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ON THE ANATOMY OF THE MISOPHRIOID COPEPODS, WITH SPECIAL REFERENCE TO *BENTHOMISOPHRIA PALLIATA* SARS

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The misophrioids are a small but phylogenetically important order of copepods, comprising only three species, which exhibit a mosaic of characters drawn from both gymnoplean and podoplean lineages.

The skeletomuscular system of *Benthomisophria palliata* is described in detail and comparative observations are made on *B. cornuta* and *Misophria pallida*. All were found to possess a carapace-like posterior extension of the cephalosome which completely encloses, both dorsally and laterally, the first pedigerous somite beneath. This structure is a posterior outgrowth of the maxilliped-bearing somite and is not derived from the tergite of the pedigerous somite that it encloses. It may represent a modification of the somitic hyaline frill common to many copepods. Its presence is apparently associated with the ability of *Benthomisophria* to gorge itself until virtually all the free space within the prosome is occupied by the gut.

The gut contents of *B. palliata* reveal that it feeds on relatively large food particles. The probable feeding mechanism is inferred from the ranges of movement possible at each of the joints of the feeding appendages and from their musculature. The probable swimming mechanism is also inferred from similar data for the thoracic limbs.

The skeletomusculature of other copepod groups is compared with that of *Benthomisophria*. The extrinsic muscles of the cephalic appendages and both the extrinsic and intrinsic muscles of the swimming legs were found to be relatively uniform throughout the Copepoda. The longitudinal trunk muscles and intrinsic muscles of the cephalic appendages were found to be more subject to modification during adaptive radiation in habit and feeding strategy respectively.

Both species of *Benthomisophria* exhibit ornamentation of the integument. This is described and a strengthening role is attributed to the intricate system of lamellae and ridges present. Laterally on the cephalosome of *Benthomisophria* species are areas of funnel-shaped cone organs standing erect from the body surface and bearing a spherical globule of secretion distally. They are positioned so that the long setae of the reflexed antenna and mandibular palp sweep over them. It is concluded that the secretion is spread over the surface of the carapace-like structure by the setae. Its function may be protective.

The gross anatomy of the other organ systems is described. The highly distensible gut has large lateral caecae which can expand to accommodate large amounts of food. The musculature of the hindgut is described, as is the postulated sequence of events during defaecation.

Adult *B. palliata* possess paired antennary glands as the functional excretory organs. The maxillary gland is absent. In other copepod groups the maxillary gland is the functional excretory organ of the adult.

The central nervous system is described. The complete absence of the nauplius eye throughout the life cycle of misophrioids is noted.

The heart is absent from *B. palliata*. In *Misophria pallida* it is a barrel-shaped structure about 40 μm long, with weakly muscular walls. It has anterior and posterior ostia only and is suspended from the dorsal body wall by short muscle fibres.

The reproductive system is described in both sexes. Male and female have paired gonads, ducts and genital openings. The oviducts open into cavities (genital antra) within the genital somite, which are closed off externally by the plate formed from the fused sixth legs. The male possesses relatively simple vasa deferentia which are poorly differentiated into functional zones.

The phylogenetic position of the misophrioids is discussed. They exhibit an unusual combination of ancestral, unique and convergent characters which makes assessment of their affinities difficult. It is tentatively suggested that the Misophrioida, which merits ordinal rank, is more closely related to the Harpacticoida than to any other order.

1. Introduction

The copepod order Misophrioida comprises just three species, *Misophria pallida* Boeck, *Benthomisophria palliata* Sars and *B. cornuta* Hulsemann & Grice. *M. pallida* is a littoral and sublittoral benthic species with a wide geographical distribution, extending from Norway to the Red Sea. It is uncommon throughout its range. The *Benthomisophria* species are bathypelagic and both are widely, if patchily, distributed, with records from both the North Atlantic and North Pacific Oceans. *B. cornuta* is rare but *B. palliata* is locally common within restricted depth horizons (Boxshall & Roe 1980). The misophrioids are important phylogenetically as they exhibit a mosaic of characters drawn from both the gymnoplean and podoplean lines within the Copepoda. As a group they have been classified variously within the Calanoida (Brady & Robertson 1873), Cyclopoida (Boeck 1864) and Harpacticoida (Sars 1903), and as a distinct group separated from and equivalent to these other orders (Giesbrecht 1892; Gurney 1927, 1933*a*; Lang 1948*a*, *b*). More recently Kabata (1979) reconsidered the ordinal relationships within the Copepoda and concluded that the misophrioids constitute a separate order formed as an early offshoot from the podoplean line.

Information on the biology and ecology of the misophrioids is sparse. Most published records comprise only a brief description and the locality data, sometimes with speculations on the phylogenetic position of the group. Sars (1903) described the swimming behaviour of *M. pallida* and Gurney (1933*a*) reared the same species from the egg to the first copepodid stage. Boxshall & Roe (1980) described the later life history stages of the two species of *Benthomisophria* and recorded observations on their depth distributions, abundance and feeding biology. Several authors have noted the presence of external integumental markings over the body surface of *M. pallida* and *Benthomisophria* species. Boxshall & Roe (1980) suggested that the surface ornamentation may facilitate distension of the body during feeding in *B. palliata*, a species that gorges until its entire prosome is distended. The morphology of the digestive tract and the skeletomuscular system has been studied and an attempt is made here to provide a functional interpretation of both these systems. The other organ systems of *B. palliata* are also described to provide the basic data on morphology and anatomy required before comparative studies in relation to other copepod orders can be undertaken.

2. Materials and Methods

All the *Benthomisophria* material examined was obtained from RMT1 + 8 samples taken in the North Atlantic at *Discovery* stations 9131 and 9541 (about 20° N, 21° W). Sampling methods and precise station data are given in Boxshall & Roe (1980). Samples were fixed initially in 5% formalin in sea water, subsequently transferred to a preserving fluid based on that of Steedman (1974), and stored in this fluid for between 1 and 3 years before the *Benthomisophria* were sorted and transferred to 70% (by volume) ethanol.

Specimens of *M. pallida* were taken from the collections of the British Museum (Natural History). This material was originally collected in Scotland in 1897 and Plymouth in 1903 (BM(NH) registration numbers 1911.11.8.42443–42447 and 42450–42452) and had been stored in 70% (by volume) ethanol at least since 1911. Material examined from the BM(NH) collections for comparative purposes included *Acanthocyclops venustus* (Norman & Scott) from Dartmoor and Ireland (registration numbers 1937.11.16.709–713) and *Centraugaptilus horridus* (Farran) from the Arabian Sea (registration number 1949.12.31.458). Specimens of

the phyllocarid malacostracan *Nebaliopsis typica* Sars were examined on loan from the *Discovery* collections at the Institute of Oceanographic Sciences (Wormley).

The two *Benthomisophria* species, *M. pallida*, *A. venustus*, *C. horridus* and *N. typica* were all examined by scanning electron microscopy (s.e.m.) with an ISI 60A microscope. Specimens were prepared by transfer from 70% (by volume) ethanol, via 50% (by volume) ethanol, to distilled water, washed three times, freeze dried in an Edwards EF2 Freeze Drier, mounted on stubs and sputter coated with palladium.

Benthomisophria cornuta was also examined by transmission electron microscopy (t.e.m.) on an AEI EM6B microscope. The anterolateral portion of the prosome was removed, rehydrated and postfixed in 2.5% (by volume) glutaraldehyde in 0.1 M sodium cacodylate buffer for 24 h at room temperature. After washing in cacodylate buffer the material was postfixed in osmium tetroxide for 4 h at 4 °C, then washed again. The material was dehydrated through graded acetones and embedded in Spurr resin. Ultrathin sections were stained with lead citrate and uranyl acetate.

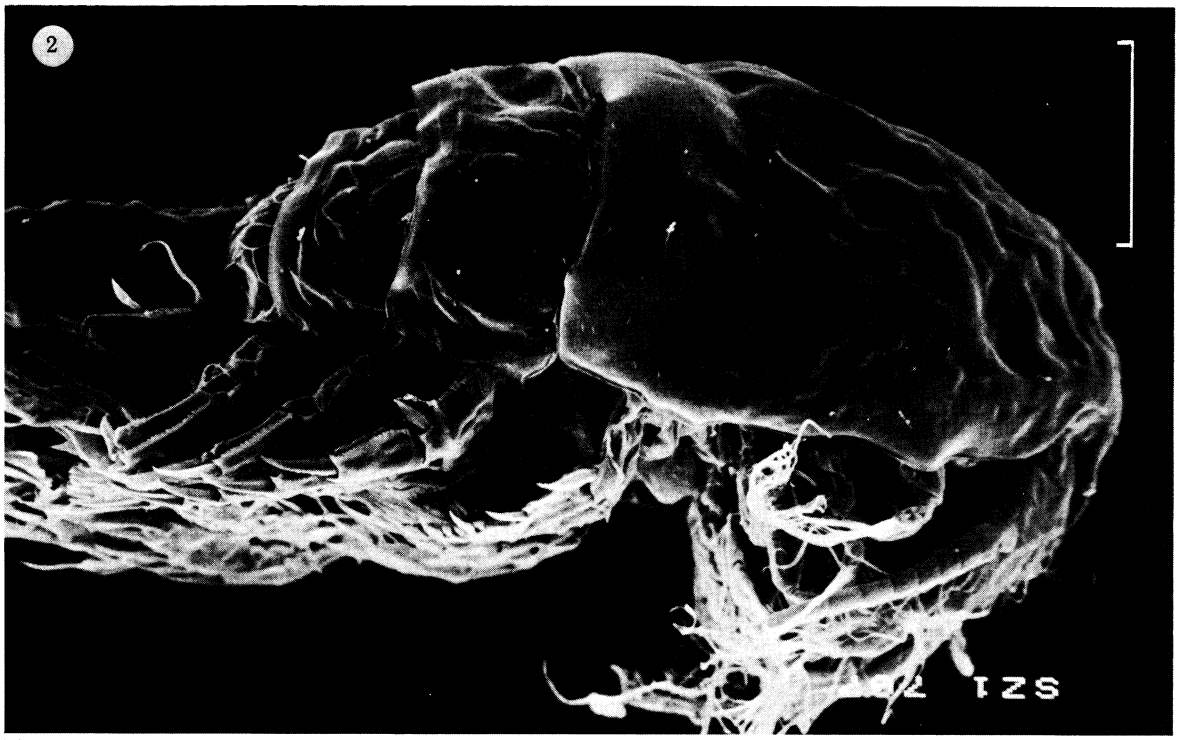
Serial sections of several specimens of *B. palliata* and *M. pallida* were examined by light microscopy. Transverse and longitudinal serial sections of 8 μm thickness were made of specimens embedded in paraffin wax and three staining techniques were employed: haematoxylin–eosin, Alcian blue with haematoxylin–eosin, and Masson's trichrome. Specimens of *B. palliata* were also dissected, in either 70% (by volume) ethanol, lactophenol or glycerol, with the aid of electrolytically sharpened tungsten wire needles. The integument was examined in specimens from which all internal tissues had been removed by heating in 10% (by mass) potassium hydroxide solution at 50 °C for 24 h. Cleared exoskeletons were washed and stained in chlorazol black before examination. All light microscope drawings were made with the aid of a camera lucida; other drawings were traced from s.e. micrographs.

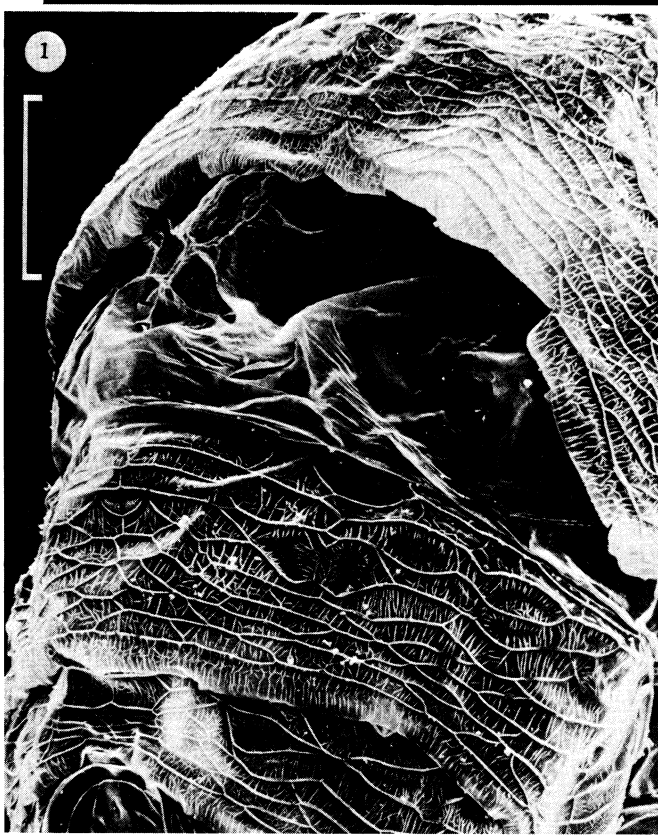
3. The skeletomuscular system

(*a*) *Trunk exoskeleton*

The basic copepod body form comprises an anterior prosome and a narrow posterior urosome. The prosome is rigid anteriorly with all the cephalic somites and the first (maxilliped-bearing) thoracic somite fused to form a single unit, the cephalosome. The cephalosome is covered dorsally and laterally by a thickened dorsal shield derived from the fused tergites. The posterior part of the prosome is semi-rigid comprising four free pedigerous thoracic somites, the second, third and fourth of which are each covered dorsally and laterally by a thickened tergite. These somites are separated dorsally and laterally by a narrow arthrodial membrane allowing some telescoping dorsally about transverse hinge lines running parallel to the ventral body surface at each intersegmental junction. Ventrally the integument of the prosome varies in thickness and allows some ventral flexure. The urosome somites are essentially thickened hoops of integument separated from adjacent somites by continuous arthrodial membrane. The anterior end of each of these somites can be telescoped inside the posterior end of the preceding one and there is freedom of movement in all directions. The conspicuous junction between the prosome and the urosome is a hinge joint with extensive dorsal and ventral arthrodial membrane permitting considerable dorsoventral movement around the midbody transverse hinge line.

The cephalosome possesses a carapace-like posterior extension which encloses the entire first





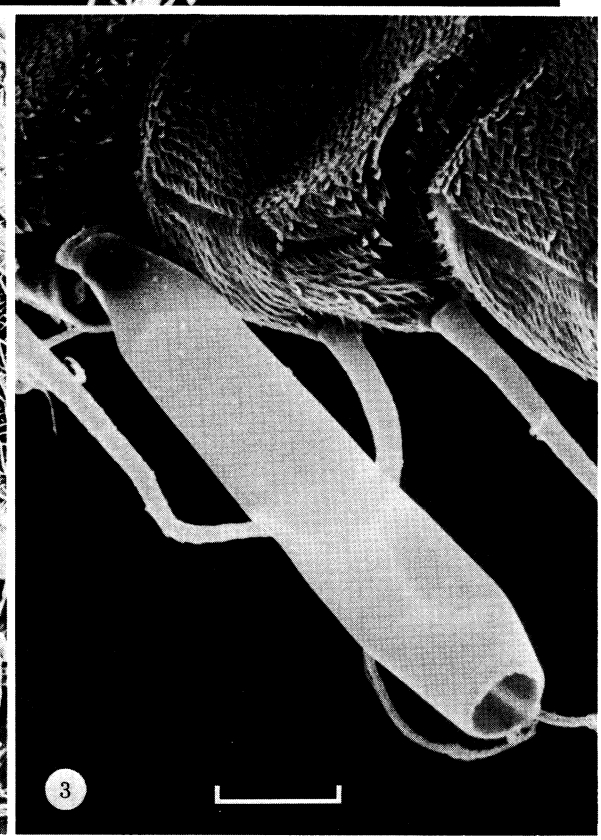


FIGURE 1. Dorsolateral view of the midprosome of a distorted *B. palliata*. The ornamented carapace-like extension of the cephalosome is raised, revealing the smooth integument of the first pedigerous somite, which it normally encloses. The ornamented tergites of the second and third pedigerous somites can also be seen. Scale bar 300 μm.

FIGURE 2. Lateral view of female *M. pallida*. The carapace-like posterior extension of the cephalosome appears as the light, raised area. Scale bar 100 μm.

FIGURE 3. Aesthetasc on the antennule of a female *B. palliata*. Scale bar 20 μm.

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pedigerous somite dorsally and laterally. This structure is derived as a backward growth from the cephalosome and not from the tergite of the first pedigerous somite which it overlays. The carapace-like extension encloses the somite beneath so completely that it cannot be easily detected and the prosome appears to be four-segmented (Hulsemann & Grice 1964; Tanaka 1966; Boxshall & Roe 1980). It can be seen in some damaged specimens (figure 1, plate 1) and in longitudinal section (figure 4). Only Sars (1909) noted the presence of this structure, in his original description of *B. palliata*. It has external ornamentation similar to that on the rest of the dorsal shield although the pattern differs in some details (see §4*a*). The integument of the first pedigerous somite beneath the carapace-like extension is thin and smooth externally. It is usually loosely folded and allows for considerable expansion of the prosome about a transverse hinge line parallel to the ventral body surface at the anterior end of the first pedigerous somite. A similar structure is present in both *B. palliata* and *B. cornuta*, and also in *M. pallida*. Its presence and extent in *M. pallida* are indicated by the raised lighter area at the posterior end of the cephalosome in figure 2, plate 1. The misophrioids are unique among the Copepoda in the presence of a carapace-like posterior extension of the cephalosome.

It is interesting here to consider the possible homologies of this carapace-like structure. In all crustacean groups that possess a carapace at least in some members (Branchiopoda, Branchiura, Cirripedia, Malacostraca and Ostracoda) it is formed as a posterior fold of the maxillary somite (Hessler & Newman 1975). The structure present in misophrioids is derived as a backwards growth apparently from the maxilliped-bearing somite. The second and third pedigerous somites bear small posteriorly directed flaps of integument dorsally and dorsolaterally along their posterior margins (figure 4, hyf). These are homologous with the hyaline frill found on the body somites of many harpacticoid copepods (Moore 1976). They comprise a double layer of integument, a dorsal layer which is a continuation of the tergite and a ventral layer which is an extension of the thinner intersomitic arthrodial membrane. The structure of the carapace-like extension of the cephalosome is the same and it is therefore probable that this unique misophrioid feature is derived as an elaboration of the posterior hyaline frill of the cephalosome.

The integument forming the carapace-like extension is relatively thick and rigid, the rigidity being enhanced by the external ornamentation. Its function appears to be protective. It encloses and protects the first pedigerous somite, the integument of which is relatively thin and highly flexible to accommodate the distension of the prosome during feeding.

(*b*) *Trunk musculature*

B. palliata possesses two major groups of trunk muscles, the paired dorsal and ventral longitudinal trunk muscles. Each dorsal longitudinal muscle is a cluster of large fibres originating anteriorly from the dorsal wall of the cephalosome in the mandibular somite (figures 5 and 13). The muscle passes posteriorly in the form of a broad band of large fibres some of which attach anteriorly in the second pedigerous somite. Several of those fibres not attaching in the second pedigerous somite have a tendinous interruption at this level which is not connected to the body wall. As the muscle continues posteriorly all the fibres attach anteriorly in the third pedigerous somite, anteriorly and posteriorly in the fourth and anteriorly in the first urosome somite. Each of these attachments forms the insertion site for one or more fibres, the final insertion site of the longest fibres being the first urosome somite.

The paired dorsal longitudinal muscles pass into the urosome in the form of a narrow

tendinous strand. Each inserts anteriorly in the first urosome somite adjacent to the site of origin of the dorsal longitudinal muscles of the urosome. As it passes down the urosome to insert dorsally on the anterior rim of the anal somite the muscle remains relatively compact (figure 7) and dorsolateral in position. At the fourth urosomal intersegment it is interrupted by an intersegmental tendon which is not connected to the body wall. A short muscle fibre originates near

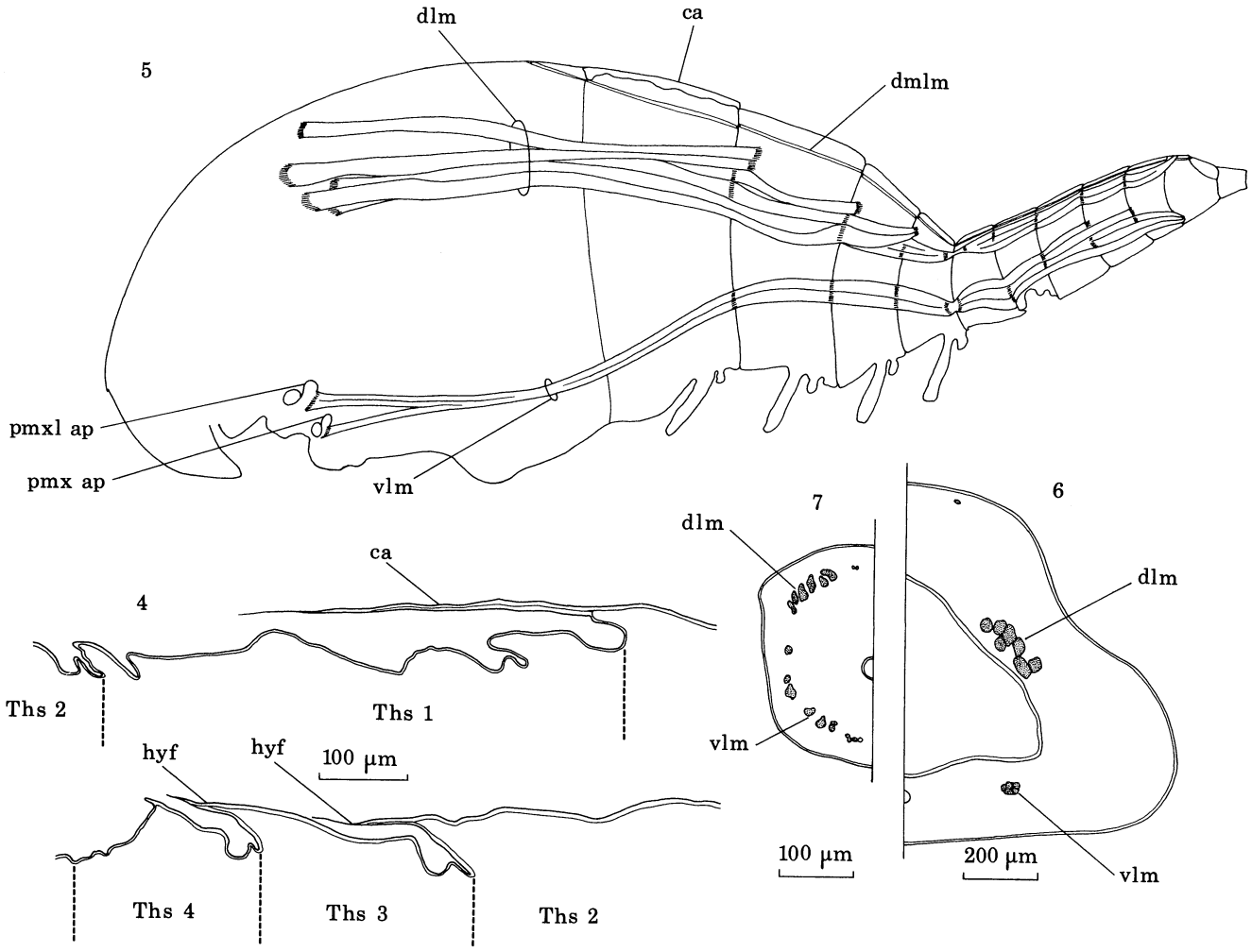


FIGURE 4. Median longitudinal section through the dorsal integument from the posterior end of the cephalosome to the posterior end of the prosome. The carapace-like extension of the cephalosome overlying the first pedigerous somite is shown, as are the hyaline frills of the posterior borders of the second and third pedigerous somites.

FIGURE 5. Median internal view of the longitudinal trunk muscles of a female *B. palliata* of body length 5.3 mm.

FIGURE 6. Transverse section through the prosome in the maxilliped-bearing somite.

FIGURE 7. Transverse section through the third urosome somite.

the dorsal midline in the posterior portion of the cephalosome. It runs posterolaterally to attach dorsolaterally on the anterior edge of the first pedigerous somite and continues posteriorly as a thin fibre passing medial to the main dorsal longitudinal muscle, attaching at each intersegmental boundary and inserting anteriorly on the first urosome somite. Adjacent to the site of

insertion of this muscle a dorsomedial urosome muscle originates which passes posteriorly to insert on the anal somite.

Each paired ventral longitudinal muscle originates from both the postmaxillulary and postmaxillary apodemes. Both these apodemes are hollow and open to the external medium at their outer ends. The ventral longitudinal muscle passes posteriorly and inserts on the anterior end of the first urosome somite, having passed the prosome–urosome boundary in the form of a broad tendinous strand. At the anterior ends of each of the second, third and fourth pedigerous somites are tendinous interruptions but these do not appear to be connected to the body wall. The muscle fibres form a compact bundle, generally rounded in cross section (figure 6). The ventral longitudinal muscles of the urosome originate at the anterior end of the first urosome somite at the position where the tendinous continuations of the prosomal ventral longitudinal muscles insert. They form a diffuse ventrolateral sheet anteriorly (figure 7) but become more compact and ventral in position posteriorly. Some fibres of this muscle attach at the anterior ends of the fourth and fifth urosome somites and it terminates at an insertion on the anterior rim of the anal somite. Some fibres attach to the body wall by thin strands, part muscle, part tendon, at the anterior ends of the second and third urosome somites (figure 61, suspt).

There are two pairs of short cephalic pleural muscles running between the dorsal and ventral surfaces of the cephalosome in the pleural region posterior to the antennules (figure 13, cplm 1–2). These muscles probably help to maintain the shape of the projecting pleural region between the bases of the antennules and antennae.

(*c*) *Skeletomusculature of the cephalosomic appendages and associated structures*

All the appendages have both extrinsic and intrinsic muscles. The muscles are identified and named according to their presumed function whenever possible; otherwise they are named by their position within the appendage. The six main functional types are promotor, remotor, extensor, flexor, adductor and abductor. The segmentation and armature of the appendages of *B. palliata* have been described by Boxshall & Roe (1980); so only features of appendage structure such as the position and range of movement of joints will be considered here.

(i) *Antennule*

The female antennule (figure 9) comprises a proximal portion of six more-or-less cylindrical segments and a twelve-segmented distal portion, separated by a major hinge joint between segments 6 and 7. The integument of the first segment is rigid, providing a firm attachment for both extrinsic and intrinsic muscles. Segments 1–6 are separated from each other by narrow rings of arthrodial membrane which allow a small amount of flexion. The antennule projects laterally and slightly ventrally from the head and movement of the limb as a whole occurs at the joint between the head and the limb base. This is basically a promotor–remotor swing about the slightly oblique medial to lateral hinge line (figure 8). There is extensive arthrodial membrane anterior to the hinge line but only a small amount posteriorly. Also at this joint there is a large apodeme formed as an intucking of the integument and open externally. It is situated posteromedially on the rim of the limb base and provides an attachment site for some of the oesophageal dilator muscles.

At the joint between segments 6 and 7 a range of movements is possible about the fulcrum. The main movement is dorsoventral flexion but there is extensive arthrodial membrane anteriorly and posteriorly, as well as laterally, which permits posterior flexion, bringing the

distal portion of the limb round into a posterolateral position. Segments 7–18 articulate with one another via a narrow ring of arthrodial membrane allowing only limited flexion at each joint.

The male antennule (figure 10) is geniculate and comprises a basal portion of nine and a distal portion of seven segments. Movement of the whole limb occurs around the head–limb base joint. The joint between segments 9 and 10 allows some dorsoventral flexion although less

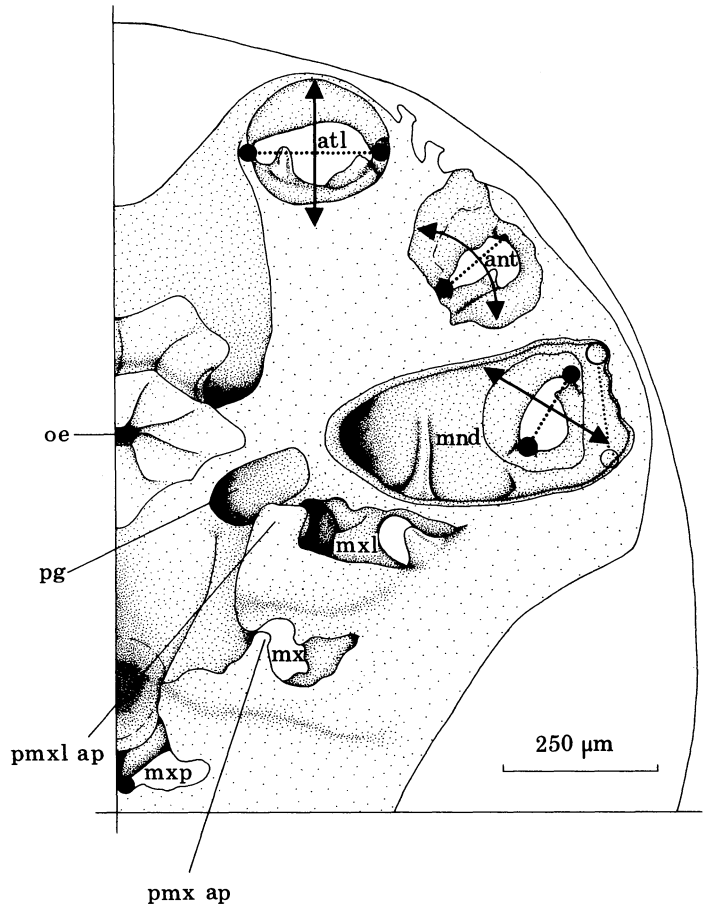


FIGURE 8. Internal view of the ventral body surface of the cephalosome, showing the bases of the appendages. The positions of the fulcra, main hinge lines and axes of movement are also marked. Those of the mandibular palp and gnathobase are shown by filled circles and open circles respectively.

than between segments 6 and 7 in the female. There is also a considerable amount of arthrodial membrane posteriorly, permitting posterior flexion about an anterior hinge line. The joints between segments 14 and 15, and 15 and 16 are modified to provide flexion of segments 15 and 16 respectively. Segment 16 is shown partially flexed in figure 10.

The extrinsic muscles of the antennule form three groups: the promotors, the remotors (both originating in the antennulary somite) and the long levator–promotor muscles originating in the mandibular somite. Promotor muscles 1 and 2 (figure 13, atl prm 1, 2) originate on the dorsal body wall and pass ventromedially to insert on the anterolateral rim of the first antennulary segment. These swing the appendage forwards about the medial to lateral hinge line. Remotor muscles 1 and 2 (atl rem 1, 2) originate on the dorsal body wall anterior to the

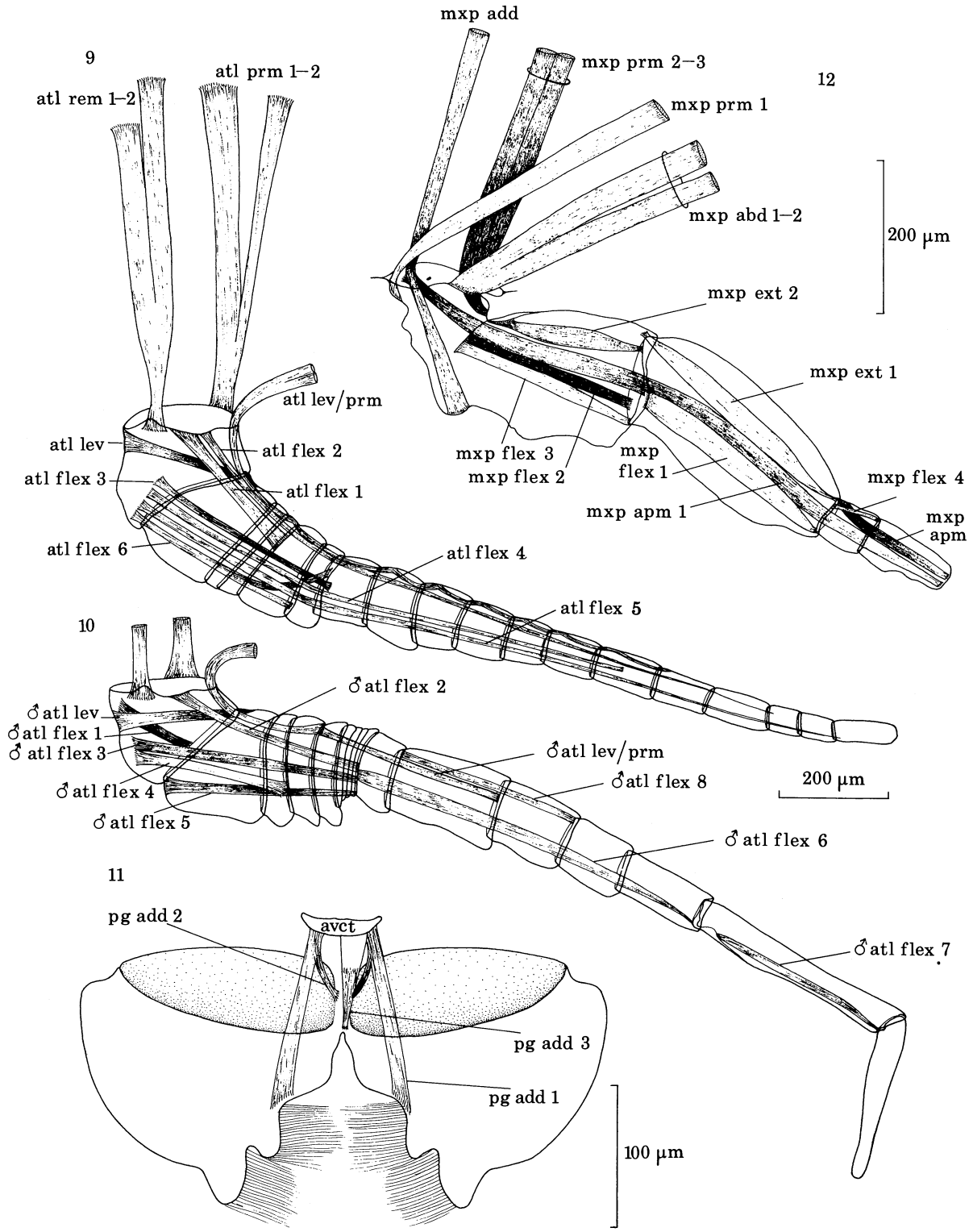


FIGURE 9. Posterior view of *B. palliata* female antennule, showing musculature.

FIGURE 10. The same for the male antennule but with only the insertion sites of the extrinsic muscles shown.

FIGURE 11. Anterodorsal view of the paragnaths, the paragnath muscles and their sites of origin on the anterior ventral cephalic tendon. The anteriorly situated paragnath adductor muscle 3 is omitted from one side.

FIGURE 12. Posterior view of maxilliped, showing musculature.

promotors and pass ventromedially and slightly posteriorly to insert inside the antennule on the posterior wall of the first segment. Contraction of these muscles swings the appendage backwards about the hinge line. There are two long oblique muscle fibres (atl lev/prm) which originate dorsally in the mandibular somite and pass anteroventrally internal to the dorsal extrinsic muscles of the antenna, uniting to form a single fibre, and into the antennule. This passes over the rim of the appendage posterolaterally and runs down the lateral wall to attach dorsally in the fourth segment. The muscle continues down the appendage, attaching dorsally in each of the eighth to thirteenth segments before inserting on segment 14. Contraction of the intrinsic portion of this muscle results in dorsal flexion (levation) of the limb. The extrinsic portion acts as both a levator and a promotor, exerting its pull posterior to the hinge line over the rim of the first antennulary segment, which therefore acts as a pulley.

Originating on the large antennular apodeme (figure 13, atl ap) are oesophageal muscles (oe dil), which are concerned primarily with dilation of the oesophagus during ingestion of large food items but which may also serve as stabilizers of the antennule–head joint.

In the female all the intrinsic muscles (figure 9) originate within the first segment. The intrinsic continuation of the oblique levator–promotor muscles has already been described. There is a short levator (atl lev) originating proximally on the medial wall and inserting proximally on the anterolateral wall of the second segment. This could produce some anterior flexion as well as acting as a levator. Two muscles originate on the posterior rim of the segment: the shorter (atl flex 1) inserts on the telescoped rim of the fifth segment and produces posterior flexion; the longer (atl flex 2) passes down the length of the appendage to insert laterally on segment 16. One muscle (atl flex 3) originates distally on the anterior wall of the first segment and inserts anteriorly on the proximal rim of segment 7. The remaining muscles all originate posterodistally in the first segment. The most lateral (atl flex 4) passes down the limb, inserts on the posterior wall of segment 13 and produces posterior flexion; another (atl flex 5) extends to the proximal end of segment 18 and acts as a depressor; the medial muscle (atl flex 6) bifurcates in segment 5, one fibre inserting posteromedially on the proximal rim of segment 6, the other posteriorly on the proximal rim of segment 7. The latter produces both posterior flexion and levation about the fulcrum between segments 6 and 7.

