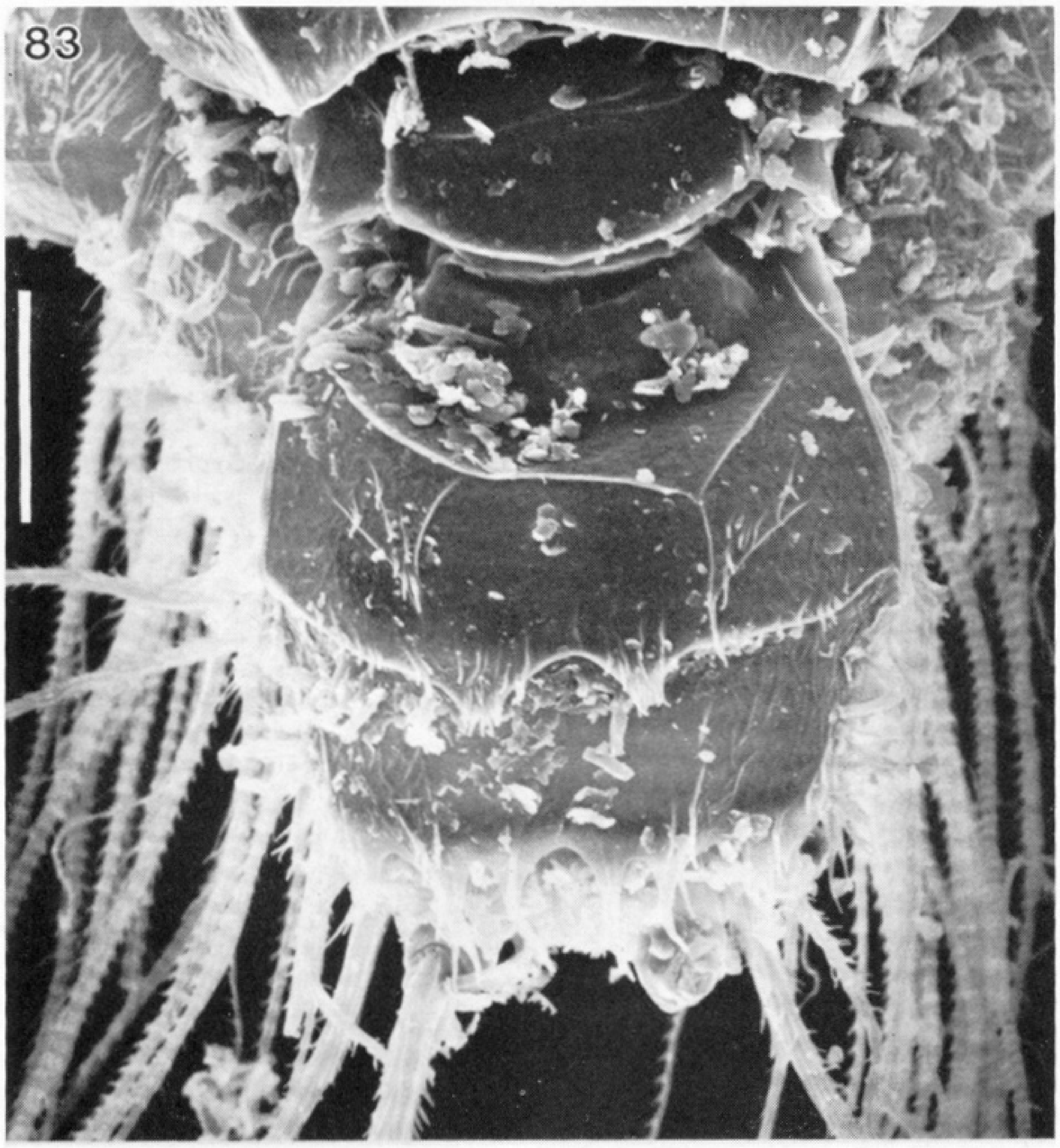
Figure 60. Dorsal view of early female *M. langi* showing wrinkled integument of trunk sac. Scale bar 40 μm.

