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FUNCTIONAL ONTOGENETIC CHANGES IN *BRANCHINECTA FEROX* (MILNE-EDWARDS) (CRUSTACEA: ANOSTRACA)

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[Plates 1–12; outrigger]

CONTENTS

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

The development of the anostracan *Branchinecta ferox* is described in a manner that emphasizes how functional continuity is maintained from the earliest nauplius (1) (length generally < 0.5 mm) to the large adult (length at least 45 mm).

The first nauplius subsists on yolk. Feeding begins at stage 2(2). Morphological specializations of the stage 2 nauplius include the use of a posteriorly located gnathobasic spine on each mandible, a purely naupliar feature, as the sole means of sweeping food particles forward between the mandibles (8, 9). The gnathobasic spines lie across the molar faces which, even if they were sufficiently developed, are therefore debarred from participation in food handling. The self-same mandibular mechanism, based on sweeping and rolling, as persists throughout life is employed. This specialization is restricted to one instar only; at stage 3 the gnathobasic spines no longer lie across the molar surfaces, which are now functional and operate in essentially the same manner as they do throughout life, but at this stage with few of the later refinements. The gnathobasic spines, however, remain as a conspicuous feature of the naupliar mandible (10) and assist the gnathobases throughout the early post-naupliar stages. They persist until an almost complete set of functional trunk limbs has been acquired.

The hitherto little-known anatomy of anostracan nauplii has been elucidated, particularly in stages 3 and 4, and is described and illustrated in detail (12–19). Particular attention is given to the complex skeleto-muscular system, whose arrangement is intimately related to locomotion and feeding. Both these activities are analysed.

Locomotion is powered entirely by the antennae (20). Because the nauplius is small it inhabits a viscous medium: a low Reynolds number environment. It therefore has no momentum and in effect levers itself through the water with the antennae, whose tips, although having a wide amplitude of beat, actually swing posteriorly for only a short distance during a cycle of movement (21, 22, 24). In the early naupliar stages the return movement of the antennae actually causes the animal to move backward slightly at this phase of the cycle (20, 21). The antennal musculature is described (26).

The exopodite spines of the antennae have a purely natatory function. They are not concerned with food collection as some have contended. The antennae are provided with specialized food-collecting spines, the distal masticatory spines (2, 5), which extract particles from suspension as the antennae beat with a frequency exceeding 5 cycles per second at room temperatures. These spines carry food particles to the vicinity of the labrum (20, 25). The labrum is provided with three sets of labral glands whose secretions, stored in conspicuous reservoirs (16, 18, 19), are discharged in a convenient position for entangling collected food particles. The distal masticatory spines are cleaned by setae of the mandibular palps (6) – transient naupliar features – as they leave the vicinity of the labrum (20). Stout, mobile, proximal masticatory spines, located near the base of each antenna (2, 12, 16, 17), sweep material forward to the mandibles. These spines are brush-like from the first feeding stage (nauplius 2) (4), and are bifid from stage 3 (12) until they cease to function at the time the full complement of trunk limbs becomes active. The mandibles pass food to the oesophagus.

Post-naupliar development is anamorphic and very gradual. Twenty instars have been identified before the acquisition of a full complement of functional trunk limbs at stage 21 (27). Maxillules and maxillae are added to the mouthparts, and trunk limbs are gradually incorporated into the locomotory/feeding mechanism, usually at the rate of one pair per instar. Such incorporation initially supplements the naupliar mechanism which continues to function until the adult mechanism is fully developed, but different naupliar elements cease to operate at slightly different times (27). There is no simultaneous development of the first six pairs of trunk limbs as has been claimed for *Artemia*, and no sudden cessation of operation of the naupliar mechanism when six pairs of trunk limbs have become active. Just before the adult system takes over, an almost complete adult mechanism and a naupliar mechanism operate hand in hand.

Various aspects of development from the nauplius to the adult are examined, particularly from a functional standpoint, beginning with some consideration of segmentation and early differentiation (28–31).

With the assumption of the adult condition, naupliar devices either are lost, as in the case of the mandibular palps, or are transformed, as in the case of the antennae which lose their role in both food handling and locomotion. The antennary glands, a conspicuous feature of the naupliar stages (14, 17, 19), also degenerate to be replaced by the maxillary glands of the adult.

Development of the posterior mouthparts (12, 16, 32–34) and of the trunk limbs (33, 35, 36) is described. All these appendages become functional before they achieve the adult condition. Concomitant changes in body form occur as size increases, and the development of other structures, such as the telson (38–41), are noted.

In order both to understand functional aspects of the adult and to make intelligible the processes involved in its development, it is necessary to have an understanding of the adult skeleto-muscular system. Its thoracic elements are therefore described in detail, particularly with reference to young adults in which the muscles, being less massive than in large individuals, are less congested (42–50, 57, 61, 62, 65, 70). Although the skeleto-muscular system is complex, its general pattern, which is metamerically repeated in the thorax, can be relatively easily appreciated from illustrations. The development of the muscles is reported (29, 30, 35).

The role in the adult of the hitherto little-studied endoskeleton is made clear and the salient features of its development from the early naupliar stages are reported. The nauplius already has a delicate, but complex, endoskeleton on hatching. This gradually extends backwards as an endoskeletal sheet (71) and establishes links with the developing thoracic endoskeleton (47–50). The latter first makes its appearance as a series of intersegmental tendons (28–30) whose subsequent fate is traced. They eventually give rise to a series of struts and sheets (42–46, 49, 57, 61, 62, 70) intimately integrated with the muscles.

Besides the major elements of the endoskeleton there are many fibrils and tendon-like sheets, used for suspending or anchoring organs, or load-spreading, as well as fibrils with contractile ends which presumably operate antagonistically to the hydrostatic pressure of the haemocoelic fluid. Examples are illustrated (54–56, 58–62, 65–70, 83).

True filter-feeding (as opposed to particle-sieving by the nauplius) begins to be practised for food collection as the trunk limbs gradually come into service. Aspects of this process in the early post-naupliar stages are described and certain points concerning filter-feeding in young adults are discussed.

The trunk limbs beat with a metachronal rhythm. The sequence within the series, and the cycle of motion of a single appendage, are described (76–78), previously unreported subtleties of these processes being reported. Notwithstanding claims to the contrary, made for other anostracans, no forwardly directed current appears to flow in the food groove. Food is moved forward mechanically by the tips of the proximal gnathobasic setae which, from an early stage of development, are specialized for this function (36, 79, 84, 95–98).

The feeding mechanism of young adults is briefly described. Contrary to certain statements in the literature, the maxillules and maxillae, especially the former, while small, are not vestigial. The maxillules fulfil a vital role in transferring food to the mandibles from the region to which it is swept by the gnathobases of the first trunk limbs.

While much food consists of suspended particles, material is also scraped from substrata by means of denticulate spines of the trunk limb endopodites (122–126). But this means large amounts can sometimes be collected quickly.

Certain glands, located near the base of each trunk limb, and others in the gnathobases of the limbs, are briefly described (79).

Filter-feeding by means of finely spaced filtering setules on the trunk limb filter setae continues until the animal attains a length of about 18 mm. Subsequently, over a very small number of moults, the endite armature of the trunk limbs is transformed. The finely spaced filtering setules (84–89) are replaced, first by somewhat more widely spaced setules (91), then by stouter, much more widely spaced structures which make up a coarse grid (92–94), and are finally lost entirely (99–101). These changes are accompanied by a drastic change in feeding habits. Hitherto a feeder on algae and particulate detritus, *B. ferox* becomes a carnivore. In at least one area in the Middle East the food consists largely of the calanoid copepod *Arctodiaptomus similis*, but the cladoceran *Daphnia atkinsoni bolivari* and other prey are also eaten. Transformation of the entire armature is accompanied by changes in the endopodite spines which lose their scraping function (128–138).

Concomitant changes take place in the labral glands. In the filter-feeding adult stages there are three sets of glands, the direct descendants of those of the nauplius, each with its own secretion-filled reservoir and exit duct (83). These degenerate after the animal has ceased to filter, and no secretions are produced from this source in large carnivorous individuals.

The trunk limbs of the post-filter-feeding stages, armed medially by the now stout endite spines, make up a median cage (133) into which prey is sucked by currents set up as in the filter-feeding stages. Such prey is forced into the food groove and passed forward mechanically by the stout gnathobasic spines (112–120), thence, via the maxillules, to the mandibles as in the filter-feeding stages. No forwardly directed current in the food groove is involved. The last pair of trunk limbs, which differ from the rest (133, 136), fence off the median chamber posteriorly.

From the stage 3 nauplius, when they first begin to handle food particles, the molar surfaces of the mandibles are elaborated to render this process more efficient. This elaboration increases and becomes very complex during the filter-feeding stages. Efficiency is increased by mandibular asymmetry (148). Each molar face has a series of more or less dorso-ventrally running ridges subdivided transversely into teeth, each produced into several cusps (153). The molar surface on the right mandible develops a groove dorsally. This is bounded by stout spines and in its depth are toothed ridges, each tooth bearing several cusps. Both the marginal spines and cusped teeth change in form with increase in size (155, 156, 163, 164, 168, 169). Dorsally on the left mandible is a series of stout teeth (159, 160) which fit into the groove of the right molar surface to produce a crushing and triturating device. The ventral margins of the molar surfaces are armed with specialized spines (166, 167, 172–174) which both fence off the triturating regions and assist in the sweeping of food particles. By the time the animal is approaching the end of the filter-feeding phase these make up a complex array (182–184).

In large, carnivorous adults the molar surfaces are somewhat less elaborate and are crushing structures (180, 181). Large posterior teeth are also developed on both mandibles (149, 150) – one of the few cases where rolling and sweeping branchiopod mandibles have acquired a biting capability. The right mandible also loses the teeth within the now enlarged groove, and the adjacent marginal teeth become reduced in number but increase in robustness.

It is stressed that the pattern of development is one of strict anamorphosis. There is no sign of the development of the first six pairs of trunk limbs as a unit whose members become functional simultaneously and which, as a mechanism of the adult-type, suddenly replaces the naupliar swimming and feeding mechanisms at this stage. Claims that this is so in the Anostraca appear to be erroneous. No such metamorphosis occurs in *B. ferox*, and evidence culled from the literature shows that the condition in this species is typical of anostracan development as a whole. Previous suggestions that the anostracan pattern of development is less primitive than that of the Cephalocarida are therefore untenable. In this respect there is nothing to support the suggestion that either group is more primitive than the other.

While we now have a reasonable idea of the major features of anostracan development from the nauplius to the adult, both in terms of gross morphology and for some of the major organ systems, we have little idea how this pattern is established and controlled. Certain hypothetical developmental models, not proposed with the Anostraca in mind, are interesting but contribute hardly at all to our understanding of morphogenesis. Possible lines of attack are briefly mentioned.

The stages between the nauplius and that stage at which all the adult appendages become functional can to some extent be regarded as motile embryos. Processes that take place in the embryo of many organisms – somite formation and the development of limbs – do so in a motile organism that has by its own efforts to maintain the energetic demands of growth and differentiation. That the Anostraca have been successful in this respect is indicated by their long survival and their enormous geographical range in a variety of climates, albeit in a restricted range of habitats which, however, include many that call for great ecological or physiological tolerance.

The entire life cycle of *B. ferox* is enacted in a single water body. Selective forces must act in very different ways on small nauplii and large adults with their different morphologies and functional needs, yet presumably do so in similar ways so far as basic physiology is concerned. The very different morphological specializations of the various stages are therefore probably accompanied by wide eco-physiological tolerance. Such a pattern is very different from that of many animals whose juvenile and adult stages differ much in morphology, each being specialized for a particular way of life and occupying niches that are not only very different but which are found in quite different environments. Such tolerance has probably contributed to the long survival of the Anostraca and probably assisted *Artemia* in the initial stages of its colonization of hyper-saline environments.

B. ferox reveals the potentialities inherent in an organism that retains two primitive attributes, anamorphic development and the retention by the adult of a substantial degree of serial homology.

1. INTRODUCTION

The basic features of anostracan development have long been known, though this has not prevented the misinterpretation of certain aspects of it in some of the most recent publications, and there is a surprising degree of divergence in accounts of the process given by different authors, even when working on the same species. Since the first description of changes taking place during development were given by Shaw (1791), a number of workers, including Prévost (1803; but see revised version in Jurine 1820), Baird (1850), Claus (1873, 1886), Sars (1896), Heath (1924), Hsü (1933) and Baqai (1963), have contributed to our knowledge of this process in several species. These and other studies vary much in quality and in the accuracy of the vital illustrations, some, such as those of Claus and Sars, being excellent, others less satisfactory. In addition the pattern of segment formation has been studied by Weisz (1946) who also (Weisz 1947) provided information on the histological development of certain tissues and organs and further elaborated his ideas on segmentation. Certain specialized aspects of development have also been well treated by Cannon (1926) and Anderson (1967), while Benesch (1969) who, for *Artemia*, has given much the most detailed account of anostracan embryology, has provided excellent information on some of the anatomical features of certain post-naupliar stages.

Notwithstanding the interest aroused by the striking morphological changes involved, scant attention has been paid to changes in function that take place throughout development. Beginning life as nauplii and gradually developing into multi-limbed adults – there are usually 11 pairs of trunk ('thoracic'†) limbs – anostracans have to face the problem of maintaining functional continuity throughout a series of profound morphological changes, which affect particularly the means of locomotion and the feeding mechanism. The feeding mechanisms of anostracan nauplii were mentioned very briefly by Cannon (1928) (for *Chirocephalus*), in somewhat greater detail by Gauld (1959) (for *Artemia*) and received passing mention from Barlow & Sleigh (1980) (for *Artemia*), but no detailed account exists. Various interpretations of the feeding mechanisms of adult anostracans have been published and are cited where appropriate, but in no case have the changes in locomotion and feeding mechanisms been followed throughout development. These changes are of considerable intrinsic interest and their correct interpretation has phylogenetic implications. In most anostracans the problems have been reduced by feeding on essentially the same kind of food throughout life – fine particles of detrital or algal origin – but in at least two species, *Branchinecta gigas* Lynch and *B. ferox* (Milne-Edwards) a change of diet takes place as the animals develop. As large adults both these animals are carnivores (Fryer 1966) and neither is capable of filter-feeding – the usual means of food collection in all post-naupliar stages in the Anostraca. Carnivorous habits are impossible in the early stages. As adults of both these species are very large, but the nauplii very small, there is an enormous increase in size during development – certainly of several tens of thousands of times volume-wise in *B. ferox*. This adds to the problem of maintaining efficient continuity in an animal that undergoes profound morphological changes yet remains active

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† Although the limb-bearing trunk segments are designated as the thorax and the succeeding apodous segments as the abdomen, these regions do not coincide with the thorax and abdomen of the Malacostraca, nor even of other branchiopods, and the terms are used simply for descriptive convenience.

throughout each stage of the life cycle except the egg. The functional changes involved during the development of either of these species are therefore likely to be even more interesting than those that take place in filter-feeding species.

This paper presents the results of a study of the changes that take place during the development of *B. ferox*, with particular emphasis on the way in which functional continuity is maintained from the first nauplius to the largest adult instar. Information on the natural history and geographical distribution of this species is given by Dimentman (1983). Here it is sufficient to say that this is a species with what appears to be a discontinuous distribution in the western part of its range – in Spain, North Africa and a closely associated group of Central European localities – and which is found also in the vicinity of the Black Sea and Caucasus and is widespread in at least part of the Levant. The eastern limits of its range are only vaguely known. Here it has been confused with the related *B. orientalis* G. O. Sars which extends across the Steppes to the vicinity of L. Baikal. Its distribution in Israel is described by Dimentman (1981). *B. ferox* frequents mostly dry regions and, like most anostracans, is an inhabitant of temporary pools. Those pools frequented are generally on alkaline or neutral soils, are often more than 1 m deep when full, and are usually flooded for more than 3 months of the year (C. Dimentman, personal communication). The ionic composition of the water clearly varies much from pool to pool and throughout the season, but *B. ferox* is not a saline-pool species.

The Anostraca is one of the most primitive groups of the Crustacea. Post-embryonic development is essentially anamorphic – precocious development of the telson rudiment is the only deviation – and as such undoubtedly reveals the primitive pattern. Although changes in form take place during development and, etymologically, the animals may be said to undergo metamorphosis, it will be shown that at no stage of development is there a sudden functional change involving the replacement of one mechanism by another, and the term metamorphosis is probably best avoided. This statement, which conflicts with some of those in the literature, has important phyletic implications, and will be fully substantiated, but deserves mention at the outset.

While anamorphic development allows changes in morphology and associated vital functions to take place gradually, and in small steps, it in some ways presents more problems to an animal than does a life cycle involving well defined metamorphosis which provides the opportunity for drastic reorganization between adjacent stages without having to evolve functional intermediates. It also presents problems such as are not encountered by animals in which segment formation occurs in the embryonic stages. Although, during anamorphic development, changes at each instar may be small, they may also be numerous, as in *B. ferox*, and each must be efficient. That a truly metamorphic life cycle has been highly successful in the Crustacea (as in hexapods of which the vast majority have such a life cycle) is shown by the success of its exponents, which include copepods, barnacles and many decapods. The anamorphic pattern has, however, also been successful as its persistence in the most primitive, and presumably among the most ancient, of all groups of the Crustacea bears testimony. Further, had the problems presented by anamorphosis not been overcome, there would have been no evolution of the metamorphic pattern.

The need for an understanding and clear exposition of morphological changes during anostracan development is made evident by recent studies on *Artemia*, for which animal much physiological and biochemical information is now available. A woeful lack of understanding of morphology is sometimes shown in this work. For example, in an otherwise excellent survey of biochemical and other features of development given by Clegg & Conte (1980) certain references to morphology, as when the development of salt organelles is mentioned, are so incoherent as to be meaningless. Unless they can be related to specific morphological landmarks, physiological and biochemical changes that take place during development lose much of their significance.

2. Materials and methods

Dried eggs, collected from temporary ponds in Israel by Dr C. Dimentman, usually hatched readily and provided a series of developmental stages that were reared at the Freshwater Biological Association's Windermere Laboratory where work on their development, functional morphology and habits was carried out. Eggs were hatched, and animals reared, in Windermere water, which is low in electrolytes, but the salt content was doubtless raised by material dissolved from the detritus that accompanied the eggs, and was further raised by the addition of algae grown in a nutrient-rich medium. No analyses were made, but the water was certainly not saline.

Rearing of the naupliar and filter-feeding stages, which were fed on *Scenedesmus* or *Chlorella*, proved easy, but great difficulty was experienced in maintaining larger, carnivorous animals which were never reared to the size found in Nature. Such animals were studied alive in Israel.

Feeding and other activities were watched under a variety of conditions, and useful information was obtained by use of a high speed cine camera, film from which could be analysed frame by frame. For morphological work, and especially for material to be sectioned, animals were usually fixed in Zenker's fluid, sections being cut from material embedded in low viscosity nitrocellulose, and usually stained with Mallory's triple stain. Dissections were performed as necessary. For the revelation of certain details recourse was had to scanning electron microscopy, material being prepared by critical point drying and subsequently coated with gold–palladium.

3. The early naupliar stages

(a) *The first nauplius*

Reviews of the hatching process of anostracan eggs are given by Davis (1968, 1981). In *B. ferox* the tiny larva that emerges (length generally <0.5 mm) is a non-feeding stage that subsists on the yolk granules with which it is abundantly provided, especially in the trunk region, but the precursors of devices that will be employed in feeding in subsequent stages are present. Its general form is shown in figure 1. In contrast to some copepod nauplii it is not discoidal but plump, its trunk being more or less circular in section.

Nauplii, which are positively phototactic, remain permanently in suspension and swim mostly with the ventral surface uppermost. They generally ascend through the water on a more or less spiral course. Every few seconds they rest and begin to sink, during which period the antennae are extended and serve as parachutes.

Neither the mandibular palps, which are unsuited to this task and whose movements are of small amplitude, nor the antennules contribute to locomotion. The sole organs of propulsion are the antennae, which are inclined somewhat ventrally. Their basic movement is a strong backward swing from a position anterior to that occupied in figure 1. Subtle refinements of this movement are described for later instars in §5 (*a*).

Distally the exopod is armed with a row of 15 natatory setae. Because of its curvature some

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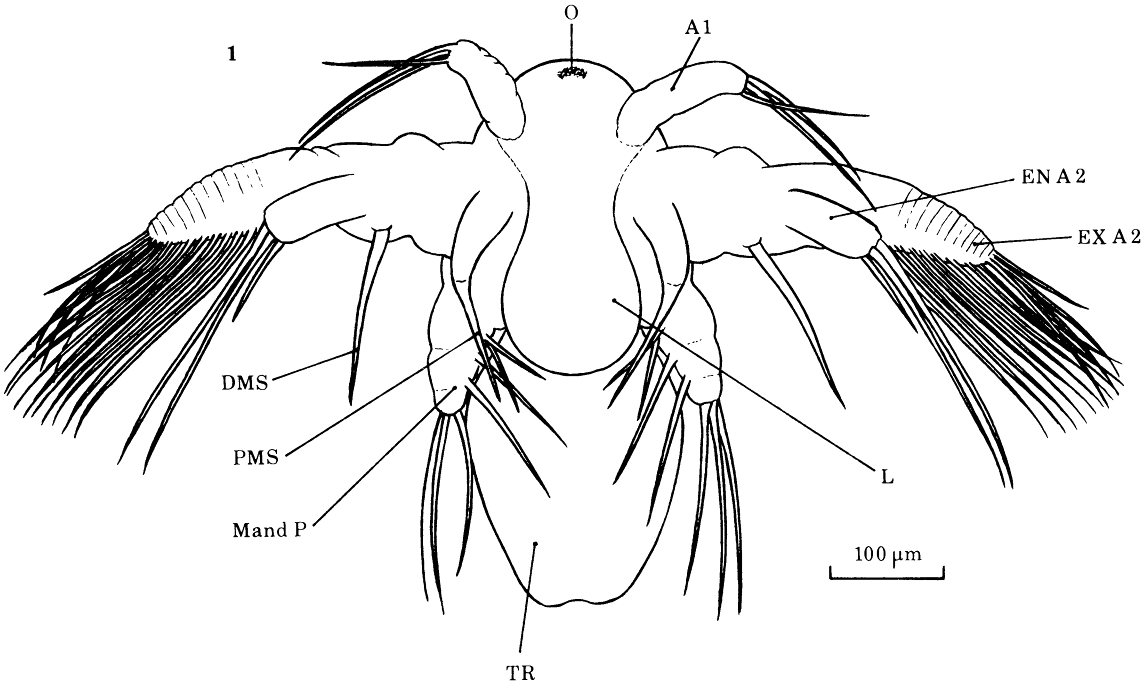

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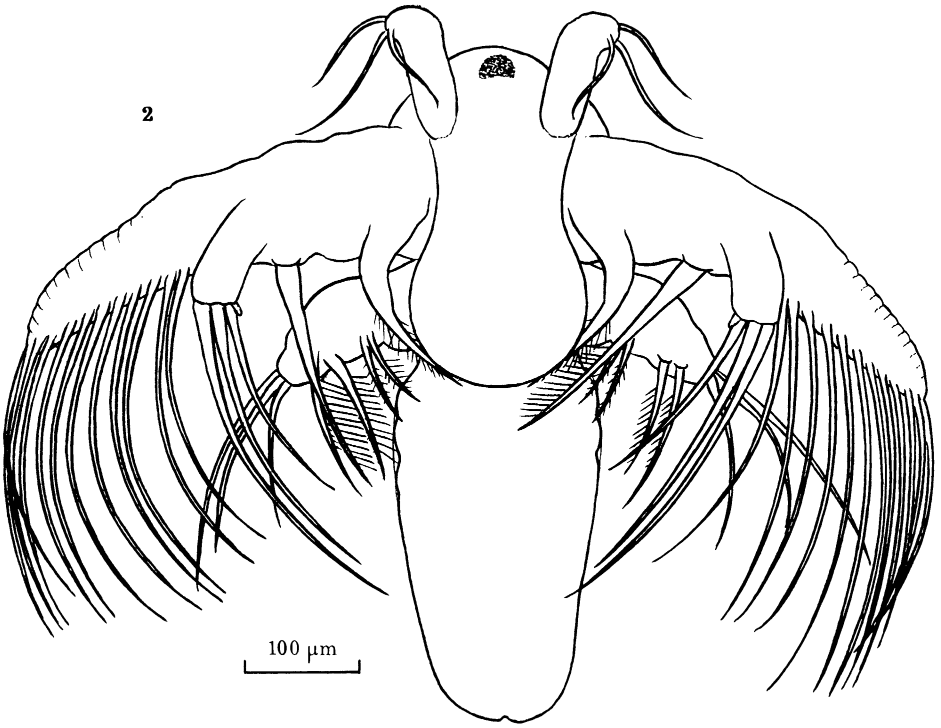


FIGURE 1. Stage 1 nauplius, ventral. (For key to lettering on this and all subsequent figures see the outrigger at the end of the paper.)

FIGURE 2. Stage 2 nauplius, ventral.

of the distalmost setae cannot be seen in figure 1. These setae lack any articulation part way along their length, a point to which reference is made later. Postero-ventrally each antenna bears two posteriorly directed spines located as shown in figure 1 – here designated proximal (PMS) and distal (DMS) masticatory spines in deference to their subsequent roles in feeding though at this stage neither is functional. Both lack the setules and spinules that later facilitate food handling, and at this stage neither can be controlled in the manner displayed in older instars.

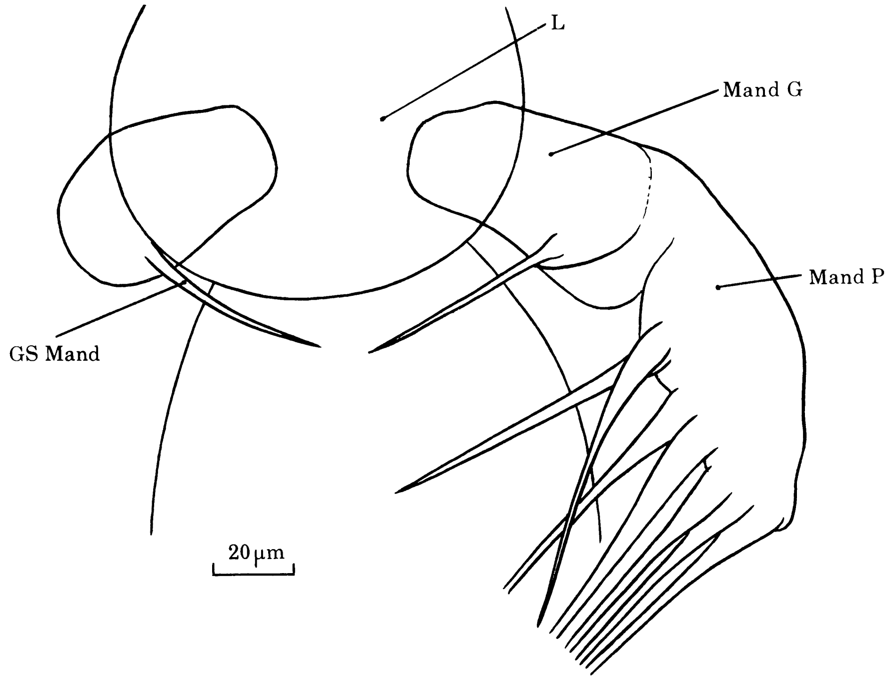


Figure 3. Mandibles of a stage 1 nauplius as seen from the ventral side. The labrum is drawn as if transparent. Note the wide gap between the prospective molar (masticatory) surfaces of the mandibular gnathobases (Mand G) and the nature and orientation of the gnathobasic spine of the mandible (GS Mand). The mandibles are non-functional at this stage.

The mandible, uniramous in the adult, here bears a palp (Mand P) whose setae (figures 1 and 3) are devoid of setules. Rudimentary gnathobases (Mand G) are already present. Because of the abundance of yolk in the labrum (L) their movements cannot be observed in the living animal but sections reveal a wide gap between their opposed molar (masticatory) surfaces, which at this stage show no elaboration (figure 3). The wide gap alone is sufficient to render the mandibles non-functional. Arising near the proximal posterior corner of the ventral face of the gnathobase and directed somewhat posteriorly is a smooth, slender spine, the gnathobasic spine (GS Mand). Its orientation and lack of any armature alone bespeak its functionless nature at this stage, but it is the precursor of an important larval adjunct to the feeding mechanism.

The precocious development and large size of the labrum are noteworthy, as is the presence towards its distal extremity of three conspicuous gland cells. These are referred to in subsequent stages, but it should be noted that even in the stage 1 nauplius a small reservoir containing the first fruits of their secretion is present in each case.

The stomodaeum is in full connection with the mid-gut but the proctodaeum is not, though in what are presumably individuals approaching the end of this instar the latter can be seen as a well marked invagination into a region that, earlier in development, is occupied by a mass of yolk granules. Here too the first trace of rectal muscles can be made out though there is no sign of these in presumably younger, yolk-packed individuals. A distinct wall seals off the posterior end of the mid-gut.

(*b*) *The second nauplius*

Although not much more than 0.5 mm in a length, the second stage nauplius (figure 2) is readily distinguished from the previous stage even to the naked eye by virtue of its more vigorous and sustained locomotion. The intermittent swimming of its predecessor is replaced by continuous activity, the larva pursuing an erratic course through open water, usually with its ventral surface uppermost. The mechanics of the process are as described for later stages in §5(*a*).

Two peculiarities of the natatory setae of the antennae are noteworthy. Neither at this nor later stages do they have a hinge or articulation about half way along their length such as is found in many branchiopod nauplii and which was indeed noted by Sanders (1963) as one of the characteristics that distinguishes them from those of non-branchiopods. A slight indication of a reduction in diameter of certain setae can sometimes be made out where an articulation might be expected, but there is definitely no genuine hinge. They also lack the setules that are usually such a characteristic feature of natatory setae in the Crustacea, whether they be on the homologous appendages of other branchiopods, such as the Cladocera, or on such different structures as the legs of copepods. The lack of both these features may be regarded as primitive on functional grounds, though non-branchiopod nauplii are successful without the former. Although they lack natatory setules, and on superficial examination appear to be naked, the setae are in fact provided with a lateral row of fine denticles that become more evident in older instars.

As indicated in figure 2, the rudiments of some of the post-mandibular appendages are recognizable at this stage. In sections rudiments of the paragnaths, maxillules and maxillae and, diminishing in distinctness from anterior to posterior, the limb buds of the first four pairs of trunk limbs and a vestige of the fifth can be distinguished. The maxillules and maxillae arise very close together and their separate rudiments can be recognized only with difficulty.

From a functional point of view the changes that take place at the first moult, though small, are highly significant. The proctodaeum opens into the mid-gut and feeding begins. There remains, however, at least at the beginning of the instar, a considerable accumulation of yolk in the alimentary canal. One sectioned individual revealed the first traces of collected food at the extreme anterior end of the gut beyond which region they were unable to pass because just behind them was an occluding mass of yolk granules.

Food collection is made possible by changes in the antennae and mandibles. Both the proximal and distal masticatory spines of the antennae undergo changes in form (compare figures 1 and 2) and acquire an armature of spinules or setules, and the larva acquires the ability to control them. The four proximal setae of the mandibular palp also develop an armature of setae, the mandibular gnathobase increases in size, and there are marked changes in the form and orientation of its gnathobasic spine.

Although often described in a perfunctory manner, the armature of the spines directly involved in food manipulation – which in the branchiopod nauplius have indeed not always been recognized as such – is of supreme importance. The general disposition of the armature of the proximal masticatory spine of the antenna is indicated in figure 2 and details are shown in figure 4, where the tip of the spine curves away from the observer and its distal part thus appears foreshortened. The brush-like nature of the armature is evident. It arises from the dorsal and lateral faces of the spine and is so arranged that when the spine swings as described in §5 (*c*) it sweeps mainly the ventral surface of the trunk behind the mandibles, though a few spinules are directed somewhat ventrally and must sweep the topographically dorsal (inner) surface of the labrum. Quite different is the arrangement on the distal masticatory spine (figures 2 and 5) whose armature consists of two rows of long, slender spinules which arise on its inner side. The ventral row is inclined ventrally, the dorsal dorsally. Thus in section the space between the rows is V-shaped (figure 5, inset), its open end being at right-angles to the ventral surface of the trunk. Any inward swing of the spine in the horizontal plane, i.e. parallel to the ventral surface, thus inevitably sweeps fine particles medially and forward.

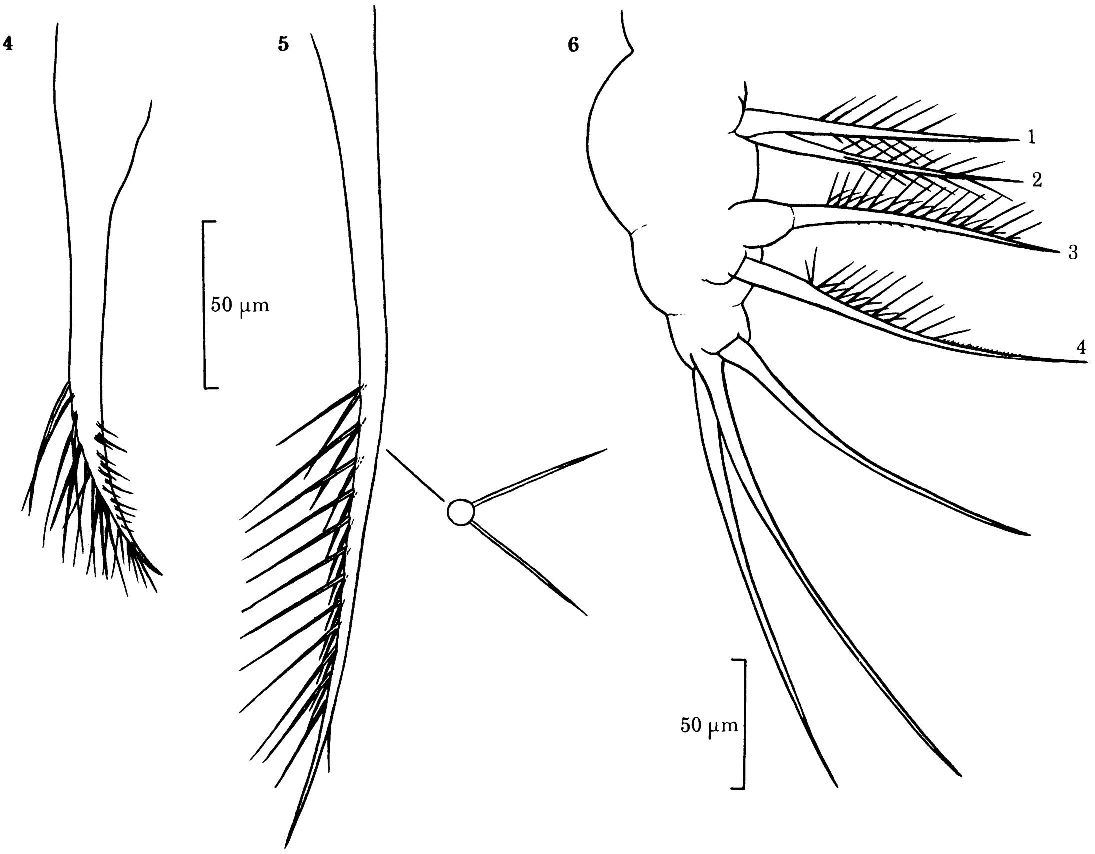
Each of the four proximal spines of the mandibular palp also bears two rows of spinules (figures 2, 6 and 7). The remarkably detailed correspondence of the armature of the mandibular palp in the naupliar stages of the extant *Chirocephalus* (Anostraca) and the Devonian *Lepidocaris* (Lipostraca) was pointed out by Scourfield (1940). That of *B. ferox* is similar but, while Scourfield says that only one row of spinules is present on each of these spines in the two former animals, two rows are present in *B. ferox*. On the two proximal spines (1 and 2) both rows of spinules lie more or less parallel to the ventral surface of the trunk: on the distal spines (3 and 4) the rows are divergent, being directed obliquely forward and dorsally and forward and ventrally from the anterior face (figures 6 and 7). Thus the proximal spines will tend to envelop any particles lying between them and the trunk, the distal to confine them laterally and sweep them inwards and forward when the palp swings inwards.

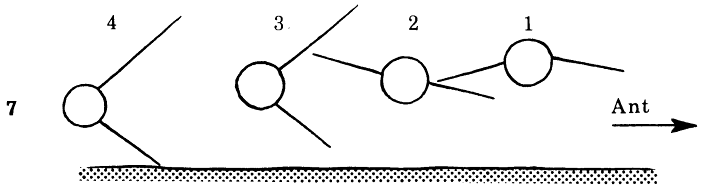
The gnathobasic spine of the mandible (GS Mand) has now been transformed into a robust structure that lies parallel to the gnathobase save that its tip curves anteriorly into the gap between the molar surfaces (figures 8 and 9). It has an armature of short spinules.

At the beginning of this instar the mandibular palps move little and are apparently ineffectual. In individuals nearing the end of the instar, however, they become much more active and engage in definite brushing movements which carry particles towards the mandibular gnathobases. These movements are not simply swings of the palps about their basal articulations but involve flexure so that their distal setae sweep briskly through a wide arc. Their working swing also includes a component that reduces the gap between their proximal spines and the ventral surface of the trunk. While they cannot fail to hold or confine particles in the vicinity of the mid-line, it is the masticatory spines of the antennae that are primarily responsible for actively sweeping them under the labrum.

At this stage there is sufficient residual yolk in the labrum to obscure movements of the mandibular gnathobases but basically they clearly operate as in subsequent stages – by the typical branchiopod roll. This causes the gnathobasic spine – an important larval specialization – to sweep material between the molar surfaces. Particularly noteworthy is the fact that the tips of the gnathobasic spines extend into the gap between the opposed molar surfaces (figures 8 and 9). This means that the molar surfaces, at this stage widely separated, could not come together even if a mechanism for achieving this existed, which it does not. They therefore play no part in the manipulation of the food. The gnathobasic spine, beautifully adapted for sweeping, is therefore the only functional part of the gnathobase at this stage. This sole responsibility is shed at the next moult though the spine continues to play a significant role in food manipulation through many succeeding instars.

Although the gnathobasic spine of naupliar branchiopods has been mentioned and illustrated by previous authors (e.g. it was clearly illustrated in *Tanymastix stagnalis* (L.) – then called *Branchipus stagnalis* – by Spangenberg as long ago as 1875†) its functional significance appears at best to have gone unrecognized, at worst to have been misrepresented. For example the similar spine present in the anostracan *Streptocephalus seali* Ryder was described as a 'sensory





FIGURES 4–7. Details of the appendage armature of a stage 2 nauplius.

FIGURE 4. Proximal masticatory spine of antenna. The tip is curving away from the observer somewhat and therefore appears foreshortened.

FIGURE 5. Distal masticatory spine of antenna. The inset shows a pair of opposed spinules sketched diagrammatically to show the angle between them.

FIGURE 6. Mandibular palp.

FIGURE 7. Diagrammatic section through the four proximal spines of the mandibular palp to illustrate the nature of their armature and its relation to the ventral surface of the animal.

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† Spangenberg says that his illustration is from an almost sexually mature animal. I suspect that this is an error. There is no trace of this spine in adults of *T. stagnalis*.

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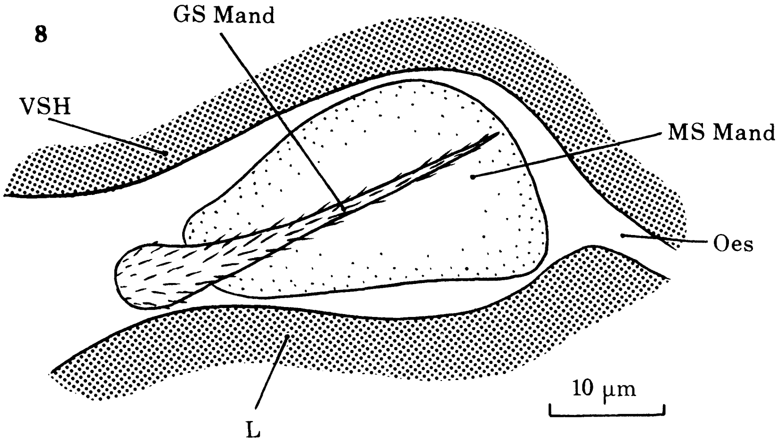

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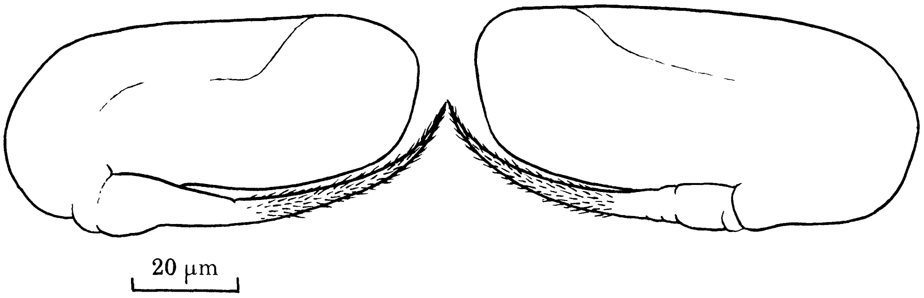

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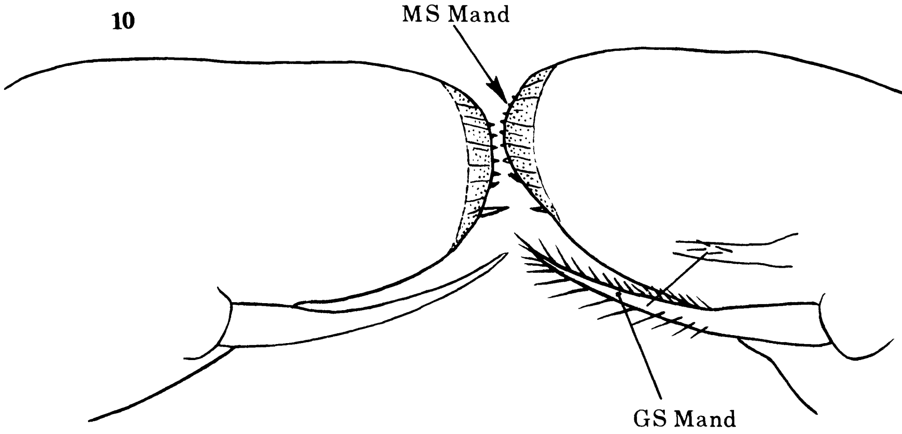

Figures 8–10. Mandibular devices in the second and third naupliar stages.

Figure 8. Longitudinal section showing in face view the molar surface of the mandible (MS Mand) of a stage 2 nauplius and the way in which the gnathobasic spine (GS Mand) curves across it. Note the transformation of this spine since the stage 1 nauplius shown in figure 3.

Figure 9. The mandibular gnathobases of a stage 2 nauplius seen from the ventral side. With figure 8 this clearly shows that the molar surfaces cannot function at this stage and enables the transient sweeping function of the gnathobasic spines to be easily visualized.

Figure 10. The mandibular gnathobases of a stage 3 nauplius seen from the ventral side. The molar surfaces are now functional. Note the change in orientation of the gnathobasic spine. The inset shows the spinules on its dorsal surface as seen by focusing through it. For the further development of the gnathobase and its spine in a stage 8 larva see figure 33.

spine' by Baqai (1963). In fact, as initially the sole food-sweeping device of the mandibular gnathobase, and later an integral part of a more elaborate mechanism, it represents a very important larval specialization. Sweeping by this spine is made possible by, and beautifully demonstrates, the rolling movements of the gnathobase proper. No other kind of movement would permit it to assist in the sweeping of particles between the opposed molar surfaces.

Noteworthy is the fact that a virtually identical spine was present on the naupliar mandibular gnathobase of *Lepidocaris rhyniensis* Scourfield, a Devonian representative of the extinct branchiopod order Lipostraca. This is clearly illustrated, but not mentioned, by Scourfield (1940). As in the Anostraca, this spine was lost when the animal became adult, no trace of it being shown in any of the excellent figures of Scourfield (1926).

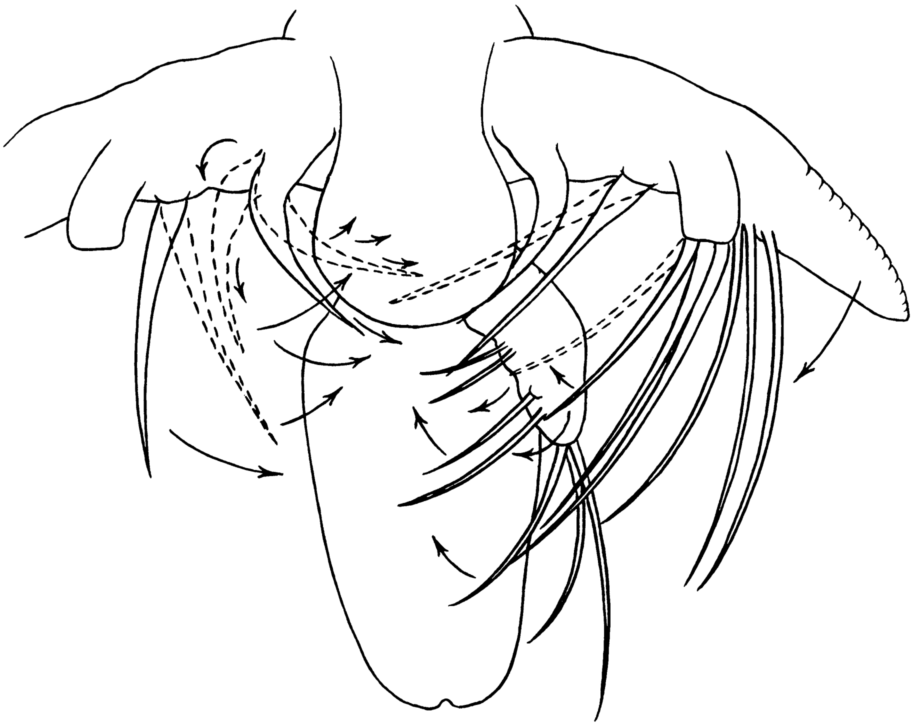

FIGURE 11. Diagrammatic representation of the independent movements of which the masticatory spines of the antenna and the mandibular palps are capable in a stage 2 nauplius. The arrows seek to indicate the sort of lunging movements in which the proximal masticatory spine of the antenna, and to some extent the mandibular palp, can indulge.

The naupliar feeding mechanism is described in §5 (*c*), but it is convenient here to indicate the independent movements of which the masticatory spines of the antennae and the mandibular palps are capable in the stage 2 nauplius. This is done diagrammatically in figure 11. Although they generally do so during feeding, the left and right masticatory spines need not necessarily operate in a synchronous manner but can move independently when occasion demands.

The antennules, which play no part in either swimming or feeding, are generally directed forward but can be swung laterally or ventrally to lie against the head (see §5 (*a*)). In life their terminal sensory setae are generally directed anteriorly, their position in figure 2 being that found in a preserved specimen.

(*c*) *The third and fourth naupliar stages*

Small but significant changes take place at the moult of the second nauplius. Locomotion is effected as in stage 2, the animal pursuing a brisk but erratic course through the water. Although the antennae propel it rapidly they do not generally display maximum possible activity, as is shown by trapped individuals which sustain extremely rapid beating for many minutes.

The armature of the antennal endopod is enhanced by the development of an inner, fourth, seta from the former rudiment and an elongation of the adjoining seta relative to its partners.

Feeding remains the responsibility of the antennae and mandibles, but while the form of the distal masticatory spines of the antennae remains unchanged the essentially proximal spines become bifurcate to facilitate sweeping (figure 12, PMS). The mandibular gnathobases are now functional, and the mandibular palps play a more active role. The rudiments of the paragnaths are more distinct (figure 12, P), the *Anlagen* of the maxillules (Mx 1) and maxillae (Mx 2) are now more easily distinguished as such and the same is true of the anterior trunk limb rudiments though only four are readily distinguished, the fifth being scarcely marked off from the succeeding undifferentiated trunk. The first such rudiment (TL 1) is clearly seen in figure 12.

The mandibular palps (Mand P), whose form is essentially as in the previous stage, now swing, usually through an angle of less than 90°, at rates of up to 6 c s^{-1} (cycles per second), and contribute actively to the transport of food particles. Whether their activity assists in locomotion is extremely doubtful, any minute contribution being purely incidental to their role in food handling.

As in the case of the antenna (see § 5 (*a*)) the working stroke of the palp is not a simple posterior swing: flexure is also important and takes place towards the end of the backward swing. This enables the three distal spines to sweep through a wide arc so that although they begin their working stroke from a lateral position, they can even pass into the space between the ventral body surface and the posterior extremity of the labrum. The four proximal spines sweep right into this space. Straightening of the palp takes place on the return stroke and so the tip describes a more or less crescentic course in relation to the trunk. Because of the nature and rapidity of the process the general impression of the movement of the distal spines is a flick towards, or even into, the pre-oral space. Although they move basically in the horizontal plane the palps are also capable of slight dorso-ventral movements so that, as can be seen by observing a nauplius so orientated that it can be viewed in optical transverse section, their proximal spines sometimes sweep near the ventral body surface (here the paragnaths), sometimes near the inner (topographically dorsal) face of the labrum. The difference between the extremes of such dorsal and ventral orientation is, however, very small.

Unless there are automatic adjustments, the palps must be moved slightly as a result of the swing and roll of the mandibular gnathobases. The forward swing of the gnathobases will actually enhance, though only slightly, the inward sweep of the palps and the roll is possibly in part responsible for the slight variation in level of the swinging proximal spines noted above.

Notwithstanding the activity of the palps, the principal agents in the transfer of food beneath the labrum and to the mandibular gnathobases are still the proximal masticatory spines of the antennae. The range of movement of each is such that it sweeps most of the region covered by the mandibular palp of its side, but as it passes ventral to the spines of the palp it will be less effective than them in dealing with particles that lie against the ventro-lateral surface of the trunk.

Morphologically trivial, but functionally profound, changes transform the role of the mandibular gnathobase between stages 2 and 3. The gnathobasic spine becomes relatively shorter and, of supreme importance, its tip no longer protrudes between the opposed molar surfaces of the gnathobases. There is thus no impediment to the coming together of these faces which, previously smooth, are now covered by thickened cuticle and armed with minute but sharp spinules (figure 10) that are sufficiently small to grip even minute particles, such as the unicellular algae that are readily ingested at this stage. It is enlargement of the gnathobases that brings the two faces together. Not only is the gap between them reduced but abduction to produce a gap such as exists in stage 2 is impossible.

It is to be noted that the food-handling spines, whether of the antennae, the mandibular palps or the mandibular gnathobases (sweeping spines), swing ventral to the rudimentary paragnaths which therefore play no part in the directing of food orally.

The fourth stage differs but little from its predecessor. The rudiments of such post-mandibular appendages as are present are somewhat more distinct and the *Anlagen* of the sixth pair of trunk limbs can just be distinguished.

4. THE ANATOMY OF THE THIRD AND FOURTH NAUPLIAR STAGES

Notwithstanding the fundamental importance of the nauplius as the larval form of a wide range of crustaceans – nauplii as a group are almost certainly the most numerous of all multicellular animals – and although many illustrations of individual larvae, some crude, others excellent, are to be found in the literature, little is recorded of the internal anatomy of the nauplius of any group of the Crustacea other than the Cirripedia. For this group we have the classic work of Groom (1894) and an elegant study by Walley (1969). The former, however, makes no attempt to deal with certain features, such as the muscular system, that are important in the present context, and in the latter the skeleto-muscular system is illustrated only diagrammatically. For the Anostraca the work of Claus (1886) on *Branchipus* and *Artemia* gives a good general impression of certain anatomical features; that of Benesch (1969), while excellent, refers particularly to features of the late-naupliar stages of *Artemia*. The account of naupliar musculature given by Baqai (1963) is inaccurate and badly illustrated.

By virtue of the acknowledged primitive nature of the Branchiopoda the nauplii of its constituent orders are likely to be of particular phyletic interest. Information having a bearing on this is an added bonus to that relevant to ontogeny yielded by anatomical study of the nauplius of *B. ferox*. Here attention is concentrated on the skeleto-muscular system, other anatomical details usually being mentioned only in so far as they are relevant to functional considerations.

Because in stages 1 and 2 details are obscured by yolk granules, stages 3 and 4 are more rewarding objects for such study and have the added advantage of being somewhat larger, though they are still sufficiently small to present difficulties. These stages are so similar in anatomy that they can conveniently be considered together. The small differences that they display illuminate certain features of ontogeny. Figures 12–19 reveal the basic features of such a nauplius.

The extrinsic musculature of the appendages originates either on a ventral endoskeleton that lies dorsal to the ventral cuticle or on the dorsal cuticle or closely associated endoskeleton. The dorsal cuticle forms what is in effect a disc-like headshield, being here thicker than that which encloses the more posterior and ventral parts of the body in an extremely flimsy pellicle. The

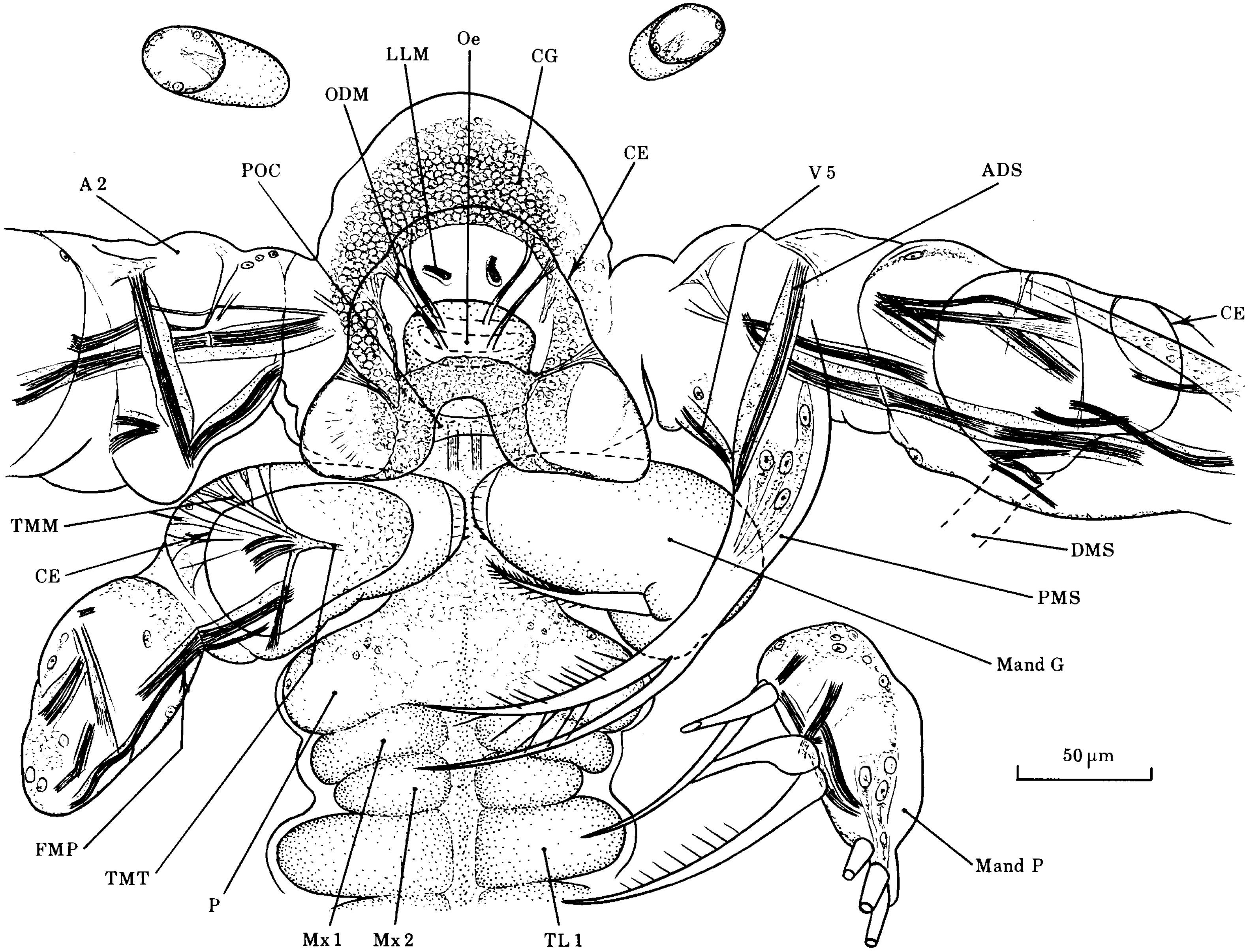

FIGURE 12. Stage 3 nauplius. Horizontal section from ventral side. This slice, which cuts very slightly deeper to the left (right hand side of the animal) than the right, cuts through the base of the labrum, removing the bulk of it and exposing the mandibles. The appendage rudiments posterior to the mandibles are not cut but are seen in surface view. Note the bifurcate nature of the proximal masticatory spine (PMS) of the antenna, some of whose muscles (V 5 and ADS) are to be seen here.

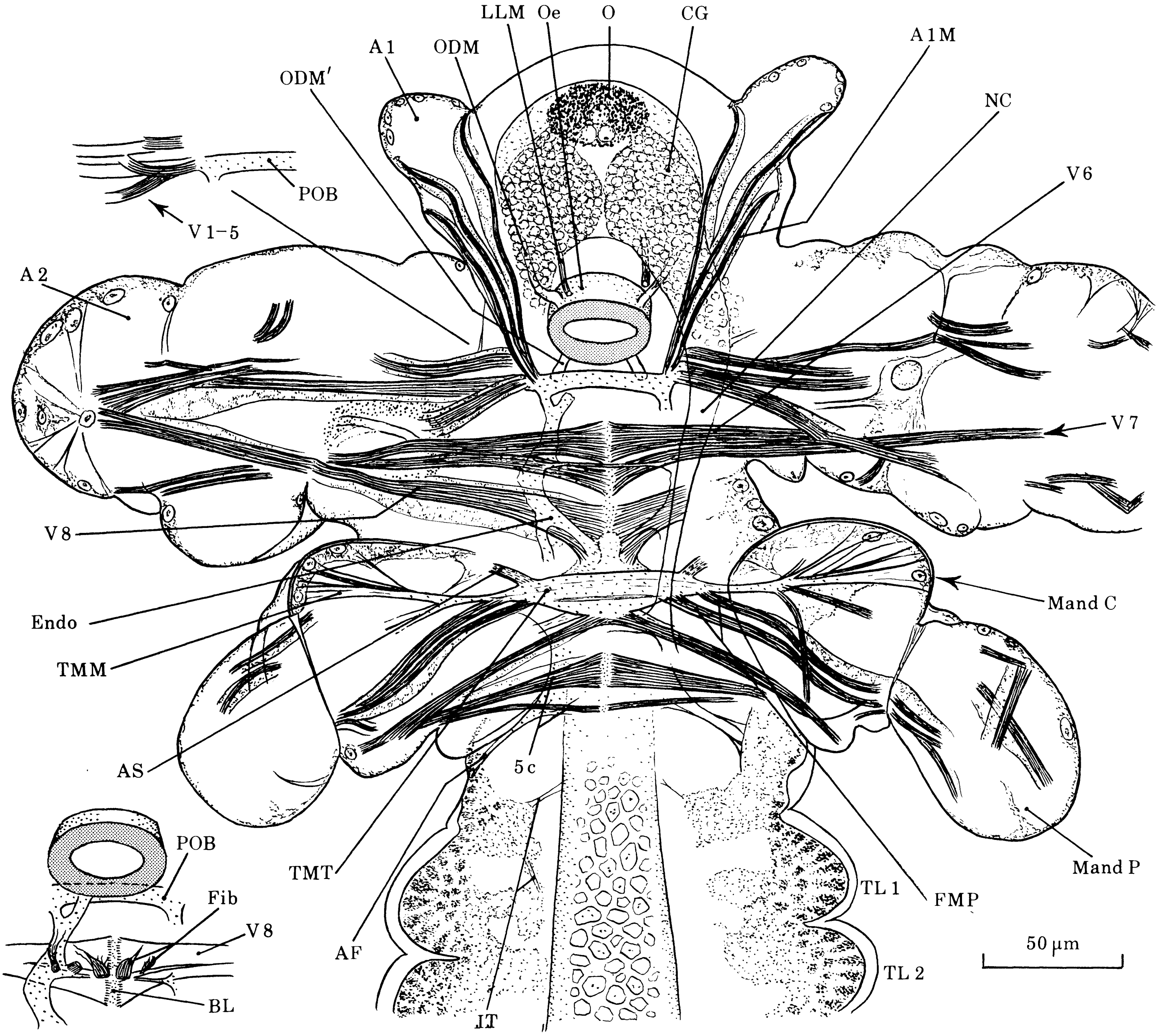

FIGURE 13. As figure 12 but deeper (more dorsal). The section shows, among others, the major ventral extrinsic muscles of the antenna (V1–8). On the right the ventral nerve cord (NC) is shown as if transparent. On the left some of the delicate endoskeleton between the post-oesophageal bar (POB) and the transverse mandibular tendon (TMT) is shown. This is for the most part extremely flimsy and, as shown where it overlies muscles V6 and 7, immediately behind the post-oesophageal bar, is not very easy to see. Where it overlies muscle V8 it has been accentuated by drawing it as if it was largely opaque – which it is not. Note the almost hair-like transverse tendon between the POB and the TMT. Further details are shown in the inset by focusing up to reveal parts of the struts (there shaded) that act as braces between the endoskeletal sheet and the ventral cuticle. Note how some of the major extrinsic muscles of the mandibular palps (FMP) take their origin on the transverse mandibular tendon.