The intrinsic musculature of the male antennule (figure 10) differs in several respects from that of the female. The intrinsic continuation of the oblique levator–promotor muscle passes from its attachment in segment 4 to insert posteriorly on the proximal rim of segment 12. The levator muscle (atl lev) is the same as in the female. There is an additional short flexor muscle (♂ atl flex 1) originating proximally on the anterior wall and inserting anteriorly on the proximal rim of the second segment. Only one muscle originates posteriorly on the proximal rim of the first segment. This (♂ atl flex 2) inserts posteriorly on the proximal rim of segment 10. Antagonistic to it is a muscle (♂ atl flex 3) originating on the midanterior wall and inserting anteriorly on the proximal rim of segment 10. One muscle (♂ atl flex 4) originates posterodistally in the first segment and inserts posteriorly on the proximal rim of segment 4. Another (♂ atl flex 5) originates proximally on the midposterior wall of the second segment and inserts ventrally on the proximal rim of segment 10. A broad muscle (♂ atl flex 6) originates on the posterior wall of segment 10 and passes down the appendage to insert ventrally on the telescoped proximal portion of segment 15. Another (♂ atl flex 7) originates on the thickened integument at the proximal end of segment 15 and inserts ventrally in segment 16. A short muscle (♂ atl flex 8) originates proximally on the anterior wall of segment 11 and passes

obliquely to its insert on the proximal rim of segment 13. The proximal intrinsic muscles produce flexion at the joint between segments 9 and 10. The distal muscles inserting in segments 15 and 16 produce medial flexion (adduction of the last two segments).

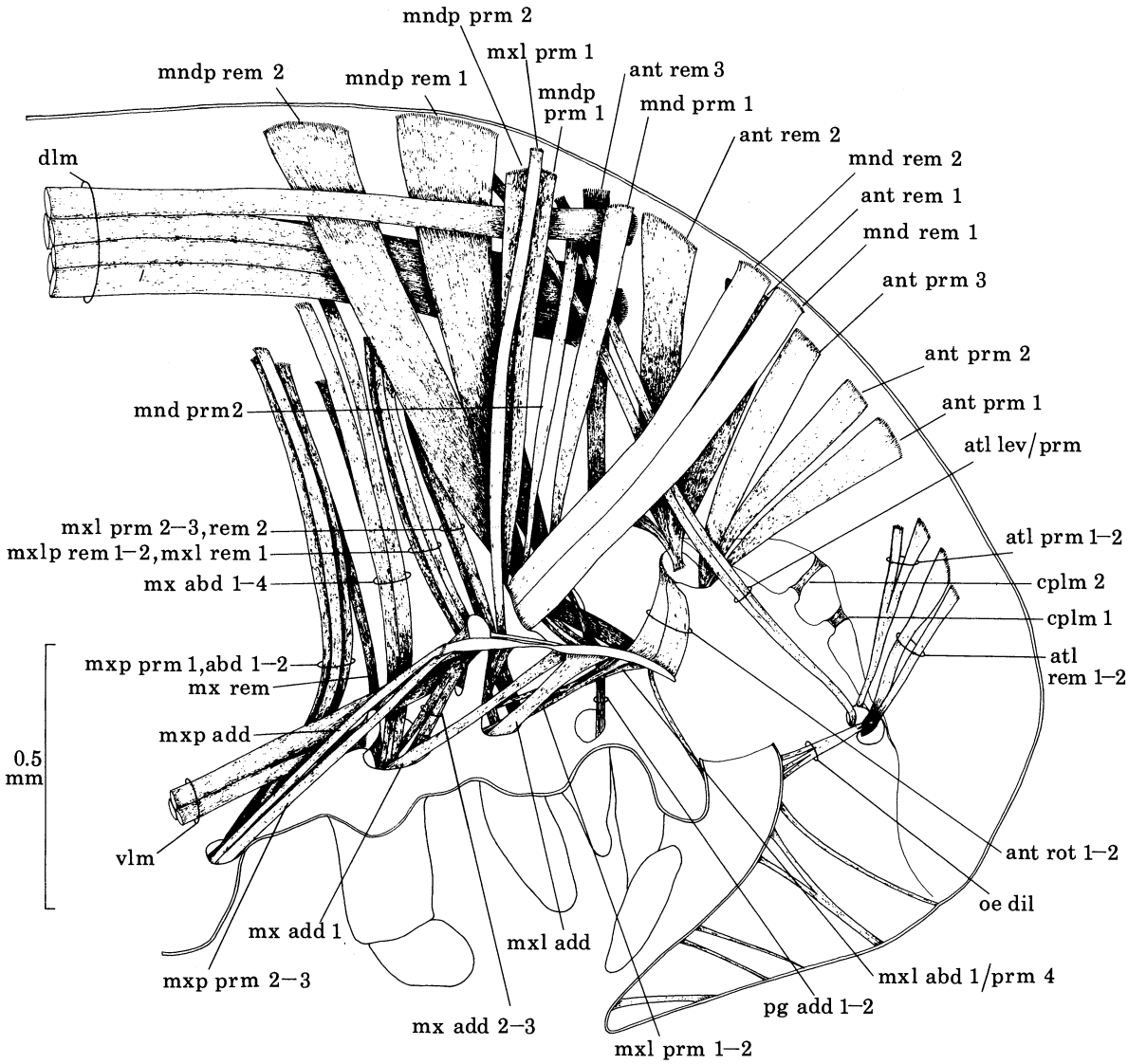


FIGURE 13. Median internal view of the musculature of the cephalosome. All other organ systems have been removed.

(ii) *Antenna*

The antenna comprises a large sympod, three-segmented endopod and five-segmented exopod (figures 14, 15) and it articulates with the head via a complex joint. There is a marked transverse hinge line along a posteromedial to anterolateral axis (figure 8) about which the limb swings, but there is also significant levator–depressor movement about a fulcrum at the posteromedial end of the hinge line. There is extensive arthrodial membrane anterior and posterior to the hinge line and lateral to the limb base. The sympod–exopod and sympod–endopod joints are both simple telescoped joints allowing a small degree of flexion in every

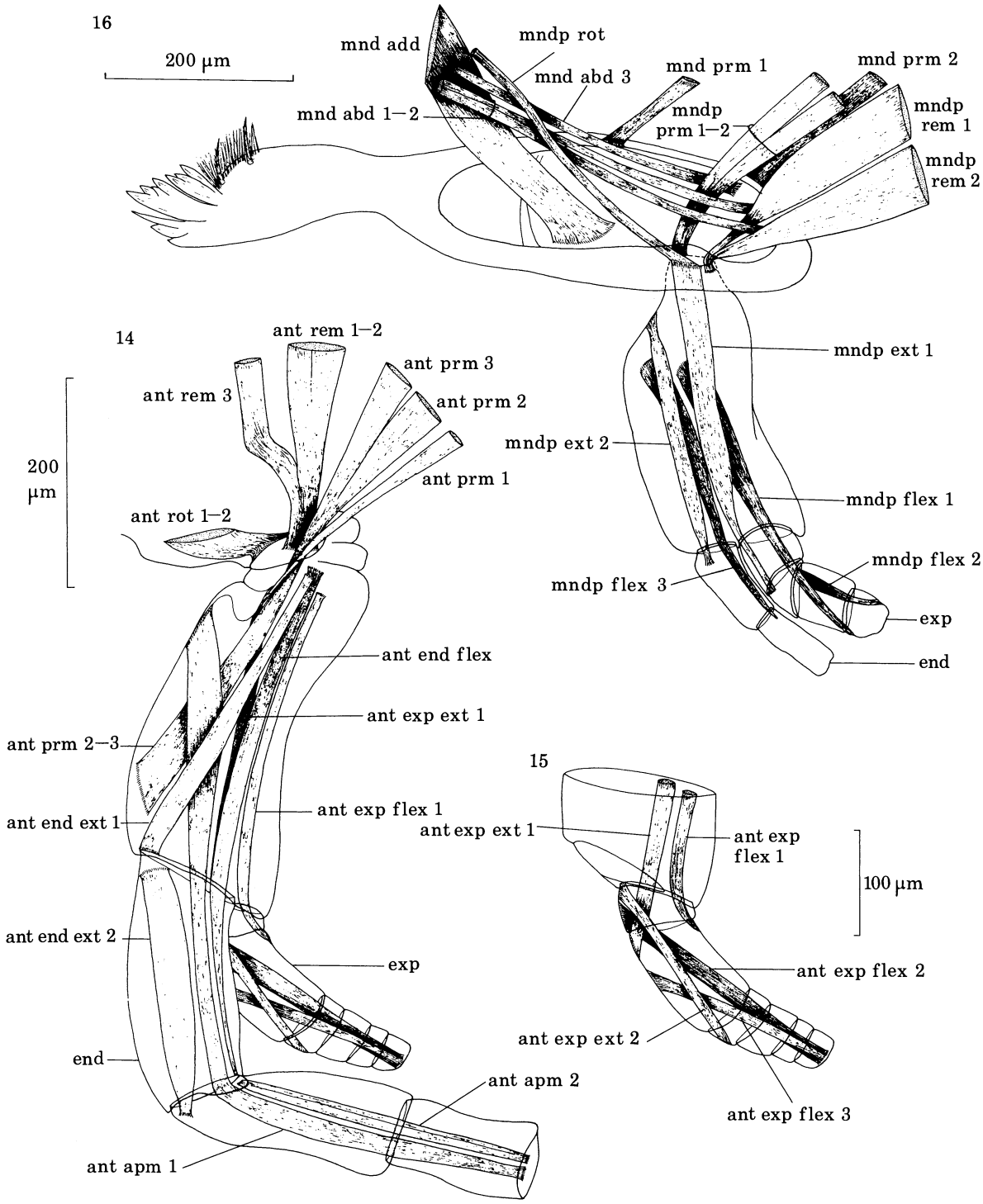


FIGURE 14. Anterior view of antenna, showing musculature.

FIGURE 15. Anterior view of antennary exopod and its musculature.

FIGURE 16. Posterior view of mandible and its musculature. Mandible remotor muscles 1 and 2 omitted.

direction. The intraexopodal joints are all similar, as is the joint between the second and third endopod segments. That between the first and second endopod segments is a hinge joint with an anterior to posterior hinge line. The integument at the apex of the endopod is flexible and deformable by the action of the muscles that insert there.

The extrinsic muscles form three functional groups; promotors, remotors and rotators. The promotors (ant prm 1, 2, 3) are broad, well developed muscles and all originate on the dorsal body wall anterior to the base of the limb (figures 13 and 14). Promotor 1 is the most anterior in origin and passes into the base of the antenna to insert on the thickened proximal part of the posteromedial wall of the sympod. Promotors 2 and 3 unite and pass posteroventrally into the limb, inserting distally on the posteromedial wall of the sympod. The remotors (ant rem 1, 2, 3) are also well developed broad muscles and all originate on the dorsal body wall (figures 13 and 14). Remotors 1 and 2 originate posterior to and at the level of the limb and pass ventrally into the limb inserting on the posterior wall just inside the rim of the sympod. Remotor 3 originates posterior to the other antennary muscles and passes ventrally and slightly anteriorly to the site of a tendinous attachment to the body wall, where it bends through an acute angle to pass anteriorly and unite with remotors 1 and 2. The position of the tendinous attachment allows the muscle to achieve a more posteriorly directed pull than it would if it had passed directly to its insertion from its dorsal origin. The rotator muscles (ant rot 1, 2) originate dorsally on the anterior ventral cephalic tendon (figure 24) and pass laterally to insert around the posterior rim of the sympod (figure 13). These may also produce some remotion.

One intrinsic muscle (figure 14, ant end ext 1) originates anteromedially in the proximal part of the sympod, passes obliquely to insert posteromedially on the proximal rim of the first endopod segment and acts as an extensor of the endopod. A broad muscle (ant apm 1) originates proximally on the posteromedial wall and passes right down the endopod to insert at its apex without attaching at any intersegmental joint. It may serve to manipulate the long setae borne at the apex of the endopod. Another long muscle (ant end flex) originates proximally on the anterolateral wall of the sympod and passes into the endopod to insert on the lateral portion of the proximal rim of endopod segment 2. This acts as a flexor of the distal part of the endopod around the hinge joint and of the first endopod segment. It is opposed by two muscles, antennary endopod extensor 1 and the short intraendopodal antennary endopod extensor 2, which originates proximally on the posterolateral wall of the first segment and inserts just inside the second endopod segment on the medial wall. Originating proximally on the lateral wall of the second endopod segment is a double-stranded muscle (ant apm 2) which passes distally to insert on the concave apex of the endopod. This muscle, with antennary apical muscle 1, is involved in manipulating the long apical setae of the endopod. Two muscles originate proximally in the sympod and pass into the exopod. One (ant exp ext 1) originates on the posterolateral wall and inserts posteriorly in the proximal part of exopod segment 2. The other (ant exp flex 1) originates anteriorly and inserts anteriorly on the proximal part of exopod segment 2. These oppose each other, extending and flexing the whole exopod. Within the exopod (figure 15) there are three muscles, an extensor (ant exp ext 2) originating proximally on the posterior wall of the first segment and inserting on the ventral wall of the third and two flexors. One flexor (ant exp flex 2) originates distally on the posterior wall of the first segment, the other (ant exp flex 3) midway along the posterior wall of the second. Both insert apically and are probably involved in manipulation of the apical setae as well as in flexion of the exopod.

(iii) *Labrum*

Anteriorly the labrum (figures 20 and 46) is rigidly fused to the rostrum and forms a massive, posteriorly directed extension of the ventral cephalic surface. Posteriorly it overlaps the mouth, enclosing the preoral food chamber ventrally. The ventral cephalic wall encloses the food chamber dorsally and the paragnaths and mandibular gnathobases form the lateral walls.

The labrum contains two pairs of labral muscles and many oesophageal muscles. One pair of double-stranded labral muscles (figure 46, lab m 1) runs dorsoventrally within the distal portion of the labrum, inserting on the posterior (dorsal) wall of the labrum just external to the oesophageal entrance. The other (lab m 2) runs more-or-less anteroposteriorly from an origin on the anterior wall towards a distal insertion on the posterior surface. Both pairs enlarge the food chamber by lowering the posterior (dorsal) labral wall. Also originating within the labrum are several of the oesophageal dilator muscles.

(iv) *Mandible*

The mandible (figure 16) comprises a sympod and a well developed biramous palp. The sympod extends medially to form a large rigid gnathobase which lies transversely and almost parallel to the ventral surface of the head so that the distal biting surface is in close apposition to that of the other mandible. The head–sympod joint is a large oval opening with small amounts of arthrodial membrane all around its circumference. Only small movements of the gnathobase are possible, primarily adduction and abduction about the indistinct hinge line between the well developed anterolateral fulcrum and the weak posterolateral fulcrum (shown as open circles in figure 8). Some promotion–remotion and some rotation (about the anterolateral fulcrum) are also possible at this joint. The palp articulates with the sympod via a simple hinge joint (shown as filled circles in figure 8). Extensive arthrodial membrane is present on both sides of this anterolateral to posteromedial hinge line. The joints within the palp are all simple telescoped joints with the ring of arthrodial membrane present at each allowing limited flexion in any direction.

The extrinsic muscles can be divided into four groups on the basis of their origins and insertions. They originate either on the dorsal body wall (figure 13) or on the anterior ventral cephalic tendon (figure 24). Muscles from both of these sites of origin pass either to the gnathobase or to the palp. The dorsal body wall muscles produce promotion and remotion of the gnathobase. The anterior promotor muscle (mnd prm 1) originates just dorsal to the origin of the dorsal longitudinal trunk muscles. It passes ventrally and slightly posteriorly to insert on the anterior rim of the gnathobase. The adjacent muscle (mnd prm 2) originates just lateral to the same dorsal longitudinal trunk muscle fibre and follows a parallel course to insert anterolaterally on the gnathobase rim. Remotor muscles 1 and 2 (mnd rem 1, 2) are better developed than the promotors. They originate medial to the antennary dorsal extrinsic muscles and pass posteroventrally to insert posteriorly on the gnathobase rim. These muscles have been omitted from figure 16 for clarity. The gnathobase muscles originating from the anterior ventral cephalic tendon are concerned with adduction and abduction. There is a single broad adductor muscle (mnd add) originating ventrolaterally near the anterior end of the tendon. This passes posterolaterally to a broad insertion inside the gnathobase, medial to the base of the palp. There are three abductor muscles, two of which (mnd abd 1, 2) are united at the origin on the anterior ventral cephalic tendon. All three run ventrolaterally passing between the dorsal extrinsic muscles to the palp before they insert on the inner side of the lateral wall of the sympod. The

four dorsal extrinsic muscles to the mandibular palp are the largest and best developed of all the cephalic limb muscles. The palp promotor muscles (mndp prm 1, 2) have a common origin dorsal to the dorsal longitudinal trunk muscles. They pass ventrally and slightly posteriorly to insert anteromedially on the proximal rim of the palp. The large palp remotor muscles (mndp rem 1, 2) originate dorsally near the midline, in the posterior part of the mandibular somite and anterior part of the maxillulary somite. They pass anteroventrally to insert posterolaterally just inside the proximal rim of the palp. These antagonistic promotors and remotors move the palp about the anterolateral to posteromedial hinge line. The single palp muscle (mndp rot) originating on the anterior ventral cephalic tendon and inserting posteriorly around the proximal rim of the palp must act as a rotator, twisting the palp around a fulcrum at the inner end of the oblique hinge line.

There are five intrinsic palp muscles: two pairs of antagonistic flexors and extensors, one pair manipulating each ramus, and a single flexor within the exopod. The exopod extensor (mndp ext 1) originates just inside the proximal rim of the palp, passes into the exopod and inserts proximally on the posterior wall of the second exopod segment. The exopod flexor (mndp flex 1) originates on the anterior wall about one-third of the distance along the protopod segment. It passes into the exopod to insert medially on the proximal rim of the apical segment. The short intraexopodal flexor (mndp flex 2) originates on the anterior wall of the second segment and inserts on the distal wall of the apical segment. The endopod extensor (mndp ext 2) originates proximally on the medial wall of the protopod and passes into the endopod to insert on the posterior wall of the first endopod segment. The endopod flexor (mndp flex 3) originates on the anterior wall of the protopod at the level of the origin of the exopod extensor. It passes into the endopod to insert proximally on the lateral wall of the apical segment.

(v) *Paragnath*

The paragnaths (figure 11) are unsegmented hemispherical lobes situated between the bases of the mandibles and maxillules on the ventral body surface. Each bears a medial and a distal process armed with long setules on their medial surfaces. The paragnath bases meet at the ventral midline forming an indented food groove. The medial walls of the paragnaths and the ventral body wall at the floor of the food groove are of thickened integument. Around the lateral margins of the paragnaths at their junctions with the ventral body wall the integument is thin and flexible.

Three muscles pass into each paragnath. All originate on the ventral surface of the anterior ventral cephalic tendon. The major, double-stranded paragnath adductor muscle (figure 11, pg add 1) passes anteroventrally from its origin via paired channels through the suboesophageal ganglion to insert on the anteromedial surface of the paragnath just proximal to the first medial process. A second muscle (pg add 2) shares the same origin but diverges as it passes the ventral surface of the ganglion and follows an anteromedial course to insert on the posterior part of the food groove. Anteriorly the third muscle (pg add 3) passes ventrally from its broad tendinous origin, via a channel at the anterior end of the suboesophageal ganglion (figure 52, ch) to insert on the anterior part of the food groove. The two muscles to the food groove must raise its floor and have the effect of adducting the distal processes of the paragnaths.

(vi) *Maxillule*

The maxillule (figure 17) comprises a large gnathobase and a distal biramous palp bearing two proximal endites. The gnathobase lies almost transversely but with the medial edge slightly anterior to the lateral edge. The head–maxillule joint (figure 8) possesses some arthrodial membrane anteriorly but very little posteriorly. Movement here is primarily a simple promotor–remotor swing about a transverse posterior hinge line. The presence of large, powerful adductor and abductor muscles inserting on the gnathobase and limb base respectively suggests, however, that adduction–abduction of the limb as a whole is also possible at this joint. This movement presumably involves some deformation of the ventral body integument as there is little arthrodial membrane medially or laterally to facilitate it. The palp is not well developed and the only significant joint is that at its base. There is some telescoping of the palp into the sympod allowing movement in all directions although there is a weakly developed fulcrum posteromedially about which some rotation of the palp takes place. The integument of the palp is thin and flexible in most areas.

The maxillule has numerous extrinsic muscles (figures 13 and 17) originating variously on the dorsal body wall, on both anterior and posterior ventral cephalic tendons and on the postmaxillulary apodeme. A promotor muscle (mxl prm 1) originates on the dorsal body wall within the mandibular somite and passes medioventrally to insert on the lateral portion of the anterior rim of the gnathobase. The dorsolateral body wall muscles originating in the maxillulary somite can be divided into anterior and posterior groups, each comprising three muscles. One muscle (mxl prm 2) of the anterior group inserts on the midanterior wall of the gnathobase just inside the rim and functions as a promotor. The other two pass into the gnathobase together and then divide, with one (mxl prm 3) passing medially to insert on the anterior wall of the gnathobase, and the other (mxl rem 2) passing posteromedially to insert on the midposterior wall of the gnathobase. These two muscles appear to act as an antagonistic promotor–remotor pair although together they may produce some abduction. The posterior group comprises one remotor muscle (mxl rem 1) which inserts on the posterior rim of the gnathobase and two others (mxlp rem, 1, 2) which pass into the limb to a common insertion proximally on the posterior wall of the palp. These two other muscles may act as remotors of the palp. Several muscles originate on the anterior ventral cephalic tendon, the largest of which is the main adductor muscle (mxl add) of the gnathobase. It originates posteriorly on the ventral surface of the tendon, passes ventrolaterally and posteriorly into the gnathobase, and inserts proximally on the posteromedial wall. A fibre (mxlp add 1) from this muscle separates off and continues ventrally into the limb to insert laterally on the proximal rim of the palp, producing adduction. Four other muscles originate on the anterior ventral cephalic tendon. Two pass posteroventrally together into the limb, one (a palp promotor, mxlp prm 1) inserting anteriorly on the rim of the palp, the other (mxlp prm 2) passing into the palp to insert on the anterolateral wall at the base of the exopod. The latter probably acts as a promotor of the exopod in opposition to an intrinsic remotor muscle (mxlp rem 4). The remaining two muscles pass ventrally and posteriorly together, with one, a gnathobase promotor (mxl prm 4), inserting on the anterior rim of the gnathobase, and the other, an abductor (mxl abd 1), inserting inside the limb on the midlateral wall. Two well developed abductor muscles (mxl abd 2, 3) originate on the posterior ventral cephalic tendon and pass ventrally and posterolaterally into the gnathobase, inserting on its anterolateral wall. Two extrinsic muscles originate on the postmaxillulary apodeme and

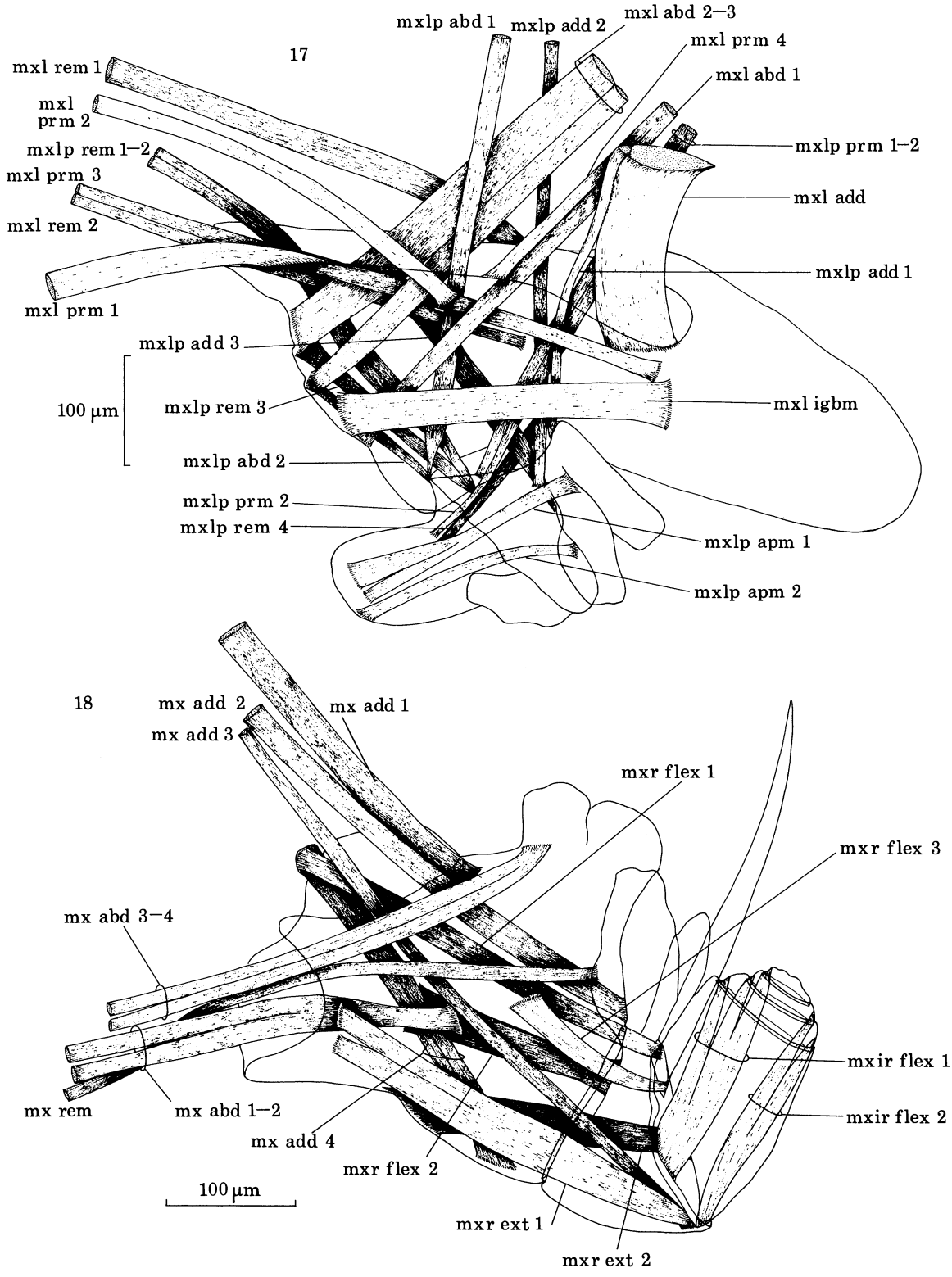


FIGURE 17. Anterior view of maxillule, showing musculature.

FIGURE 18. Anterior view of maxilla, showing musculature.

pass anteroventrally into the limb. One (mxlp abd 1) functions as a palp abductor and inserts laterally on the proximal rim of the palp; the other functions as an adductor–promotor (mxlp add 2) and inserts medially on the anterior wall of the palp.

There is a single intragnathobasic intrinsic muscle (mxl igbm) passing transversely from the anterolateral wall to the anteromedial wall. Its function is unclear as there is little flexibility in the integument of the gnathobase but it may assist the abductor muscles by giving greater rigidity to the gnathobase as a whole. Two short muscles originate on the posterolateral wall of the gnathobase, a palp abductor (mxlp abd 2) inserting laterally on the proximal rim of the palp, and a palp remotor (mxlp rem 3) inserting on the posterior wall of the palp. Another short muscle (mxlp rem 4) originates distally on the posterior wall of the gnathobase. It passes ventrolaterally to insert on the posterior wall of the exopod and acts as an exopod remotor in opposition to an extrinsic promotor (mxlp prm 2). A longer muscle (mxlp add 3) originates proximally on the posterior wall of the gnathobase and passes into the palp to insert on the posterior wall near the base of the endopod and is probably an adductor of the palp. Of the two transverse muscles within the palp, one (mxlp apm 1) originates on the anterolateral wall near the base of the first endite, the other (mxlp apm 2) on the posterolateral wall near the base of the endopod. The former divides and has a double insertion subapically on the anterior wall of the exopod. The latter inserts apically. Both serve to manipulate the fan of setae at the apex of the exopod.

(vii) *Maxilla*

The maxilla (figure 18) is uniramous and six-segmented. The sympod bears four endites, each armed with strong medially directed setae, and the ramus bears a strong claw proximally. The head–maxilla joint (figure 8) is provided with some arthrodial membrane on three sides but not posteriorly, although there is some flexible integument posteriorly between the basal rim of the sympod and the base of the postmaxillary apodeme. The movements at this joint are a promotor–remotor swing about the slightly oblique posterior hinge line, together with some adduction–abduction about a weak anteroposterior hinge line. The base of the ramus is telescoped inside the sympod and there is a complete ring of arthrodial membrane allowing some movement in all directions at this joint, although the main movement is flexion about an anteroposterior hinge line located medial to the middle of the joint. The remaining intraramal joints are simple telescoped joints each with a complete ring of arthrodial membrane permitting a small amount of flexion.

The extrinsic muscles (figures 13 and 18) originate on the dorsolateral body wall, on both ventral cephalic tendons and on the postmaxillary apodeme. Four muscles originate on the dorsolateral body wall of the maxillary somite and one in the maxilliped-bearing somite. The latter muscle (mx rem) passes ventromedially into the limb to insert distally on the anteromedial wall of the first segment, and perhaps functions as both remotor and abductor. The other four dorsolateral muscles form two pairs, each with a common insertion. One pair (mx abd 1, 2) inserts on the midanterior wall of the first segment, the other (mx abd 3, 4) on the medial wall proximal to the first endite. All appear to act primarily as abductors about the weak anteroposterior hinge line, although they may also produce some remotion. A single large muscle (mx add 1) originates posteriorly on the ventral surface of the anterior ventral cephalic tendon and passes posteroventrally towards its insertion on the posterior wall just inside the limb. This acts as a combined promotor and adductor, swinging the limb forwards and towards the ventral midline. Two muscles originating on the posterior ventral cephalic tendon have a

similar combined function. One of these (mx add 2) inserts distally on the medial wall of the first segment; the other (mx add 3) passes deep into the sympod inserting on the lateral wall at the distal extremity of the second segment. Two muscles originate on the anteroventral surface of the postmaxillary apodeme and pass directly into the limb. There is a double-stranded adductor muscle (mx add 4) passing ventrolaterally to insert on the lateral wall in the distal part of the first segment. The other (mxr flex 1) inserts medially on the proximal rim of the ramus near the base of the claw, acts as a flexor of the ramus, and may also be involved in manipulating the claw.

A short, well developed muscle (mxr flex 2) originates on the midposterior wall of the first segment and inserts posteriorly on the proximal rim of the second segment. It produces posterior flexion of the second segment. Another short flexor muscle (mxr flex 3) originates on the distal part of the anterior wall of the first segment and inserts on the posteromedial wall of the ramus just distal to the base of the claw. As well as producing flexion this muscle may be used in manipulating the claw. A large extensor muscle (mxr ext 1) with a double origin on the proximal part of the anterior wall of the first segment passes under the anterolateral surface of the sympod and inserts on the lateral rim of the ramus. A second extensor (mxr ext 2) originates posterolaterally in the middle of the first segment and inserts posteriorly on the proximal rim of the ramus. This inserts lateral to the anteroposterior hinge line and, while acting as an extensor, may also produce some anterior flexion of the ramus. Within the ramus two antagonistic flexor muscles (mxir flex 1, 2) originate proximally in the basal segment of the ramus and subdivide into strands which insert on the more distal segments.

(viii) *Maxilliped*

The maxilliped (figure 12) is uniramous and four-segmented. The joint between it and the head is complex and allows a wide range of movements. There is extensive arthrodial membrane anteriorly, anteromedially and laterally and movement occurs about a marked posteromedial fulcrum. The limb as a whole is capable of adduction–abduction, promotion–remotion and some rotation. The joint between the first two segments is a hinge joint allowing adduction of the more distal parts. The more distal joints are similar telescoped joints, each with a ring of arthrodial membrane permitting limited flexion.

The extrinsic muscles (figures 12 and 13) originate on the dorsolateral body wall, the posterior ventral cephalic tendon and the postmaxillary apodeme. Three muscles originate on the dorsolateral body wall and pass first ventrally, then ventromedially and posteriorly to approach the limb base from in front at an acute angle. Two of these muscles (mxp abd 1, 2) insert together around the posterolateral part of the proximal rim of the first maxilliped segment, and probably act as abductors–remotors, swinging the limb backwards and away from the midline. The third (mxp prm 1) inserts just inside the first segment on the medial wall and acts as a promotor. A single muscle (mxp add) originates on the posterior end of the posterior ventral cephalic tendon and passes posteroventrally into the maxilliped at an acute angle. It passes anteromedially over the rim of the first segment to insert on the anteromedial wall near the middle of the segment. Its function is difficult to interpret, but it probably produces some adduction and promotion. The remaining pair of extrinsic muscles (mxp prm 2, 3) originate on the postmaxillary apodeme and pass posteroventrally into the maxilliped, inserting on the thickened lateral wall just inside the first segment. These produce promotion, with some rotation towards the midline around the posteromedial fulcrum.

One intrinsic muscle (mxp apm 1) runs the whole length of the appendage, originating on the

anterior wall near the proximal end of the first segment and inserting at the apex of the limb. It produces some medial flexion of the distal-most segments in opposition to two short muscles, one (mxp apm 2) originating laterally at the proximal end of the third segment and inserting on the apex of the limb, and the other weaker muscle (mxp flex 4) originating distally on the second segment and inserting proximally on the lateral wall of the terminal segment. Flexion and extension of the joint between segments 2 and 3 is achieved by the action of a pair of antagonistic muscles. The medial flexor (mxp flex 1), originating proximally within the second segment and inserting medially on the proximal rim of the third segment, opposes the lateral extensor (mxp ext 1) which originates distally on the lateral wall of the first segment and inserts laterally on the proximal rim of the third segment. Movement between segments 1 and 2 is similar, extension being produced by a muscle (mxp ext 2) originating proximally on the thickened wall of the first segment and inserting laterally on the proximal rim of the second segment. This muscle is opposed by two flexor muscles, an anterior (mxp flex 2) originating on the anterior wall of the segment and inserting anteromedially on the proximal rim of the second segment, and a posterior (mxp flex 3) originating on the thickened part of the posterior wall and inserting medially on the rim of the second segment.

(*d*) *The feeding mechanism*

Study of the skeletomusculature of the mouthparts has revealed the range of movements possible for each appendage. Examination of s.e. micrographs of the oral region of several specimens of *Benthomisophria* with their mouthparts preserved in different positions confirms that these movements occur. It is possible to postulate the likely feeding mechanism from these data.

Two primary modes of feeding are employed by planktonic copepods, filter feeding on relatively small particles, and raptorial feeding (including predation) on relatively large particles. These two modes are not mutually exclusive as many filter feeders, such as *Oithona nana*, have the capacity to feed raptorially on larger food items (Lampitt 1978). The gut contents of *B. palliata* reveal that it is primarily a raptorial feeder on relatively large prey items (Boxshall & Roe 1980). The oesophagus is adapted for the passage of large particles and the presence of large portions of prey in the gut suggests that the function of the mouthparts is to seize prey, tear it into manageable fragments and force it into the oesophagus, as in the cyclopoid *Macrocyclops albidus* (Fryer 1957) rather than mastication of prey.

The planes of movement of each of the oral appendages are indicated in figure 8. The maxilliped is capable of adduction–promotion (swinging anteromedially) and abduction–remotion (swinging posterolaterally), and also some rotation about the posteromedial fulcrum. *B. palliata* is carnivorous and this limb is probably used to grasp prey and push it anteriorly towards the maxillae. The maxillae are capable of promotion–remotion about a slightly oblique hinge line, and some adduction–abduction. These movements probably serve to push prey anterodorsally towards the mouth. The strong medial and distal setae on the ramus (figure 19, mxs) may penetrate the prey and assist in the process of breaking it into manageable fragments. When the limb is adducted the setae on the endites (figure 19, es) are directed anteromedially, passing medial and proximal to the maxillulary gnathobase setae. They form a lateral barrier preventing the loss of food particles during fragmentation. The hemispherical ventral expansion of the body surface between the bases of the maxillae (figures 19 and 20, ims) bears several rows of stout spinules on its anterior and ventral surfaces which must help to prevent struggling prey from slipping posteriorly. The maxillule is capable of movements that

probably enable it to assist in forcing food particles anteriorly and slightly dorsally beneath the labrum. The line of strong distal setae on the gnathobase (figure 19, mxls) of each maxillule assists in forcing food anteriorly under the labrum and between the paragnaths into the path of the blades of the mandibular gnathobase. These setae may also be used to fragment the food. Much of the complex extrinsic and intrinsic musculature of the maxillule is associated with the palp which probably has a range of functions both mechanical and sensory. Some of these can be inferred from s.e. micrographs of the palp *in situ* in a series of specimens.