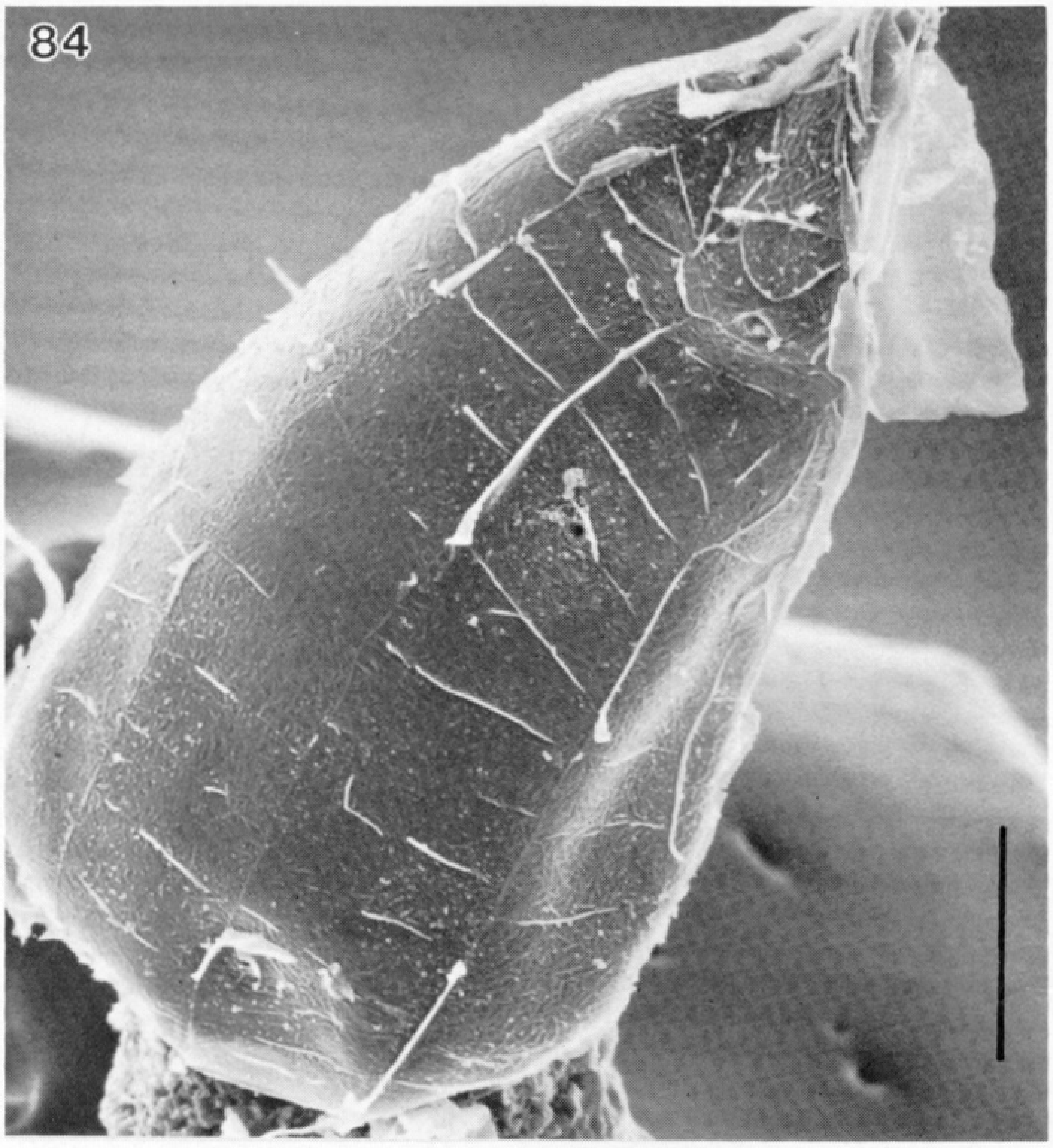
Figure 61. Posterior view of early stage female *M. langi* showing posterior rim of cephalic shield. Scale bar 5 μm.