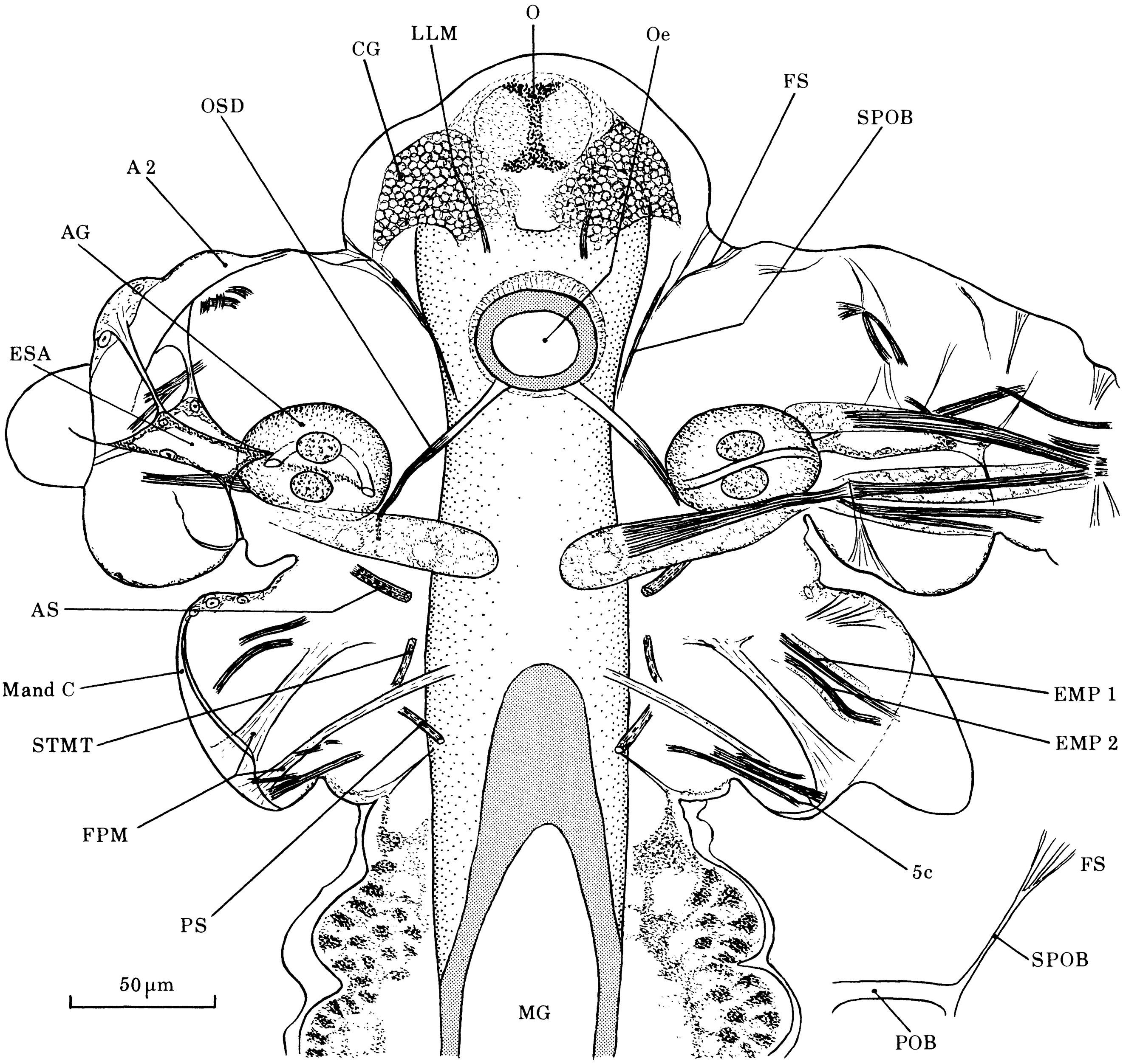

FIGURE 14. As figure 13 but deeper (more dorsal). Note here the absence of extrinsic antenary muscles (cf. the more ventral figure 13 and the more dorsal figure 15). The inset (semi-diagrammatic) shows how the post-oesophageal bar, which lies ventral to this section (see figure 13), is suspended.

ventral endoskeleton is illustrated in part, particularly in figures 13, 18 and 19. Some elements of it are easy, others extremely difficult, to see. Just behind the oesophagus there is a prominent transverse bar, here called the post-oesophageal bar (POB), from whose lateral extremities supporting ligaments run obliquely forward, dorsally and outward (figures 14, 16 and 17, SPOB) to insert as a splayed-out array of fibrils very dorsally near the bases of the antennae (figure 17, Fib). The post-oesophageal bar and its lateral wings serve as the place of origin for a variety of muscles. All three antennulary muscles (A1M) originate near the outer extremities (figures 13 and 16) as they do in naupliar *Artemia* (Anostraca), *Triops* (Notostraca) (Dahl 1952) and both larval and adult *Hutchinsoniella* (Cephalocarida) (Hessler 1964).

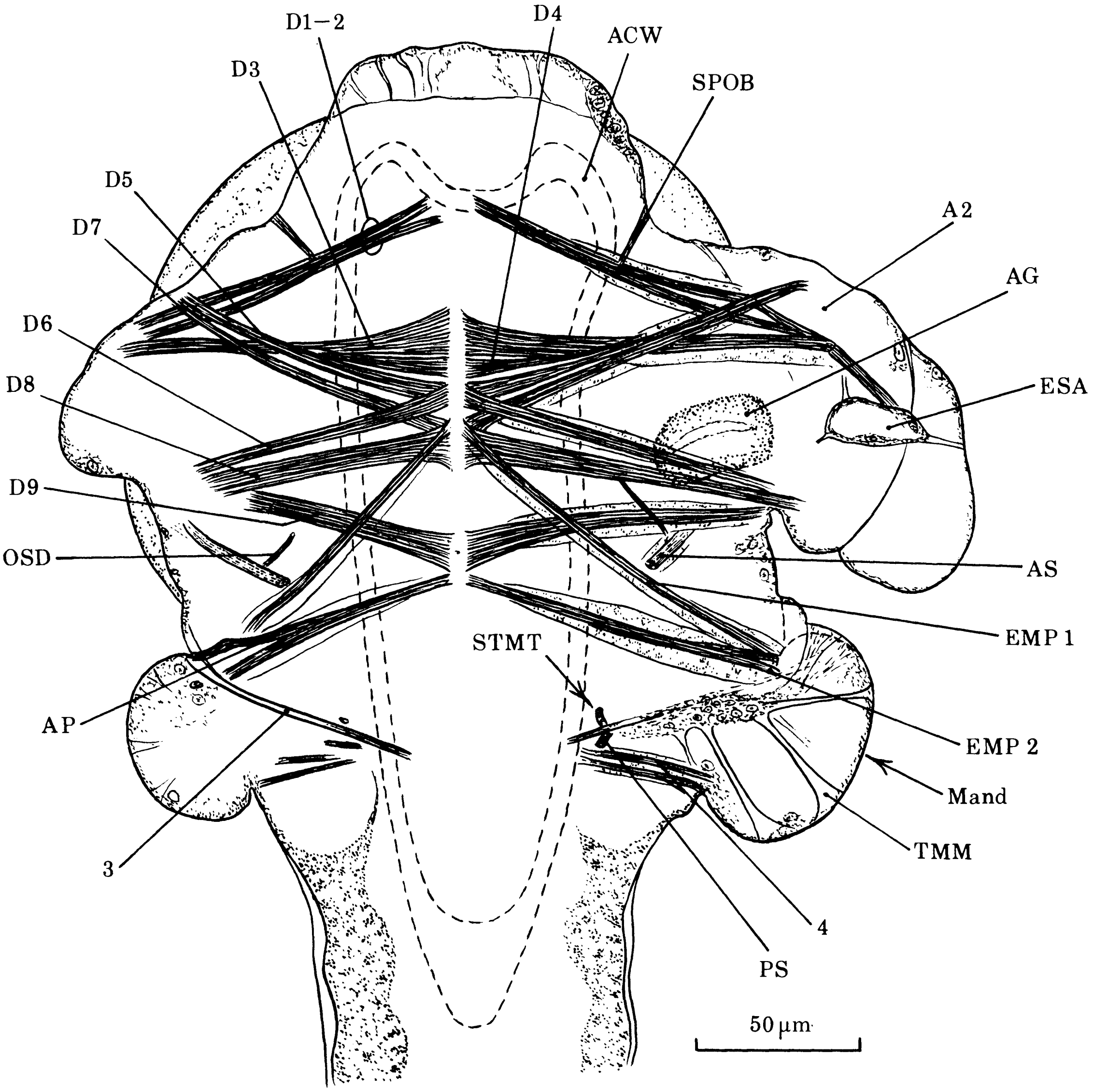

FIGURE 15. As figure 14 but deeper (more dorsal). That (dorsal) portion of the alimentary canal which is present in this slice overlies the muscles but for clarity is here indicated only by dashed lines. Note that the dorsal region is not flat but markedly concave internally.

The major anterior ventral extrinsic muscles of the antennae (V1–5) also originate on the anterior lateral prolongations of the post-oesophageal bar (figures 13 and 19). These prolongations fan out into sheets which become easier to see in later instars. The anteriormost antennal extrinsic muscle, the origin of which is not seen on the left hand side of figure 13 in fact takes its origin on this sheet. The post-oesophageal bar itself is utilized as the place of origin of a pair of what one would expect to be oesophageal dilator muscles (figure 13, ODM′) but which in stage 3 appear to be fibrous structures in which no contractile fibrils have been made out. Posteriorly the bar gives rise on each side to a delicate strap of fibrous material (figure 13, Endo) that extends backward in the horizontal plane. The exact shape of these straps is difficult to ascertain but each ultimately unites on its side with the transverse mandibular tendon (TMT) complex. About midway between the post-oesophageal bar and the transverse mandibular tendon is a slender transverse uniting strand only about 1 μm in width but which

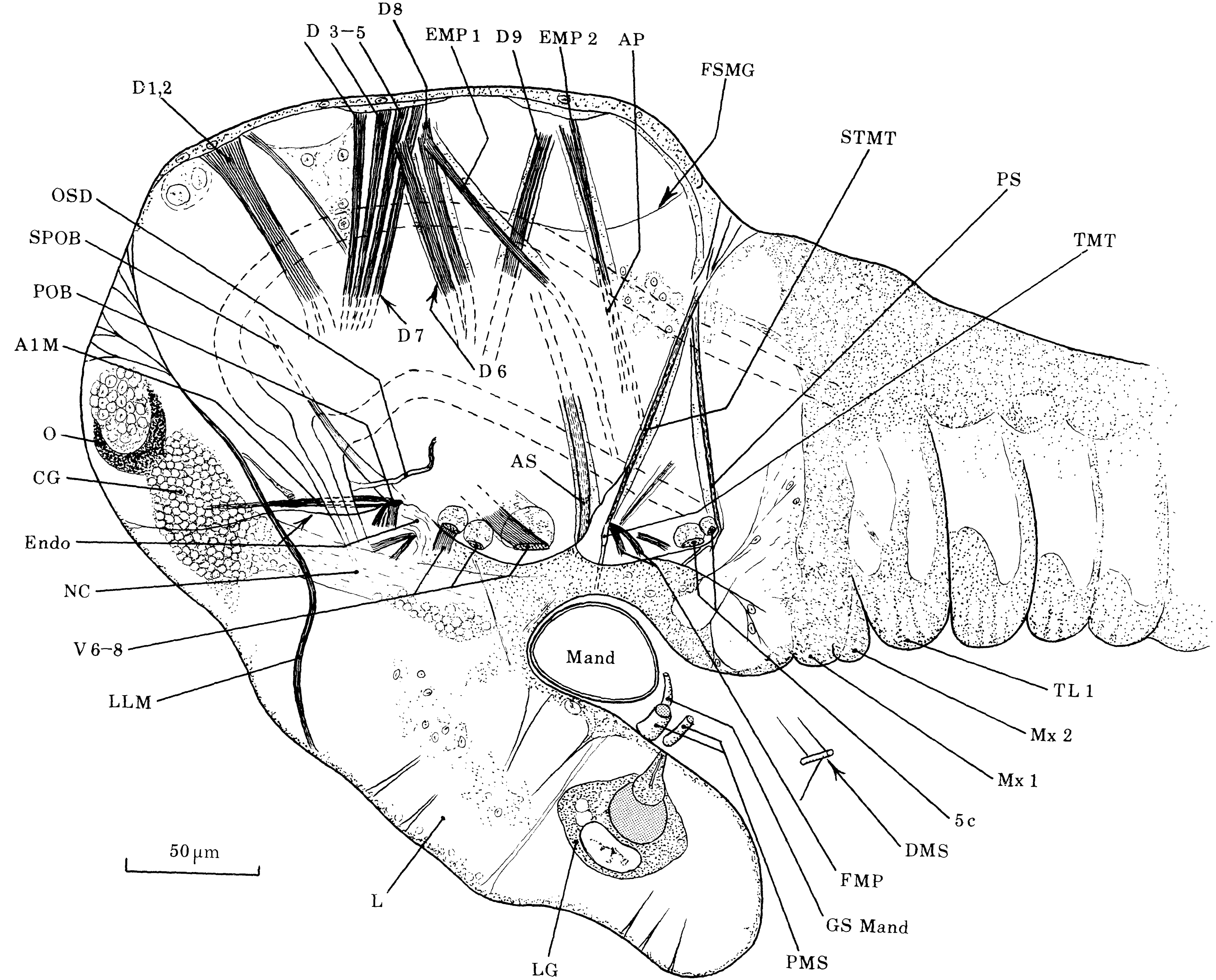

Figure 16. Stage 4 naupius. Longitudinal section somewhat to the right of the mid-line, the section cutting a little more to the right anteriorly than posteriorly. The alimentary canal, which lies to the observer's side of the dorsal series of muscles, is indicated only by dashed lines. The dorsal antennary and mandibular muscles run obliquely into the plane of the paper and, to facilitate understanding, their course, as ascertained from more lateral sections, is extended by dashed lines. Muscles of the ventral series dive more steeply into the plane of the paper.

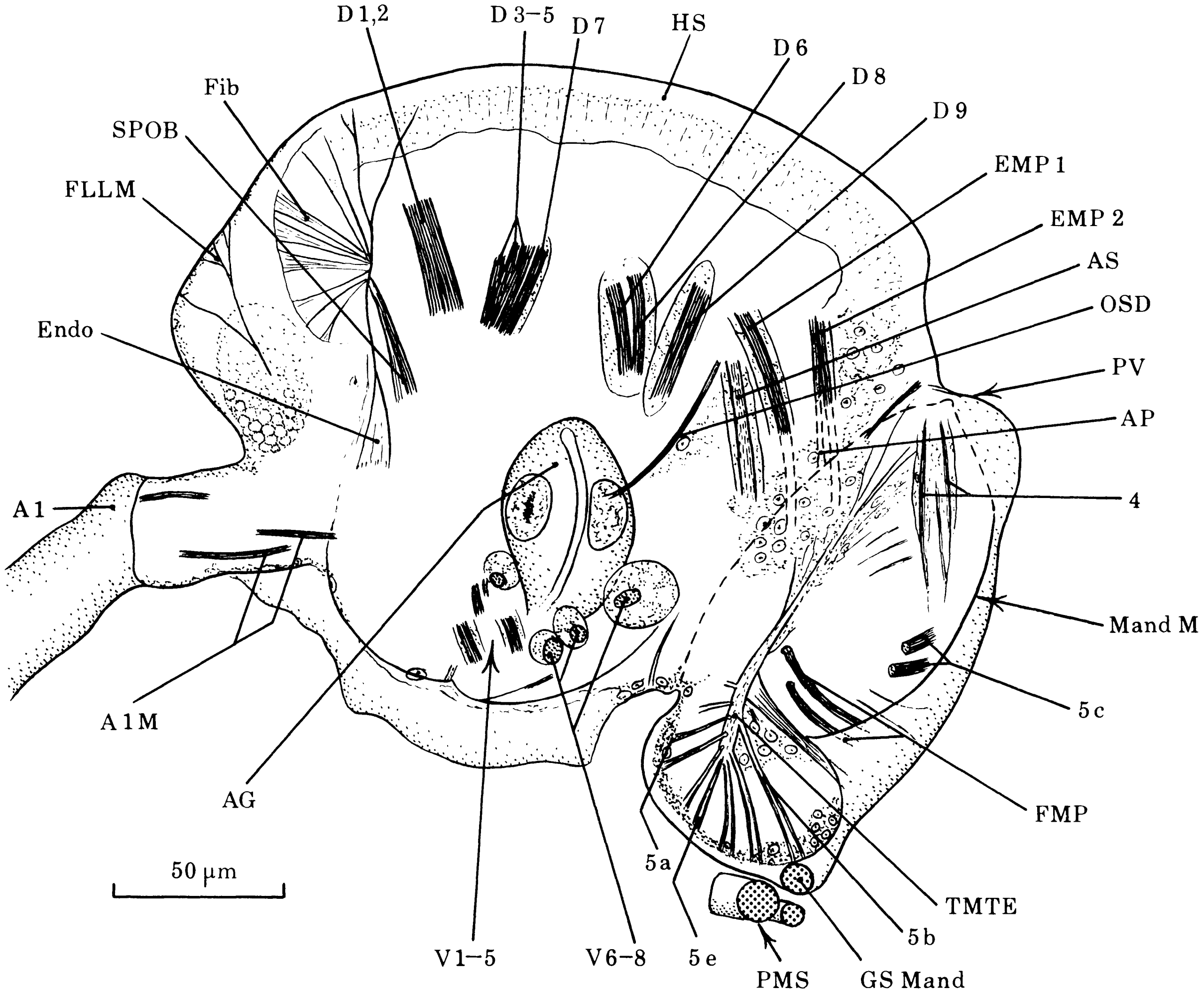

FIGURE 17. As figure 16 but more lateral. Dashed lines indicate the lateral (oblique) continuation of certain muscles beyond the limits of the section.

nevertheless appears to brace the two longitudinal straps. Anterior to this each longitudinal strap gives rise to a thin, again more or less strap-like strand, which runs anteriorly, ventral to the post-oesophageal bar (figure 13, lower inset) and apparently unites with the oesophagus. Although even more tendinous in appearance than the oesophageal dilator *Anlagen* that originate on the post oesophageal bar, these strands also appear to be differentiated into oesophageal dilator muscles in later instars.

Extending ventrally from the essentially horizontal network of bars and sheets of the endoskeleton are several fibrous struts that link it with the ventral cuticle. These are indicated, rising towards the observer, in the lower inset of figure 13 (Fib). The median pair can be seen through the ventral cuticle in figure 12. Each pair of the posterior ventral muscles (V 6–8) (see below) is united in the mid-line by a binding ligament (figure 13, inset, BL) that appears to pass between V 7 and V 8 as a median strap, but is very difficult to see. Fibrils from the fibrous struts shown in this inset presumably link the median binding ligament to the ventral cuticle, which would grant the anticipated stability, but details are very difficult to make out.

Posterior to the transverse mandibular tendon the endoskeleton extends backward as a delicate sheet and terminates beneath the rudimentary paragnaths where fibrils extending ventro-laterally from its corners anchor it to the cuticle (figure 13, AF). These fibrils are perhaps the homologues of the intersegmental endoskeletal struts that develop posteriorly as development proceeds and of which the first traces, between the maxillules and maxillae, and between the maxillae and first trunk limb, are to be seen at this stage (figure 13, IT). If this is indeed the case they must represent the mandibular/maxillulary intersegmental struts. They are assisted by additional anchoring fibrils (shown for stage 4 in figure 18, AF) that span the gap between the endoskeletal plate and the ventral cuticle.

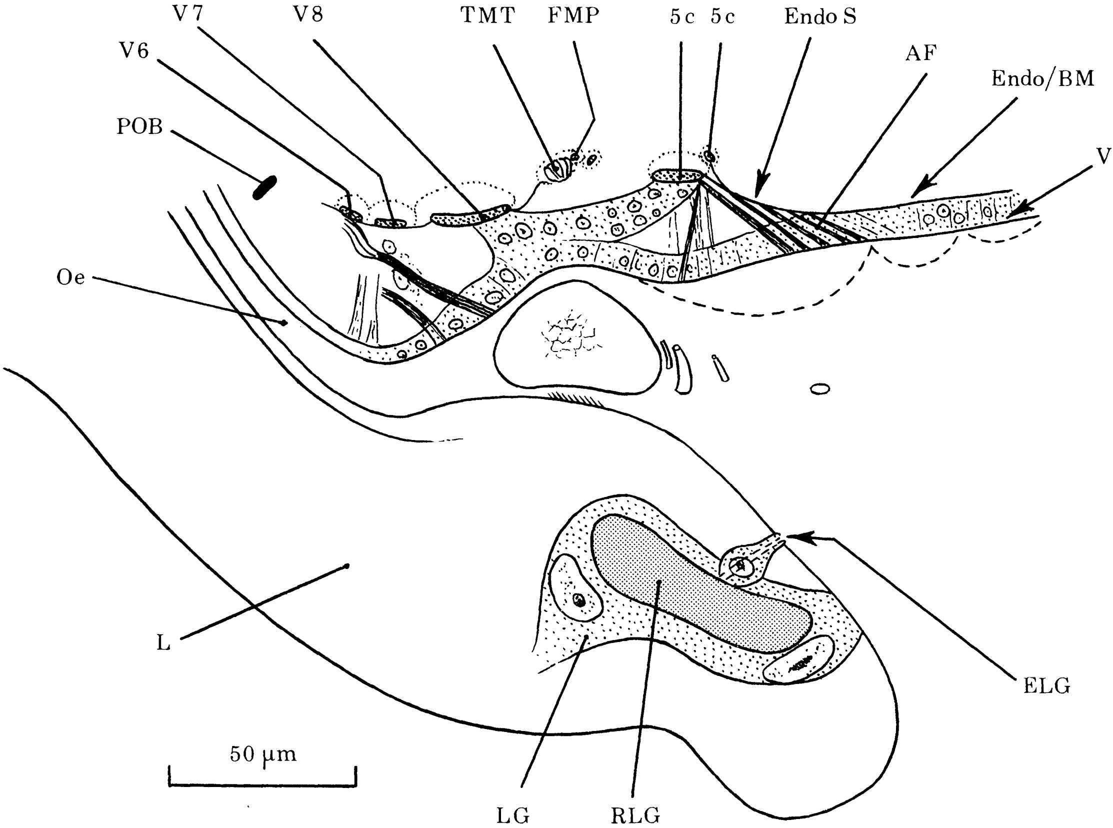

FIGURE 18. As figure 16 but not far from the mid-line and showing aspects of the endoskeleton, at this stage entirely cephalic. Note how, posterior to the 5c muscles, the endoskeletal sheet (Endo S) peters out and how it is firmly anchored by fibrils (AF) to the ventral cuticle (VC).

The muscular system of the third and fourth naupliar stages is illustrated in figures 12–19 which allows description to be reduced to a minimum. The antennulary muscles require no comment. There are two series of extrinsic antennary muscles, dorsal and ventral. For convenience members of the ventral series are designated V 1, 2, 3, ... from anterior to posterior; members of the dorsal series are designated D 1, 2, 3,... The origins of the muscles of the ventral series, eight in number, are seen in figure 13. The association of V 1–5 with the post-oesophageal bar and its prolongations, and the origins of V 6–8 on a median binding ligament, have already been noted. Posterior to V 8 the binding ligament is associated with the transverse mandibular tendon complex (figures 13 and 18). Some of the more lateral parts of the ventral muscles can be seen in figure 14, and they can be seen cut transversely in figures

16 and 17. The course of some of them is indicated in figure 19, which reveals how in some cases they traverse the appendage from a dorsal origin.

The dorsal antennary muscles, nine in number, originate in the sequence shown in figure 15. More distal portions of these muscles are seen in several figures, and figures 16, 17 and 19 make clear how they have a markedly dorso-ventral inclination, instead of extending predominantly horizontally as do members of the ventral series. A note of complexity is introduced here as the two posteriormost arise posterior – one markedly so – to a muscle (EMP1) that runs obliquely posteriorly and ventrally *en route* to the mandibular palp.

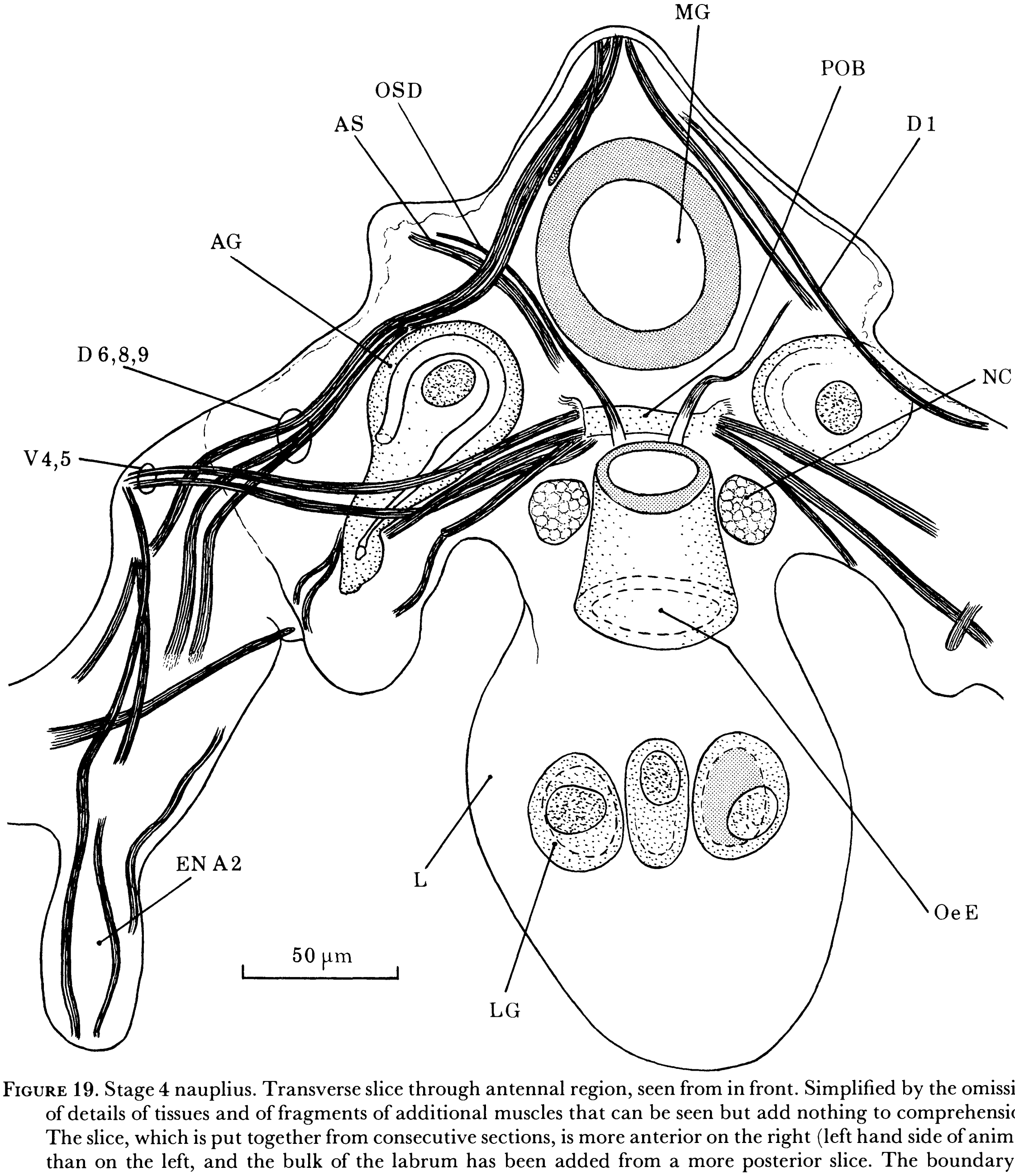

FIGURE 19. Stage 4 nauplius. Transverse slice through antennal region, seen from in front. Simplified by the omission of details of tissues and of fragments of additional muscles that can be seen but add nothing to comprehension. The slice, which is put together from consecutive sections, is more anterior on the right (left hand side of animal) than on the left, and the bulk of the labrum has been added from a more posterior slice. The boundary of each labral gland reservoir is indicated by a dashed line. In one case the reservoir is shown as seen by deep focusing but in all cases it is in fact obscured by the cell cytoplasm.

Intrinsic antennary muscles, some of which are to be seen in the illustrations, call for scant comment here, but the provision of muscles (e.g. figure 12, ADS) that enable the angle of attack of the masticatory spines to be altered, and grant independent movements, is noteworthy.

Further information on antennary musculature, based on an older instar in which the arrangement is essentially the same as in earlier stages, is given in connection with antennary activity (§5(*b*), figure 26).

The anteriormost dorsal extrinsic mandibular palp muscle (EMP1) has a companion (EMP2) that inserts immediately behind the posteriormost dorsal antennary muscle. As these two muscles enter the mandible they come to lie close together (figure 15) and remain so as they continue to the palp. Both are extremely long. They traverse the head, passing obliquely backward and ventrally, pass through the lateral part of the mandible, enter the palp and continue distally, the posterior originating near its tip. They function as extensors of the palp. Besides these two extrinsic palp muscles – a purely larval specialization – the skeleto-muscular system of the mandible embraces a complex array of muscles and suspensors from which the adult arrangement is directly derived.

Originating so closely alongside the posterior mandibular palp extensor muscle (EMP2), and lying so close to it over much of its length as to make the two difficult to separate, is another muscle (figures 15, 16 and 17, AP) that inserts somewhat dorsally on the anterior margin of the mandible. This becomes easier to see in later instars when, like the palp muscles, it can be seen in action in the living animal. It serves as an accessory promotor roller.

Three pairs of suspensors are conspicuous. A median pair (figures 14–16, STMT) suspends the transverse mandibular tendon. At this stage these suspensors appear to be tendinous, as is the case in older individuals, though red-staining tissue is present and it is possible that this may indicate contractile fibres.

Arising close to the point at which each such suspensory ligament arises from the transverse mandibular tendon, and inclining forward and outward as it rises dorsally, is another suspensor (AS) that inserts dorsally and laterally on the headshield (figures 13–17). This is muscular. The contractions of which it is therefore capable presumably enable it to maintain rigidity in the cephalic endoskeletal sheet, and the fact that it is muscular and not tendinous possibly indicates that this sheet is subject to slight distortion at this stage. Muscular suspensors have also been described in the cephalic region of the Cephalocarida by Hessler (1964) and in the nauplius of the barnacle *Balanus balanoides* (L.) by Walley (1969) who, on the basis of sarcomere length and features revealed by electron microscopy, suggested that they are probably slow muscles – in contrast to the fast muscles that actuate the appendages. Slow muscles can maintain contractions over long periods of time during sustained depolarization, an attribute well suited to their role as suspensors.

Behind the suspensors of the transverse mandibular tendon, and supporting the posterior cephalic endoskeletal sheet, is another pair of suspensors (PS) each member of which inclines forward and laterally as it ascends to insert alongside the suspensor of the transverse mandibular tendon of its side (figures 14–16). This pair of suspensors too is muscular.

An array of muscles responsible for mandibular movements is already present (see especially figures 13 and 17), but some of those that are massive in the adult are as yet feebly developed. This is so particularly in the case of the promotor and remotor roller muscles which, following the terminology employed by Manton (1964) and used also in the Cladocera (Fryer 1963, 1968, 1974), are designated 3 and 4 respectively. The promotors are, however, assisted by the accessory promotors (AP) already noted. By contrast some of the transverse mandibular muscles are well developed as is made particularly apparent in figure 13. The 5c muscles, which insert on the posterior edge of the mandibular gnathobase and originate on a uniting ligament in the mid-line, and also a series of transverse muscles (TMM) that originate on the transverse mandibular tendon are already formed. The transverse tendon serves from these early stages the function that it will fulfil throughout life and the fate of some of the muscles originating on it can be followed from the third (and probably earlier) nauplius to the adult. It also serves as a transient site of anchorage for certain palp muscles. The short peripheral muscles of the 5a, b and e series are most readily apparent in figures 12, 13 and especially 17, where they are separately labelled. While some of the larger transverse muscles are clearly differentiated as such, some of the muscles-to-be appear at this stage to be entirely tendinous (see especially figure 14, FPM), though they certainly become functional muscles in later instars.

The mandibular palp has its own muscular system, two components of which, the extensors EMP1 and 2, have been noted above. Other elements are indicated particularly in figures 12 and 13. The major flexors (FMP) are of particular interest in that they utilize the transverse mandibular tendon as their site of origin.

Others muscles already of functional significance in the early instars include the labral levator (figures 12–14 and 16, LLM) and the various oesophageal dilators (ODM) readily apparent in the figures.

Posteriorly the oesophagus is provided with a pair of long suspensors, or bracers (OSD), which appear to serve also as dilators for they are in part muscular (cf. the suspensors of the cephalic endoskeleton). These extend posteriorly beyond all the extrinsic antennal muscles. Their course can be followed in different planes in figures 14 and 15, 16 and 17, and 19.

The antennary gland (AG) is a conspicuous feature of the larva in the early instars and is seen from various aspects in figures 14, 17 and 19. The labral glands (LG) and the three associated secretion-filled reservoirs (RLG) are also already conspicuous (figures 16, 18 and 19) and their exit ducts can be seen in some sections (figures 16 and 18). Other anatomical features, such as parts of the nervous system, and the ocellus (O), are indicated in the figures but require little comment, though the large volume of the cerebral ganglion (figures 12–14 and 16, CG) and the massive nature of the nerve cords (figures 13 and 16, NC) relative to total volume are noteworthy. The mid-gut (MG) is at this stage a simple tube, there being no sign of anterior caeca.

5. Swimming and feeding in the naupliar stages

Apart from a brief mention by Cannon (1928) relating to *Chirocephalus* and a more detailed account by Gauld (1959) for *Artemia*, nothing seems to have been recorded about the swimming and feeding of anostracan nauplii until some information for *Artemia* was given by Barlow & Sleigh (1980). Nauplii of other crustaceans have been considered from these standpoints very briefly by Cannon (1924) (Conchostraca) (see also Cannon & Manton 1927) and in more detail by Storch (1928) (Copepoda), Lochhead (1936) (Cirripedia), Norris & Crisp (1953) (Cirripedia) and Gauld (1959) (Cirripedia and Copepoda). As Gauld showed, branchiopod nauplii differ in various ways from those of non-branchiopod crustaceans, a matter confirmed by the morphological comparisons of Sanders (1963). The differences have phyletic implications but in the context of functional morphology are important chiefly in that the branchiopod type differs markedly from the non-branchiopod nauplius and that comparisons are of less value in helping to appreciate the anostracan mechanism than the superficial similarity of all nauplii might suggest. It is worth noting also that not all accounts of non-branchiopod naupliar mechanisms are in agreement; Gauld for instance was unable to confirm some of Storch's observations on the nauplii of calanoid copepods.

(*a*) *Swimming*

In *B. ferox* locomotion is similar in the various early stages and much of the following account applies to all but is based mostly on observations on stages 2–5 with additional observations on later stages. Propulsion is entirely by means of the antennae which beat at between 5 and 6 c s^{-1} at room temperatures. Barlow & Sleigh (1980) report a rate of 8–10 c s^{-1} in *Artemia* nauplii at 20 °C, falling to 6–7 c s^{-1} in older stages. In arthropods propulsion by a single pair of limbs is unusual but the antennal-powered swimming of the nauplius has been retained by the adult in two branchiopod orders, the Conchostraca and the Cladocera. Because the nauplii are small their forward movement has scarcely any momentum: inertia is scarcely relevant. Their small size means that to them water is a viscous medium (a low Reynolds number environment) and they must use viscous forces to lever themselves through it. Each backward swing of the antennae (described in more detail below) which can be likened to the working stroke of an oar in a rowing boat, propels the animal forward only during the period of swing. At the end of the stroke forward movement virtually stops. Notwithstanding the fact that, as they make their forward, recovery, stroke, the antennae are so orientated as to reduce resistance to the water (drag), they exert a force that actually pushes the nauplius backward slightly. This can be seen by simple observation in the feebly swimming stage 1 nauplius and is clearly revealed by high-speed cine-photography in older larvae. Lacking the momentum that is so beneficial in larger, streamlined, aquatic animals, the nauplius is in a similar situation to a walking terrestrial animal, where forward movement is directly related to the thrust of a limb, but whereas there is no penalty for making the recovery stroke in the latter such is incurred in the nauplius of *Branchinecta*.

Gauld (1959) described the stroke of the antennae of *Artemia* as 'a very simple one'. While this is basically true of the general movements of *B. ferox*, superimposed on the simple movements are some subtle refinements. Muscular co-ordination of the naupliar antenna is indeed of a high order, involving numerous muscles, both extrinsic and intrinsic, which suggests the existence of well developed proprioceptors. Furthermore, while for the most part a rhythmic cycle of activity is followed, this is not rigidly stereotyped. The sequence and degree of contraction of individual muscles can be modified according to need, e.g. for turning or backing away from an obstacle, which shows that the repetitive excitatory stimuli, presumably arising in the cerebral ganglia, can be modified. The angle of attack of the antennae can clearly be altered to enable the nauplius to rise in the water, and the masticatory spines are also capable of independent movements of considerable magnitude that when necessary can be superimposed on those that take place during the basic cycle (figure 11).

A swimming nauplius generally lies ventral surface uppermost. In the following account the region above such a swimming animal is referred to as dorsal; the region below it as ventral. At the beginning of the working stroke the antennae are extended anterior to the body (figure 20A) so as to be directed more or less forward. The posterior origin of muscles D5 and D7 confers a useful mechanical advantage here. The annulated exopod, and the endopod, are rotated forward so that their setae are directed to a considerable extent dorsally. At this stage the distal masticatory spine, which lies in the horizontal plane, is directed more or less at right angles to the trunk and lies remote from the labrum and mandibles, and the proximal masticatory spine, which lies in the same plane, is directed essentially backwards, and also lies well clear of the labrum.

As the antennae swing backwards in the horizontal plane (figure 20B) they are fully extended and, during the early part of the cycle, rotate even further forward so that their widely spread armature of setae presents a large area in a plane not far from vertical to the horizontal axis of the body. This rotation is initially sufficient to more than offset the forward impetus given by the at first more lateral than posterior thrust of the antennae, and the nauplius actually moves back by a minute amount (region of graph immediately to right of position A in figure 21). Very quickly, however, the swing of the antennae begins to be more posterior and more effective and impels the animal forward, tending at the same time to lift the anterior end a little. Forward movement is at first slight. (The distance traversed since the previous position illustrated is indicated by the length of the line on each outline shown in figure 20 and the time interval between successive positions is also recorded.)

As the antennae continue their backward swing (figure 20C) the nauplius accelerates rapidly. Although the time interval between positions B and C is only 90% of that between A and B, forward motion is more than 6.5 times greater. During this phase of the backward swing the distal portion of each antenna, and the endopod, begin to rotate backward so that formerly more or less dorsally directed setae gradually become directed more posteriorly. This inevitably gives a little lift. By the time the antennae are extended laterally, with some dorsal inclination, in which position they are fully stretched (figure 20C), the proximal masticatory spines are approaching the margin of the labrum, and the distal portions of the distal spines, which travel more quickly, lie just outside the proximal spines.

Rapid forward progression continues as the antennae continue to swing back beyond the mid-point, but speed decreases as their angle of attack becomes less effective and is considerably reduced by the time they lie as shown in figure 20D. By the time that they have reached this position the proximal masticatory spines have swung into the gap between the labrum and the trunk and the distal spines are approaching it. This position represents more or less the posterior limit of swing of the antennal protopods though, by dint of flexure, the more distal portions continue the propulsive phase of the cycle somewhat further. Such flexure, which causes the antennae to present a crescentic profile when viewed ventrally (figure 20E), is permitted by the annular nature of the exopods and an appropriate band of muscle along the posterior margin of each exopod. This is shown in figure 26 for a stage 8 nauplius which, being somewhat larger than those used in the preparation of figure 20, enables muscles more easily to be traced, but the pattern is the same in both. It is interesting that although in this position the animal has a shape that is more 'streamlined' than at any other phase of the cycle, and has just received a powerful propulsive thrust, forward motion has virtually ceased: a graphic illustration of the irrelevance of streamlining as a means of reducing drag at low Reynolds numbers. In larger animals streamlining reduces the loss of energy to the wake: here the wake is unimportant, or non-existent.

Although only incidental to locomotion, two other movements that accompany the backward swing of the antennae (except in the earliest instars) are conveniently recorded here, namely a forward and ventral swing of the antennules and a lateral (forward) swing of the mandibular

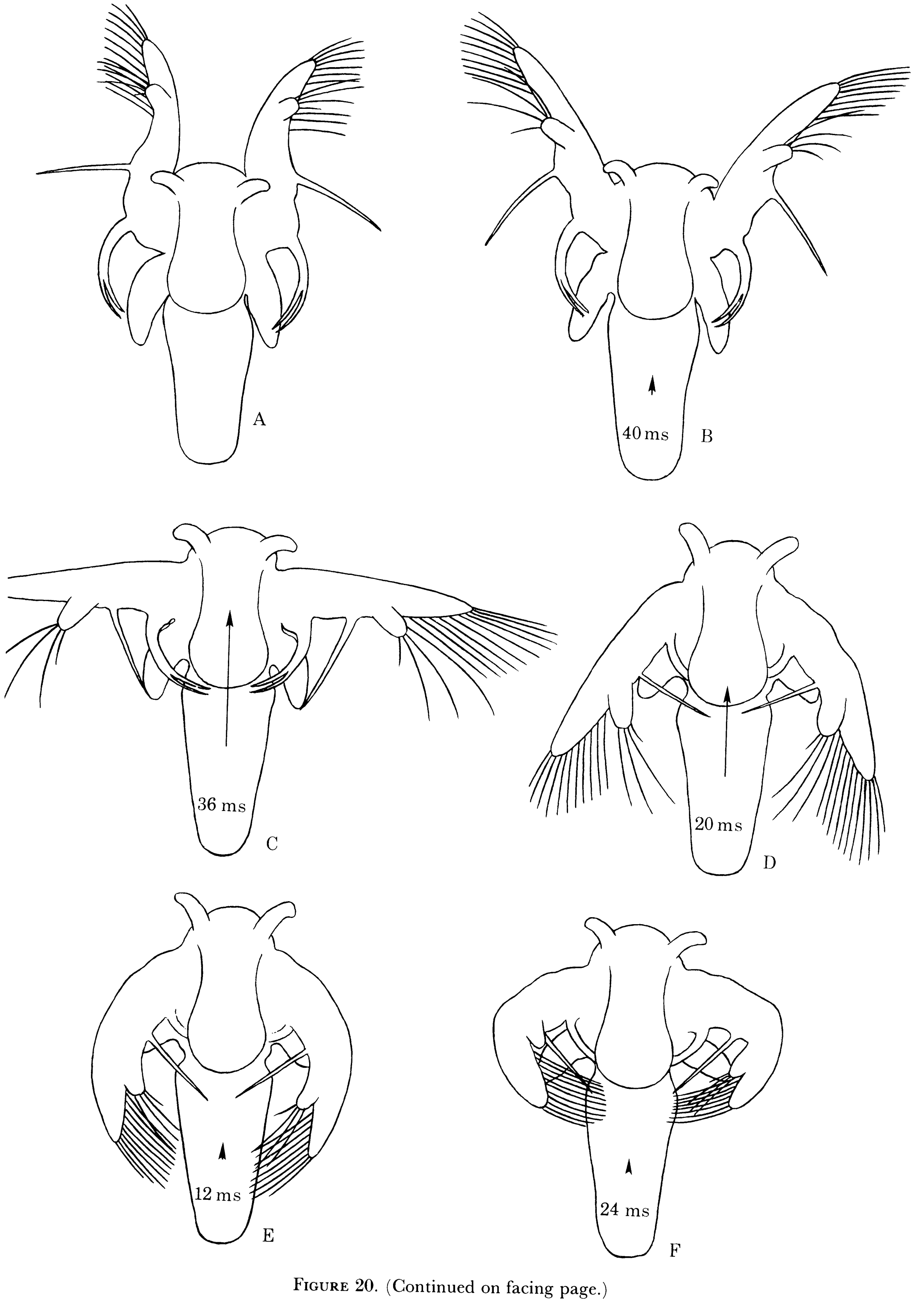

FIGURE 20. (Continued on facing page.)

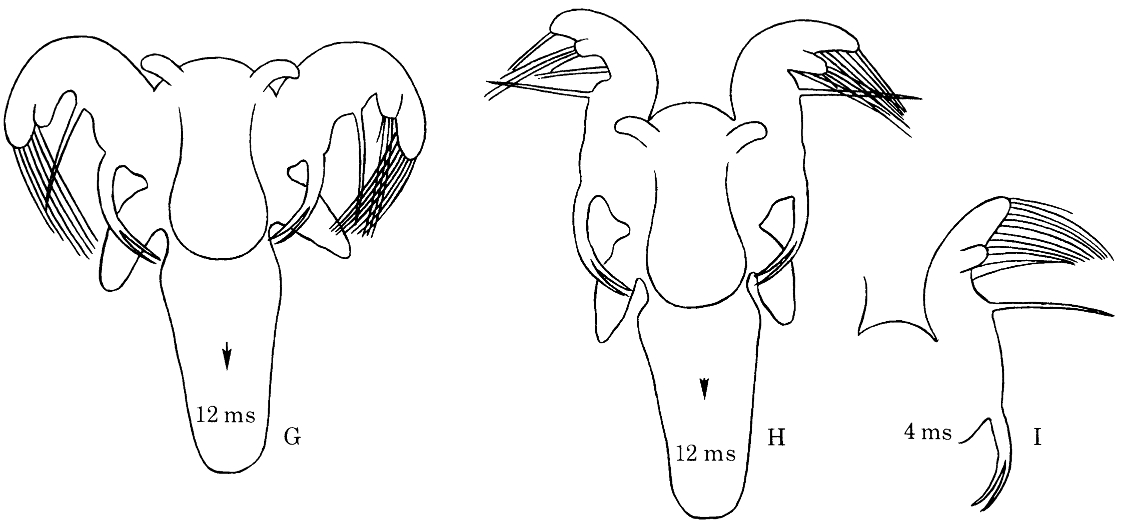

FIGURE 20. Simplified outlines made from cine film of a complete cycle of locomotory (and feeding) activity of the antennae of a stage 4 nauplius swimming horizontally, ventral surface uppermost. Natatory setae are indicated only by single lines and only sufficient of these are shown to reveal their disposition. Setae of the mandibular palp are omitted. The apparent increase in length of the nauplius (shortest at A, longest at E) is the result of a slight lift of the head end during the early part of the cycle, followed by a slight sinking towards the end. Arrows indicate the distance and direction moved from the previous position. The time interval (which is not the same in each case) is also indicated. The distance moved in B is a net movement which includes a small backward component (see figure 21): in all other cases movement is exclusively in the direction shown. See figure 21 for a graphical representation of this cycle.

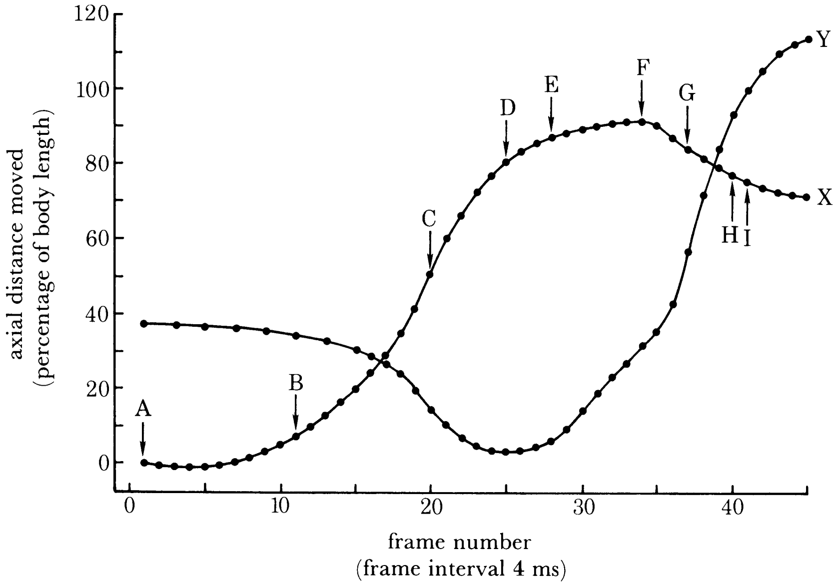

FIGURE 21. Progression in a stage 4 nauplius, swimming horizontally, ventral surface uppermost, at room temperature, throughout a single cycle of movement of the antennae. The points of curve X were obtained by plotting at intervals of one frame the location of the anteriormost point of the body from greatly enlarged images cast by a film made at 250 frames per second. Trivial discrepancies arise from the difficulty of plotting the anteriormost position exactly and because the anterior end lifts somewhat during the cycle, but these in no way obscure the clear pattern. Lettered arrows indicate the points in the cycle that correspond to those showing the disposition of the appendages in figure 20. Curve Y plots the axial position of the tip of the antennal exopodite throughout the same cycle of movement: initially, where the movement is small, at intervals of two frames; later at intervals of one frame. The relatively small amount of posterior movement is clearly shown. (The minor discrepancy between the distance from the antennal tip and the anterior end of the body at the beginning and end of the cycle is probably due to a slight lift of the anterior end during the course of the cycle.)

palps (figure 20A–E). What in larger animals would be a wilful disregard of the principles of streamlining on the part of the antennules is particularly noteworthy. This movement is certainly not passively induced, and the muscles responsible (figures 13 and 17, A1 M) are indeed readily identified. The extension of the sensory antennules at this phase of the cycle enables the environment ahead of the nauplius to be explored at just the time when information from this region is most valuable.

The very last, and minute, forward push is given by the antennae just after the stage shown in figure 20E, and these appendages then begin the return phase of the cycle. The protopod begins to swing forward but the exopod flexes even more (figure 20F) so that it presents little resistance on the return stroke. The setae are also bunched. Nevertheless resistance is sufficient not merely to retard progress but to reverse it, and as the antennal protopods pass the horizontal position the nauplius actually moves backwards (figure 20G).

The exopods remain curved backward throughout the time that the protopods are swinging forward and it is only after the latter are directed fully forward that the exopods begin to swing forward (cf. figure 20G, H), thereby reducing resistance to a minimum. During this phase of the cycle the endopod and exopod rotate forward to return their setae to the position taken up at its beginning. This is the most efficient phase of the cycle during which to undertake this operation: resistance that would push the animal backward as the antennae move forward has been avoided; rotation now neither pushes the animal backward nor impedes forward progression but merely depresses the head end slightly.

Progression throughout the cycle illustrated in figure 20 is shown graphically in the lettered curve (X) of figure 21.

Although figure 20 shows the successive positions of the antennae during a cycle of activity and the distance moved by the nauplius between one such position and the next, it cannot reveal the important fact that the antennae do not move backward through the water to the extent that the illustrations might imply. Because of the viscous nature of the medium to an animal of such small dimensions, the antennae do not so much propel the nauplius by pushing water backward as lever it forward by pressing against a relatively unyielding medium. During the backstroke, therefore, the absolute backward movement of an antenna is small as can best be appreciated by consideration of the trajectory described by the tip of the exopodite, which of course has the maximum amplitude of any part of the antenna. The axial distance moved by an exopodite tip throughout a cycle of movement is plotted in figure 21, curve Y, and the actual course of the tip is shown in figure 22, where successive positions corresponding to the frame numbers used in figures 20 and 21 are plotted. The position of the anterior end of the nauplius at different phases of the cycle is also indicated. Figure 24 shows the swimming of a nauplius in a diagrammatic manner, but uses actual plots of the trajectory of the tip of the antennal exopodite. This clearly reveals the short backward component of motion, that is the very small distance that the exopodite tip actually moves backward through the water. More proximally the distance moved is of course even less. Figure 23 shows the approximate trajectory of the tip of the endopodite. While it is not easy to plot successive positions of this region with absolute accuracy this is irrelevant; the very small backward component is very evident and has important repercussions in relation to the interpretation of the feeding mechanism (§5(*c*)).

The lack of any hinge or articulation in the antennal setae has been noted (§3(*b*)) and is reflected in a difference between the swimming mechanisms of the nauplii of *B. ferox* and *Artemia*. The latter has setae that are hinged in the typical branchiopod manner. According to Gauld

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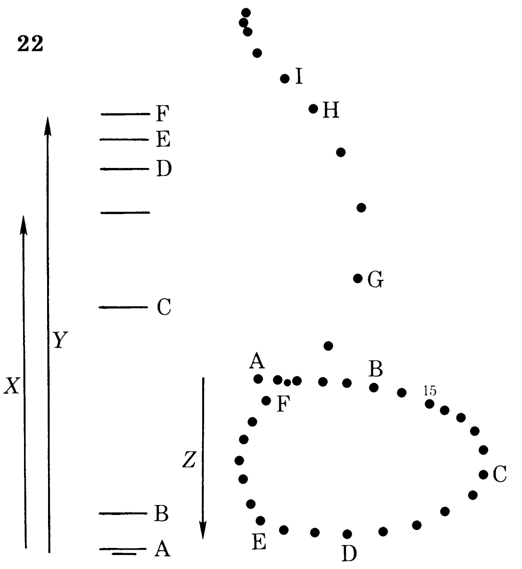

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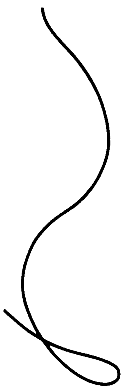

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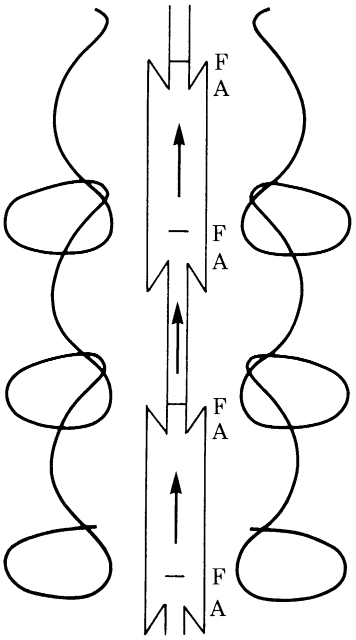

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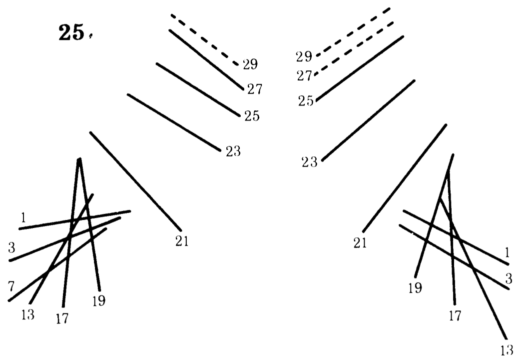

Figures 22–25. Antennal movements of a swimming nauplius.

Figure 22. The trajectory of the tip of an antennal exopodite during a cycle of movement, plotted from the data used in figures 20 and 21. The spots show the position of the exopodite tip at intervals of 8 ms up to position 15, then at intervals of 4 ms. Letters correspond to positions illustrated in figure 20 and indicated on the graphs in figure 21. Corresponding positions of the anterior end of the nauplius throughout the cycle are shown to the left where *X* shows the net, *Y* the gross, forward movement. *Z* shows the actual posterior distance moved by the tip of the antennal exopod.

Figure 23. The trajectory of the tip of the antennal endopodite during the same cycle of movement. Note the very small absolute backward component.

Figure 24. Diagrammatic representation of a swimming nauplius showing three cycles of antennal movement. The trajectories shown are for the tip of the exopodite.

Figure 25. The movement of the distal masticatory spines of the antennae through the water during part of a cycle of activity, based on outlines from a cine film. The numbers correspond to the frame numbers used in figures 20–22. Note the small backward component during the early part of the cycle and the long broadside sweep from about frame 13 to frame 29. Dashed lines are used where the outline of the spine was not distinct.

(1959), during the recovery stroke each seta trails, evidently as a result of passive flexure at the hinge, so that resistance to the water is reduced to a minimum. The lack of hinges prevents passive trailing of these setae in *B. ferox*, as can be seen particularly well in figure 20H, I. The device employed appears to be more akin to that of the nauplius of certain copepods, cirripedes, euphausids and penaeid prawns in which variation in the effective area of the setal paddles is brought about 'by flexing and extending the apical segments of the exopodite of the limb so that the setae...are opened and closed like a fan' (Gauld 1959).

It is interesting that *B. ferox*, a branchiopod *par excellence*, departs from the rule of having hinged natatory setae on the antennae and displays what Sanders (1963) recognized as a non-branchiopod character. One can only speculate as to whether this is a secondary specialization by loss of a hinge (of which faint suggestions can sometimes be seen) or a primitive attribute. A simple seta is presumably more primitive than one that is hinged. This deviation does not invalidate the recognition of branchiopod and non-branchiopod naupliar types.

The account of Barlow & Sleigh (1980) of the swimming of the nauplius of *Artemia* shows that, as expected, the process is similar to that of *B. ferox*. Barlow & Sleigh also employed cine-photography, but most of their observations are based on animals glued to a fine needle of glass so that the nauplius remained stationary and propelled water backwards with its antennae. While facilitating filming, this method has the disadvantage that the early, very small, stages that in effect lever themselves through a viscous medium, may perform unnaturally as the antennae have to be forced through water on which they would normally push. While this will be partially offset by the lack of forward movement of the whole animal, the forces involved are unlikely to cancel each other out exactly. In nauplii that have in some way been trapped, I have seen the distal portion of the antennal exopod bend forward in a shallow U towards the end of the working stroke exactly as one would expect if it were forced through relatively unyielding viscous fluid. This has never been seen in a free-swimming individual. In spite of such problems, larger, tethered nauplii observed by Barlow & Sleigh clearly behaved in a very similar manner to those of *B. ferox*.

(*b*) *Mobility and musculature of the antenna*

The antenna owes its great mobility – readily apparent from figure 20A–I which, however, show only the orthodox swimming movements – to the essentially jointless nature of the protopod and its complex musculature, shown for a stage 8 nauplius in figure 26. Although the branchiopod nauplius is primitive, its antennal musculature is more complex than, for example, that of a malacostracan walking limb. The lack of joints proximally extends even to the union of the protopod with the head. Here, while there is the suggestion of strengthening in what would be the rim region of a jointed appendage, it has proved impossible to recognize any particular pivotal regions, or indeed clearly to demarcate the appendage from the head.

There is, however, a simple joint between the protopod and the endopod and there are appropriate flexor and extensor muscles. The pivots appear to be more or less anteriorly and posteriorly located when the antenna is viewed in the horizontal plane. Likewise the exopod has a recognizable, but not particularly distinct, articulation with the protopod.

Well defined annuli are formed in the cuticle of the essentially cylindrical exopod. Even here, however, there appear to be no pivotal points between adjacent rings though there is more arthrodial membrane anteriorly, where the walls of the rings are thickest, than elsewhere (figure 26, inset). Here each ring telescopes inside its proximal, and larger, partner and it is easy to

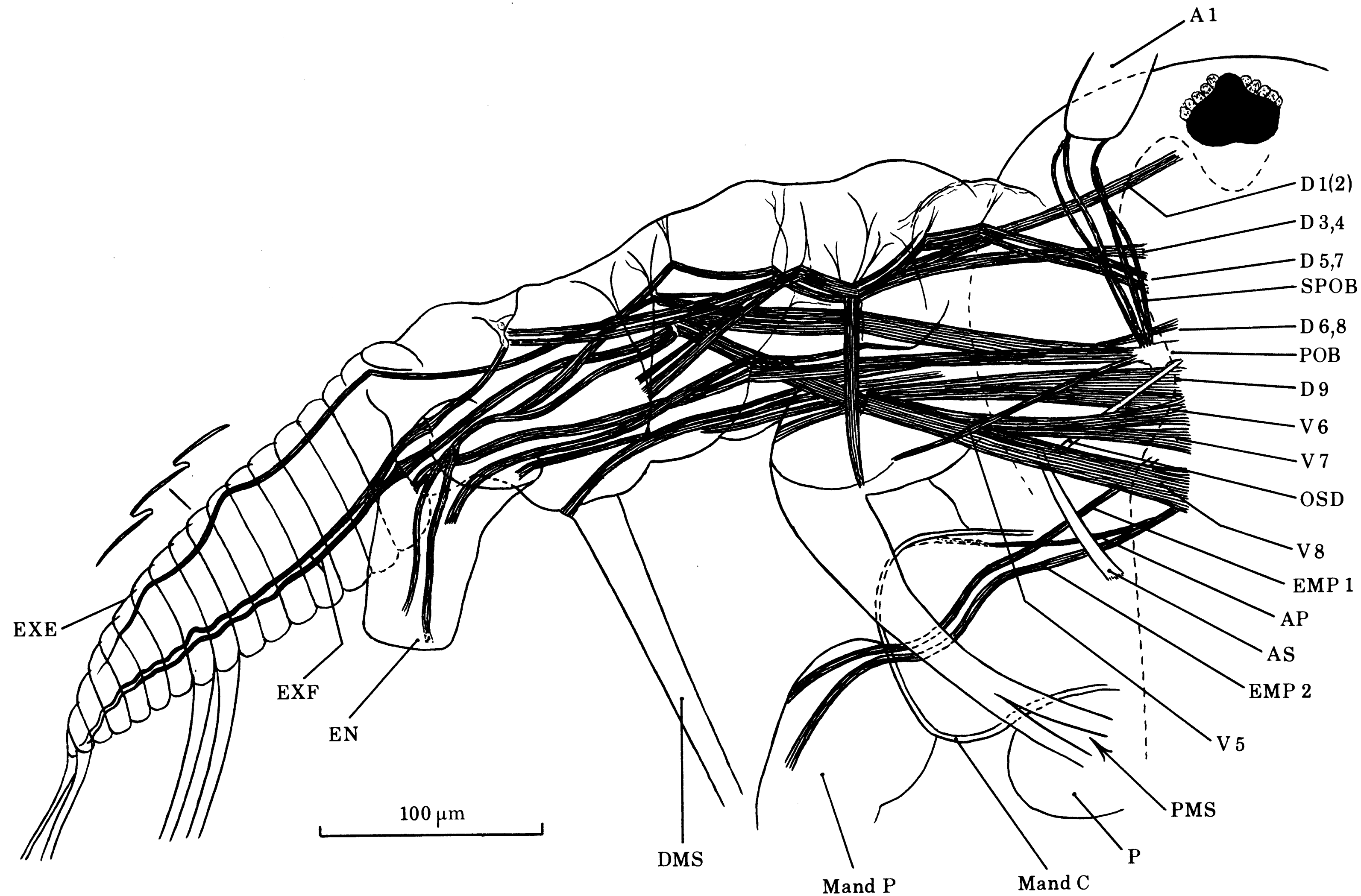

FIGURE 26. The antennary musculature of a stage 8 nauplius, ventral. All non-muscular soft tissues are omitted and only a few of the suspensory fibrils of the muscles are shown. The two dorsally originating mandibular palp muscles (EMP 1 and 2) and muscle AP are also shown but no other mandibular muscles. Muscle AP inserts on the mandibular margin dorsal to the outline seen ventrally, the margin at that level being indicated by a dashed line. The outline of the alimentary canal is indicated by a dashed line simply as a landmark but is treated as if transparent. In fact it obscures the proximal extremities of all the dorsally originating segmental muscles. The inset shows, in a simplified manner and to a larger scale, the arrangement of the anterior region of the exopod rings.

see how, when the exopod is flexed, as it is in the latter part of the cycle portrayed in figure 20, the arthrodial membrane will permit the necessary pulling apart of the rings anteriorly that inevitably accompanies flexure. It is also easy to see how, in conjunction with the exopod flexor and extensor muscles of the protopod, the relatively simple intrinsic flexor (EXF) and extensor (EXE) muscles of the exopod give rise to the shape changes shown in figure 20. Thickening of the cuticular rings more posteriorly appears to be strengthening associated with the insertion of the natatory setae.