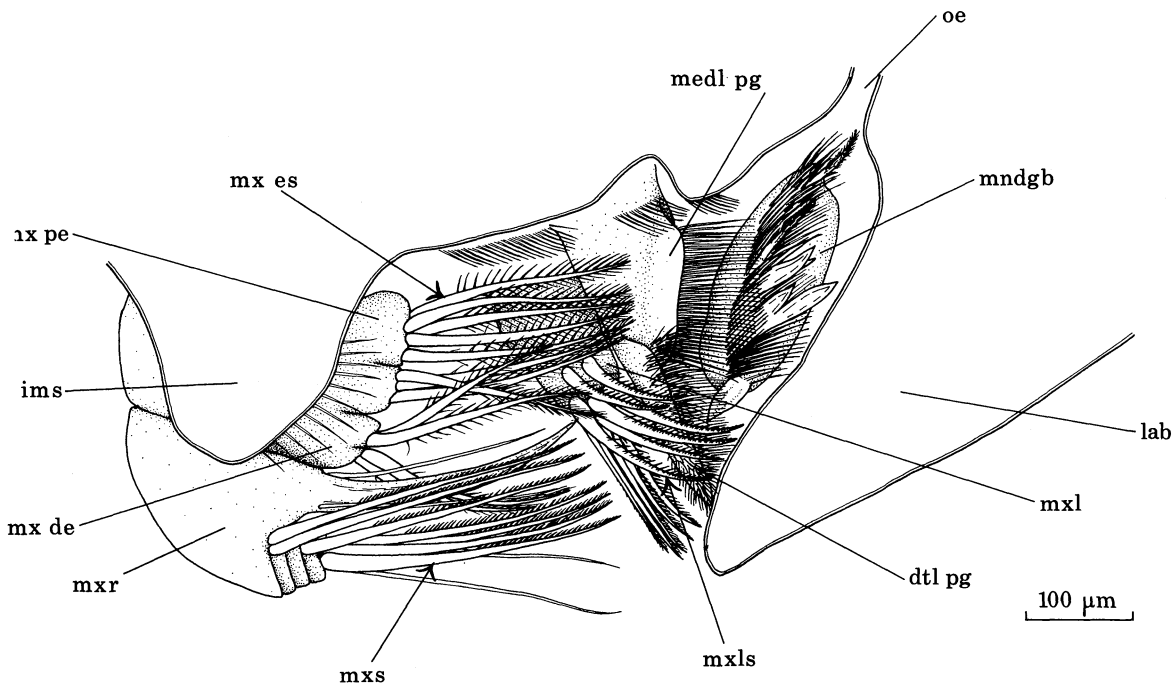


FIGURE 19. Median section through cephalosome of *B. palliata* showing mouthparts of left side *in situ*. The maxilla is adducted and the maxillule slightly abducted.

The palp possesses four fans of setae (figure 20), one formed by the distal setae from both endites, one distally on endopod segment 1, one on the apex of endopod segment 2 and the fourth on the apex of the exopod. The enditic setae are directed anteromedially, overlying the paragnath. The fan of setae on endopod segment 1 is directed anteriorly, overlying the middle portion of the mandibular gnathobase and extending lateral to the labrum as far as the base of the antennule. The fan on the apex of the endopod is directed ventrally and posterolaterally, overlying the sympod and exopod of the maxillule, and extending over the area between the mandible and the maxillule. The fan of apical setae on the exopod is directed posterolaterally, extending over the area lateral to the second maxilla and maxilliped. These fans of setae probably serve partially to block off the lateral ends of the gaps between the limbs and thereby reduce the flow of water through these channels during feeding movements, which may carry away small fragments of food. They may also serve to clean debris from the ventral surface of the mouthparts. Some of the maxillulary palp setae, particularly those on the ventrally directed endopod are probably sensory and make contact with prey being manipulated and fragmented by the other mouthparts.

The mandibular gnathobase extends medially from the base of the limb and passes into the

preoral food chamber dorsal to the labrum. The apical blades lie inside this chamber which is enclosed ventrally by the labrum, dorsally by the ventral body surface and laterally by the paragnaths and gnathobase itself. The labral glands discharge into this preoral chamber by means of paired pores. The muscles of the gnathobase can swing its armed apex anterodorsally and posteroventrally, fragmenting the prey and forcing it into the oesophagus.

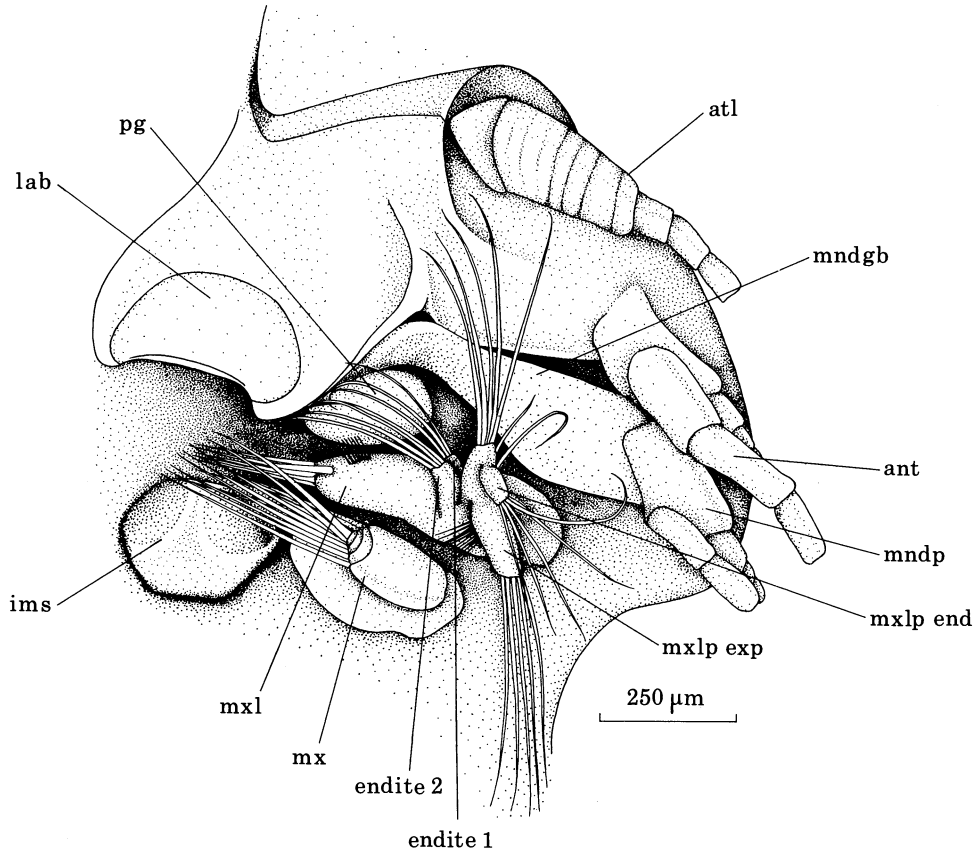


FIGURE 20. Ventrolateral view of the cephalic appendages of the left side *in situ*, drawn from s.e. micrographs. The fans of setae on the maxillulary palp can be seen.

The mandibular palp and antenna are morphologically and functionally very similar. The range of possible promotor–remotor and rotational movements indicates that the primary action undertaken by both limbs is to sweep the long setae of the rami anterodorsally and posteroventrally across the pleural areas of the cephalon and the carapace-like extension of the cephalosome. The pleural areas bear numerous cone organs which raise globules of secretion up into the path of these long setae (see §4*c*). The extrinsic muscles of the mandibular palp and antenna are well developed with a large cross-sectional area relative to the muscles of the other cephalic appendages. Their function is clearly of great importance. In a filtering particle feeder, such as *Calanus*, the swimming vortex, and consequently the feeding vortex, result from the vibration of the antennary endopod, mandibular palp and distal part of the maxillule (Cannon 1928). In *Calanus*, however, these limbs are essentially directed ventrally and only the antennary exopod is recurved. Cannon (1928) found the recurved exopod difficult to interpret but suggested that it may assist in forming the feeding currents and also serve to reduce drag on the

base of the antenna as a whole. In *Benthomisophria* the whole antenna is recurved, as is the mandibular palp. The function performed by these limbs is clearly linked in some way to that of the secretory cone organs and is discussed further below (see §4*c*).

(*e*) *The thoracic swimming legs*

(i) *Skeletal structure*

The four pairs of thoracic swimming legs are essentially the same and the description given here of the second pair applies equally to all. The structure of the ventral body wall of the pedigerous somites is also described as it has been shown to be of significance in the locomotion

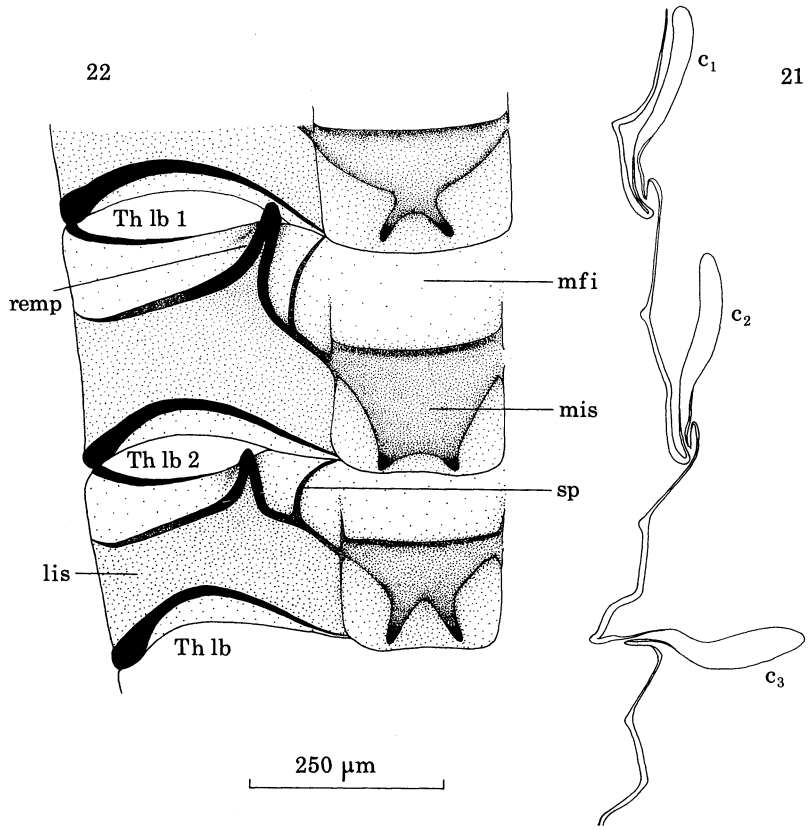


FIGURE 21. Median longitudinal section through the ventral integument of the first to third pedigerous somites, showing the differences in thickness of integument within the somites. The attachment of the coupler of the thoracic leg to the median intersegmental sclerite and to the median flexible integument is also shown.

FIGURE 22. Internal view of ventral body surface on left side of first to third pedigerous somites. The intensity of shading indicates the degree of sclerotization of the integument.

of *Calanus* (Perryman 1961). The two members of each pair are united by a rigid, flattened hollow structure called a coupler (figure 23, c) or interpodal bar. This represents a ventral outgrowth of the thoracic sternite (Hartog 1888), and unites a pair of legs into a single functional unit. It comprises two transverse half cylinders of integument, fused together distally and fused laterally to the medial margins of the limb coxae. The proximal portion of the coupler projects into the body slightly, the anterior half cylinder projecting further in than the posterior. Both half cylinders are joined to the body wall proximally (figure 21). The anterior articulates

along a transverse hinge line with the large subrectangular median intersegmental sclerite: the posterior is fused posteriorly to a large expanse of flexible integument. The ventral body wall (figure 22) therefore comprises median intersegmental sclerites (mis) alternating with median

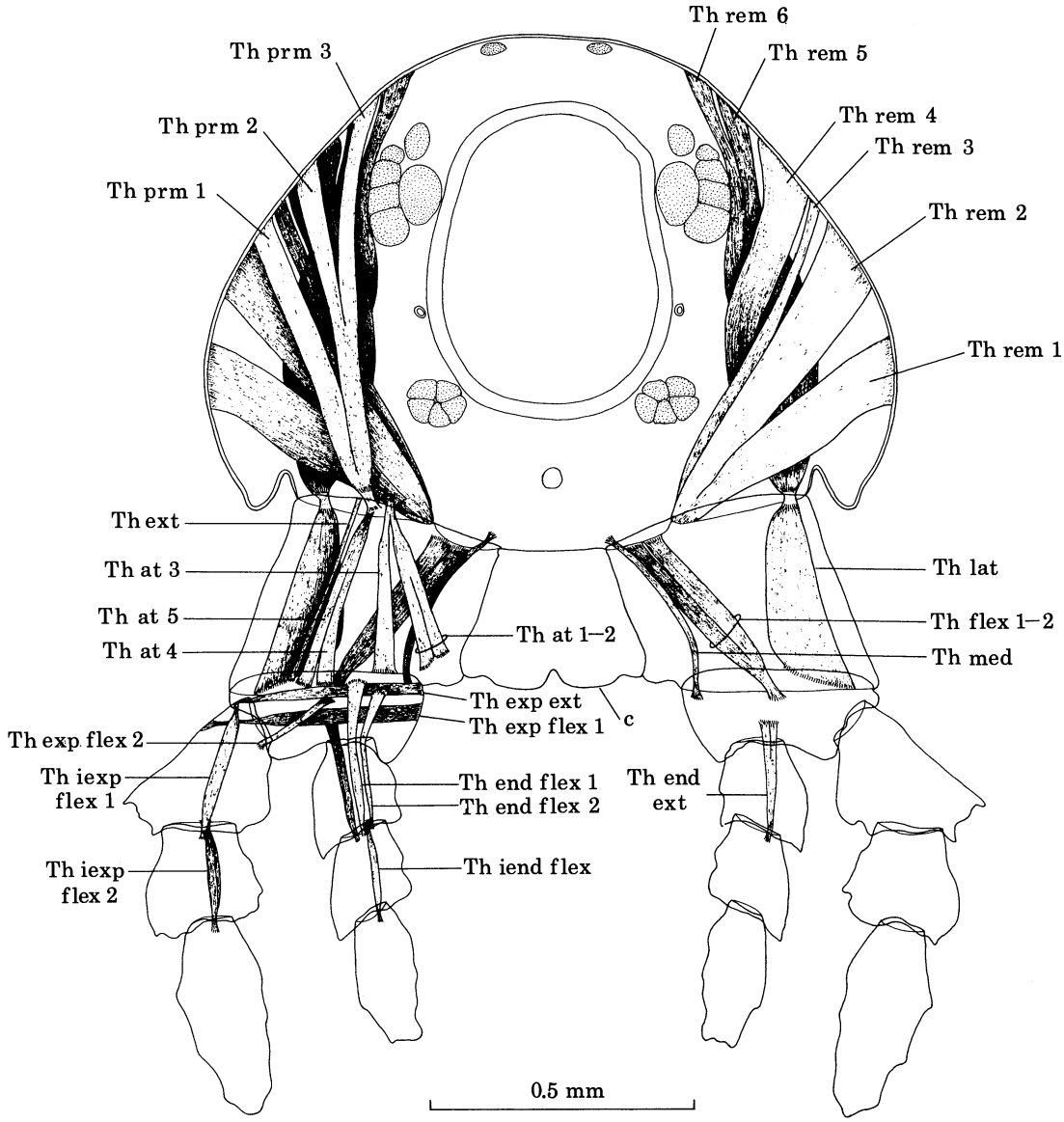


FIGURE 23. Anterior view of the second pedigerous somite with its pair of legs, showing the musculature. Anterior muscles omitted from one side.

areas of flexible integument (mfi). There are no rigid transverse intersegmental bars or vertical intersegmental plates in *Benthomisophria*, though the slight transverse ridge on the intersegmental sclerite may represent the vertical intersegmental plate present in *Calanus* (Perryman 1961). The median intersegmental sclerite is thickened anteriorly, the thickened area extending posteriorly in the form of a bifid fork the tips of which form the points of articulation with the coupler. The lateral intersegmental sclerites (figure 22, lis) are bordered posteriorly by the thickened anterior proximal rim of the leg base. Anteriorly they are sclerotized and produced

into a large anteriorly directly remotor process which projects over the opening of the limb base. The sclerotized anterior edge of the sclerite lateral to the process forms the skeletal hoop of Perryman (1961). Anteriorly the sclerite is fused to an area of flexible integument where some of the main limb remotor muscles insert. Medial to the remotor process the sclerotized anterior edge curves posteromedially before giving rise to an anteroventrally directed sclerotized spur which ends at the proximal end of the coxa–coupler junction.

Each thoracic swimming leg (figure 23) comprises a coxa, basis and two three-segmented rami, all of which are flattened. The coxa articulates with the somite via a well developed transverse hinge joint at which the only movement possible is a simple promotor–remotor swing. The proximal rim of the coxa is thickened anteriorly and posterolaterally, either side of the hinge line. The coxa–basis joint possesses some arthrodial membrane posteriorly but none anteriorly. The anterior margin is flexible and acts as a hinge line allowing some posterior flexion of the basis. The basis–endopod joint is a simple hinge joint allowing bilateral flexion about an anteroposterior hinge line. Some posterior flexion may also be possible. The intra-endopodal joints are similar to this proximal joint. The basis–exopod joint is similar, with lateral, medial and posterior arthrodial membrane allowing flexion about the anteroposterior hinge line, with some posterior flexion in addition. The intraexopodal joints allow medial flexion and some posterior flexion.

(ii) *Musculature*

The main extrinsic limb muscles (figure 23) originate dorsolaterally on the body wall and insert on the ventral body wall adjacent to the base of the limb, and on the coxal rim itself. These are arranged into a promotor group and two remotor groups, each comprising three muscles. Promotor muscles 1 to 3 (Th prm 1, 2, 3) originate on the mid-dorsolateral body wall and pass ventrally to a common insertion on the middle of the thickened anterior rim of the coxa, extending onto the anterior wall of the coxa just inside the proximal rim. Contraction of the promotors swings the limb pair forwards. The anterior group of remotor muscles originates laterally on the body wall and passes ventromedially to insert on the ventral body wall posterior to the limb base. Remotors 1 and 2 (Th rem 1, 2) have wide origins and large cross-sectional areas and unite with the narrower remotor muscle 3 (Th rem 3) to form a broad insertion on the area of thin integument lateral to the remotor process, as well as on the lateral surface of the process itself. Contraction will pull the area of thin flexible integument around the insertion upwards and swing the limb backwards. The posterior group of remotor muscles (Th rem 4–6) originates high on the dorsolateral body wall. Remotor 4 originates ventral to remotors 5 and 6 and passes obliquely across their anterior surfaces before turning ventrally to pass with them towards their common insertion located laterally on the thin ventral body wall just posterior to the limb base. Contraction of these muscles raises the flexible body wall producing the remotor swing of the legs and also raises the skeletal hoop to some extent. The remotor swing of the thoracic leg is achieved by the indirect action of remotors 1 to 6, which insert on the ventral body wall posterior to the limb base.

Several minor extrinsic limb muscles originate or insert on the ventral body wall near the limb. A large lateral muscle (Th lat) originates distally on the posterior wall of the coxa and passes dorsally, narrowing to a tendinous portion which extends through the limb base, over the proximal rim to a common insertion on the ventral body wall with remotor muscles 4 to 6. A narrow medial muscle (Th med) originates on the ventral body wall just posterior to the

medioproximal angle of the coxa, through which it passes to insert proximally on the medial side of the posterior wall of the basis. Two muscles (Th at 1, 2) originate on the anterior wall of the coxa near the mediodistal angle and pass obliquely into the body to insert on the ventral body wall just anterior to the limb base. They share an insertion with a third muscle (Th at 3) which originates anteriorly on the proximal rim of the basis. Two muscles (Th at 4, 5) originate on the midanterior wall of the basis and pass over the proximal rim of the coxa to insert at a common site on the ventral body wall anterior to the limb base. The functions of all these minor extrinsic muscles originating or inserting on the body wall close to the limb base are difficult to determine and they are here identified by anatomical position rather than function. Many act indirectly as they pass over the proximal rim of the coxa which acts as a pulley. Most appear to be involved in movement of the whole limb, though some (for example the Th med) may help to move the basis relative to the coxa. At present it is not possible to assign functions to each of them with certainty.

Two intrinsic muscles (Th flex 1, 2) originate posteriorly on the proximal rim of the coxa and pass obliquely down to insert together on the midposterior wall of the basis. They produce posterior flexion of the basis. A thin extensor muscle strand (Th ext) originates anteriorly on the proximal rim of the coxa and passes down the limb to insert on the anterior wall of the basis. Two transverse muscles originate on the lateral wall of the basis and pass horizontally into the base of the exopod. The proximal muscle (Th exp ext) inserts near the outer proximal angle of exopod segment 1 and produces extension around the anteroposterior hinge line. The distal muscle (Th exp flex 1) inserts about one-third of the way along the lateral exopod margin and produces medial flexion about the same hinge line. It acts with a short oblique muscle (Th exp flex 2) that originates on the midposterior wall of the basis and inserts near the medioproximal angle of exopod segment 1. Within the exopod a single muscle (Th iexp flex 1) originates near the outer proximal angle and inserts proximally in the middle of the anterior wall of segment 2. A similar muscle (Th iexp flex 2) originates distally in the middle of the posterior rim of segment 1 and inserts proximally on the anterior wall of segment 3. These produce some flexion of the distal exopod segments. Extension is presumably brought about by integumental elasticity. In KOH-cleared specimens the exopod returns to the extended position if flexed mechanically.

The endopod is moved as a whole by three muscles originating in the basis. The single extensor muscle (Th end ext) originates on the posterior wall of the basis and inserts proximally on endopod segment 2. Two flexors (Th end flex 1, 2) originate proximally on the anterior wall of the basis and also insert proximally on endopod segment 2. These produce medial flexion of the whole ramus and of the second segment relative to the first. A single muscle strand (Th iend flex) originates distally in endopod segment 1 and inserts proximally on segment 3. This produces medial flexion of the distal segment.

(iii) *The swimming mechanism*

Swimming movements in calanoid copepods are of two kinds, slow almost continuous swimming achieved by the anterior cephalic appendages, and the rapid jumping movements typical of copepods (Cannon 1928). Cyclopoid copepods also exhibit a jumping pattern of locomotion (Strickler 1974). Jumping is effected by the metachronal movements of the four pairs of thoracic swimming legs, starting with the fourth pair and passing anteriorly. During the recovery stroke the four pairs swing forwards essentially simultaneously to their anteriorly

directed resting position (Storch 1929; Strickler 1974). Strickler (1974) reported that in *Cyclops* the antennules beat 2 ms before the swimming legs start to beat. He also noted that a dorsoventral flapping movement of the urosome is involved in jumping locomotion, especially during escape jumping, and that turning is controlled by the urosome and antennules. The uniformity in the skeletomusculature of the swimming legs in the Copepoda as a whole (see §3*f*) indicates that the mechanics of the jumping movements in free swimming forms is similarly uniform and it is here assumed that jumping locomotion in *Benthomisophria* is fundamentally the same process as in cyclopoid and calanoid copepods.

Manton (1977), using the work of Perryman (1961) on *Calanus*, identified the presence of a coupler uniting the members of each pair of swimming legs as the key to the achievement of rapid jumping. The anatomy associated with the coupler permits a promotor–remotor swing of these limbs through 110° in contrast to the 50–60° range common to most other crustaceans. In *Benthomisophria* the promotor–remotor swing was estimated by comparing specimens fixed with their limbs protracted and those with them retracted. A swing through an angle of about 110° was measured. This is achieved in the absence of the system of transverse intersegmental bars and vertical intersegmental plates, movement of which contributed to the total swing in *Calanus* (Perryman 1961). The postulated sequence of actions comprising a complete promotor–remotor swing in *Benthomisophria* is basically the same as that of *Calanus* described by Perryman (1961). At rest the limbs are anteriorly directed. Contraction of the powerful remotor muscles 1 to 6 swings each pair backwards by raising the area of flexible integument around its common insertion posterior to the limb base. The insertion of the remotors outside the limb on the adjacent body wall rather than on the limb base itself is a device to reduce the range of swing of the muscle fibrils on their tonofibrils attached to the body wall (Manton 1977). As each limb pair swings back the anterior hoop of the coupler, which is longer than the posterior hoop (figure 21), deforms the posterior portion of the median intersegmental sclerite, with which it articulates by bending it upwards. At the midpoint of the remotor swing, when the limb is perpendicular to the ventral body surface, the proximal end of the anterior hoop of the coupler projects well into the body and this is the point of maximum deformation of the median intersegmental sclerite. In the second half of the remotor swing the limb continues backwards to the fully retracted position. This phase is accompanied by dorsal intucking of the median flexible integument posterior to the posterior hoop of the coupler (Perryman 1961). During this phase the remotor muscles are assisted by the elasticity of the thickened median intersegmental sclerite as it reverts to its non-deformed state. This effect will operate in reverse during the promotor swing. The sclerite will be deformed during the first phase and its elasticity will assist in the second. However, during the remotor swing the effect is accentuated by the posterodorsal pull on the remotor process of the immediately anteriorly situated pair of limbs exerted by the remotor muscles 1 to 3. This in turn produces an anteroventral force at the distal points of the sclerotized fork of the median intersegmental sclerite articulating with the anterior hoop of the coupler of the succeeding (immediately posterior) pair of limbs. This accentuation effect is manifested only if the remotors of each pair of limbs contract when the pair of legs immediately posterior to them is already at the midpoint of its remotor swing. Contraction during the initial phase of remotion would produce an antagonistic rather than an accentuating effect. For this accentuating effect to operate, leg 3 must commence its remotor swing when leg 4 is halfway through its swing, followed by leg 2 when leg 3 is halfway through its swing, and so on. This is exactly the sequence recorded by Strickler (1974) during swimming in *Cyclops scutifer*. Here each

leg completes its remotor swing in about 4 ms. The fourth pair moves first, the third pair starts to move about 2 ms later, the second pair 2 ms later still, and so on. The accentuating effect can therefore operate as leg 4 is at the midpoint of its remotor swing before the remotors of leg 3 contract raising the remotor process and producing an anteroventral force on the coupler of leg 4 transmitted via the median intersegmental sclerite.

(*f*) *Comparisons with other copepod groups*

Little published information is available on the musculature of copepods. Lowe (1935) and Perryman (1961) have provided an account of the trunk and extrinsic limb musculature in *Calanus* and this information on calanoids is supplemented by Hessler's (1964) work on *Metridia lucens* Boeck. Hartog (1888) described the intrinsic limb musculature of *Cyclops* and Lang's (1948*a*) monograph contains observations on the trunk and limb musculature in certain harpacticoids.

The arrangement of the major trunk muscles is similar in calanoids, cyclopoids, harpacticoids and misophrioids. The calanoids differ from the rest in that some oblique fibres of the dorsal longitudinal trunk muscles, absent from the other groups, originate on the postmaxillulary apodeme. Hessler (1964) identified the tendency, within the Copepoda, of the longitudinal trunk muscles to form long strands independent of the body wall. The condition exhibited by cyclopoids and misophrioids is intermediate between that of harpacticoids in which the longitudinal muscles attach at every intersegmental boundary, either directly to the body wall or indirectly by functional tendons (Lang 1948*a*), and that of calanoids in which these muscles tend to lose their attachments to the body wall at some intersegmental boundaries.

Cephalic pleural muscles have also been reported in cyclopoids by Hartog (1888) who found a series of short muscles connecting the two walls of the pleura. The pleural muscles that he illustrates (Hartog 1888, fig. 5, pl. 3) are in the maxillary somite and are clearly more extensive in *Cyclops* than in *Benthomisophria*. In *B. palliata* they are restricted to the preoral region, and their absence from the more posterior part of the cephalosome may be attributed to the configuration of the dorsal shield in the region of the reflexed antenna and mandibular palp.

The ventral cephalic tendons (the free endosternites of Lowe (1935)) are difficult to observe in copepods and the only complete description of these structures available is that for *Calanus finmarchicus* (Lowe 1935). In *B. palliata* there are two ventral cephalic tendons (an anterior and a posterior) lying posterior to the oesophagus and ventral to the gut in the anterior part of the cephalosome. They (figure 24) are connected by a pair of strands (suspt 1) which are tendinous at both ends but muscular in the middle. There are pairs of suspensory tendinous strands attaching both cephalic tendons (suspt 2, 3) to the postmaxillulary apodeme and attaching the posterior one (suspt 4) to the postmaxillary apodeme. There is another pair of suspensory tendons (suspt 5) arising anteriorly and passing anterolaterally to attach to the lateral body wall in the antennary somite. These tendons have a muscular middle portion (figure 46, suspt 5).

Most of the ventral extrinsic muscles of the cephalic appendages originate on the ventral cephalic tendons. The three pairs of paragnath adductor muscles originate on the ventral surface of the anterior half of the anterior ventral cephalic tendon. The oesophageal dilator muscles have an elongate common origin along the dorsal surface of the anterior half of the same tendon, from which they radiate anteriorly (figure 46). The anterior half is flattened anteriorly and grooved posteriorly, while the posterior half has a marked double keel providing

a large surface area for muscle attachment. The posterior ventral cephalic tendon is V-shaped in cross section and flattened posteriorly.

The general arrangement of the cephalic tendons and the muscles originating on them is the same in *Calanus* and *Benthomisophria*, though there are marked differences in proportions. The ventral tendons in *C. finmarchicus* are more elongate and their suspensory tendons are similarly longer and thinner. The posterior part of the anterior tendon is poorly developed by comparison

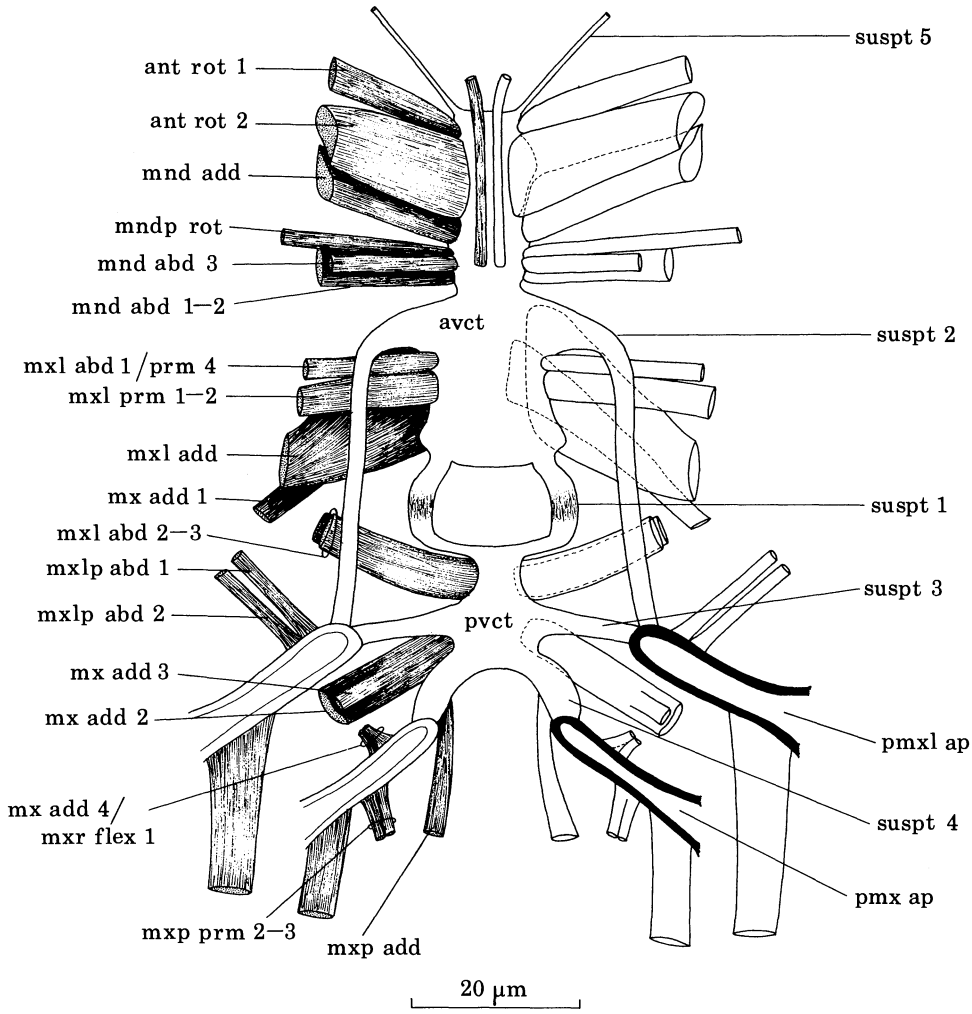


FIGURE 24. Semidiagrammatic dorsal view of anterior and posterior ventral cephalic tendons, reconstructed from serial transverse sections. The sites of origin of the ventral extrinsic muscles to the appendages are shown. The paragnath adductor muscles originate from the ventral surface of the anterior ventral cephalic tendon and cannot be seen in dorsal view.

with that of *B. palliata*, which is massively developed and on which the large maxillulary adductor muscle originates. Maxillary adductor muscle 1, which originates on the posterior part of the anterior tendon, is wrongly identified by Lowe (1935, fig. 1) as one of the maxillulary muscles, although Perryman (1961) identified it correctly as a maxillary muscle (muscle no. 41 in fig. 9 of Perryman (1961)). A more significant difference between *Calanus* and *Benthomisophria* is the location of the maxillulary muscle origins. The large maxillulary adductor

TABLE 1. EXTRINSIC MUSCLES OF THE CEPHALOSOMIC APPENDAGES: A COMPARISON BETWEEN *BENTHOMISOPHRIA* AND *CALANUS*

(*Calanus* data from Perryman (1961).)

appendage	muscle (*Benthomisophria*)	muscle (*Calanus*)	remarks
antennule	atl rem 1	1	
	atl rem 2	2	
	atl prm 1, atl prm 2	3	single origin in *Calanus*
	atl lev/prm	4	originates in mandibular somite
	—	5	absent from *Benthomisophria*
	oe dil	6	simple in *Calanus*, subdivided in *Benthomisophria*
antenna	ant prm 1	7	
	ant prm 2, ant prm 3	10, 11	these insert distally in segment 1 in *Benthomisophria* but proximally in segment 2 in *Calanus*
	ant rem 1, ant rem 2, ant rem 3	8, 9, 12	precise homologies cannot be ascertained; all three are better developed in *Benthomisophria* than in *Calanus*
	ant rot 1, ant rot 2	13	these insert proximally in segment 1 in *Benthomisophria* but in segment 2 in *Calanus*
mandible	mnd rem 1, mnd rem 2	14 (+15?)	a powerful double-stranded muscle in *Benthomisophria*
	mnd prm 1	16	
	mnd prm 2	17	
	—	18, 19	?absent from *Benthomisophria*
	mnd abd 1, mnd abd 2	20b, 21?	
	mnd abd 3	20a	
	—	22	?absent from *Benthomisophria*
	mndp prm 1	23	
	mndp prm 2	24	
	mndp rem 1	25a	these are the largest and most powerful of all cephalic appendage muscles in *Benthomisophria*
	mndp rem 2	25b	
	—	26	?absent from *Benthomisophria*
	mndp rot	27?	
	mnd add	28	well developed in *Benthomisophria*
maxillule	mxl prm 1	29	originates in the mandibular somite
	mxl prm 2	30a?	many of the muscles present in *Benthomisophria* are absent from *Calanus*; either the musculature is simpler in *Calanus* or it is inadequately described by Perryman (1961); the homologies proposed here are necessarily tentative
	mxl prm 3	30b (part)	
	mxl prm 4	32 (part)	
	mxl rem 1	31 (part)	
	mxl rem 2	30b (part)	
	mxlp rem 1, mxlp rem 2	31 (part)	
	mxlp prm 1, mxlp prm 2	32 (part)	
	mxl abd 1	32 (part)	
	mxl abd 2, mxl abd 3	34	originates on posterior ventral cephalic tendon
	mxl add, mxlp add 1	33	originates on anterior ventral cephalic tendon
	mxlp add 2	—	?absent from *Calanus*
	mxlp abd	—	?absent from *Calanus*
maxilla	—	35	?absent from *Benthomisophria*
	mx abd 1, mb abd 2	37	inserts more proximally in *Benthomisophria*
	mx abd 3, mx abd 4	36	these muscles have a common insertion in *Benthomisophria*, but separate insertions in *Calanus*

TABLE 1 (*cont.*)

	mx rem	38/39?	this originates in the maxilliped-bearing somite in *Benthomisophria* as does 39 in *Calanus*, but inserts well inside the limb as does 38
	mx add 1	41	
	mx add 2	—	?absent from *Calanus*
	mx add 3	—	?absent from *Calanus*
	mx add 4 mxr flex 1	40	these muscles have a common origin on the postmaxillulary apodeme
maxilliped	—	42	?absent from *Benthomisophria*
	mxp prm 1	43a+b	
	mxp prm 2 mxp prm 3	45	originate on postmaxillary apodeme in *Benthomisophria* but apparently on postmaxillulary apodeme in *Calanus*
	mxp abd 1	44a	
	mxp abd 2	44b	
	mxp add	46	

TABLE 2. THE INTERNAL MUSCLES OF THE THORACIC SWIMMING LEGS OF COPEPODS REPRESENTING SIX ORDERS

Misophrioida (*B. palliata*)	Calanoida (*Eucalanus attenuatus*)	Cyclopoida (*Acanthocyclops gigas*)	Harpacticoida (*Sunaristes paguri*)	Siphonostomatoida (*Cribropontius normani*)	Poecilostomatoida (*Copilia mirabilis* ♀)
Th lat	+	m ext bas	fl Pr 1–2	IX	4
Th med	+	fl 4	ex Pr 8	XIII?	flb_2 (part)
Th at 1 Th at 2 Th at 3	+	fl 2	ex Pr 7 ex Pr 6	X?	1 (in b_1 segment)
Th at 4 Th at 5	+		ex Pr 4 ex Pr 5	XI	2+3 (in b_1 segment)
Th flex 1 Th flex 2	+	m ext bas	fl Pr 3 fl Pr 4	XII	flb_2 (part)
Th ext	+	fl 3?	ex Pr 1 (or 3?)	?	?
Th exp ext	+	m abd ex	abd Exp p	VI	1 (in b_2 segment)
Th exp flex 1	+ (2 strands)	m add ex	2 add Exp p	VII	2 (in b_2 segment)
Th exp flex 2	+	m add ex	1 add Exp p	VIII	3 (in b_2 segment)
Th iexp flex 1	+	m add p ex	ex Exp/fl Exp	II	1°–2°
Th iexp flex 2	+	m add p ex	fl Exp	I	2°
Th end ext	?	m abd p end	1 fl Enp	IV	3x
Th end flex 1	+	m add p end	ex Enp	V	1x
Th end flex 2	+	m add p end	2 fl Enp		2x
Th iend flex	+	m add p end	2 fl Enp	III	2x
present account	present account	Hartog 1888	Lang 1948*a*	Giesbrecht 1899	Riester 1931

muscle (figure 24, mxl add) in *Benthomisophria* originates from the anterior tendon, whereas Perryman (1961) shows the largest maxillulary muscle (no. 34) originating on the posterior tendon. Lowe (1935) shows all but one of the maxillulary muscles originating from the posterior tendon, the one exception being the wrongly identified maxillary adductor muscle 1. As both Perryman's and Lowe's figures are semidiagrammatic it is difficult to determine whether this difference is real and the two muscles are not homologous or whether it represents a difference in interpretation.