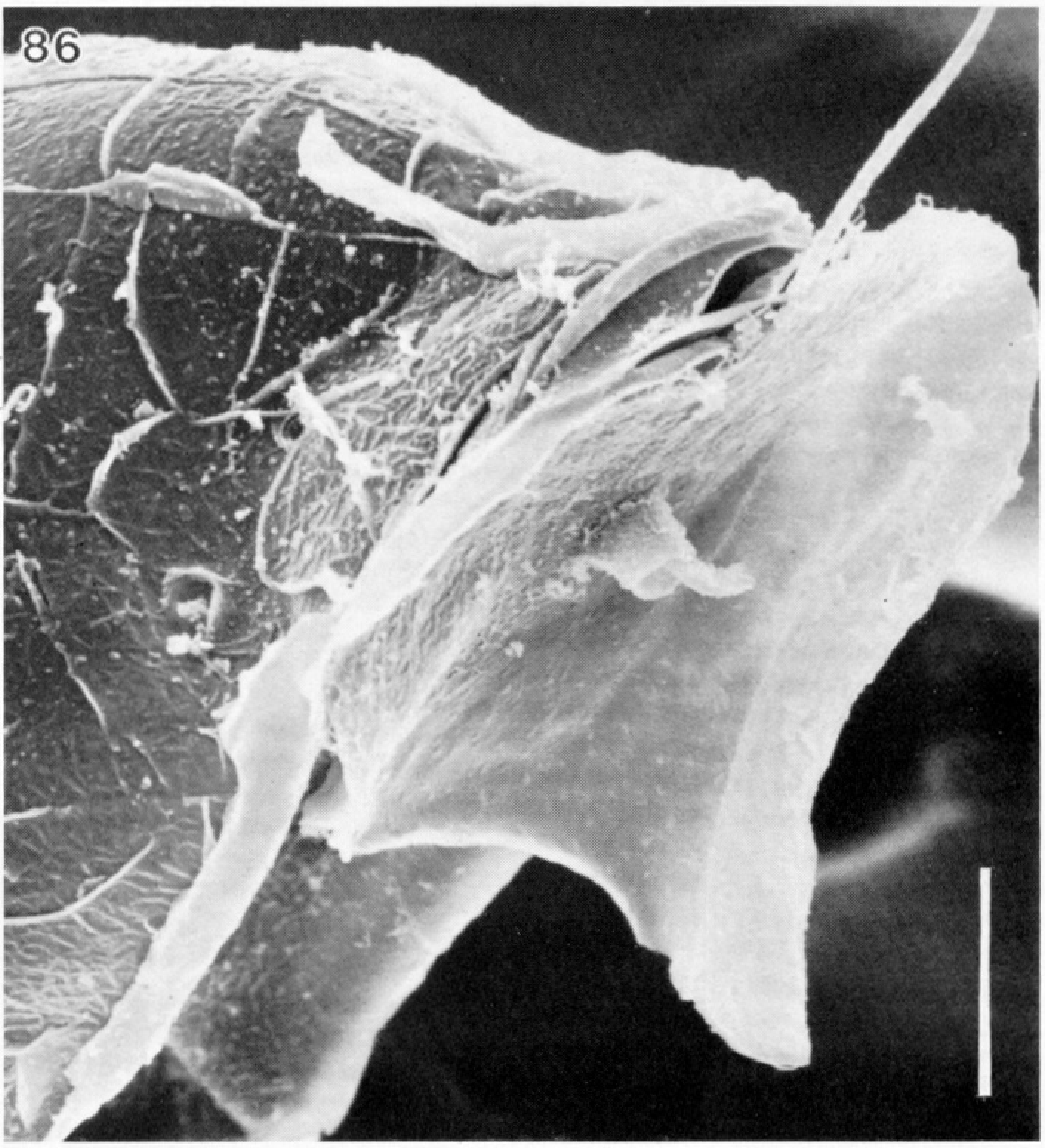
Figure 62. Lateral view of head showing ornamentation and associated pores. Scale bar 12 μm.

Figure 63. Dorsal view of rostral area of *M. langi* female. Scale bar 2 μm.

Figure 64. Dorsal view of *O. birdi* tantulus attached to pereopod of its host tanaid. Scale bar 25 μm.







Description of plate 7

Figure 83. Dorsal view of abdomen of tantulus of *O. birdi*. Scale bar 5 μm.

Figure 84. Lateral view of head shield of female *O. curtus* showing ornamentation and pore pattern. Scale bar 10 μm.

Figure 85. Highly folded, convoluted integument of trunk sac of adult female *O. curtus*. Scale bar 10 μm.

Figure 86. Head of *O. curtus* still attached to a torn fragment of host integument, showing puncture point at centre of oral disc and the tubular structure penetrating the host's integument. Scale bar 2 μm.