Hydrostatic pressure may be involved in exopod extension, and certainly plays a part in maintaining turgor here as well as in the limb as a whole.

Although for the most part lacking true joints, the antennal protopod has a complex system of internal fibrils, sometimes expanded to give small sheets, that sling or support the muscles and provide points of attachment (both origins and insertions) of muscles. It is sometimes difficult to decide from simple observation whether a given set of fibrils merely supports a muscle or represents a point of attachment.

While the role of some of the muscles is self-evident – e.g. the powerful posterior ventral muscles, V 6, 7 and 8, clearly make a major contribution to the remotor swing of the antenna – it is not easy to appreciate how the appendage is swung to the extreme point of promotion (figure 20). The secret seems to lie in the various muscles, or segments of muscles, that traverse the protopod from a posterior origin and insert more anteriorly and proximally and which, with the major extrinsic promotors, extend different regions (pseudo-segments) of the appendage, while the anteriorly located horizontal sections of muscles assist by their tendency to shorten the leading edge of the protopod. Again hydrostatic pressure also conceivably plays a part.

Both proximal and distal masticatory spines enjoy considerable independent movement. The proximal spine is actuated entirely by muscles, but while the abduction movement of the distal spine is controlled by a powerful muscle this has no antagonist, adduction presumably being affected by cuticular elasticity, perhaps aided by hydrostatic pressure. It is interesting that it is the working stroke that is so powered, but no real load is imposed on this spine as it sweeps orally.

Aided by its annulations, the exopod is much more flexible than is manifest during ordinary swimming. When necessary it can be bent sharply forward, an attribute perhaps seldom called upon in Nature but one that is not infrequently displayed in the confines of the small cells in which some of the observations were made, or when movements are restrained.

(*c*) *Feeding*

As it swims the nauplius also collects and manipulates its food. Both Cannon (1928) and Gauld (1959) believed that the natatory setae of the antennae were responsible for the collection of food particles in anostracan nauplii and Barlow & Sleigh (1980) believe that Gauld's explanation 'is probably true'. Gauld correctly described how these setae sweep inwards towards the end of the power stroke and then pass around the posterior end of the labrum beneath which he thought they swept particles. Barlow & Sleigh (1980) describe how the setae actually pass beneath the labrum in *Artemia*, but this is not the case in *B. ferox* where, on the recovery stroke of the antennae, they begin to be withdrawn laterally before they reach the labrum (figure 20E, F).

While the action of the natatory setae is such that they may occasionally bring material to the posterior end of the labrum, as Barlow & Sleigh record, I believe their function to be concerned solely with locomotion. In *B. ferox* they lack any setules such as would enable them to collect suspended particles as they sweep backward, and there appears to be no means of transferring from the antennal setae to the proximity of the mouth any particles so caught.

The most fundamental objection to the idea that the natatory setae collect food particles, however, is the fact that, especially in the early instars, they scarcely move through the water. As described in §5(*a*), and illustrated in figures 21–24, the distance moved even by the tip of the exopodite during what, if they acted as filters, would be the filtering phase of a cycle, is small, and that moved by more proximal regions even less. If they were to filter, they would be extremely inefficient. Their role is not food collection but the propulsion of the nauplius. The selective forces favouring these activities are diametrically opposed.

Further, in the form of the distal masticatory spines, the nauplius possesses apparatus specialized for the sieving of particles and for conveying them towards the mouth. As figure 20A–D shows, as the antennae swing backward these spines, which are armed with sieving setules (figure 5), sweep through a wide arc.

However, for the same reason as the natatory spines actually sweep only a short distance through the water during the working stroke of the antennae, so too during the initial phase do the distal masticatory spines, at least in early instars. This, however, does not prevent them from sweeping through a considerable volume of water. The positions occupied by these setae during certain phases of a cycle of movement are shown in figure 25, where numbers correspond to the frame numbers used in figure 21. (For some of the actual positions see figure 20.) These show how, during that phase of the cycle in which the nauplius is moving forward most rapidly, and during that in which the antennae begin their return stroke, the distal masticatory spines sieve a considerable volume of water and inevitably collect and convey towards the labrum any particles that they encounter. These are swept into the vicinity of the openings of the three ducts of the labral glands. Figure 16 shows the relation of one of these spines to the duct exits in a stage 4 nauplius. Some collected particles may therefore become entangled at this stage of the cycle.

As the distal masticatory spines leave the neighbourhood of the labrum and swing anteriorly and laterally during the return phase of the antennal cycle, they sweep past the proximal setae of the mandibular palp which are actually moving in the opposite direction (figure 20E, F, and see also G and H to show the further movement of the palps). Figure 2 shows the relative positions of the setae and spines concerned in a stage 2 nauplius, a condition that holds good also in older nauplii. Gauld (1959) comments on the combing function of the mandibular palps in *Artemia*, but admits that they cannot effectively clean all the antennal setae (fewer in number in *Artemia* than in *B. ferox*) which he believes to be the collectors of the food. This is even more true in *B. ferox*, but no such problem confronts the mandibular palp setae when it is only the distal masticatory spine that they have to clean. It is spines 3 and 4 of the palps, and essentially the long ventral spinules of these, that are important here. The arrangement and movements of the mandibular palp spines (figures 6 and 7) are suitable both for entrapping particles and for carrying them towards the labral gland secretions and within the ambit of the very mobile proximal masticatory spines of the antennae. The way in which the mandibular palps can flex to assist sweeping was noted in §3(*c*) and is indicated in figure 11. The proximal masticatory spines of the antennae pass freely beneath the labrum and convey material to the vicinity of the mandibular gnathobases. Their brush-like armature (figure 4 for a stage 2 nauplius; figure 12 for stage 3 and subsequent stages) is well suited to this task.

Material arriving behind the mandibles is dealt with by the gnathobases which, from their earliest movements, operate with the typical branchiopod roll (Manton 1964; Fryer 1963, 1968, 1974). Morphological and functional changes in the mandibular gnathobase and its associated spine between stages 2 and 3 are described in §3 and the ontogeny of the mandibular armature is dealt with in § 15.

Although the above sequence is re-enacted with seemingly monotonous regularity, and the appendages concerned are apparently incessantly active, it is not rigorously stereotyped. By virtue of their basal articulation and musculature the proximal masticatory spines enjoy wide freedom of independent movement and can swing independently through an arc of at least 60°. This enables them to sweep beneath the labrum right up to the level of the mandibular gnathobases. Nor need left and right spines operate in a synchronous manner. Similar, but less spectacular, independent mobility is exhibited by the distal spines.

Although there is only a single food-collecting spine on each side, each sweeps almost incessantly and covers a considerable distance during each cycle of movement, the cycle being repeated more than five times every second at room temperatures. In the situations inhabited by *B. ferox* suspended particulate matter is generally abundant, thus facilitating the collection of sufficient material. Further, the 'mesh size' of the spines is such that relatively large algal cells or detrital particles can be handled.

To anticipate later development, Barlow & Sleigh (1980) note that in *Artemia* the antennae continue to beat after the trunk limbs become operative, as is also the case in *B. ferox*, and that progression becomes smoother as the efficiency of the trunk limbs increases, but that even in individuals in which many trunk limbs are active there is a jerk when the antennae perform their working stroke. They also remark that by the time several trunk limbs are active the antennae 'no longer curve over the ventral surface to bring water and filtered particles to the mouth' but come to rest after travelling through 180° – as they must because the anterior trunk limbs prevent any further swing – before the recovery stroke. This further confirms the purely natatory function of these setae. Even if they did collect food, which they do not, they could not function in such instars. However, the food-collecting distal masticatory spines are still functional, and continue to collect food particles at this time. The restricted amplitude of beat of the natatory setae in no way interferes with the ability of the distal masticatory spines to transport particles to the developing mouthparts – as can be seen from the photograph (fig. 3) in the paper of Barlow & Sleigh.

Concerning the labral gland secretions, it is only fair to record that, in the limited number of early nauplii sectioned, no extruded material has been found in the vicinity of the exit ducts, though the presence of secretions in the reservoirs is easy to demonstrate even in the first, non-feeding, stage and is shown in a stage 4 larva in figures 16, 18 and 19. Secretions have been seen in the oesophagus of a stage 4 nauplius but their presence there is ambiguous. Extruded secretions have been found in copious amounts in later stages and are almost certainly involved from the outset. It was Cannon who first emphasized the importance of entangling labral gland secretions though he was only able to infer, not prove, their origin in any branchiopod, larval or adult, and Gauld (1959) was unable to demonstrate such secretions in the nauplius of *Artemia*. Unequivocal proof of the origin of similar secretions in several anomopod cladocerans (Fryer 1962, 1963, 1968, 1974) vindicates Cannon's belief.

Cannon (1924) and Cannon & Manton (1927) believed that the shape of the labrum of the branchiopod nauplius causes water to be sucked under it and towards the mouth region as the animal moves forward. This is unproven and I doubt whether such suction is involved. The hypothetical sketch of such currents given by Cannon & Manton (1927) shows currents passing orally but does not indicate how these leave the sub-labral space – as they must. Likewise Gauld (1959) found no evidence of Cannon's 'backwash' currents in the nauplius of calanoid copepods in which, although details of the feeding mechanism are different from those of branchiopods, a similar labrum is present.

While a comparison of naupliar feeding mechanisms is not necessary here, it is worth noting that the mechanism in *B. ferox* is clearly similar to that of *Artemia* and quite different from that of those non-branchiopod nauplii – copepods and cirripedes – for which information exists. In the non-branchiopod nauplii the mandibles are the chief collectors of food (Lochhead 1936; Norris & Crisp 1953; Gauld 1959).

6. A NOTE ON THE NUMBER OF INSTARS

It is not easy to ascertain the number of moults from stage 4 onwards nor to define individual instars. Limits of variation within an instar are difficult to ascertain and, in the early stages, it is not easy to define for example when a somite should be regarded as demarcated or a limb bud recognized as free. Later on it is equally difficult to be sure just when an appendage first begins to move or becomes functional. A limb that moves little at the beginning of an instar may show considerable activity at the end, though this does not involve external morphological changes. From the point of view of the continuity of function these are minor problems as they do not obscure the general pattern.

Notwithstanding the difficulties involved in defining instars, and even if allowance is made for some individual variation, the number recognizable is greater than generally recorded in anostracan development, including that of congeneric species. Following the initial recognition of numerous instars on morphological criteria, considerable success was achieved in rearing individual larvae in separate vessels at 10 °C. The sequence of development observed is shown in figure 27.

Comparisons with other species are not always easy as some previous work is clearly erroneous and different observers disagree in their accounts of the same species, but enough can be gleaned from some accounts to show that the sequence is not identical in all species. For example the careful work of Nourisson (1964) showed that all 11 trunk limbs of *Chirocephalus diaphanus* Prévost are fully differentiated by stage 10 and, notwithstanding certain errors on the part of Bernice (1972), the same is probably true of *Streptocephalus dichotomus* Baird, said by her to achieve this condition at stage 9. Heath (1924), who was aware of some of the difficulties and who certainly missed some stages, indicates, but without being specific on the point, that all trunk limbs are functional at stage 8 in *Linderiella occidentalis* (Dobbs) and that the entire life cycle involves 17 instars. On the other hand, although Hentschel (1968) gives no details of the last few such stages in *Artemia salina* (L)†, he refers to stage 17 as the last larval stage. The careful study of Benesch (1969), who recognized all limbs as functional at stage 18 (17 in his terminology as the hatching stage was designated as stage 0), is in agreement, and the discrepancy between these findings and those of Weisz (1947), who reported all trunk limbs to be functional at stage 20 (19 in his terminology), is sufficiently small to indicate that the

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† For a note on taxonomy see p. 331.

number of stages involved is greater in *Artemia* than in *Chirocephalus* and *Streptocephalus*. More surprising is the belief expressed by Daborn (1975), partly on the basis of erroneous observations by others, and partly as a result of an uncritical and erroneous assumption (1974) that in the huge *B. gigas* Lynch, which shows many similarities to *B. ferox*, the adult number of segments and the appearance of genital structures is attained at stage 7 and that the full life cycle involves 19 instars. At stage 7 in *B. ferox* only the three naupliar appendages are functional, and the number of instars is far more than suggested for *B. gigas*.

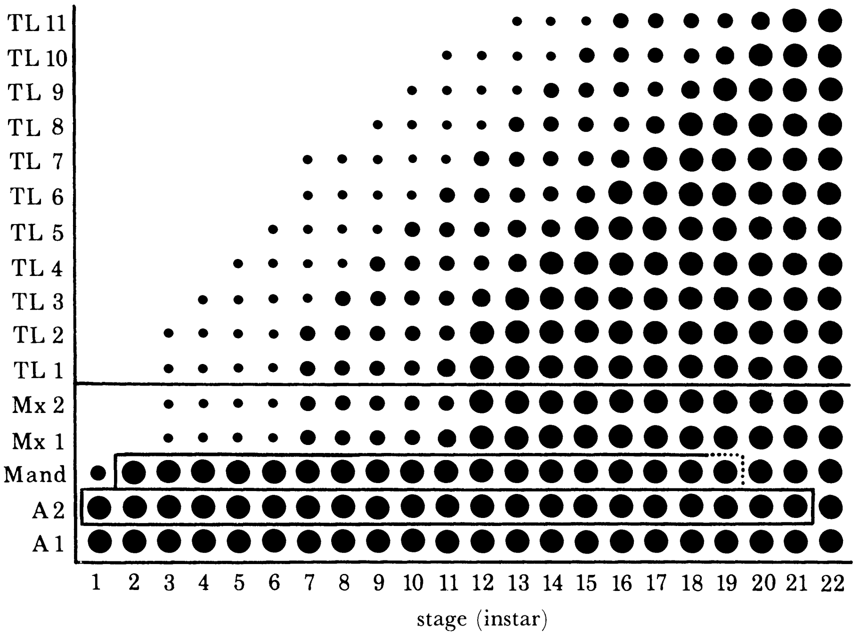


FIGURE 27. The sequence of appendage development in *Branchinecta ferox* from hatching as a non-feeding nauplius to the time that an adult way of life is pursued. Many additional instars succeed those indicated here. Stages in which the mandibular palps are functional and in which the antennae are either entirely responsible for, or assist in, locomotion and food manipulation are boxed. Four categories of development are indicated by successively larger circles: • appendage bud free; ● appendage with at least 1 seta; ⬤ appendage able to move but non-functional; ⬤ appendage functional but not necessarily fully differentiated (e.g. it may later accrue more spines or setae). While in most cases the assignment to these categories presents no problem the distinction is occasionally blurred, but this does not alter the general pattern. Limb buds are recognizable before they are free but are not indicated here. As the maxilla is virtually immobile the criterion used to assess it as functional is that the appendages before and behind it have become so. Although the maxillule is shown as functional at stage 12 its contribution at this stage is probably small.

The principal features shown in figure 27 are not affected by any minor discrepancies that may be due to difficulties of definition noted above. It is the pattern of development that is important. This is of considerable phyletic interest, differing as it does from that on which phylogenetic conclusions have recently been based (see § 16). No attempt has been made to ascertain the total number of instars. Animals are about 4.0 mm in length (exclusive of terminal setae) by the time that they reach stage 22; females begin to produce eggs at a length of about 17.5 mm and may continue to grow to a length of at least 45 mm.

7. FUNCTIONAL ASPECTS OF DEVELOPMENT FROM STAGE 5 ONWARD

(*a*) *Segmentation and differentiation*

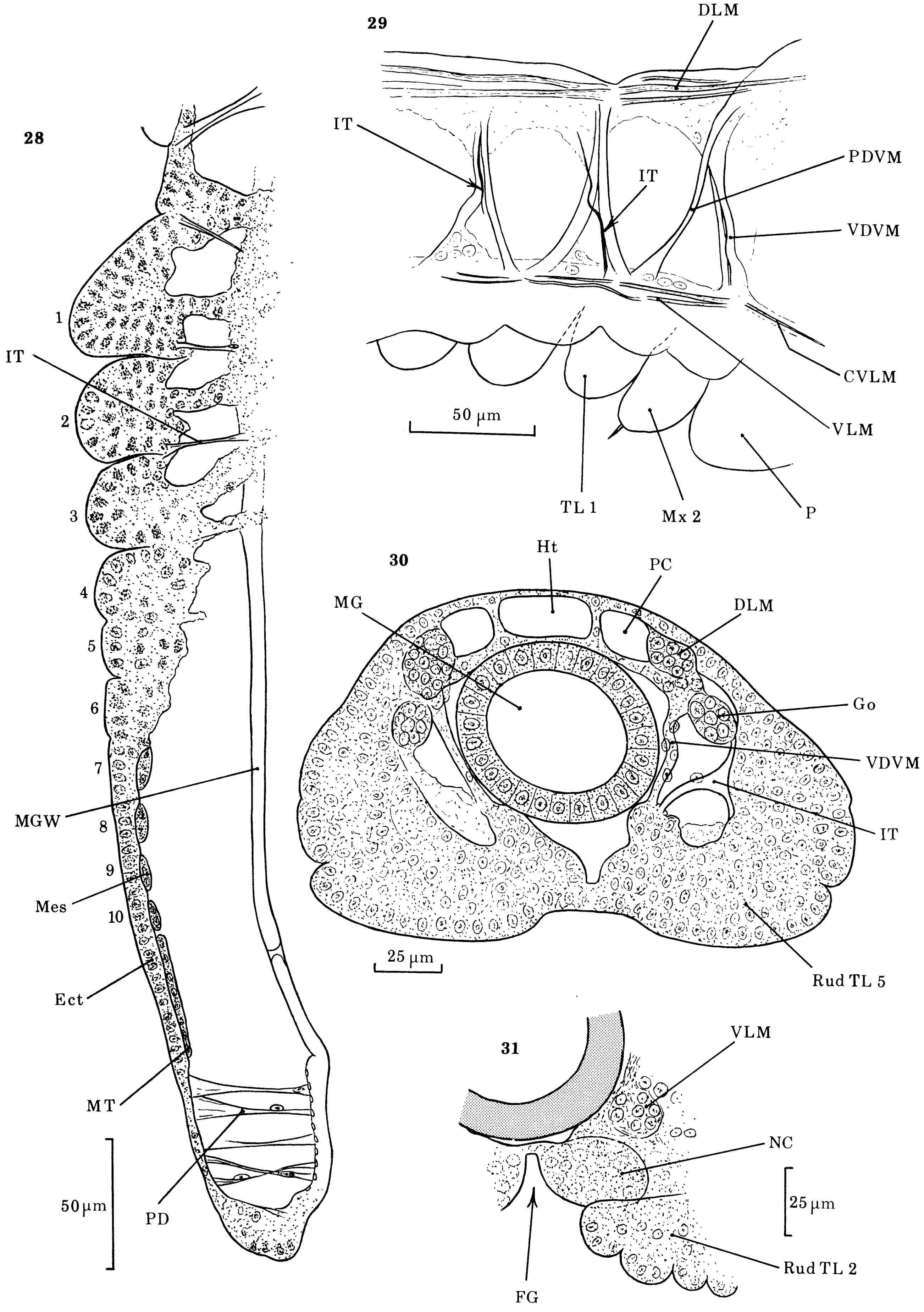
While the basic features of naupliar and post-naupliar development are well known in outline, certain points require elaboration and the timing of certain events, which has important phylogenetic implications, calls for careful description if the functional continuity of the process is to be understood. Valuable information on segmentation and differentiation is given for *Streptocephalus* and *Artemia* by Claus (1886) and for *Artemia* by Fränsemeier (1939), Weisz (1947), Anderson (1967) and Benesch (1969). Here remarks are confined to points essential to understanding or relevant to functional considerations.

Externally stage 5 differs little from the preceding stage, though an additional limb bud can be recognized and the posterior mouthparts are more distinct (figure 32). As in earlier instars segmentation can be traced much further back internally than externally (figure 28). Mesodermal somite bands (Mes) are differentiated in the tissues derived from the mesoteleoblasts (MT) before the overlying ectoderm (Ect) follows suit, a matter well treated in *Artemia* by Fränsemeier (1939) and in *Artemia* and the conchostracan *Limnadia* by Anderson (1967). Although Benesch (1969) says that a clear answer to the question of whether segmentation is initiated in the mesoderm or the ectoderm is not possible, the early signs of such in the mesoderm in *B. ferox* is readily apparent.

Anderson (1967) illustrates the early segmentation of the thoracic mesoderm in *Artemia*. Benesch (1969), however, throws doubt on the validity of these illustrations. Because he apparently failed to observe such signs of segmentation in well fixed material, he believes the condition observed by Anderson to be an artefact of fixation. However, my sections of *B. ferox*, prepared by a different method, reveal a very similar situation (figure 28) to that shown by Anderson. The answer is perhaps that this segmentation is at first seen only laterally and ventrally – being related to the subsequent development of trunk limbs – and would not be seen in a dorsally located horizontal section. Figure 28 is of a thick slice cut more or less in the mid-line and reveals the segmentation. Such is also seen in longitudinal sections, and is indeed depicted by Fränsemeier (1939) whose figure 6 shows many similarities to a longitudinal slice of a stage 5 larva of *B. ferox*.

From figure 28 it would appear that the dilator muscles/fibrils of the anus (PD), which lie posterior to the mesoteleoblasts, cannot be derived from mesoderm, and indeed the proctodael dilators were among the muscles of *Chirocephalus* that Cannon (1926) described as being of ectodermal origin. In the first naupliar stages, however, there is in the proctodael region a mass of mesoderm, from which the muscles are derived (cf. also: Anderson 1967; Benesch 1969). Having been differentiated, the telson, within whose precursor these muscles lie, is pushed back as a unit posterior to the teleoblasts. Appearances are therefore deceptive. A valid point made by Cannon (1926) is that, in *Chirocephalus*, these muscles are functional before they have any evident nerve supply, and this is true also in *B. ferox*. A possible explanation is that they are activated by stretch – now believed to be a general property of striated muscle. Pressure from the gut could stretch and activate the circular muscles, which also appear to lack a nerve supply, whose contraction could in turn activate the dilators.

Although the dilators of the anus are functional at this stage, and indeed have been so from stage 2, it is nevertheless difficult, and sometimes impossible, to make out their muscular nature even in well fixed preparations. They have the appearance of ligaments and would be classed



FIGURES 28–31. For description see opposite.

as such if their function were not known and one relied solely on histological criteria. Some of the transverse mandibular muscles present similar problems in early instars (§4).

Early stages in the formation of the thoracic endoskeleton in the form of intersegmental strands (IT), already to be seen at stage 4, are now more readily seen. These continue the sequence of intersegmental strands recognizable between maxillule and maxilla and between maxilla and trunk limb 1 which are detectable as early as stage 3 (figure 13). Clearer also are strings of cells, detectable in stage 4, that will give rise to dorso-ventral muscles. Similar strings of cells, the precursors of the dorsal longitudinal trunk muscles, can be traced at least as far back as thoracic somite 5 and perhaps into somite 6. (These are too dorsal to be seen in figure 28.) The first strands of the muscle fibres become recognizable in the next instar – by which time at least one additional limb bud is free (figure 27) – and have been detected in both the dorsal longitudinal and in the dorso-ventral series.

An excellent histological account of the development of the dorso-ventral muscles of *Chirocephalus diaphanus* has been given by Cannon (1926) who describes the way in which the muscle fibres form within the strings of primordial cells and how, as is also the case in *B. ferox*, there is differentiation dorsally and ventrally that ultimately gives rise to their fibrous attachments. The arrangement of these muscles, and details of the endoskeleton with which they are associated, are described for later stages below.

With each succeeding moult additional limb buds become free posteriorly in the sequence indicated in figure 27 and first the anteriormost, then succeeding trunk limbs, begin to differentiate, as do the posterior mouthparts (figures 29, 32–35).

(*b*) *Changes in the cephalic appendages*

The first movements of a post-mandibular appendage take place at stage 11 when the maxillules and first trunk limbs acquire this distinction but this does not render them functional, the burden of locomotion still being borne entirely by the antennae, that of feeding by the antennae and mandibles.

DESCRIPTION OF FIGURES 28–31

FIGURES 28–31. Early stages of differentiation.

FIGURE 28. Horizontal section of a stage 5 larva showing the development of limb buds anteriorly, the origin of the intersegmental endoskeletal tendons (IT), and the way in which the mesoteloblasts (MT) extend posteriorly, budding off mesoderm (Mes) which indicates somites not visible externally.

FIGURE 29. Longitudinal section of the left side of a stage 8 larva to show the position of the intersegmental endoskeletal tendons (IT) and the developing muscles. The full length of the anteriormost tendon shown is indicated though not all of it can be seen at one level of focusing. Its expanded dorsalmost portion, which also lies most laterally (see figure 30), only comes into view by focusing down. For convenience the dorsal longitudinal muscles (DLM) are shown more clearly than is indeed the case. Of the post-mandibular mouthparts only the maxilla (Mx2) can be seen. At this stage it lies internal to the maxillule (see figure 32).

FIGURE 30. Transverse section of a stage 9 larva in the vicinity of the rudiment of trunk limb 5 to show particularly the developing intersegmental endoskeletal tendon (IT) (seen to the right). The developing vertical dorso-ventral muscle (VDVM) is also clearly seen on the right. The rudiments of the dorsal longitudinal muscles (DLM) are well developed (muscle fibres are differentiated just anterior to this section): those of the ventral longitudinal series, already recognizable anterior to this section (see figures 29 and 31) develop in the ridge of tissue ventral to the tendon and vertical dorso-ventral muscle. Whether the tissues immediately ventral to the gut have been pulled away during fixation or display the correct orientation is uncertain. The rudiment of the gonad (Go) does not at this stage extend very far in the anterior–posterior direction.

FIGURE 31. The same as figure 30, but in the vicinity of the developing trunk limb 2 (Rud TL 2) to show the rudiment of the ventral longitudinal muscles (VLM). Note the more advanced development of this limb than of trunk limb 5 (figure 30), endite rudiments being recognizable.

The antennae change little throughout the stages in which they function as organs of locomotion and food manipulation. Although in *Artemia* they have been reported as ceasing to operate in these capacities by the time that the first six pairs of trunk limbs are functional (a conclusion that is questioned in §16), in *B. ferox* they remain fully effective in both roles until 10 pairs of trunk limbs are functional, and partially so at the next instar (21), when all 11 pairs of trunk limbs are functional. Until instar 20, at which trunk limb 11, although able to move, is clearly non-functional, there is no sign of degeneration of any of the antennal structures involved in either feeding or locomotion, unless it be that the proximal masticatory spines are slightly distorted. At stage 21, however, these spines are much distorted and cease to contribute to food handling. Their distal companions sometimes show slight signs of distortion but are still potentially functional though they are unlikely to contribute significantly and can no longer be cleaned. The natatory setae are relatively shorter at this than at the preceding stage but are still functional. There is individual variation in the rate at which these setae are lost. In stage 22 from two to eight rudiments remain distally on each antenna, and the endopods may or may not retain short setae. At all events, at this stage, although the antennae still often beat regularly, their contribution to locomotion is clearly of no importance, if indeed they contribute at all. All that remain of the proximal masticatory spines are very short rudiments, and the distal spines are now somewhat distorted. Although the swinging of the antennae carries them beneath the labrum, their active role is now virtually, if not completely, at an end. Locomotion has become the responsibility of the trunk limbs alone while food collection and manipulation are carried out by the trunk limbs and mouthparts. At the next stage (23) the antennae, although capable of a little movement, no longer beat regularly, their endopods are reduced to unarmed rudiments, the proximal masticatory spines have gone, and the distal are reduced in length and are without function. They disappear at the next moult as, one moult later, do the remnants of the endopods.

In the early larval stages the antennal muscles are very conspicuous in the cephalic region (figures 12–17) but when the antennae cease to beat their role ceases and they naturally diminish (figure 42, Rem D). Subsequently a complex antennal musculature develops in the adult, especially in the male where the antennae serve as claspers, but is in no way concerned with feeding or locomotion.

On purely morphological criteria it is impossible to be certain when the antennary gland ceases to function, except when it is clearly degenerate. It probably remains active until about stage 18, though the maxillary gland, whose development in *Artemia* is described by Benesch (1969), is certainly functional before this. The end sac retains its integrity for at least four more instars during which other remnants can also be detected, and traces of it have been seen even later. Such persistence of the end sac has a parallel in the Cladocera where, although never functional, it is sometimes readily detectable in sectioned material of even large adults.

The gnathobases of the mandibles, functional in an essentially adult manner from stage 3, change only a little at each moult but gradually become more massive as their musculature becomes elaborated. Their opposed molar surfaces acquire a thicker armour of sclerotized chitin as development proceeds. Here, posteriorly, a stout denticle gradually develops (seen at stage 8 in figure 33). The ontogeny of mandibular armature is dealt with in §15. During the early instars the sweeping posterior gnathobasic spine of the mandible (GS Mand) plays an important part in the feeding process and persists until stage 18, in which instar it is relatively smaller than initially and its role is clearly reduced. It disappears at the next moult.

The mandibular palp retains the basic structure already evident in the second naupliar stage (figure 6) throughout its active existence, but its proportions gradually change. As development proceeds its spines display accelerated growth. Thus by about stage 15 the four proximal spines, about the same length as the palp in stage 2, are twice its length. This allometric growth enables the spines to keep pace with the ever increasing size of the mandibular gnathobases which gradually carry the palps further and further away from the mid-line. The contribution made by the palps towards the end of their active existence is not easy to determine, but they probably assist until stage 18. At stage 19 they are still active and retain their full complement of spines but while they can still clean the distal masticatory spines of the antennae they can probably do no more than flick particles towards the molar region of the mandibular gnathobases. Their role is then at best very minor, and in any case by this time the stream of food particles is effectively directed between the mandibular gnathobases from behind, and they lie beyond its confines. A marked degeneration of the palp armature is evident after the next moult (stage 20). One or both of the proximal spines have gone at this stage, while the median pair is much,

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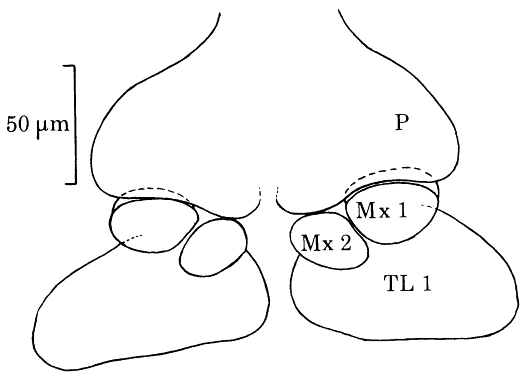

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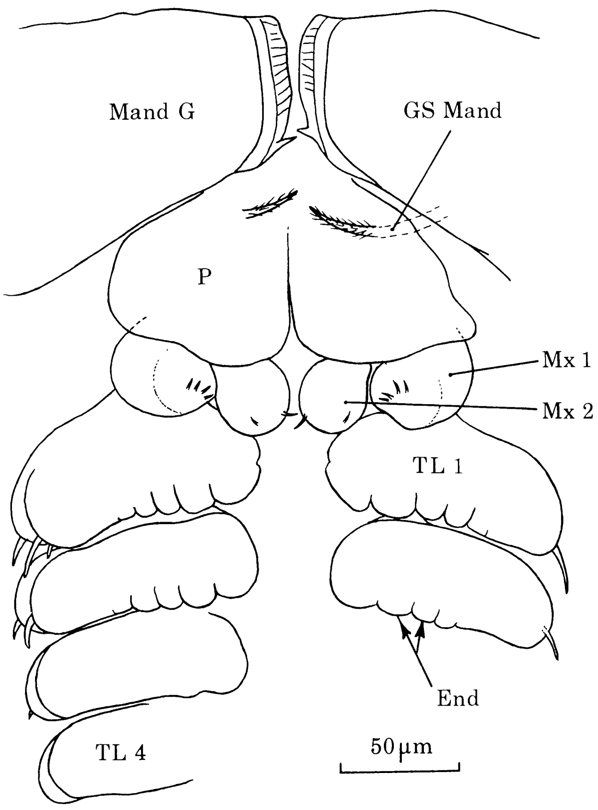

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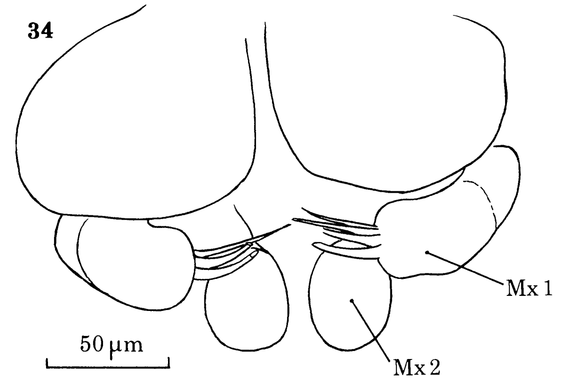


FIGURES 32–34. Early differentiation of mouthparts and trunk limbs.

FIGURE 32. Outline of the rudiments of the posterior mouthparts and first trunk limbs of a stage 5 larva as revealed by a horizontal slice. At this stage no armature is detectable on any limb.

FIGURE 33. Horizontal slice of a stage 8 larva showing the development of the mouthparts and anterior trunk limbs. The first signs of armature on the maxillules and maxillae are detectable in the preceding stage. At this stage all the trunk limbs are immobile.

FIGURE 34. Horizontal slice through the posterior mouthparts of a stage 12 larva; shown in outline only.

and the distal trio drastically, reduced, but there is some variation. At stage 21 the rudimentary palp usually bears two short median and two minute terminal spines and, although completely non-functional, is still capable of very feeble movement. A remnant of the palp, now removed laterally from the scene of its former operations, persists for several more stages but is minute and functionless.

Traces of spines or setae are detectable on the maxillules and maxillae in the seventh instar and are clearly seen in the next stage (figure 33) though these appendages are still far from functional. Movements of the maxillules begin at stage 11. Armature is much more evident by stage 12 (figure 34) though these appendages still probably make no significant contribution to food handling until after the next moult.

(*c*) *Early development of the trunk limbs*

An early sign of differentiation of a trunk limb is the appearance of a small terminal spinule, such being first recognizable in stage 7. As moulting continues further rudiments of armature appear and endites become recognizable. Early stages of ontogeny are reproduced by the sequence shown by limbs 4 to 1 of the eighth instar larva illustrated in figure 33.

As in other features, the trunk muscles develop from in front backwards so that by the time an individual has reached the twelfth instar (figure 35) the segmental trunk musculature of the first somite displays in essentials those features that are present in the adult while the most

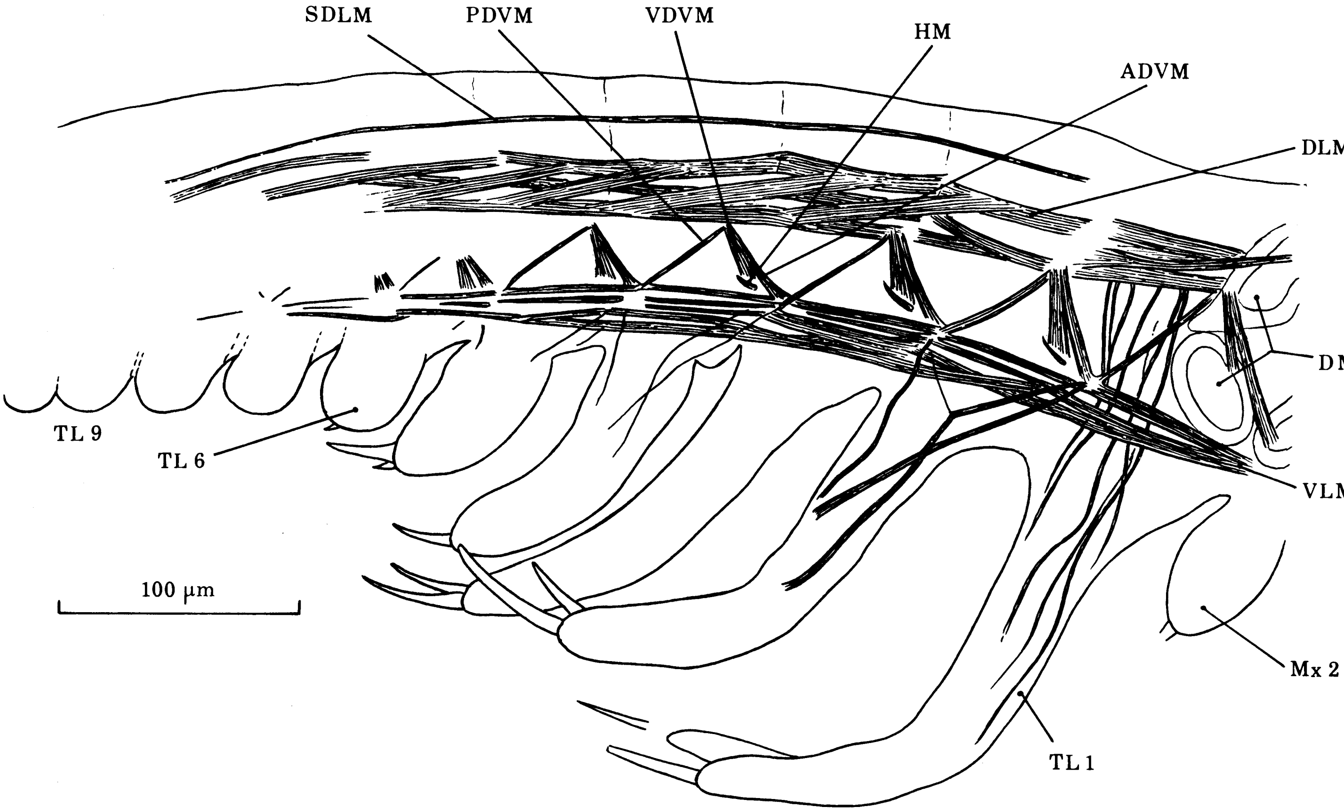


FIGURE 35. Longitudinal slice through an individual at stage 12. The posterior–anterior sequence reflects the temporal sequence of development of trunk limb 1. Note especially the great disparity in development between trunk limbs 1 and 6.

posterior trunk somites are still devoid of muscles. Proceeding from back to front therefore reveals a series of stages, somite by somite, that illustrates the ontogeny of the anteriormost. The development of the trunk musculature goes hand in hand with that of the limbs and their muscles, extrinsic and intrinsic.

As figure 35 makes clear, development of the trunk limbs and their muscles is progressive and there is no indication that the first six pairs begin to function simultaneously (or that the first six somites constitute a unit) as described for *Artemia* by Anderson (1967) (see discussion in §16). There is in fact a four moult interval between the time at which the first and sixth trunk limbs begin to function, which they do before they are fully differentiated.

The first movements of the trunk limbs begin at stage 11 and involve the first pair only. Although rudimentary setae are already present on their gnathobases, where they make their appearance two stages earlier, these are clearly incapable of handling food of any kind. It is also unlikely that the feeble beating of which these limbs are capable contributes anything to locomotion. Movements of the maxillules also begin at this stage, but these are also too feeble to assist in food transfer, and in any case the maxillules do not lie on the route followed by particles collected by the naupliar feeding apparatus all of which lies ventral to the paragnaths.

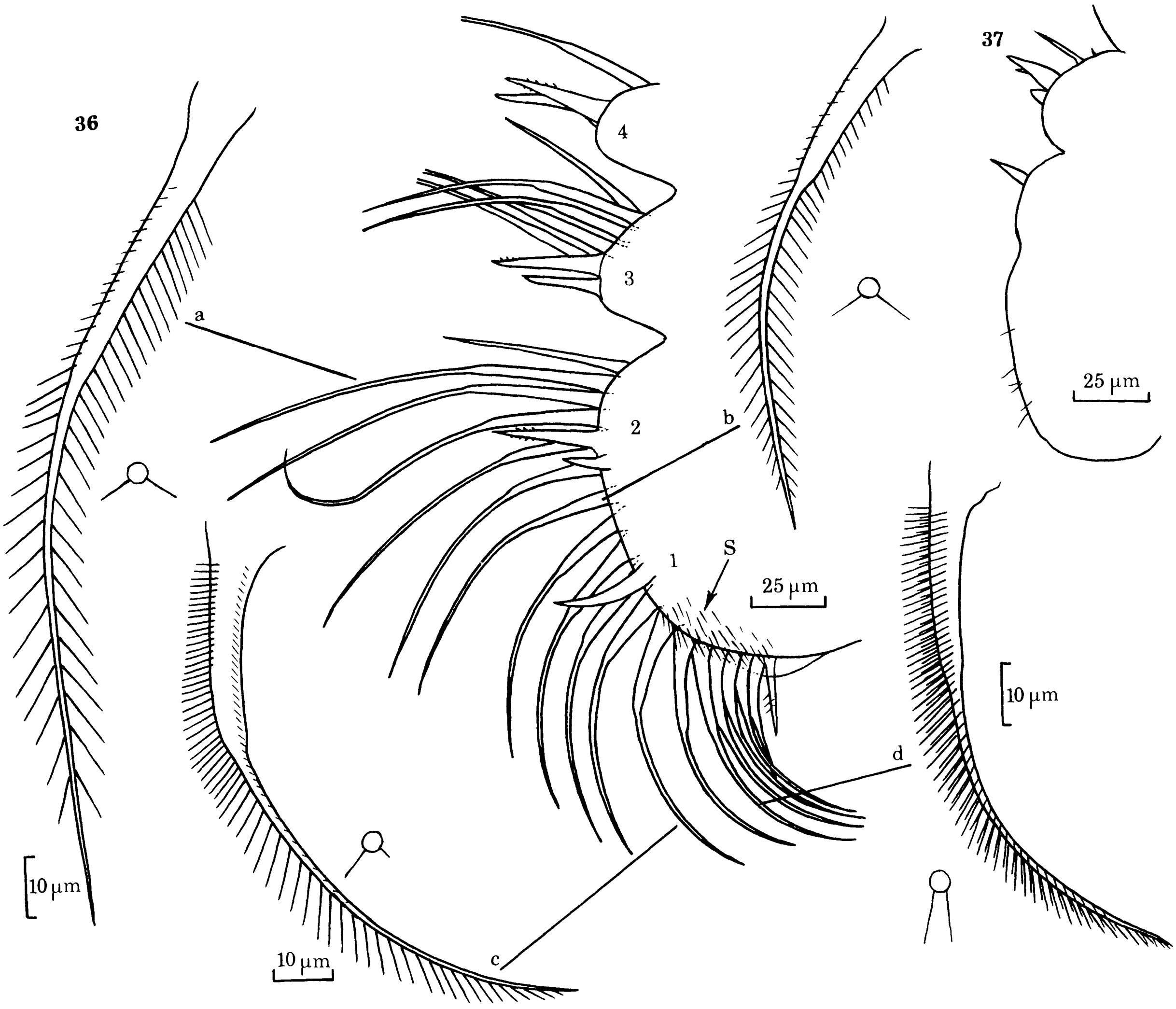
After the next moult two pairs of trunk limbs become both active and functional and the third pair is capable of movement but not of handling food particles. The beating of the first two pairs now for the first time brings a contribution to locomotion from the thoracic appendages but the main burden still falls on the antennae, and the small trunk limb contribution does not change the jerky progression so characteristic of the stages propelled largely or entirely by the antennae.

The contribution made to feeding by the thoracic limbs is also negligible at this stage, the antennae continuing to play the dominant role. During that part of the cycle of movement when the space between the trunk limbs is enlarging, water, and therefore particles, are sucked into the mid-ventral space, and some material at least accumulates posterior to the maxillae, as can be demonstrated by the use of carmine particles. Any such material passes first between the maxillae and then between the maxillules – whose spines lie against the inner faces of the wedge-shaped paragnaths – to the mandibles. The assistance rendered by the maxillules appears to be negligible at this stage. Particles collected by the naupliar apparatus are swept across the ventral surface of the paragnaths (topographically dorsal as the animal usually swims ventral side uppermost) and their handling does not involve any post-mandibular appendages.

At stage 13 the third trunk limb becomes functional. Figures 36 and 37 show how different is the development of the proximal region limbs 1 and 4 at this stage. The first limb now has a well armed gnathobase (numbered 1) to which is fused the next endite (numbered 2). The proximal region of the fourth limb has an unarmed gnathobase and its second endite bears only a single spine. Although this limb is capable of movement, and is armed with several spines distally, it can contribute nothing to the handling of food. The compound nature of the basal portion of trunk limb 1 is indicated by the two distinct sets of heavy armature on the inner face. This consists of a single stout spine on the gnathobase and two spines on endite 2. For simplicity of description, and on functional grounds, this compound proximal structure is referred to simply as the gnathobase though for correctness of homology the next endite distally is called endite 3.

At stage 13 the gnathobase of trunk limb 1 bears, in all, 19 marginal setae of which 7 probably belong to endite 2, and of which the most distal (no. 19) can be ignored for present purposes.

Seta 18 (figure 36, inset a) bears long marginal setules arranged much as in a filter seta, the angle between which is oblique (but extremely difficult to measure accurately), the gaps between adjacent setae varying from about 2 μm proximally to almost 5 μm distally. More proximal setae are shorter and the gaps between their setules smaller – about 2 μm in the middle region of seta 13 (figure 36, inset b). Towards the proximal end of the gnathobase the setae are progressively more curved in connection with their function of sweeping particles along the food groove, and the setules that they bear lie closer together proximally than on the more distal setae (figure 32, inset c). The angle between them also becomes less obtuse and, on several of the most proximal setae, acute. On seta 6 the two sets of setules are directed in essentially the same direction (figure 36, inset d). Indeed without careful focussing at high magnifications it is easy to believe that only a single row is present. The gaps between adjacent setules are



FIGURES 36 AND 37. Early stages of the differentiation of the trunk limbs and their armature.

FIGURE 36. The basal endites of the first trunk limb of an individual at stage 13. Insets give details of four of the setae of the gnathobase (actually the fused gnathobase and endite 2). The arrangement of the setules on the various setae, as seen in transverse section, is indicated in each case on the basis of inspection but the angles involved have not been measured.

FIGURE 37. The basal endites of the fourth trunk limb of the same individual to the same scale.

less than 2 μm wide over much of the length of the seta and not much more than 1 μm proximally. These proximal setae are clearly adapted to sweeping material forward along the food groove mechanically, the swing of the gnathobase being ideally suited to provide the necessary motive force. In connection with this function the two most proximal setae also lie more laterally than the rest, number 2 being partly hidden behind its adjacent companions when the gnathobase is viewed laterally from the inside (figure 36), and therefore help to span the gap between the row of gnathobasic setae and the wall of the food groove.

Even at stage 13 a few spinules are present proximally on the face of the gnathobase of trunk limb 1 (figure 36, S). These increase in number as development proceeds (e.g. see figure 84) and eventually form a pelage of spinules over the face of this compound endite on all limbs (figure 79, figure 134, plate 6, and figure 185, plate 12). Their presence on the first limb is particularly noteworthy.

With each successive moult an additional pair of trunk limbs becomes active. The thoracic contribution to feeding and locomotion is therefore gradually increased – not abruptly so (see §16). This is reflected by smoother progress during swimming as more and more trunk limbs become functional, their beating being virtually incessant. A forward lurch with each stroke of the antennae is, however, noticeable as long as these appendages remain active. The gradual incorporation into the series of several pairs of limbs that are simultaneously active, but slightly out of phase, reduces the load on any one pair, which adds its contribution to locomotion by pushing water already set in motion by other pairs. The phase difference is apparent from an early stage: ultimately it gives rise to the metachronal rhythm so characteristic of individuals with the full complement of limbs.

That the trunk limbs increasingly contribute to food collection is readily shown by means of a dilute suspension of fine carmine particles. Even at stage 15 (five pairs of trunk limbs functional) particles are rapidly accumulated in the food groove. At this stage true filter-feeding is practised. Aspects of the mechanism involved are noted below. Although no attempt has been made to elucidate details at each stage it is clear that the same principles hold good throughout.

Trunk limb development proceeds in a regular manner until the full complement of limbs becomes active at stage 21 (figure 27), the only point to note being that, from the outset, limb 11 differs from its companions in accordance with functional demands. Complete takeover of responsibility for both locomotion and feeding by adult structures is achieved at stage 22 by which time the animal is about 4 mm in length. Other than for the few stages that follow this, no attempt has been made to ascertain the exact number of instars, individuals being referred to simply by size. Growth increments of course become greater at each moult as size increases.

As figure 36 makes clear, the trunk limbs become functional long before they have acquired the full complement of spines and setae on their endites. The appendage illustrated was in fact functional in the previous instar. As development proceeds additional setae are incorporated at each moult until the full complement is acquired. By stage 21, the first at which all trunk limbs are functional, the compound gnathobases of limbs 1 to 11 bear respectively 39, 37, 35, 33, 32, 30, 28, 25, 22, 19 and 13 setae including any rudimentary setae that may be present (see figure 84 for trunk limb 1). The much smaller number of setae on the last than on the preceding trunk limb reflects not merely its late development but its distinctive function as a gate that seals the posterior end of what, at this stage, can be called the filter chamber. It never develops as many setae as the other ten and the form and armature of those present are of a distinctive kind.

The number of setae on the compound gnathobase continues to increase in instars beyond that at which all the limbs are functional and, as size increases, changes take place in their form and armature. These are associated with changes in the feeding mechanism and in the nature of the food consumed. There are also associated changes in the nature of the heavy armature of the compound gnathobase and in that of the more distal endites and the endopodites. An account of these (§ 12) is deferred until the feeding habits of the early trunk limb-using instars have been described.

(*d*) *Development of the abdomen, telson and other features*

By virtue of the anamorphic pattern of development, the abdomen is formed after the thorax. From the time that its full complement of segments is laid down, however, its growth is positively allometric with respect to that of the thorax; so large adults have a relatively longer abdomen than do small individuals. This is the case in *Artemia* (Gilchrist 1960) and apparently in Anostraca generally. A hitherto unemphasized feature relevant to locomotion is the development on the telson of a pair of initially unarmed papillae which develop an armature, first of a naked terminal seta (figure 38), then of lateral setae on each side (figure 39). The papillae elongate and become somewhat flattened dorso-ventrally and the number of setae increases (figure 40). With increasing size the setae also begin to acquire a row of horizontally directed setules on each side (figure 40) and the telson begins to act as a stabilizer. Eventually there

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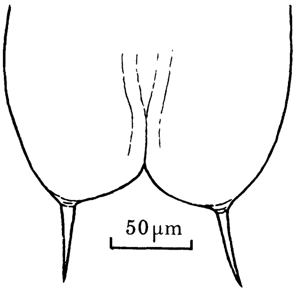

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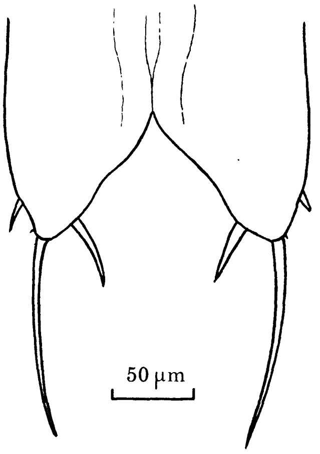

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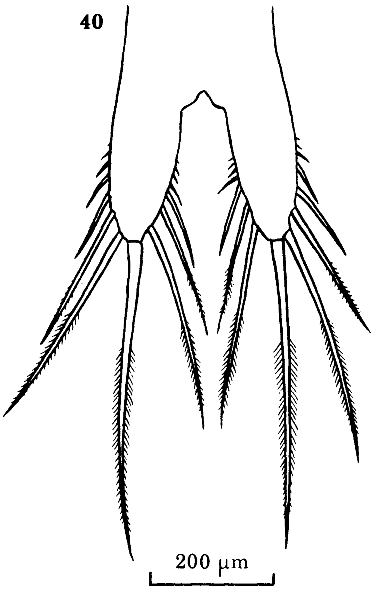

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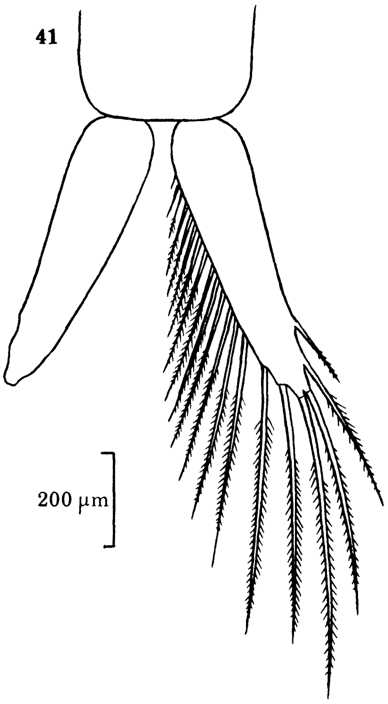

Figures 38–41. Stages in the development of the telson.

Figure 38. Stage 11.

Figure 39. Stage 14.

Figure 40. Stage 20. This is the instar immediately before that at which the full complement of trunk limbs becomes functional.

Figure 41. An individual about 8.1 mm in length.

are 11 or 12 setae on each side. This is the maximum reached on the outside. With increasing length of the ramus the number of setae to the inside continues to increase while the external armature gradually disappears (figure 41), and the rami become articulated with the telson, relative to which their position can be altered by the pull of simple muscles. The rami continue to increase in length and gradually their tips curve outwards. The setae of their inner margins increase in number until there are about 52 on each side in individuals 44 mm in length. Because these setae are armed laterally with horizontal rows of setules, each ramus is functionally a flat plate and the pair, located at the end of the now long, slender abdomen, serve as stabilizers which help the animal to maintain smooth progression in its chosen plane. They also facilitate changes of direction by enhancing the rudder-like function of the abdomen. They may be more important in females – which are burdened with a large egg pouch – than in males. By enabling the abdomen to exert more force they also assist in escape from awkward situations, a few rapid flicks enabling an individual to dart swiftly away. Likewise a trapped individual violently threshes its abdomen.

Development of other features, such as the pedunculate eyes and anterior caeca of the alimentary canal, takes place concomitantly with that of the features described above and in a manner readily appreciated by reference to the illustrations of previous investigators. For example Claus (1886) has provided excellent information on such features as the paired eyes and median ocellus in *Branchipus*, and Sars (1896) shows how the caeca develop in *Branchinecta*.

8. The pattern of the adult skeleto-muscular system

The gross features of development that are externally apparent are accompanied by complex internal changes of profound functional significance. These include the laying down and development of the muscular system. Inseparable from, and developing with, the muscular system is the endoskeleton, a system that has received little attention in branchiopods. The understanding of any account of how the skeleto-muscular system develops presupposes, or is at least facilitated by, a knowledge of the adult condition – if only to make the nomenclature intelligible. Accordingly, although this disrupts a progressive account of ontogeny, the adult condition is described first. This account is complete in itself, provides a frame of reference for the account of development, and is the key to the understanding of much functional morphology.

References to anostracan trunk musculature are usually incomplete and the illustrations often either inadequate or difficult to elucidate, but that of Hessler (1964) for *Eubranchipus*, given for comparison with his excellent account of the cephalocaridan *Hutchinsoniella*, is accurate and helpful. Information is also supplied by Cannon (1926) for *Chirocephalus*, though Benesch (1969), who also makes certain specific criticisms, refers to this work as 'zu schematisch'. Cannon's paper is indeed more useful for its account of muscle development than as a guide to muscle pattern. Benesch's own account of the musculature of a late larval stage of *Artemia* is conveyed mainly by means of two detailed, but unfortunately cramped, illustrations showing an essentially adult pattern in the thorax, and an accompanying table, and is the most detailed available. All these authors use different nomenclature, which does little to facilitate understanding. That of Hessler, used also in his account of the skeleto-musculature of *Hutchinsoniella*, is probably the most satisfactory and is used here wherever possible.

Although highly complex, the trunk musculature of *B. ferox* can be understood relatively easily by reference to adequate illustrations. It is of the type whose basic features are common to a wide range of arthropods in which the segments are capable of movement relative to one another. In this case the permitted movement is considerable and the body can be markedly flexed when occasion demands but can also maintain the necessary stability when swimming. Its salient features, as seen in an individual at stage 24, are shown in figures 42–44, 49 and 50. The animal is now about 5.2 mm in length, including the telson. Although the muscles are small, in some ways they display their basic arrangement more clearly than do those of large individuals in which they become more massive and the dorso-ventral series more congested. This can be seen for example by comparing the longitudinal muscles, as seen in transverse section, in an individual at stage 24 (figure 43) with those of a 36 mm individual shown in figure 146. The same is true of the extrinsic trunk limb muscles, very slender in the earliest adult instars, which become more massive and more congested. Some such are seen in figure 146 (ETLM).

Reduced to essentials, the thoracic musculature consists of paired bundles of dorsal and ventral longitudinal muscles and pairs of segmentally arranged dorso-ventral and horizontal muscles. Anteriorly the dorsal longitudinal muscles (DLM) extend into the head where the anteriormost bundle of fibres originates dorsally in the mandibular segment and others more posteriorly (figure 42). The more posterior origin of certain of these muscle bundles on a dorsal intersegmental tendinous sheet of endoskeleton between the maxillary and first thoracic segments (DITS MX2/TS1) is seen in figure 49. As shown in figure 42 the arrangement of the cephalic extension of each dorsal longitudinal muscle is relatively simple, as is the case in the first thoracic segment where, however, additional bundles of muscle fibres are present. More posteriorly complexity is introduced by a twisting of the component bundles of muscles of this series, each bundle making a spiral and returning, four segments posteriorly, to a similar point to that from which it began. The whole complex of muscles is suspended by transverse intersegmental tendinous sheets (DITS), labelled between trunk segments 3 and 4 in figure 42 (DITS, TS3/4) and shown for other intersegments, and by numerous tendinous fibrils (Fib), indicated only in segment 4 of figure 42 but present in all segments. The way in which some muscle fibres of a bundle extend between adjacent segments while others of the same bundle originate on the intersegmental endoskeletal sheets is shown in figure 49 and diagrammatically in the inset to that figure. On each side, above the main group of bundles of dorsal longitudinal muscles there is also a slender bundle of fibres constituting a superior dorsal longitudinal muscle (SDLM) which originates at what is probably the posterior limit of the head and extends backwards independently of the main bundles.

The arrangement of the ventral longitudinal muscles (VLM) is shown in figure 42. Like those of the dorsal series, these extend into the head where there is a robust, ventrally inclined, anchoring muscle, the cephalic ventral longitudinal muscle (CVLM). As are their dorsal equivalents, the ventral longitudinal muscles are suspended by transverse intersegmental tendinous sheets (VITS), labelled between thoracic segments 1 and 2 in figure 42 (VITS TS1/2). There are also ventral anchoring fibrils (VA) running obliquely forward to the base of the trunk limbs where they are attached anteriorly. These are referred to in the description of the endoskeleton.