The extrinsic muscles of the cephalic appendages in *Calanus* and *Benthomisophria* are compared in table 1. Their great similarity is obvious. Their intrinsic musculature has not been described in sufficient detail in *Calanus* to permit comparison. Considerable variation in intrinsic musculature

between the major copepod groups may be expected, however, as great adaptive radiation in feeding strategies and morphology of the feeding appendages has taken place within the Copepoda. The close similarity between the extrinsic muscles in calanoids and misophrioids suggests that both gymnoplean and podoplean lines have retained the ancestral condition from their most recent common ancestor, the ancestral stock of the whole Copepoda according to the system of relationships proposed by Kabata (1979).

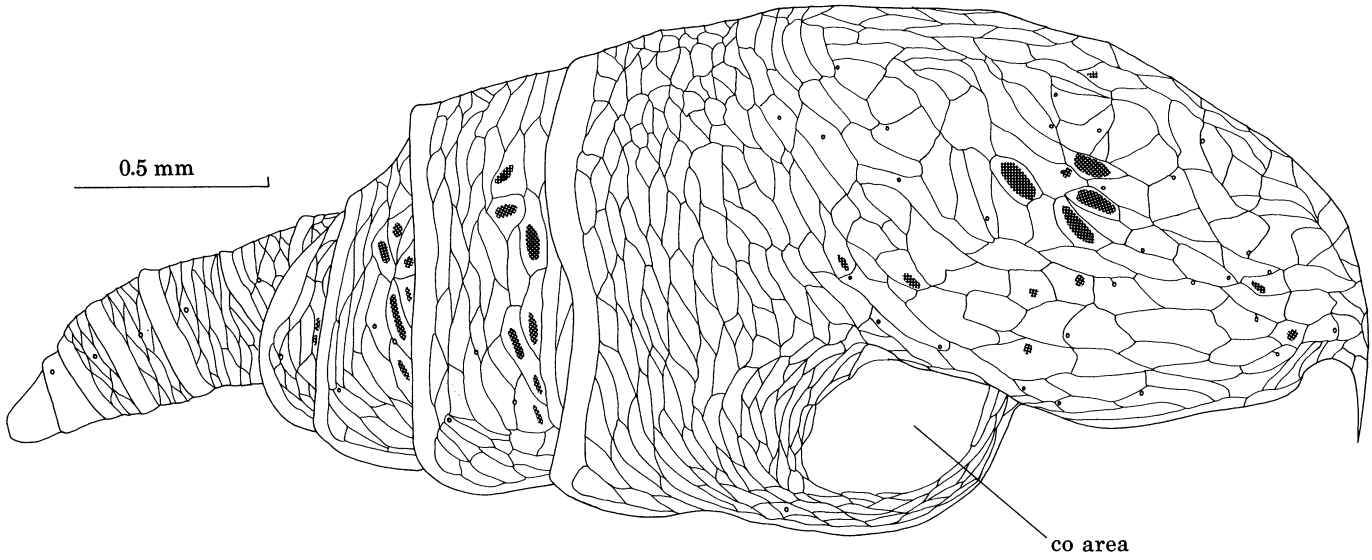


FIGURE 25. Lateral view of female *B. palliata*, drawn from serial s.e. micrographs. The primary lamellae ornamenting the body surface can be seen, as can the positions of pores in the integument. The stippled areas represent sites of muscle attachments marked externally by the pattern of secondary lamellae. Ornamentation is omitted from the area occupied by cone organs.

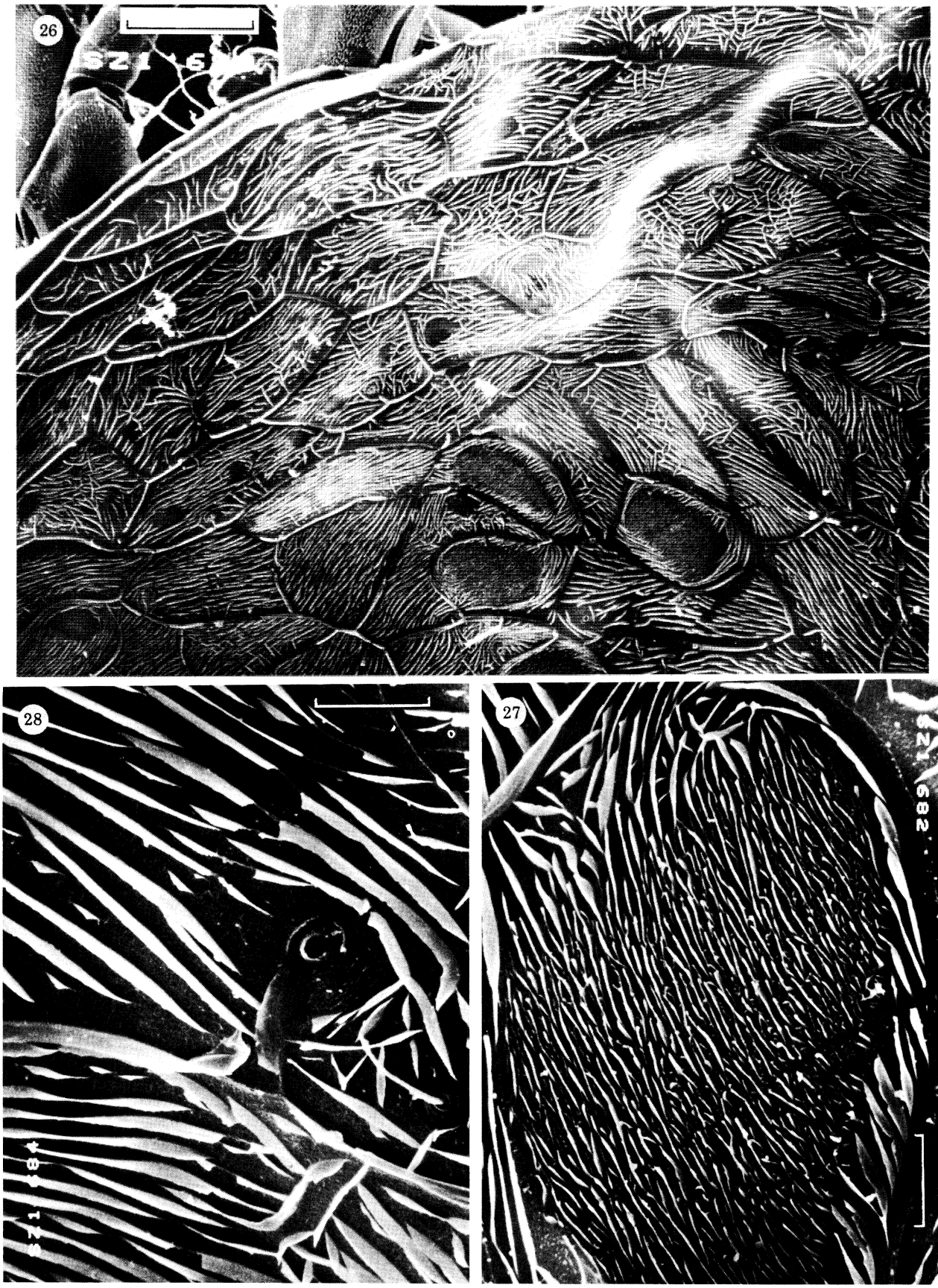
The musculature of the swimming legs is also similar in *Calanus* and *Benthomisophria* although Perryman (1961) has represented the extrinsic muscles in *Calanus* as large blocks whereas in *Benthomisophria* these are subdivided into strands each with a discrete site of origin on the dorsolateral body wall. Swimming leg protractor muscles 1 and 2 and the retractor muscles 1 to 3 of *Calanus* are homologous with promotor muscles 1 to 3 and remotor muscles 1 to 6 of *Benthomisophria* respectively. The intrinsic muscles of the swimming legs are remarkably uniform throughout the whole of the Copepoda. The basic pattern can be recognized in all the orders and there is little variation even in the details of origins and insertions of small muscle fibres. Published information on the intrinsic muscles of copepod swimming legs is summarized in

DESCRIPTION OF PLATE 2

FIGURE 26. Dorsal view of lateral portion of cephalosome of *B. palliata*, showing the surface ornamentation, which comprises a system of primary lamellae delimiting areas containing numerous more-or-less parallel secondary lamellae. Scale bar 75 μm.

FIGURE 27. Detail from figure 26 of an area of closely packed fine lamellae marking externally the site of origin of a dorsal longitudinal trunk muscle fibre. Scale bar 10 μm.

FIGURE 28. Detail from figure 26, showing an integumental pore and an associated sensilla. Scale bar 10 μm.



FIGURES 26–28. For description see opposite.

(*Facing p.* 156)

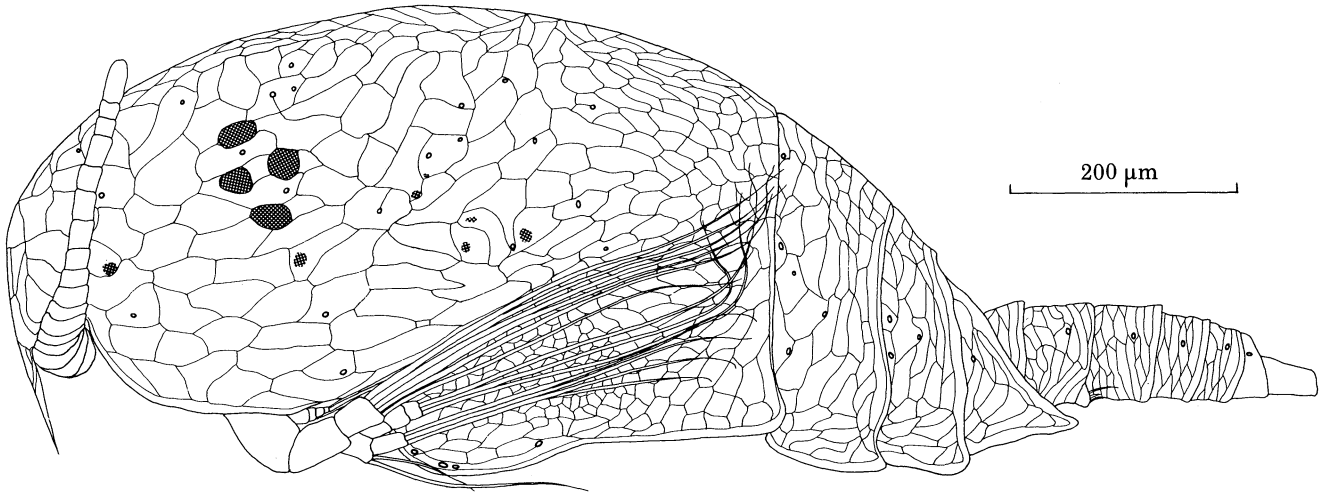
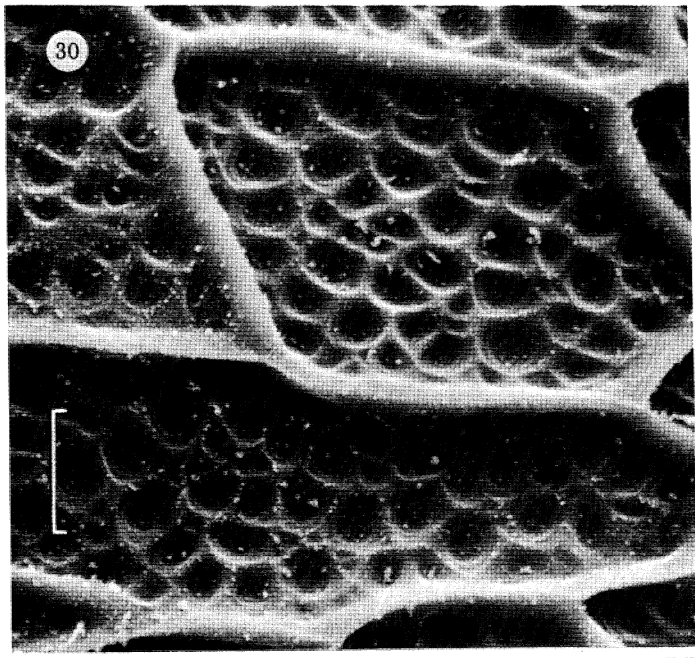
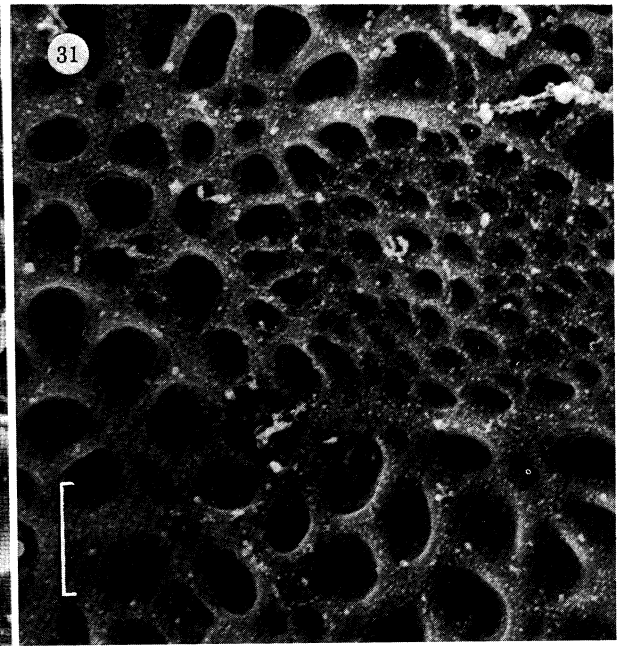


FIGURE 29. Lateral view of female *B. cornuta* drawn from serial s.e. micrographs. The major ridges ornamenting the body surface can be seen, and the stippled areas represent sites of muscle attachments marked externally by the pattern of surface pits. The positions of pores in the integument are shown, and the antennule, reflexed antenna and mandibular palp are drawn *in situ*.





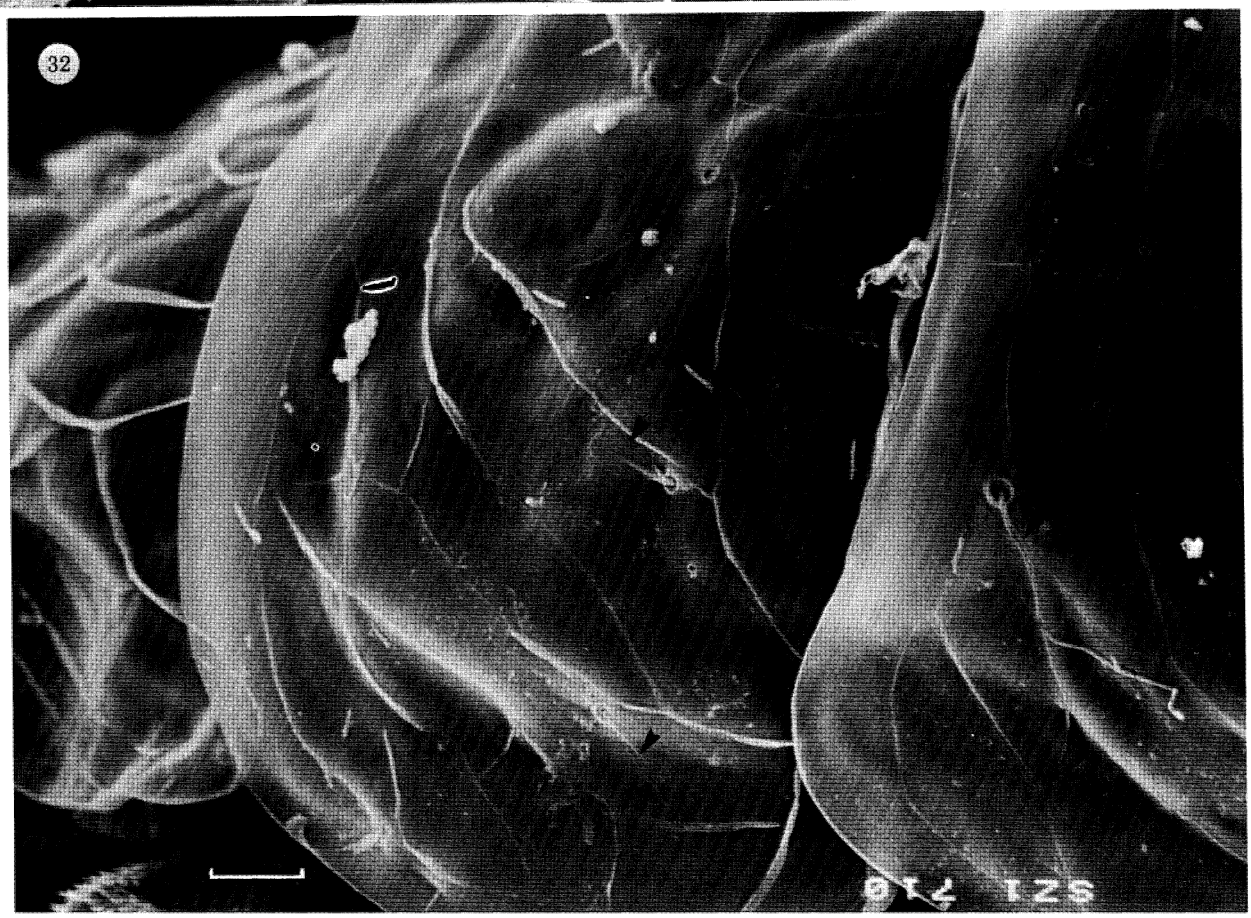


FIGURE 30. Detail of surface ornamentation on cephalosome of *B. cornuta*. The system of ridges delimits areas containing numerous surface pits. Scale bar 10 μm.

FIGURE 31. Detail of surface ornamentation on cephalosome of *B. cornuta* marking the site of origin of a dorsal longitudinal trunk muscle fibre by the presence of smaller, densely packed pits. Scale bar 10 μm.

FIGURE 32. Lateral view of the pleural region of second to fourth pedigerous somites of *M. pallida*. The poorly developed surface ornamentation of fine lamellae can be seen. The positions of oar-shaped sensillae are marked by arrows. Scale bar 10 μm.

Description of plate 4

Figure 33. Lateral view of cephalosome of *B. cornuta*. The area of cone organs on the side of the body can be seen. Most of the cone organs are intact, still bearing the apical globule of secretion. Scale bar 100 μm.

Figure 34. Lateral view of the area of cone organs on the cephalosome of *B. palliata*. Most of the cone organs have been damaged and have lost their globules of secretion. Scale bar 100 μm.

Description of plate 5

Figure 35. Detail from cone organ area of *B. cornuta*. The cone organs visible show continuous gradation in the size of the globule of secretion. Scale bar 2 μm.

Figure 36. The same, showing a large globule formed by coalescence of the globules of two separate cone organs. Scale bar 2 μm.

Figure 37. The same. The globules of secretion of these organs are slightly displaced, showing the rim of the hollow cone. Scale bar 2 μm.

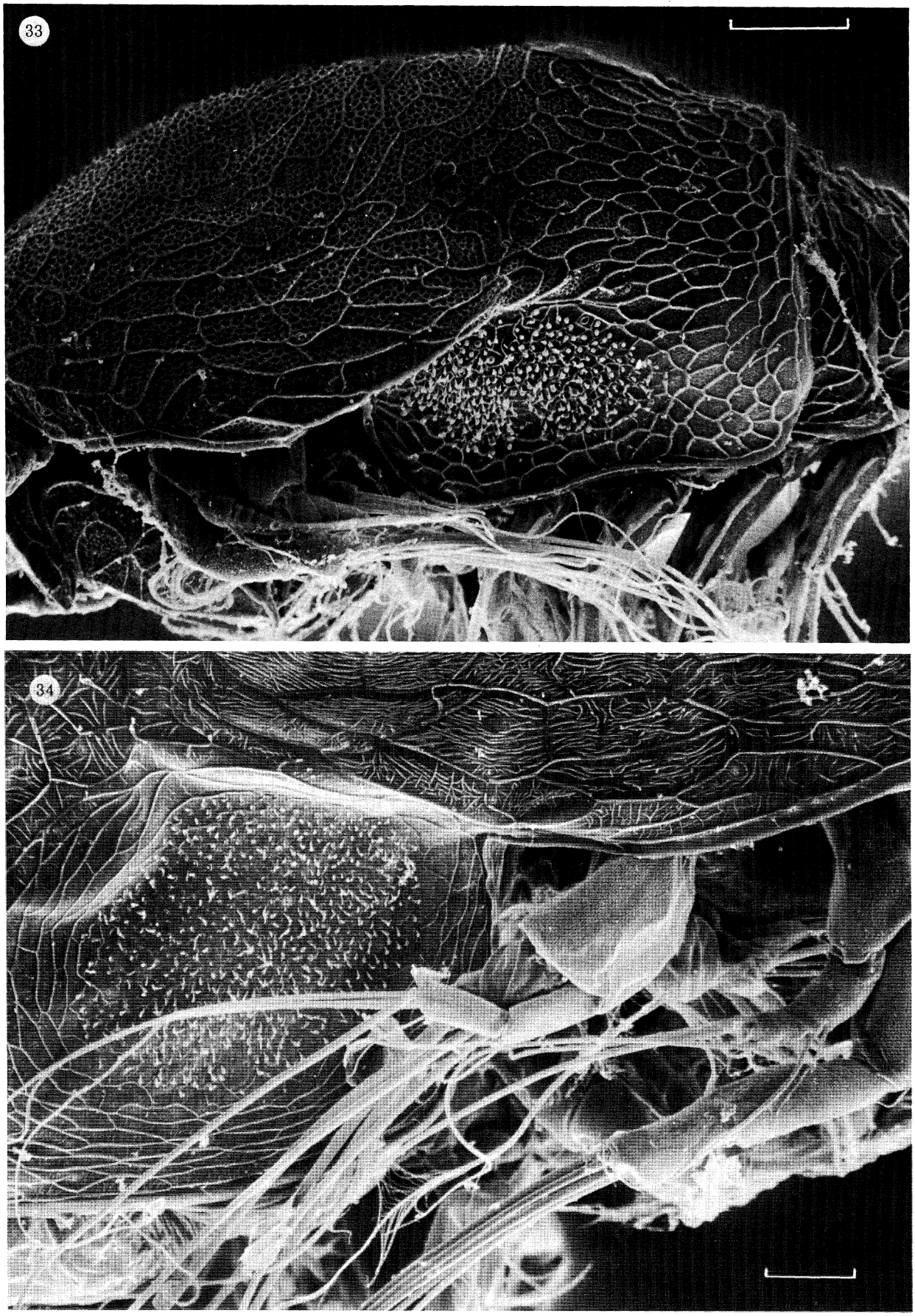
Figure 38. Detail from cone organ area of *B. palliata* in which the cone organs have been damaged and lost their globules of secretion or had them displaced. Scale bar 2 μm.

Description of plate 6

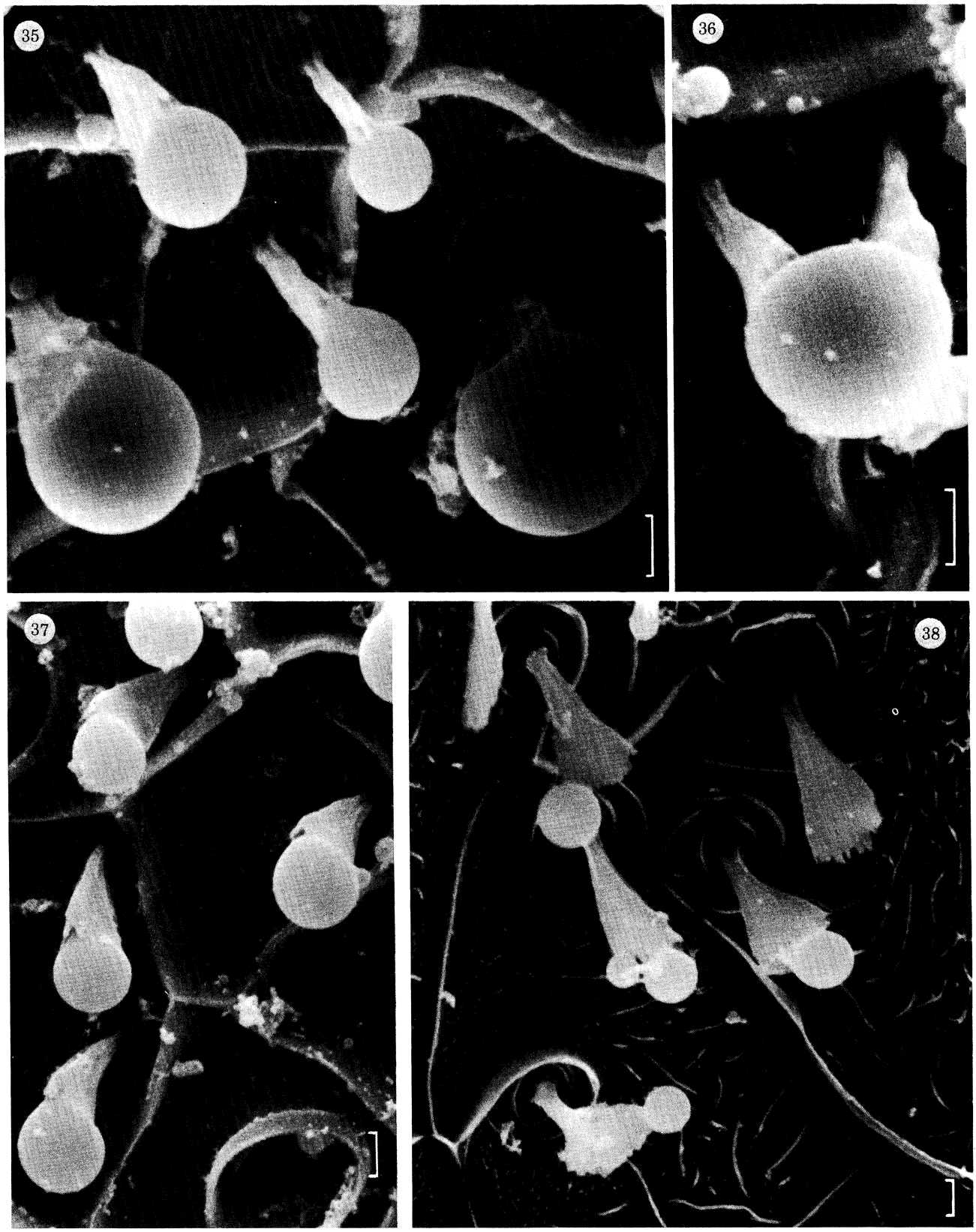
Figure 39. Section through collapsed cone organ and its basal pore through the integument. The epicuticular nature of the wall of the cone is apparent. Scale bar 2 μm.

Figure 40. The same. The double lining (internal and external) of epicuticle on the cone wall can be seen. Scale bar 2 μm.

Figure 41. The same. The tubules originating from underlying glandular cells can be seen entering the basal pore of the cone organ. Scale bar 2 μm.

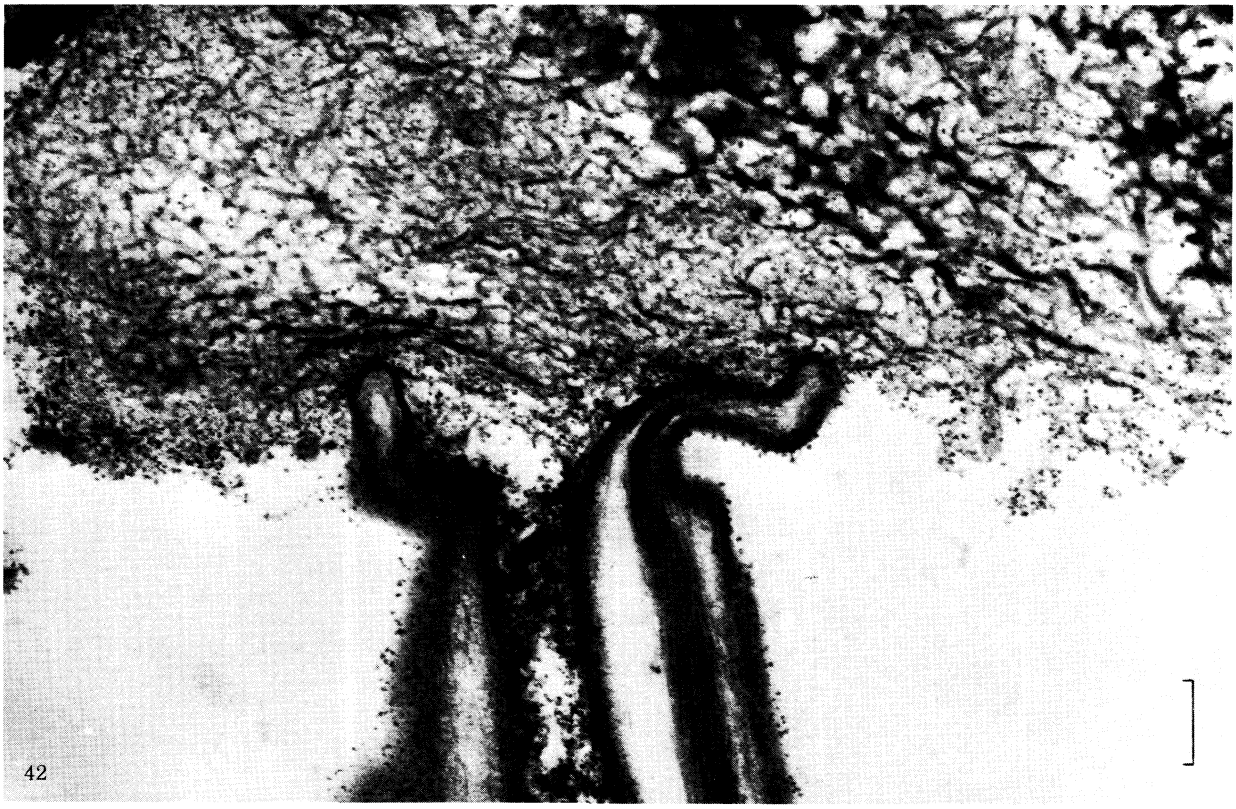


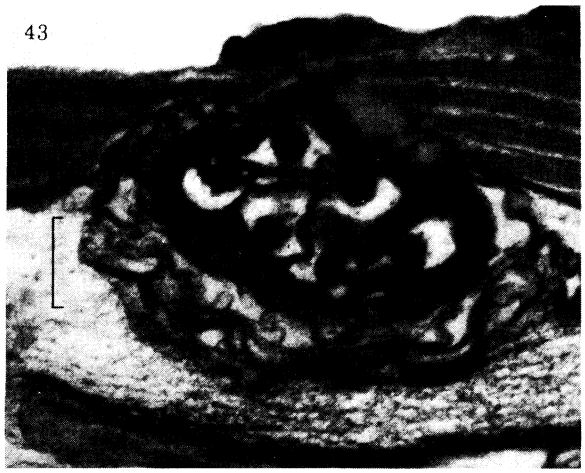
FIGURES 33 AND 34. For description see opposite.

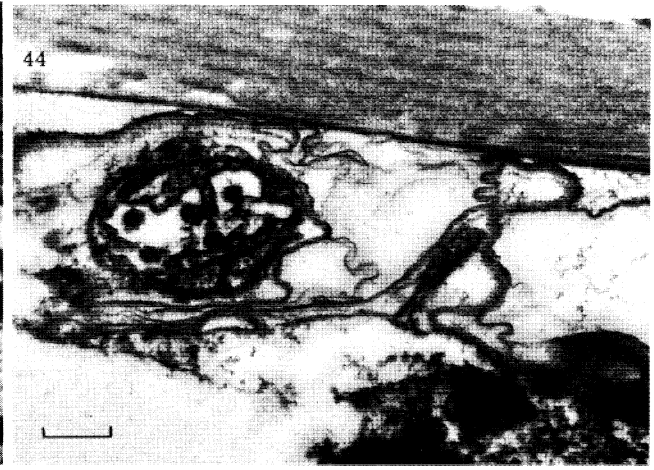


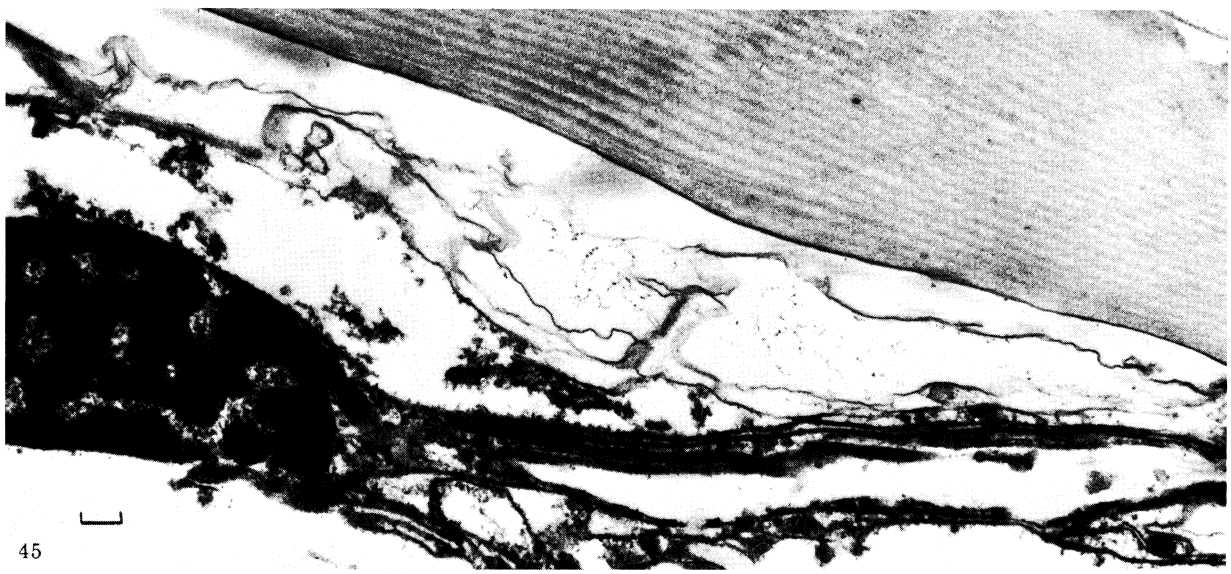
FIGURES 35–38. For description see facing plate 4.

FIGURES 39–41. For description see facing plate 4.









FIGURES 42–45. For description see opposite.

table 2 although the determination of homologies is sometimes not possible from the inadequate and occasionally inaccurate illustrations available.

Much basic anatomical work is still necessary but it is already possible to make some generalizations about copepod musculature. First, it is remarkably conservative in evolutionary terms. The same patterns of muscles can be recognized in both gymnoplean and podoplean lines, as well as in the constituent orders of the latter. Clearly these patterns are retained, largely unaltered, from the condition exhibited by the ancestral copepod stock. The intrinsic and extrinsic muscles of the swimming legs and the extrinsic musculature of the cephalic appendages are the clearest examples of retained ancestral conditions. The longitudinal trunk muscles and the intrinsic muscles of the cephalic appendages are more subject to evolutionary modification during adaptive radiation (as a swimmer, crawler or burrower) and in feeding strategy. It is these latter groups of muscles that may in future provide the best evidence for elucidating phylogenetic relationships between the orders within the Copepoda.

4. The structure and ornamentation of the integument

(*a*) *External ornamentation*

Except for the limb-bearing ventral surface and the anal somite the whole body of adults of *B. palliata* is ornately patterned (figure 25). The patterning comprises a reticulate system of simple lamellae standing out perpendicularly from the surface. Each lamella comprises just a single layer of epicuticle. The primary lamellae delimit small irregularly shaped areas of integument and on both the prosome and anterior urosome somites the surface within these areas is covered with many similar but smaller lamellae (figure 26, plate 2). On the anterior portion of the cephalosome these secondary lamellae are arranged more-or-less parallel to each other and have few interconnections, whereas over the carapace-like structure they are irregularly orientated with many interconnections. The first pedigerous somite has a smooth surface (figure 1) usually completely concealed within the carapace-like structure. The second to fourth pedigerous somites have their secondary lamellae orientated more-or-less anteroposteriorly, with an intermediate number of interconnections. Urosome somites 1 to 5 typically have the areas delimited by the primary lamellae elongated with their long axes running around the circumference of the somite. These areas contain many small, irregularly orientated secondary lamellae. A few longitudinally orientated lamellae are present on the hyaline frills around the posterior borders of these somites. The anal somite and uropods have a dense covering of pointed denticles.

Certain areas on the prosome contain closer-packed secondary lamellae (figure 27, plate 2). Study of the skeletomusculature of *B. palliata* reveals that these areas of fine secondary lamellae

Description of plate 7

Figure 42. Section through the tip of a collapsed cone organ. The fibrous nature of the secretion when fixed can be seen. Scale bar 2 μm.

Figure 43. Transverse section through a bundle of tubules lying immediately beneath the integument and passing between the glandular cells and the basal pore of the cone organ. Scale bar 2 μm.