The dorso-ventral and horizontal trunk muscles are best understood by comparing figures 42, 43 and 49. Spanning the region between the dorsal and ventral longitudinal muscles and the lateral body wall, these form, with their associated tendons, an internal girder system that

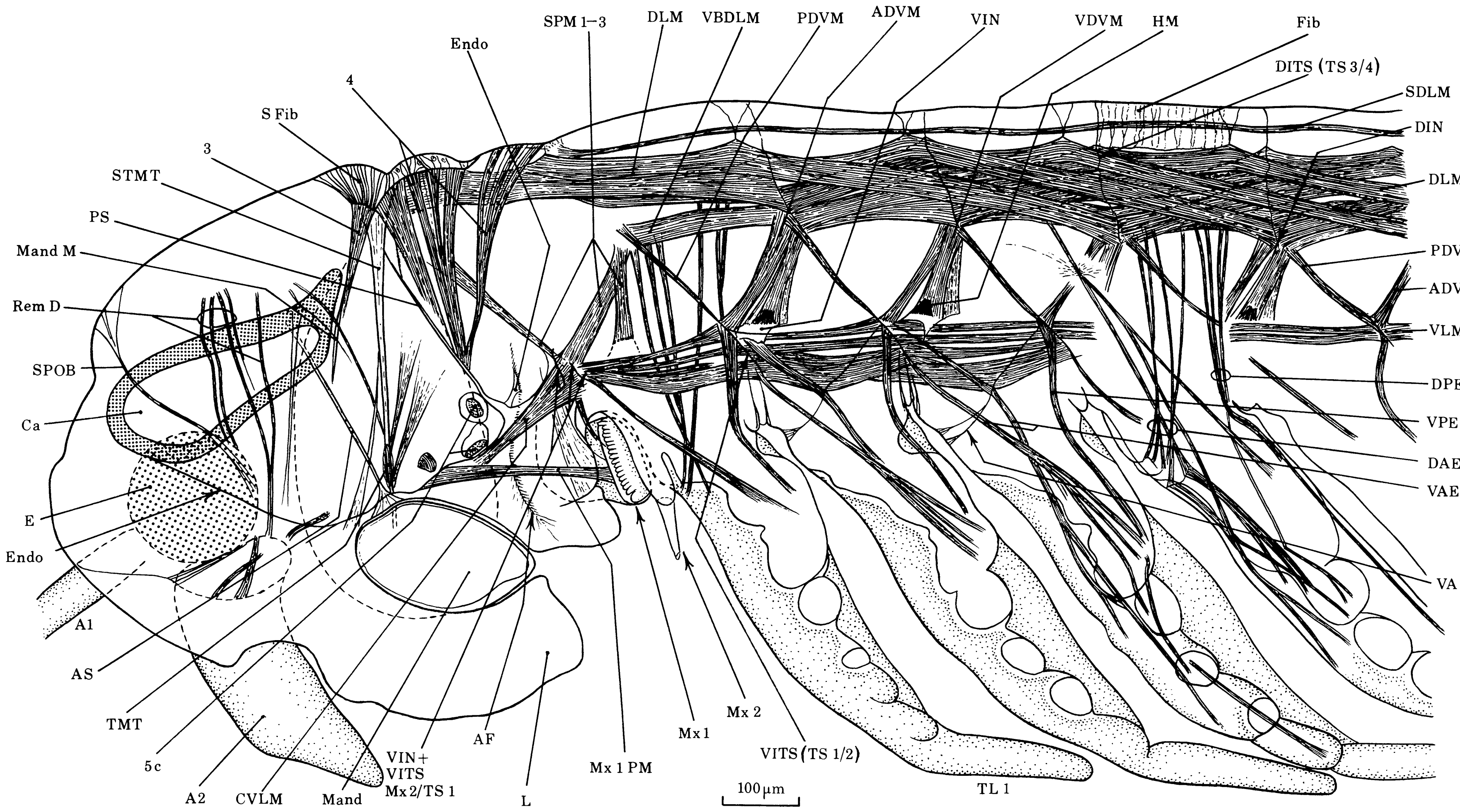

FIGURE 42. Median longitudinal slice through an individual at stage 24 to show the basic features of the musculature and some elements of the endoskeleton. Understanding of the arrangement in three dimensions is facilitated by comparison with figures 43–50, especially figures 43 and 49. Different elements of the trunk limb musculature are shown in different limbs. The extrinsic muscles shown in trunk limb 4 lie deeper in the plane of the paper, that is more laterally, than the muscles of trunk limb 3. The outline of the mandible, the bulk of which lies lateral to most of the structures shown, is indicated by a dashed line. That portion of its margin (Mand M) that is shown appears as a result of deeper focusing. Note how the cephalic musculature, dominated by antennary muscles in the naupliar stages (cf. figure 16), now pertains particularly to the mandibles. Remnants of the dorsal antennary muscles (Rem D) still traverse the head. These pass lateral to the caecum (Ca) of the alimentary canal, as does the suspensory ligament of the post-oral bar (SPOB). Many additional transverse mandibular muscles that can be seen and traced by deeper focusing on this thick slice are omitted for clarity.

fulfils several functions and is anatomically and functionally continuous with the extrinsic muscular system of the thoracic limbs. Each set of dorso-ventral muscles consists, on each side of the thorax, of a compound vertical dorso-ventral (VDVM), an anteriorly descending oblique (ADVM), and a posteriorly descending oblique muscle (PDVM), just as described by Hessler (1964) in the Cephalocarida. All incline inwards as they descend as is seen most obviously in figures 43 and 49. The horizontal muscles (HM), which in fact rise slightly as they pass laterally, are difficult to decipher in longitudinal slices but are clearly seen in horizontal (figure 49) and transverse (figure 43) slices. Cannon's (1926) sketches of the muscles of *Chirocephalus* are diagrammatic and, in the lateral view, somewhat confusing. His outer dorso-ventral muscle is clearly what is here called the horizontal muscle which rises somewhat as it passes laterally, as it does in *B. ferox*.

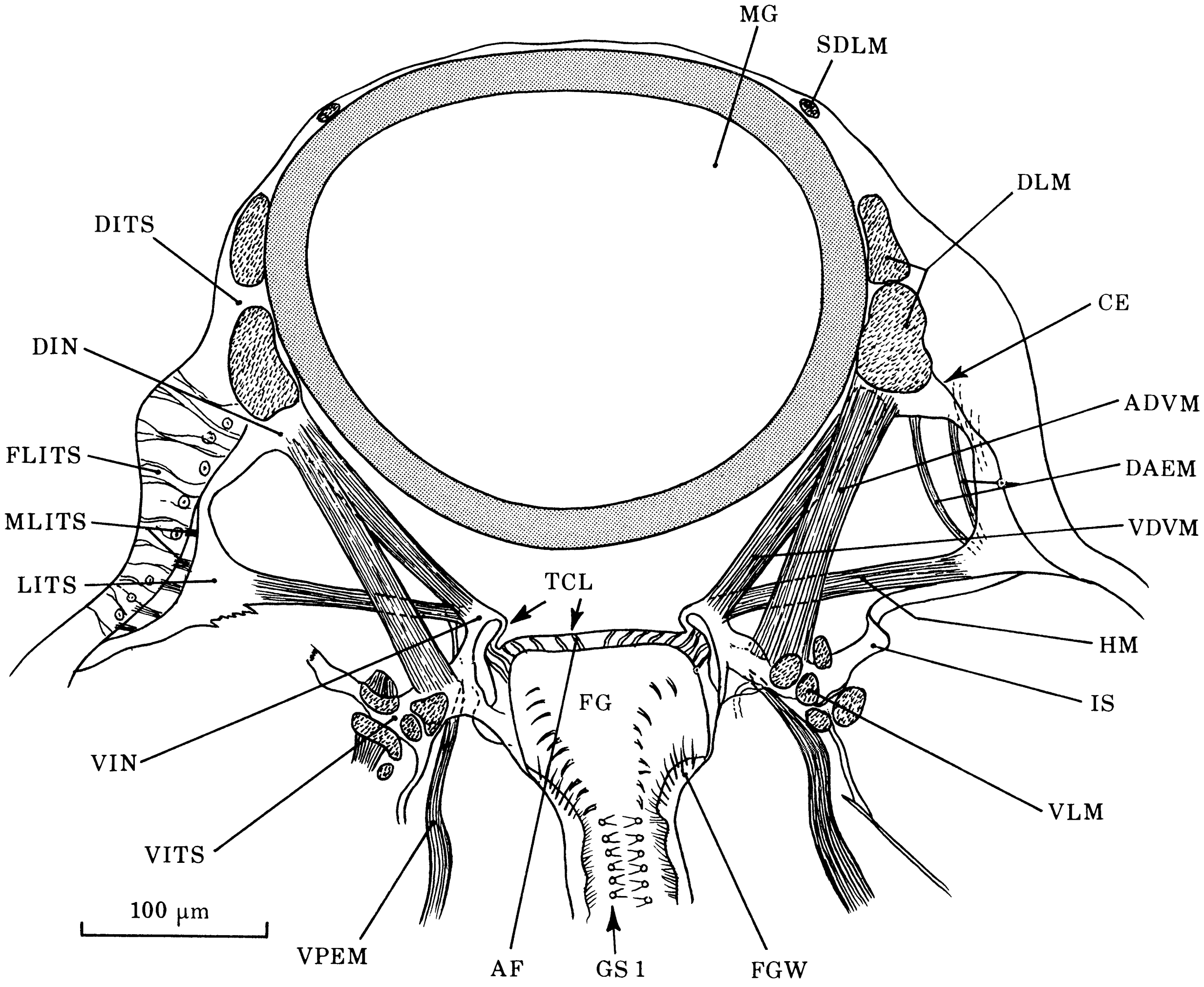

FIGURE 43. Transverse slice of an individual at stage 24 at the level of the intersegment between thoracic segments 1 and 2. The section lies just anterior to the heart. The arrangement of the longitudinal trunk muscles has been somewhat simplified and most of the extrinsic limb muscles have been omitted. The nature of the intersegmental tendinous sheets (DITS and VITS), to be seen in part in longitudinal (figure 42) and horizontal (figure 49) sections, is more apparent in this plane and the anchorages of the horizontal trunk muscles (HM) are readily apparent. At this early stage the longitudinal muscles and the intersegmental sheets are much less bulky than in large individuals (cf. figure 146). The thick cytoplasmic sheet with which many of the muscles are invested is omitted. See also figures 44 and 46.

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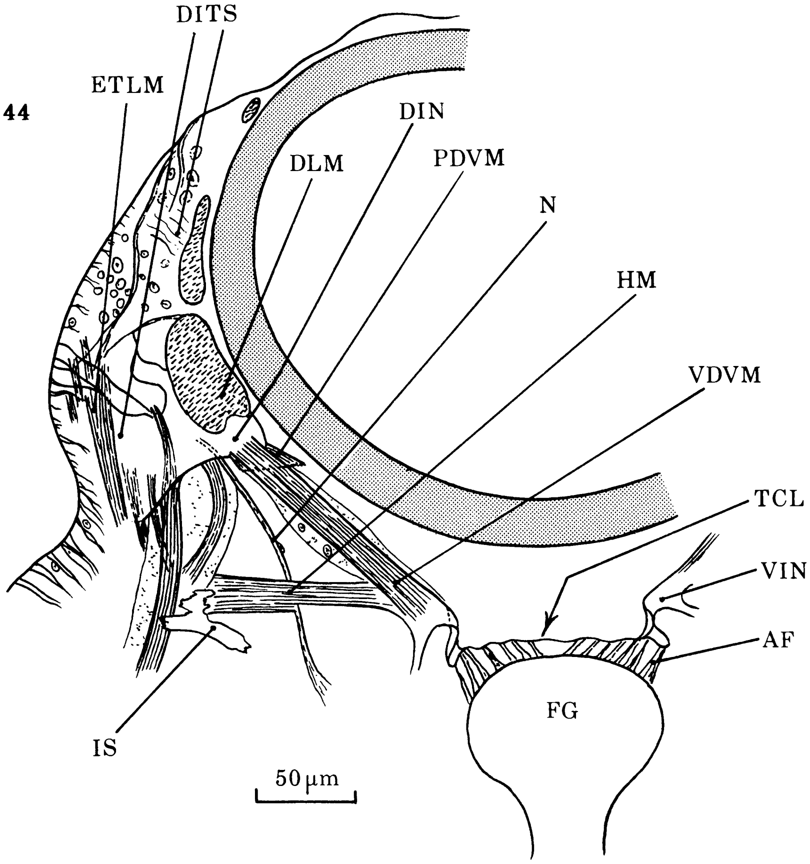

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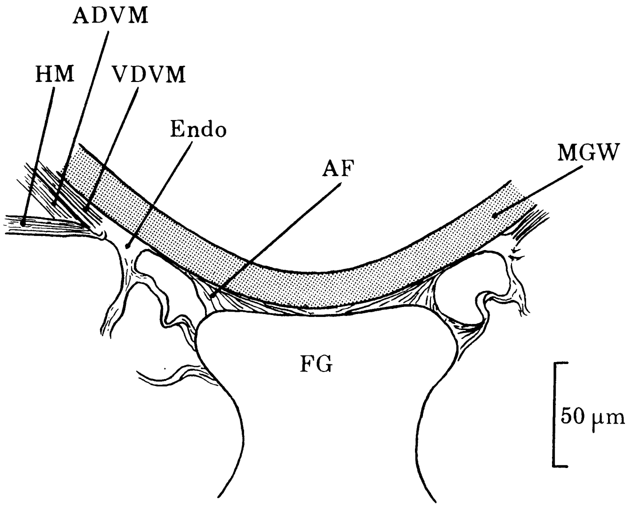

Figures 44 and 45. Further details of the skeleto-muscular system.

Figure 44. Transverse slice immediately behind that shown in figure 43, showing the complexity of the dorsal tendinous mass which consists of the intersegmental node (DIN) and the contiguous intersegmental sheet (DITS), the dorsal anchorage of the posteriorly descending dorso-ventral muscle (PDVM) (not seen in figure 43), and the dorsal origins of some of the numerous extrinsic trunk limb muscles (ETLM) whose upper extremities can be seen through the intersegmental sheet. Some cytoplasmic muscle sheaths are shown. Note how the cross-sectional shapes of both trunk and food groove change over a short distance (cf. figure 43).

Figure 45. Transverse section (stage 24) showing the close juxtaposition of the roof of the food groove and the alimentary canal at the level of thoracic intersegment 3/4. (Compare with the wide gap between the gut wall and food groove roof at more anterior intersegments (figures 43 and 44).)

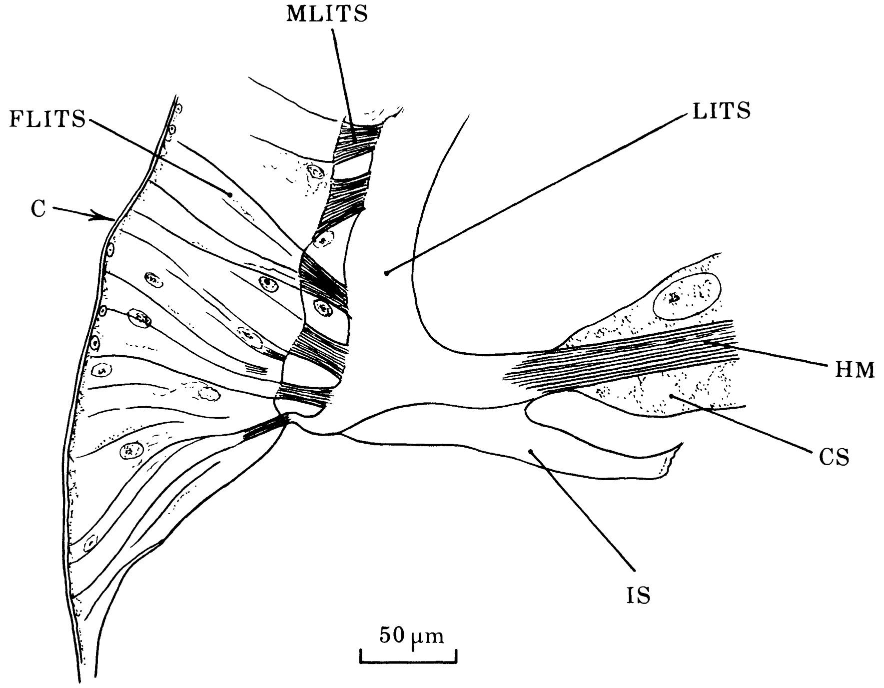

Figure 46. Transverse section (stage 24) showing the lateral anchorage of one of the horizontal trunk muscles at thoracic intersegment 2/3. Note the muscles of the intersegmental endoskeletal sheet (MLITS).

Providing support and anchorage for the trunk muscles is a tendinous endoskeleton, which also provides sites of origin for various extrinsic limb muscles. Ventrally is a series of transverse intersegmental sheets or struts, the transverse connecting ligaments (figures 43 and 44, TCL). These lie in the horizontal plane and each is anchored to the ventral exoskeleton above the roof of the food groove (topographically the bottom as *B. ferox* swims inverted) by a series of

Description of figures 47 and 48

Figures 47 and 48. Endoskeletal features in the head–thorax boundary region.

Figure 47. Horizontal slice, viewed from the ventral side at the level of the ventral longitudinal muscles (VLM), showing the posterior part of the cephalic endoskeleton of an individual at stage 22. The food groove (FG), which curves ventrally at this point as it passes forward, is cut through in the posterior part of the figure revealing some of the gnathobasic setae of trunk limb 1 (GS 1) in the groove itself. Note the anchoring fibrils (AF) of the cephalic portion of the endoskeletal sheet (Endo S), the way in which the ventral intersegmental tendinous sheet (VITS) at the maxillary–thoracic segment 1 intersegmental boundary is anchored (A) to the walls of the food groove, and the link between the cephalic and thoracic components of the endoskeleton.

Figure 48. Horizontal slice of the same individual as that shown in figure 47 and immediately dorsal to it, viewed ventrally. The slice passes through the anterior extremity of the thorax at the level of the ventral longitudinal muscles (VLM) and the roof of the food groove (FGR). Figure 49 assists in location. Various features of the endoskeleton are shown. Anteriorly the posterior extremity of the cephalic portion of the endoskeletal sheet (Endo S) is seen extending backwards and somewhat dorsally before becoming anchored to the roof of the food groove which here begins to curve slightly ventrally as it passes forward. (Although figure 50 is a transverse slice, the present figure reveals the posterior extension of the endoskeletal sheet there portrayed.) More posteriorly the intersegmental endoskeleton of thoracic segments 1/2 is seen. On the left can be seen the fibrils (FFG) that anchor this system over a considerable length of the lateral wall of the food groove. On the right, by deeper focusing is revealed the sheet-like nature of that part of the tendon system (Endo) that, still more ventrally, is utilized by the ventral extremities of the dorso-ventral muscles and of which part is to be seen on the left hand side of figure 49. Towards the middle of the inter-segmental region, and seen through the roof of the food groove, are the anchoring fibrils (AF) (cf. figures 43–45).

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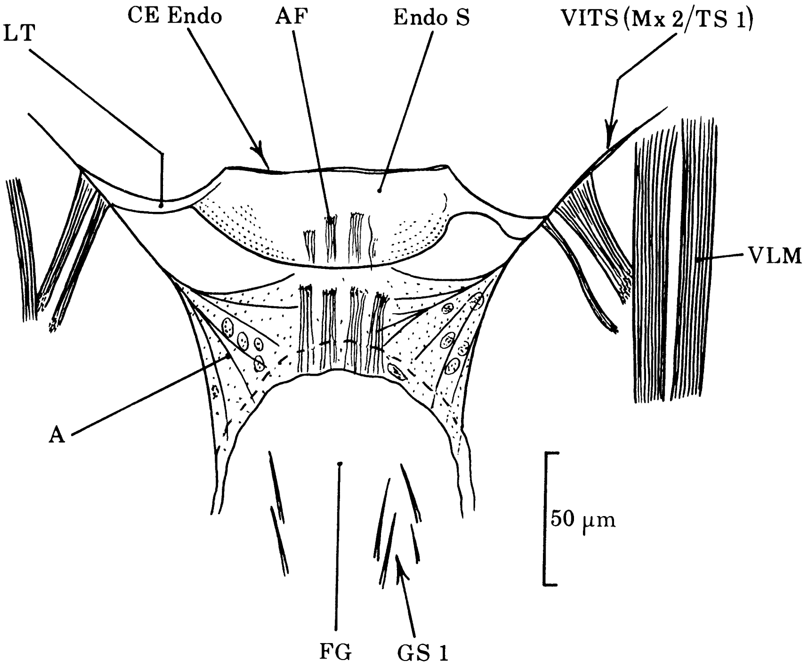

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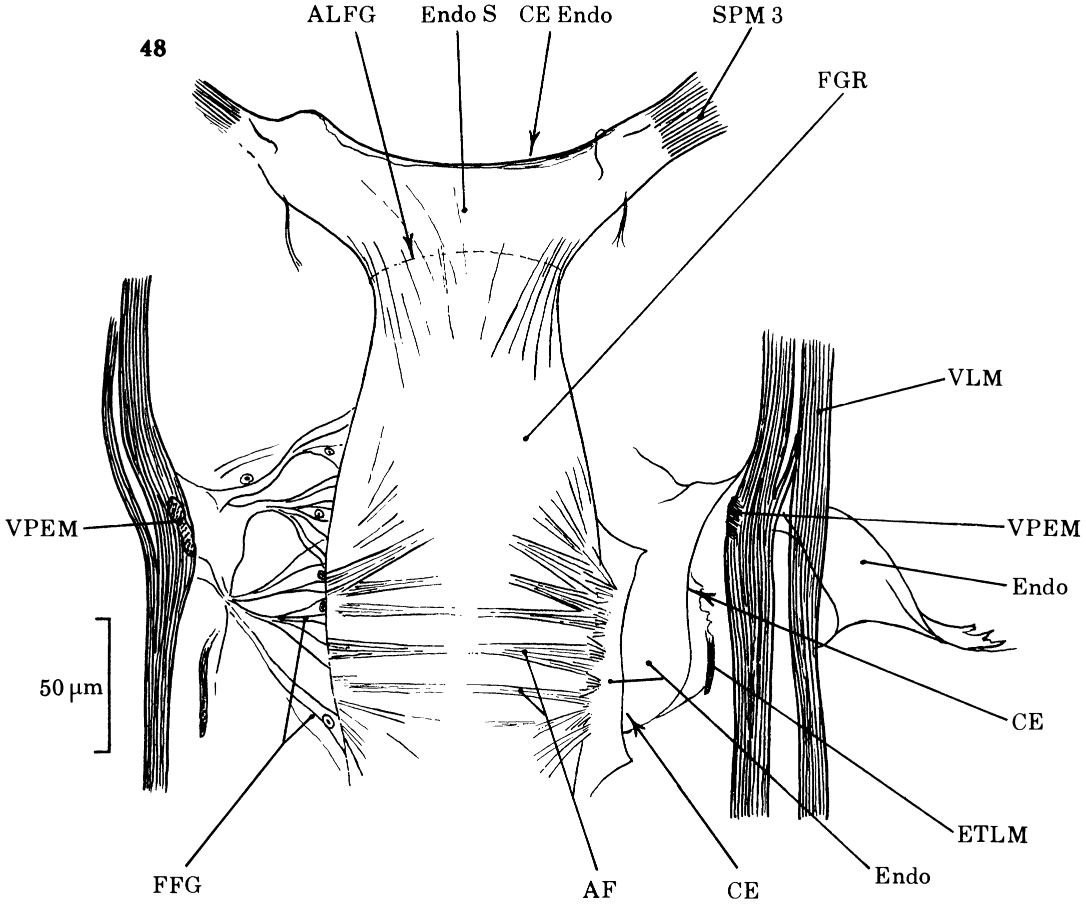

FIGURES 47 AND 48. For description see opposite.

fibrils (AF), thereby assuring its rigidity. Because the food groove is bound to the endoskeletal system it too is braced.

In the case of thoracic intersegment 1/2 (TS 1/2) (figure 43), towards each lateral edge of the food groove, the transverse connecting ligament gives rise to a more or less dorsal, almost apodeme-like projection which expands to form a ventral intersegmental node (VIN) which

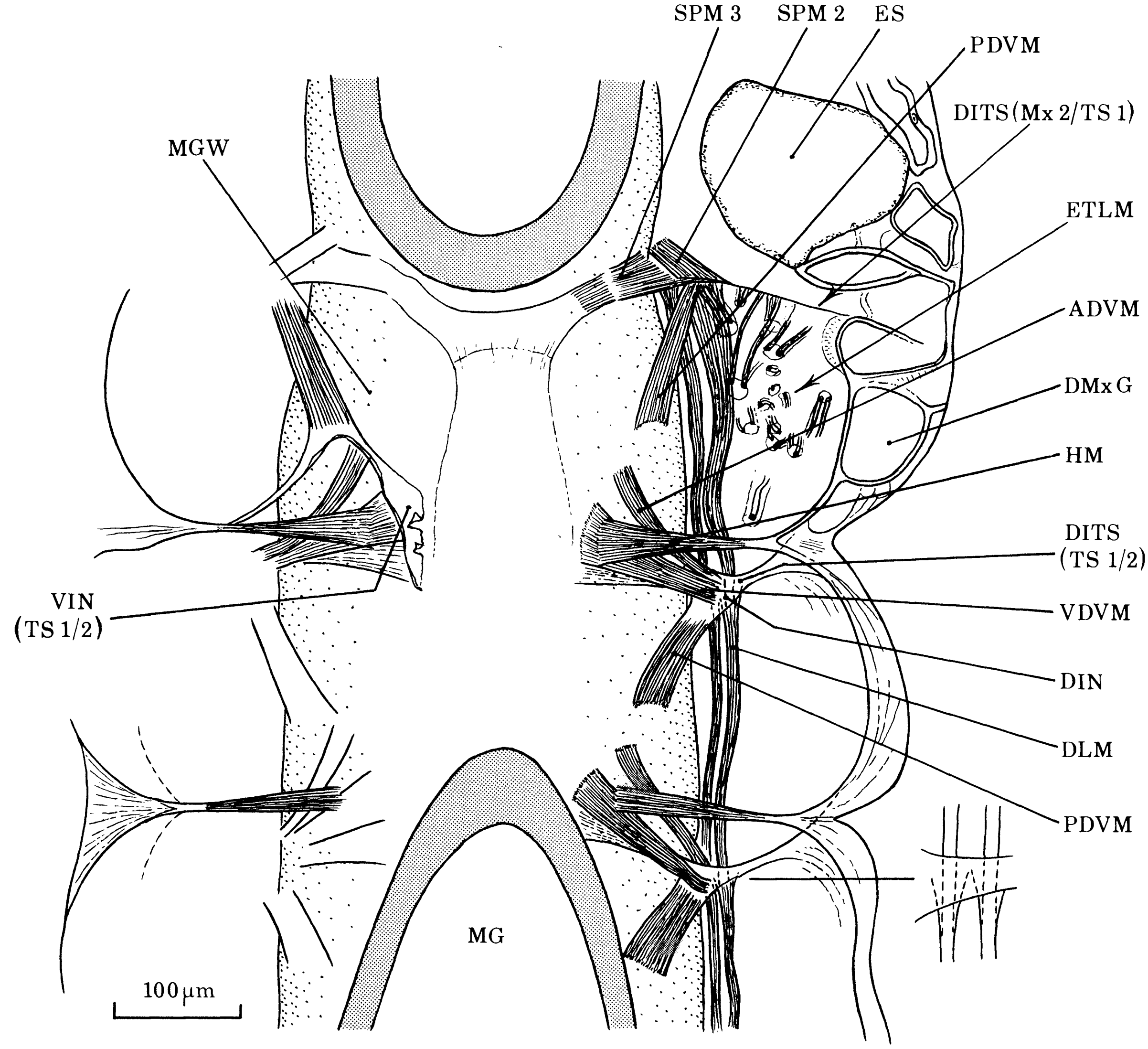

FIGURE 49. Horizontal slice of the same individual as shown in figures 47 and 48, and immediately dorsal to that shown in figure 48, viewed ventrally. The slice cuts between the dorsal and ventral longitudinal trunk musculature and just includes the ventralmost strands of the dorsal series (DLM). The horizontal trunk muscles (HM) rise slightly towards the observer as they approach the mid-line. The inset shows diagrammatically how some elements of the dorsal longitudinal muscles originate on the intersegmental tendinous sheets (DITS) of the endoskeleton. Antero-medially there has been added from a more ventral slice an indication of the posterior limits of the cephalic endoskeletal sheet and its anchorage to the roof of the food groove, for details of which see figure 48. To show clearly what has been superimposed, a distinct break is left in the muscle (SPM3) involved. A slight undulation of the alimentary canal has resulted in the mid-gut (MG) being sliced twice in this section. The anterior section is related to the curvature near the oesophageal entrance to the mid-gut. Extrinsic trunk limb muscles are shown only on one side of the first thoracic segment; they are of course present in each leg-bearing segment. Although the dorsal intersegmental tendinous sheet (DITS) is labelled between trunk segments 1 and 2, only the ventralmost fragment of this is actually visible, but a strap-like lateral extension that binds this to the lateral exoskeleton is very clearly seen.

serves as the point of anchorage for the vertical dorso-ventral and horizontal trunk muscles (see also figure 42). More laterally the node curves ventrally and, passing somewhat anteriorly, expands greatly and forms a tendinous sheet, the ventral intersegmental tendinous sheet (VITS), seen in face view in figure 43, edge on at each intersegment in figure 42. This supports and serves for the anchorage of the ventral longitudinal muscles and also, in its dorsal portion, the posteriorly descending oblique dorso-ventral muscle from the segment in front (too anterior

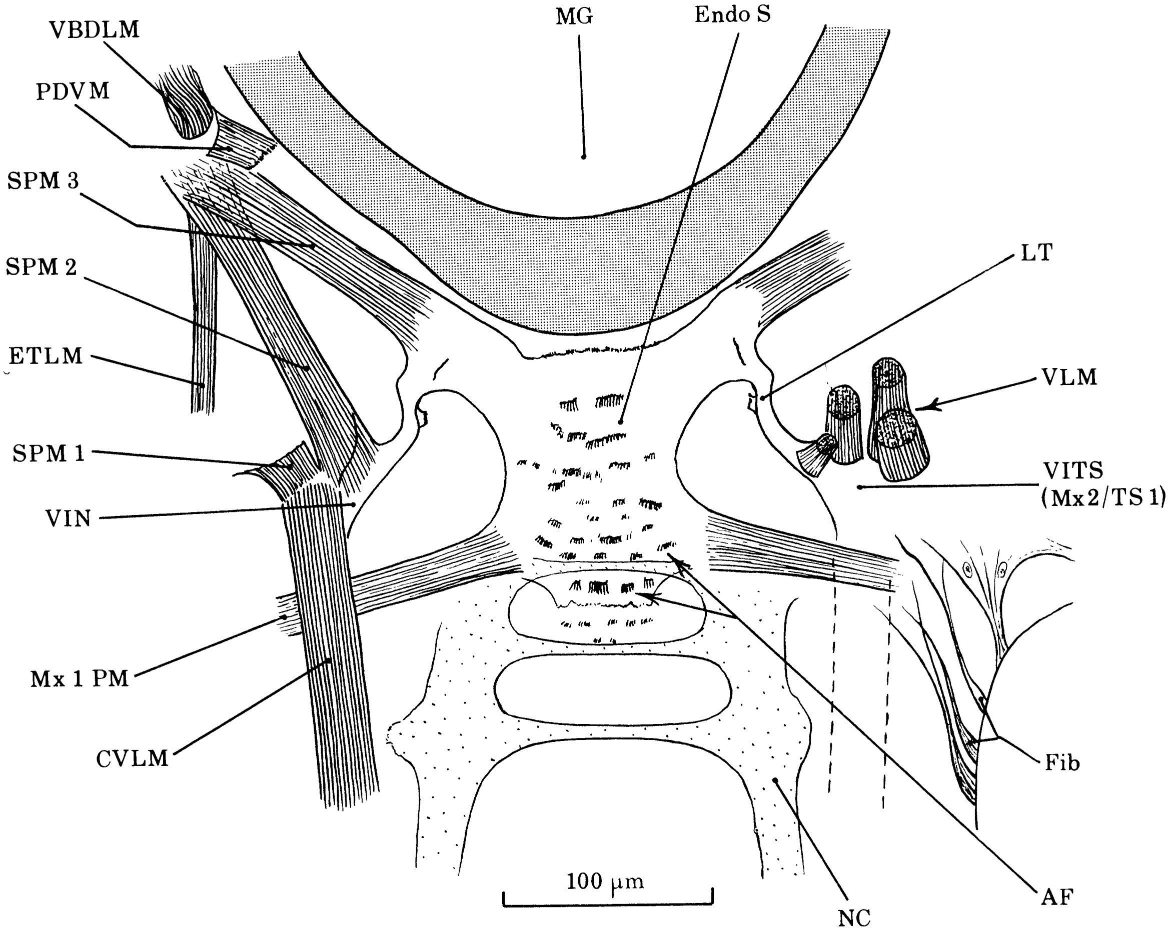

FIGURE 50. Transverse section at the level of the ventral maxillary/trunk segment 1 intersegmental node of an individual at stage 24 to show part of the ventral endoskeletal sheet (Endo S) as it passes from the head into the thorax. Although this is a transverse slice, cutting slightly more posteriorly dorsally than ventrally, the head is here curved ventrally and the endoskeletal sheet rises as it passes posteriorly and is here seen in part in face view. As it is a very thin sheet the numerous fibrils (AF) that anchor it to the ventral exoskeleton are easily seen through it. Details of these in a much larger individual are shown in figures 65–68, plate 3. Note how the ventral endoskeletal sheet is continuous with the ventral intersegmental node (VIN) – seen on the left – and with the ventral intersegmental tendinous sheet (VITS) – seen on the right – at the maxillary/thoracic segment 1 boundary. The endoskeletal sheet curves posteriorly just behind this section and almost immediately becomes anchored to the roof of the food groove as shown in figure 47. Its course can be followed in longitudinal section in an earlier stage in figure 71. On the left of the figure the ventral intersegmental node lies just anterior to the level at which the ventral longitudinal muscles originate (cf. figure 42). The anterior extremities of the latter (VLM) are indicated in a simple manner on the right. The cut ends lie posteriorly and these muscles are running away from the observer. The nerve cords are indicated only for topographic purposes. The maxillulary promotor muscle inserts beneath the endoskeletal sheet. On the right are shown various fibrils and fibrous sheets (Fib) that are continuous with and serve to brace the major element of the endoskeleton. Although their connections are not shown, being here obscured in part by muscles (omitted or indicated by dashed lines), their arrangement and function are readily apparent.

to be seen in figure 43), and for a massive ventro-posterior extrinsic trunk limb muscle (VPEM) of the limb in front of it. The sheet is anchored ventrally by fibres, some of which can be seen in figure 42, that run to the cuticle between the trunk limbs. From it extends laterally and somewhat posteriorly a strap (figure 43, IS) that extends to the lateral body wall. Although this seems in some cases to merge with the tendinous lateral expansion of the horizontal muscle it generally seems to maintain a separate identity laterally.

The horizontal muscle is continuous with a lateral tendinous expansion, the lateral intersegmental tendinous sheet (LITS), which originates on the body wall and extends dorsally (figures 43 and 46 and, for a much older individual, figure 146). The arrangement is, however, more complex than this bald statement implies. Not only is there a system of suspensory fibrils (FLITS) between the exoskeleton and the basement membrane, but between the latter and the lateral intersegmental tendinous sheet are several bundles of short muscle fibres (figures 43 and 46, MLITS) which presumably maintain the correct tension over the whole length of the union more accurately than would the unaided generalized pull of the horizontal muscles.

Ventrally the endoskeleton sends a process, the ventral anchor (figure 42, VA), from the vicinity of the ventral intersegmental node towards the anterior region of the base of the trunk limb anterior to it. Such anchorage to a moving part may be dictated by necessity and is a curious arrangement which involves a special refinement. Although the extreme bases of the limbs move relatively little, compensation has to be made for this and the anchors incorporate muscle fibres adjacent to their attachments to the cuticle. Delicate in early instars (figure 42), these become more robust in older individuals. Even by stage 25 (figure 60, plate 2) an array of muscle fibres is present.

At intersegment TS1/2 there is a considerable gap between the transverse connecting ligament (TCL) and the mid-gut (MG) (figures 43 and 44). At intersegment TS2/3, where the arrangement is virtually identical, the gap is smaller, and at intersegment TS3/4 (figure 45), and all succeeding thoracic intersegments, the ligament is closely associated with the wall of the mid-gut. This brings the dorso-ventral muscles closer against the outer wall of the mid-gut and makes it less easy to see the arrangement in transverse sections than anteriorly, though it is essentially similar at all intersegments.

The dorsal longitudinal muscles are served by intersegmental tendinous sheets (DITS) in the same way as are the ventral. As clearly seen in figure 42 the dorsal sheets lie posterior to their ventral partners. Each serves also to anchor the various dorso-ventral muscles dorsally at a dorsal node (DIN), as seen particularly clearly in transverse and horizontal sections (figures 43 and 49). Figure 43 also shows how this endoskeletal complex is continuous with the lateral intersegmental tendinous sheet (LITS). Dorso-laterally the tendinous sheet unites with the cuticle of the exoskeleton. In part it here breaks up into fibrils but details are difficult to elucidate and define as, at its posterior border (immediately behind the level shown in figure 44), a veritable jungle of extrinsic limb muscles (ETLM) takes its origin among these fibrils, some of them on the sheet itself, some perhaps directly on the cuticle.

The way in which the posteriorly descending oblique dorso-ventral muscle (PDVM) utilizes the dorsal node of one intersegment and the ventral node of the next behind is most readily seen in longitudinal sections (figure 42) but its dorsal anchorage is clearly shown in figure 49, and can also be seen in figure 44.

The arrangement of the muscles at both dorsal and ventral maxilla/trunk segment 1 nodes differs from that at the corresponding thoracic nodes. Running obliquely backward and ventrally from the head to the ventral node is a muscle (SPM 1), most easily appreciated in figure 42, that is clearly the cephalic homologue of the posteriorly descending oblique dorso-ventral muscle of the thoracic segments. As this helps to brace and suspend the ventral endoskeletal sheet it is designated simply as a suspensor muscle of such. Hessler (1964) has shown how muscles serve a similar function in the Cephalocarida. Of the muscles descending from the dorsal node, the anteriormost (SPM2) runs obliquely forward to the ventral node and is clearly the morphological homologue of the anteriorly descending oblique dorso-ventral muscle of each thoracic segment. The adjacent muscle (SPM 3) is the homologue of the vertical dorso-ventral muscle but is here a single and not, as in the thorax, a compound muscle. In figure 42 it is cut through just about where it unites with the endoskeletal sheet, part of which, as seen in the adjacent slice, is indicated by a dashed line. The course of this muscle can easily be followed in figures 49 and 50. Both muscles SPM 2 and 3 also help to brace and suspend the ventral endoskeletal sheet in the region where it passes from head to thorax and are thus again simply designated as suspensors of the endoskeletal sheet. Their location is more strategic for the maintaining of tension in the sheet than that of the more anterior suspensors (AS and PS) which, muscular in the early nauplii (§4), now appear more fibrous – like the adjacent suspensor of the transverse mandibular tendon (STMT) – but possibly retain some contractile ability in early adult instars.

The ventral Mx 2/TS 1 intersegmental node marks the anterior limit of the ventral longitudinal muscles and is unique in respect of the muscles that converge upon it (figure 42). The unique muscles are the suspensors SPM 1 and 2 just described and the cephalic ventral longitudinal muscle (CVLM) noted earlier. There is no horizontal muscle.

In its entirety the skeleto-muscular system of the thorax, and that of the head, with which it is continuous, constitutes a system of struts and braces that grant rigidity to the trunk while at the same time permitting the necessary degree of flexibility.

The basic features of the mandibular muscular system of the Anostraca (based on *Chirocephalus*) have been described by Manton (1964). *B. ferox* differs only in details and a description is not called for here, but to supplement Manton's diagrammatic figures a series of thick transverse slices of the mandibles of an individual at stage 19, i.e. before the mandibular muscles have become massive, is shown in figures 51–53, plate 1. These not only give a good overall impression of the arrangement of the muscles and reveal such key figures as the transverse mandibular tendon (TMT) and its suspensors (STMT), but show the shape of the mandibles, the region of their articulation (Art), and their relationship to the labrum (L) and to such features as the mid-gut (MG) and the tubules of the maxillary gland (D MxG).

Some elements of the musculature of the maxillules can be seen in figures 42, 50 and 80. Not seen in figure 42 as they lie more laterally are two dorsally originating muscles which are the homologues of the dorsally originating anterior and posterior extrinsic trunk limb muscles.

Extrinsic trunk limb musculature is shown in part in figure 42. The arrangement of the muscles, extrinsic and intrinsic, is described and illustrated for *Chirocephalus* by Preuss (1957) and for *Artemia* by Benesch (1969), and is essentially similar in *B. ferox*. Important information on the function of individual trunk limb muscles is given by Preuss (1957).

While that part of the muscular system described above displays the adult pattern by the time that the full series of thoracic limbs becomes functional, individual muscles gradually become more massive as growth proceeds. Of necessity there is a concomitant increase in the robustness of certain parts of the endoskeleton, and a considerable development of fibrous suspensors and bracers. Some of these developments are seen in figures 57–62, plate 2, and figures 146 and 147, which serve also to illustrate certain points dealt with later. The strengthening, and increase in size, of endoskeletal elements is well seen by a comparison of figure 50 and figure 65, plate 3. In the former the endoskeletal sheet (Endo S) is extremely flimsy and difficult to make out, even in well fixed preparations: in the latter it is readily seen and, being blue- and blue-purple-staining with Mallory, contrasts strongly with the red-staining muscles whose massive development is also seen.

In addition to the major elements of the endoskeleton, *B. ferox* makes extensive use of fibrils and tendon-like sheets in various parts of the body, especially in large adults. Their roles are various. They serve, for example, to suspend organs, such as the tubules of the maxillary gland, and, as assistants to the dorsal intersegmental tendons, the dorsal longitudinal muscles (figure 42). Often fibrils are associated with contractile fibres with which they merge imperceptibly. Large numbers of such fibrils, contractile at each end, span the cavity of the trunk limbs where they presumably operate antagonistically to the hydrostatic pressure of the haemocoelic fluid. In the limbs too they provide firm anchorages for muscles and brace the narrow 'joint' regions. Examples of the use of fibrils in several contrasting situations are illustrated in plates 1–3 and figure 83.

The labrum of branchiopods is often described as a 'fleshy' lobe. Figures 55 and 56, plate 1, show how the specialized distal lobe acquired by large individuals of *B. ferox* (§13(*a*)) is spanned by a reticulum of fibrils many of whose extremities are red-staining with Mallory and presumably contractile, though muscle striations are not always apparent. Fibrils (S Fib) and a fibrous sheet (FSH) used for suspending the labral glands are shown in figure 83. A particularly instructive example of the use of fibrils for load-spreading and anchorage of muscles is illustrated in figures 58 and 59, plate 2, which show some of the fibrils that form part of a system involved in the anchorage of oesophageal dilators and the support of antennal muscles, details of which are irrelevant here. A further example, figure 54, plate 1, shows bracing fibrils (B Fib), some of whose attachments are contractile, in a thoracic limb.

9. DEVELOPMENT OF THE ENDOSKELETON

Any account of the development of the endoskeleton inevitably involves reference to the concomitant development of the muscular system. Early stages of the ontogeny of the latter in *Streptocephalus* and *Artemia* are described by Claus (1886) and Benesch (1969), and the sequence of development of the trunk muscles in *Chirocephalus* is reported by Cannon (1926).

DESCRIPTION OF PLATE 1

FIGURES 51–53. A series of thick transverse slices through the mandibles of an individual at stage 19, as seen from in front and revealing the various mandibular muscles and parts of the endoskeletal suspensory system. The shape of the mandibles and the topographical relations between mandibles and labrum are also apparent. The sequence is from anterior to posterior. The mandibular promotor muscles (3) – the antagonists of the remotors (4) – lie anterior to the section shown in figure 51 and are therefore not seen.

FIGURE 54. Bracing fibrils with contractile extremities located near the base of a thoracic leg of a 41 mm adult.

FIGURE 55. Thick horizontal slice through the ventral part of the labrum of a 44 mm individual (ventral), showing the distal lobe protuding between the first thoracic limbs.

FIGURE 56. As figure 55, showing the reticulum of fibrils, many with contractile extremities, that span the cavity of the distal lobe.

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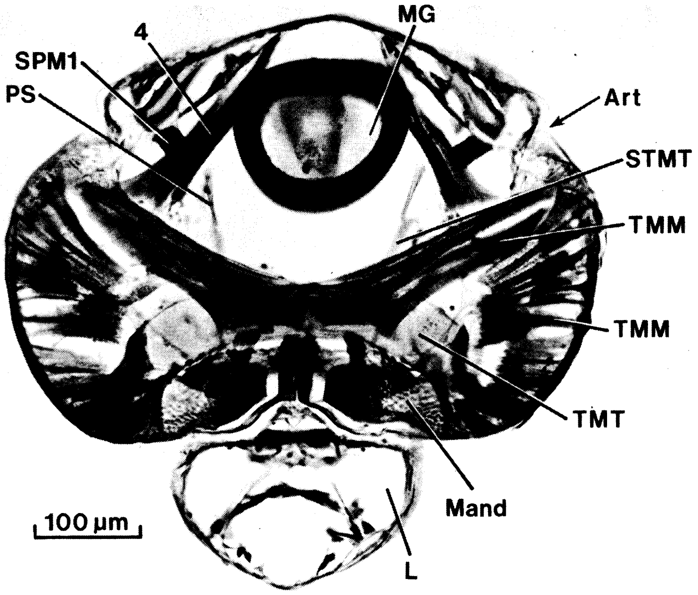

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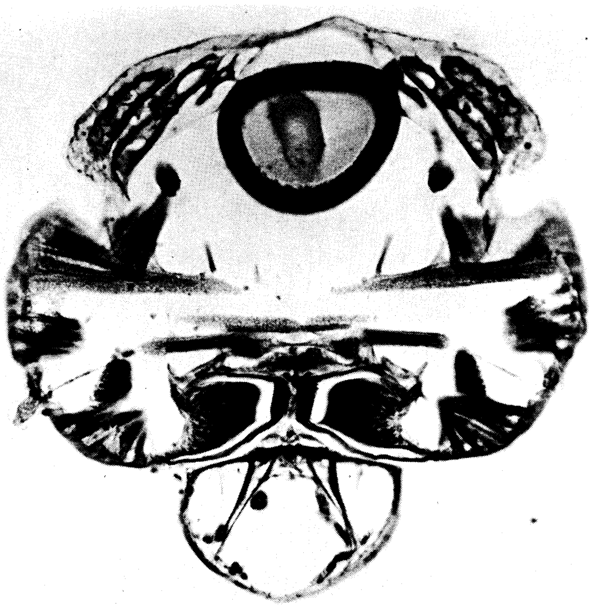

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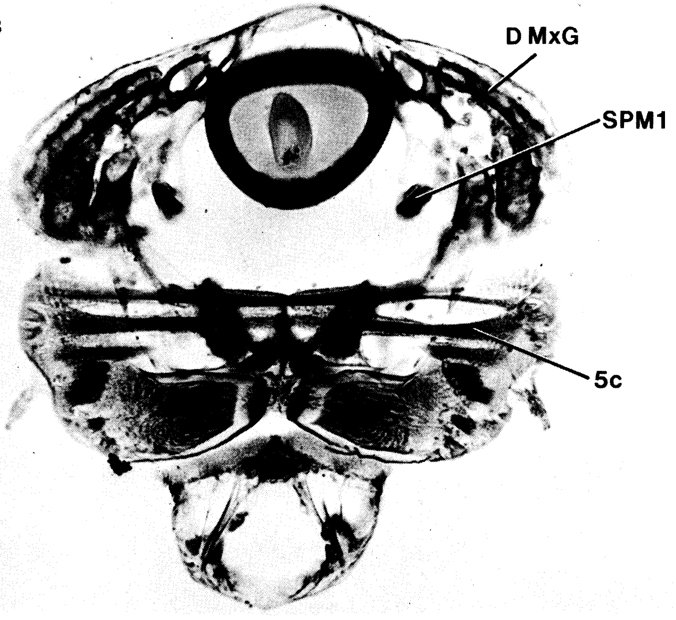

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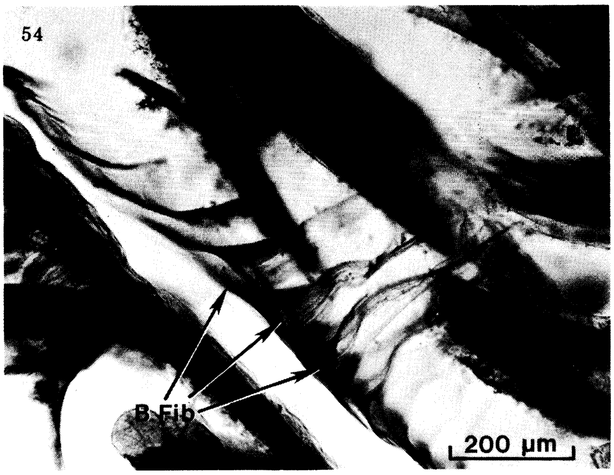

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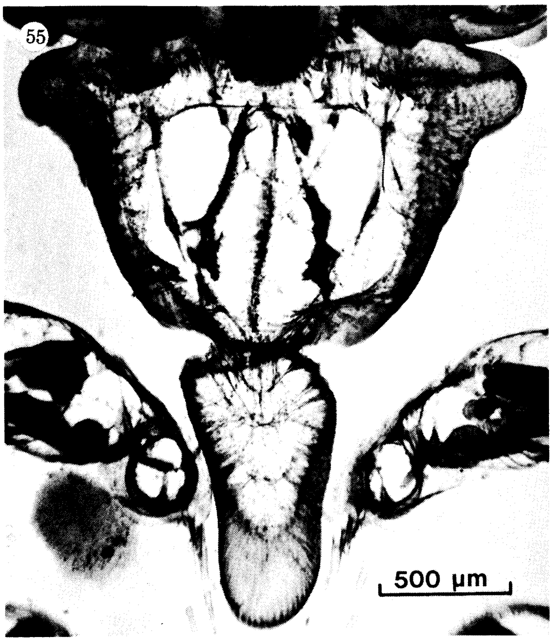

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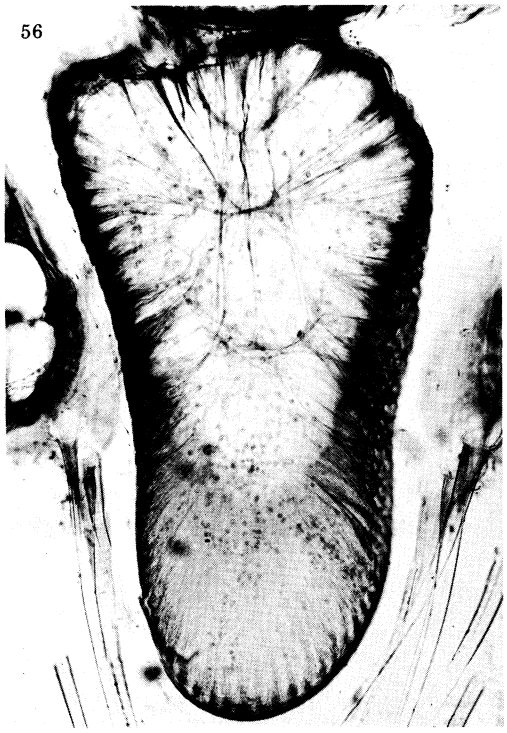

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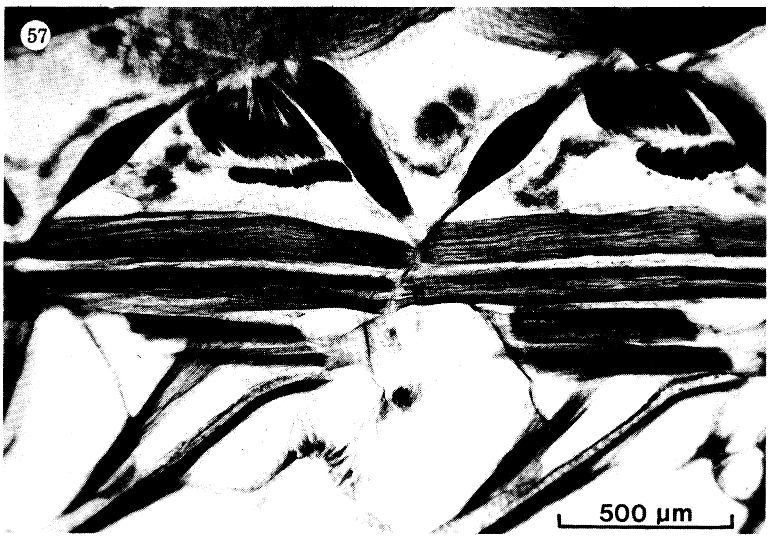

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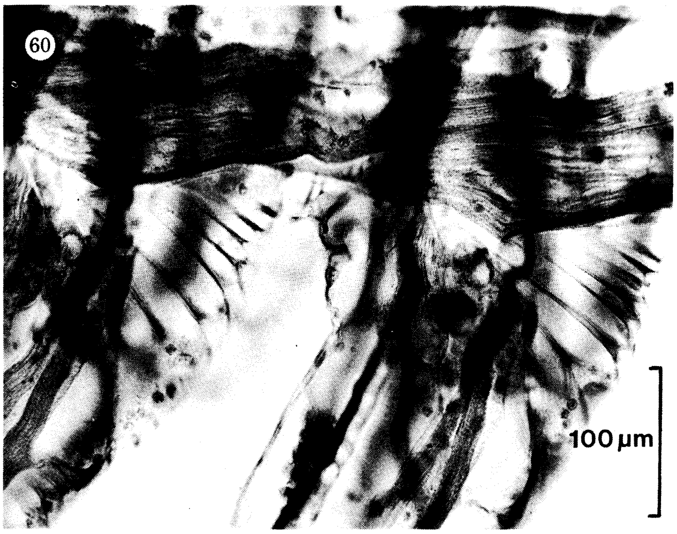

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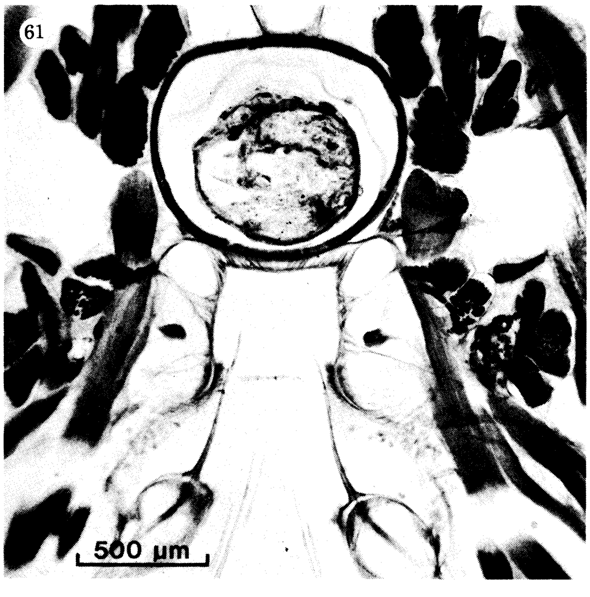


62

DESCRIPTION OF PLATE 2

Some features of the skeleto-musculature, particularly of large individuals.

FIGURE 57. Longitudinal section at the level of thoracic intersegment 6/7 to show the massive development of the trunk muscles in a 44 mm individual (cf. figure 42 for the same muscles in a much earlier instar).

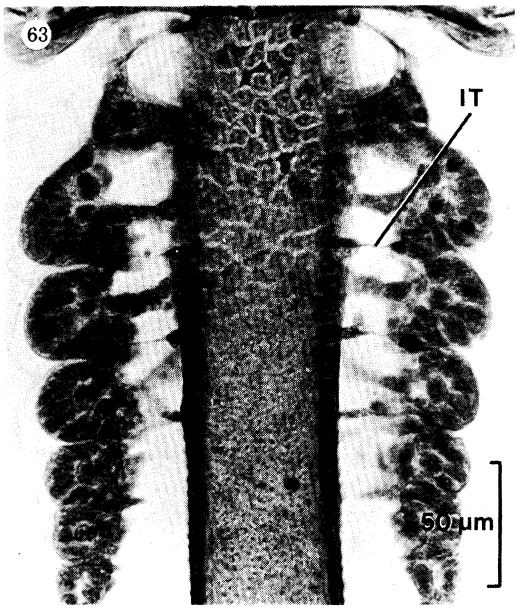
FIGURE 58. Horizontal section at the extreme anterior end of the body of a 36 mm individual, showing the region between the bases of the antennae (seen on each side) to illustrate the use of fibrils for load-spreading and the anchorage of muscles.

FIGURE 59. As figure 58, showing the load-spreading fibrils in greater detail.

FIGURE 60. Longitudinal section at the level of the ventral longitudinal muscle of an individual at stage 25 showing the anchoring fibrils at the base of trunk limbs 4 and 5.

FIGURE 61. Thick transverse section of a 36 mm individual at the level of a transverse connecting ligament of the endoskeleton, which lies just beneath the mid-gut and can be seen anchored by fibrils to the food groove roof (see figure 62 for details). The gnathobases seen at the bottom of the photograph are those of trunk limb 4. Note the massive development of the trunk muscles, of which the dorsal and ventral longitudinal bundles are cut transversely, in comparison with the condition in younger individuals (cf. figure 43).

FIGURE 62. As figure 61, showing details of the endoskeleton and fibril system and the massive nature of the ventral longitudinal muscles, here cut transversely.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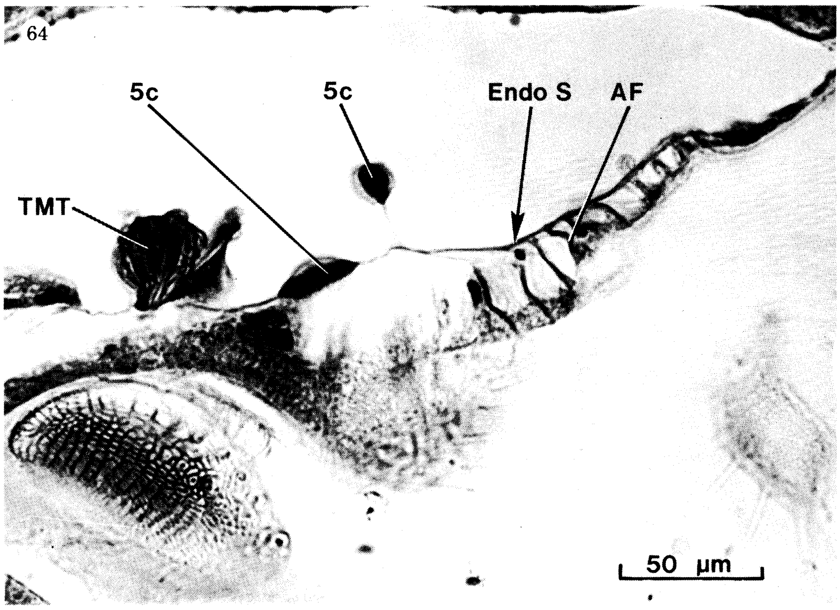
IT
50 µm


64
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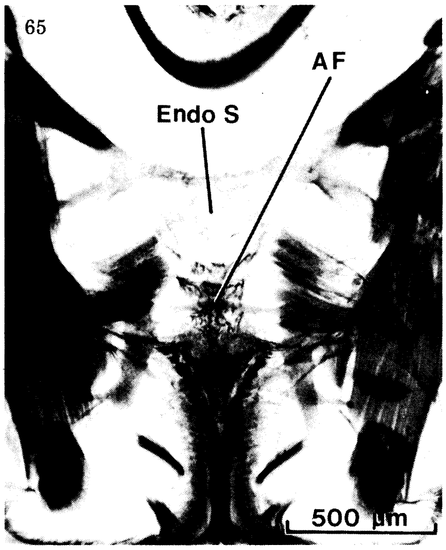
65
AF
Endo S
500 µm


66


67


68


69
200 µm


70

Here, therefore, the development of the muscular system, the later stages of which are easy to appreciate in the light of information given in §8 and by reference to figures 29, 30 and 35, is mentioned only briefly in connection with the development of the endoskeleton.

Although the ventral cephalic endoskeleton of the earlier naupliar stages is partly sheet-like there is a tendency for it to form transverse bars, of which the post-oesophageal bar (POB) and the transverse mandibular tendon (TMT) are very obvious (figure 13). Its shape at any given stage is difficult to ascertain and even more difficult either to describe or illustrate as it changes much over short distances and the sheet does not everywhere lie in the same plane. Some idea of its configuration at stages 3 and 4 is to be obtained from figures 13 and 16–19 (see §4 for brief description).

As can be seen in figure 13, posterior to the mandibles the endoskeleton takes the form of a delicate sheet, and figure 18 shows how, at stage 5, this (Endo S) is anchored to the ventral cuticle by means of fibrils (AF). As development proceeds the cephalic region increases in length, the maxillules and maxillae gradually differentiate, the ventral endoskeletal sheet extends posteriorly (figure 71), the number of anchoring fibrils (AF) increases, and the sheet eventually becomes anchored to the roof of the food groove just behind the ventral intersegmental node of the maxillary/first thoracic segment.

The posterior region of the cephalic endoskeleton is shown for a stage 14 larva in figure 71. This makes clear how the transverse mandibular tendon (TMT) is an elaboration of the endoskeletal sheet (Endo S), and how the sheet also extends anteriorly. Although its post-mandibular portion rises posteriorly, the endoskeletal sheet gradually approaches the cuticle of the ventral body wall (VBW) which here rises more steeply and, at the posterior limit of the anchoring fibrils (AF), it merges imperceptibly with the basement membrane of the ventral cuticle. Its posterior limit lies within the thorax as can be seen from the positions of the two relevant ventral intersegmental nodes, indicated by black spots, but as the maxillary/thoracic segment 1 node (Mx 2/TS 1) lies well forward (cf. the level of the maxillule (Mx 1) and maxilla (Mx 2)) the intrusion is not great.

In older individuals fine fibrils are present which bind that portion of the endoskeletal sheet that lies anterior to the transverse mandibular tendon to the cuticle that overlies the mandibles,

DESCRIPTION OF PLATE 3

Some details of the endoskeleton.

FIGURE 63. The genesis of the thoracic endoskeleton as seen in a horizontal section of a stage 5 larva. Intersegmental tendons (IT) can be seen developing at the first two thoracic intersegments.

FIGURE 64. Longitudinal section of the mandibular region of a stage 4 larva to show the endoskeletal sheet (Endo S) and its anchoring fibrils (AF). Note also the armature of the masticatory surface of the right mandible.

FIGURE 65. Transverse section of a 36 mm individual just behind the level of the mandibles, viewed from in front, showing the ventral endoskeletal sheet (Endo S) and the fibrils (AF) that anchor it to the ventral cuticle (cf. figure 50 for the same region in a much earlier stage).

FIGURES 66–68. The anchoring fibrils shown in figure 65, more highly magnified and immediately posterior to the level of that figure, shown at successively deeper levels of focusing. In figures 66 and 67 the endoskeletal sheet is curving away from the observer as it rises and is not in focus; in figure 68, where it is beginning to pass backward in approximately the horizontal plane, its cut edge is seen as a somewhat more definite, but still vague, curved outline.

FIGURE 69. Longitudinal slice of a 41 mm individual showing some of the mass of fibres used in muscle anchorage near the base of a thoracic leg.

FIGURE 70. Thick transverse section of a 36 mm individual showing a ventral intersegmental node and adjacent parts of the endoskeleton. (See figure 43 and figures 61 and 62, plate 2, for location).