Figure 44. The same. Scale bar 2 μm.

Figure 45. Section through a glandular cell, showing long tubules arising from it. The cell contains areas of densely staining secretion. Scale bar 2 μm.

correspond to sites of muscle origin on the internal surface of the integument. These sites are found primarily on the anterodorsal part of the cephalosome and on the dorsolateral parts of the pedigerous thoracic somites.

The lateral areas of the cephalosome (figure 25) just posterior to the level of insertion of the mandibular palp are each provided with clusters of cone organs. These cone organs are described in detail below (see §4*c*). Around these lateral areas the surface ornamentation comprises primary and secondary lamellae as elsewhere, but within them the lamellae are small and irregularly orientated. There are crescent-shaped lamellae positioned in association with many of the cone organs, typically anterodorsally of the base of the cone organ.

The rostrum is covered with lamellae and is fused to the labrum which is covered with tiny flattened denticles, similar to those on the anal somite. Most of the appendages are also covered, at least in part, with minute flattened denticles.

The surface ornamentation of *B. cornuta* (figure 29) is similar to that of *B. palliata* in extent but comprises a reticulate system of primary ridges delimiting small, irregularly shaped areas of integument. Within each area on the prosome the surface is pitted with shallow depressions of variable size (figure 30, plate 3). The ridge-delimited areas are larger on the cephalosome than on the posterior extension of the cephalosome over the first pedigerous somite. The areas on the urosome are typically elongated around the circumference of the somite and each urosome somite has a smooth hyaline frill around its posterior border. The body surface between the ridges on the urosome somites is smooth. As in *B. palliata* the pitting is finer (figure 31, plate 3) at the sites of muscle origin on the internal surface of the prosomal integument. The lateral areas of the cephalosome, in the zone overlain by the setae of the antenna and mandibular palp, are each provided with clusters of cone organs. The body surface between the cone organs has relatively smaller primary ridges and sparser pitting than on the rest of the prosome.

The pits in *B. cornuta* are superficial, penetrating only as far as the inner procuticle. The ridges between pits are composed mainly of outer procuticle and the surface of the pits and ridges is covered with thin epicuticle. The inner and outer layers of the procuticle are laminate in *B. cornuta* but the fibrous organization of the laminae could not be ascertained because of inadequate fixation.

In both *B. palliata* and *B. cornuta* the detail of the ornamentation on the carapace-like extension of the cephalosome is different from that on the cephalosome proper. The areas delimited by the primary lamellae or ridges are smaller on the extension and there are more interconnections between the secondary lamellae in *B. palliata*. These modifications must strengthen and provide greater rigidity to the structure, which is only attached anteriorly and is not supported by the somite that it encloses. The areas of fine secondary lamellae or pits are associated with the position of major muscle origins and this also suggests a strengthening function for the external ornamentation of lamellae and ridges as a whole.

The body surface ornamentation of the littoral *Misophria pallida* was examined for comparison with the bathypelagic *Benthomisophria* species. Its ornamentation is weakly developed but a reticulum of fine lamellae is present over parts of the urosome and prosome (figure 32, plate 3). The lamellae are simple flaps of epicuticle standing perpendicular to the body surface, as in *B. palliata*. The integument between them is smooth. Lamellae are absent from the cephalosome but can be seen on the free thoracic somites. They are very fine on the second pedigerous somite but better developed and more conspicuous on the third and fourth. On the urosome they are fine and inconspicuous. *M. pallida* also possesses a carapace-like posterior extension of the

prosome enveloping the first pedigerous somite (figure 2). The lateral portions of the cephalosome do not extend ventrally and the antenna and mandibular palp are not reflexed over the dorsolateral surface of the cephalosome as in *Benthomisophria* species. There are no cone organs. Pedigerous somites 2 to 4 and the anterior urosome somites each have a smooth hyaline frill around their posterior border.

(*b*) *Comparative anatomy of the copepod integument*

The basic organization of the integument is the same throughout the Copepoda, with a thin epicuticle overlying a thicker procuticle which comprises several laminae and which is frequently subdivided into inner and outer layers (Bouligand 1966*b*; Raymont *et al.* 1974; Gharagozlou van Ginneken 1975). The procuticle is a network of chitin and protein filaments forming bow-shaped patterns in section due to their helicoidal arrangement (Gharagozlou van Ginneken & Bouligand 1973, 1975). As a greater diversity of copepod species has been studied more elaborations of this basic integumental structure have been reported. Bouligand (1966*a*, *b*) observed a poorly developed system of external microvilli on the integument of the endoparasites *Lamippe aciculifera* Zulueta and *Linaresia mammalifera* Zulueta. He also recorded the presence of vertical pore canals in the integument of the latter. These endoparasitic copepods lack a functional alimentary canal and it has been suggested that their specialized integumental structure is related to an absorptive role for the cuticle in nutrition. A recent study by Gharagozlou van Ginneken & Bouligand (1975) of integumental structure in the highly ornamented free-living harpacticoids *Porcellidium viride* (Philippi) and *P. fimbriatum* Claus revealed the presence of well developed external microvilli and vertical pore canals. The vertical pore canals terminate in ampullae just beneath the epicuticle and are in contact with it via numerous intermediate vesicles.

Gharagozlou van Ginneken & Bouligand (1973) identified four layers (e1 to e4) within the epicuticle of the harpacticoid *Cletocamptus retrogressus* Schmankenwitsch. The same authors (1975) identified levels e1 to e3 in the epicuticle of *Porcellidium* and regarded them as probably homologous with the same levels in *Cletocamptus retrogressus*. The external microvilli in *Porcellidium* are formed by the e1 and e2 levels of the epicuticle. In *Benthomisophria cornuta* four levels could be recognized within the epicuticle at high magnifications, and the entire epicuticle appeared to be involved in the formation of cone organs. The cuticle of *Alteutha depressa* (Baird) has also been studied by Gharagozlou van Ginneken (1976) and was found to be similar to that of *Porcellidium*, with external microvilli and vertical pore canals. These two genera belong to closely related harpacticoid families, the Peltidiidae and Porcellidiidae. It was suggested that the pitted surface, external microvilli and vertical pore canals had an important role in water retention during low tide in these intertidal taxa. Previously Gharagozlou van Ginneken & Bouligand (1975) suggested that in *Porcellidium* the microvilli and pore canals may have a function related to the presence of significant bacterial populations distributed over the highly pitted body surface.

Most planktonic copepods have a basically smooth external body surface although some, such as *Centraugaptilus horridus*, are densely covered with spinules. Reticulate ornamentation has been reported from the planktonic harpacticoid *Aegisthus aculeatus* Giesbrecht (Boxshall 1979) although the markings have not been studied in detail. The freshwater cyclopoid *Acanthocyclops venustus* also has integumental markings on the urosome but s.e.m. studies showed these to be a system of narrow grooves in the integument. The functional significance of all these markings is

poorly understood but the adaptive advantages conferred must outweigh the disadvantage of increasing hydrodynamic drag in the free swimming forms.

In the bathypelagic *Benthomisophria* species the integumental ornamentation is not a water retention system as suggested for *Alteutha* and *Porcellidium*. It functions partly as a strengthening system giving rigidity to the integument, especially in areas around muscle insertions. The surface ornamentation in *Benthomisophria*, together with the secretion of the cone organs, may be associated in some way with the presence of a surface flora of microorganisms, but the absence of epibionts from specimens studied by s.e.m., and the presence of lamellae on the surface of the sublittoral *Misophria pallida*, which lacks cone organs, both suggest that this interpretation is unlikely.

The integument of many crustaceans exhibits a more-or-less regular hexagonal structure (Cals 1973; Gharagozlou van Ginneken 1974; Mauchline & Ballantyne 1975) which often corresponds with the arrangement of the underlying epidermal cells. In *Nebaliopsis typica* the hexagonal structure of the integument is marked by a system of external lamellae. In most copepods the hexagonal structure is not apparent but in *Centraugaptilus horridus* Mauchline (1977) found it laterally on the first and second pedigerous somites. Scanning microscopy reveals that this hexagonal structure, though visible by transmitted light, is not represented by any external markings in *C. horridus*. It is unlikely that the pattern of ornamentation in *Benthomisophria* species corresponds with the arrangement of epidermal cells because of the irregularity of the patterning, the relatively great differences in size and shape of the areas enclosed by primary lamellae or ridges, and the presence of patterning on the carapace-like posterior extension of the cephalosome, which is an integumental structure and does not have an underlying cellular component.

(*c*) *The cone organs*

(i) *Structure*

Both species of *Benthomisophria* possess cone organs on the ventrolateral extension of the cephalosome (figures 33 and 34, plate 4). In *B. cornuta* there are approximately 250 of these in a patch on each side of the body, whereas in *B. palliata* there are approximately 530. Each cone organ arises from a basal pore through the integument and consists of an inverted hollow cone surrounded by a shallow depression and carrying a spherical globule of secretion at its distal extremity. Because they are hollow (figure 35, plate 5) they have often collapsed in specimens prepared for s.e.m. The cone has a serrated distal margin, clearly visible in some specimens, especially those from which the globules of secretion have been lost (figures 37 and 38, plate 5). All the cones are of similar height, about 4 to 5 μm in *B. cornuta* and 7 to 8 μm in *B. palliata*. The globules of secretion vary in diameter from about 2.7 to 6.7 μm. Their liquid nature is demonstrated by the coalescence of globules from adjacent cones where these have come into contact before fixation (figure 36, plate 5), and by their fragmentation into several smaller spherical globules where mechanical damage has occurred. In all the *B. palliata* examined under s.e.m. most cones had lost their globules; only those around the anteroventral periphery of the area were intact and many of these showed obvious signs of damage, with their globules displaced or fragmented (figure 38). It is assumed that the globules are lost as a result of mechanical damage sustained during catching and catch-handling procedures.

The walls of the cone organs are double, consisting of an outfolding of the epicuticle (figures 39 and 40, plate 6) so that each cone is lined both inside and out with epicuticle. The basal aperture of each inverted cone encircles a pore through the integument which is not lined with

epicuticle (figure 41, plate 6). The large apical aperture of the cone is a simple circular opening at which the globule of secretion is located, with the greatest diameter of the sphere at the level of the rim of the cone.

Passing into the pore canal at the base of each cone are several narrow tubules (figures 41, plate 6, 43 and 44, plate 7). These all terminate within the pore canal, discharging their contents into the lumen of the cone organ. The tubules originate from glandular cells containing densely staining droplets of secretion (figure 45, plate 7). It was not possible to trace all the tubules from a single cone organ through serial t.e.m. sections but it was apparent that the tubules discharging via any one cone organ originated from more than one glandular cell. The glands are located as an extensive but shallow mass occupying an area similar to that occupied by the cone organs on the surface. The gland mass may be several cells deep and occupies most of the available space between the integument and the gut wall when the animal is fully gorged (figure 54, plate 8).

The chemical nature of the secretion has not yet been ascertained. The globules are not membrane-bound. When fixed the secretion is rather fibrous (figure 42, plate 7).

(ii) *Function*

The cone organs, which are clearly secretory, are situated on either side of the cephalosome in such a position as to allow the long setae of the antenna and mandibular palp to sweep dorsoventrally across them. In the course of this sweeping movement these setae presumably come into contact with the raised globules of secretion. As they do so some or all of the secretion presumably adheres to them. The cone organs raise the globules several micrometres above the body surface and the gradation in size of globules indicates that secretion is a continuous process. The secretion could be either retained on the setae, smeared over the posterolateral surface of the cephalosome, or dispersed in the surrounding water. Without knowledge of the chemical nature of the secretion and without opportunity to observe living material it is difficult to determine the role of the cone organs. Possible interpretations are numerous. (i) The secretion may be used in the feeding process by being retained on the setae and used to entrap motile prey. (The difficulty of preventing the secretion from fouling the copepod's own limbs is a problem with this interpretation.) (ii) The secretion may be smeared over part of the body surface as a means of protection or of preventing the establishment and growth of micro-organisms. (This is supported by the observation that the area covered by the sweep of these setae is largely the surface of the carapace-like extension of the cephalosome, which is the only area of the body devoid of integumental pores as it has no underlying cellular component.) (iii) The secretion may possess an odour repellent to predators. (iv) It may serve as a chemical signal attracting potential mates. (v) It may be bioluminescent. (This is regarded as unlikely in an organism apparently devoid of photoreceptors.)

Analysis of the chemical nature of the secretion should give an indication as to which if any of these possible interpretations is correct. The antennae and mandibular palps are large well developed limbs and have relatively large and powerful muscles to move them. The main movement sweeps their setae up and down over the areas of cone organs. There is, therefore, a considerable anatomical and physiological investment in structures associated with the cone organs, and their function is of major significance to the animal. On the basis of the little evidence available it appears most likely that the role of the cone organs is to bring their secretion into contact with the antennary and mandibular setae so that it can be spread over the

surface of the carapace-like structure, which is the only area of the body surface devoid of pores and underlying integumental organs. The secretion is probably defensive or protective in nature.

No other copepods or crustacean groups are known to possess organs like the cone organs of *Benthomisophria*. Some calanoids of the family Augaptilidae have well defined areas of pores laterally on the pleurites of the first and second pedigerous somites (Mauchline 1977). The pores appear to be the openings of subintegumental secretory glands. Material of *Centraugaptilus horridus* was examined by s.e.m. and it was found that the pores are not associated with any external structure. They are simple elongate pores about 6 μm long with a well defined lip and are arranged in two pairs of areas laterally on the first thoracic pleurite. These areas are raised above the surrounding surface, which is smooth and unarmed rather than covered with regularly spaced slender spinules up to 20 μm long as it is over the rest of the body. These areas of pores are sited, as in *Benthomisophria*, so that the long setae of the reflexed antennary exopod and mandibular palp brush over them. They may have a similar function to the cone organs. Mauchline (1977) suggested a possible bioluminescent function for these glands in *Centraugaptilus* but this appears unlikely.

(*d*) *Integumental sensillae and pores*

The body surface of *B. cornuta* is punctuated with pores which are distributed over the surface in a definite pattern (figure 29). There are no pores through the carapace-like extension of the cephalosome. Each urosome somite has a pair of lateral pores. The anal somite has a pair of ventral pores, and the uropods bear a pair of dorsal and a pair of ventral pores, all of which are secretory gland openings (figure 57). The pores are elliptical with axes of between 5 and 6 μm and 2.5 and 4 μm, and they typically have a small membranous flap around their circumference.

The distribution of the pores in *B. palliata* (figure 25) is broadly similar to that in *B. cornuta*, most occurring on the cephalosome. There are no pores in the carapace-like structure and few on the free thoracic somites. Others occur on the urosome somites and uropods as in *B. cornuta* although they are circular and smaller (diameter 2–3 μm) and have a slight raised lip.

There are no sensillae on the ornately patterned parts of the surface of *B. cornuta*. A few simple sensillae are distributed around the margins of the dorsal shield and along the bases of the hyaline frills at the posterior margins of the second to fourth pedigerous and the urosome somites. *B. palliata* has similar but more numerous simple sensillae similarly distributed. It has for example, 12 posterior marginal sensillae positioned around the circumference of urosome somite 3, compared to four in *B. cornuta*. *B. palliata* also has sensillae distributed over the patterned parts of the body surface. These sensillae often appear to be associated with pores (figure 28, plate 2).

The integument of *Misophria pallida* is provided with sensillae and pores, though the positions of the latter could not be mapped on the material available. Sensillae are distributed over the cephalosome and free thoracic somites as well as around their margins and those of the urosome somites. In addition, *M. pallida* possesses a small number of oar-shaped sensillae (marked by arrows in figure 32). Each originates from a shallow pit with a raised rim and consists of a thick-walled tapering proximal section and a broad thin-walled distal section. Two pairs of these sensillae are present on the second and third pedigerous somites. They appear to have collapsed during preparation for s.e.m. and it is assumed that they were originally inflated. They do not have a terminal pore like the chemosensory aesthetascs.

The adults and copepodid stages of both *Benthomisophria* species bear large aesthetascs on their antennules. In *B. palliata* these are about 100–110 μm long with an apical pore about 13 μm in diameter (figure 3, plate 1).

The positions of sensillae and pores on the body surface may be species-specific and pore signatures have proved to be useful taxonomic characters in both calanoid (Fleminger 1973; Fleminger & Hulsemann 1977) and poecilostomatoid (unpublished data) groups. A variety of sensory and secretory functions has been attributed to these integumental organs although the assumption that several of these appeared only at maturity and therefore represented secondary sexual characters has had to be questioned since the discovery that these organs develop sequentially through the ontogenetic stages like any complex character (Mauchline & Nemoto 1977).

5. The anatomy of other organ systems

(*a*) *The digestive tract*

(i) *Oesophagus*

The mouth is situated in the anterior fifth of the ventral surface of the cephalon. It is overlain by the large posteriorly directed labrum and opens into the oesophagus, which passes first dorsally, then posterodorsally towards the midgut. The integument-lined oesophagus opens into the midgut at the level of the junction between the anterior midgut caecum and the anterior part of the midgut itself. The oesophageal musculature is well developed and complex (figure 46). A series of broad circular muscle bands encloses the oesophageal epithelium and basement membrane, extending from just inside the mouth opening to the junction with the midgut. The circular muscles at each end of the oesophagus function as sphincter muscles (figure 46, sphn) closing off the oesophagus at the mouth and junction with the midgut. The others function as oesophageal constrictors. The oesophagus is dilated by numerous muscle strands (oe dil) which radiate outwards from along its length. These originate at several sites within the anterior three somites, including the anterior and lateral surfaces of the labrum, the postantennulary apodeme and the anterior ventral cephalic tendon, as well as the ventral and lateral body wall. They insert on thickened areas of the oesophageal wall. They dilate the lumen of the oesophagus considerably and enable the copepod to swallow relatively large items, the maximum size of which is limited by the diameter of the nerve ring surrounding the oesophagus. Sequential contraction of the dilators alternating with the constrictors produces a peristaltic wave that carries the food towards the midgut.

(ii) *Midgut*

The midgut comprises three main regions; anterior, posterior and the anterior midgut caecum (figure 47). The midgut caecum is typically a subspherical chamber though the wall is highly convoluted in some specimens. It is situated at the anterior end of the midgut and separated from it by a muscular valve consisting of several strands of circular muscle which can completely close off the caecum from the rest of the midgut. The wall of the midgut caecum contains a high proportion of epithelial cells possessing balloon-like extrusions distally. These are probably equivalent to cell type 2 of the harpacticoid *Tigriopus californicus* (Sullivan & Bisalputra 1980). The remaining cells are simple columnar epithelial cells lacking distal extrusions.

The anterior midgut is extremely distensible and when fully distended (figure 49) occupies

most of the free space within the prosome from the level of the mouth to the posterior end of the second pedigerous somite. It bears large lateral caecae which can greatly increase its capacity. When distended its wall is stretched and the epithelial cells become flattened. When empty it is partly collapsed in on itself (figure 48) and is suspended by connective tissue strands. The epithelial cells revert to a columnar morphology and many cells bearing balloon-like extrusions can be observed, though in relatively smaller numbers than in the anterior midgut caecum. The

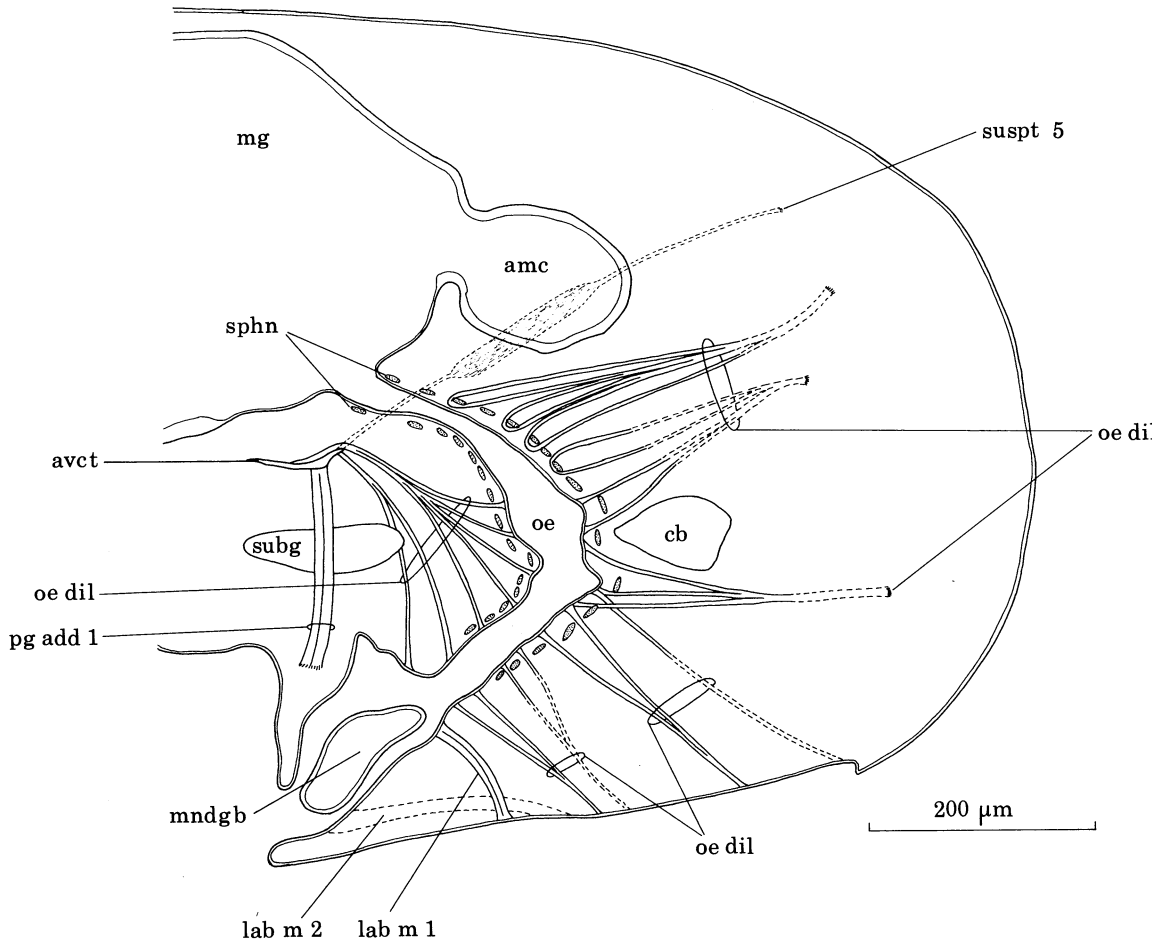


FIGURE 46. A thick median longitudinal section through the anterior end of the cephalosome, drawn from three adjacent serial sections of 8 µm thickness. The medial elements of the complex oesophageal musculature are shown. Continuations of the oesophageal dilator muscles passing laterally out of the plane of the 24 µm composite section towards insertions on the body wall are represented by hatched lines, as are other structures lying completely lateral to the plane of the section.

anterior midgut is encircled by regularly spaced bands of circular muscle along its length. Longitudinal muscles were not observed.

In the third pedigerous somite the anterior midgut narrows abruptly to its junction with the posterior midgut, which extends as a simple tube through the urosome to its junction with the hindgut. The junction between anterior and posterior portions of the midgut is marked by six thick bands of circular sphincter muscles. The wall of the posterior midgut has a similar structure to that of the anterior midgut but is thinner and the epithelial cells are more flattened

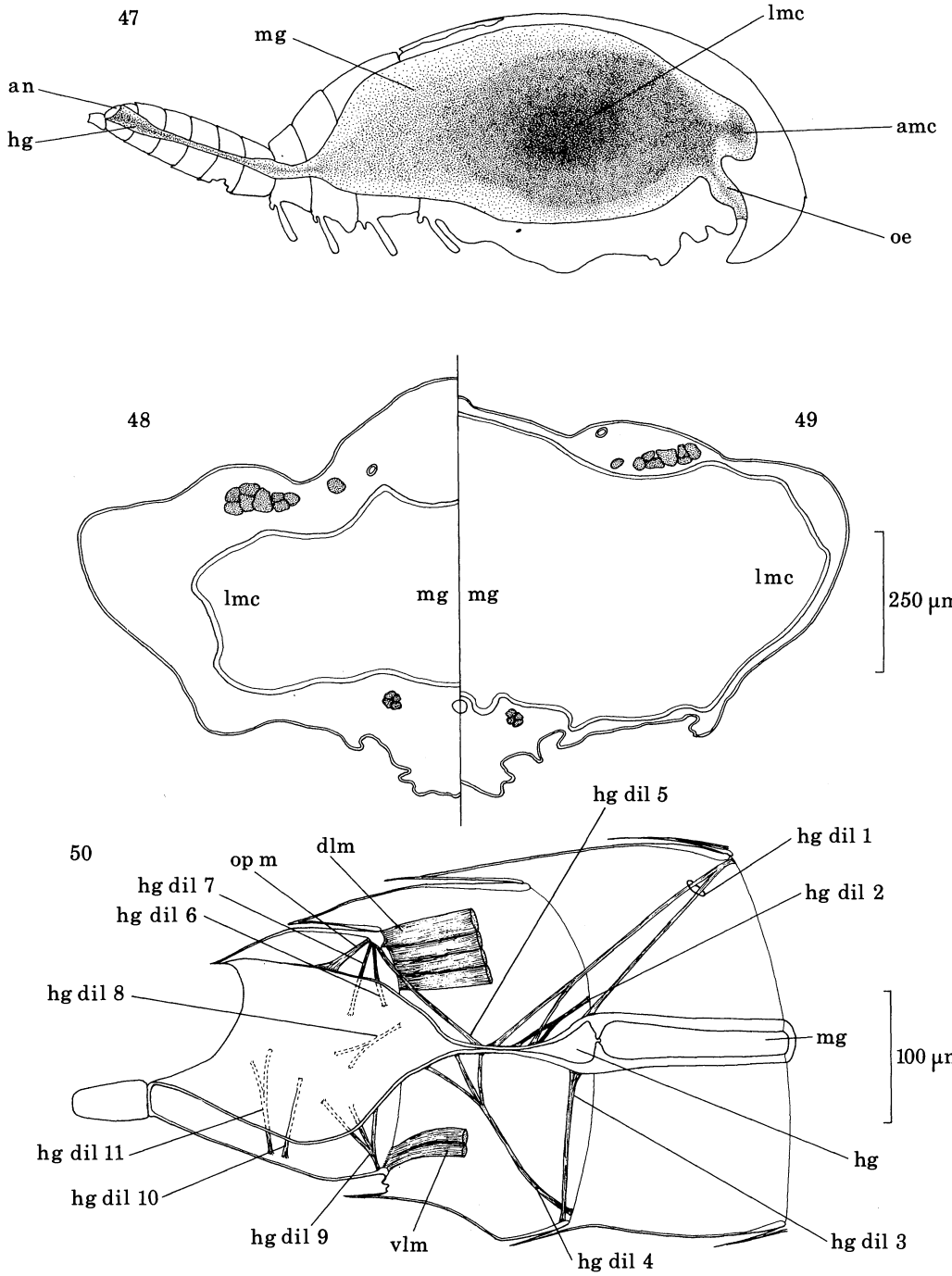


FIGURE 47. Median internal view of the gut of a female *B. palliata* of body length 5.3 mm.

FIGURE 48. Transverse section through the maxilliped-bearing somite. The specimen has a partially collapsed gut, largely devoid of contents.

FIGURE 49. The same. This specimen has a distended gut, full of food, which occupied virtually all the free space within the cephalosome.

FIGURE 50. Median internal view of the last three urosome somites, showing the hindgut and its musculature. Only the insertions of the longitudinal trunk muscles are shown.

and squamous and are more widely spaced. Few of the cells possess distal extrusions. The posterior midgut is well supplied with longitudinal muscle strands and some narrow circular muscle bands are distributed along its length. It extends as far as the posterior boundary of the fourth urosome somite, where there is a valve between it and the hindgut formed by enlarged cells projecting into the lumen.

(iii) *The hindgut*

The hindgut (figure 50) is about 300 μm long and opens via the anus onto the dorsal surface of the anal somite. Its wall comprises a layer of flattened epithelial cells on a basement membrane. It is well supplied with longitudinal muscles but only a few circular strands were observed, in its anterior part within urosome somite 5.

Several paired and median unpaired muscles are involved in the defaecating process. These are shown in figure 50 with the anus open. One pair (hg dil 1) originates on the anterior rim of urosome somite 4 just dorsal to the dorsal longitudinal trunk muscles. Each muscle divides as it passes towards its insertion on the hindgut at three dorsolateral sites in the front half of somite 5. Inserting laterally in the same region is a muscle pair (hg dil 2), each of which bifurcates midway between its lateral origin on the anterior rim of somite 5 and its insertion. Another pair (hg dil 3) originates ventrally on the anterior rim of the same somite and passes vertically to insert just behind the midgut–hindgut valve. A pair (hg dil 4) originates just lateral to muscle hg dil 3 and each passes posteromedially to insert ventrally and ventromedially on the hindgut in the posterior part of urosome somite 5. Inserting dorsolaterally at the same level is a pair of unbranched muscles (hg dil 5) which originates dorsally on the posterior rim of the anal somite. Two other pairs of muscles (hg dil 6, 7) share the same origin, passing medially to insertions in the anterior part of the anal somite. Also originating mid-dorsally is the median opercular muscle (figure 50, op m), which inserts on the hindgut near the base of the small anal operculum. A pair of muscles (hg dil 8) originates laterally on the anterior rim of the anal somite and each has a double insertion on the lateral wall of the hindgut. A median muscle (hg dil 9) originates ventrally on the anterior rim of the somite, divides into three strands and inserts on the ventral and ventrolateral wall of the hindgut. Two pairs of muscles (hg dil 10, 11) originate on the ventrolateral body wall in the middle of the anal somite. The muscles of the anterior pair are unbranched. The posterior pair bifurcate at midlength, and all insert on the ventrolateral wall of the hindgut.

All of these muscles (hg dil 1–11) orginate on the body wall and are dilators. There are few circular constrictors of the hindgut and these are restricted to its anterior portion. The dilators are therefore presumably opposed by the elasticity of the tissues and/or turgor pressure which force the hindgut walls inwards to close its lumen. In figure 50 the hindgut is shown with the dilators of the anterior part relaxed and the lumen occluded by the walls, which become convex (in longitudinal section) by contraction of the circular muscles, and also perhaps by their own elasticity and pressure of the body fluids. The posterior part is shown with the dilators contracted, the very flexible walls concave and the lumen greatly expanded. The anus is open. Opening results from combined action of the dorsal longitudinal trunk muscles, the opercular muscle, and hindgut dilators 6–11. The first insert dorsally on the proximal rim of the anal somite and tend to enlarge the anus by telescoping the dorsal side of the anal somite inside the preceding somite. Simultaneously dilators 6 to 11 and the opercular muscle pull outwards the flexible wall of the posterior hindgut, which had previously bulged inwards to occlude the lumen.

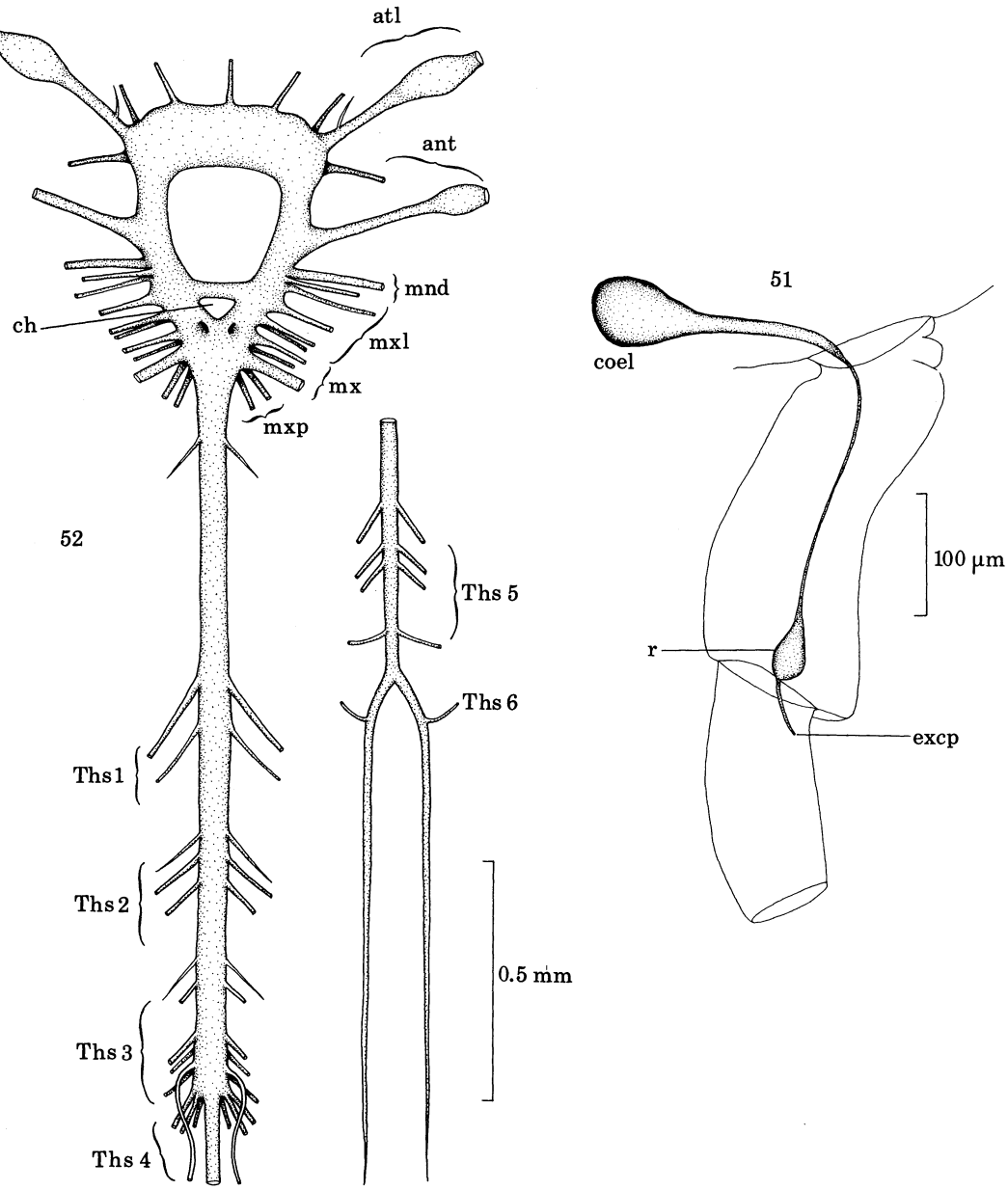


FIGURE 51. Anterior view of antennary gland of an adult *B. palliata*.

FIGURE 52. Dorsal view of the central nervous system of *B. palliata* drawn from a dissection *in situ*. The sites of origin of the main nerves to the cephalic appendages and thoracic somites are shown. Note the absence of any optic centres from the cerebrum.

Defaecation probably commences with a faecal pellet passing through the hindgut-midgut valve into the anterior hindgut. At this stage the anterior part of the hindgut is dilated, the posterior part is not and the anus is closed. Then the anus is opened, the posterior part of the hindgut is dilated and the anterior part is constricted, resulting in the rapid voiding of the faecal pellet, after which the anus is closed again.

(*b*) *The excretory system*

The maxillary gland, characteristic of the adult stages of all other copepod groups thus far studied, is not present in adult *B. palliata* but the antennary gland (figure 51) is well developed. It comprises a pear-shaped coelomic vesicle of about 50 μm diameter lying just dorsal to the antennary rotator muscles within the cephalon, and a broad coelomic funnel of 9 μm diameter extending to the base of the antenna. The junction between funnel and vesicle is constricted by some large cells which may act as a valve. The funnel narrows to a tubule of diameter 3 to 4 μm as it enters the limb. At the apex of the protopod it enters an excretory reservoir 26 μm in diameter. The reservoir empties via a duct of diameter 1.8 μm which terminates in a pore on the lateral margin of the first endopod segment.

The lumen of the gland is filled with excretory material in the form of spherical granules (figure 53, plate 8) from the coelomic vesicle to the distal reservoir and duct. The granules vary in diameter from about 1.4 to 1.8 μm and stain darkly with haematoxylin–eosin. There is presumably little liquid excretory material as these granules are densely packed in the lumen.

(*c*) *The central nervous system*

The central nervous system is shown in figure 52. The cerebrum is about 435 μm wide, about 130 μm long and about 150 μm deep. It is oval in section, is not divided externally into lobes, and is situated anterior to the oesophagus. From its posterolateral angles arise two massive circumoesophageal commissures which pass posteroventrally around the oesophagus and unite to form the single ventral nerve cord. Where the commissures unite the nerve cord is thickened, forming the suboesophageal ganglion, which is marked by three dorsoventral channels through which all the paragnath adductor muscles pass. The ventral nerve cord passes posteriorly through the prosome into the urosome. Just posterior to the boundary between urosome somites 1 and 2 it bifurcates, each branch continuing posteriorly in a ventrolateral position into the paired uropods on the anal somite.