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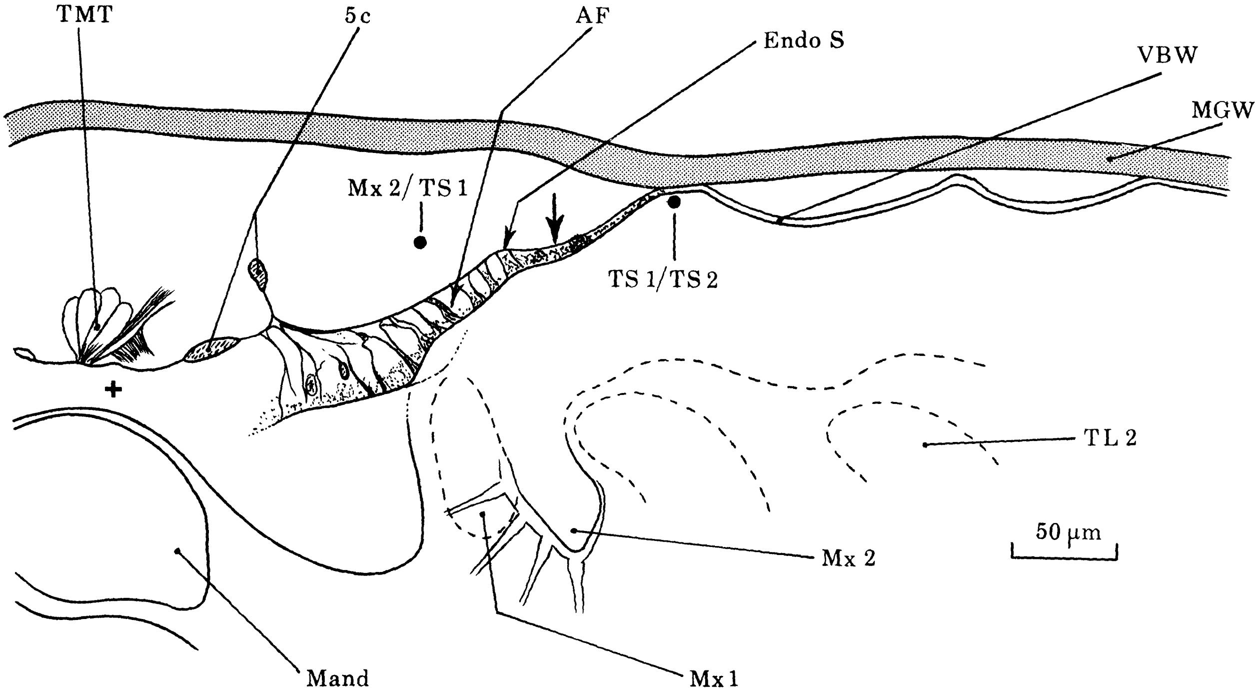

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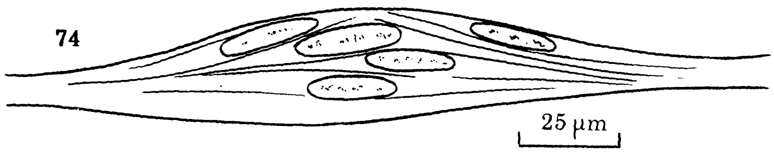

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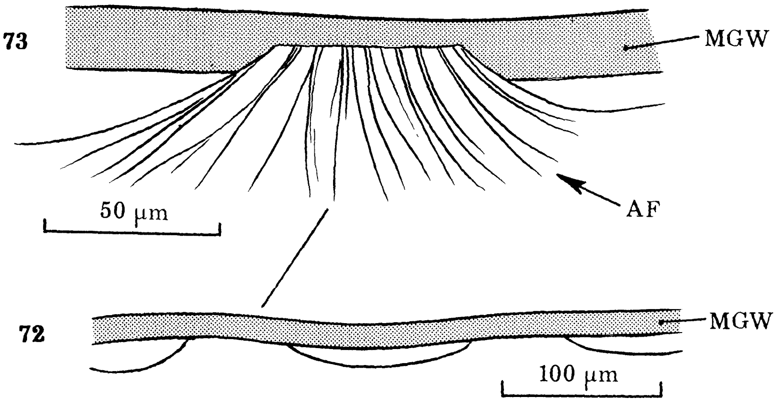

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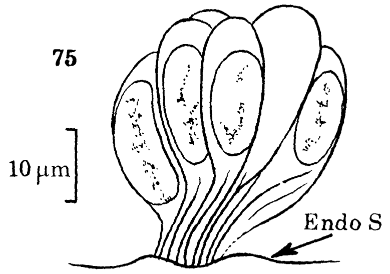

Figures 71–75. Endoskeletal details in some early instars.

Figure 71. Longitudinal section through the postero-ventral part of the head and adjacent structures of an individual at stage 14 to show the posterior sheet of cephalic endoskeleton (Endo S) and its anchorage by fibrils (AF) to the ventral cuticle. The approximate region where the endoskeleton merges imperceptibly with the basement membrane is indicated by a vertical arrow. The region (more lateral) of each relevant ventral intersegmental node is shown by a black spot, the anteriormost being the maxilla/thoracic segment 1 node, the next that of thoracic segments 1/2. The positions of the maxillule (Mx 1) and gnathobases of the first two trunk limbs (TL) (either nearer to or further from the observer) are indicated by dashed lines. Note how the transverse mandibular tendon (TMT) is an elaboration of the endoskeleton (for details see figures 74 and 75) and how, near the mid-line, the ventral body wall (here the roof of the food groove) is closely associated with the mid-gut wall. In the region ventral to the transverse mandibular tendon, indicated by +, fibrils later develop that anchor the endoskeletal sheet to the cuticle, but no such have been detected at this stage.

but such have not been detected at the stage (14) illustrated. As the animal grows, the fibrils (AF) that anchor the posterior cephalic endoskeletal sheet become more robust and their ventral ends splay out and become more numerous, thereby keeping pace with the increasing mechanical demands made upon them. In individuals 20 mm or more in length they are vastly more massive than the delicate fibrils from which they originated.

The ontogeny of the endoskeleton also involves independent activities in the thorax. Here, at a very early stage of development, on each side of the body a fibrous tendon (IT) develops at each intersegmental boundary and extends antero-ventrally from the ectoderm to deeper-lying regions (figure 28 and figure 63, plate 3). These intersegmental tendons soon come to lie much deeper within the body as a result of the development of initially relatively undifferentiated tissues both laterally and ventrally (figure 30). They eventually become more or less transverse straps (figure 43, IS), whose inner extremities expand to provide the ventral endoskeletal node (VIN) and a fibrous sheet (VITS), that between them eventually support the ventral longitudinal muscles, the muscles of the dorso-ventral series, and a major extrinsic trunk limb muscle (VPEM) as described in §8. The lateral extremity is expanded from an early stage of development (figure 30).

The development of the tendons is associated with that of the dorso-ventral muscles whose arrangement is described in §8 (compare figures 43 and 44). Of these, as in *Chirocephalus* (Cannon 1926), the vertical dorso-ventral (figure 30, VDVM) differentiates first. The anteriorly descending oblique dorso-ventral muscle (ADVM) develops later than the vertical and horizontal (HM) muscles and indeed were it to do so earlier there would be nowhere for it to become attached. Cannon (1926) describes only its primordia but his diagrammatic figure shows its ventral end located somewhat laterally in *Chirocephalus* as it is in *B. ferox*.

The endoskeletal tendon also expands laterally (compare figures 30 and 43) to give rise to a delicate sheet (LITS) which extends dorsally up the lateral cuticular wall of the thorax and merges with the expanding dorsal tendinous attachment of the vertical dorso-ventral muscle to give rise to a dorsal endoskeletal mass that eventually differentiates into a node (DIN) and a sheet (DITS). These serve the dorsal longitudinal muscles (DLM) and the dorsal extremities of the dorso-ventral muscles in the same way as their ventral equivalents serve the ventral longitudinal muscles and ventral extremities of the dorso-ventral muscles.

In its early stages, the intersegmental endoskeletal tendon (IT) is closely associated with the developing horizontal muscle (HM) which indeed seems to differentiate in its dorsal portion though there is a clear separation later when the tendon forms an intersegmental strap (IS).

DESCRIPTION OF FIGURES 71–75 (*cont.*)

FIGURE 72. Longitudinal section, stage 22, towards the posterior end of the thorax showing how at each intersegmental boundary the ventral fibres of the thoracic endoskeleton are closely associated with mid-gut wall.

FIGURE 73. As figure 72. Ventral fibres of the thoracic endoskeleton at an intersegmental boundary. The region of figure 72 here shown more highly magnified is indicated.

FIGURE 74. The transverse mandibular tendon of an individual at stage 14, as seen in optical section from the ventral side, to show its cellular nature. It is contiguous on its ventral surface with the delicate endoskeletal sheet (cf. figures 71 and 75).

FIGURE 75. Transverse section of the transverse mandibular tendon of an individual at stage 14, as seen in longitudinal section of the whole animal. Note the continuity of the tendon with the ventral cephalic endoskeletal sheet (Endo S). Note also the laminar nature of the tendon and the elongate cells associated with its production.

This strap, which links the dorsal and ventral elements of the endoskeleton, persists throughout life. However, as the animal increases in size, the bulk of the ventral longitudinal muscles becomes proportionately greater (compare figure 43 with figures 146 and 147) and the strap therefore relatively shorter.

The intersegmental sheets also become elaborated in the vicinity of the food groove to whose rigid lateral walls they become anchored by means of numerous fibrils (figure 48, FFG) and across whose roof they expand in the horizontal plane to form a cross link, the transverse connecting ligament (figures 43 and 44, TCL), which becomes anchored to the roof of the food groove by means of fibrils (AF).

During the early post-naupliar stages the transverse connecting ligaments, which form ventral intersegmental cross struts on the roof of the food groove, give the impression of being closely associated with the ventral region of the mid-gut (figure 71). This apparent association continues throughout development at the more posterior intersegments, as is indeed inevitable because the roof of the food groove lies close against the gut wall (figure 45). However, anteriorly, where there is more space between the gut and the food groove roof, as development proceeds the first two thoracic intersegmental connecting ligaments separate from the gut wall (figures 43 and 44), thereby emphasizing that the connection is with the rigid food groove walls and not with the mobile wall of the gut.

As shown in figure 50 the cephalic and thoracic portions of the endoskeleton are continuous in the adult, the posterior end of the cephalic sheet (Endo S) being united on each side to the ventral maxillary/first thoracic intersegmental node (VIN) by a tendon (LT). Further details of the region of transition between the cephalic and thoracic components of the endoskeleton are illustrated in figures 47 and 48 and figures 65–68, plate 3. In figure 47 the ventral maxillary/first thoracic intersegmental tendinous sheet (VITS) and the way that it is anchored to the food groove walls are clearly seen. Other elements of the thoracic endoskeleton are seen in figures 42–49, figures 57, 61 and 62, plate 2, and figure 70, plate 3, details being explained in their respective captions. Comparisons of transverse and horizontal sections are particularly informative, e.g. in revealing the arrangement of the anchoring fibrils on the roof of the food groove at each intersegment.

Thus is built up a complex endoskeleton that combines the advantages of lightness, flexibility and great strength. Its lightness is readily apparent; for the most part it is made up of extremely thin sheets. Mechanical flexibility can be inferred from some of the actions of which adults are capable, from manipulation and from its blue-staining reaction to Mallory. Its strength can be most easily appreciated by manipulation of the transverse mandibular tendon; which is, however, more robust than the thin sheets. Apart from its intrinsic mechanical properties, about which very little is known for any branchiopod, the strength of the system depends on the principle that thin sheets can possess relatively great tensile strength – as can readily be tested by pulling in diametrically opposite directions on a sheet of paper. The flexibility of the endoskeletal sheets suggests that the individual chitin fibres of which they are composed tend to have a parallel arrangement (see Wainwright *et al.* 1976), doubtless arranged in line with the muscles whose contractions they resist, as are isolated groups of fibrils.

Many of the major muscles are attached to the edges of endoskeletal sheets and pull in essentially the same plane as the sheet, those of the dorso-ventral series (e.g. figure 43) being good examples. Such sheets are also admirably suited to the slinging and supporting at regular intervals of the longitudinal trunk muscles without involving heavy, inflexible structures.

The transverse mandibular tendon (TMT) bears particularly heavy loads and from the second naupliar stage onwards has to withstand pulls from the transverse mandibular muscles (TMM) that are oblique to its long axis (see figure 13 for nauplius, and figure 51, plate 1, for an individual at stage 19). It is therefore more robust than the rest of the endoskeleton, most parts of which consist of a thin sheet. It is made up of several sheets (figures 74 and 75), closely associated ventrally, but more widely separated dorsally where cells with conspicuous elongate nuclei that presumably secrete them can be seen, especially in early instars. Even in very large individuals (over 40 mm in length), however, these cells and their nuclei can still be seen in transverse sections cut near the middle of the tendon, though the cells are now much compressed and not inflated like those of early instars. In this region therefore the endoskeleton is more than merely a cell product, though it is clearly the products that confer the requisite mechanical properties on the tendon.

There are interesting, and in some cases puzzling, differences between the development of the endoskeleton as described here and such parts of the process in *Chirocephalus* as were described by Cannon (1926). Although concerned particularly with the development of the muscular system, Cannon's observations, which are well described and clearly illustrated, show that dorsally the endoskeleton in *Chirocephalus* arises essentially by conversion of the fibrils of the dorsal extremities of the dorso-ventral muscles into tendofibrils which spread to form a rigid plate, a process involved also in *Branchinecta*. Intersegmental tendons such as are present in *Branchinecta* are not described. Ventrally it is reported that the dorso-ventral muscles narrow down to a tendon that runs directly to the cuticle in the mid-ventral region, and there are no indications, at least in the early stages, of any endoskeletal elaboration such as is so conspicuous in *Branchinecta*. Cannon's observations were confined to the early stages of development, to which his detailed illustrations apply, and events that take place in *B. ferox* suggest that in later stages ventral elaboration takes place. However, his diagrams (p. 407) of trunk muscles – intended as such and not as detailed figures – show no such elaboration save a possibly tendinous link between the ventral longitudinal muscles and the mid-ventral exoskeleton, to which he notes that they retain a connection by means of 'a thin chitinous sheet which is a development of the basal membrane of the ectoderm of this region'. Nothing like the strap-like intersegmental tendon of *B. ferox* is shown, yet without such a device there can be no means of preventing the ventral longitudinal muscles from sagging and no rigid place of attachment for the anteriorly and posteriorly descending dorso-ventral muscles (labelled 'connective muscle' in Cannon's upper figure).

To elucidate this mystery sections were cut of an adult *Chirocephalus diaphanus*. These revealed that a strap-like tendon, very similar to that of *B. ferox*, is indeed present and clearly serves the same functions. (In the animal sectioned the ventral longitudinal muscles were more massive than in the stage 24 individual shown in figure 43 but less so than in the 36 mm individual shown in figures 146 and 147, and the strap was accordingly relatively shorter than in the former but longer than in the latter.)

That, as expected, *Branchinecta* and *Chirocephalus* are similar in this respect, removes an apparent anomaly. In the development of the endoskeleton, *Branchinecta* resembles the malacostracans *Hemimysis* (Manton 1928) and *Nebalia* (Manton 1934) in that in all cases the trunk endoskeleton originates from intersegmental bars, and one would not have expected it to show greater resemblance to these remotely related crustaceans than to its fellow anostracan *Chirocephalus*.

There is no strap-like tendon in the cephalocaridan *Hutchinsoniella*, to whose excellently described skeleto-muscular system (Hessler 1964) that of *Branchinecta* bears many general similarities, but there the horizontal muscle links the ventral endoskeletal mass with the lateral body wall and thus supports the ventral longitudinal muscles at each intersegment.

10. SOME ASPECTS OF FILTER-FEEDING IN THE EARLY POST-NAUPLIAR STAGES

The feeding mechanism of most anostracans involves the filtration of fine particles throughout adult life by means of setae borne on the trunk limbs which, as one of the consequences of the metachronal rhythm of their beat, draw suspended material into the mid-ventral region. This process has been studied by various authors (Lundblad 1920; Storch 1924–25, 1929; Cannon 1928, 1933, 1935*a*; Eriksson 1934). Many of its essential features are agreed upon by these investigators and even by Lowndes (1933) who misinterpreted certain important aspects, and are conveniently summarized by Manton (1977). Controversial matters, however, remain. Here the feeding mechanism is not described in detail: attention is merely drawn to certain features that either have a bearing on unsettled points or amplify earlier accounts, and mention is made of the transition between the naupliar and adult mechanisms.

On certain points Cannon was adamant. Thus he maintained that, during that phase of the cycle of trunk limb movement when the interlimb space is being reduced in volume, this space becomes subdivided by contact of adjacent limbs. He further claimed that as a consequence of this, while most water is expelled outwards (postero-laterally), thereby driving the animal forward – though the main propulsive thrust actually occurs immediately before this phase of the cycle – that discharged from the proximal compartment enters the food groove in which it passes forward. This intermittent current he refers to (1933) as being squeezed between the filter setae of the compound basal endite – here simply termed the gnathobase. He also maintains that it leaves the inter-limb space by a definite exit groove which he said is present in 'all the Anostraca which I have studied' (Cannon 1935*a*), and is the main means of moving food forward along the food groove. By contrast Storch maintained that food is swept along the food groove by the gnathobasic setae, not only in the Anostraca but in all branchiopods.

While not denying that some water may enter the food groove from the inter-limb space at the appropriate phase of the cycle (see below) I cannot confirm the subdivision of that space in the manner described by Cannon. Of particular relevance here is the fact that the trunk limbs begin to function before they are fully developed and are able to collect food particles and transfer them anteriorly when only a few anterior pairs are operative. It is even more difficult to see how the inter-limb spaces become sub-divided in individuals with only partially developed limbs than it is in adults. This does not mean that, as adjacent limbs approach each other, some water is not squeezed into the median chamber. However, I cannot trace an exit groove in *B. ferox* though there is inevitably a depression between adjacent limb bases which might be thought to be such. Cannon's illustration of an exit groove (1933, fig. 2*b*) is very clear, but the so-called groove is no more than the space between the 'toe' of the gnathobase and the corm of the limb and is an inevitable consequence of the projection of the former from the latter.

I also find it difficult to agree with Cannon as to which phase of the cycle of movement constitutes the suction phase. Cannon gives a good general account of this cycle – though some details call for modification – and explains clearly how, of a pair of adjacent limbs, it is the posterior that is ahead in the cycle. This being so, suction can only begin following the point when, on its forward stroke, the posterior limb has reached its maximum swing but the anterior limb continues to swing forward – thereby widening the inter-limb space. This space continues to widen as the posterior limb begins to swing back while the anterior either is still swinging forward or has reached the maximum forward position but has not begun to swing backward, and for some time after it has begun to do so but is still accelerating. The essence of this is correctly presented by Manton (1977). Cannon holds that suction takes place during the forward stroke during which he claims that the inter-limb space is increasing in volume (1928, p. 809). In fact, during this phase of the cycle, in *B. ferox* at least, adjacent limbs lie close together, the inter-limb spaces are almost obliterated, and several pairs of limbs move forward essentially simultaneously (figure 77). Thus as a wave of anteriorly moving limbs is built up, trunk limb 11 moves against trunk limb 10, both move forward so that trunk limb 10 abuts on trunk limb 9, all three move forward until trunk limb 9 meets trunk limb 8, and so on, so that eventually a wave of six pairs of trunk limbs is moving forward, the pace being about the same for each. It is only at about the time that trunk limb 5 is being incorporated into this wave that trunk limb 11 begins to separate from the posterior end of the series and move back, thus initiating the development of a gap between it and trunk limb 10, to be followed by the opening up of successive gaps between trunk limbs 10 and 9, 9 and 8, and so on. It is as this gap develops that suction occurs.

Although Cannon's clear sketch (1933, figure 1) shows the general features of a set of anostracan limbs at a given instant in a swimming and feeding animal, it is idealized and reveals neither the full subtlety of the process nor the correct relative positions of the limbs during the forward stroke such as are revealed by cine-photography. Such an idealized illustration also obscures an important attribute of the limbs – great flexibility. The flexibility, and the fact that, with one exception noted by Preuss (1957), the anostracan limb lacks joints, deserve emphasis. It is indeed ironical that, while undoubted arthropods – literally, jointed limbed animals – the Anostraca (and the Cladocera) owe much of their success to the lack of joints in the limbs, movements of which, often of great subtlety and precision, exploit their jointless nature. Preuss (1957), who lists individual muscles, has described some of the details of limb flexure and extension in *Chirocephalus*, without which abilities neither swimming nor feeding would be possible in the manner now practised. The single joint lies between what is here recognized as the exopodite and the corm. In *B. ferox* there are two flexors and an antagonistic extensor. Preuss indicates that four muscles are involved, but these muscles are particularly easy to see in large individuals of *B. ferox* and there are only three. It is, however, the principle rather than the details that are important, and there may be differences between different species.

Figure 78*a–n* shows the successive positions of the distal portion of a limb during a cycle of movement (for description see caption) and figures 76 and 77 show the positions of the entire set of trunk limbs at different phases of a cycle. Besides lying close to their fellows, forwardly moving limbs are much flexed, their distal portion being bent backward so as to lie, at least in the case of the posterior limbs, more or less at right angles to the basal region of the corm (figure 76). As they move forward they keep a low profile, thereby offering minimal resistance to the water during what, locomotion-wise, is their return stroke. They are also rotated so that their anterior faces lie, not at right angles to the long axis of the trunk when the animal is viewed from below, but oblique to it, the inner part of the corm lying anterior to the lateral. This also reduces resistance to the water on the forward stroke. At the end of the forward stroke

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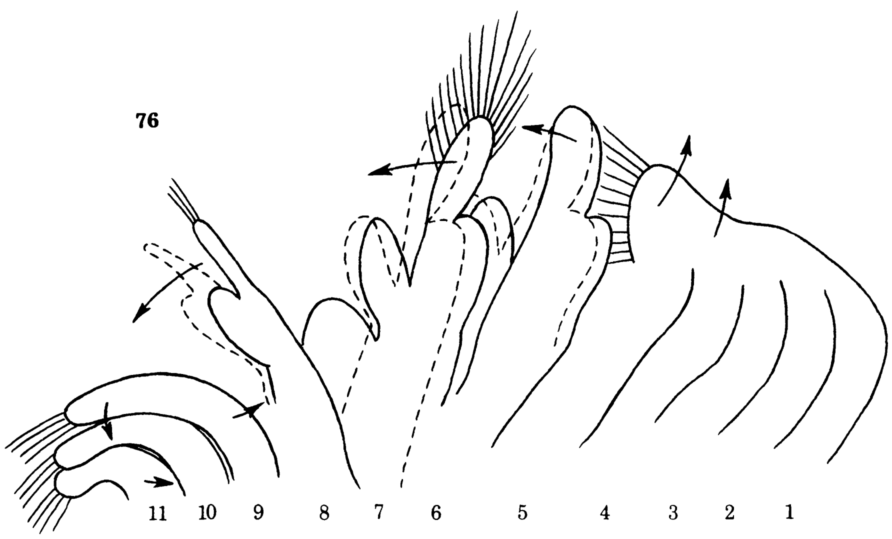

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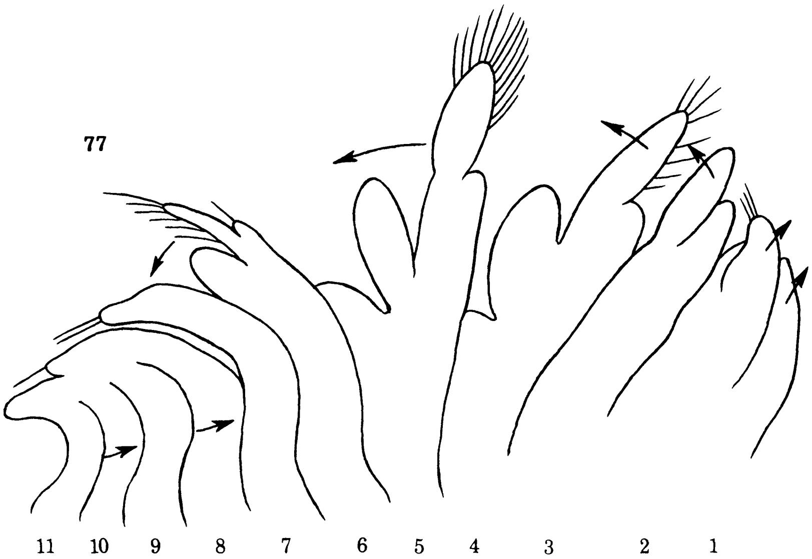

FIGURES 76 AND 77. The sequence of trunk limb movement in a filter-feeding adult.

FIGURE 76. Outlines of the trunk limbs, seen laterally, at a particular instant during a cycle of movement, prepared from cine-film. Trunk limb 4 is beginning to extend prior to commencing its backstroke; trunk limb 5, which is further ahead in the cycle, has extended further; trunk limb 6, more or less fully extended, is beginning to swing backwards; trunk limbs 7 and 8 are doing so more rapidly; the distal portion of the trunk limb 9 is still swinging, but now essentially towards the trunk so as to fold the limb, and its proximal region has already reached the end of the backstroke and is beginning to move forward. Trunk limbs 10 and 11 are moving forward, the movement being essentially at the proximal end of the limb while the distal region remains flexed. At this stage trunk limbs 1–5 are so closely packed that their individual outlines are difficult to make out. To further illustrate the sequence, the positions occupied by trunk limbs 6, 7 and 8 immediately following those shown are indicated by dashed lines, the time interval being the same in each case.

FIGURE 77. The same but at a different phase of the cycle. Trunk limbs 1–4 are extending, and in the case of 3 and 4 beginning to swing backwards, trunk limbs 5 and 6 are swinging backwards, trunk limb 7 is flexing as it reaches the end of its backstroke, and trunk limbs 8–11 are swinging forward, at least proximally. Note the bunched nature of the forwardly moving limbs and the virtual absence of any inter-limb spaces.

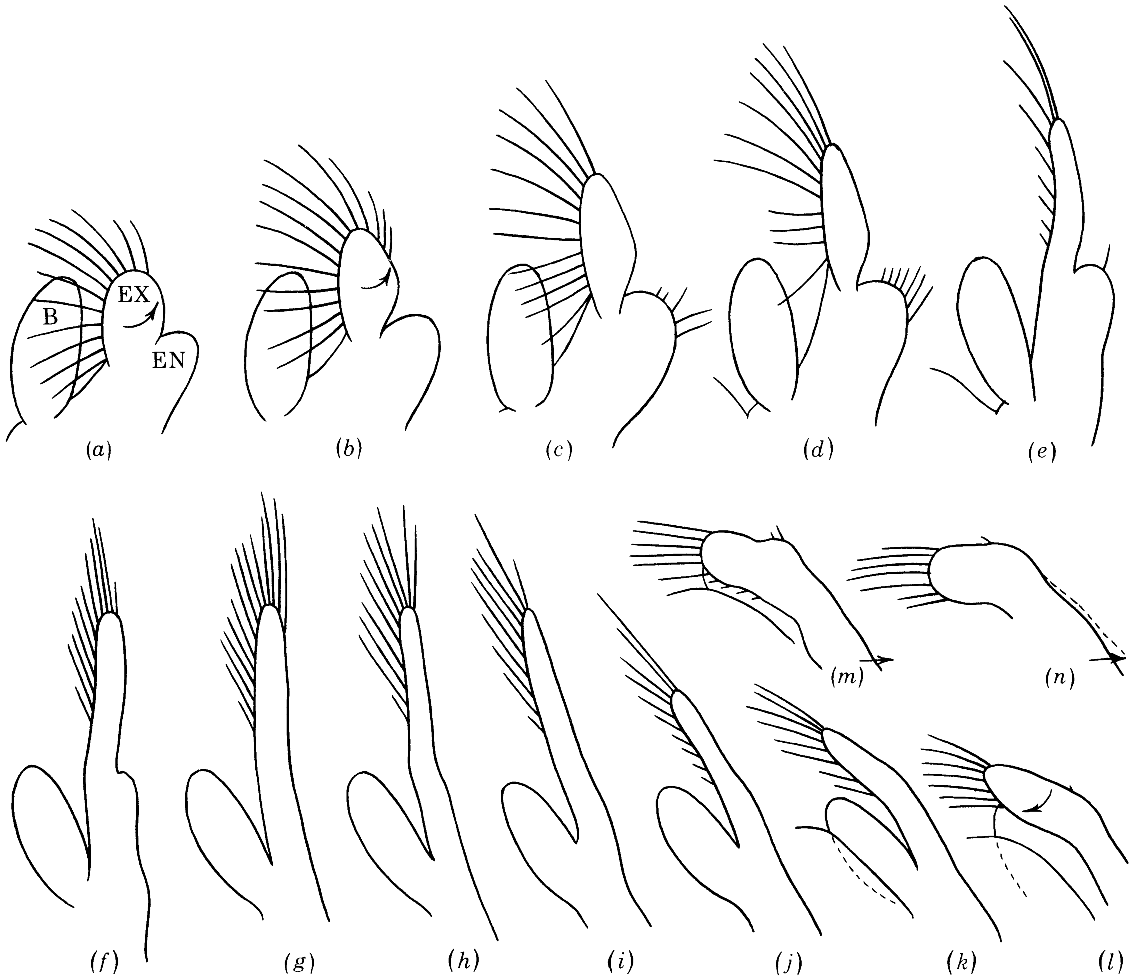

FIGURE 78. Sketches, prepared from cine film, of the distal part of a trunk limb, viewed from the inside. These show the successive positions, particularly of the exopodite, from the time when the limb begins to extend from the body prior to 'spreading' and delivering the working stroke as it swings posteriorly to the point when it begins to fold close to the trunk for the return (forward) stroke. The same base-line is used for each figure. Note how in (*a*)–(*e*) the exopod not only rises relative to the bract, itself rising somewhat, but rotates so as to lie more or less at right angles to the direction of motion. The setae seen at (*e*) are those on the inside of the exopod, those at (*f*) on the outside. The rotation is reversed towards the end of the back stroke. At (*m*) and (*n*), as the limb folds against its posterior partner, its proximal regions are already beginning to swing forward, as indicated by the arrows, and, in (*n*), by the dotted line.

a limb straightens out in such a way that it appears to unfold and rear up as it becomes fully extended in order to present the maximum surface area to the water on the working backstroke (figures 76, 77 and 78). The distance that a forwardly moving limb extends from the body is usually only about 65 % of that from the tip to the base of a fully extended limb. As the limb begins to move backward it also rotates so as to bring its face to a position at right-angles to the long axis of the trunk, the most efficient position for developing maximum thrust on the working stroke (figure 78*d*–*f*). This rotation also has the effect of widening the inter-limb space more rapidly towards the mid-line than laterally, thereby promoting suction from the mid-ventral space via the filter plates to the inter-limb space.

Suction in the mid-line (into the median chamber) is not uniform along the length of the trunk limb series but is at a maximum in the vicinity of whichever successive pairs of limbs are in the suction phase. An effect of the metachronal rhythm of the limbs is that this region of maximum suction moves forward along the length of the trunk limb series, and as one such region reaches the anterior end another is being established posteriorly. Because of the speed of the limb beat such waves of maximum suction quickly follow each other, the effect being essentially that of continuous suction, though there is a time when, as two limbs come together at the end of the backstroke and water is expelled from the inter-limb space, some is probably forced through the endite setae into the median chamber. This is not quite the same as Cannon's spurt along the so-called exit groove. Because the suction continues elsewhere within this chamber there is no likelihood of particles being lost at this stage as water is entering over much of the mid-ventral region and, as waves of suction move anteriorly, the tendency will be for any dislodged particles to do likewise. This is not the same as an anteriorly directed food stream, of whose existence, like Storch, I am dubious. Like him I find that food is swept forward along the food groove mechanically, certainly in large adults and probably throughout life, and is not propelled by currents. To facilitate such mechanical transport the most proximal gnathobasic setae are modified for sweeping from the outset.

An apparently important argument against the role of the gnathobasic setae as sweepers of food along the food groove raised by Cannon & Manton (1927) and reiterated by Cannon (1928) is that this armature is overlain by that of the limb in front and that if it did sweep food forward it 'would push it in between successive limbs and not in the food groove'. That this is not in fact the case has already been shown for the large, carnivorous, *B. gigas* (Fryer 1966), nor does it happen in *B. ferox*. Large, non-filter-feeding individuals (§ 14), which cannot pass food along the food groove by the means postulated by Cannon, and which very obviously do so by mechanical means, show that they suffer from no such disability as he envisaged.

Telling evidence against the passing of material along the food groove by means of currents, even in the filter-feeding stages, is provided on those occasions, especially after food has been collected by scraping (§ 12), on which large amounts accumulate in the groove. Material piles up from behind and sometimes extends over a distance of several limb bases. Such accumulations seem unlikely to be put together by currents and there can of course be no flow of water along the blocked food groove. Further, if hydraulic transport prevailed there would be no need for the proximal gnathobasic setae to curve forward along the food groove or to be modified for sweeping, as in fact they are, and as indeed they are in a wide range of anomopod cladocerans which pass food forward mechanically along a similar, though shorter, food groove (Fryer 1963, 1968, 1974).

That some currents flow anteriorly in the groove is not denied. The forward swing of the gnathobasic spines inevitably causes such, which will not entirely be cancelled out on the return stroke, and there may be some contribution from water leaving the inter-limb spaces as Cannon suggested, but this is not the same thing as the stream that he envisaged. Cannon emphasized his belief that this stream is intermittent, but it is clear that he believed that the successive pulses of which he thought it was composed followed each other in such a way that it is functionally continuous. Such currents could facilitate the movement of particles along an empty food groove and would perhaps explain the movement of such with greater rapidity than might be expected that I saw in *Chirocephalus bairdi* (Brauer), a species that I have not studied in detail. Barlow & Sleigh (1980) also say that they find no reason to doubt the existence of Cannon's anteriorly directed current, and record the rapid anterior travel of small particles along the food groove of *Artemia*, which they say is clearly visible. Such observations call for further study. Those who think that currents are the main propulsive agent must also explain how these can pile up food in the food groove, and how such masses are eventually moved forward. While particles can sometimes be seen to move forward in the food groove of *B. ferox* without apparently being swept, such movement is easily explained by the currents set up by the swinging sweeping setae, and definite sweeping can be seen. No anteriorly directed currents were detected in *Hutchinsoniella* (Cephalocarida) which also passes particles forward by means of a series of metachronally beating limbs (Sanders 1963).

Certain other points also require mention. Suction into the inter-limb spaces, much of it from the mid-ventral region, takes place as the gap between two adjacent limbs widens, and continues until this gap reaches its maximum extent. The further from the limb base the wider is the gap as viewed laterally. It is also wedge-shaped as seen ventrally, at least until the limbs that bound it fore and aft have rotated so that their faces are at right-angles to the long axis of the body. The wedge-shaped nature of the gap as seen from the side explains the increasing length of the setae of the gnathobase towards its distal end and the even greater length of the setae on the adjacent endite when this becomes functional (see figure 84 for trunk limb 2 in an individual at stage 21). The distal setae have to span the gap at its widest point.

Filtration takes place during this suction phase of the cycle. The most distal setae have the most widely spaced setules in early instars (figure 36). As velocity is greatest distally, and there are mechanical limits to the size of the interstices through which water can pass at an adequate velocity, a too close arrangement there would probably result in bending of the setules or the setae that bore them, or even breakage of the setules. A similar arrangement prevails in the rapidly beating filter-bearing trunk limb 3 of the anomopod cladocerans *Disparalona* (Chydoridae) (Fryer 1968) and *Bosmina* (Bosminidae) (G. Fryer, unpublished observations). Proximally, velocity decreases, and in the depth of the food groove is probably nil. It is here that the gnathobasic setae are specialized, not for filtration, but for sweeping. The probable passage of a little water between the filter setae from the inter-limb space as the latter is cyclically obliterated has already been noted. This will inevitably dislodge particles from the filters. During this phase the cleaning setules (or spinules) borne on the face of the gnathobase (seen for example in figures 79 and 84, S) and described by Cannon for *Chirocephalus*, cannot clean the overlying setae of the limb in front as the relative motion of adjacent limbs is in the wrong direction for this. Only as the limbs are moving apart can this device be effective, and this is the suction phase during which any particles so removed from the filter will be promptly sucked back onto it. This is not to deny that these setules play an important part in cleaning the filters but, distally at least, their role may not be exactly that previously envisaged. Furthermore such setules occur on the face of the first trunk limb, yet there are no filter setae for these to clean (see below). In *B. ferox* they are relatively robust, more spinule-like than setule-like, on all limbs, especially in later stages, and they must, however slightly, help to sweep material towards the food groove as the limb makes its backstroke. Their orientation also enables them to frustrate the escape of flocculent particles.

Observations (chiefly on large individuals where they are easiest to make) show that there is much direct suction of particles towards the food groove, filtration of which is carried out by setae towards the proximal end of the gnathobase, but not in the depths of food groove. Any particles first sucked against the distal setae will be ejected into the mid-ventral space and move further towards the food groove, perhaps being caught again by the more proximal setae as they do so, but will eventually come within the ambit of the more proximal sweeping setae of the gnathobase.

Each lateral food groove wall bears a narrow band of anteriorly directed stiff setules (shown

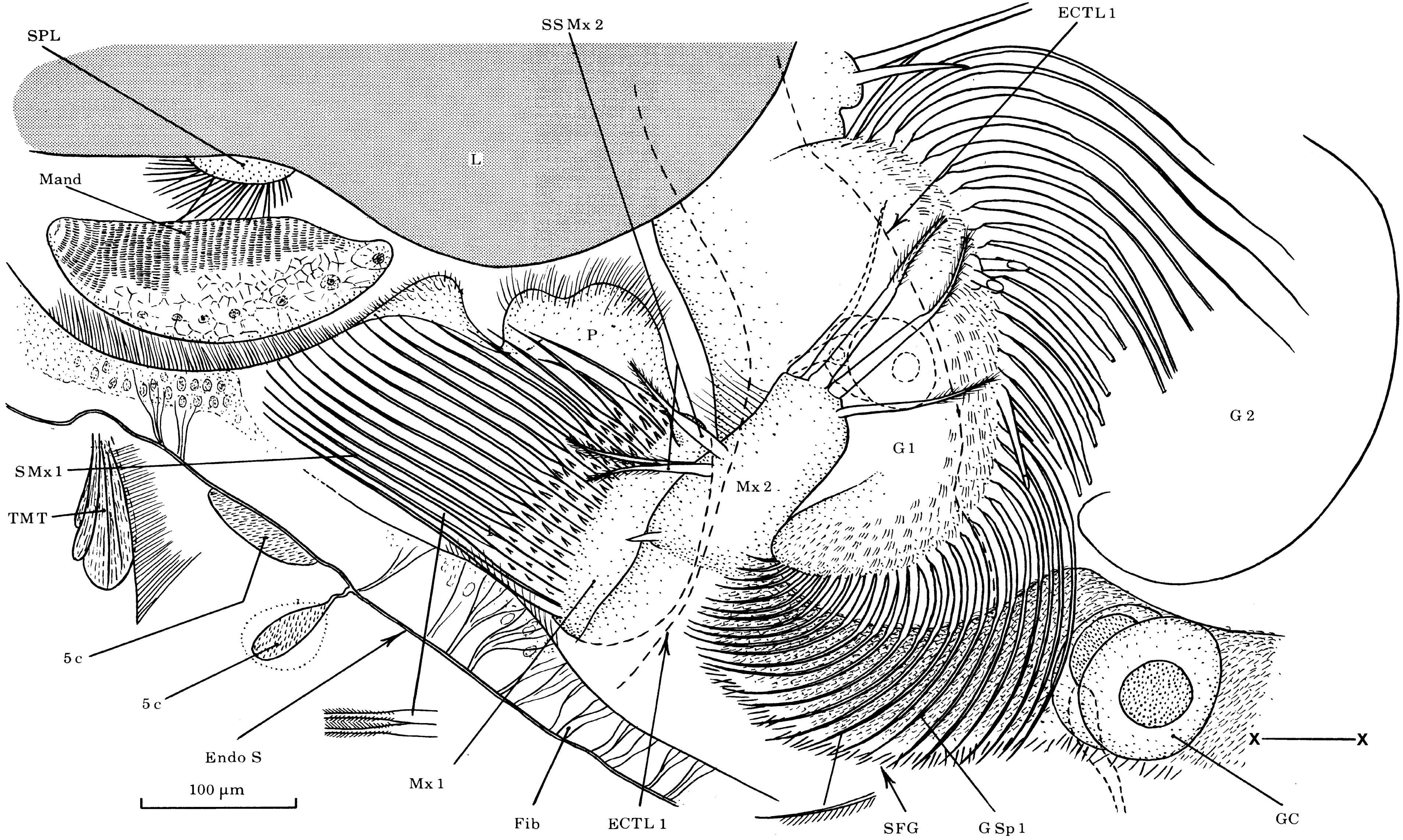

FIGURE 79. Median longitudinal section, ventral surface uppermost, in the vicinity of the mouthparts of an individual at stage 26, and showing also the gnathobase of trunk limb 1 (G1) and, in outline, that of trunk limb 2 (G2). A pair of giant gland cells (GC) such as is shown adjacent to the base of trunk limb 2 is present also at the base of trunk limb 1 but is omitted for clarity. Outlines of the somewhat similar gland cells located within each gnathobase are indicated by a dashed line in gnathobase 1. The anterior end of the food groove is here curved ventrally: more posteriorly it lies in the horizontal plane as indicated by × — ×. The relation of the endoskeletal sheet (Endo S) to the anterior extremity of the food groove is made plain. Setules are omitted from the setae of the maxillule (but are indicated in an inset) and from the setae of the gnathobase. The latter are in any case so fine that an oil immersion objective is necessary for their clear resolution, even distally where (see inset) they are stoutest. Note, in addition to the row of coarse spinules along the food groove (SFG), the very fine setules, shown somewhat schematically, that clothe the upper part of its lateral wall.

for an individual at stage 26 in figure 79, SFG) – in earlier stages these are finer spinules – and, adjacent to them, a broader band of fine setules. These clean those gnathobasic setae which swing within the food groove, and strip off any adhering material on the return stroke. The stiff spinules, which become more numerous as size increases (figure 109, plate 4), are strategically located for the latter function. When the filtering setae are transformed to spines (§12) the entire assemblage becomes spiniform (figures 112, plate 5, and 134, plate 6).

Food reaching the anterior end of the food groove is passed between the maxillae (Mx2) by the gnathobases of the first trunk limbs (G1), swept by the maxillules (Mx1) to the mandibles (Mand), between which it is rolled and swept into the atrium oris, and is then sucked up the oesophagus by peristalsis, a process that can be easily envisaged by reference to figure 79.

The maxillules and maxillae are essentially similar to those of other anostracans described by Cannon & Leak (in Cannon 1933) and only brief comment is needed. In view of the fact that anostracan maxillules have recently been described as vestigial, however, the well developed nature of these appendages (figures 79–82, Mx1) and the formidable array of spines

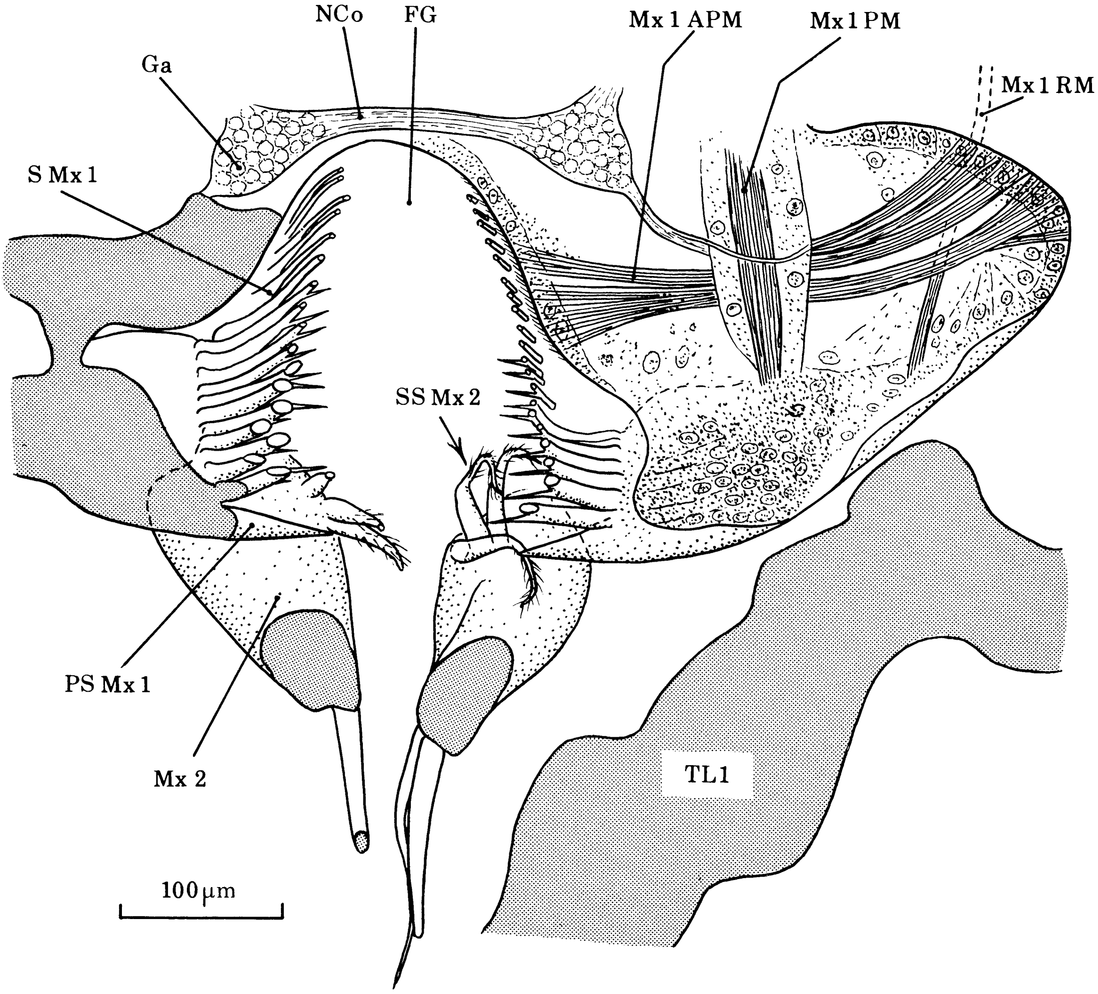

FIGURE 80. Horizontal section through the maxillules and maxillae of an individual at stage 25. Viewed from the ventral side. The location of the adjacent trunk limb 1 is also indicated. This section cuts just below the tip of the maxilla (Mx2). The food groove is here curving ventrally, i.e. rising towards the observer anteriorly; hence its appearance almost in transverse section anteriorly. The cytoplasmic sheath is shown only on one muscle.

(S Mx1) that they bear even in these early, filter-feeding stages deserves emphasis. Ventral to this row of spines and, because of the oblique orientation of the maxillulary armature, posterior to it, is a stout, simple spine (figure 79 and figures 80 and 82, PS Mx1). Behind the battery of spines of the maxillule, seen in face view in figure 79, the wall of the extreme anterior end of the food groove is densely setose, doubtless to prevent clogging of this otherwise uncleanable appendage. Some of these setules can be seen in figure 80 (right hand side). Each maxillule swings vigorously, and is capable of a powerful forward thrust as its robust promotor muscle (figure 80, Mx1 PM), assisted by an accessory promotor (Mx1 APM), makes plain.

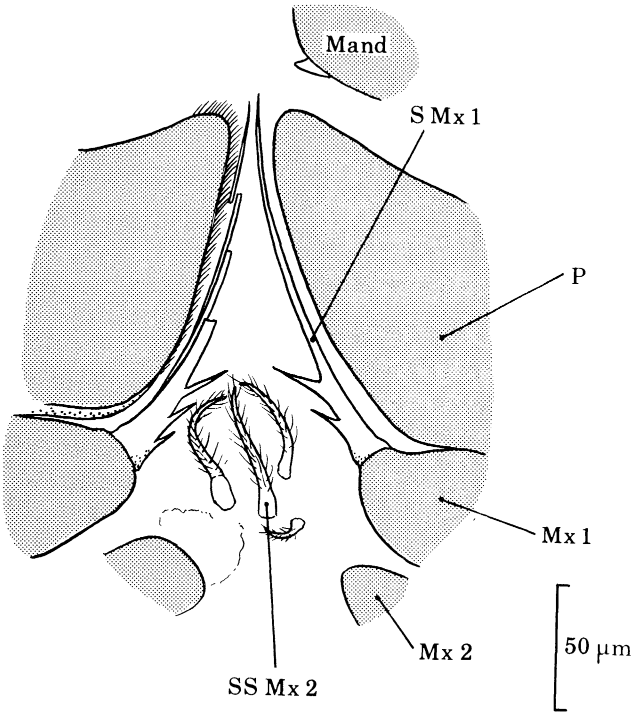

FIGURE 81. Transverse section through the maxillules (Mx1) and soft setae of the maxillae (SS Mx2) of an individual at stage 24, ventral surface uppermost. For clarity only one of the spines of the maxillule (S Mx1) is shown on the right. The posterior tooth of the mandible (Mand) is seen on the right. The reason why this appendage is located so ventrally in a transverse section at this level is made clear by reference to figure 79 which shows how the food groove curves ventrally in this region.

The maxilla (figures 79–82, Mx2) has the soft setae (SS Mx2), here three in number, typical of anostracans and anomopod cladocerans. These are directed forward, perhaps to help deflect labral gland secretions onto the food and, in the filter-feeding stages, possibly to some extent serve to prevent the escape of food particles from the oral region. There are fewer stiffer terminal setae (four only in the early filter-feeding stages, increasing to six later) than in the species of *Branchinecta* described by Cannon & Leak, but more than in certain other anostracans. Their function cannot be observed but can be deduced with reasonable confidence. They wipe the face of the gnathobase of the first trunk limb, against which they lie (figure 79 and figure 134, plate 6), which cannot otherwise be cleaned, and are themselves kept clean by its coat of spinules. They possibly also help to confine food in the vicinity of the food groove. The distal portions of the maxillae, down to the level of their soft setae, lie more or less in contact, thereby forming, with the food groove, a tunnel into which the 'toe' of the gnathobase of each thoracic leg 1 swings, past the bases of these appendages, towards the maxillules. The mandibles have devices that reduce the chances of material escaping from between their opposed molar surfaces (§15), but any that does so is prevented from slipping backward as they make their return roll by an array of spinules dorsal to their molar surfaces (topographically ventral in an animal swimming inverted) and, on the other side, by a spinous pad (figure 79, SPL) on the adjacent surface of the labrum. Details of mandibular action in relation to the armature of the molar surfaces, and of changes in this armature during ontogeny, are given in §15.

The labral glands present in the naupliar stages continue to function until, and during, the filter-feeding stages of adulthood. Their arrangement in an individual at stage 24 is shown in

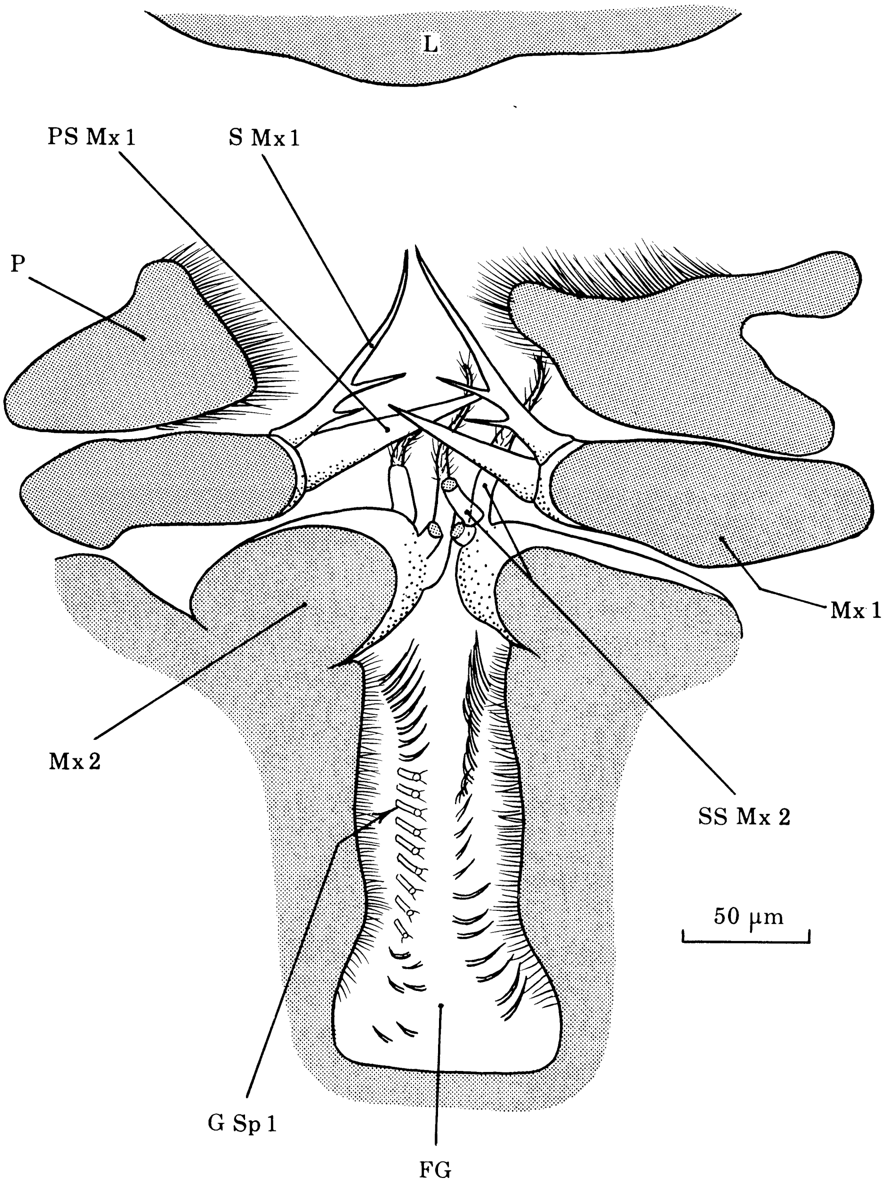

FIGURE 82. Transverse section through the maxillule (Mx1) and maxillae (Mx2) of the same individual as shown in figure 81 but immediately posterior to it. The slice cuts just anterior to the posterior ventral tooth (PS Mx1) of the maxillule. The setae in the food groove are those of the gnathobase of trunk limb 1 (GSP1). On the left some of these are shown as seen by deeper focusing, i.e. more remote from their tips.

figure 83, only two of the three ducts being visible in this section. Each gland (LG) has an enormous secretion-filled reservoir (RLG) from which a conspicuous duct cell (DCLG) with a large nucleus (DCN) and an intracellular duct (DLG) leads to the exterior (ELG). There appear to be three cells (SC) encircling the union of duct and reservoir, and what may be tiny fibrils, the whole presumably making up a sphincter. Each gland unit is suspended by fibrils (S Fib) and fibrous sheets (FSH). The subsequent fate of these glands is described in §13(*b*).

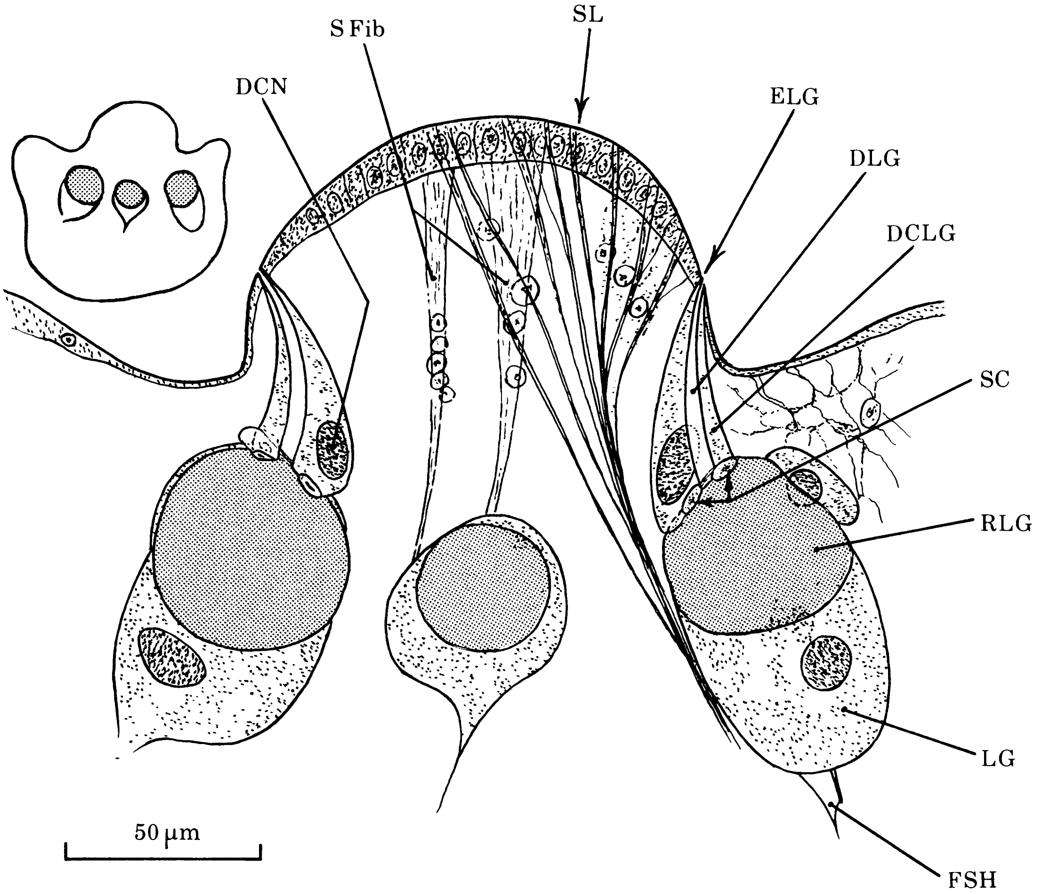

Figure 83. Transverse section through the topographically upper (morphologically ventral) part of the labrum of an individual at stage 24 to show the reservoirs of the labral glands (RLG) and, in the case of the lateral pair, the exit ducts (DLG). The inset shows the locations of the glands in relation to a section through the whole labrum. Note that the labrum is here shown as seen in an animal dorsal surface uppermost.

As this section and figure 27 make clear, development in *B. ferox* is a gradual process during which the trunk limbs become functional throughout a sequence of ten instars. Furthermore, each limb begins to function before its individual development is complete. In view of statements to the contrary, it should be emphasized that as the anterior members of the trunk limb series come into service as organs of locomotion and food collection they supplement, and operate in collaboration with, the cephalic, naupliar appendages that have earlier been responsible for these activities. There is no sudden replacement of one mechanism by another, either locomotory or feeding. Clearly the efficiency both of swimming and of the adult-type feeding mechanism increases progressively as more and more trunk limbs are incorporated and as each gradually becomes better developed. The last pair of trunk limbs never becomes filtratory and serves to seal off the posterior end of the median chamber.

11. A NOTE ON CERTAIN GLANDS

As there is no feeding current to carry away excretory products, the opening of the maxillary gland on the maxilla, and therefore close to the mouth, calls for comment. Observations on other branchiopods, which drink much water (Fox 1952; Fryer 1970), indicate that the chief function of the gland is to pump out water, and so the urine must be extremely dilute. The enormous size of the gland can also scarcely be accounted for on the basis of nitrogenous excretion. There will always be sufficient movement of water in the vicinity of the maxilla quickly to disperse any discharged products.

As shown in figure 79 there is at the base of each trunk limb a pair of enormous gland cells (GC) whose gross appearance can be readily seen in the living animal. The same is true of other anostracans (Spangenberg 1875; Claus 1886; Cannon 1933; Debaisieux 1952; Dornesco & Steopoe 1958). Debaisieux erroneously refers to them as 'les glandes segmentaires abdominales' and Dornesco & Steopoe, who do not cite him, curiously also refer to them as 'les glands abdominales'. They are of course thoracic. Cannon, who makes no reference to the earlier observations, merely indicates the position of these cells, which he refers to as a 'conspicuous bun-shaped gland'. In fact additional smaller cells are present, there being a small gland cell, which is always packed with concretions, apparently jammed between the two large cells, and a delicate duct system which passes from this more or less dorsally to open on the food groove wall. According to Dornesco & Steopoe, in *Chirocephalus* the duct consists not merely of the elongate duct cell but includes also a minute cell that links its proximal end to the small concretion cell. The small gland cell and the beginning of the duct can be made out only vaguely in figure 79 as they lie beneath the cuticle of the food groove wall, and are indicated only by dashed lines. As Claus (1886) was already aware, these cells are intimately associated with the segmental ganglia of the ventral nerve cords.

Lundblad (1920), who mentions these cells without giving details, suspected that they produce a secretion that binds together food particles that accummulate in the food groove. Cannon (1933) also originally suggested that each gland 'most likely exudes viscid material' into the food groove, but subsequently (1935*a*) changed his ideas and believed that the secretion possibly has a coagulative effect on the labral gland secretions. This is extremely unlikely, not least because the duct persists in large adults in which labral gland secretions are no longer produced, and in which there is no effective means of bringing their secretions, especially in the case of the remotely lying posterior segmental glands, into contact with any anteriorly produced secretions (§14(*b*)). Dornesco & Steopoe (1958) showed that the large gland cells produce mucus. The most likely function of this seems to be that suggested by Lundblad, but this remains unproven. No secretions are visible in any sectioned material, either within or at the exit of the duct – both duct and, especially, the exit being in fact often difficult and, in the case of the latter, sometimes impossible to make out. Debaisieux in fact failed to find it. The glands may be responsible for some of the mucoid material sometimes seen in the food groove or near the limb bases (§13(*b*)) but there is no proof of this. Of historic interest is the abandoned suggestion of Claus, based on the presence of secretion granules in the median cell, and its superficial resemblance to an otocyst, that these glands may function as such.

Similar glands are located within the gnathobase as in other Anostraca (Spangenberg 1875; Claus 1886; Cannon 1933; Debaisieux 1952; Dornesco & Steopoe 1958). These are indicated by dashed lines in figure 79. As Dornesco & Steopoe have shown, each displays the same five-celled arrangement as the glands at the limb base. Although Cannon described such a unit as a 'pear-shaped gland with a conspicuous opening' in *B. ferox* the opening is often difficult to see even when the duct is clear. Cannon (1933) originally suggested that these produced a viscid substance, later (1935*a*) a coagulant of the labral gland secretions. Dornesco & Steopoe showed that the large gland cells produce mucus, but apparently in smaller amounts than their counterparts in the glands at the limb base. Again their function remains obscure.

12. MORPHOLOGICAL FEATURES OF THE TRUNK LIMB ARMATURE AND AGE-RELATED CHANGES IN THE FEEDING MECHANISM

Apart from the positive allometric growth of the abdomen, from the time the full complement of trunk limbs becomes functional, changes in gross form are small, though size increases greatly. Filter-feeding by means of finely spaced filtering setules continues until a length of about 18 mm is achieved, subsequent to which, over a very small number of moults, striking changes in the nature of the endite armature of the trunk limbs take place. These are related to changes in feeding habits, including the kind of food taken, but do not involve any fundamental changes in limb structure or activity. The trunk limbs continue to be used for locomotion in the typical anostracan manner.