Anteriorly the cerebrum gives rise to a lateral pair and an unpaired median nerve which passes anteroventrally to a small median organ of uncertain homology. Each of the lateral pair passes anteriorly and then dorsally to terminate at a small organ situated in the hypodermis just dorsal and medial to the origin of the antennulary remotor muscles. These nerves branch several times and appear to supply three other pairs of small glands (see §5*d*). Three pairs of nerves arise from the anterolateral angles of the cerebrum. The most medial arises ventrally and each one passes towards an antennule, giving off a branch towards a pair of glands located ventrally near its base. The large nerve arising at the angle itself is the antennulary nerve and it forms a ganglion at the base of the limb. It gives rise to a small branch proximally which passes towards the antennulary muscles. A pair of antennary nerves arises ventrally from the lateral part of the cerebrum. The main pair of antennary nerves and the two pairs of mandibular nerves arise from the posterior region of the circumoesophageal commissures. The nerves to the maxillules (four pairs), maxillae (three pairs) and maxillipeds (two pairs) arise in sequence from the dorsal and ventral areas of the lateral surface of the suboesophageal ganglion. A pair of large labral nerves emerges from the ventral surface of the suboesophageal ganglion. These pass anteroventrally around the oesophagus and into the labrum. The ventral nerve cord gives off two pairs of nerves to each of the four pairs of swimming legs. These arise from the nerve cord a considerable distance anterior to the muscles that they innervate and they follow an oblique

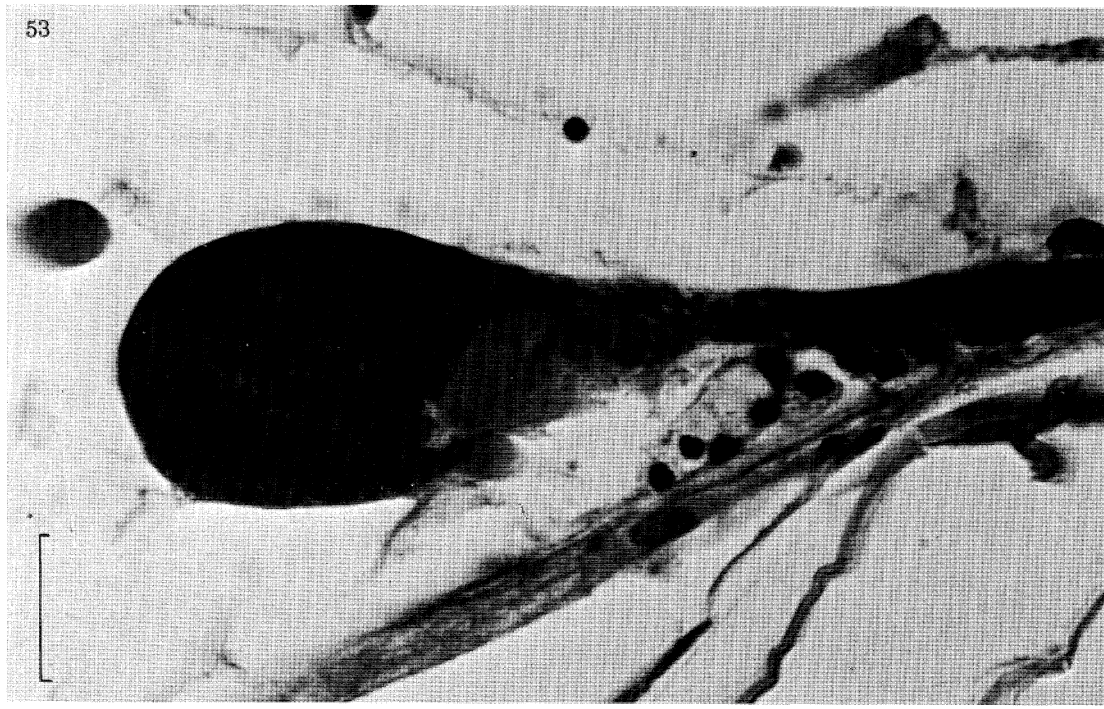


FIGURE 53. Section through the coelomic vesicle of the antennary gland of an adult *B. palliata*. The granular nature of the contents of the vesicle and funnel is apparent. Scale bar 25 μm.

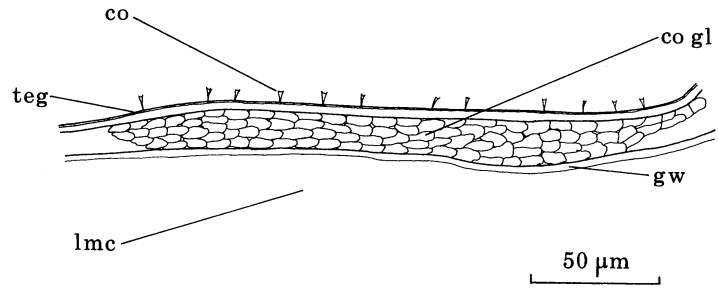


FIGURE 54. Transverse section through lateral cone organ-bearing area of cephalosome, showing the mass of glandular cells sandwiched between the gut wall and integument.

(*Facing p.* 168)

posterolateral course. Throughout its course through the prosome the ventral nerve cord gives rise to nerves supplying the dorsal and ventral longitudinal trunk muscles. The nerves supplying the fifth legs arise from the nerve cord within the last prosome somite. The nerve cord bifurcates at the level of the anterior end of the genital somite and the paired longitudinal nerves pass towards the uropods. Just posterior to the bifurcation each gives rise to a sixth leg nerve. No other large nerves arise from the nerve cords in the succeeding urosome somites.

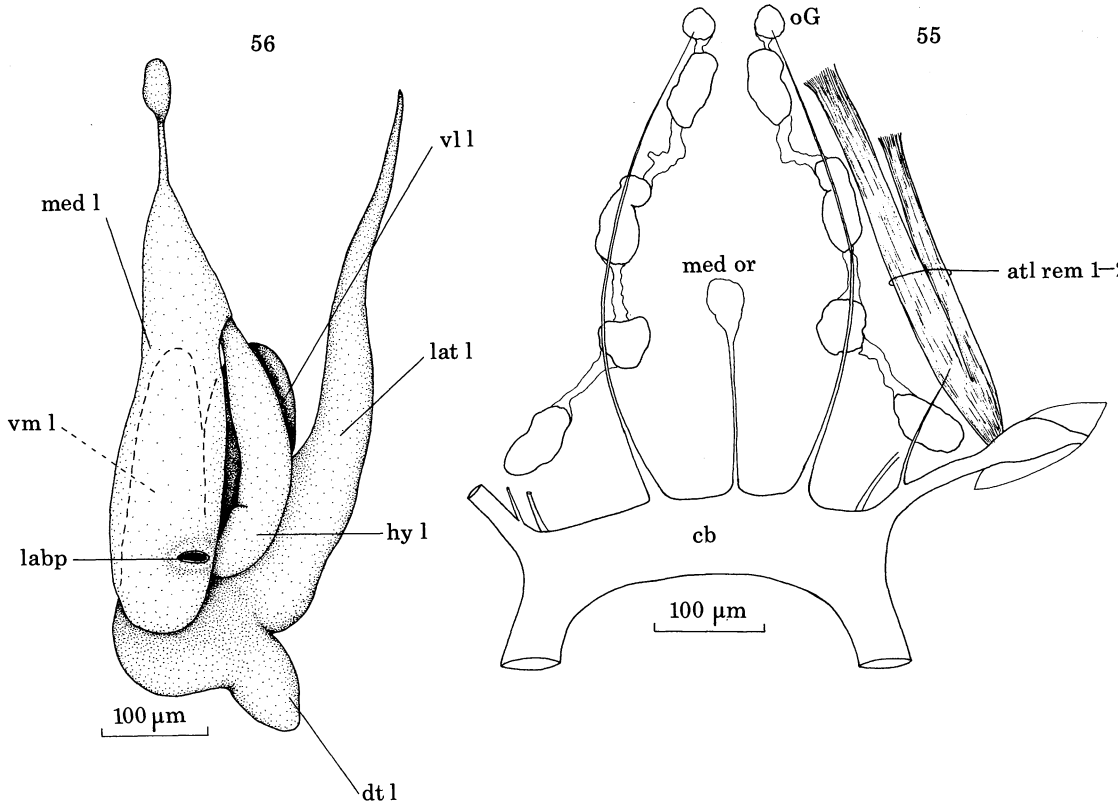


FIGURE 55. Dorsal view of cerebrum and the anterior nerves passing to the various small glands located beneath the anterior surface of the cephalosome. Drawn from a dissection *in situ*.

FIGURE 56. Dorsal view of the labral gland complex drawn from a dissection with the aid of a three-dimensional reconstruction from serial sections.

(*d*) *Glands*

(i) *The labral glands*

The glands contained within the labrum (figure 56) are the largest in *Benthomisophria*. They occupy most of the space within the proximal part of the labrum and extend anterodorsally into the cephalon. They are regarded here as a pair of multilobed glands rather than a complex of paired glands as they secrete via a single pair of pores through the dorsal surface of the labrum. The pores are sited in the distal half of the labrum and open into the preoral food chamber posteroventral to the mouth. The staining properties of the labral gland secretions vary not only from lobe to lobe but also between the different regions of any one particular lobe.

There are six main lobes in each gland (figure 56): medial, lateral, distal, ventromedial,

ventrolateral and hyaline. The first five appear to produce a similar secretion of a coarse granular consistency and discharge into a common lumen just beneath the pore. Their contents become finer-grained and less eosinophilic the further away from the common lumen. The hyaline lobe produces an extremely fine-grained secretion and discharges directly into the pore rather than into the common lumen.

Richard (1891) examined the labral glands of several freshwater cyclopoid and calanoid copepods. In all cases the paired labral glands discharge into a pair of common chambers which empty via a single pair of pores. By contrast Lowe (1935) found that, in *Calanus*, each component gland (lobe) of the paired labral gland complex empties individually by its own pore on the dorsal surface of the labrum. The labral glands of *Benthomisophria* are clearly of the type reported by Richard (1891).

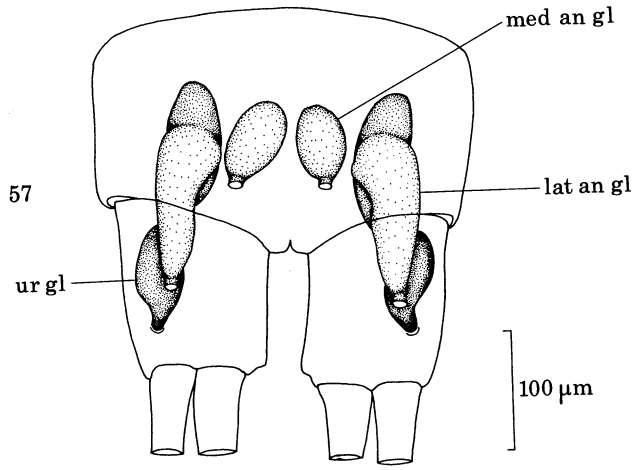


FIGURE 57. Ventral view of anal somite and uropods, showing secretory glands.

(ii) *Frontal glands*

There are five pairs of small glands beneath the hypodermis of the anterior surface of the head (figure 55). Their innervation is described above (see §5*c*). Each of the most dorsally situated pair of glands comprises a small cluster of cells similar in appearance by light microscopy to the organ of Gicklhorn in *Euchaeta norvegica*, as described by Elofsson (1966). Elofsson (1970) has since described the ultrastructure of this organ and now regards it as a photoreceptor that has been derived independently of the nauplius eye complex of crustaceans. The other four pairs of glands are probably secretory. The dorsal-most contains globules of slightly eosinophilic material, as does the most ventrally situated pair close to the base of the antennule. The middle two pairs contain a finely granular secretion that stains light purple with haematoxylin–eosin. Strands of connective tissue link most of these glands. They probably discharge onto the anterior body surface via pores through the integument. Their homologies with the frontal glands of other crustaceans cannot be ascertained without detailed histological examination of better-preserved material.

In the frontal area there is also a small median unpaired organ innervated by a short nerve from the cerebrum. Its homology is also uncertain though it is possible that it represents a vestige of the nauplius eye.

(iii) *Urosomal and perianal glands*

In the urosome of *B. palliata* a pair of glands is situated near the ventral surface of each of the third to fifth somites. These appear to be absent in males. They contain globules of eosinophilic secretion similar to that found in some of the frontal glands. In both sexes there are two pairs of glands in the anal somite (figure 57), one opening via pores on the ventral surface of the anal somite, the other via pores on the ventral surface of the uropods. The lateral gland is divided into two areas, an anterodorsal area which stains reddish purple with haematoxylin–eosin, and a posteroventral area, which also acts as the duct and stains dark purple. The more medial gland is bladder-like, having a large lumen with fine grained vacuolate contents staining light reddish purple with haematoxylin–eosin. Another small pear-shaped gland is found within each uropod. Each opens via a distal pore on the dorsal surface and the secretion stains dark reddish purple.

(*e*) *The circulatory system*

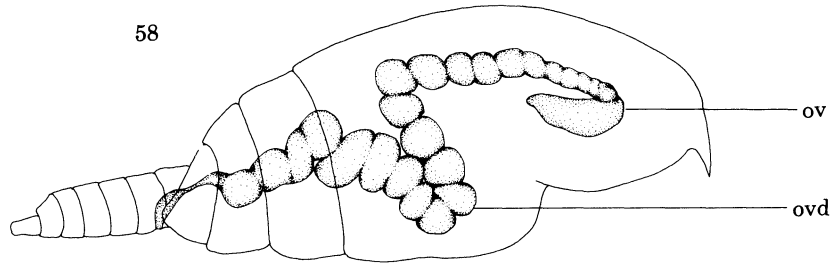
Misophria pallida is the only podoplean copepod known to possess a pulsating dorsal vessel (heart), but, although its presence has been widely quoted and regarded as of great phylogenetic significance, it has never been properly described. According to Giesbrecht (1892, pp. 4, 5) it is more primitive in structure than that of calanoids and he could not detect ostia with certainty. In the present study particular emphasis was placed on the search for the heart, yet no structure that could be identified with certainty as such was found in either dissected or serially sectioned specimens of *B. palliata*. In sectioned specimens a number of membranous structures was present dorsal to the gut in the second and third pedigerous somites but no musculature was associated with them and no consistent form could be recognized in the different specimens examined. It is concluded therefore that no heart is present in *B. palliata*. Its absence may be linked to the capacity for extreme distension of the gut as this would cause compression of organs in the middle of the prosome.

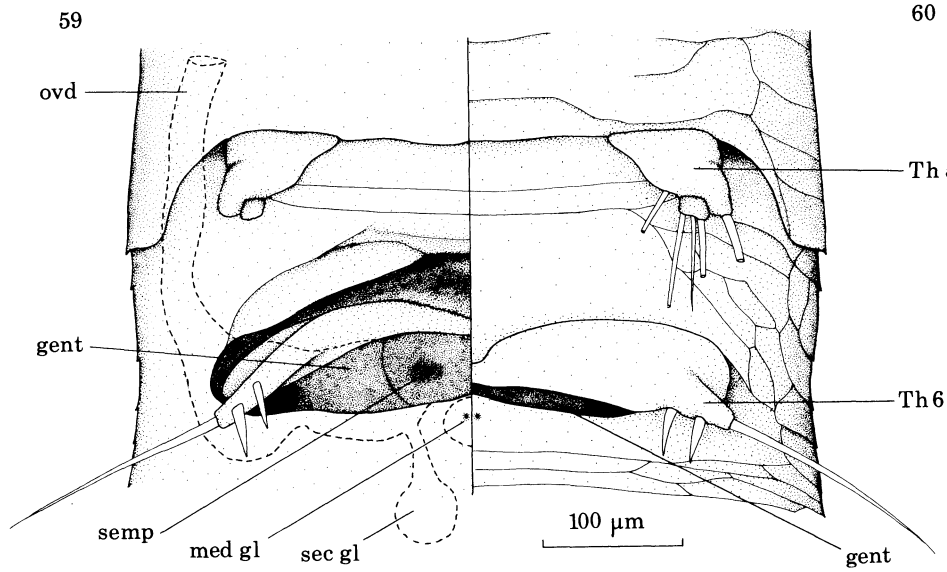
A mature female of *M. pallida* was serially sectioned and a structure that is presumed to be the heart was found within the prosome. Its position in the cephalosome, dorsal to the gut and between the paired ovaries, is more anterior than in *Calanus* (Lowe 1935). It is barrel-like, about 40 μm long with a maximum diameter of 17 μm and has thin walls sparsely supplied with muscle fibres. It appears to have only two ostia, anterior and posterior, and is suspended from the dorsal wall of the cephalosome by short muscle fibres at each end. Lateral ostia could not be discerned but this may be due to the state of preservation of the material, which had been stored in alcohol for over 70 years. This description of the heart is still far from complete and observations on fresh or live material are required to supplement it.

(*f*) *The reproductive system*

(i) *Female*

The ovaries are paired and lie dorsomedially in the cephalosome. Each is about 0.5–0.6 mm long in a mature female and is more-or-less cylindrical with rounded ends but tapering posteriorly. An oviduct emerges from the lateral wall of each ovary near the anterodistal angle (figure 58). It passes posteriorly between the dorsal wall of the gut and the body wall until it reaches the level of the cephalosome–first pedigerous somite boundary, where it turns ventrally. This descending segment passes laterally and ventrally around the gut until it nearly reaches the





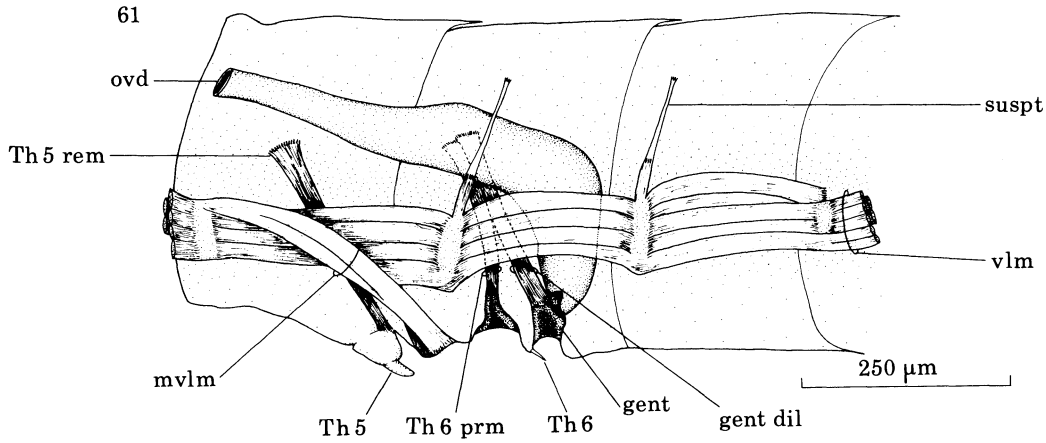


FIGURE 58. Lateral view of right side of an adult female *B. palliata* of body length 4.8 mm, showing right ovary and oviduct.

FIGURE 59. Ventral view of genital somite of adult female with fused sixth legs partially protracted and the genital antra partially opened. The positions of the oviduct and secretory gland are shown by hatched lines. Drawn from a partially cleared whole mount.

FIGURE 60. Ventral view of genital somite of adult female with the opening to the genital antra almost completely closed by the fused sixth legs. Drawn from a s.e. micrograph.

FIGURE 61. Median internal view of urosome somites 1–3 of an adult female, showing the musculature associated with the genital apparatus. The seminal receptacles, dorsal longitudinal trunk muscles, gut and nerves are omitted. The tendinous connections between the ventral longitudinal trunk muscles and the body wall can also be seen.

ventral body wall, where it turns posterodorsally through about 180° and passes to the middle of the first pedigerous somite. Here it turns posteriorly and passes towards the prosome–urosome boundary. In a gravid female the oviducts are filled with eggs as far as the posterior end of the third pedigerous somite. It continues as a slightly flattened tube full of secretion positive to periodic acid–Schiff reagent (PAS), passing dorsolaterally through the fourth pedigerous somite and the first urosome somite into the genital somite. It turns ventrally through 90° and gradually increases in diameter before opening into the lateral wall of the genital antrum (figure 61).

The genital antra (figure 59, gent) are paired integument-lined cavities, formed as invaginations of the ventral wall of the genital somite posterior to the sixth legs. The antra meet in the midline, forming a continuous, transverse bilobed cavity. This is usually closed off by the fused sixth legs which act as a ventral wall for the cavity. The antrum in figure 60 is slightly open. Also opening into the antra on each side are the seminal receptacles. These are nearly spherical organs positioned just lateral to the midline and just dorsal to the antra. Each receptacle appears to open via a posteromedially situated pore in the dorsal wall of the antrum. Sperms are stored in the seminal receptacles and were also observed in the antrum near the oviducal openings. Paired secretory glands are present ventrally in the third urosome somite and ducts from these pass anteriorly into the genital somite opening via pores in the posterior walls of the antra. A median gland is present at the ventral midline immediately posterior to the antra. The contents of this gland are strongly PAS-positive and it appears to open onto the ventral body surface through a pair of pores. It is possible that the function of this secretion may be spermatophore release. Such a role has been attributed to glands opening in a similar position in the calanoid *Labidocera aestiva* Wheeler (Blades & Youngbluth 1979).

The musculature associated with the genital apparatus is simple (figure 61). The ventral longitudinal trunk muscles extend through the genital somite passing just dorsal to the antra and seminal receptacles and medial to the oviducts. They originate on the ventral wall of the first urosome somite and attach in the second and third somites via suspensory connections that are partly muscular and partly tendinous. In succeeding somites most of these muscles attach directly to the body wall. Two large fibres (figure 61, mvlm) from the dorsal side of the ventral longitudinal muscle bundle diverge in the first urosome somite and pass medially and ventrally to insert anteriorly on the body wall of the second urosome somite at the ventral midline. These presumably act as levators, raising the ventral body wall and possibly assisting indirectly in the release of eggs from the genital antra. Also within the first urosome somite are the paired extrinsic muscles (Th5 rem) of the fifth leg. These originate anteriorly on the lateral body wall and pass posteroventrally and medially to insert posterolaterally on the proximal rim of the fifth leg. They act as remotors, though the range of possible movements is limited to a small degree of promotor–remotor swing. Promotion is presumably achieved by cuticular elasticity as no antagonistic muscles are present.

Within the genital somite there are two pairs of muscles associated with the genital antra and sixth legs (figure 61). The sixth legs are fused to form a transverse plate which can swing forwards and backwards about a transverse hinge line extending between two fulcra, one at each of the proximal anterolateral angles of the sixth leg plate. A pair of muscles (Th6 prm) originates on the dorsolateral body wall and passes ventrally and slightly posteriorly towards ventrolateral insertions on the body wall anterior to the sixth legs. Their contraction raises the ventral body wall, causing the sixth leg plate to swing forwards and upwards thereby opening the antra to

the outside (figure 59). These promotors may be assisted by the levators (mvlm) originating from the ventral longitudinal muscle bundle. Together these muscles can cause marked depression in the ventral surface of the somite anterior to the sixth legs. Opposing them is a pair of muscles (figure 61, gent dil) that originate just dorsal and posterior to the promotors and pass ventrally and slightly posteromedially to insert in the flexible anterior wall of the genital antra posterior to the base of the sixth leg plate. They dilate the antral cavity into a large subspherical space and also produce remotion of the sixth legs, causing them to swing downwards and backwards to close off the antral openings. These antral dilator–remotor muscles may be opposed in part by cuticular elasticity because at rest the anterior wall of the antral cavity is highly convex, bulging out largely to occlude the cavity. In this resting state the antral cavity is a semispherical concavo–convex space which is crescentic in outline when sectioned.

(ii) *Oviposition*

Benthomisophria produces relatively large lecithotrophic eggs. None of the 214 adult females examined bore egg sacs and it is probable that species of this genus release their eggs without the formation of a typical copepod egg sac. Gurney (1933*a*) found that a female *M. pallida* bears two to four large eggs, loosely attached to the genital somite but not apparently enclosed in a definite egg sac. If oviposition is similar in *Benthomisophria* then the PAS-positive secretion observed in the distal segment of the oviduct may be the material with which the eggs are coated and by which they are loosely attached to the urosome.

The genital antra are large enough to accommodate only a single egg each and it can be assumed therefore that eggs are released singly from each oviduct. Each egg is probably drawn from the oviduct opening into the antrum by dilation of the antral cavity. Once inside the antrum fertilization can occur as the egg passes through the sperms gathered near the mouth of the oviduct and more sperms may be released from the seminal receptacles. During this part of the process the external openings of the genital antra are closed by the sixth legs. Once the antra contain a pair of eggs the combined contraction of the promotors and levators swings the sixth legs forwards and opens the antra. The two eggs are then pushed out by the bulging of the anterior wall due to cuticular elasticity as the antral dilator–remotor muscles relax. The process can then begin again.

(iii) *Male*

The paired testes lie dorsolaterally in the first pedigerous somite (figure 62). In a mature male each testis is about 0.2 to 0.3 mm long and is more-or-less cylindrical with rounded ends. Spermatogonia occupy the more posterior region, mature sperms the more anterior region. A vas deferens emerges from the lateral wall of each testis within the anterior third, passes ventrally until it reaches the midlevel of the body and turns through 90° to pass towards the urosome. It increases in diameter in the second and third pedigerous somites, and is slightly dilated in the fourth. In the genital somite it follows an oblique course, dorsolateral to ventrolateral, gradually increasing in diameter towards the genital aperture.

Each genital aperture is closed off by a plate formed from the fused sixth legs, which extends across it, parallel to the ventral body surface. Each aperture is situated dorsal to the sixth leg and posterior to its base. The dorsal surface of the sixth leg is flexible and slightly convex, thereby closing off the genital aperture. The ventral surface of the sixth leg is rigid except for a transverse strip of arthrodial membrane proximally along its anterior rim.

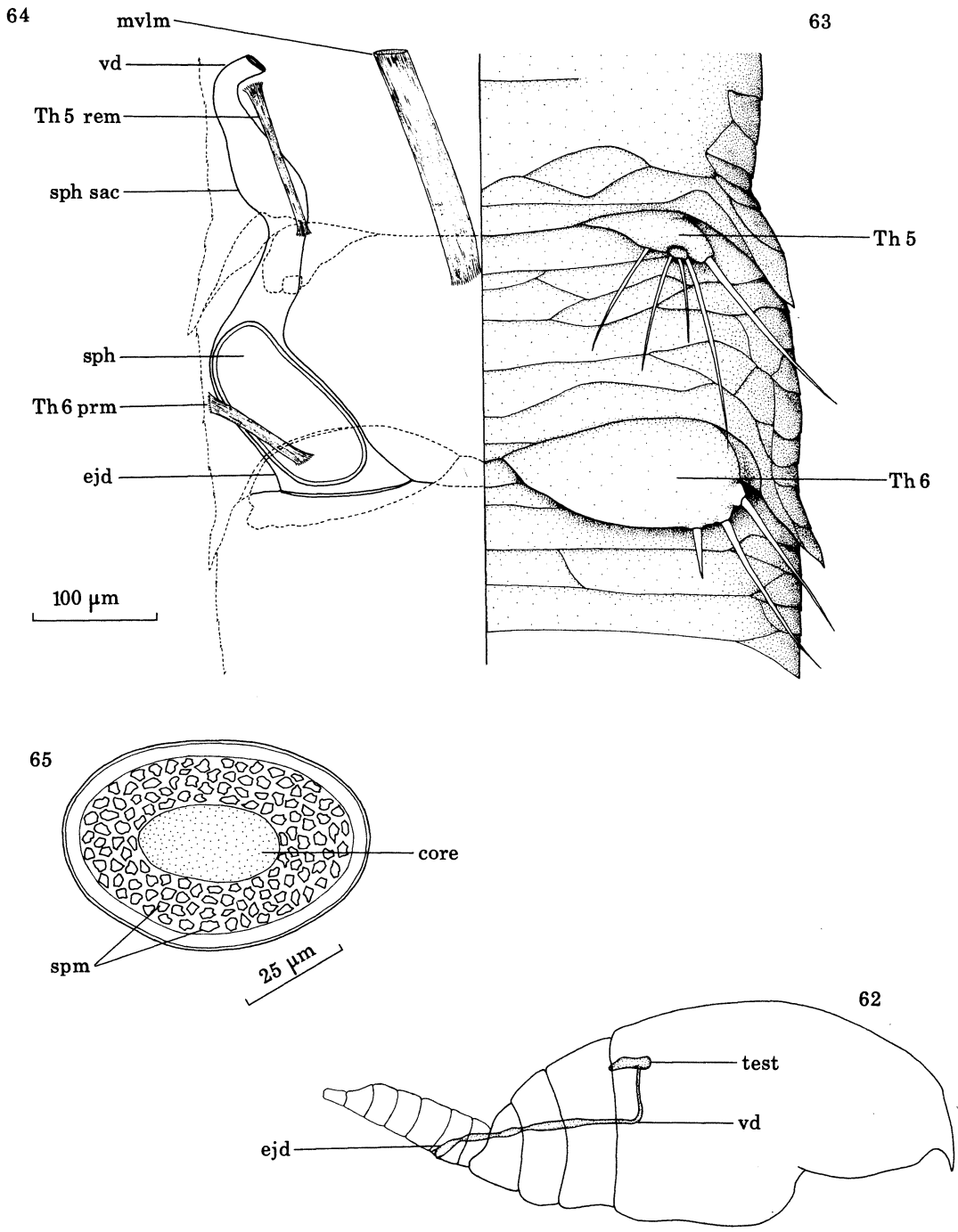


FIGURE 62. Lateral view of right side of an adult male *B. palliata* of body length 4.2 mm, showing right testis and vas deferens.

FIGURE 63. Ventral view of genital somite of adult male, showing external morphology. Drawn from a whole mount.

FIGURE 64. Ventral view of internal structures of genital somite of adult male. A spermatophore can be seen within the ejaculatory duct and the musculature associated with the genital apparatus is illustrated. The external features are shown in hatched outline.

FIGURE 65. Transverse section through a mature spermatophore. A dense granular core is present, surrounded by sperms.

The vas deferens is relatively simple in *Benthomisophria*, showing much less marked differentiation into functional regions than in other copepod groups. The initial descending segment is a narrow tube with walls 4–5 μm thick and showing little sign of secretory activity. The lumen is about 3 μm in diameter here and typically contains a single row of sperms. The posteriorly directed segment passing through the second pedigerous somite has walls about 9 μm thick but the diameter of the lumen remains at 3 μm. In the third and fourth pedigerous somites the wall is thickened and actively secretory. It is in this segment that the spermatophore is formed. This spermatophore sac frequently contains a spermatophore in the process of formation. A fully formed spermatophore is usually present in the dilated ejaculatory duct at the obliquely angled end of the vas deferens.

The spermatophore (figure 64) is about 200 μm long, about 60–70 μm in diameter, and typically slightly curved. Its wall is about 3.5 μm thick and comprises a thin outer integumental layer staining green with Masson's trichrome, and a thicker inner layer staining orange/brown (figure 65). Inside a fully formed spermatophore the sperms are arranged peripherally within a matrix, around a densely staining central core. This appears to be homogeneous but is presumably composed of densely packed Q-bodies (as reported in male *Diarthrodes* by Fahrenbach (1962)) which swell to force out the contents of the spermatophore once extruded. When inside the ejaculatory duct the spermatophore wall at its inner end is continuous with secreted material in the lumen of the vas deferens and this may be drawn out to form a neck on the spermatophore. Naturally extruded spermatophores have not been observed and it is not known whether they possess necks.

The mature spermatophore lies in the ejaculatory duct near the closed genital aperture. The aperture is opened by a short muscle fibre (figure 64, Th6 prm) originating laterally on the body wall at the middle of the somite and inserting proximally on the thickened ventral surface of the sixth leg. As it contracts the anterior part of the sixth leg swings dorsally and the posterior part swings ventrally, opening the aperture.

(iv) *Comparisons with other copepod groups*

In calanoids both sexes possess a single median gonad and a single genital opening. Mature females possess paired oviducts (uteri) which are often sac-like and extend into the anterior regions of the cephalosome. Mature males possess only one vas deferens, usually the left, which may be markedly differentiated into functional regions (Herberer 1932). Female harpacticoids possess a single median ovary and paired oviducts but the genital openings of the female are paired (Fahrenbach 1962) though the mechanism of opening may ensure that both always open simultaneously as in *Benthomisophria*. In harpacticoids the testis is median and has a single vas deferens, most frequently on the left side (in 70% of specimens) but sometimes on the right (Lang 1948*a*; Fahrenbach 1962). Female cyclopoids, poecilostomatoids and monstrilloids usually possess a single median ovary with paired ducts and genital openings which are often dorsal or dorsolateral in position. Males of these groups also usually possess a single testis with paired vasa deferentia and genital openings. In many siphonostomatoids both sexes possess paired reproductive organs, ducts and genital openings, though a single median gonad occurs in some species.

The presence of paired gonads and genital openings clearly represents the ancestral copepod condition. The single median gonad found in members of several copepod groups may represent either the fused paired gonads of the ancestral type, as indicated by the presence of bilateral

ducts and genital openings, or the gonad of one side only, as indicated by the presence of a single asymmetrical duct and genital opening. The occurrence of sinstral and dextral alternatives of the latter condition suggests that it has arisen independently several times. The gross morphology of the copepod reproductive system in both sexes is variable both within and between groups and is highly plastic evolutionarily. Its value in assessing phylogenetic relationships between groups is therefore limited. It can, however, be concluded that the paired system found in misophrioids and members of some other groups represents a retained ancestral condition, as does the poorly differentiated male duct in *Benthomisophria*.

6. The phylogenetic position of the Misophrioida

Misophrioids, like most groups, exhibit a mosaic of ancestral and derived character states but their affinities with other copepod orders have proved difficult to assess as they share few derived features with other orders. This difficulty is reflected by the variety of phylogenetic positions to which the group has been assigned since its discovery by Boeck in 1864. It has been placed in the Calanoida, the Cyclopoida and the Harpacticoida as well as being accorded separate status and equivalent taxonomic rank, as the Misophrioida. Most have subscribed to the view that it represents a distinct and equivalent taxon (Giesbrecht 1892; Gurney 1927; 1933*a*; Lang 1948*a*, *b*; Kabata 1979), though Sars (1903) and Wilson (1932) referred it to the Harpacticoida. Sars (1903) laid great stress on the common possession of a single egg sac in *Misophria* and the harpacticoids as evidence of phylogenetic affinity. As Gurney (1927), and later Lang (1948*a*, *b*), pointed out, this character is variable within the Harpacticoida and has little phylogenetic significance, an opinion reinforced by Gurney's (1933*a*) observation that female *M. pallida* bear '2 to 4 eggs loosely attached to the genital somite but not, apparently, enclosed in a definite egg sac'.

Misophrioids are readily distinguishable from calanoids by the possession of the podoplean division of the body into prosome and urosome, the major articulation being immediately posterior to the fourth pedigerous somite (fifth thoracic somite). Podoplean segmentation is shared by all copepod groups other than the Calanoida. Misophrioids also differ from calanoids in the presence of a pair of legs on each of the first and second urosome somites, and in the bilaterally symmetrical condition of the modified male antennule and male reproductive system. They show a superficial resemblance to some calanoids, such as *Pseudocyclops*, in general facies and in the structure of certain limbs, such as the maxillules, but in view of the fundamental differences in body segmentation these similarities must be due to convergent evolution. The most important character shared by misophrioids and calanoids is the possession of a pulsating dorsal vessel (heart). The structure of the heart in misophrioids is difficult to discern (see §5*e*) but it is poorly developed compared to that of *Calanus* (Lowe 1935). However, it is assumed that it is homologous with that of *Calanus* and represents an ancestral condition retained in both groups. The Misophrioida is the only podoplean group to possess a heart and it is upon this character more than any other that its separation from the other podoplean orders has been based. Supplementary characters have also been used: misophrioids differ from harpacticoids in the relatively large number of antennular segments (misophrioids have 16–18, harpacticoids never more than 10); they differ from cyclopoids in the condition of the antenna (misophrioids have both rami well developed; cyclopoids typically have a reduced exopod).

This study has revealed several new characters that serve to separate misophrioids from all

other copepod groups. The presence of a carapace-like posterior extension of the cephalosome enclosing the first pedigerous somite is unique to the misophrioids. It is suggested that this structure has evolved secondarily in association with opportunistic macrophagy. It is unlikely to represent an ancestral condition lost in all other groups though it does indicate the presence of a potential within crustaceans for the independent evolution of carapaces and carapace-like structures, as suggested by Hessler (in Hessler & Newman 1975). The absence of the nauplius eye at all stages of the life cycle of misophrioids presumably represents the primitive condition of the ancestral misophrioid stock and is another diagnostic character. Its loss by the free-living ancestral misophrioid stock may be interpreted as evidence for a bathypelagic origin of this group. This interpretation is supported by the presence, in the littoral and sublittoral *Misophria*, of the carapace-like structure, here regarded as an adaptation to the typically bathypelagic feeding strategy of opportunistic macrophagy. Indeed, the gut of *M. pallida* is less distensible than that of *Benthomisophria* species and transverse sections show that there is relatively much less room available within the cephalosome of this species for expansion of the gut. One may therefore speculate that the carapace-like structure in *Misophria* is largely vestigial.

The presence of functional antennary glands and the absence of maxillary glands in adult misophrioids is unusual. The antennary gland is the functional excretory organ in the nauplii of calanoids (Grobben 1881), cyclopoids (Hartog 1888) and harpacticoids (Fahrenbach 1962) but is lost in the adults, whose functional excretory organs are the maxillary glands. This neotenic retention of the antennary gland in the adult is, to my knowledge, unique within the Copepoda.