Any description of these changes is complicated by the fact that the arrangement of setae is not uniform over the whole of the compound gnathobase – for simplicity here referred to simply as the gnathobase. From an early stage the proximal setae are modified for sweeping food particles forward, the more distal for filtration. There is a gradual transition between the two types. The general pattern is most easily appreciated from figures 36, 84 and 79 which portray progressively older individuals. A further complication is that the arrangement of the setules is not uniform over the entire length of a seta. From an early stage the setae of endite 3 – the first free endite beyond the gnathobase – are functionally continuous with the distal members of the gnathobasic series. These continue the trend of becoming more coarsely armed towards the distal end of the series.

For simplicity the changes taking place in the distal filtering setae of the gnathobase are considered first: changes in the proximal sweepers are considered separately. Even so the account has to be generalized because of the differences that exist even between adjacent setae.

From the early stages of development of the trunk limbs there is a tendency for the setules of the posterior row to be longer than those of the median row especially, but not only, on those setae in the region where filtration occurs. Seta 8 of trunk limb 1 of a stage 13 larva (figure 36) shows this in an extreme form. In the filtering region the long setules interdigitate with the shorter setules of the adjacent, more distal, setae. Figure 85 shows the arrangement of setules on a group of adjacent setae of leg 1 at stage 21 in a region well removed from the tips of the setae. Here the filtering surface is made up entirely by the rows of long posterior setules. The role of the much shorter, median setules is to support those of the posterior series and, as each of the latter fits between a pair of median setules, to maintain the even spacing throughout their length. In the upper part of figure 85 a posterior filtering setule has been dislodged and has become hooked under the wrong median setule, thereby clearly demonstrating the use of the latter. The same holds good in older stages and is revealed by the scanning electron microscope (see, for example, figures 104 and 108, plate 4). In figure 104 (of an 11.5 mm individual), where the fine tips of the long setules, supported by the short setules, have remained *in situ* during preparation, they tend to retain their form even though they are somewhat distorted; where they are unsupported their tips suffer considerable distortion. To anticipate further, the arrangement is particularly easy to see as development proceeds and the setules become coarser and more widely separated (figures 92–94). While there is usually a good setule by setule correspondence between adjacent setae, occasional discrepancies occur, presumably to allow for differences in the distance between adjacent setules on adjoining setae and perhaps differences in curvature.

At stage 21 the gaps between the setules in the general vicinity shown in figure 85 are about 1.4–1.7 μm wide, but the more distal the location of a filter seta on the gnathobase the wider are the gaps between adjacent setules of the posterior row. Those setae located towards the distal end of the gnathobase therefore have more widely spaced setules than those illustrated. Such is the case over much of the length of the seta, but, at the same time, towards the tips of the distal setae the gaps between setules gradually become wider – as shown for a distal seta at stage 13 in figure 36. The situation in the stage 21 individual is the same though the setules are now far more numerous. The widening gaps, both on the distal setae and towards the tips of the setae, are related to the length of the distal setae as mentioned in the previous section. Excessive pressure on closely spaced setules, especially those remote from the base of the seta, would cause the seta to bend. Towards the proximal end of the series of filter setae the tips tend to be modified for sweeping. In spite of these trends there is a considerable area where the arrangement of setules is such as to give rise to a relatively uniform meshwork (see, for example, figure 103, plate 4, for an 11.5 mm individual).

Although the gnathobasic setae increase in number as the animal grows – there are 19 on trunk limb 1 at stage 13, 39 at stage 21, and 46 at stage 26 – their arrangement and armature remains essentially similar until the animal reaches a length of about 18 mm, by which time about 56 marginal setae are present. (There is some variation, and the presence or absence of a rudimentary seta at the proximal end of the series is not always easy to ascertain.) During this increase the width of the gaps between setules increases, but only slightly (see below). Details of the arrangement of the gnathobasic setae and their armature as revealed by scanning electron microscopy in individuals 11.5 and 14 mm in length are shown in figures 103–111, plate 4.

In an 18 mm male the heavy gnathobasic spine belonging to the gnathobase proper lies at about the level of seta no. 36 counting from the proximal end. This serves as a convenient marker. The heavy armature belonging to endite 2, which is incorporated with the gnathobase, lies in the vicinity of seta 42. Figure 89 shows the spacing of setules in the middle region of setae 36–38. The gaps between setules average a little over 2 μm in width. Although this represents an increase of approximately 30 % from stage 21, the absolute increase in relation to the great increase in size of the animal is small. Towards their tips the armature of these setae changes. The setules of the posterior row become more akin to those on sweeping setae while those of the median row gradually diminish in size and, near the tip, disappear (figure 90).

Figure 91 shows the middle region of setae from the same vicinity on leg 1 in a male 18.9 mm in length, and probably one instar more advanced. A distinct widening of the gaps between setules is apparent; each now usually has a width of 2.5 μm or rather more. Figure 93 shows similar setae in a male 19.4 mm in length†. An increased width in the gaps between the setules

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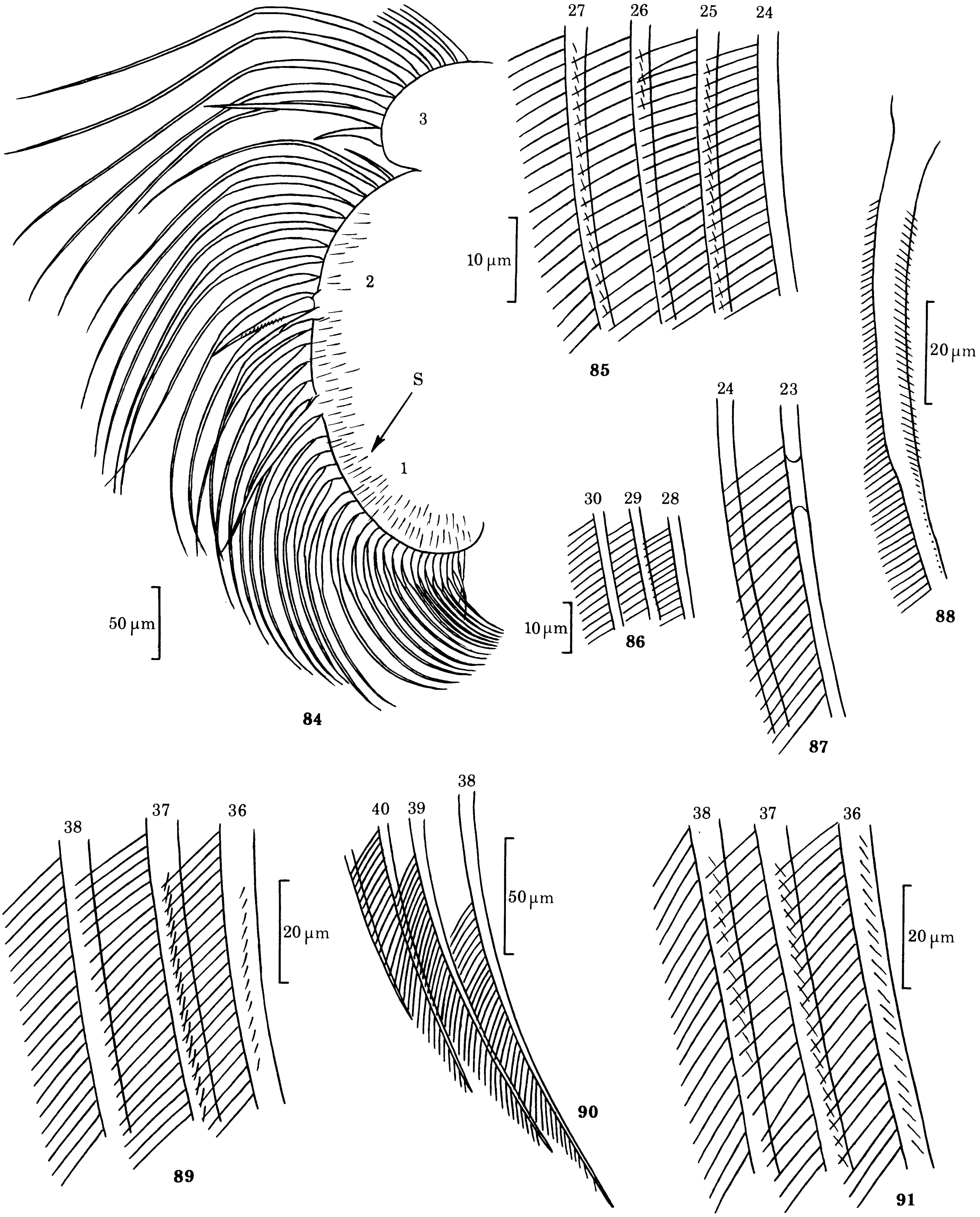
† Discrepancies in the apparent increase in size per moult reflect several kinds of variation and are of no consequence: it is the pattern rather than absolute size or instar number that is important.



Figures 84–91. For description see opposite.

is now very apparent; each is about 6 μm wide. Even in setae nearer to the proximal end of the series, whose setules lie closer together (figure 94), the gaps are wider than those in more distal setae in the 18.9 mm individual. On setae towards the distal end of the series they are even wider (figure 92). Figure 100 shows setae of the same region of a 20 mm male. These are now distinctly spiniform. No setules span the gaps between adjacent setae, the only traces of the posterior series being a row of short spinules on some of the setae. On somewhat more proximal setae (see especially the inset showing seta 32) the posterior row is represented by short stiff setules or spinules very different from the array previously present. On some proximal setae traces of the median row also persist, but nowhere are filtratory setules present. Details of more distal setae in the series are shown in figure 99.

Similar spiniform setae from an individual 21 mm in length, and probably just one instar older, are shown in figure 101, and proximal examples from an individual 23 mm in length in figures 112–114, plate 5. Figure 112 shows the spines *in situ* in the food groove and also the underlying array of stiff spinules of which there is now a band on each lateral wall of the food groove just inside the margin. Their location is best appreciated from transverse sections (figures 145 and 146 for a still larger, 36 mm, individual in which the arrangement is the same).

Similar changes take place at about the same size in both sexes but the examples illustrated in the line drawings were all taken from males in order to avoid any confusion that might arise if one sex undergoes the changes slightly before the other. Details of the trunk limb morphology of large carnivorous adults are given in § 14 (*a*).

From now on changes are slight but the spiniform setae become ever more spine-like, and in the largest adults are robust spines. Changes, though of a less subtle nature, also occur in the most proximal setae. Figures 95–98 and 102 show how these are transformed into stout spiniform structures. In a 19.4 mm individual the two anteriormost setae are brush-like (figure 98 shows the first seta) and are set more laterally than the rest so that they sweep the food groove wall. This offset condition is still maintained after their transformation to stouter structures as can be seen in a 21 mm individual in figure 102. Indeed the anteriormost spines are brush-like even in large adults.

Description of figures 84–91

Figures 84–91. Trunk limb armature during the filter-feeding stages.

Figure 84. Gnathobase and adjacent endite (endite 3) of trunk limb 1 of an individual at stage 21. (In this and all figures up to figure 102, a right hand limb is involved.)

Figure 85. Details of the middle region of gnathobasic setae 24–27 of trunk limb 1 of an individual at stage 21 to show the nature of the armature. In all, 39 setae are present at this stage. The setules of the median row on each seta, although much shorter than the posterior row, appear foreshortened here. The difference is therefore exaggerated. Note how one of the posterior setules of seta 25 has been displaced and caught by the wrong median setule.

Figure 86. The same. Setae 28–30 to the same scale as in figure 88 to permit a meaningful comparison of size.

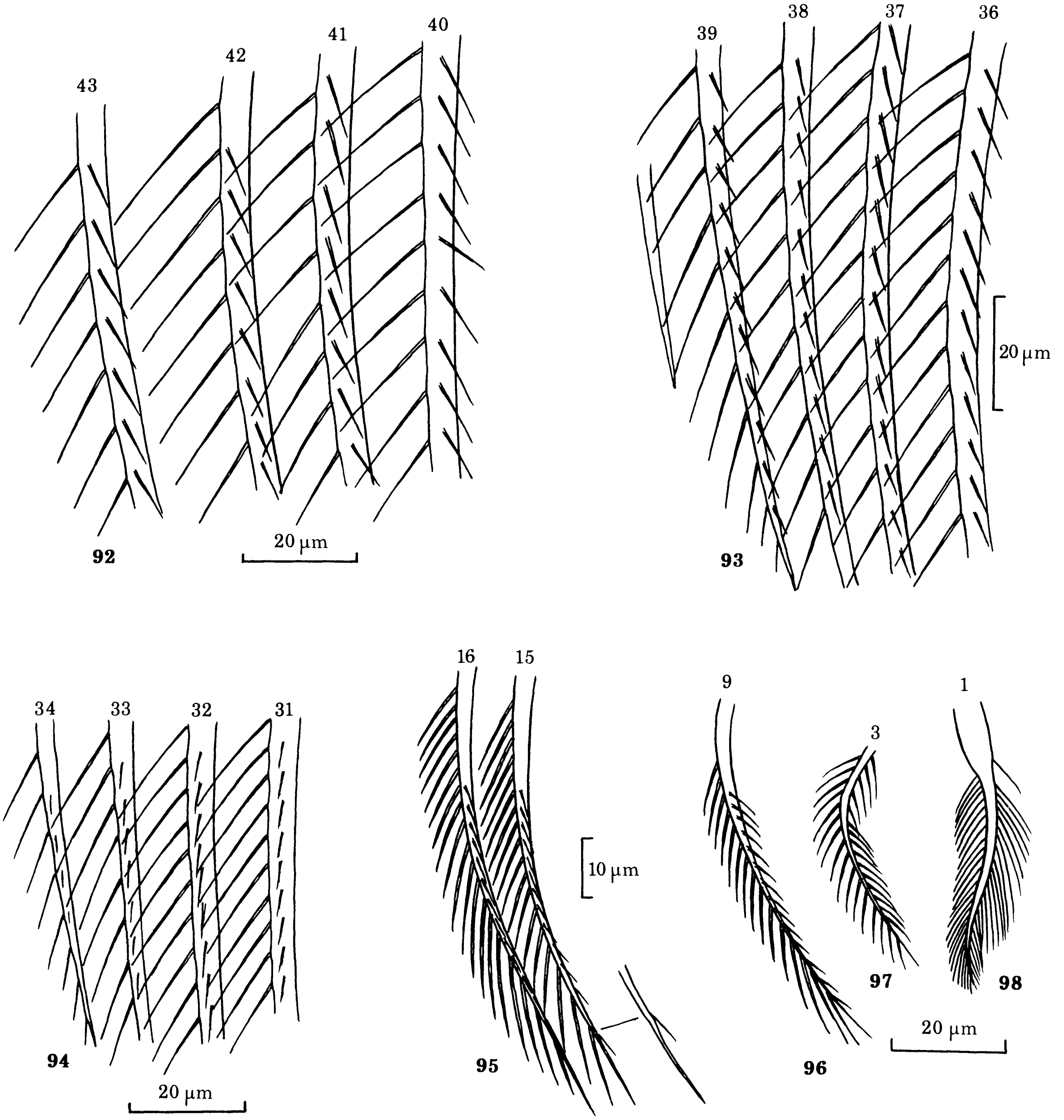
Figure 87. The same. A pair of adjacent setae to show the 'plug' in one of them. Median setules omitted.

Figure 88. The same. Proximal region of seta 24 to show the homology of the median row, whose nature differs in different regions of the seta.

Figure 89. Details of the middle region of gnathobasic setae 36–38 of leg 1 of a male, length 18 mm. Some 56 setae are present at this stage.

Figure 90. The tips of setae 38–41 of the same limb.

Figure 91. Details of the middle region of gnathobasic setae 36–38 of leg 1 of a male, length 18.9 mm. Some 54 setae are present. (Note the variation in the number of setae present. Although larger and showing further development in its setae than the 18 mm individual, the gnathobase of this animal has two fewer setae.)



FIGURES 92–98. Gnathobasic setae of trunk limb 1 of a 19.4 mm male, i.e. during the transition from filter-feeding to raptatory behaviour.

FIGURE 92. Details of the middle region of setae 40–43. There are 56 setae present.

FIGURE 93. Setae 36–40 and somewhat more distally as indicated by the tips of setae 39 and 40.

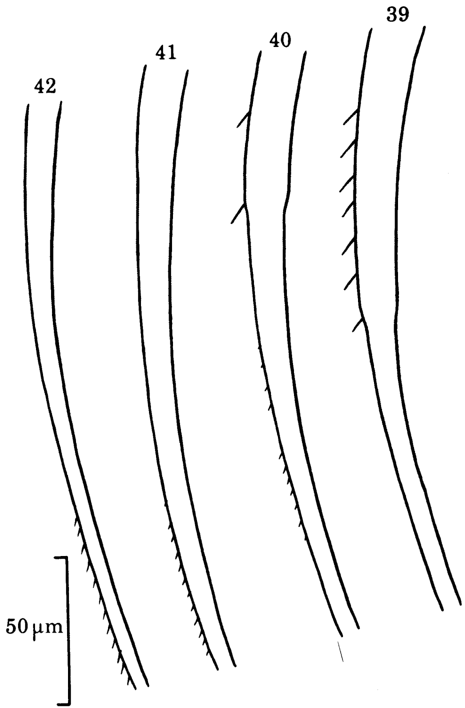
FIGURE 94. Approaching the distal end of setae 31–34.

FIGURE 95. The tips of setae 15 and 16. Note the progressively wider gaps between setules both from the proximal to the distal setae of the series and as one proceeds distally along individual setae.

FIGURE 96. The tip of seta 9.

FIGURE 97. The tip of seta 3 which has been twisted clockwise to reveal the arrangement of the setules, both rows of which are directed obliquely towards the observer. The seta itself has been distorted by this twisting.

FIGURE 98. Seta 1. Note that this is the entire seta, not just the tip of a longer structure.



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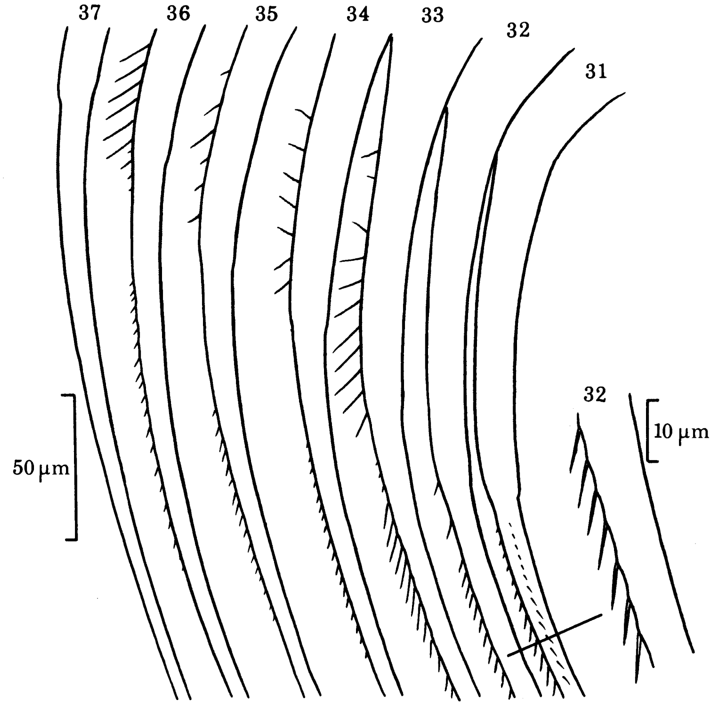

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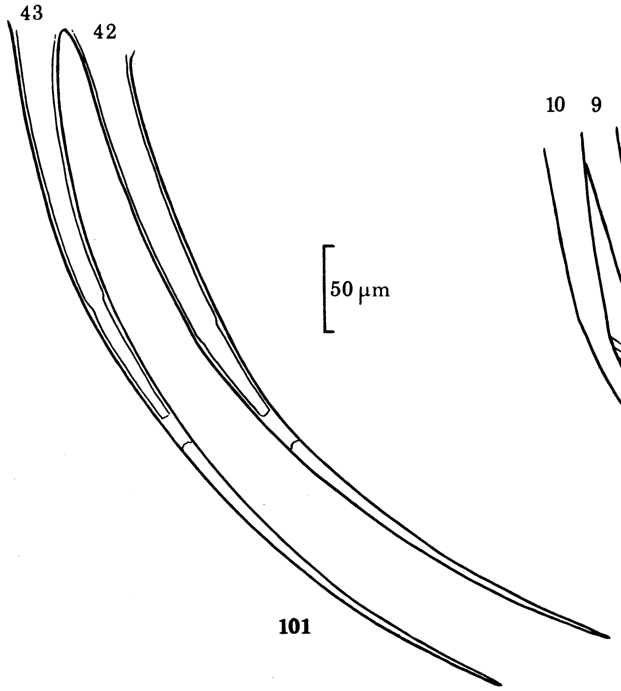

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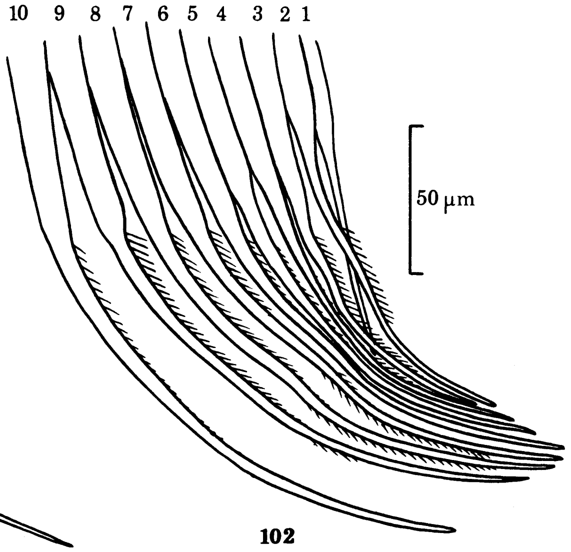

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FIGURES 99–102. .Gnathobasic setae of carnivorous adults.

FIGURE 99. Proximal and median regions of gnathobasic setae 39–42 of trunk limb 1 of a male, length 20 mm. There are 53 setae present.

FIGURE 100. The same, setae 31–37. Inset shows details of seta 32. Note the marked change in armature between this and the individual 19.4 mm in length (figures 92–94). Because of the difference in scale a larger proportion of the setae illustrated is seen here than in figures 92–94.

FIGURE 101. Gnathobasic setae 42 and 43 of trunk limb 1 of a male, length 21 mm.

FIGURE 102. The ten most proximal setae – here spiniform – of the gnathobase of trunk limb 1 of a male, length 21 mm. Note how seta 1 lies behind seta 2 and will therefore block any gap that might have existed between this plate of sweeping setae and the wall of the food groove.

Differences from spine to spine complicate any description of the situation in large adults and a detailed account is not necessary here, the general pattern being readily intelligible from figures 133–136, plate 6. Certain details are shown in figures 115–121, plate 5. The proximal gnathobasic spines tend to retain spinules distally (see, for example, figures 115 and 116). These spines often have sharply pointed tips (see, for example, figures 117–119) and the spinules just behind the tip are frequently stout to facilitate the transport of material along the food groove (figures 117–120). The short, anteriormost gnathobasic spines, mostly hidden by the overlying spines of the limb in front in figure 133, plate 6, tend to retain a brush-like nature even in the largest individuals (figure 121, plate 5). This is particularly the case on the first trunk limb where, unlike those on the succeeding limbs, these spines receive no assistance from a limb in front and bear the sole responsibility for passing food between the maxillae to the maxillules. The main impetus is from less proximal spines lying deeper in the food groove: the brushes assist but are perhaps as important in keeping clean the adjoining food-groove wall.

The change from filtering to spiniform setae marks a reversal in the trend for the number of elements on the gnathobase margin to increase with age. The maximum acquired by trunk limb 1 is about 56, a number recorded in both 18 mm and 19.4 mm individuals. It drops to about 53 at 20 mm, about 50 at 27 mm, and about 41 at 40 mm. Numbers are not given precisely as there is some variation. During development the posterior trunk limbs inevitably lag behind the anterior in acquiring their full complement of gnathobasic setae, and indeed always have slightly fewer than the anterior limbs.

These morphological changes are correlated with fundamental changes in feeding habits. The coarsely armed setae described for the 19.4 mm male are present for only a brief period, probably during only one instar, and are clearly unable to extract such fine particles as those of earlier stages, and the spiniform setae and spines that replace them are adapted for quite other purposes. However, even when all the setules have been lost, the gaps between the setae themselves are still initially not very wide – only about 30 μm in the vicinity of setae 38–43 for example (figure 99), and considerably less proximally – so that although filtering in the sense in which it is generally understood in filter-feeding crustaceans cannot take place there is still the possibility of extracting quite small particles from currents and, even if such extraction is not practised, the setae form a cage the walls of which have a relatively fine mesh.

Description of plate 4

Details of the armature of the gnathobasic setae in individuals 11.5 mm (figures 103–106) and 14 mm (figures 107–111) in length, revealed by scanning electron microscopy. Note: critical point drying involves some shrinkage of material. The sizes given are those of the final preparations. The small discrepancy involved is irrelevant in an anatomical context.

Figure 103. Arrangement of setae on right trunk limb 1.

Figure 104. Mid-region of setae 20–22 of left trunk limb 4. Note the supporting role of the row of short setules and how the tips of the long setules are distorted where they have been deprived of this.

Figure 105. Near the tips of the seta on right trunk limb 10.

Figure 106. The brush-like tip of seta 25, right trunk limb 1.

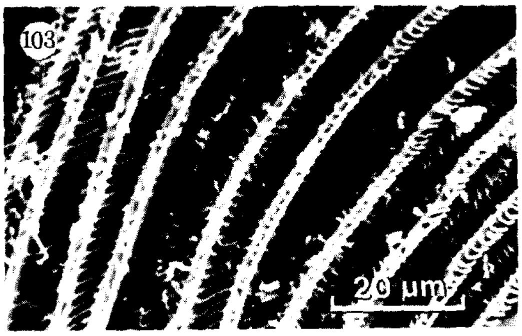
Figure 107. Left trunk limb 2 showing the arrangement of the setules near the base of the setae.

Figure 108. The same, approaching the tips of the setae.

Figure 109. Left trunk limb 9, approaching the tips of the setae, with two setae broken off to reveal the underlying array of stiff spinules.

Figure 110. The brush-like tips of the setae of left trunk limb 2 *in situ* in the food groove.

Figure 111. The same, just behind the tips.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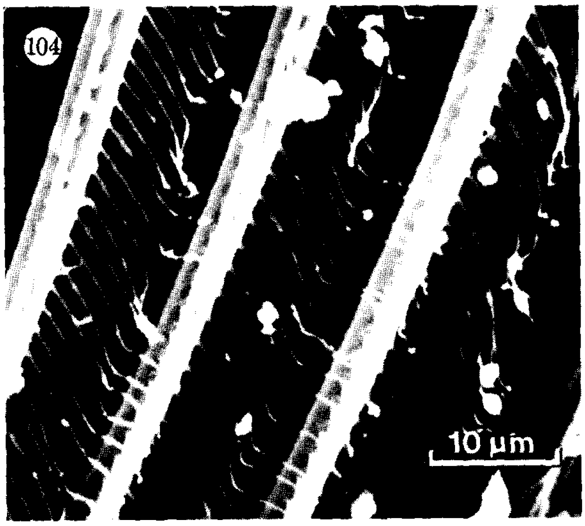
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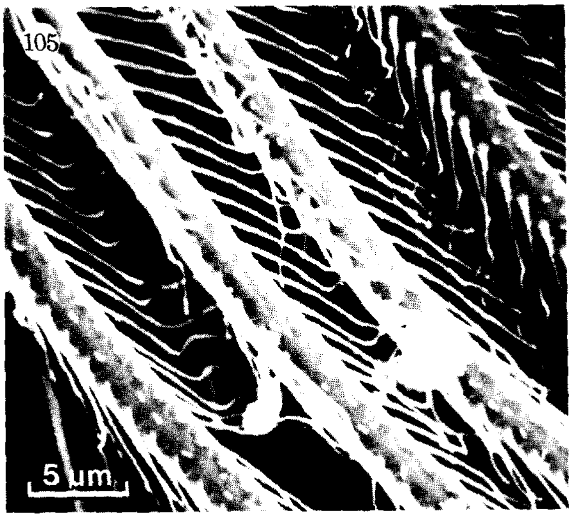
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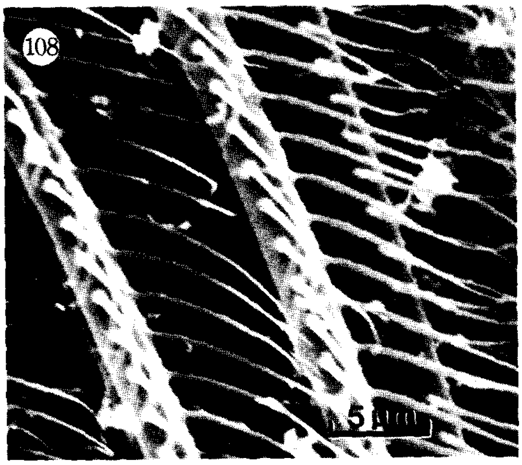
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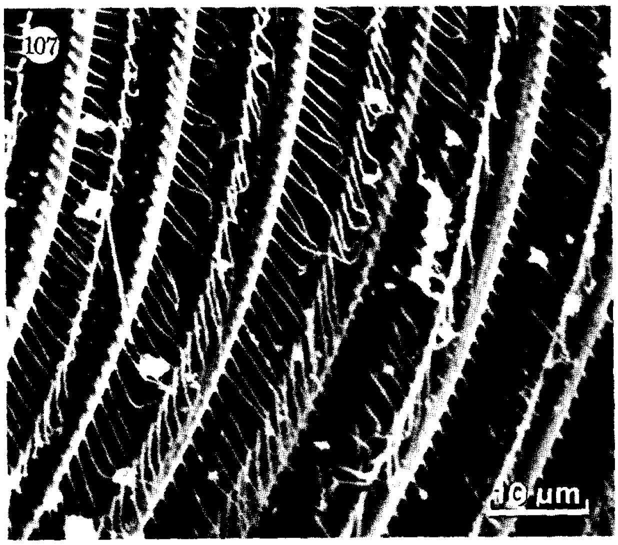
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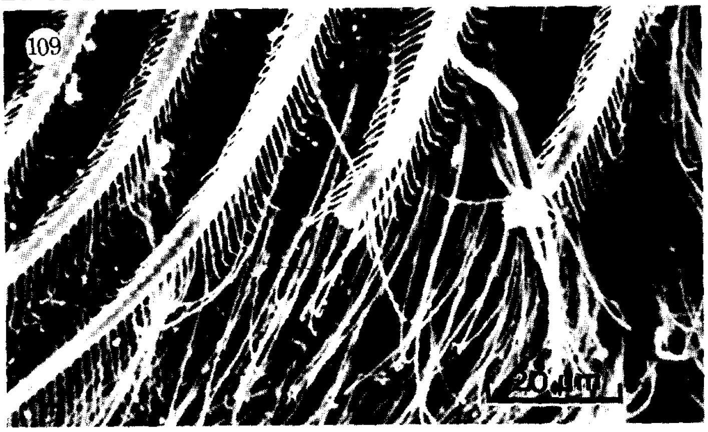
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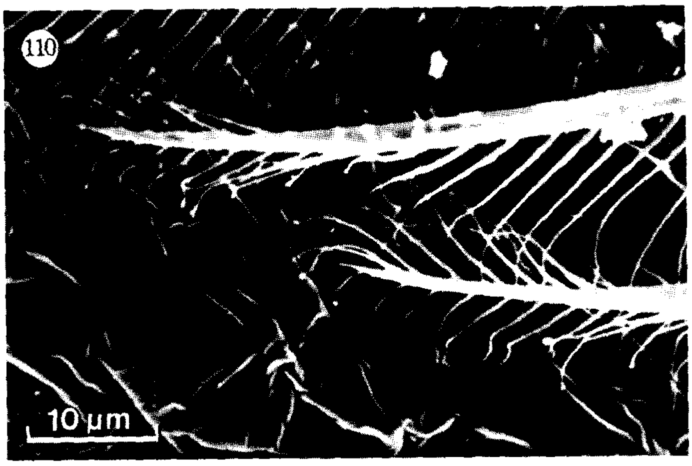
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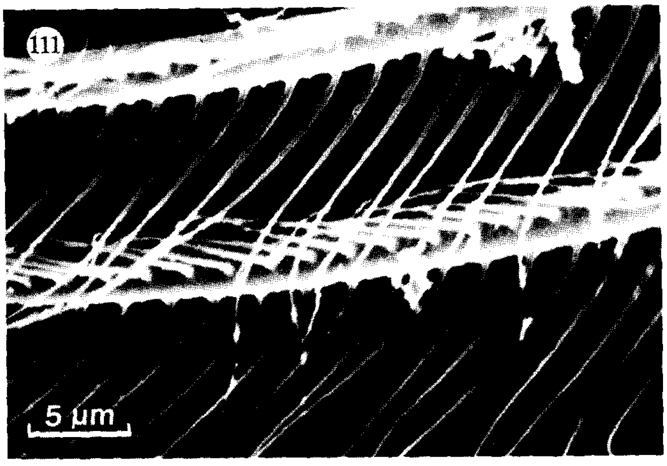
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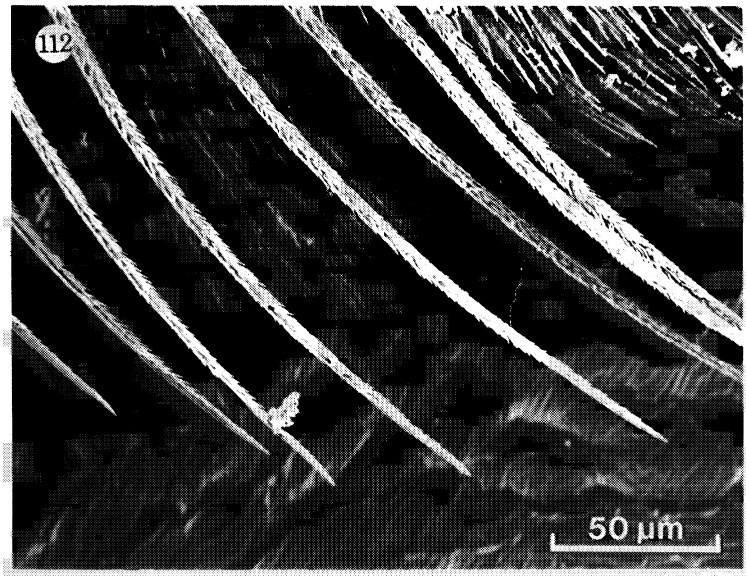

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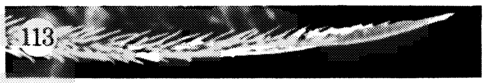

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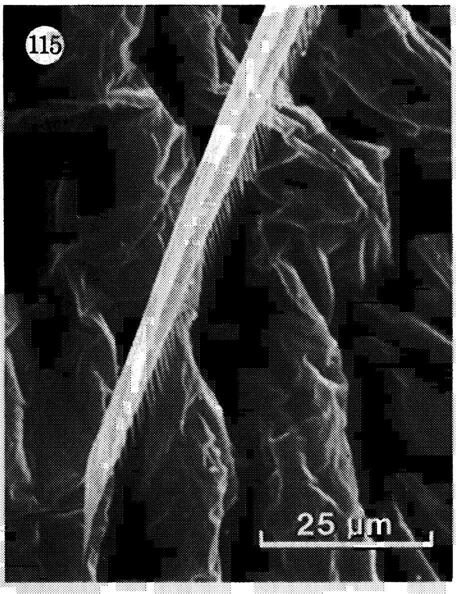

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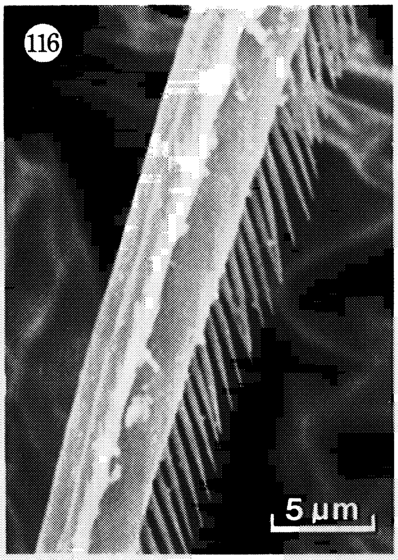

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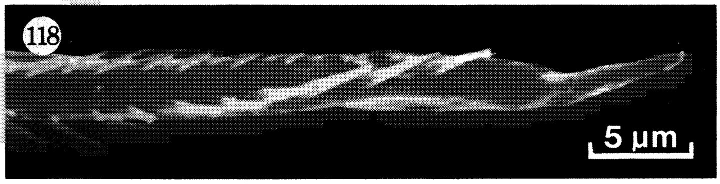

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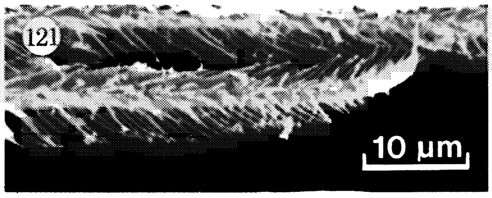

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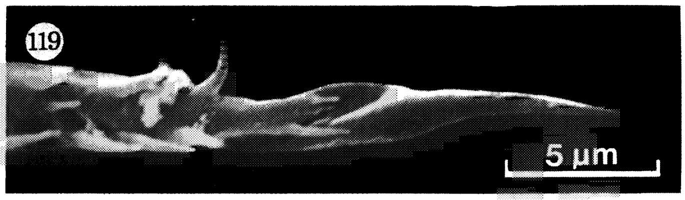

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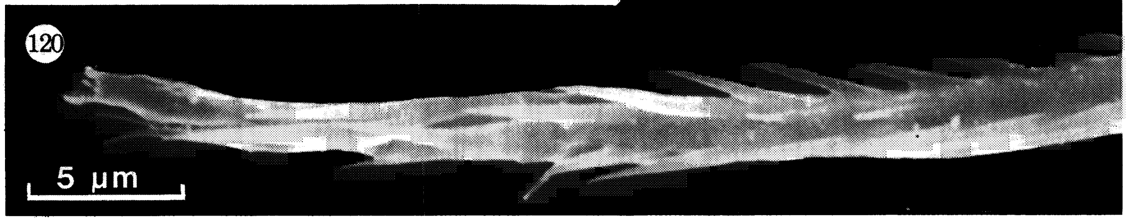


Other changes, especially in the armature of the endopodite, accompany those of the gnathobasic armature as size increases. From an early age the endopodite armature is modified for scraping (figures 122–126 and 129–130) in a manner already described for other Anostraca (Fryer 1966). Individuals of various ages, but not large carnivores, have frequently been observed to descend to the substratum, invert themselves, scrape with the endopodites and, after returning to the normal dorsal-surface-down position, swim away carrying a load of detritus which they proceed to manipulate. Persistent scraping of the vertical walls of glass vessels has also been seen. When scraping a hard surface the animals appear to press themselves against it and either move slowly forward or, at times, remain virtually stationary. Pressure may be achieved in part by suction caused by modified limb beats, for the limbs undergo such as they scrape. Their exact disposition during this process has not been ascertained but they are certainly more laterally spread than during swimming. From the point of view of nervous co-ordination, and as an indicator of evolutionary potential, such behaviour reveals a versatility that would be unsuspected in animals observed only in stereotyped swimming and filter-feeding.

The scraping endopodite spines are assisted for a short time by the three or four most distal spines of endite 6. It is doubtful whether any such assistance is forthcoming in leg 1 at stage 21, the first at which all limbs are functional. At this stage the three distalmost of the four spines present are slightly denticulate but this is probably to increase their efficiency in passing food medially and not as scrapers. Gradually, however, the number of spines in this row increases to 10 and, in a 12 mm individual, at least the four distalmost help to scrape, for which purpose they are toothed like the endopodite scrapers but in a less robust manner.

The number of endopodite scrapers increases with age/size. Figures 122, 124 and 126 show the full complement at stages 13, 19 and 21; figures 129 and 130 show only the more distal members of certain older stages. The full complement of 12 on the median margin, of which, initially, all save the most proximal spine are scrapers, is acquired by the time that the animal is about 26 mm in length.

Scraping enables large amounts of food to be collected during the filter-feeding stages with far less effort than is required to extract a comparable volume of particles from suspension. It is in animals behaving in this manner that the packing of the food groove with particles over a considerable length is most frequently seen. Once the ability to filter fine particles is lost, no good purpose is served by collecting such material and the endopodite armature is transformed, usually within the space of a few instars, from a set of beautifully formed scrapers to an array of stout spines (figures 131 and 132 and figures 186 and 187, plate 12). There appears to be

Description of plate 5

Figure 112. Distal portions of some of the more anterior gnathobasic spines of left trunk limb 2 of a 23 mm individual, within the food groove. Note the underlying band of stiff spinules on the food groove wall.

Figure 113. The tip of a single spine of trunk limb 3.

Figure 114. As figure 112 but of right hand side.

Figure 115. Distal portion of a gnathobasic spine of a 45 mm individual in food groove.

Figure 116. Details of a more proximal region of the same spine.

Figure 117. Distal portion of the gnathobasic spines of a 43.5 mm individual in food groove.

Figure 118. Details of the tip of the right hand spine shown in figure 117.

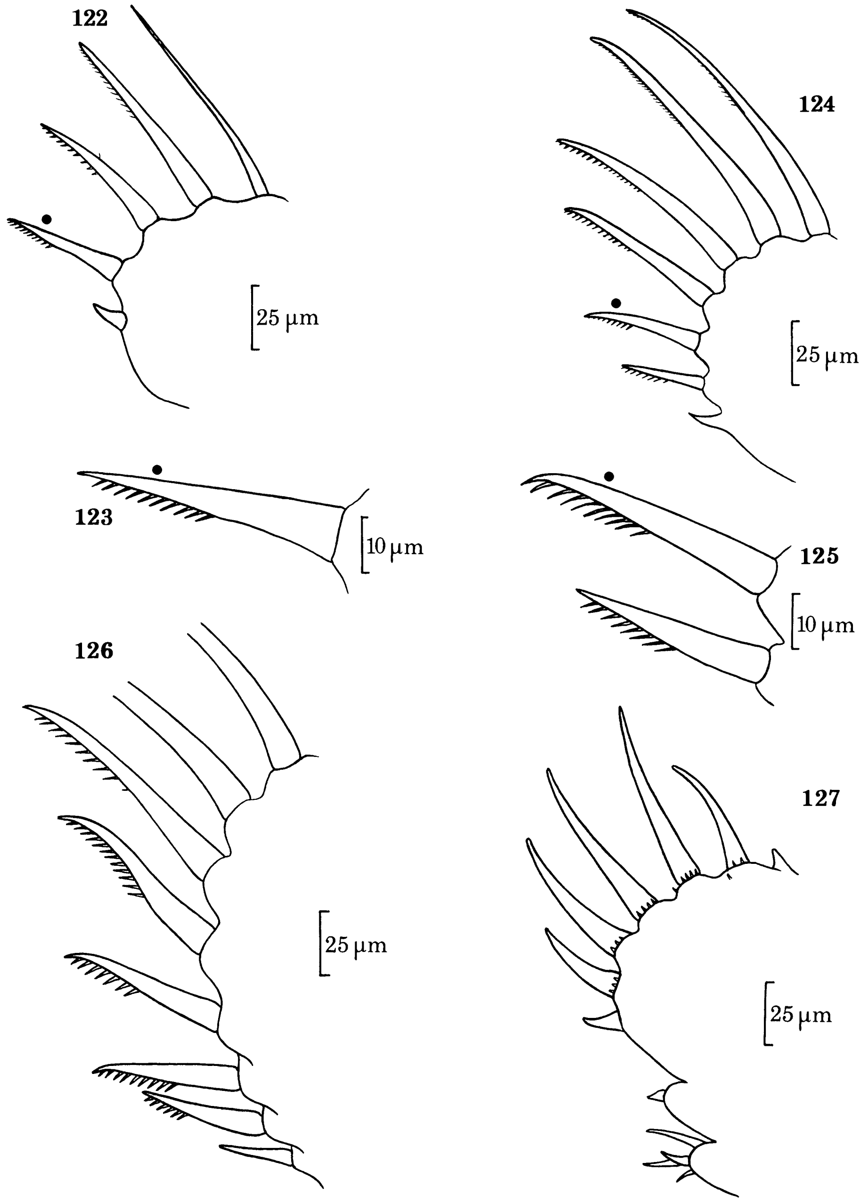
Figure 119. Tip of another gnathobasic spine of a 43.5 mm individual.

Figure 120. Tip of a gnathobasic spine of trunk limb 6 of a 43.5 mm individual.

Figure 121. Anteriormost gnathobasic element of trunk limb 3 of a 45 mm individual to show its brush-like nature.

some variation here. For example the spines of the 23 mm individual in figure 186, plate 12, still retain some scraper-like characteristics.

With increase in size the endopodite spines acquire independent mobility. (Some such may be possible in animals less than 20 mm in length but this is difficult to ascertain.) In larger individuals each endopodite spine is pivoted (figures 186 and 187, plate 12). The mechanism involved is essentially the same as that which grants great mobility to the cheliped bristles of



Figures 122–127. Development of the endopodite in the early instars.

Figures 122–127. Development of the endopodite in the early instars.

Figure 123. Proximal spine of same.

Figure 124. Distal part of endopodite of trunk limb 1 of an individual at stage 19.

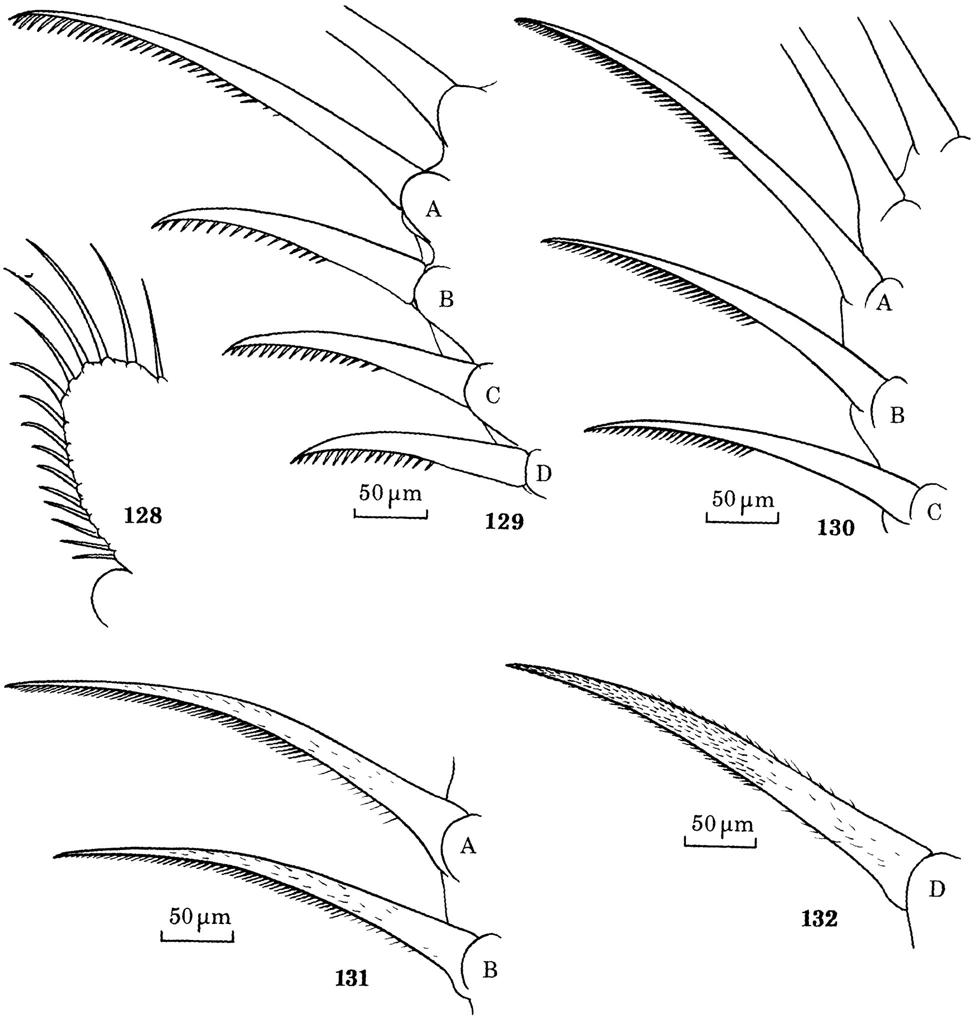
Figure 125. The two proximal spines of same.

Figure 126. Distal part of endopodite of trunk limb 1 of an individual at stage 21.

Figure 127. Endopodite and adjacent endites of trunk limb 11 of an individual at stage 21.

atyid prawns, described and illustrated by Fryer (1977) – an interesting example of convergent evolution in remotely related organisms. As in *Atya* no muscles are involved and extension is therefore dependent upon hydrostatic pressure generated in the haemocoelic fluid, which causes the spines to pivot along the hinge line, which is clearly displayed in figures 186 and 187, plate 12. Pressure causes the spines to rise towards the observer. Their return follows from the elastic, spring-like nature of the cuticle at the opposite side of the spine when pressure is released.

Loss of the ability to filter and the associated changes in endopodite armature are accompanied by a change in diet. Algae and detritus are largely replaced by animal matter, for *B. ferox* now becomes carnivorous. Although it has not been possible to check this in the field at the appropriate season, the loss of setules, which precludes subsequent true filter-feeding,



FIGURES 128–132. Changes in the endopodite armature of larger adults.

FIGURE 128. Outline of endopodite of trunk limb 1 of a male, length 18.9 mm, to show the number and relative size of the marginal spines.

FIGURE 129. The same, showing details of part of the distal endopodite armature. The spot identifies the same spine in figures 128 and 129.

FIGURE 130. Part of the distal endopodite armature of trunk limb 1 of a male, length 20 mm.

FIGURE 131. Endopodite spines of trunk limb 1 of a male, length 21 mm.

FIGURE 132. Endopodite spine of trunk limb 1 of a male, length 40 mm.

presumably coincides with the assumption of carnivorous habits. In Israel large adults feed largely on diaptomid copepods (§ 14 (*b*)).

The absolute number of setae involved in food collection is smaller in *B. ferox* than in anostracans that filter-feed throughout life. Thus on trunk limb 1 the number of gnathobasic setae never exceeds about 56 towards the end of the filter-feeding stage and subsequently becomes reduced to about 41 in large adults. Endite 3 bears only eight or nine marginal spiniform setae. By comparison a 15.5 mm male of the purely filter-feeding *Streptocephalus torvicornis* (Waga) had 112 setae on the gnathobase and 25 on endite 3 of trunk limb 1 – which is smaller than leg 2 in this species. Other anterior legs had more setae (maximum 131 and 29). For *Chirocephalus diaphanus* (adult) Cannon (1928) shows 80+ and 16 setae.

In this as in other respects *B. ferox* shows marked specializations for a carnivorous adult diet, but less so than *B. gigas*, the adult gnathobase and endite 3 of which bear only 23 and 11 spines respectively.

13. ONTOGENETIC CHANGES IN THE LABRUM AND THE LABRAL GLANDS

(*a*) *The labrum*

The precocious development of the labrum in the branchiopod nauplius, where it is conspicuous from the outset (figures 1 and 2), is well known. *B. ferox* is no exception. Some of the details of this organ and its conspicuous glands in the naupliar stages are shown in figures 16, 18 and 19. Its general form as seen in longitudinal section in an individual at stage 24 is indicated in figure 42. Because this slice is cut just lateral to the mid-line it does not reveal the presence, at the tip, of a rudimentary projection. As growth proceeds this becomes ever more distinct and eventually forms a finger-like distal lobe. Such is well marked for example in animals about 15 mm in length, and even more so at 23 mm (figure 133, plate 6). In this and larger individuals the lobe (figure 55, plate 1), whose cavity is traversed by a reticulum of bracing fibrils (figure 56, plate 1) (see § 8), articulates with the rest of the labrum and can be flexed towards the food groove by an array of muscle fibres. Such flexure is perhaps of assistance in securing prey in these carnivorous individuals (§ 14 (*b*)). This suggestion is not supported by observations, but the proximal region of the extension is flanked on its oral face by the paragnaths and overlies the maxillae, thereby enabling a confined space to be demarcated just behind the maxillae. Flexure of the extension might even help to push large food items orally.

(*b*) *The labral glands*

Changes also take place in the labral glands as size increases. Their condition in an individual at stage 24 is shown in figure 83. They are located just proximal to the base of the distal lobe. A similar situation prevails in the glands of individuals 16 mm in length but the lateral glands are now located more laterally, presumably an adjustment to changes in the shape of the labrum, and the median gland is relatively reduced in size. At about 19.5 mm the lateral glands are relatively smaller in relation to the labrum than in earlier stages but are still present at 22 mm, by which stage the median gland has degenerated, though two cells, evidently the rudiments of it, remain, and a small reservoir that appears to contain a little secretion also persists. At 36 mm the lateral glands are still present but whether they still function is uncertain. In a well fixed individual a reservoir was present and full of secretion on one side, as was the dubiously functional duct, while at the other side the gland appeared to be degenerating. Of the median gland only some very degenerate cells remained but it was still possible to recognize the duct cell. At 41 mm even the lateral glands are represented only by some apparently degenerate rudiments though what appears to be a trace of secretion in a closed reservoir has been detected. The duct cell can still be seen but its proximal end is rounded off and in no way connected to the remains of the former reservoir system.

The loss of labral gland secretions is clearly related to the change in diet. Such are not required in the handling of large food items such as copepods. A small problem remains. Even in large individuals in which the labral glands are non-functional, occasional traces of mucoid material are to be encountered in the food groove or near the limb bases. Their origin is unknown but their presence, which recalls earlier disputes about the nature of secretions found in the vicinity of the labrum in anostracans (Nicholson & Yonge 1935; Cannon 1935*b*), cautions against the attribution of all such material to the secretion of labral glands unless its derivation from that source has been unequivocally proved. Likely sources of these secretions are the glands opening into the food groove and on the gnathobases of the trunk limbs discussed in §11, but this is not proven.

14. CARNIVOROUS FEEDING BY LARGE ADULTS

(*a*) *Trunk limb morphology and associated features*

The salient features of the trunk limbs of filter-feeding anostracans are reasonably well known and are illustrated for example by Sars (1896) and Cannon (1928, 1933). An illustration of a typical trunk limb of the large, carnivorous *Branchinecta gigas* is also available, and the major differences between this species and typical filter-feeders, not only in the nature of the armature but in the orientation of endites 4–6, have been pointed out (Fryer 1966). Large adults of *B. ferox* to some extent stand between the filter feeders and *B. gigas* in that, while the armature of the limbs is non-filtratory and shows other modifications, the orientation of the endites is but little different from that of filter-feeders. Such was already known from the examination of a few preserved specimens of *B. ferox* used for comparison with *B. gigas* (Fryer 1966). Additional relevant facts are now available.

The food-handling portions of the trunk limbs of a 23 mm individual are shown *in situ* in figures 133–136, plate 6. Apart from an increase in robustness of the spines, the arrangement in larger individuals differs scarcely at all from that seen here (see figure 137, plate 7). A series of horizontal sections through the whole series at three different levels is given for a 44 mm individual in figures 141–143. Between them these illustrations enable the arrangement of the limbs and the manner in which they operate to be visualized relatively easily, for although the complete system is mechanically complex and its operation demands co-ordination of a high order, the principles of both its construction and its operation are relatively simple.

Most structural features are self-explanatory but attention is drawn to the armature of endites 4–6 which is seen on trunk limb 3 of a 45 mm female in figures 137 and 140, plate 7. On this limb, which is representative of legs 2–10, though there are small differences within the series, the armature of each of these endites consists basically of two rows of spines, an outer row (OS) homologous with the row of filter setae in filter-feeding species, and a median row (MS) of shorter, stouter spines that represent the heavy armature of each endite. These two components can be readily separated on most of the limbs in figure 141. In contrast to the situation in filter-feeding species, the number of spines in the outer row is reduced, that in the median row increased. Thus endites 4 and 5 each have a median row of nine spines (figure 140, plate 7) (two is common in filter-feeders though the number may be increased in the male) while the outer row is reduced to four longer spines on endite 4 and three on endite 5. Although partly obscured by the spines of the median series, all the outer spines can be seen in figure 140, plate 7. Endite 6 bears 13 median and four outer spines. The median spines are inserted in an arc distally and almost begin a second row. All the median spines of these three distal endites are directed medially and towards the food groove and for the most part somewhat posteriorly. Some, especially on the most distal endites, are directed more anteriorly: their orientation differs from endite to endite, according to their location on the endite, and from limb to limb. They inevitably force towards the food groove any material with which they come in contact during the working stroke of the limb.

Trunk limbs 1 and 11 differ from the rest. The distal endites of trunk limb 1, apart from being more squat than on adjacent limbs, are directed more medially so that their medial spines, which are more numerous than on adjacent limbs and are not confined to a single row, extend towards their partner on the opposite limb and close off the anterior end of the feeding cage (figures 133, plate 6, and figure 141). The posterior end of the cage is similarly guarded by trunk limb 11 whose armature differs strikingly from that of other limbs. The distinctive nature of the gnathobasic spines, which extend more or less transversely across the median gap, is readily seen in figures 133 and 136, plate 6, and the way in which the armature of more distal endites closes off the cage can be seen in figures 141 and 142.

Although the gnathobasic spines which push food along the food groove are superficially smooth, scanning electron microscopy reveals that many of them are in fact armed with two rows of short, stout spinules, presumably derived from the longer setules of earlier instars. Additional scattered spinules are also present on some spines. Figures 112–114, plate 5, show several such gnathobasic spines of a 23 mm individual. Figure 112 shows how these extend into the food groove, the bottom (morphologically the roof) of which lies below the level of the photograph. The upper part of the photograph shows the pelt of stiff spinules which extends as a band along each wall of the food groove adjacent to its open side and is a characteristic feature of large adults. Its ancestry has been noted in §10. Details of gnathobasic spines from individuals 43.5 and 45 mm in length are shown in figures 115–121, plate 5.

Figure 102 shows how the most proximal gnathobasic setae of trunk limb 1 of a 21 mm individual have rather conspicuous spinules. This feature is retained by these spines, but not by those of succeeding gnathobases, even in the largest animals. The first gnathobase is the only

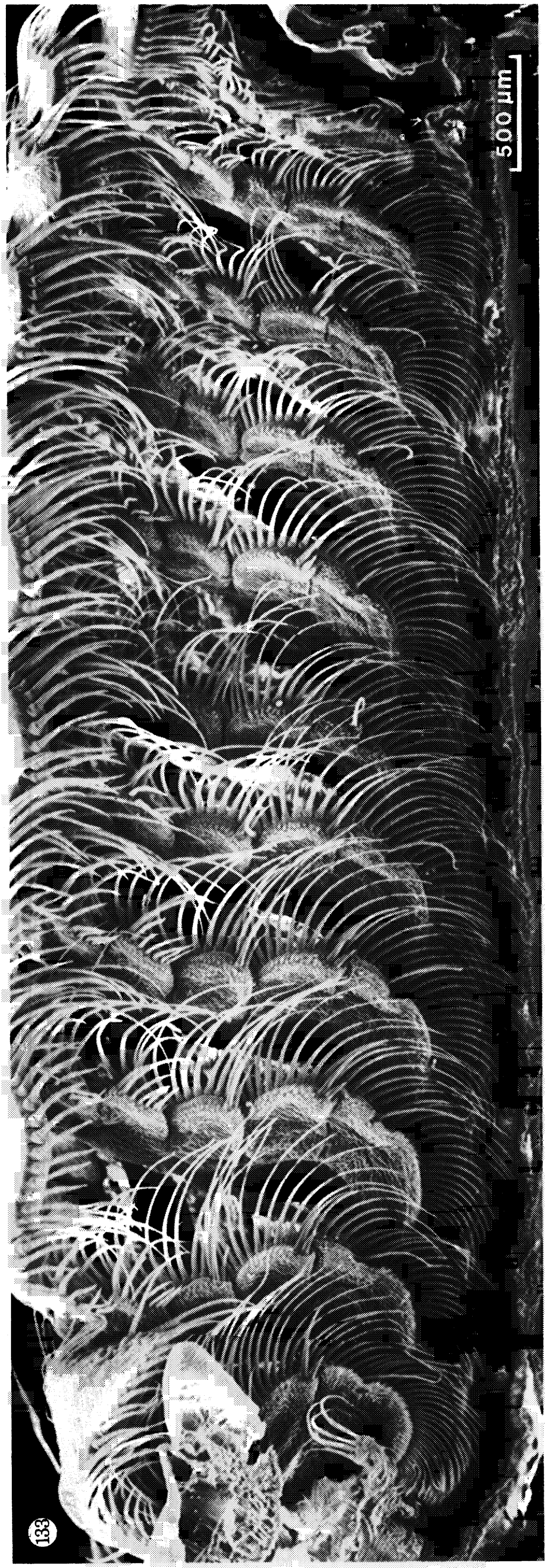
DESCRIPTION OF PLATE 6

FIGURE 133. The complete series of left trunk limbs of a 23 mm female seen from the median side. Between this face and that of the right series, which are mirror images, lies the median chamber. The photograph was obtained by scanning electron microscopy of a bisected individual. The endopodites are flopped somewhat posteriorly and medially; otherwise the arrangement of the limbs, and especially of the endites, gives a good impression of their disposition in life. Anteriorly part of the maxillule can just be made out anterior to the readily seen maxilla. Posteriorly the endopodite of the tenth limb lies partly, that of the eleventh entirely, posterior to the limits of the photograph. The labrum is cut medially just to the observer's side of the mid-line and reveals the clearly demarcated distal lobe.

FIGURE 134. The maxilla and the gnathobase of the first trunk limb.

FIGURE 135. The gnathobases and adjacent endites of trunk limbs 3 and 4.

FIGURE 136. The gnathobases and adjacent endites of trunk limbs 10 and 11. Note the distinctive nature of the latter.