Finally the misophrioid life cycle is different from that of free-living representatives of other copepod groups. Free-living calanoids (Marshall & Orr 1955), harpacticoids (Thia-Eng 1975), poecilostomatoids (Gibson & Grice 1978) and cyclopoids (Oberg 1906) commonly have six naupliar stages and this appears to be the ancestral copepod number. This number is reduced to five in some free-living cyclopoids (Gurney 1933*b*). The presence of just a single nauplius in the life cycle of the Misophrioida (Gurney 1933*a*) is therefore highly unusual. Perhaps more significant is that the misophrioid nauplius is of the lecithotrophic type (yolk-filled and possessing more simply constructed limbs than those of the planktotrophic type). The possession of a lecithotrophic nauplius is typically associated with parasitism or symbiotic relationships in copepods and is common to many parasitic poecilostomatoids and cyclopoids and to the siphonostomatoids. Some parasitic copepods with lecithotrophic nauplii still possess a large number of naupliar stages, five in the cyclopoid *Notodelphys affinis* (Dudley 1966), but in many the number is reduced to two, typical of most siphonostomatoids (Boxshall 1974), and in a few the nauplius phase of development is lost altogether (Kabata & Cousens 1973). A reduction in the number of stages in a form possessing a non-feeding lecithotrophic nauplius is readily understandable. The adoption of this strategy by misophrioids can be interpreted as further evidence of their bathypelagic origin as it is typical of many bathypelagic forms.

The possession of several unique characters in combination with ancestral features indicates that the misophrioids represent an ancient lineage with a long history independent of the main podoplean line. This would appear to justify their separation at the ordinal level, as the Misophrioida. Having established this independent status it is necessary to determine affinities. The phylogenetic scheme relating the copepod orders proposed by Kabata (1979) is largely adopted here. Additionally the order Mormonilloida is recognized as an independent branch from the podoplean line (Boxshall 1979).

The unique features of misophrioids are of little help in assessing interordinal affinities within the podoplean line; neither are the relatively primitive features such as the possession of gnathostomatous mouthparts, as these are retained in at least three other orders (Harpacticoida, Cyclopoida and Mormonilloida). There are, however, a few shared derived characters that can be used although most belong to evolutionary trends involving loss or reduction of appendages or segments, as is common in many other crustacean groups, and these provide poor evidence of affinity. More reliable is the common possession of a derived state of a complex system comprising many integrated parts. After considering the whole suite of characters exhibited by misophrioids the only complex system of this nature identified was the double genital antrum of the adult female. This oviposition system is found in *Benthomisophria* and *Diarthrodes*, a harpacticoid (Fahrenbach 1962), but not in any other copepod groups, although few have been studied in sufficient detail for reliable comparisons to be made. On this basis alone the Harpacticoida are here regarded as the sister group of the Misophrioida and these lineages and their common ancestral stock comprise the sister group of the line leading to the remaining podoplean groups. Establishing relationships between taxa on the basis of a single character, albeit a complex one, is far from ideal and the affinities of all podoplean orders should be reassessed continually as more anatomical information becomes available. In particular the oviposition system and the functional morphology and anatomy of the mandibles and maxillules, the most diverse of the cephalic appendages, would appear to be promising areas for study.

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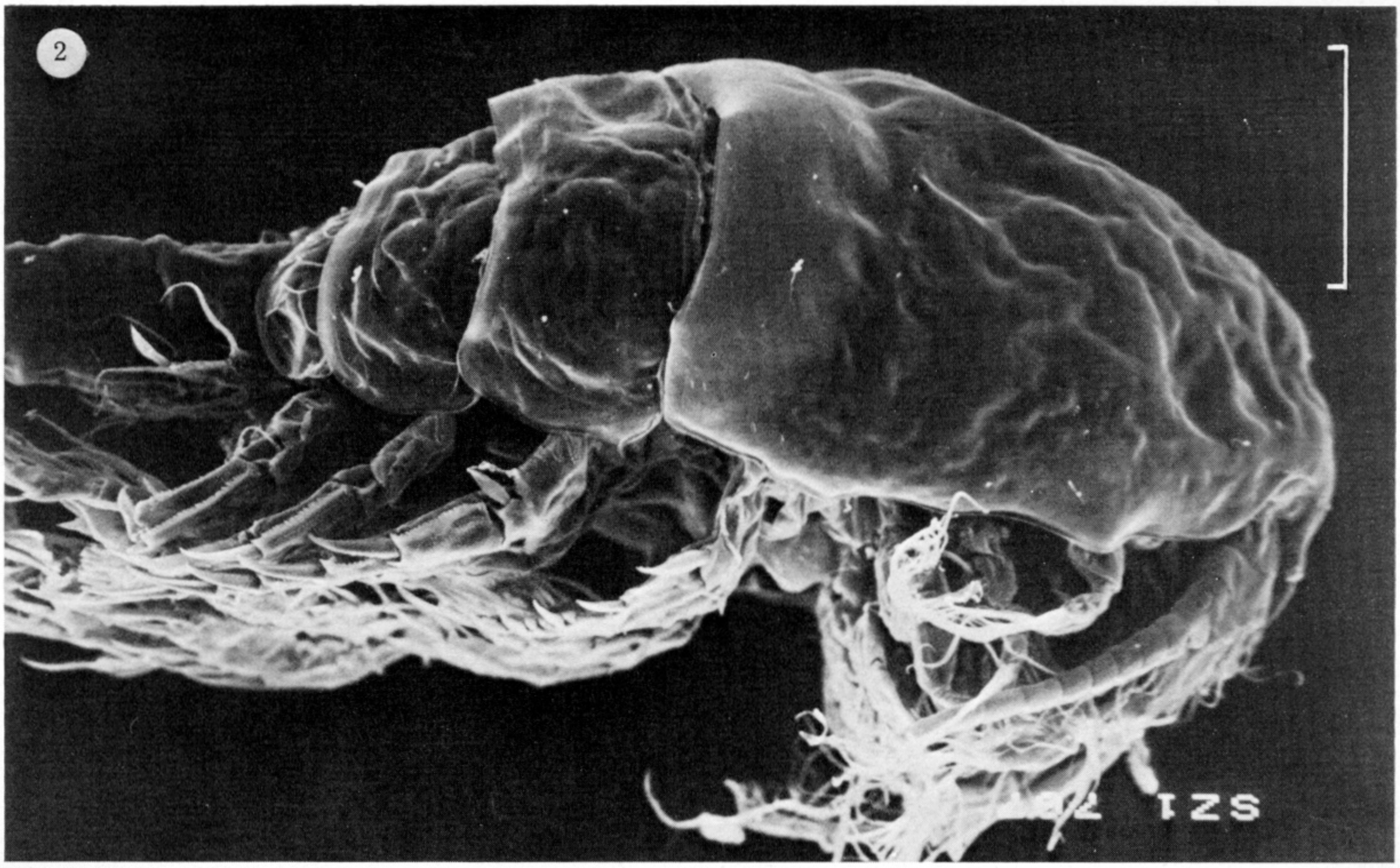
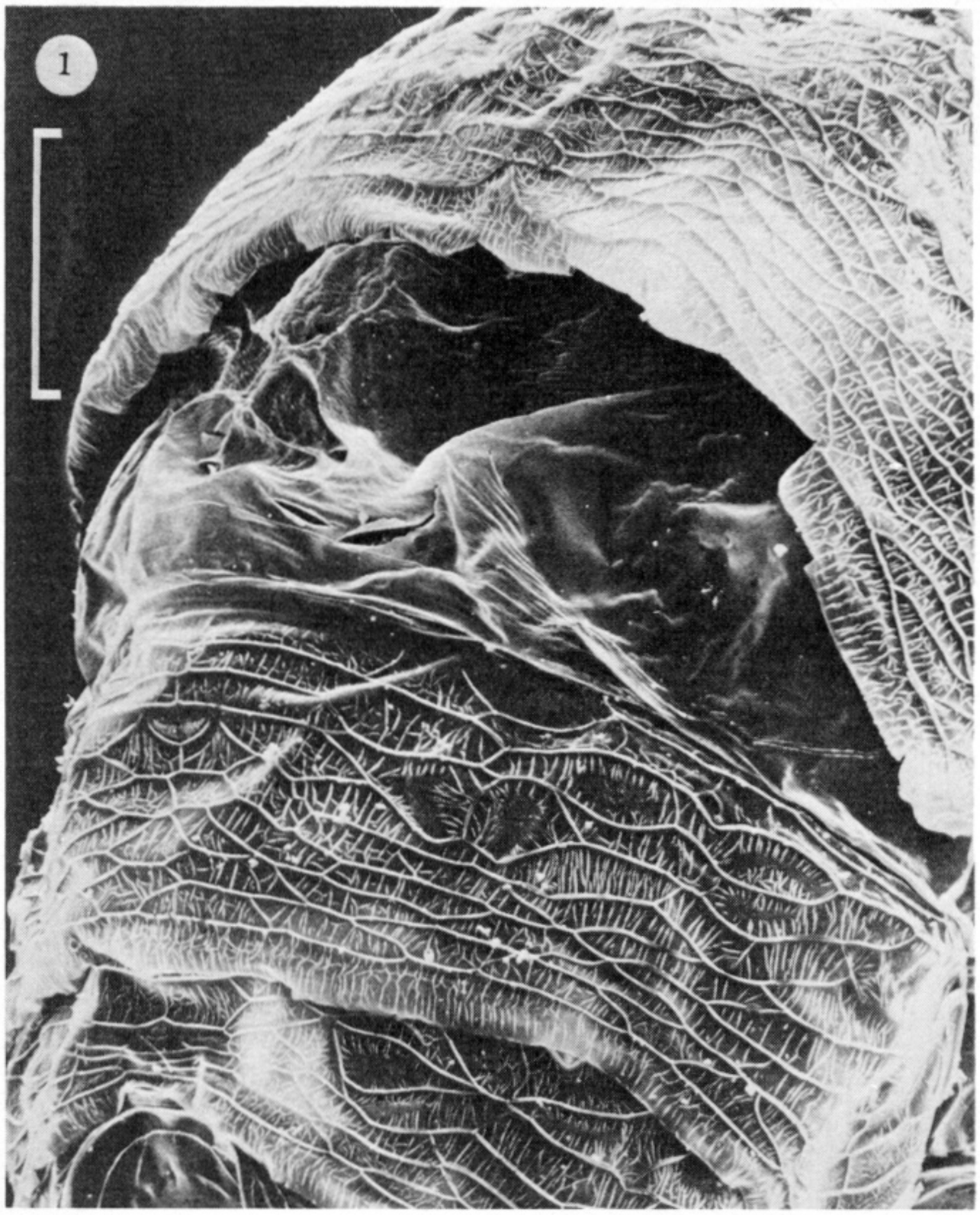




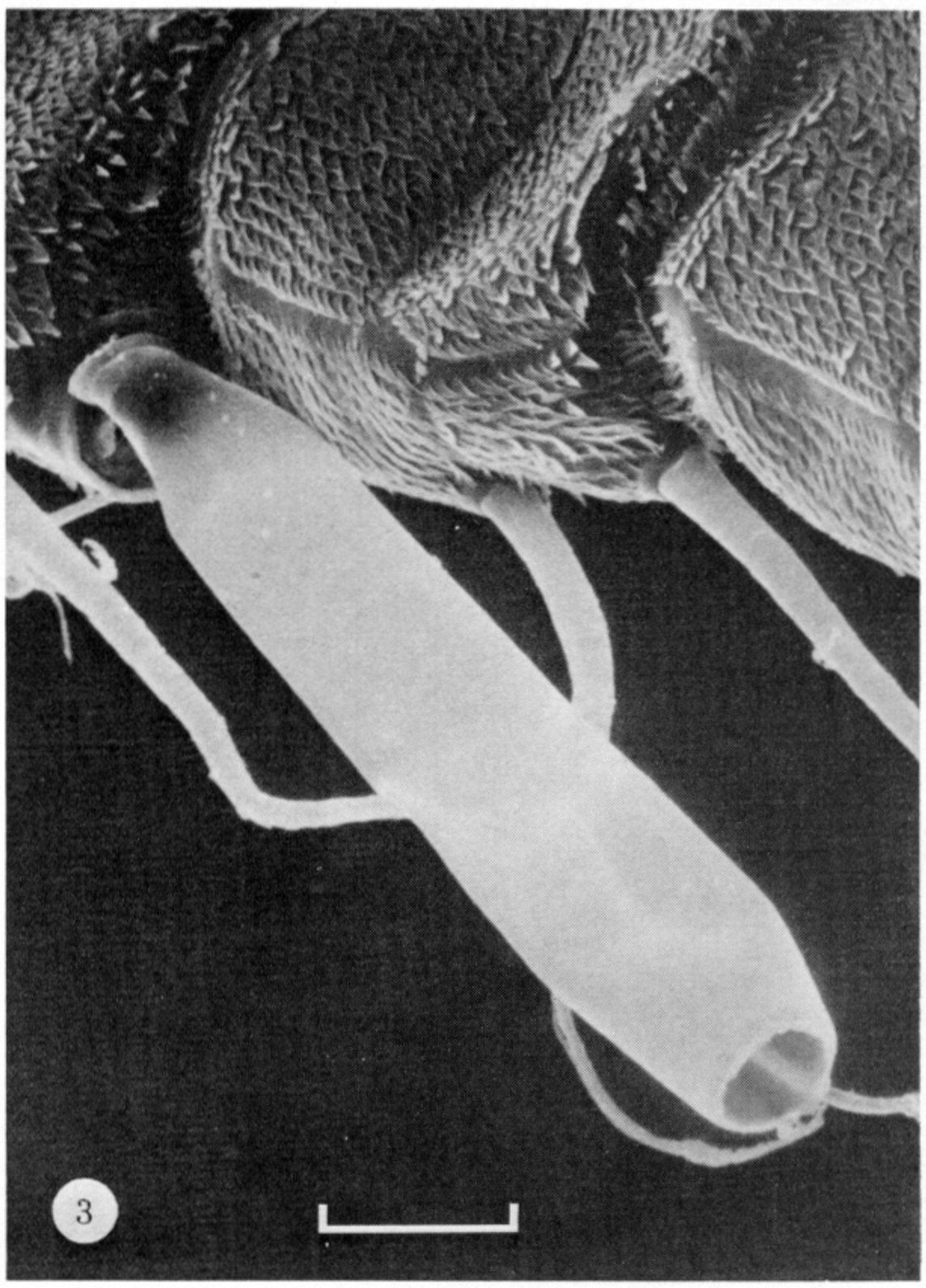
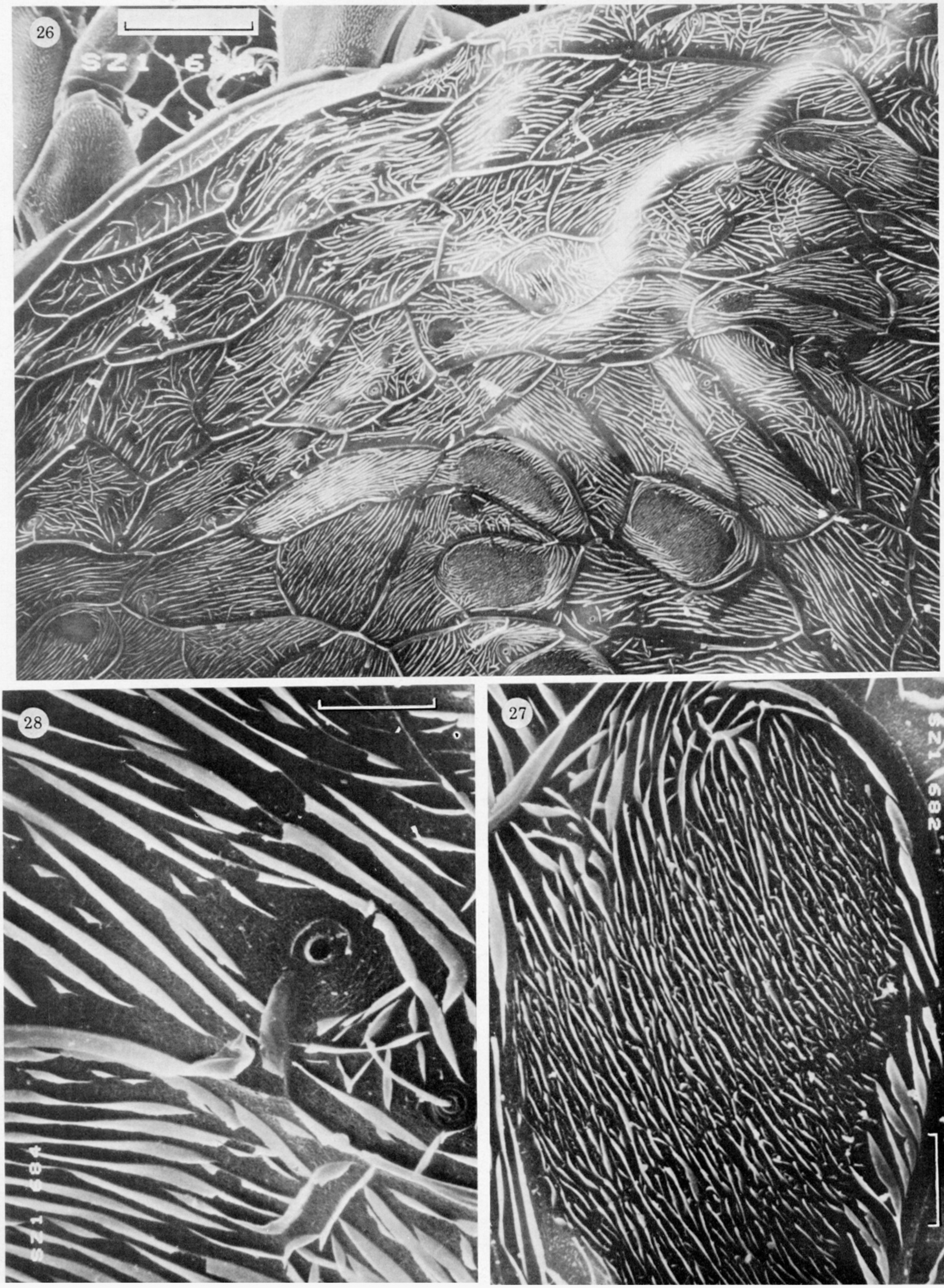


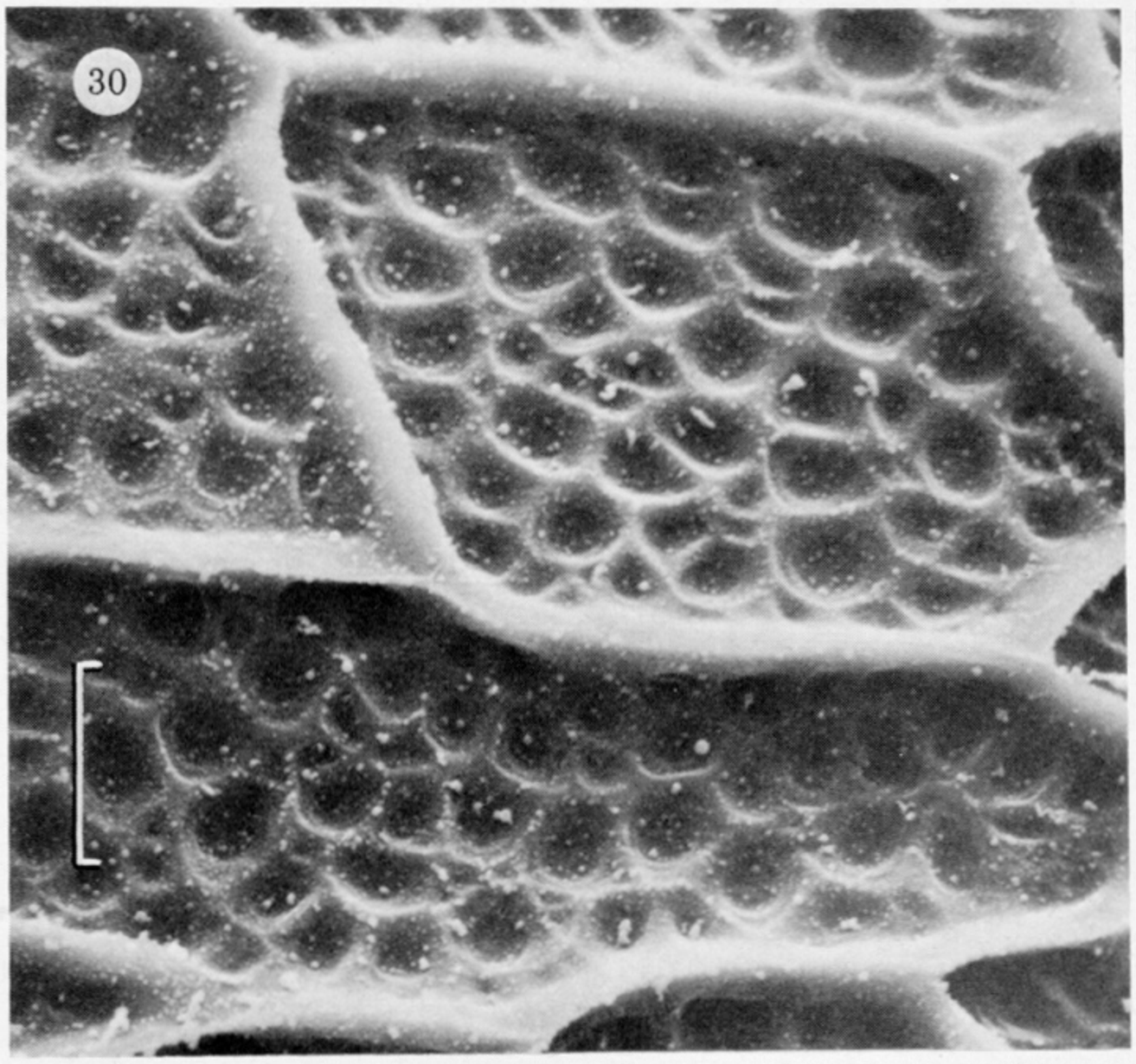
FIGURE 1. Dorsolateral view of the midprosome of a distorted *B. palliata*. The ornamented carapace-like extension of the cephalosome is raised, revealing the smooth integument of the first pedigerous somite, which it normally encloses. The ornamented tergites of the second and third pedigerous somites can also be seen. Scale bar 300 μm.

FIGURE 2. Lateral view of female *M. pallida*. The carapace-like posterior extension of the cephalosome appears as the light, raised area. Scale bar 100 μm.

FIGURE 3. Aesthetasc on the antennule of a female *B. palliata*. Scale bar 20 μm.



FIGURES 26–28. For description see opposite.



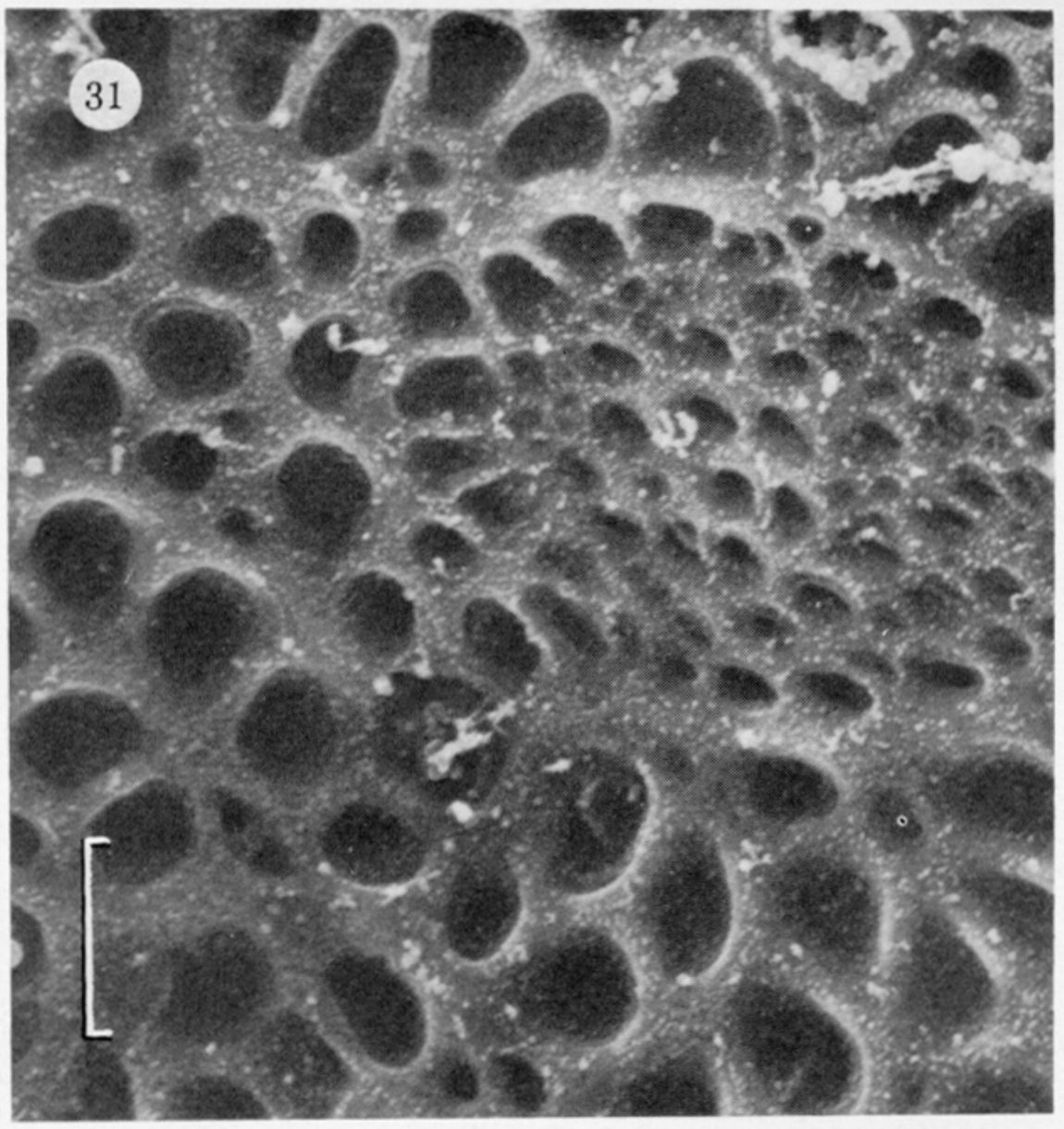
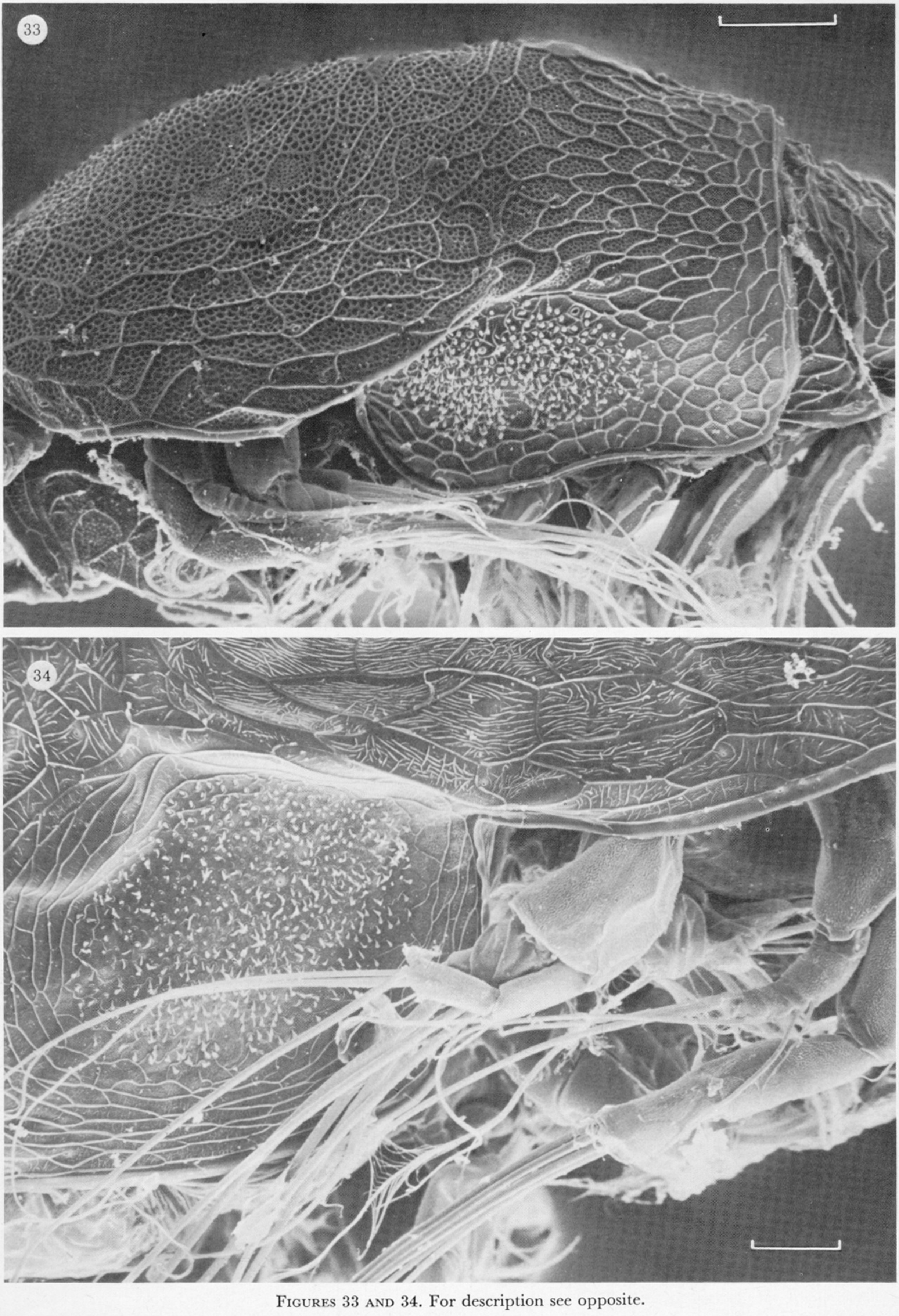


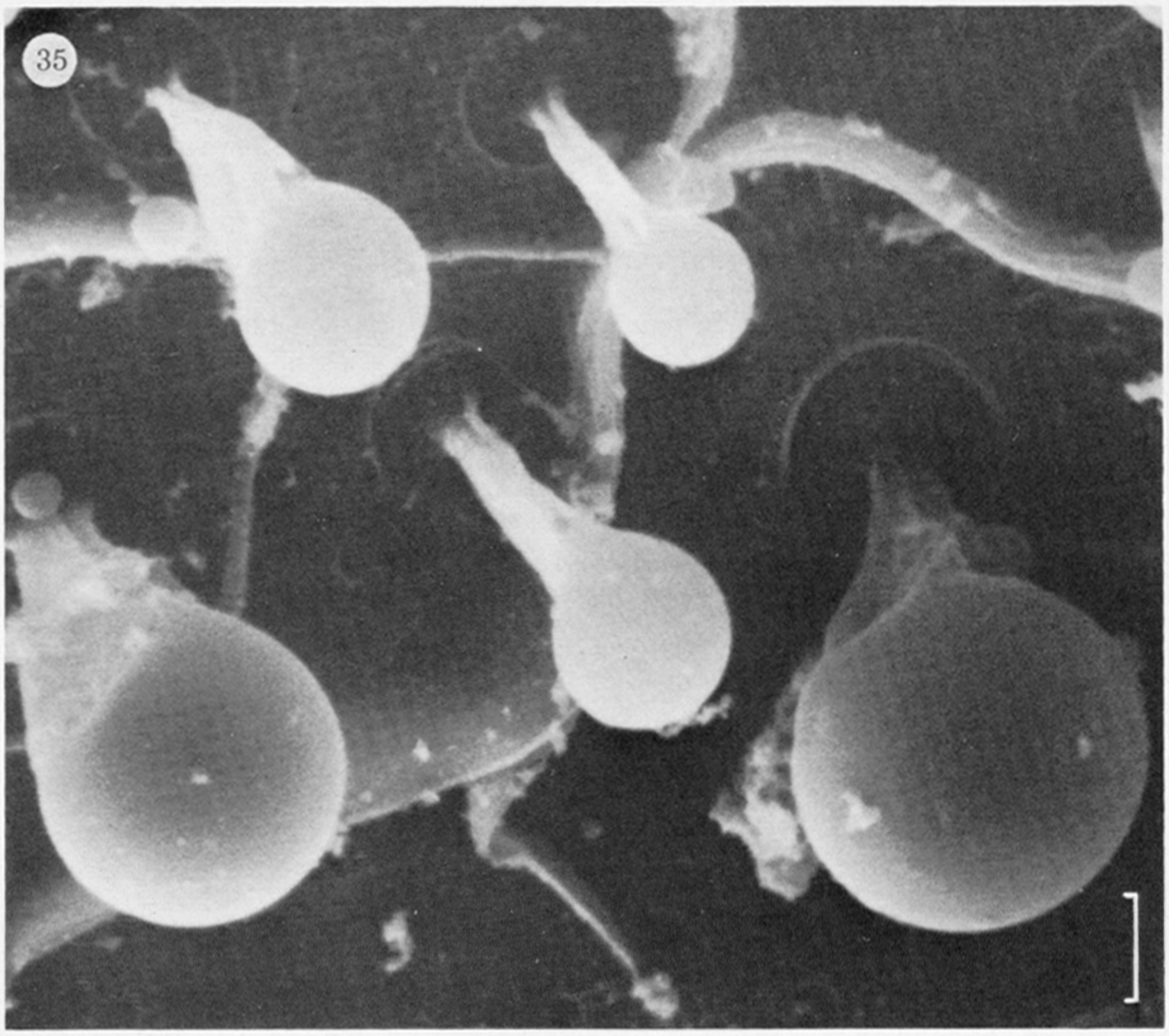
FIGURE 30. Detail of surface ornamentation on cephalosome of *B. cornuta*. The system of ridges delimits areas containing numerous surface pits. Scale bar 10 μm.

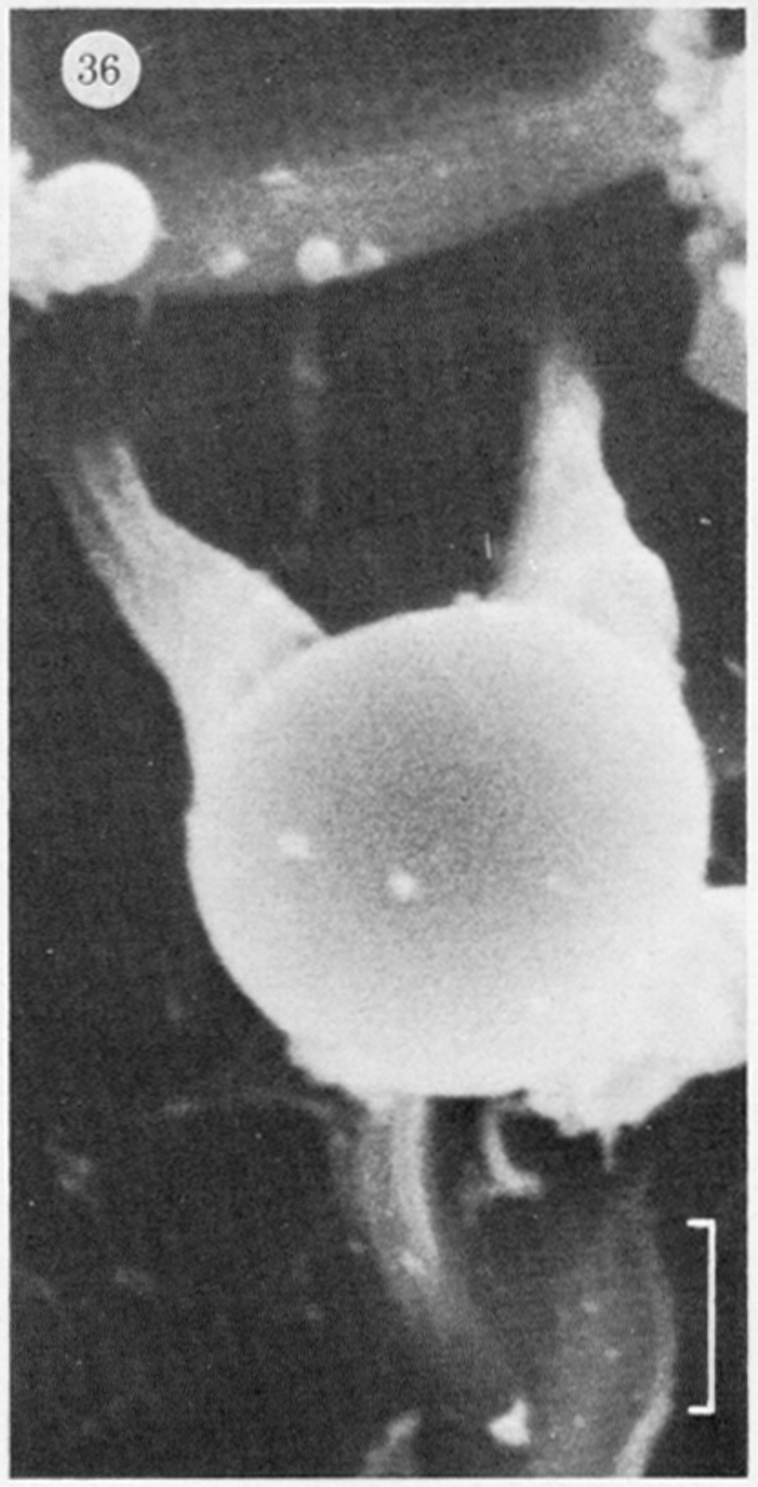
FIGURE 31. Detail of surface ornamentation on cephalosome of *B. cornuta* marking the site of origin of a dorsal longitudinal trunk muscle fibre by the presence of smaller, densely packed pits. Scale bar 10 μm.