500 µm
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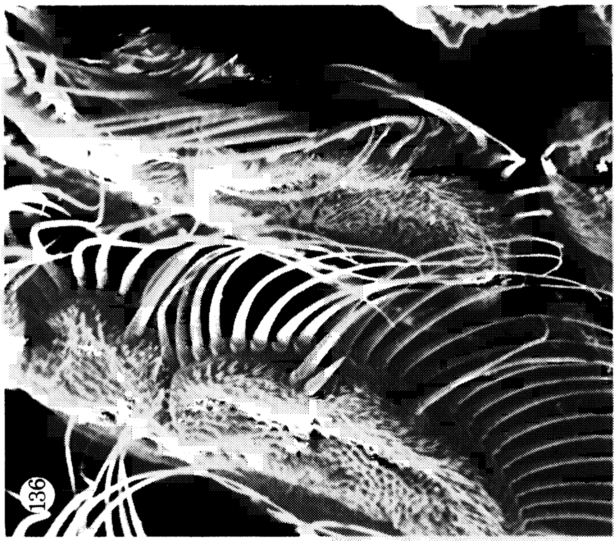
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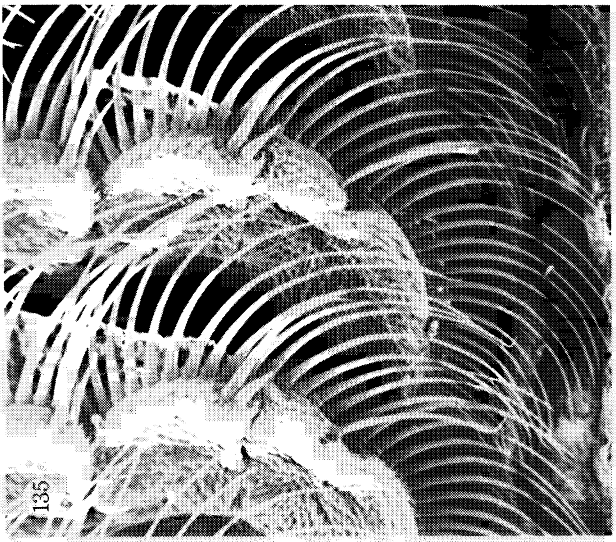
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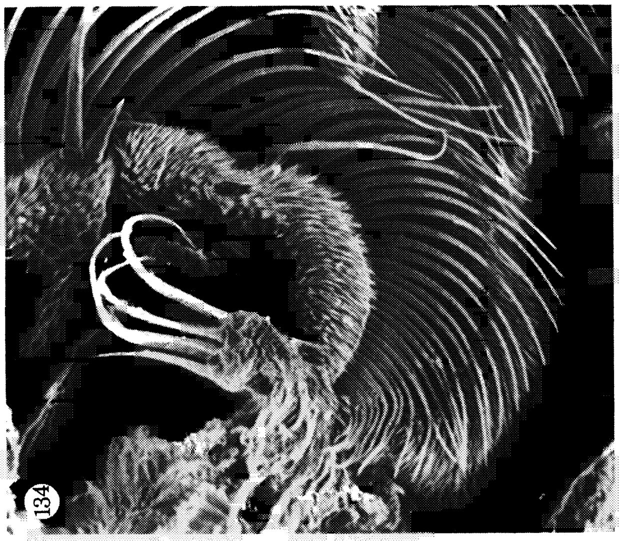
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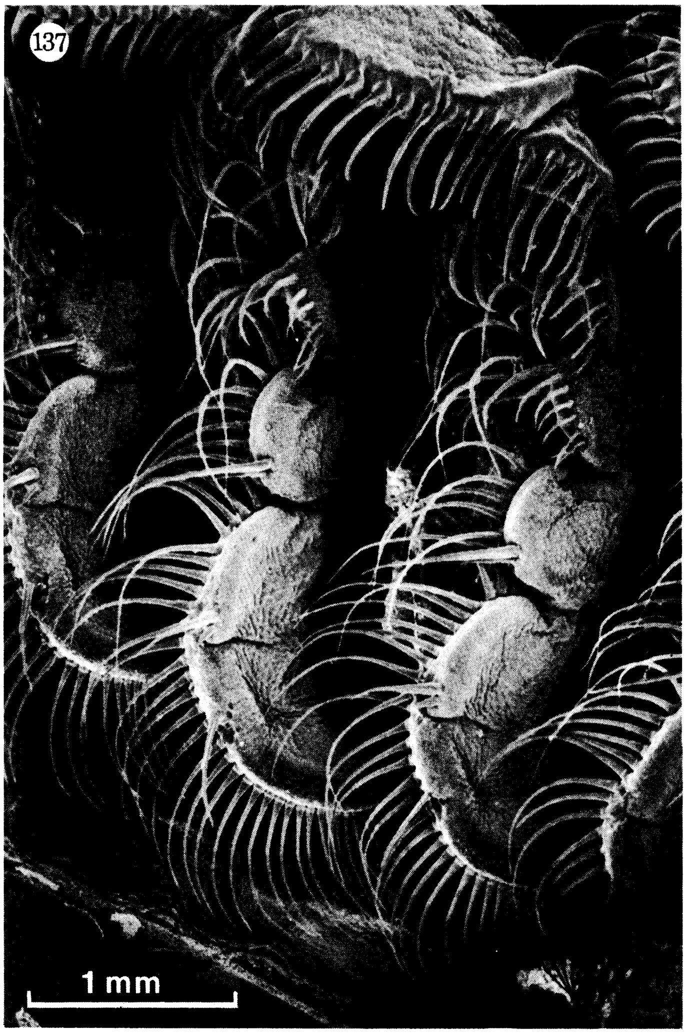
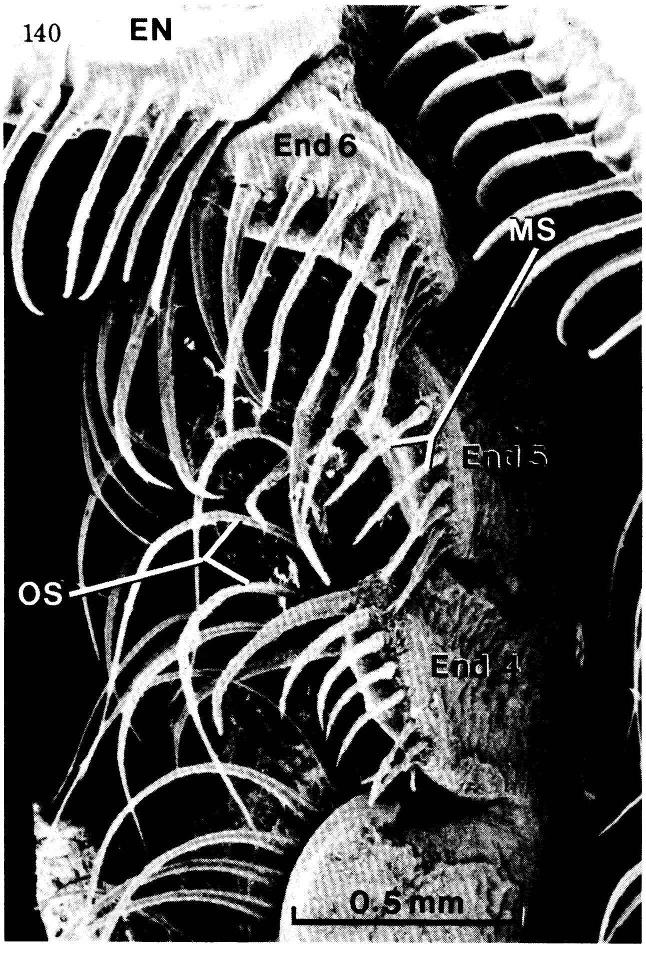

137
1 mm


138
0.5 mm


139
200 µm


140
EN
End 6
MS
End 5
OS
End 4
0.5 mm

one whose proximal spines are not overlain by spines of the gnathobase behind and therefore they alone are responsible for the forward transport of food whereas their homologues on more posterior limbs receive assistance. This suggests that the spinules enhance efficiency but are not employed on more posterior gnathobases as they would there be a mechanical liability as they slid past the spines of the adjacent gnathobase.

(*b*) *Feeding habits*

Large adults living in pools near Jerusalem feed predominantly on the copepod *Arctodiaptomus similis* (Baird) and to a lesser extent on the cladoceran *Daphnia atkinsoni bolivari* Richard. Some detritus is also ingested. Most live material was collected from a turbid pool at El Khadr which, although several metres deep when full, dries out annually. Here *B. ferox* was plentiful and *A. similis* extremely abundant. Like other calanoid copepods, *A. similis*, of which females attain a length of about 1.4 mm, has an extremely swift and efficient escape reaction. Nevertheless it is caught with ease by *B. ferox* whose gut often contains several dozen individuals. As these are invariably a bright orange-red their presence is revealed even to the naked eye.

When *B. ferox* was placed in a commodious vessel and supplied with large numbers of *A. similis* these were readily captured. So efficient is collection that two *Branchinecta* cleared several dozen copepods within about 2.5 h, not even a single straggler escaping.

While feeding takes place during the course of normal swimming, looping movements are sometimes performed that are perhaps particularly associated with this activity. Copepods are drawn into the median cage (figure 133, plate 6, and figures 141–143) by very powerful suction which takes place along the entire length of the trunk limb series. While this can be inferred from watching the capture of prey by free-swimming individuals, it is more clearly observed in a restrained animal, held ventral surface uppermost, so that its limbs may beat freely, and provided with a dense population of *A. similis*. The copepods in the vicinity of the median entrance to the cage can then be seen attempting to swim away from it, in an upward and slightly posterior direction, irrespective of their position along much of the length of the cage. A suspension of particles (*Chlorella* powder was used) also reveals this suction and the high velocity of the currents involved. Even in a partly narcotized animal in which limb movements are slowed, suction is still powerful. Currents are set up by the same means as in earlier, filter-feeding, stages and their course is the same. When a cloud of *Chlorella* powder is sucked into the cage it passes between the spines of the gnathobases, where in earlier stages particles would be filtered, and is discharged laterally. Only an occasional particle passes into the food groove where lateral suction is inoperative. Copepods sucked into the cage are too large to escape via the lateral exits between the rows of endite spines and are prevented from doing so ventrally by the inflowing current, and to some extent by the tips of the endite spines that form its lateral walls, and especially by the median series of spines of the more distal endites (4–6). The

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DESCRIPTION OF PLATE 7

FIGURE 137. A 45 mm individual. Right trunk limbs 3 and 4 *in situ*. Parts of trunk limbs 2 and 5 can also be seen. In order to portray the limbs in a vertical position the animal is canted so that the anterior end of the food groove, at the bottom of the picture, is inlined downwards towards the right.

FIGURE 138. The same, Trunk limb 1, endites 4–6 and endopodite. The white material towards the proximal end of the limb is a coagulated mass of secretion.

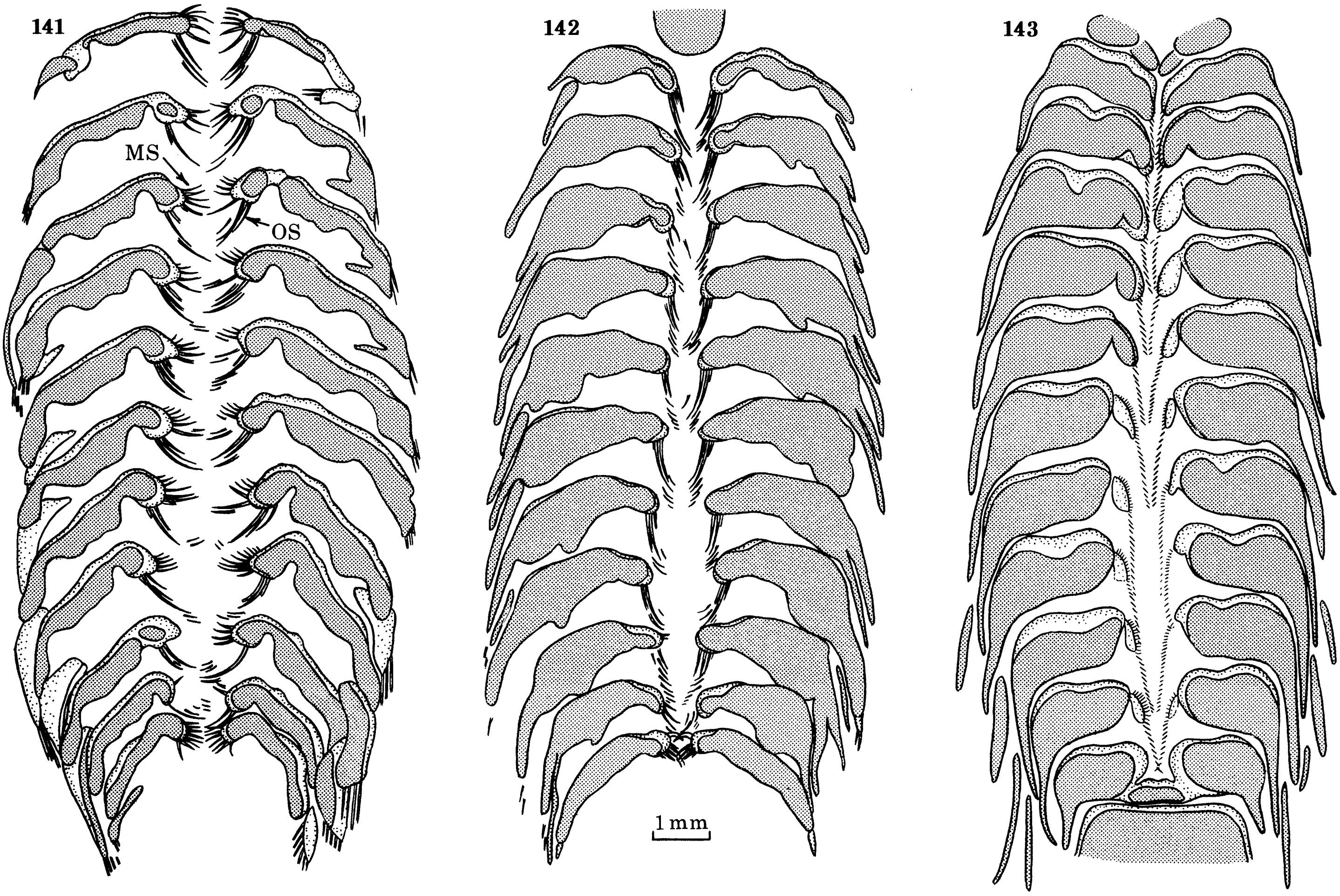
FIGURE 139. The same. Trunk limbs 3 and 4, proximal armature.

FIGURE 140. The same. Trunk limb 3, endites 4–6 and part of the endopodite.

orientation of the latter (figures 133, plate 6, and figure 140, plate 7) is such that, should pumping momentarily cease – and this has not been seen – a narrowing of the cage would enable them very effectively to perform the function of a one-way valve.

In preserved material the distal endopod spines curve towards their counterparts on the opposing limb and give the impression that they can effectively close the ventral entrance of the cage. In life, however, there is almost invariably a wide gap ventrally along the entire length of the cage in feeding animals and only rarely and briefly have the opposing endopods been seen so to come together – and this particularly posteriorly. Such a closing device is in fact not usually required and is not employed. The endopod spines are thus not actively engaged in either the capture or the retention of prey but help to guide it into the chamber. Although the cage is bounded anteriorly by the endite spines of trunk limb 1 little indication of prey seeking to escape via this route was observed. The posterior gate of the cage, formed by the spines of the last pair of trunk limbs, remains closed as these limbs beat, but with a smaller

141 142 143



Figures 141–143. Thick horizontal slices through the trunk limbs of a 44 mm individual.
Figure 141. At the level of the distal endites.
Figure 142. At the level of endite 3.
Figure 143. At the level of the tips of the gnathobases showing many of the proximal gnathobasic setae.

amplitude than the more anterior limbs, and there is thus no posterior escape route for the prey.

While prey is transported towards the food groove mainly by suction, the endite spines also make a contribution. Any contact with the median spines of the distal endites inevitably leads to the prey being swept posteriorly and towards the food groove. As the groove is approached, the spines of the heavy armature of endites 1–3 can make a similar contribution, but their action has a more median, or even anterior, component, and is of smaller amplitude. That such mechanical processes are involved at times is shown by the fact that while, very approximately, the inflow to the cage in the mid-ventral line is vertical to it, captured copepods have been seen to enter it well forward and pass back along much of its length before entering the food groove. The distal gnathobasic spines, whose curvature in two planes can be seen in figure 133, plate 6, guide the prey towards the food groove and medially, and their tips contribute actively to its transport, perhaps more so anteriorly than posteriorly, their orientation on the latter limbs being somewhat more medial than on the anterior limbs.

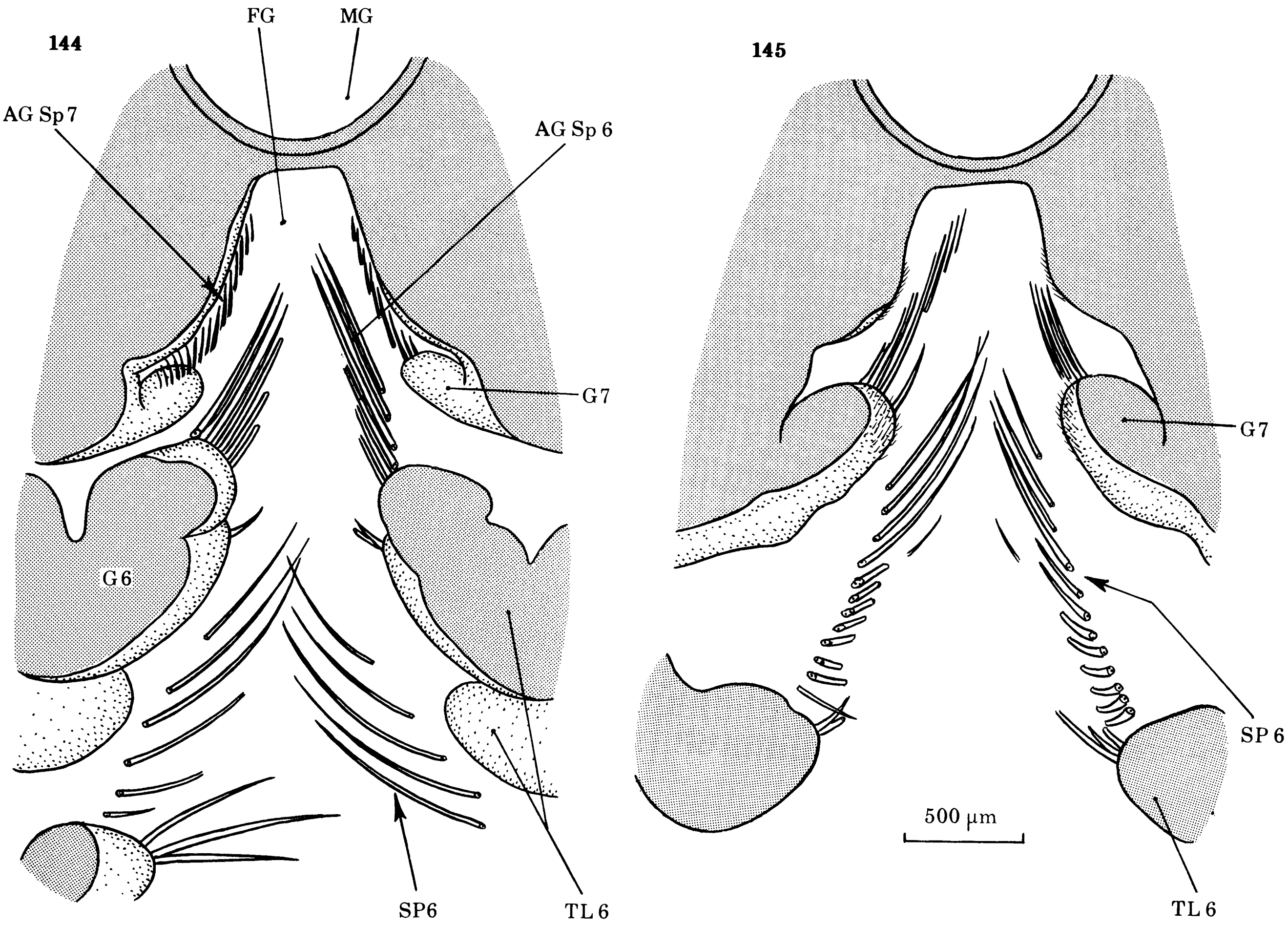
Within the depths of the groove the prey lies in a region of dead water and is passed forward mechanically by the tips of the proximal gnathobasic spines as in earlier, filter-feeding, stages. That there is no anteriorly directed current in the food groove is seen by the way that fine particles make their lateral exit with no tendency to move forward as they approach it, and by the behaviour of the very few such particles that find their way into it. These move forward very slowly, being swept by the marginal gnathobasic spines – which are not equipped to deal efficiently with such – or by the eddies inevitably set up by the movement of these spines. The role of the stiff spinules of the food groove wall (figure 146) – to clean the gnathobasic spines and to strip from them any adhering material as they make their return sweep – is easy to appreciate.

The most proximal, and therefore most anterior, marginal spines of the gnathobase (figure 144, AG Sp7) keep close to the lateral wall of the food groove as the animal feeds. The more distal spines extend medially somewhat further into the cage (figures 145 and 146, G Sp7) – an inevitable consequence of the fact that they overlie the gnathobase behind (see also figure 143). In life they appear to do so to a lesser extent than is suggested by sectioned material.

When prey is abundant, material often piles up at the anterior end of the food groove, or even along much of its length, as do fine particles in the filter-feeding stages. This is further evidence of the lack of anteriorly directed currents, and also shows that Cannon's argument about food being pushed between successive limbs if mechanical transport were to be employed – as it is – is without foundation. Material is clearly not pushed in this undesirable way but along the food groove. The spines in any case lie too deeply within the food groove, and below the fringing cleaning spinules, for this to happen.

Food reaching the mouthparts is dealt with in essentially the same manner as in earlier stages. The maxillules, still as illustrated in figure 79 but more robust and with stouter spinules on the lateral margins of the distal portion of each spine, play a vital role in passing material from the gnathobases of the first trunk limbs to the mandibles. Information on the mandibles of large individuals is given in §15. Although copepods are damaged during this part of the feeding process, which appears to rupture the cephalothorax, they are not usually completely dismembered and are often seen virtually intact within the gut.

When prey is abundant, diaptomids are sometimes taken into the cage, pass posteriorly, and are there released, not via the gate between the last trunk limbs but ventrally. An unanalysed

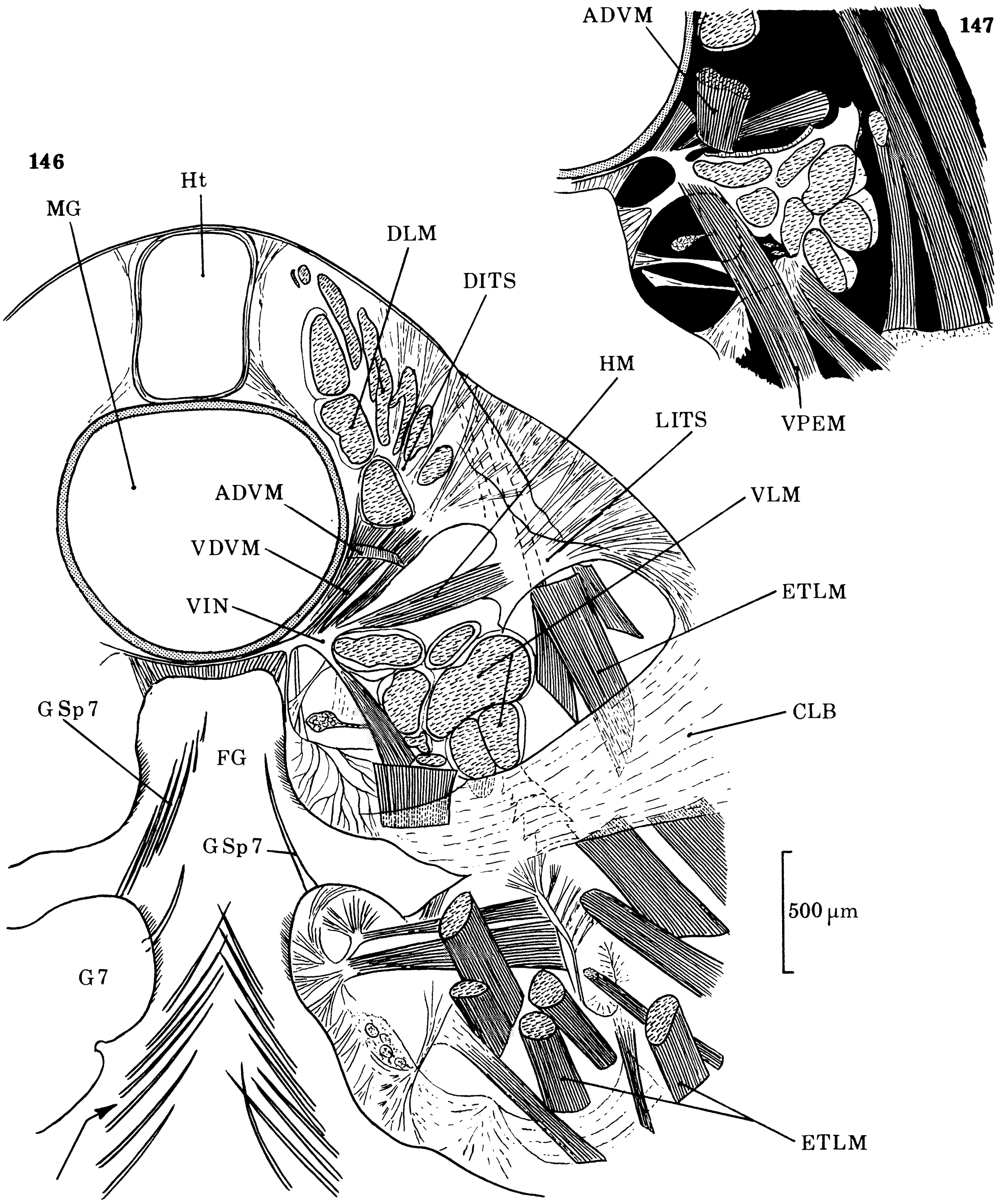


Figures 144 and 145. Thick transverse slices through the food groove region of a 36 mm individual viewed from in front to show the relations of the gnathobases of successive trunk limbs. The series continues posteriorly with figure 146. In figure 144 the extreme anterior (proximal) tip of the gnathobase of trunk limb 7 (G7) is to be seen adjacent to the food groove wall. Note the proximity of its spines (AGSp7) to the wall of the food groove and their relation to the overlying spines of the gnathobase of trunk limb 6 (AGSp6). It is clear that gnathobase 7 cannot push material far into the gap between gnathobase 6 (G6) and the food groove wall and that as it swings forward (which it does *after* gnathobase 7) the armature of gnathobase 6 will carry forward the material carried to the anterior limit of the field of action of gnathobase 7. In figures 145 and 146 respectively progressively more of gnathobase 7 is to be seen.

wriggling motion seems to assist this process. Such prey appear to be undamaged. Large *Daphnia atkinsoni*, which have long posterior spines, appear to present handling problems. *Branchinecta* was often seen to take these animals into the cage, where they remained for some time perhaps half way along its length and not very far within it, and then reject them during a bout of violent wriggling.

15. The ontogeny of the mandibular armature

The mandibular mechanism of the anostracan *Chirocephalus* was described by Manton (1964); that of cladocerans, which employs similar principles but is more specialized, by Fryer (1963, 1968, 1974). In all these branchiopods the basic movement is that of sweeping combined with



FIGURES 146 and 147. Successive transverse slices through an intersegmental region of the thorax of a 36 mm individual to show some details of the adult skeleto-muscular system, and, with figures 144 and 145, the arrangement of the gnathobase and proximal trunk limb armature. Because the ventral intersegmental tendinous sheet of the endoskeleton is somewhat oblique, scarcely any of it is seen in the vicinity of the ventral longitudinal muscles (VLM) in figure 146 and that part of it which supports these muscles is shown in figure 147 where it is depicted in white against a black background. Because its configuration changes over very short distances it is almost impossible to draw an exact outline but the general shape can be deduced from these two figures. The way in which the longitudinal muscles assume more massive proportions and occupy a progressively larger portion of the thoracic haemocoele as the animal grows is easily appreciated by comparing these figures with figure 43 which is from a much smaller individual. To the right of figure 146 only one gnathobasic spine (GSp7) is shown for simplicity.

rolling. During sweeping the molar (masticatory) surfaces swing forward across each other, the narrow gap that separates them posteriorly being obliterated, to appear anteriorly at the end of the remotor sweep; during rolling the anterior and posterior margins are alternately pulled dorsally. Sweeping is effected by the various transverse muscles, rolling by the massive remotor and somewhat less massive promotor muscles which originate dorsally. Details of these extremely complex muscular systems are given in the papers cited and some of the muscles involved in *B. ferox* can be seen in an individual at stage 19 in figures 51–53, plate 1.

In most branchiopods the molar surfaces of the mandibles are elaborated for the most efficient trituration and transport of the food, and this efficiency is generally enhanced by skeletal asymmetry. Several authors have indicated the ridges and teeth into which the cuticle of the molar surface is drawn out in so far as this can be revealed by light microscopy, the observations of Ocioszynska-Bankierowa (1933) being particularly informative for the Anostraca. Scanning electron microscopy enables a far clearer picture to be obtained and reveals extremely elegant refinements that are clearly functional in nature. Most of these are indeed easily understood in the light of mandibular movements.

As from an early stage the animal swims inverted it is convenient to describe the molar regions as seen with the ventral surface uppermost. Asymmetry is best visualized if the right and left molar surfaces are viewed and described as shown in figure 148. Folding of these towards each other, as one shuts a book, brings them into correct juxtaposition. Code letters facilitate description.

The mandibles become functional in the stage 2 nauplius, but it is only at stage 3 that their molar surfaces acquire their first fine spinules on the thickened and, even at this stage, presumably somewhat sclerotized cuticle, and begin to handle food particles (§3 (*c*)). Slight signs of skeletal asymmetry are already apparent (figures 10 and 12). From this stage on, these appendages, although increasing enormously in size, continue to employ the same mechanism but their molar surfaces gradually change in relation to the change in size and nature of the particles – and eventually large food items – with which they have to deal. Gradually each molar surface begins to display signs of differentiation into what at first appears as a reticulum but soon resolves itself into a series of ridges running more or less dorso-ventrally, while the margins of this area develop minute teeth. Each ridge becomes divided into several blunt-crowned teeth. On the dorsal margin of the molar surface of the left mandible a series of minute knobs, about four or five can first be distinguished posteriorly, are recognizable from an early stage. By stage 6 they can be clearly seen with the light microscope in a good preparation.

As development proceeds the ridges become more distinct in number: 11 are distinguishable in the mid-region, with a reticulum of teeth fore and aft, by stage 11. By stage 15 the molar regions display the essential features that, with considerably modification of detail, are to prevail throughout life. The major portion of the molar area of the right mandible is occupied by ridges of thickened cuticle which, for the most part, run more or less dorso-ventrally (figure 152, plate 8). Each ridge is subdivided transversely into a row of teeth, each produced into a series of rounded cusps, generally three or four per tooth. Anteriorly the ridges become close-packed and difficult to discern and here the predominantly rounded cusps are close-set (figure 154, plate 8). Posteriorly there is a progressive tendency for individual teeth to be unicuspid, the cusps being sharply pointed and forwardly directed (figures 151 and 152, plate 8).

The ventral margin is bordered by a row of stout spines which here show in rudimentary form the specialization that will render them distinctive in older individuals. Their nature in regions A, B, and C can be seen from figures 152, 153 and 154, plate 8, respectively. Their function is best indicated by reference to older stages.

Dorsally there is posteriorly a stout tooth (figure 151, plate 8) and an accompanying spine, but the most distinctive feature is a groove which, bounded by a few specialized marginal spines, extends anteriorly, gradually becoming shallower as it does so and petering out between regions E and F. Within it are toothed ridges, fewer in number and much more widely separated than those of the main molar surface and with only two teeth in each row in the depths of the groove (figure 155, plate 8). Each tooth has several cusps, about six in the middle of the groove, and these are stout and sharply pointed. Each ridge terminates in a marginal tooth which projects more or less at right angles to it and differs somewhat from row to row (figures 155 and 156, plate 8). These teeth fence off the groove. Anteriorly the teeth of the groove merge imperceptibly with those of the main ridges (figure 156, plate 8).

The left mandible has a denticulate molar region which is more or less a mirror image of that of the right, but its teeth are arranged in fewer dorso-ventral ridges and tend to be more robustly cusped. As in the right mandible the teeth are arranged in clusters rather than rows fore and aft (figures 157 and 158, plate 8). Ventrally the molar surface is bounded by a row

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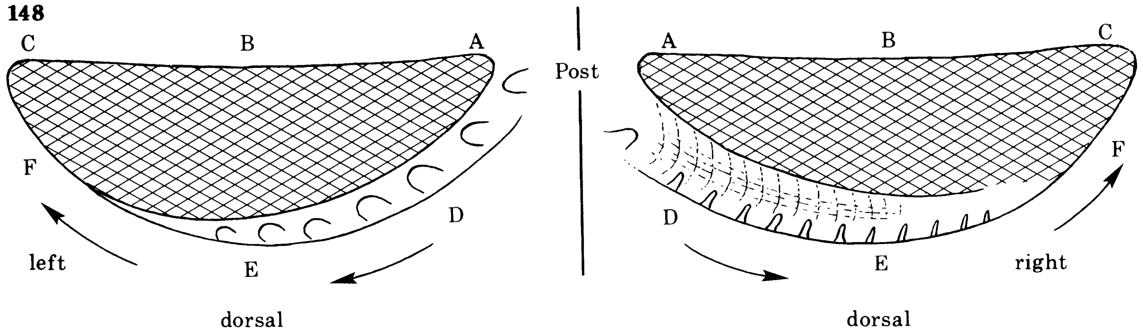

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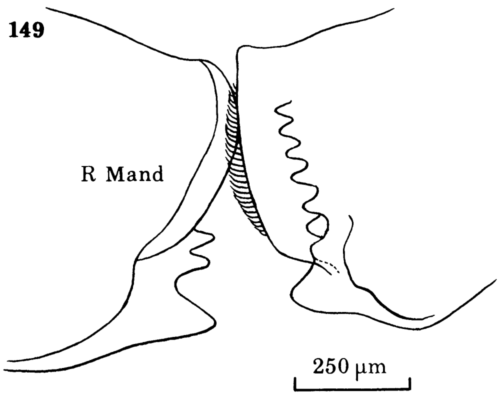

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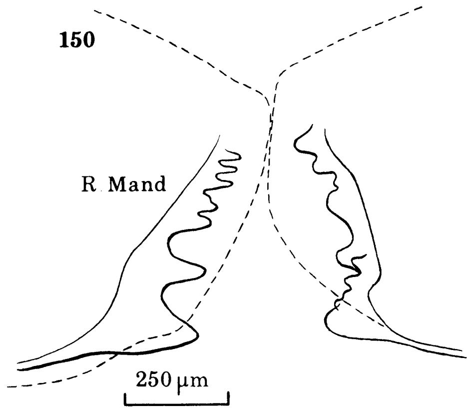

FIGURES 148–150. Details of mandibular armature.

FIGURE 148. The molar regions of the mandibles (diagrammatic). These oppose each other, as in life, if folded towards each other along the vertical line between them. Arrows indicate the direction of remotor roll which assists in the forward transport of food particles.

FIGURE 149. Thick horizontal section through the molar regions of the mandibles of a 35 mm individual, viewed ventrally. The left mandible is drawn as if transparent to reveal the row of dorsally lying teeth.

FIGURE 150. The same in a 44 mm individual. Here the dashed outline of the mandible lies ventral to (topographically above) the stout teeth.

of spines similar to those of the right mandible but differing in detail (figures 157 and 158, plate 8). Like the right mandible, the left has a stout, pointed tooth posteriorly (figure 160, plate 9), accompanied by a robust spine. Here, however, this is the end member of a row of seven stout, widely spaced teeth, of which the posterior three are shown in figure 159, plate 9, which occupy an area just below the dorsal edge of the molar surface and extend anteriorly to the area between E and F, diminishing in size as they do so, the dimunition corresponding with the decrease in depth of the groove of the right mandible into which they fit. Apart from the posteriormost, these are more or less wedge-shaped, appearing bluntly rounded when the molar region is viewed face-on (figures 159 and 160, plate 9), but are seen to be pointed when viewed obliquely dorsally (figure 162, plate 9). While the consequences of the tooth–groove arrangement are readily apparent, functional considerations are best discussed for older stages.

In the tooth–groove system of both mandibles the cuticle is perforated by three (left) and four (right) pores, circular in section and only about 0.3 μm in diameter (figure 161, plate 9, and figure 155, plate 8). Probably too fine to serve as ducts conveying secretions to the exterior, these are presumably spanned by thin cuticle and may be sensillae. What may be a sensilla of a different kind lies posterior to the pores of the left mandible (figure 159, plate 9).

By the time that an individual has reached 11 or 12 mm in length, the right mandible, while still clearly displaying the pattern already described, has undergone several changes. The number of ridges, and teeth per ridge, of the molar surface is vastly increased and the number of ridges in the groove has also increased, but to a lesser extent. The individual teeth of the latter ridges are also somewhat more numerous, about four per ridge, and their cusps more numerous, more robust and more rounded than in earlier stages (figure 163, plate 9). The marginal teeth of these rows are similar to those described for stage 15 but are now continuous anteriorly with a marginal row of spines scarcely differentiated at that stage. These are stout, rise at right-angles to the molar surface, and have their tips bent sharply forwards. Their form and the gradual transition of spine form along the dorsal margin is best appreciated from figures 164 and 165, plate 9. A remarkable development of the marginal spines is now also exhibited ventrally. Posteriorly these are hook-like and their tips are directed downwards and somewhat anteriorly over the ridges of the molar surface which they overhang (figure 166, plate 9). In the vicinity of B their orientation gradually changes and they are more forwardly directed (figure 167, plate 9), as they are anteriorly.

Parallel developments take place in the left mandible but these and further elaboration of the right mandible can easily be appreciated from the condition in an individual about 17 mm

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Description of plate 8

Details of the molar surfaces of the mandibles of a stage 15 larva. Code letters of regions refer to those shown in figure 148.

Figure 151. Right mandible. Extreme posterior tooth (whose companion spine is here damaged) and region D

Figure 152. Right mandible. Region A.

Figure 153. Right mandible. Region B.

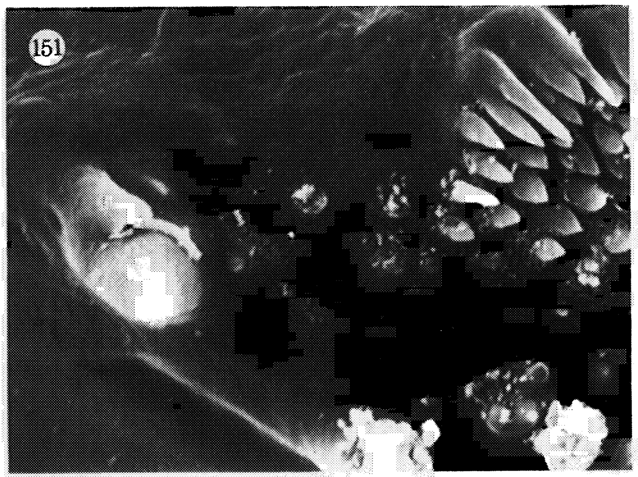
Figure 154. Right mandible. Region C/F.

Figure 155. Right mandible. Region E.

Figure 156. Right mandible. Region E and anterior to it.

Figure 157. Left mandible. Region A/D.

Figure 158. Left mandible. Region C/F.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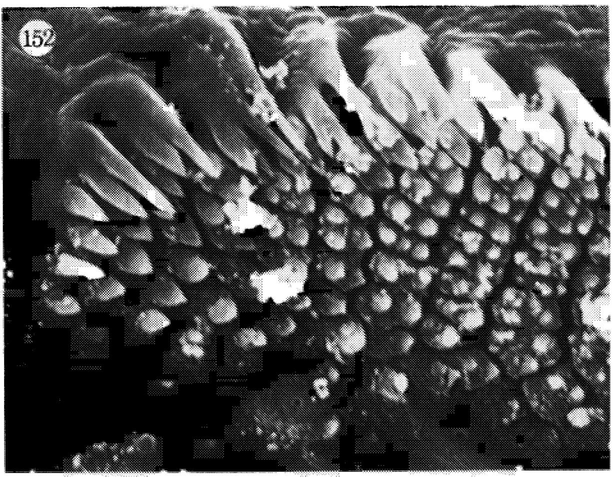
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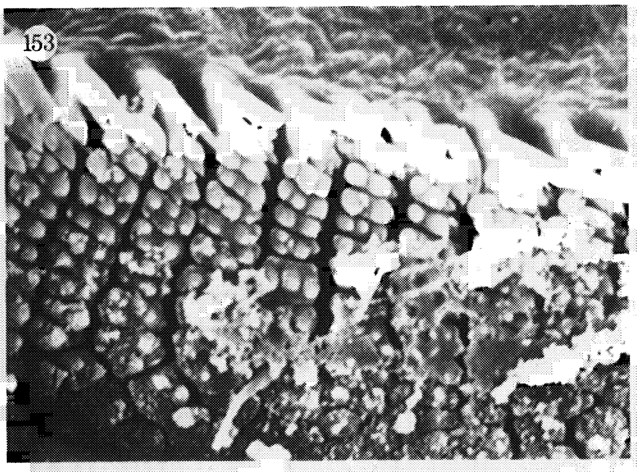
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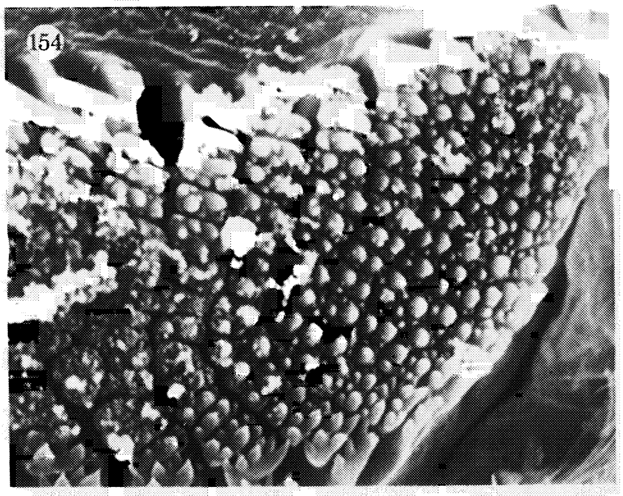
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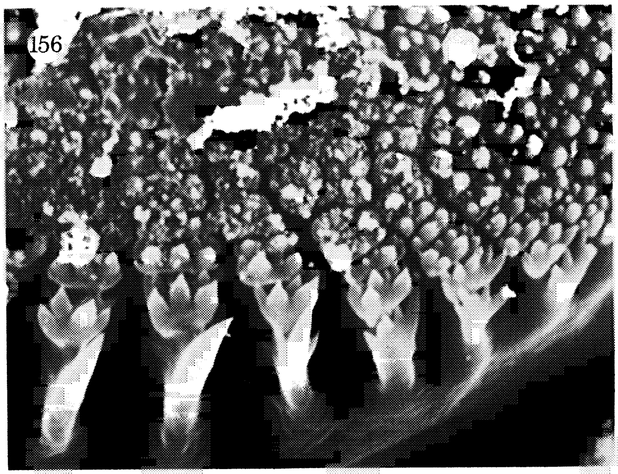
155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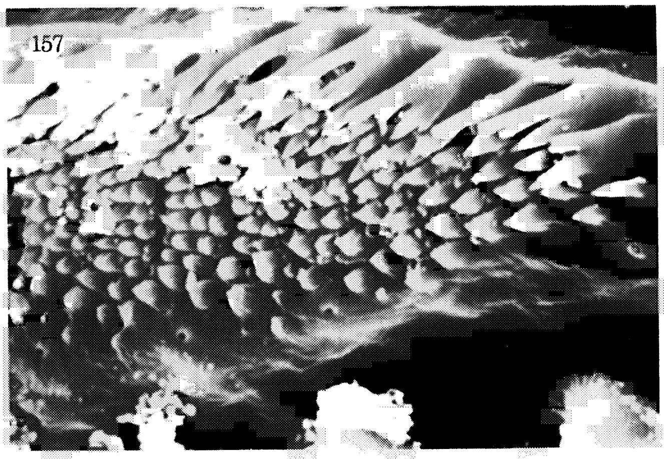
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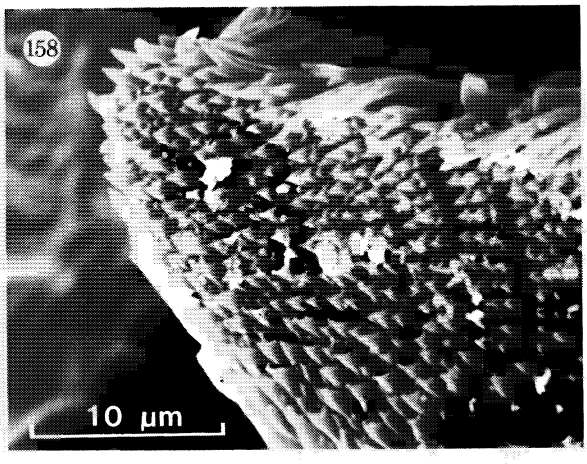
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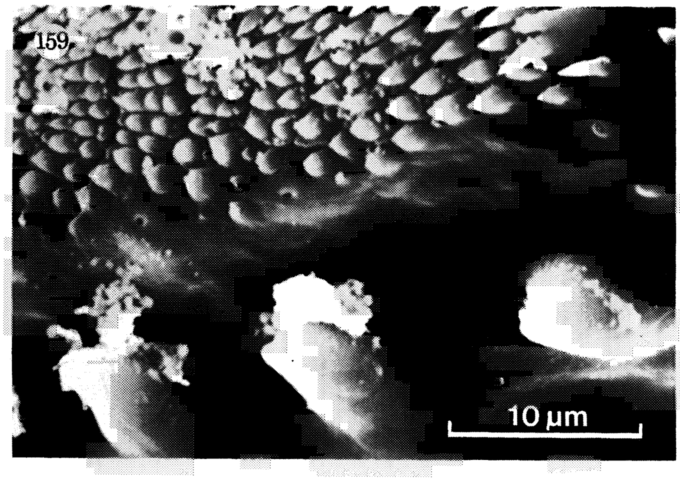
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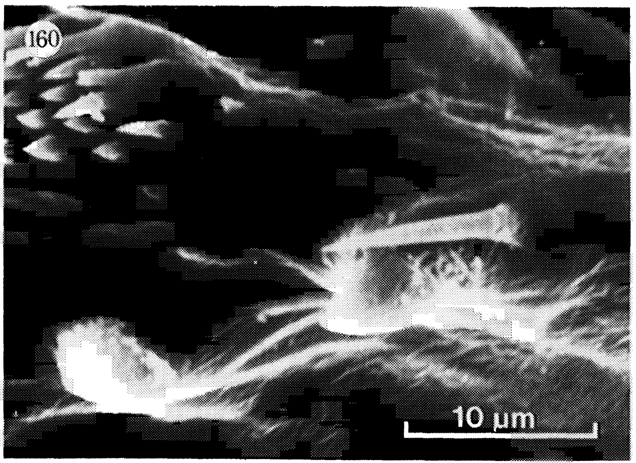
10 µm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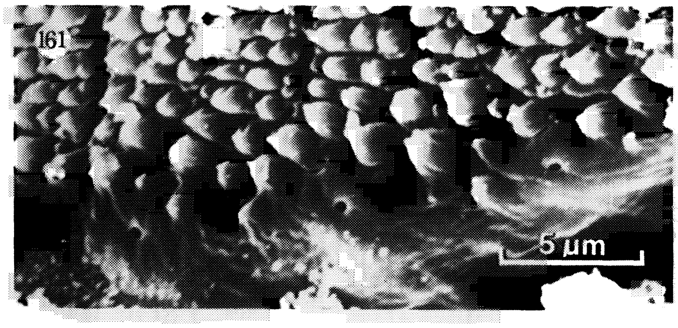
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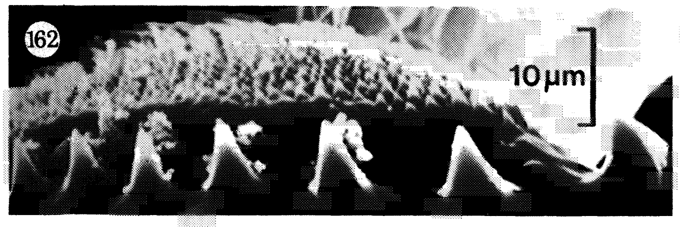
5 µm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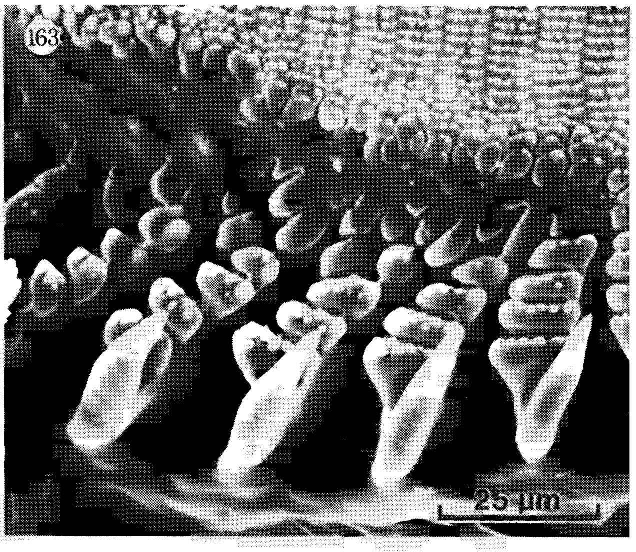
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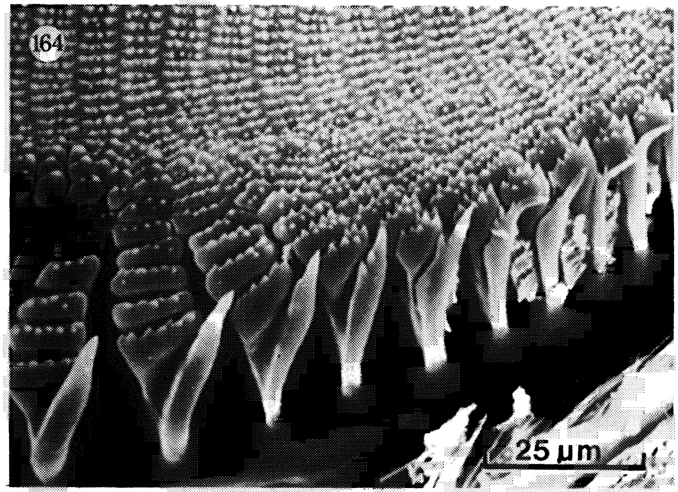
25 µm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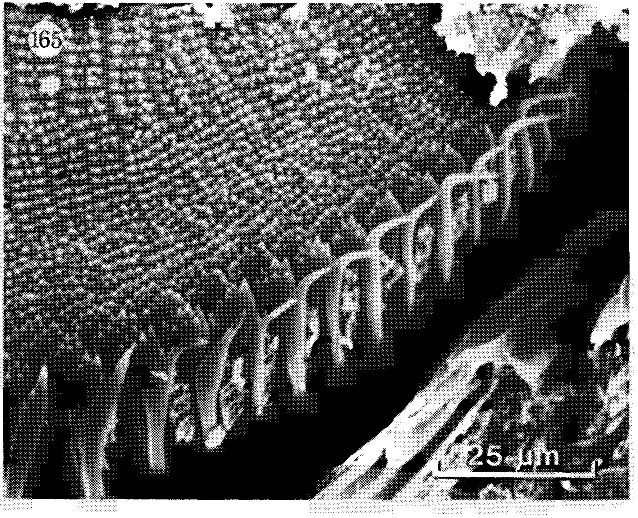
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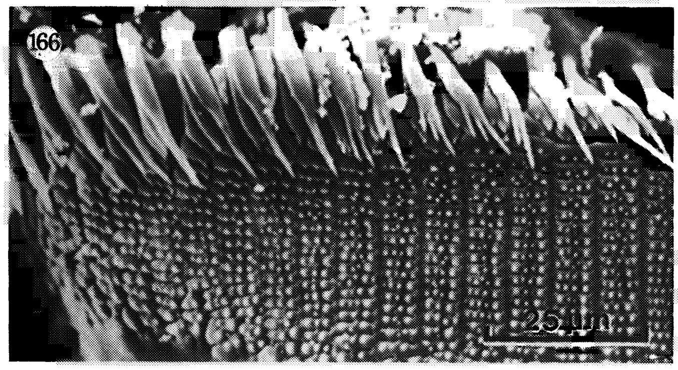
25 µm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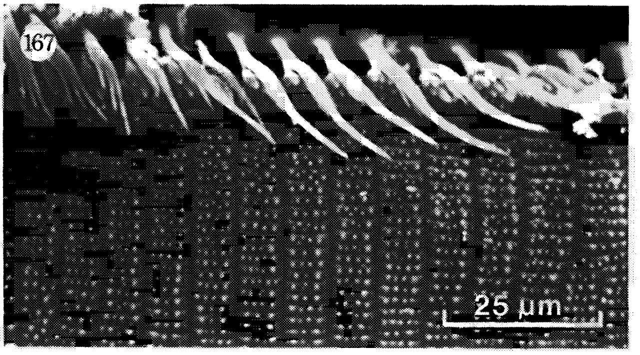
25 µm


167
25 µm

DESCRIPTION OF PLATE 9

Details of the molar surfaces of the mandibles at different stages of development. Code letters refer to those shown in figure 148.

FIGURE 159. Stage 15, left mandible. Region D.

FIGURE 160. Stage 15, left mandible. Region of extreme posterior tooth.

FIGURE 161. Stage 15, left mandible. Pores in the cuticle adjacent to the dorsal teeth.

FIGURE 162. Stage 15, left mandible. Dorsal teeth, viewed obliquely from above.

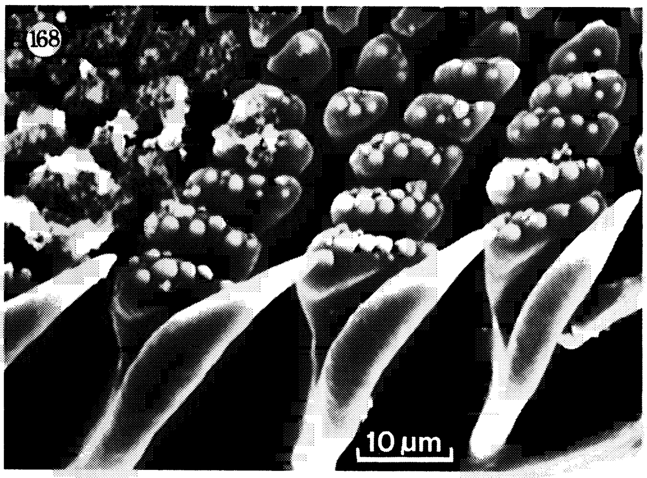
FIGURE 163. An 11.5 mm individual, right mandible. Dorsal groove in region E.

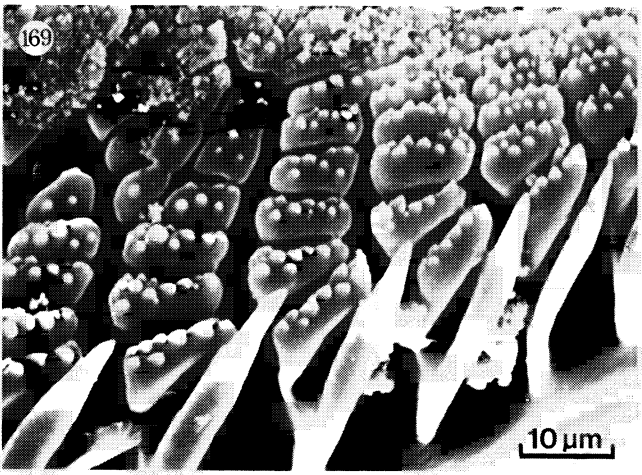
FIGURE 164. The same, right mandible. Region E and anterior to it.

FIGURE 165. The same, right mandible. Region F and posterior to it

FIGURE 166. The same, right mandible. Region A.

FIGURE 167. The same, right mandible. Region B.


(168)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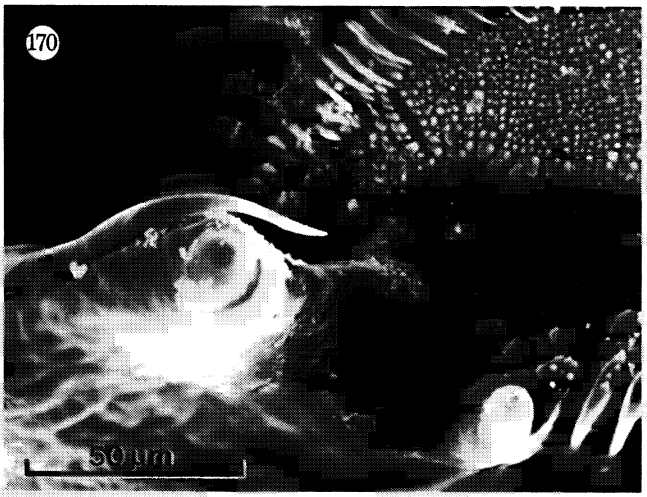
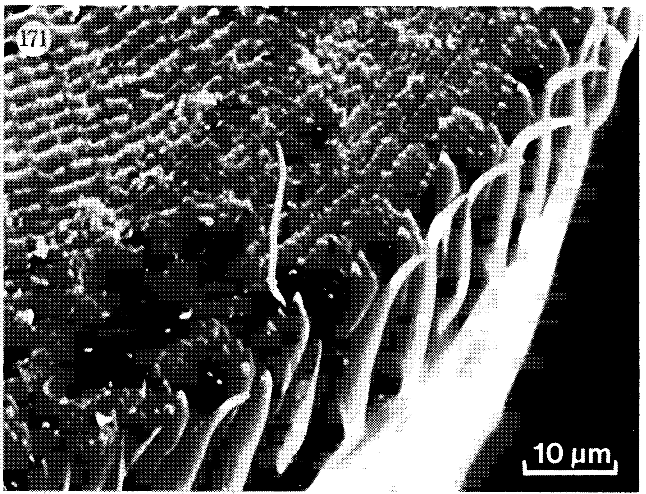

(170)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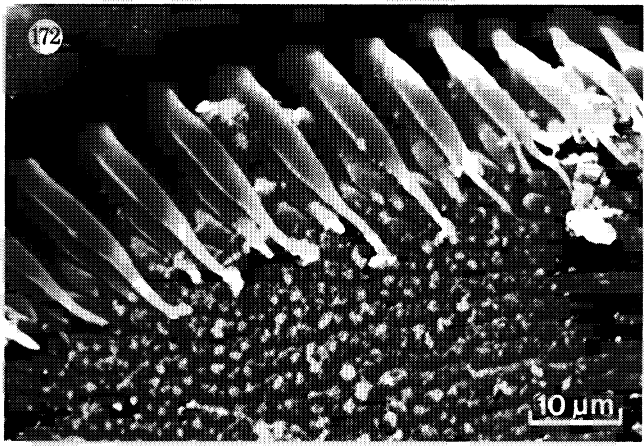
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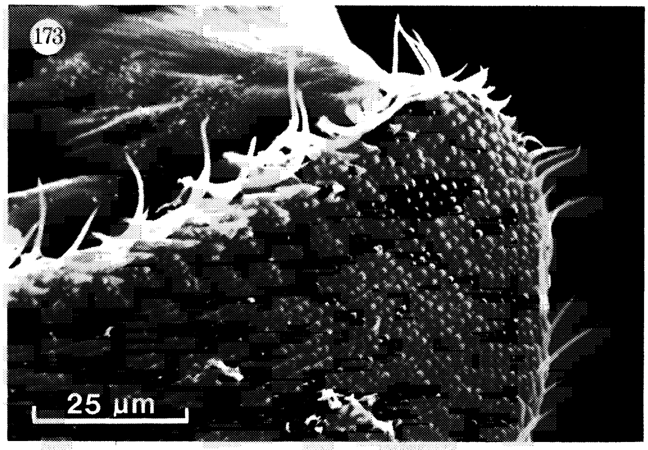
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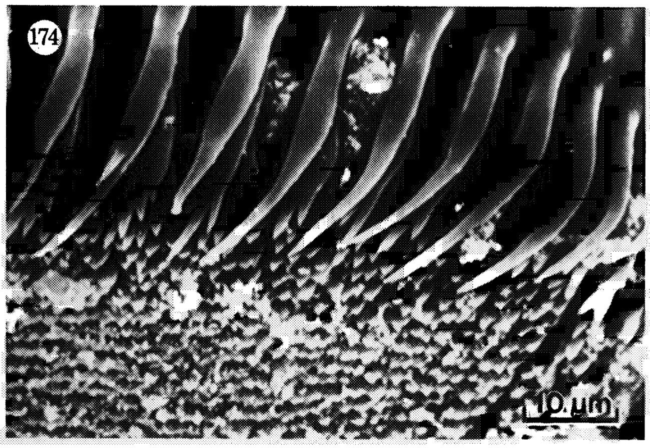
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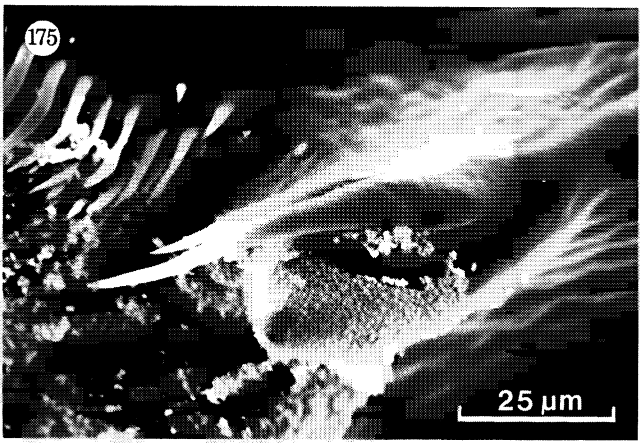

(175)

DESCRIPTION OF PLATE 10

Details of the molar surfaces of the mandibles of an individual 17 mm in length. Code letters refer to those shown in figure 148.

FIGURE 168. Right mandible. Region D.

FIGURE 169. Right mandible. Region E.

FIGURE 170. Right mandible. Posterior tooth.