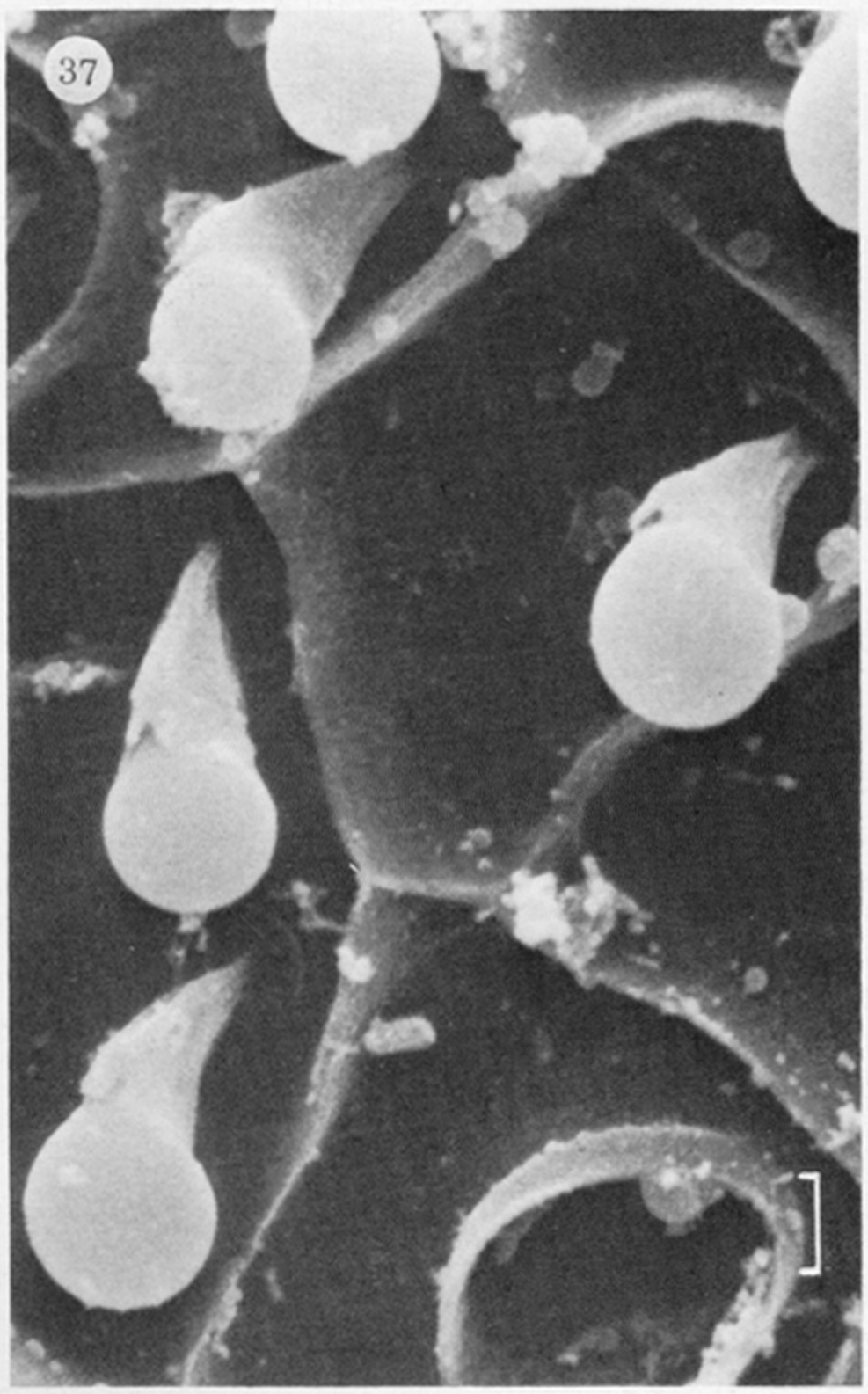
FIGURE 32. Lateral view of the pleural region of second to fourth pedigerous somites of *M. pallida*. The poorly developed surface ornamentation of fine lamellae can be seen. The positions of oar-shaped sensillae are marked by arrows. Scale bar 10 μm.

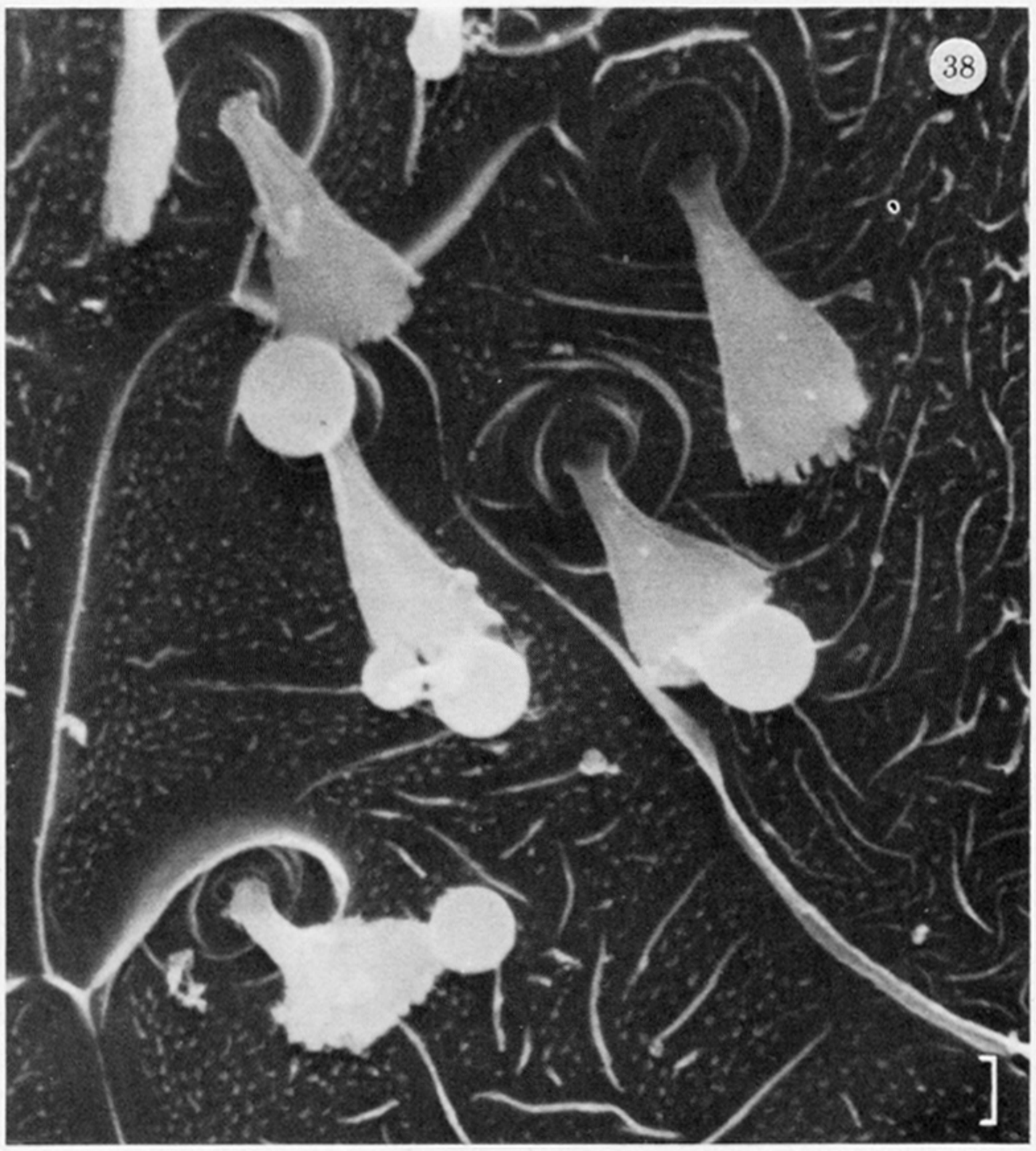


FIGURES 33 AND 34. For description see opposite.









FIGURES 35–38. For description see facing plate 4.

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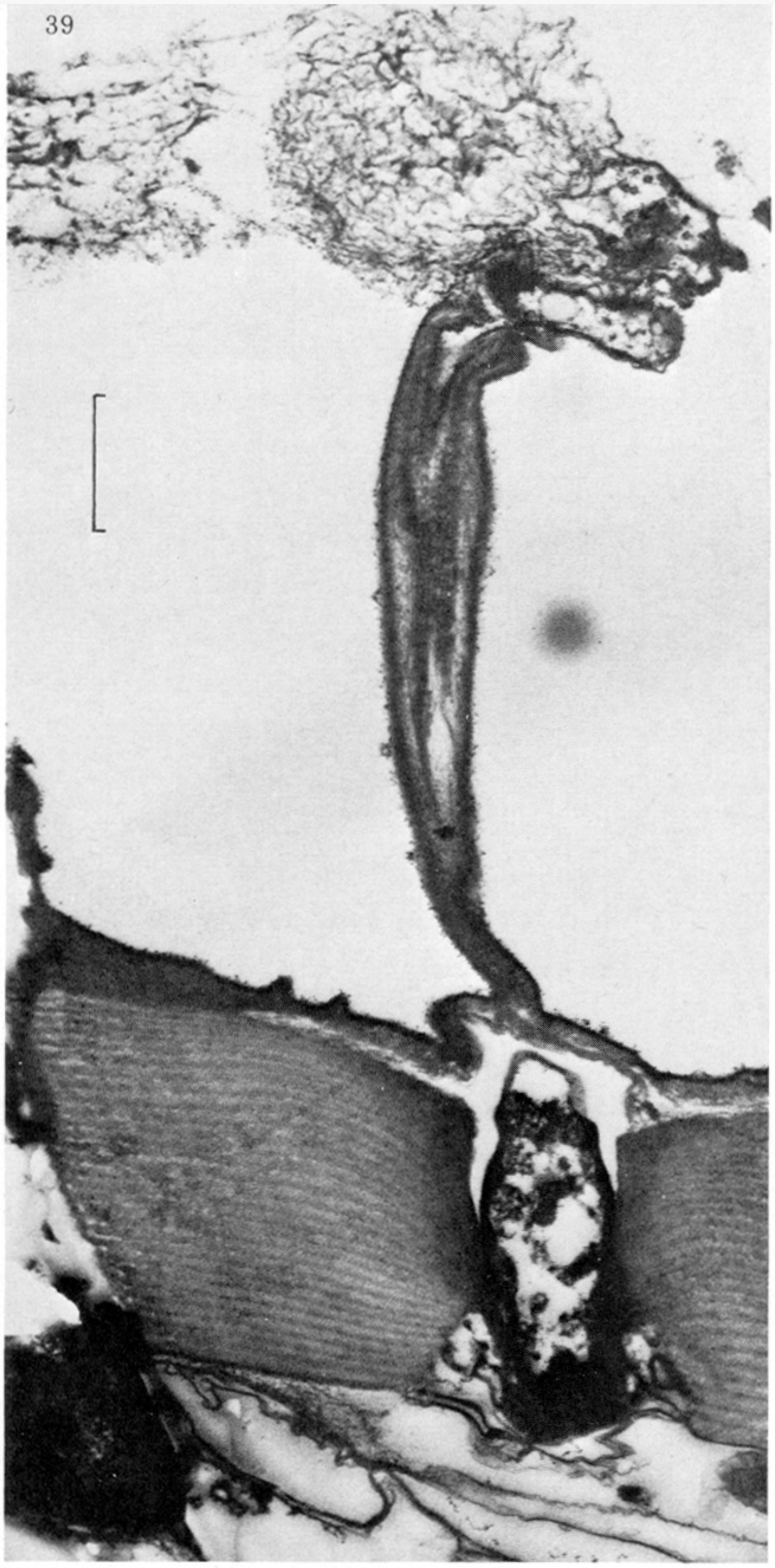

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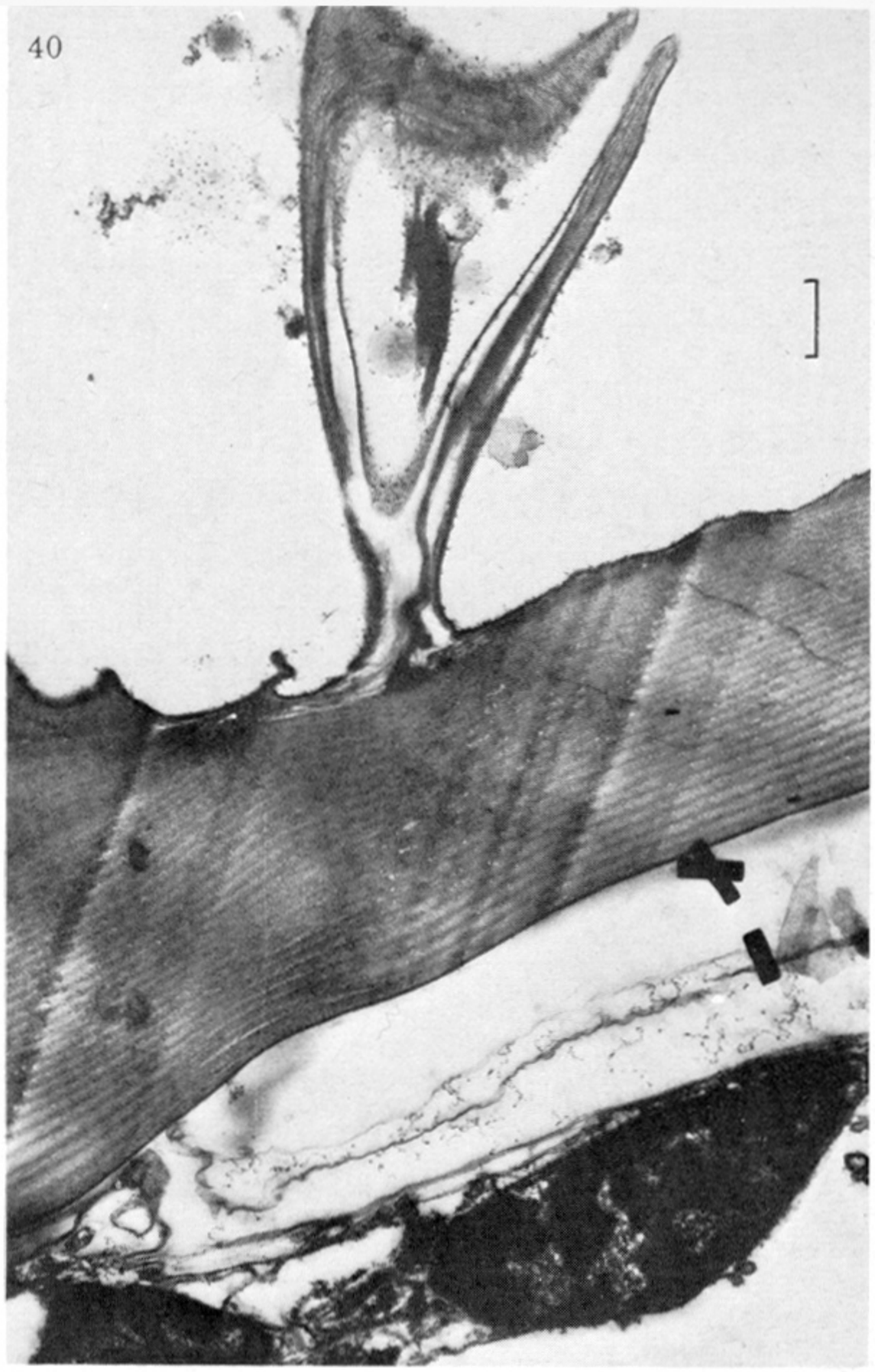

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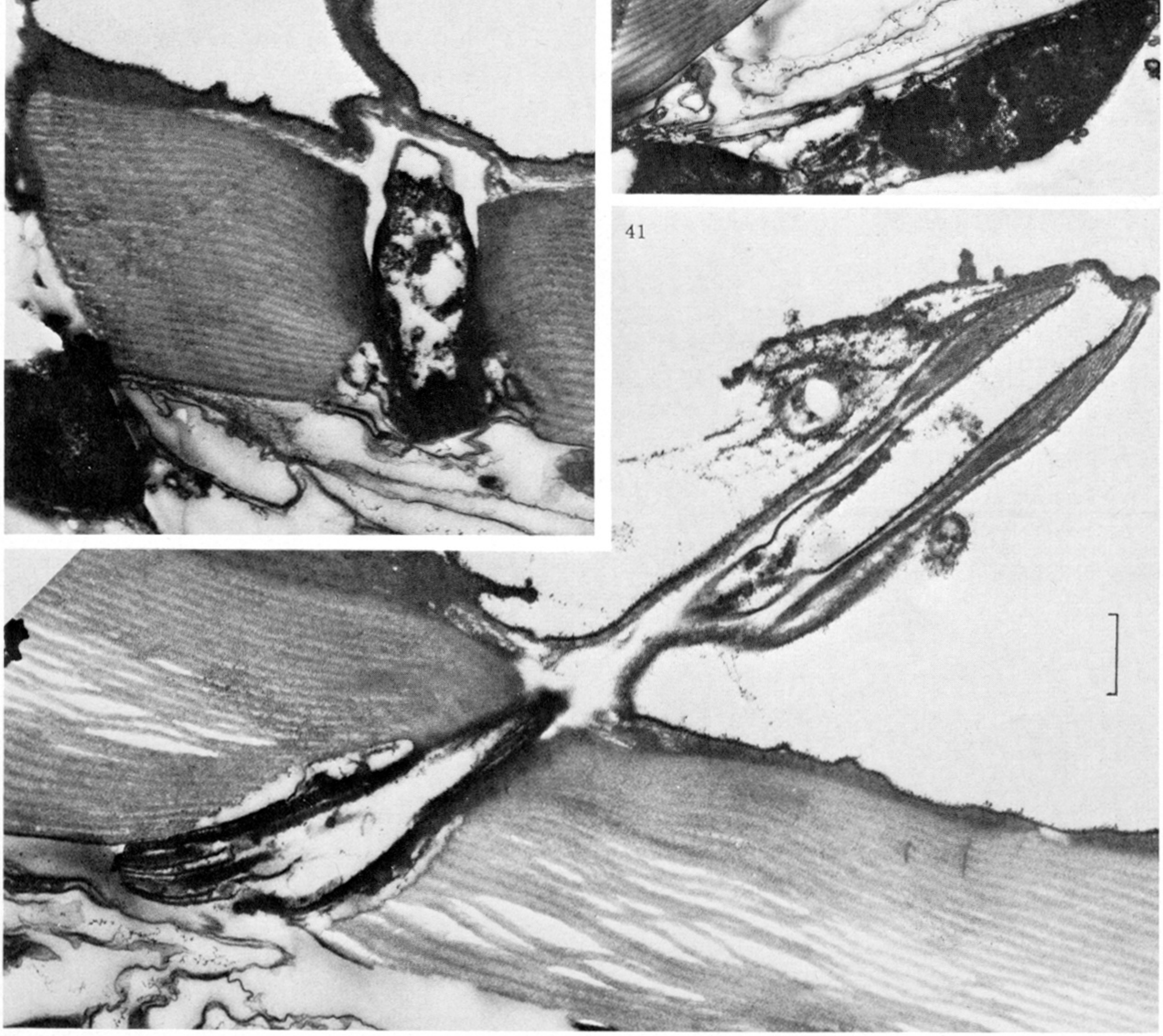
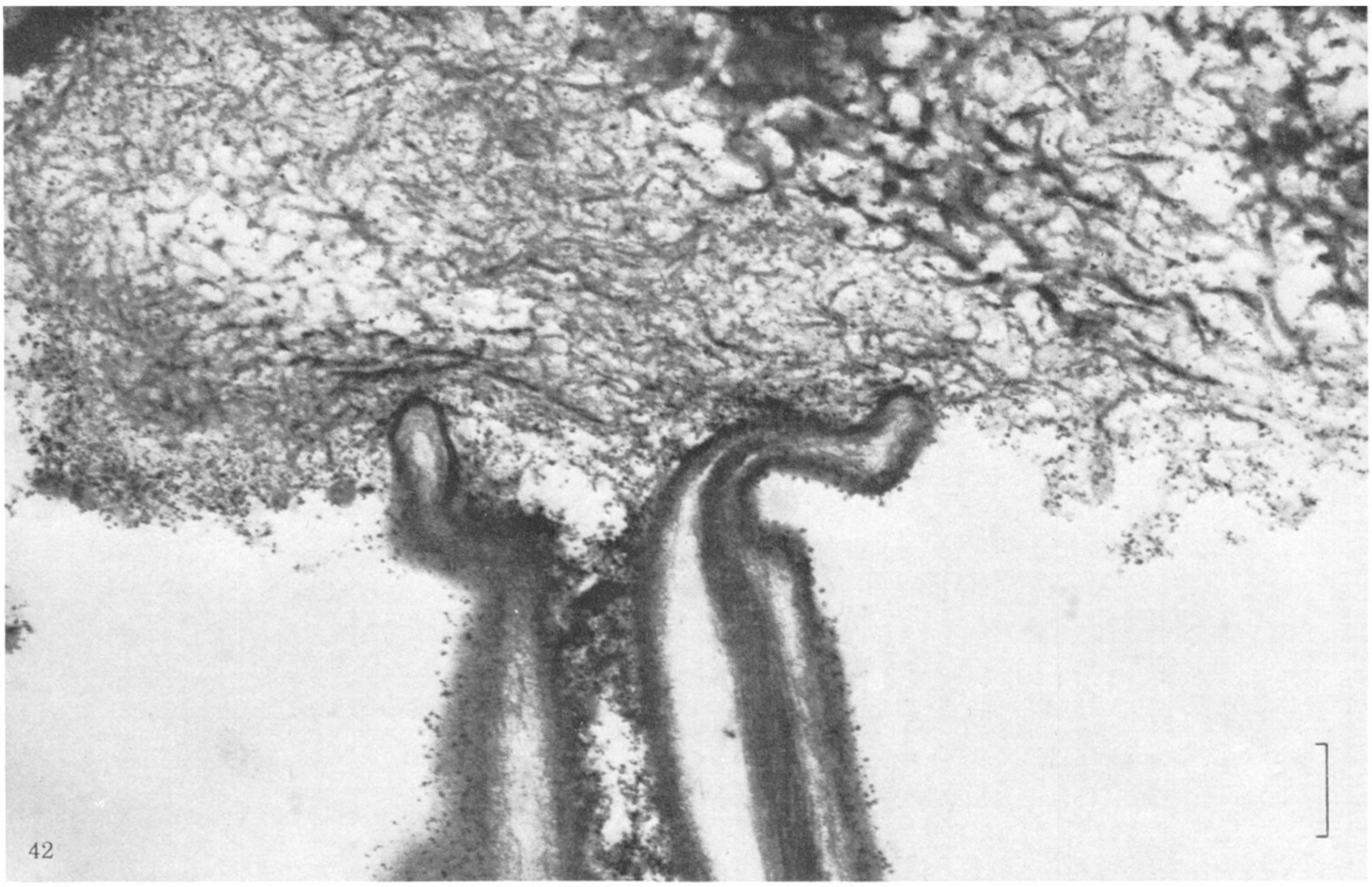
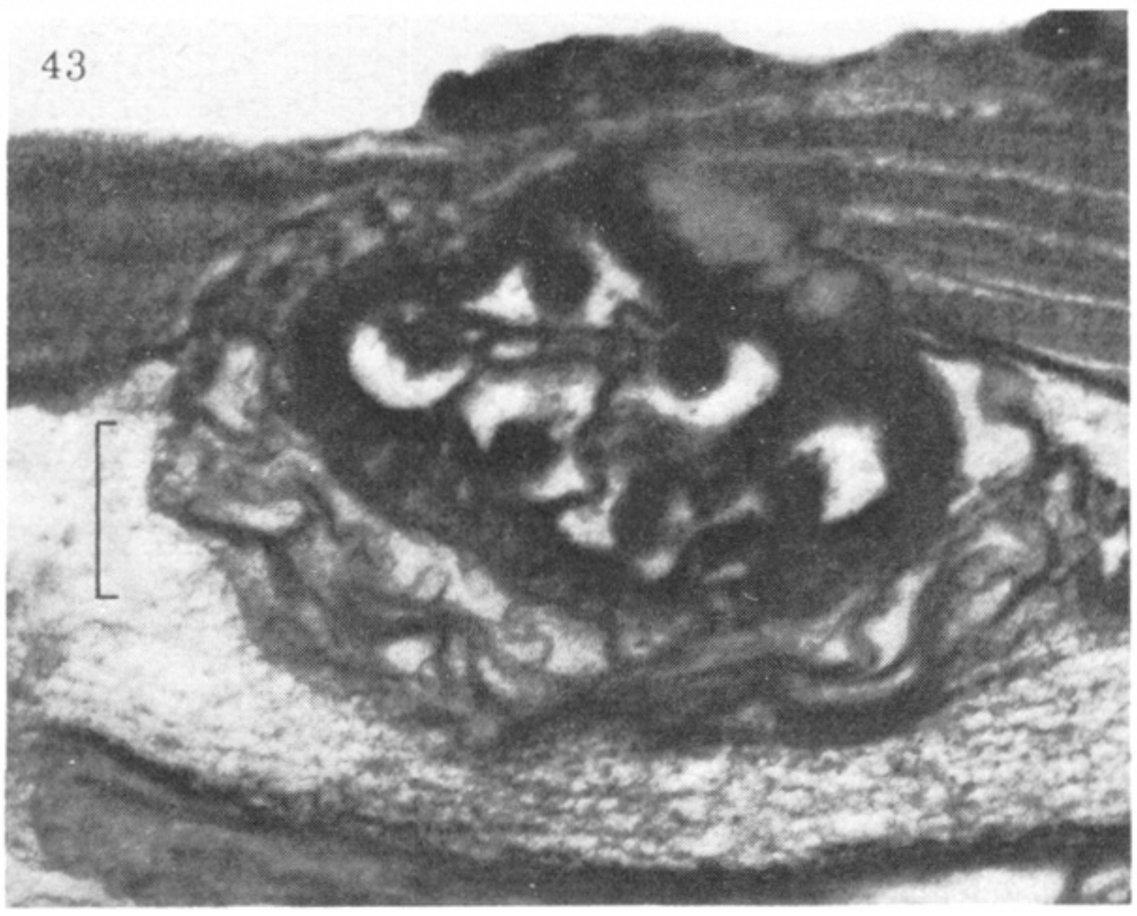
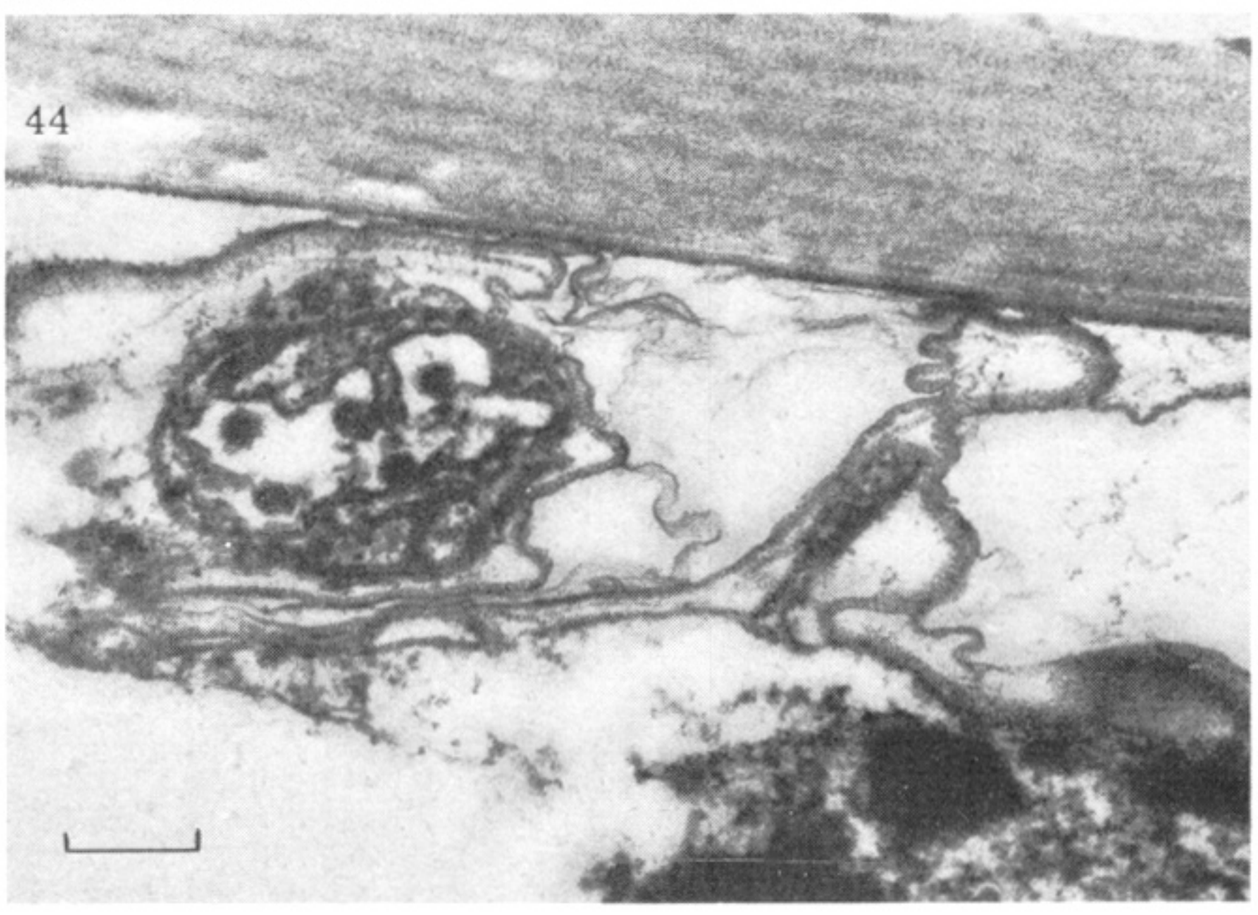
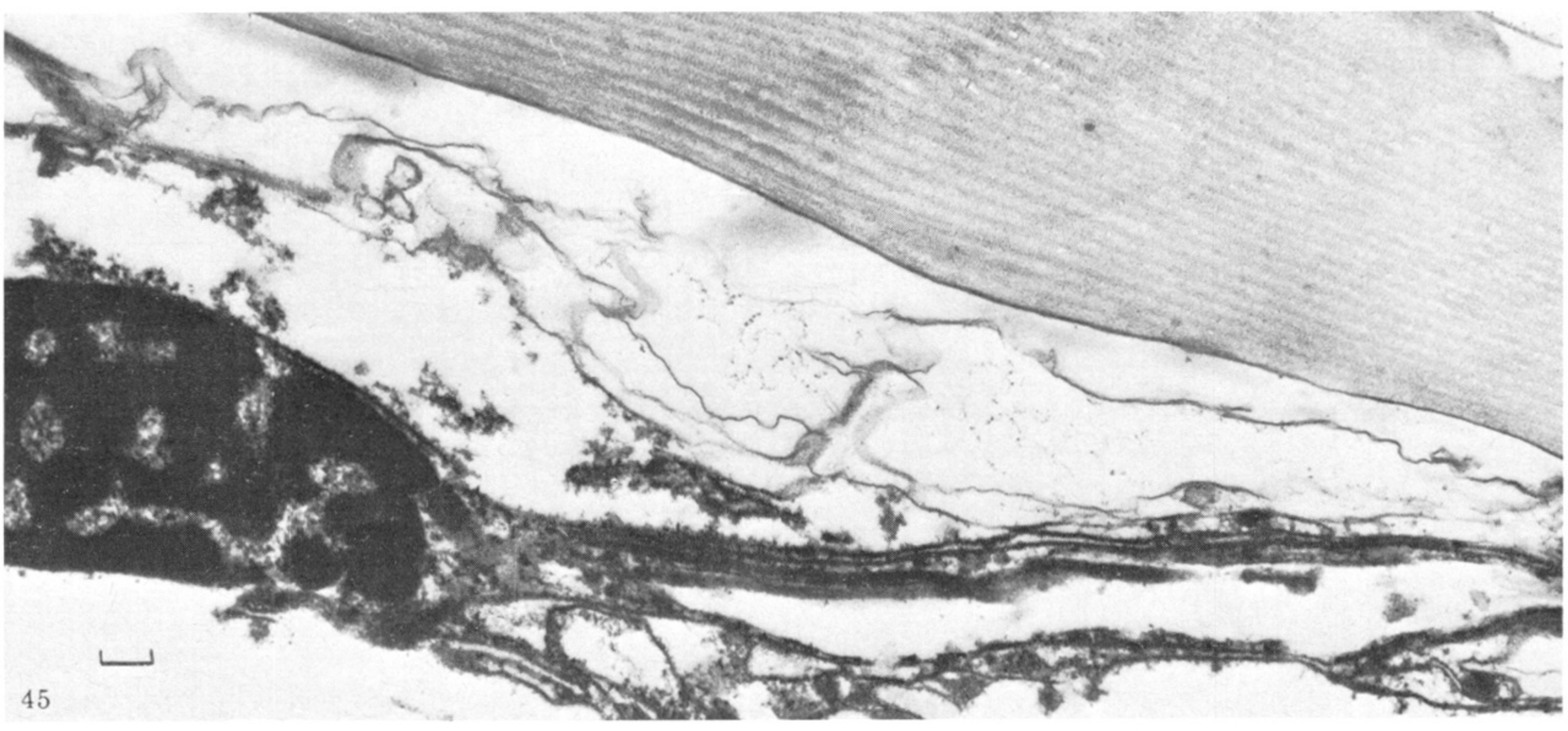


FIGURES 39–41. For description see facing plate 4.









FIGURES 42–45. For description see opposite.

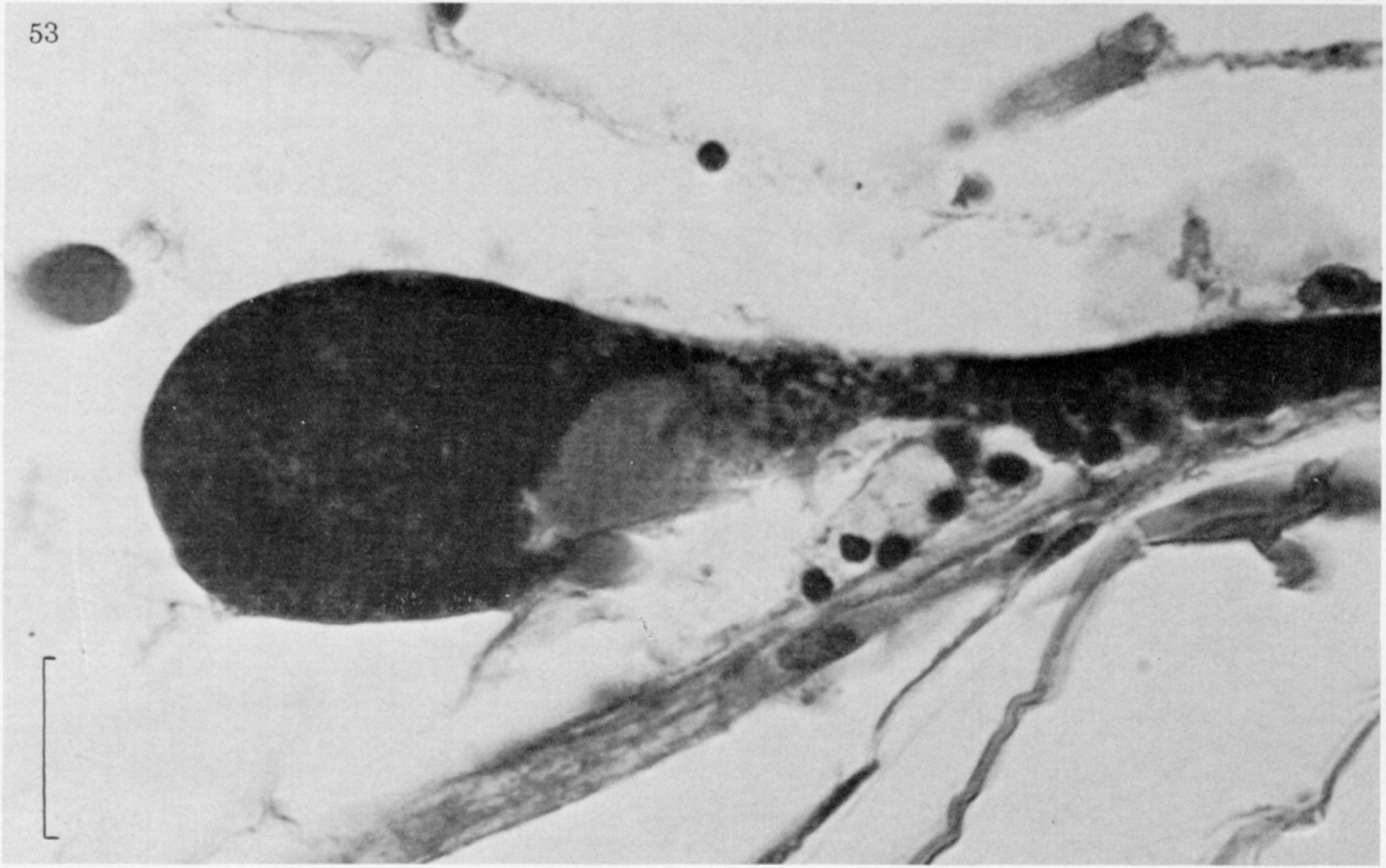


FIGURE 53. Section through the coelomic vesicle of the antennary gland of an adult *B. palliata*. The granular nature of the contents of the vesicle and funnel is apparent. Scale bar 25 μm.