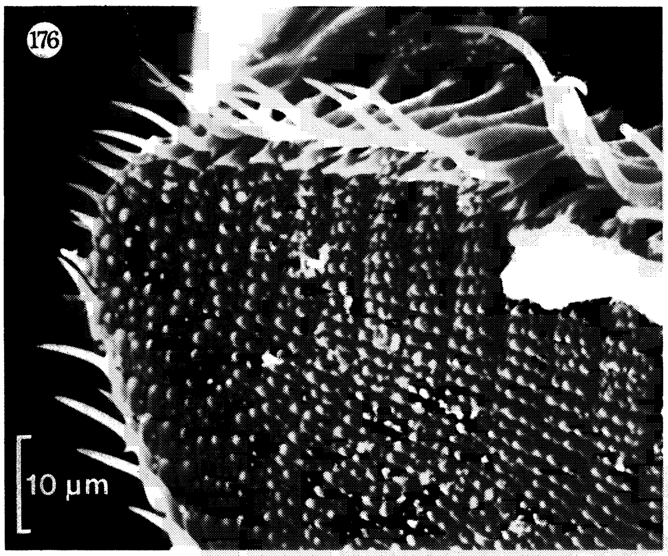
FIGURE 171. Right mandible. Region F.

FIGURE 172. Right mandible. Region A.

FIGURE 173. Right mandible. Region C.

FIGURE 174. Left mandible. Region A.

FIGURE 175. Left mandible. Posterior tooth.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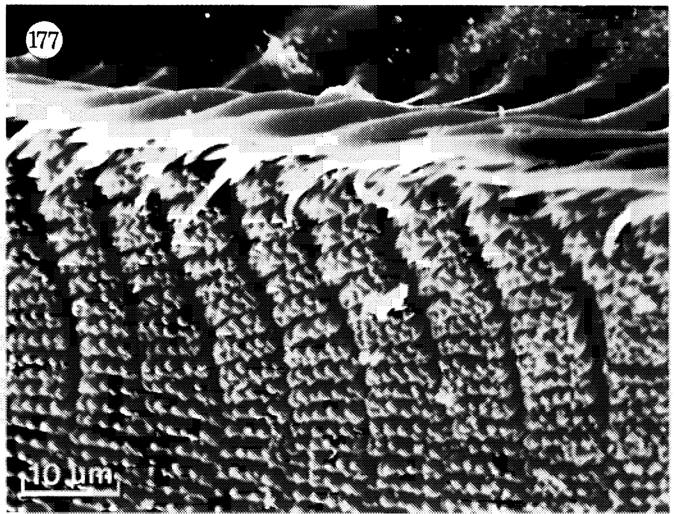
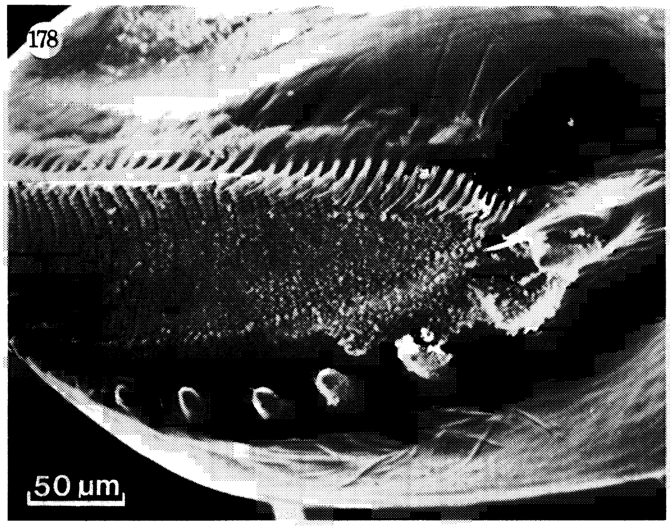
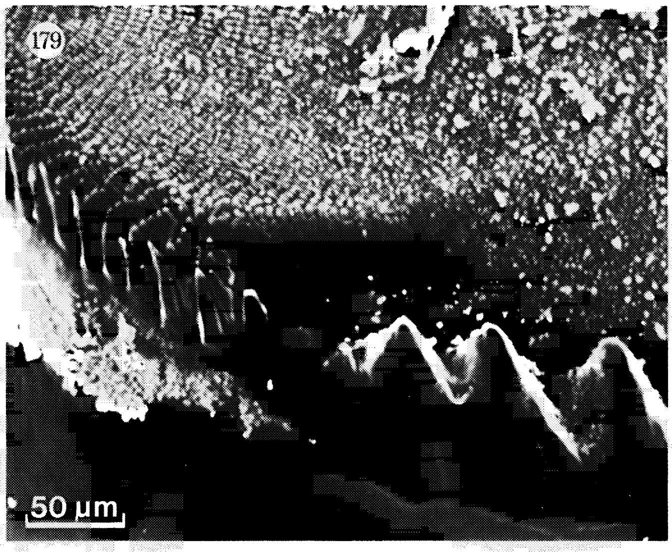
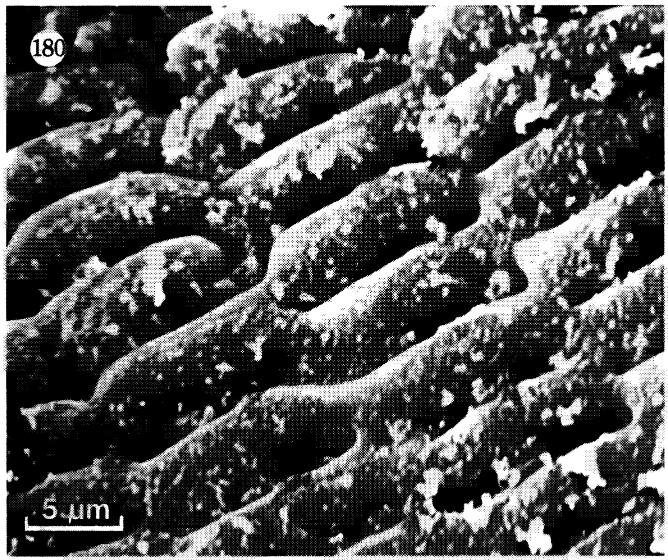
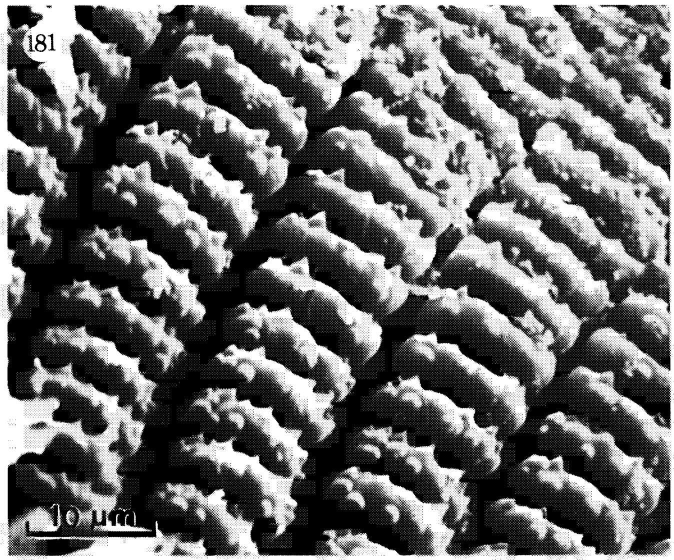
10 µm


177
10 µm


178
50 µm


179
50 µm


180
5 µm


181
10 µm

Description of plate 11

Details of the molar surfaces of the mandibles in individuals of various sizes. Code letters refer to those shown in figure 148.

Figure 176. A 17 mm individual, left mandible. Region C.

Figure 177. The same, left mandible. Somewhat anterior to region B.

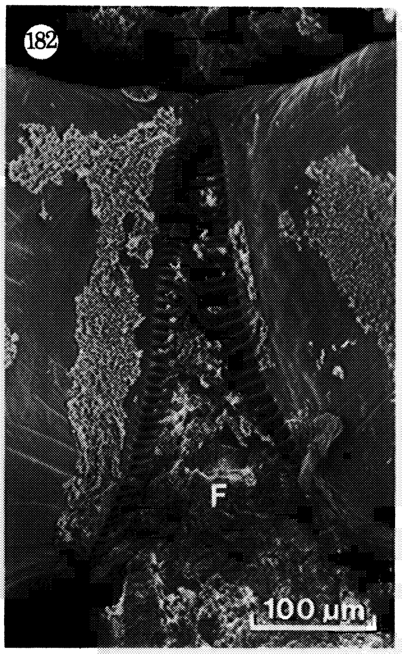
Figure 178. The same, left mandible. Showing much of the molar surface and the row of large dorsal teeth.

Figure 179. A 44 mm individual, left mandible. Region E.

Figure 180. A 43.5 mm individual, right mandible. Ridges of molar surface in anterior region.

Figure 181. A 43.5 mm individual, left mandible. Molar surface in ventral region.

(182)



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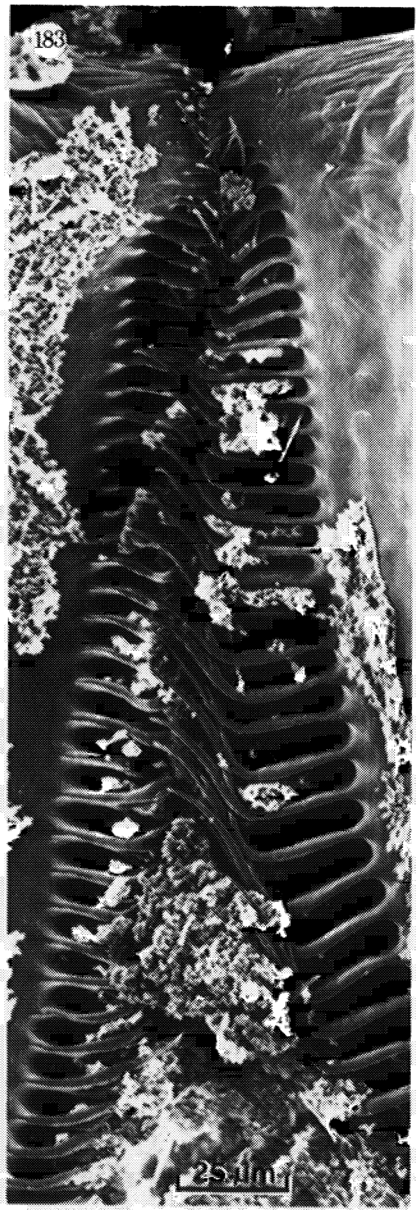
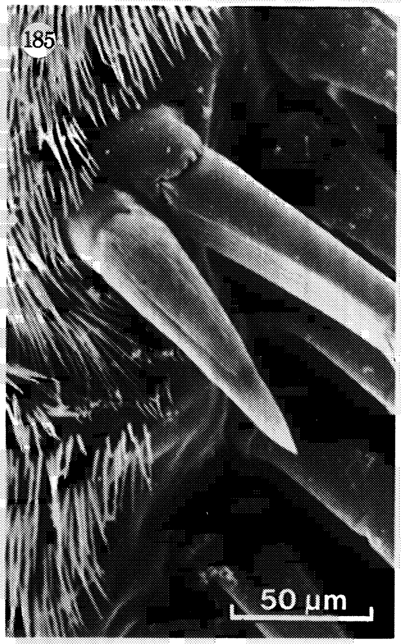
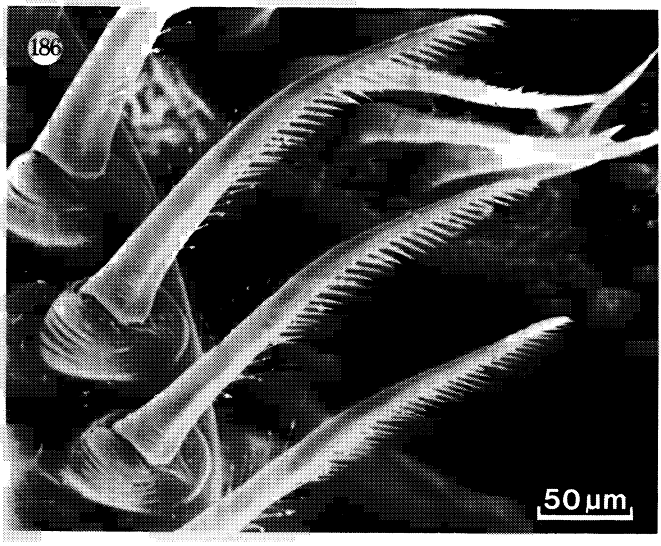


(184)

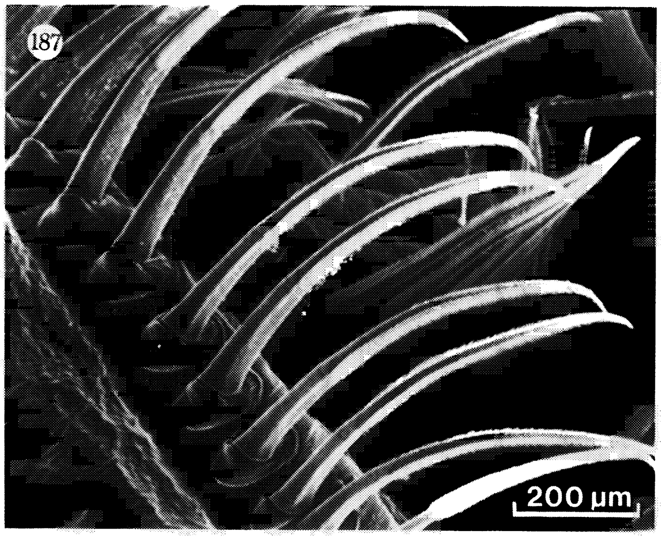
(185)



(186)



(187)



in length. At this stage the right mandible has the now familiar form but there is a general increase in robustness as can be seen for example in the teeth at the posterior end of the dorsal groove (figures 168 and 170, plate 10). The dorsal marginal teeth in the vicinity of E, and also anteriorly where they are directed forward, can be seen in figures 169 and 171, plate 10, respectively. Posteriorly the stout tooth and its accompanying robust spine (figure 170, plate 10) are conspicuous. Adjacent to them, the extreme posterior end of the molar surface, that is posterior to the ridges, bears short, stout, somewhat anteriorly directed spines. The armature of the ventral margin in the vicinity of A and C respectively is shown in figures 172 and 173, plate 10.

The left mandible retains the earlier developed features of its molar surface and dorsal teeth and is now elaborated marginally. Posteriorly the largest dorsal tooth now has a bifid spine as its companion (figure 175, plate 10) instead of the simple spine formerly present, and the entire series, still of seven teeth, is of course more robust. The marginal teeth, while similar to those of the right mandible, differ in detail. Their transition from the posterior to the anterior end in regions A, somewhat anterior to B, and C is shown in figure 174, plate 10, and figures 177 and 176, plate 11, respectively. The last figure also shows the anteriormost spines of the dorsal margin.

As individuals of this size exhibit features common to the filter-feeding stages it is convenient to discuss function here and at the same time give further morphological details. Appreciation of function is aided by reference to figure 182, plate 12, which shows the ventral surfaces of the mandibles of an 18 mm individual as revealed by removal of the labrum. Here a mass of particulate food (F) arriving via the maxillules from the food groove is seen posteriorly. This is passed forward as the mandibles sweep. The wedge-shaped gap disappears, to appear anteriorly as the food is pushed out towards the oesophageal entrance. This action is accompanied by remotor rolling. Arrows on figure 148 indicate the general direction of the remotor roll produced by the remotor roller muscles (muscle 4). This movement is reversed by the promotor rollers (muscle 3). It is easy to see how, when the transverse muscles contract and the mandibles begin to sweep, the large posterior tooth and its accompanying spine (right mandible) or spines (left) will help to drag towards their molar surfaces material that approaches in an antero-ventral direction. It is also easy to see how the simultaneous remotor roll and swing of the mandibles drives the distal portions of the posterior spines of the ventral margin (region A) more or less along the line of their own axes, forcing food downwards and forward so that in the next cycle of movement it will tend to lie between the opposed, ridged, molar surfaces or within the scope of the tooth–groove system. Further forward (region B and

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Description of plate 12

Figure 182. Mandibles of an 18 mm individual viewed ventrally after removal of labrum. The food mass (F) can be seen entering the V-shaped gap between the mandibles from behind. Note that in this view the right mandible lies on the left side of the photograph.

Figure 183. The same, showing details of the ventral marginal spines.

Figure 184. The same, showing details of the ventral marginal spines in the anterior region.

Figure 185. Trunk limb 3 of a 23 mm individual, showing the heavy armature of endite 2 (incorporated into the functional gnathobase) and the pelage of stiff spinules which clothes the median face of the gnathobase. The bases of the gnathobasic spines can also be seen lying more deeply in the photograph.

Figure 186. Exopodite spines of trunk limb 3 of a 23 mm individual.

Figure 187. Exopodite spines of trunk limb 4 of a 44 mm individual.

anterior to it) the marginal spines are concerned with the forward transfer of particles rather than with forcing them between the molar surfaces, and also serve to prevent the escape of material ventrally. Any such escaping material would be an embarrassment though complete loss is prevented by the overlying labrum. Figures 183 and 184, plate 12, show the intricate way in which these spines intermesh. That they effectively confine food particles between the molar surfaces in this region is self evident. It also appears that the right hand series is more important for sweeping than the left. The latter will, however, sweep forward any stray particles that come to lie between the mandibles and the labrum. Anteriorly the spines on both sides clearly assist in sweeping material forward and towards the oesophageal entrance as the gap between the opposed anterior extremities of the mandibles widens.

Although it is impossible to follow the course of any given particle between the mandibles it seems likely, indeed almost inevitable, that, because the fine triturating surfaces occupy only a small proportion of the vertical distance across the molar face posteriorly, much of the food initially enters the groove. Pushing by the ventral marginal spines in region A must also contribute to this. That the postero-dorsal tooth–groove system is a grinding device is readily apparent. As the mandibles make their forward sweep and remotor roll, particles are dragged and swept into the groove, crushed as between upper and nether millstones, and passed forward Some large particles are probably broken here before passing to the finer triturating system anterior to the groove. Material emerging from the groove anteriorly joins that moving forward between the ridged areas of the molar surfaces, such merging being an inevitable consequence of the shape of the molar regions and of the funnel-like gap within which they lie. The marginal teeth of the groove system, which have a retaining role, are continuous with those of region F, which clearly help to push material forward. That the finely toothed molar surfaces can deal with very fine particles is indicated by transverse sections of individuals with no particles between these surfaces, which are then sometimes in contact.

The intricate association of the opposed molar surfaces in the tooth–groove mechanism and of the armature of the ventral margins makes it imperative that the mandibles should roll simultaneously. While there may be scope for very slight discrepancies in this respect there can be no possibility of any significant phase difference that would permit one mandible to sweep across the other.

Changes that take place in the mandibles as size increases and the diet changes from fine particles to copepods and other relatively large items (§14) are both quantitative and qualitative in nature. An increase in size is itself clearly important. Associated with this is an increase in size of the teeth involved in the tooth–groove system (figure 179, plate 11) and a general coarsening of the triturating molar surfaces. Particularly important is the massive development of the posterior teeth (figures 149 and 150). Similar, indeed even more massive, teeth are present in the huge *B. gigas* which devours smaller anostracans (Fryer 1966), but those of large *B. ferox* are still very impressive and constitute one of the few cases where the rolling mandibles of branchiopods have acquired a biting capability, here a combination of biting and crushing. The teeth also serve to pass large food items forward.

In a 44 mm individual (figure 150) the groove of the right mandible occupies a relatively larger proportion of the molar face than in smaller animals and is very deep. Further, the rows of teeth that lie within it and are so conspicuous a feature in early stages, are now indistinguishable save at its extreme anterior end, and the number of marginal teeth, of which the three posterior in particular are now very robust, is reduced to six that can be assigned to the groove proper. These are additional to the posterior tooth, which has lost its companion spine. At least the two posterior members of this row of marginal teeth, therefore, now to some extent resemble those of the left mandible but are less robust.

A groove is now present internal to the row of stout teeth on the left mandible (figure 179, plate 11) though this is less deep than that of the right. As a result there is posteriorly a deep cavity between the molar regions of the mandibles (figure 150). This increases the scope of the posterior teeth and facilitates the engulfing of large objects.

While the original ridged arrangement can still be made out over much of the molar surface, the ridges are confluent in many parts of the right mandible (figure 180, plate 11) and the teeth mostly lack any cusps. A few cusped teeth are present ventrally but in some areas even the ridges are indistinguishable. On the left mandible, however, there are considerable expanses, especially ventrally, where ridges of teeth are still clearly differentiated (figure 181, plate 11). Such teeth are well suited to gripping objects such as copepods and crushing them against the furrowed surface of the right mandible.

The ontogenetic changes in the food-handling regions of the mandibles are analogous to, but more subtle than, those between the milk and adult dentitions of mammals, and display interesting parallels to those in other crushing and grinding structures that have to deal with different foods at different stages of the life history, such as the pharyngeal teeth of certain cichlid fishes. The gradual changes seen in these primitive crustaceans in some ways represent a more impressive evolutionary achievement than does the replacement of milk dentition in mammals. Analogous end points in the grinding devices of unrelated groups of animals are not entirely unexpected, but the striking similarities, even though on an utterly different scale, between the teeth of the groove region in the filter-feeding stages and the pharyngeal bones of certain cyprinid fishes deserve emphasis. While composed of different materials and operated in a completely different manner the dental patterns involved have many features in common.

16. PHYLETIC AND FUNCTIONAL IMPLICATIONS OF THE PATTERN OF DEVELOPMENT

The careful work of Sanders (1963) on the development of the cephalocaridan *Hutchinsoniella macrocantha* Sanders revealed its primitive pattern of development, which he rightly emphasized. This pattern he compared with those of other crustacean groups including the Branchiopoda. For this purpose he had to rely on the descriptions of previous workers, his data on the Branchiopoda being based largely on information provided for the anostracan '*Artemia salina*'[†] by Heath (1924). This, however, is inadequate and inaccurate, suggesting as it does that the full complement of trunk limbs have achieved definitive form by stage 6 and that only four moults are necessary for the accomplishment of this process from a stage at which no trunk limbs are present. Blake (1979), who gives certain measurements, seems uncritically to have accepted Heath's erroneous sequence, and his results do nothing to reveal the true situation. Although not corresponding exactly, the accounts of Weisz (1947), Hentschel (1968) and

[†] What was formerly believed to be a single entity, *Artemia salina*, with a world-wide distribution, is now known to be a complex of species which differ in mode of reproduction and degree of ploidy (many old-world populations being polyploid). (See Barigozzi (1980) for general review.) A frequently used species is the bisexual, diploid, North American form now known as *A. franciscana* Kellogg. Heath's animals were presumably of this species, as would be Anderson's referred to below. It is unlikely that the different species differ in their pattern of development.

Benesch (1969) show that more stages are involved than are described by Heath and that that process is more gradual than he indicated. Sanders also cited Heath's observations on *Linderiella occidentalis* (Dobbs) – called *Branchinecta occidentalis* by Heath and subsequently assigned at different times to both *Chirocephalus* and *Pristicephalus* – as confirming that several limbs and segments may be added at a single moult. While development of this species has not been restudied it is certain that Heath missed some stages and that, while useful, his description cannot be relied upon in all details. Early stages in the development of *Artemia* have also been studied by Anderson (1967) who, both here and in an important book (Anderson 1973), has drawn phyletic conclusions from this work and that on the conchostracan *Limnadia stanleyana* King. On the basis of his interpretation of development he has also made certain suggestions concerning the ontogeny of feeding mechanisms in the Anostraca, which he compared with the situation in the Cephalocarida. While Anderson's morphological and cytological work was carried out meticulously, some of his statements relating to development (repeated also in Anderson 1979) are fundamentally at odds with observations made on *B. ferox*, and are not in agreement with some of those reported for *Artemia* by Weisz (1947), Gauld (1959), Hentschel (1968) and Benesch (1969), nor with my own brief observations on this animal. The situation in *B. ferox* indeed leads to entirely different phyletic conclusions.

According to Anderson (1967) the first six pairs of trunk limbs of *Artemia* become functional simultaneously. This is shown in a chart (figure 17, p. 79) and is emphasized several times in the text. Furthermore they are reported to achieve this condition 'coincident with metamorphosis at the ninth moult' (p. 80). At the ninth moult the feeding function of the antennae is also reputedly lost (see, for example, p. 85) and the swimming function of these appendages 'is also lost simultaneously...in association with the development of six pairs of natatory phyllopods' (p. 85). Concerning the mandibles it is also stated that after this moult 'in Anostraca...only the gnathobases persist into the adult' (p. 85). The existence of a definite stage at which metamorphosis takes place, with the replacement of the naupliar feeding and swimming apparatus by a device of the adult type as a result of six pairs of trunk limbs becoming functional simultaneously, is reiterated and emphasized in the book (Anderson 1973) and in a later paper (Anderson 1979). For example, the naupliar feeding mechanism is stated to sustain the larva 'until metamorphosis when the naupliar ingestive apparatus is eliminated and feeding by means of the trunk limbs suddenly commences' (Anderson 1973, p. 300).

Anderson lays great stress on the difference between what he believes to be the process found in *Artemia* and that found in the Cephalocarida. Thus in 1967 he suggests (p. 88) that in the Branchiopoda 'instead of attaining the functional condition progressively through a long series of moults as in Cephalocarida, the first six segments develop almost simultaneously after hatching. As a result, they all attain the functional condition at the same stage, after only nine moults in Anostraca...and it is at this stage that metamorphosis occurs and the naupliar feeding apparatus is lost'. Likewise in his book (1973) he emphasizes that 'the sharp transition from naupliar feeding to adult feeding at metamorphosis in the Branchiopoda is in marked contrast to events in the Cephalocarida' (p. 300). He regards the alleged change in feeding mechanism in the Branchiopoda as an adaptation of the more primitive cephalocaridan condition and stresses that this includes 'a synchronous precocious development of the first six trunk segments and a sudden transition from one to the other at metamorphosis, after fewer naupliar stages than in the Cephalocarida' (p. 301).

The development of *B. ferox* does not conform to that described by Anderson for *Artemia*.

As shown in figure 27 the first six pairs of trunk limbs do not become functional simultaneously: they do so over a sequence of five instars, of which the first is stage 12. The naupliar feeding mechanism is not suddenly replaced by apparatus of the adult type: the naupliar mandibular palps contribute until eight or nine trunk limbs are functional and the antennae continue to do so until the full complement of trunk limbs has achieved this status. The antennae do not cease to be used for locomotion at a stage with six pairs of functional trunk limbs: they assist in the process up to and including the time when all trunk limbs are functional and often beat regularly, though probably ineffectually, in the succeeding stage.

That the facts shown in figure 27 are substantially correct can be checked by reference to figures 33 and 35. Figure 33 shows the anterior trunk limbs in a stage 8 larva. None of these is yet capable of movement. There is here no sign of the simultaneous development of an anterior block of six trunk limbs. On the contrary, progressive development from front to back is clearly shown. Figure 35 shows a longitudinal slice through a stage 12 larva in which, while the first two pairs of trunk limbs are functional, but are differentiated to different degrees, the sixth pair consists of no more than a rudimentary papilla devoid of muscles and incapable of any movement. As this figure shows, such progressive differentiation of the limbs goes hand in hand with the gradual development of the trunk musculature along an anterior–posterior gradient.

Furthermore, the situation described for *B. ferox* appears to be general in the Anostraca, though the number of stages involved evidently differs in different species. Indeed, as long ago as 1791, Shaw, who was the first to describe the development of any anostracan, recorded of *Chirocephalus* that 'On the seventh day after hatching, they approach pretty nearly to the form of the complete animal, except that they still retain the two long pairs of rowers or arms: the legs however, or fins, are at this period very visible', and his illustration, simple as it is, shows an individual at the seven-limbed stage with well developed antennae. Prévost's account (originally published in 1803, but see Jurine (1820)) of the development of *Chirocephalus diaphanus* was accompanied by a clearer illustration (plate 21, figure 2) of an individual 'à l'état qui précéde celui d'adulte' which shows a complete series of trunk limbs, diminishing in size posteriorly, *and* natatory antennae still armed with food-collecting spines. Mandibular palps are also shown. Other early illustrations are those of Baird (1850, pl. 5, figs 6 and 7), which show two early post-naupliar stages of *C. diaphanus* that clearly illustrate the progressive nature of the development of the trunk limbs, and Claus (1873, pl. 2, fig. 7), which shows this even more clearly for *Branchipus stagnalis* (= *B. shaefferi* Fischer). Even more convincing, in his figures of what he correctly described as the last larval stage of *Branchinecta paludosa* (Müller), Sars (1896) beautifully portrays an animal with the full complement of functional trunk limbs, which also possesses antennae that are clearly used to assist in locomotion. More recently Nourisson (1964), after stating that the full complement of trunk limbs of *C. diaphanus* is differentiated at stage 10 (much earlier than in *B. ferox*), notes that in the *next* stage the larval antennae progressively cease their role in locomotion – which they have clearly retained throughout the development of the full complement of trunk limbs. Similar patterns are shown by *Chirocephalus bairdi* (Brauer), which I have reared but not studied in detail, and by *Siphonophanes grubei* (Dybowski), whose development is described and illustrated (apparently with some stages missed) by Oehmichen (1929) and Valousek (1950).

It may be that Anderson was misled by his findings concerning the conchostracan *Limnadia stanleyana*. Here, as in *L. lenticularis* L. (Sars 1896), there is what could be described as a metamorphosis at which the larval feeding apparatus is replaced by the adult mechanism, consisting at that stage of six pairs of trunk limbs. With this, and the situation in the Cephalocarida (in which the enditic process of the antennae is lost before the full complement of trunk limbs is functional) in mind, and the concentration of his observations most carefully on the early stages of development of *Artemia*, Anderson may have misinterpreted the situation in the latter, for it appears that the pattern in this animal is also of the kind observed in *B. ferox*. Although Weisz (1947) did not pay particular attention to this point, his diagrammatic figure of what he refers to as a stage 16 larva shows eight pairs of functional trunk limbs, and antennae that appear still to subserve locomotion, and he notes (p. 73) that the antennae gradually begin to change at stage 17. He had earlier noted that the end of stage 19 marks the time when what he calls the 'gnathobase' and setae have been lost by the antennae (Weisz 1946). Similarly, Gauld (1959) specifically states that, as late as the stage in which eight pairs of trunk limbs are functional swimming organs, 'the essential structure of the mouthparts', which in this context includes the antennae, 'is unchanged'. This is borne out by the photograph in Barlow & Sleigh (1980) which shows an individual with an apparently full complement of trunk limbs and well developed antennae, and by their reference to antennal beat as preceding that of trunk limb 11. Likewise Hentschel (1968) says that at stage 6 'Die ersten zwei bis drei Extremitätenpaare bewegen sich aktiv' – a situation quite other than a simultaneous development of the first six pairs. Benesch (1969) gives more details and shows that the first pair of trunk limbs becomes fully developed at what he designates as stage 8 (actually the ninth stage as he calls the newly hatched nauplius stage 0) and that limbs are added at the rate of one pair at each stage. Indeed, commenting on the comparison of the Cephalocarida and Anostraca, he specifically states that 'Ich selbst fund nie Stadien mit derart simultan entwickelten Extremitäten'. In his table (tbl. 5a, pp. 362–363) he clearly enumerates such a sequence but (possibly as an error) indicates two pairs of trunk limbs achieving full development between stages 14 and 15 (15 and 16).

Benesch also shows that the antennae are still present when nine pairs of trunk limbs have achieved full development, being at that stage armed with 'lange bis kurze Borsten', which are degenerating at the next stage which has ten pairs of trunk limbs fully developed and the eleventh pair almost so. He notes also that the mandibular palp is still present, though short, at the nine-limbed stage and persists as a knob-like rudiment at the ten-limbed stage. The pattern that he describes is in full accord with that observed in *B. ferox*. My own observations on *Artemia* (presumably *A. franciscana*) hatched from commercially supplied eggs also showed a progressive development of the trunk limbs and retention of the larval functions of the antennae beyond the stage with six pairs of trunk limbs.

The early stages of *Lepidocaris*, a representative of the extinct branchiopod order Lipostraca, so clearly illustrated by Scourfield (1940), show that there too the trunk limbs developed sequentially, the anterior pairs being ahead of the posterior exactly as in the Anostraca. Development of the first six trunk limbs as a block certainly did not occur. Trunk limb 1 shows considerable differentiation at the time that the trunk limb 6 was no more than a narrow transverse lobe. Furthermore, the antenna of the larval *Lepidocaris* had a bifid proximal masticatory spine just as does that of *B. ferox* from stage 3 onwards, and this persisted until the trunk limbs were well developed. The best preserved of all known specimens, an individual rather more than half the maximum adult length, in which the full complement of body somites is recognizable, simultaneously reveals the persistence of the masticatory spine and well differentiated trunk appendages (Scourfield 1926, fig. 4). Just how well developed were the posterior trunk limbs is not certain, but a comparison of this stage with that shown in fig. 2 of Scourfield (1940) makes it clear that differentiation must have extended well back and that the anterior trunk limbs and the antennae for a time operated simultaneously as food collectors.

Relevant also is that *Lepidocaris* retained natatory antennae throughout life. Adult locomotion clearly involved contributions both from these appendages and from the trunk limbs, just as is the case in the Anostraca during the period that the trunk limbs are gradually developing.

Thus there is no fundamental difference in the pattern of development of the Cephalocarida and the Anostraca (or the Lipostraca), though the first two have slightly different starting points. In the stage 1 nauplius of *Hutchinsoniella* the maxillule is distinctly, but incompletely, differentiated and a rudiment of the maxilla is present (Sanders 1963). *Lightiella incisa* Gooding (Cephalocarida) is even more advanced at hatching for, although the youngest known stage is not necessarily that at which hatching occurs, even late embryos have one trunk segment more than the stage 1 nauplius of *Hutchinsoniella* (Sanders & Hessler 1964). In all three groups the process is essentially one of anamorphosis. In the Cephalocarida, after a trunk limb has become functional there is often an interval of one, or even two, instars before the limb immediately behind it achieves this condition, whereas no such lag has been detected in *B. ferox* and the limbs become functional in a regular sequence, for the most part an additional pair becoming functional after each moult. These, however, are merely modifications of a common theme, not profound differences.

It might indeed be argued that changes are more gradual in the Anostraca, certainly in *B. ferox* and *Artemia*, than in the Cephalocarida. Although development is gradual in *Hutchinsoniella*, some structures 'show abrupt and profound changes in a single moult' (Sanders 1963), and the same is true of *Lightiella* (Sanders & Hessler 1964). Thus in *Hutchinsoniella*, at the moult following stage 13 the naupliar enditic process of the antenna disappears, as does the palp of the mandible, and there are changes in the maxillule, this moult in fact being recognizable as the dividing line between naupliar and juvenile stages of development. In *B. ferox* there are no such abrupt changes. Here the proximal masticatory spine (the equivalent of the enditic process in *Hutchinsoniella*) is gradually reduced and is present as a non-functional remnant in two instars beyond that at which it last has a role, and the distal masticatory spine persists throughout an additional instar. Subsequent changes in the antennae are of course greater in the Anostraca than in the Cephalocarida in relation to different functions, but these do not nullify this comparison. Likewise in *B. ferox* the role of the mandibular palp is gradually reduced and the palp itself persists as a minute vestige for several instars beyond that at which it last functions.

Another difference between the nauplii of these groups that may have a bearing on this is that both trunk segments and limbs are demarcated earlier in development in the Cephalocarida than in the Anostraca. This facilitates an early improvement in the efficiency of food collection and perhaps represents an advanced feature in the Cephalocarida, though too much weight should not be placed on this. Such comparisons are particularly hazardous as the cephalocarid nauplius is, as Sanders (1963) so clearly showed, of the non-branchiopod type and therefore differs from that of the Anostraca in several ways, whose significance is not easy to assess in the phyletic sense.

It is not only in appendages that gradual changes take place in *B. ferox*. The development of the furca (figures 38–41) provides an additional example. In the Cephalocarida the furca is precociously developed and changes relatively little during development.

The phyletic implication of this situation is that it can no longer be claimed that the Cephalocarida shows a more primitive pattern of development than the Anostraca. In this respect there is nothing to support the idea that one group is more primitive than the other, unless one were to argue that the situation displayed by *B. ferox* is slightly more primitive than that found in the Cephalocarida, an argument with which the presence of the greater number of trunk limbs in the former could, though tenuously, be made to agree. Constituent members of both groups show modifications of the basic pattern among themselves. If one can rely on existing descriptions these are the greater in the Anostraca for the simple reason that more species are involved. Within this order it may be that *B. ferox* displays the primitive pattern particularly clearly but the indications are that such modifications as are found in other species are essentially superficial.

In the belief that in the Anostraca six pairs of trunk limbs suddenly become functional and replace the naupliar feeding apparatus, Anderson (1967) put forward certain suggestions concerning the maxillules. These he regarded as being vestigial in the Branchiopoda. Likewise, and quite wrongly, Weisz (1947) described their motion in *Artemia* as 'extremely limited' and stated that 'the appendage as a whole is rightly considered vestigial'. While small, the maxillules are certainly not vestigial in the Anostraca, as this account (see figures 79–82) makes clear, and they play a vital role in the feeding mechanism. Anderson suggested that what he designated as their 'secondary vestigiality' is 'associated with larval enlargement of the sublabral space and specialization of the antennal and mandibular brushes sweeping through this space, to the functional exclusion of the maxillules'. This suggestion is interesting but not supported by facts. The naupliar appendages are certainly responsible for the initial collection of food but, as this account has shown, do not prevent the maxillules from operating in collaboration with them as soon as they have developed to a sufficient degree. In *B. ferox* they possibly contribute at stage 12 and definitely do so from stage 13 onwards, thus working in conjunction with the antennae and mandibles throughout several stages (figure 27). Anderson also suggested that 'their continued vestigiality after metamorphosis can be explained on the basis of substitution of a mid-ventral, forwardly directed food current in branchiopods for the primitive setal forward food transfer of the Cephalocarida'. As described here, and elsewhere for other branchiopods Anostraca (Fryer 1966), anomopod cladocerans (Fryer 1963, 1968, 1974)), and as Storch maintained long ago, there is in fact no such current; so this hypothesis falls down.

Anderson also suggested that the arrangement of the branchiopod naupliar feeding apparatus, with its 'vestigial' maxillules and maxillae, means that the first pair of trunk limbs remains widely separated from the mandibular gnathobases 'as long as the naupliar feeding apparatus persists'. 'Food transfer from the trunk limbs to the mouth, therefore, is not possible until this apparatus is lost at metamorphosis, so that progressive augmentation of naupliar feeding by trunk limb feeding as in Cephalocarida cannot occur in branchiopods.' (p. 87). This is not so. As shown for *B. ferox*, as soon as the first two pairs of limbs are able to operate they begin to contribute to food collection and, gradually augmented by additional pairs of more posterior limbs, do so through several stages during which the naupliar apparatus is still active. The maxillules help to bridge the gap between the first pair of trunk limbs and the mandibles from a very early stage. While they probably make no significant contribution when two pairs of trunk limbs are active, they certainly do so from the three-limbed stage and continue to do so throughout life – whether the naupliar feeding appendages are involved or not. The same appears to be true of *Artemia* and doubtless of all anostracans.

17. THE PATTERN OF ANOSTRACAN ONTOGENY: SOME DEVELOPMENTAL, ECOLOGICAL AND EVOLUTIONARY CONSIDERATIONS

Because its superficial aspects can be described in relatively simple terms, the anamorphic pattern of development of the Anostraca has about it a deceptive air of simplicity. In reality, notwithstanding speculations that do little to promote real understanding, how this pattern is established and controlled remains essentially unknown. It is indeed ironical that, while there have been striking advances in our knowledge of the molecular events involved in cell differentiation, we know relatively little about what controls and determines the behaviour of developing tissues, or somite formation, and almost nothing is known about these processes in the Anostraca. For example the regular addition of somites and the budding off of limbs during the early instars, when changes in form from one instar to the next are most marked and most rapid, lend themselves to superficial description and can be portrayed in simple, but informative, diagrammatic form, as in figure 27, but we have scarcely any understanding even of what determines, say, the change in pattern between the establishment of the last thoracic and first abdominal somites or their subsequent, quite different, individual developmental histories. Weisz (1946) has suggested that the presence or absence of appendages is determined in part by the size of the segments when these are first laid down, and by the time available for appendage rudiments to form 'appendageal tissues', and (Weisz 1947) that the ratio of ectoderm to endoderm per unit area determines whether or not an appendage bud develops. While it is possible to make correlations of this sort it is difficult to see how they help understanding as the manner of determining these 'determinants' remains unexplained, and there appears to be an element of circularity in the arguments.

Repeating patterns, such as the regular formation of segments along an anterior–posterior gradient, of which the Anostraca present one of the best examples among the Crustacea, have prompted the putting forward of models of various kinds, though not with the Anostraca in mind. Favourites include those of the reaction-diffusion type in which chemical morphogens, reacting together and diffusing through tissues, have been claimed as able to explain not only repeating patterns but even the main phenomena of morphogenesis (Turing 1952). More recently, so-called escapement models have come into vogue. These draw analogies between this pattern of development and escapement mechanisms, such as those of clocks, which release measured amounts of potential energy at precisely measured intervals of time (see, for example, Cooke 1981). Such models, while interesting, are largely hypothetical and do little to help those wrestling with the realities of morphogenesis in an animal such as *B. ferox*.

An explanation of the 'simple' anamorphic pattern of development in the Anostraca in genetic terms is still utterly beyond us. It comes into the category of 'the formation of complex structures such as patterns' for which 'no explanation in terms of genes and their products is immediately in sight' (Gurdon 1977). Some clues may be obtained, however, via dietary studies such as those of Hernandorena (summarized 1980). In *Artemia* changes in the levels of purine and pyrimidine supplies available during development have been found to change the timing of events and the expression of genetic information. Reduction in the adenylic/cytidylic acid ratio induces the development of supernumerary, but incomplete, ovisacs on the two abdominal segments behind that which carries the normal ovisac in the female. As Hernandorena notes, the genetic message coding for the development of these structures is not translated during normal development, but it is under this particular dietary régime. Likewise genetic messages coding for the development of the posterior trunk limb, which are of course translated during normal development, are not so translated in animals deprived of folic acid and thymidine. Development of the posterior appendages of such individuals is reduced or aborted. Such a negative effect is interesting but appears less spectacular, and may prove less informative, than the induction of supernumerary structures, which involves positive morphogenetic activity.

Concrete advances in our knowledge of other organisms, such as that on mutations which affect segment number and polarity in *Drosophila* larvae (Nüsslein-Volhardt & Wieschaus 1980), and recent work on compartments and polyclones in the same insect, may also give clues. However, in spite of their lowly phylogenetic status, the Anostraca are in many ways mechanically much more complex than *Drosophila* larvae, which makes it unlikely that analogous studies of the former type can be made in this group. Such mutations, even if not physiologically lethal, would probably render the swimming/feeding mechanism inoperative. Work on compartments and polyclones in the Anostraca would be technically difficult, and we also lack the cytogenetic background information available for *Drosophila*. The only anostracan for which much such information is available is *Artemia* – where the situation is complicated by polyploidy and a confused state of taxonomy.

Some understanding may also come from selective destruction experiments by the use of a laser microbeam system such as has been used with good effect on the nematode *Caenorhabditis elegans* (Sulston & White 1980; Kimble 1981). Here single cells can be destroyed without apparently damaging adjacent cells. In any work on the Anostraca the target would probably have to be less precise, and the use of this technique, for example for the selective destruction of particular limb buds, may prove of greater value in the study of functional morphology, as in analysis of swimming and feeding mechanisms, than of morphogenesis.

As it is our ignorance is profound. To give one concrete example we have no idea what determines that, in most anostracans, there are only trivial differences between thoracic segments 9 and 10 and their appendages, (and their anterior homologues), much greater differences between the appendages of segments 10 and 11, and profound differences between segment 11 and the first abdominal segment (with its egg sac in the female), and the naked abdominal segment 2 with which it is fused, and the succeeding naked segments. Comparative studies using *Polyartemia* (with 19 pairs of thoracic limbs) as well as 11-legged species may help here.

In one sense the sequence of stages between the nauplius and stage 21 in *B. ferox* can be regarded as a series of motile embryos. What in many organisms are essentially embryological processes – the addition of trunk somites and the development of limbs which, initially, are not even present as rudiments – take place during this phase of development. Each stage must not only survive but meet the energetic demands of growth and differentiation, not by drawing on provided energy as does an embryo, but by its own efforts. Clear evidence of success in this respect is to be seen in the wide geographical range of the Anostraca – all continents including Antarctica and embracing a diversity of climates from arctic to tropical – and in their survival through a long period of time. High fecundity has doubtless helped, but would in itself be no compensation for mechanical inefficiency. In the latter connection it is noteworthy that in neither the nauplius nor the adult are most of the limbs specialized for one particular function but have to subserve at least two. The naupliar antennae are the sole organs both of locomotion and of food collection and the trunk limbs of the adult subserve both these functions and also probably those of respiration and ionic regulation. This is in striking contrast to many other crustaceans, even including many branchiopods, in which specialization of a limb for a single function, or for a single function with a supplementary role, such as respiration or brood care, is frequent.

The entire life cycle of *B. ferox* is enacted in a single, sometimes small, water body. This is typical of the Anostraca but is a particularly striking case as there are more changes in diet and feeding mechanisms than is usually the case. Although physical and biological features of the environment change throughout the season that the ponds contain water, which presumably involves changes in selection pressures, it is scarcely feasible for early and late stages of the life cycle to be selected for general responses to particular conditions as different stages to some extent co-exist. Furthermore, conditions vary from pond to pond, and seasonal changes are not necessarily the same from year to year even in one pond. Studies on genetic variability, using electrophoretic techniques, would be informative here. Although habits and feeding mechanisms change during the course of the life cycle, all stages exist in an essentially similar physical environment and all swim in relatively open situations. Thus selection, which must act in very different ways on small nauplii and large adults, with their different morphologies and functional needs, presumably does so in similar ways so far as basic physiology is concerned. One might therefore expect that the often very different morphological specializations of the different stages would be accompanied by wide eco-physiological tolerance. Such a pattern is different from that displayed by many of those animals whose juvenile and adult stages differ much in morphology, each being specialized for a particular way of life and occupying niches that not only are very different but that are found in quite different environments, e.g. many larval and adult crustaceans and insects. The apparently inevitable broad eco-physiological tolerance, like the specializations for life in temporary water bodies (whose advantages include the fact that they are usually predator-free and competitor-poor) may have been an essential ingredient in the long survival of the Anostraca. Such tolerance was also probably a necessary preliminary stage in the processes of physiological adaptation that allowed the ancestors of *Artemia* to colonize saline water. These include the development of such features as a relatively impermeable cuticle, except for the epipodites (or neck organ of the nauplius) which excrete sodium chloride, and active uptake of water by the gut which enable the haemolymph concentration to be stabilized at a level tolerable to cells and tissues. Although a freshwater group *par excellence* the Anostraca must be able to withstand the high salinities sometimes encountered in drying ponds. *Artemia* now habitually frequents hyper-saline environments.

B. ferox illustrates that the potentialities for an animal that develops by anamorphosis and, as an adult, retains a substantial degree of serial homology (two primitive attributes) are greater than often supposed. Its achievements invite caution in assessing the ways of life of extinct groups, such as the trilobites, which displayed little tendency towards serial specialization during the enormous period of time through which they existed, but which may have had more diverse feeding habits than is sometimes assumed.

From an initial mechanism that enables naupliar anostracans both to swim and to collect food, anamorphosis permits a gradual transition to an entirely different mechanism that again subserves both these vital functions. Gradual transition has probably been facilitated in *B. ferox*, and in the Anostraca in general, by use of essentially the same kind of food – particulate organic matter – throughout. This second mechanism, which involves striking serial homology, then displays a further potentiality by undergoing what are relatively small mechanical changes but which lead to a dramatic change in the kind of food taken and the way in which it is handled, and which completely change the animal's ecological role. Predation is an unexpected capability in multi-legged animals that employ a metachronal limb beat and lack prehensile appendages, and whose close relatives and immediate ancestors are essentially filter-feeders, but at least two anostracans, of which *B. ferox* is one, have made this remarkable transition. Students of extinct, and indeed extant, groups whose hallmark appears to be uniformity should always bear in mind the possibility of such cryptic radiation.

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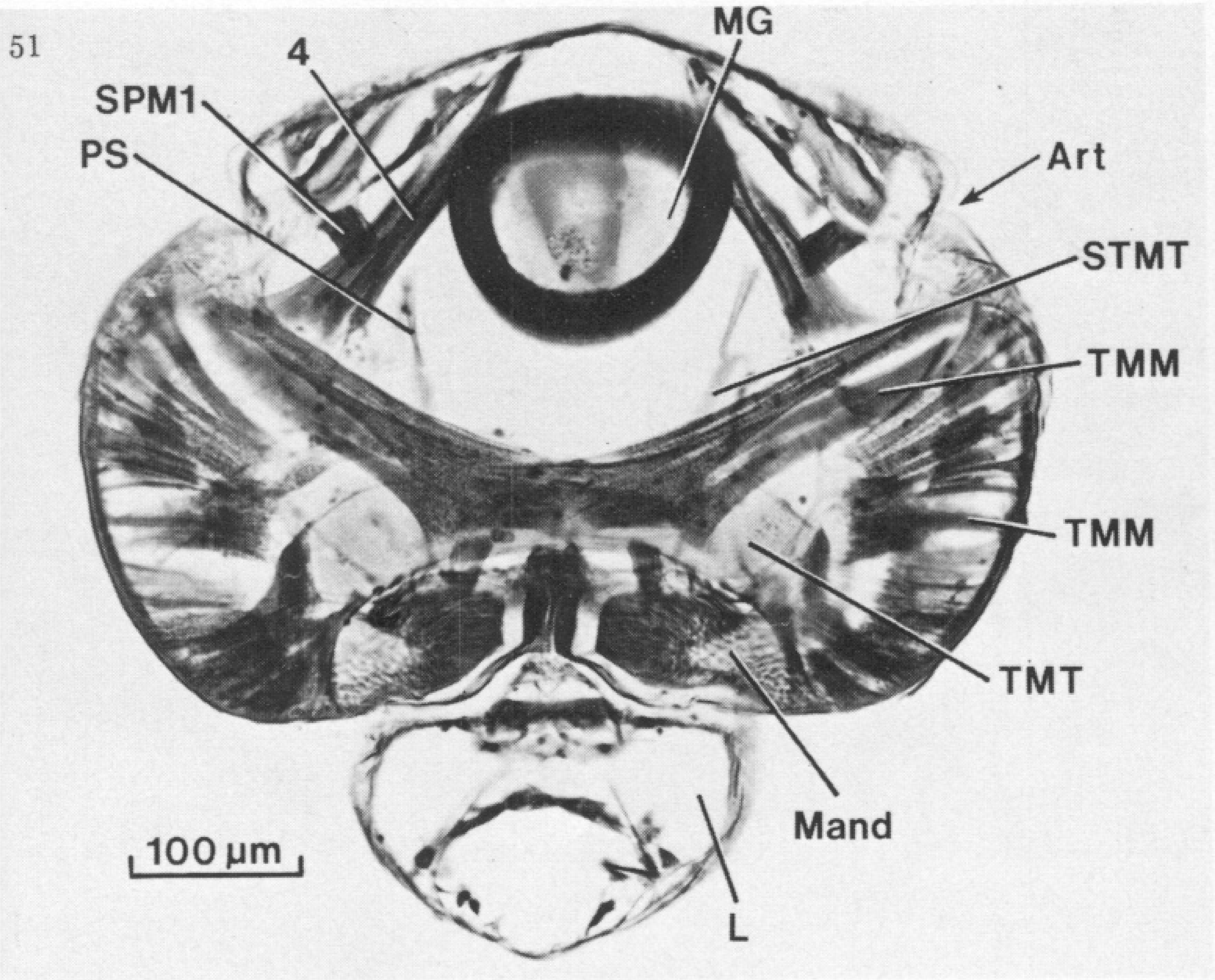
LIST OF ABBREVIATIONS USED IN FIGURES

A	anchorage of maxillary/trunk segment 1 intersegmental tendinous sheet
A1	antennule
A2	antenna
ACW	wall of alimentary canal
ADS	adductor muscle of proximal masticatory spine of antenna
ADVM	anteriorly descending oblique dorso-ventral muscle
AF	anchoring fibrils of endoskeletal sheets and ligaments
AG	antennary gland
AGSp6, 7	anteriormost gnathobasic spines of trunk limb 6, 7
ALFG	anterior limit of food groove
A1 M	antennular muscle
AP	accessory promotor roller muscle of mandible
Art	region of dorsal articulation of mandible
AS	anterior suspensory ligament
B	bract
B Fib	bracing fibrils
BL	binding ligament
C	cuticle
Ca	caecum
CE	cut edge
CE Endo	cut edge of endoskeletal sheet ('upper' edge when viewed ventrally)
CG	cerebral ganglion
CLB	cuticle near base of limb
CS	cytoplasmic sheath
D 1, 2, 3,...	dorsal series of naupliar appendage muscles
DAEM	dorsally originating anterior extrinsic trunk limb muscles
DCLG	duct cell of labral gland
DCN	duct cell nucleus
DIN	dorsal intersegmental node of endoskeleton
DITS	dorsal intersegmental tendinous sheet of endoskeleton
DLG	duct of labral gland
DLM	dorsal longitudinal muscle
DMS	distal masticatory spine of antenna
D MxG	duct of maxillary gland
DPEM	dorsally originating posterior extrinsic trunk limb muscles
E	eye
Ect	ectoderm
ECTL1	edge of corm of trunk limb 1
ELG	exit of labral gland reservoir
EMP1, 2	extrinsic extensor muscles of mandibular palp
EN	endopod
End	endite(s)
Endo	endoskeleton
Endo/BM	endoskeleton here merging with basement membrane
Endo S	endoskeletal sheet
ES	end sac of maxillary gland
ESA	end sac of antennary gland
ETLM	extrinsic trunk limb muscles
EX	exopod
EXE	extensor of antennal exopod
EXF	flexor of antennal exopod
F	food mass
FFG	fibrils anchoring endoskeleton to lateral wall of food groove
FG	food groove
FGR	food groove roof
FGW	food groove wall

Fib	tendinous fibrils
FLITS	fibrils of lateral intersegmental tendinous sheet
FLLM	fibrils anchoring labral levator muscle
FMP	extrinsic flexor muscle of mandibular palp
FPM	fibrous precursor of transverse mandibular muscle
FS	fibrils of suspensor of post-oesophageal bar
FSH	fibrous sheet suspending labral glands
FSMG	fibrous suspensor of mid-gut
G 1, 2,...	gnathobase 1, 2,... of trunk limbs
Ga	ganglion
GC	gland cell
Go	gonad (rudiment)
GS 1, 2, ...	gnathobasic setae of trunk limb 1, 2, ...
GS Mand	gnathobasic spine of mandible
GSp 1, 2, ...	gnathobasic spines of trunk limb 1, 2, ...
HM	horizontal muscle
HS	'headshield'
Ht	heart
IS	intersegmental strap
IT	intersegmental endoskeletal tendon
L	labrum
LA	lateral anchorage of endoskeletal sheet
LG	labral gland
LITS	lateral intersegmental tendinous sheet
LLM	labral levator muscle
LT	lateral tendon of endoskeletal sheet
Mand	mandible
Mand C	mandibular cuticle
Mand G	mandibular gnathobase
Mand M	mandibular margin
Mand P	mandibular palp
Mes	mesoderm
MF	muscle fibres
MG	mid-gut
MGW	mid-gut wall
MLITS	muscles of lateral intersegmental tendinous sheet
MS	median spines of endite
MS Mand	molar surface of mandible
MT	mesoteloblast
Mx 1	maxillule
Mx 1 APM	accessory maxillulary promotor muscle
Mx 1 PM	maxillulary promotor muscle
Mx 1 RM	maxillulary remotor muscle
MX 2	maxilla
MX 2/TS 1	maxillary/thoracic segment 1 boundary
N	nerve
NC	nerve cord
NCo	nerve commissure
O	ocellus
ODM	oesophageal dilator muscles
ODM′	oesophageal dilator/suspensor
Oe	oesophagus
OeE	oesophagus near entrance
OS	outer spines of endite
OSD	suspensor/dilator of oesophagus

P	paragnath
PC	pericardial cavity
PD	proctodeal dilator muscles
PDVM	posteriorly descending oblique dorso-ventral muscle
PMS	proximal masticatory spine of antenna
POB	post-oesophageal bar
POC	post-oesophageal commissure
PS	posterior suspensory ligament
PS Mx 1	posterior ventral spine of maxillule
PV	pivot of mandible
Rem D	remnants of dorsal naupliar antennary muscles
RLG	reservoir of labral gland
R Mand	right mandible
Rud TL 2, 5	rudiments of trunk limbs 2, 5
S	spinules
SC	sphincter cells
SDLM	superior dorso-longitudinal muscle
SFG	spinules of food groove wall
S Fib	suspensory fibrils
SL	topographically dorsal (morphologically ventral) surface of labrum
S Mx 1	spine of maxillule
SP 1, 2,...	spine of trunk limbs 1, 2,...
SPL	spinous pad of labrum
SPM 1, 2, 3	suspensor muscles of ventral endoskeletal sheet
SPOB	suspensor of the post oesophageal bar
SS Mx 2	soft setae of maxilla
STMT	suspensor of transverse mandibular tendon
T	tendon between endoskeletal sheet and intersegmental elements
TCL	transverse connecting ligament of endoskeleton
TL 1, 2,...	trunk limbs 1, 2,...
TMM	transverse mandibular muscles
TMT	transverse mandibular tendon
TMTE	end of transverse mandibular tendon
TR	trunk rudiment
TS 1/2, 2/3,...	boundary of thoracic segments 1 and 2, 2 and 3,...
TS 1, 2,...	thoracic segment 1, 2,...
V 1, 2,...	ventral series of naupliar appendage muscles
VA	ventral anchor
VAEM	ventrally originating anterior extrinsic trunk limb muscle
VBDLM	ventralmost bundle of dorsal longitudinal muscles
VBW	ventral body wall
VC	ventral cuticle
VDVM	vertical dorso-ventral muscle
VIN	ventral intersegmental node of endoskeleton
VITS	ventral intersegmental tendinous sheet of endoskeleton
VLM	ventral longitudinal muscle
VPEM	ventrally originating posterior extrinsic trunk limb muscle
VSH	ventral surface of head
3	mandibular promotor (or promotor roller) muscle
4	mandibular remotor (or remotor roller) muscle
5 a, b, e	adjustor (transverse and levator) muscles
5 c	transverse mandibular muscles

51



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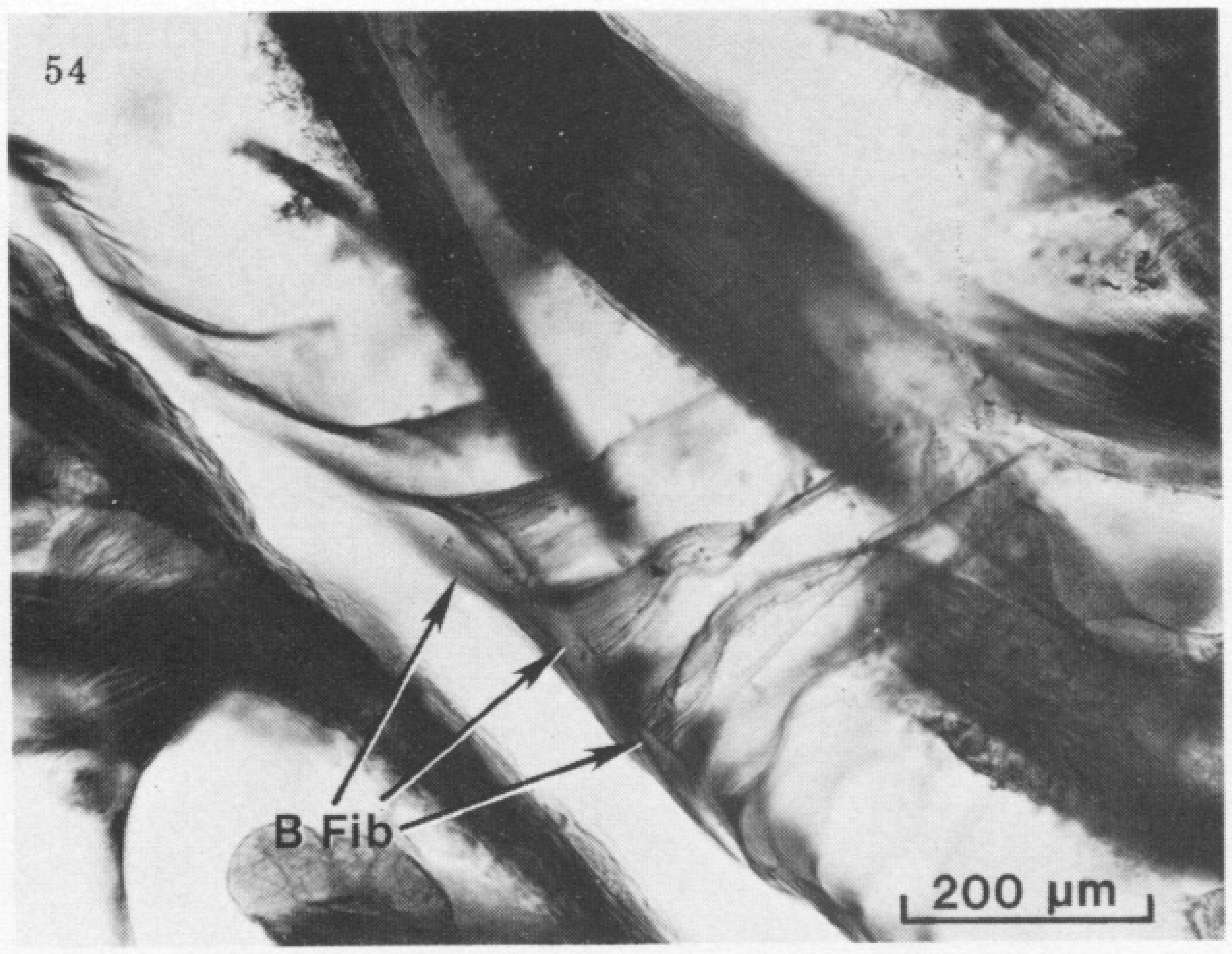

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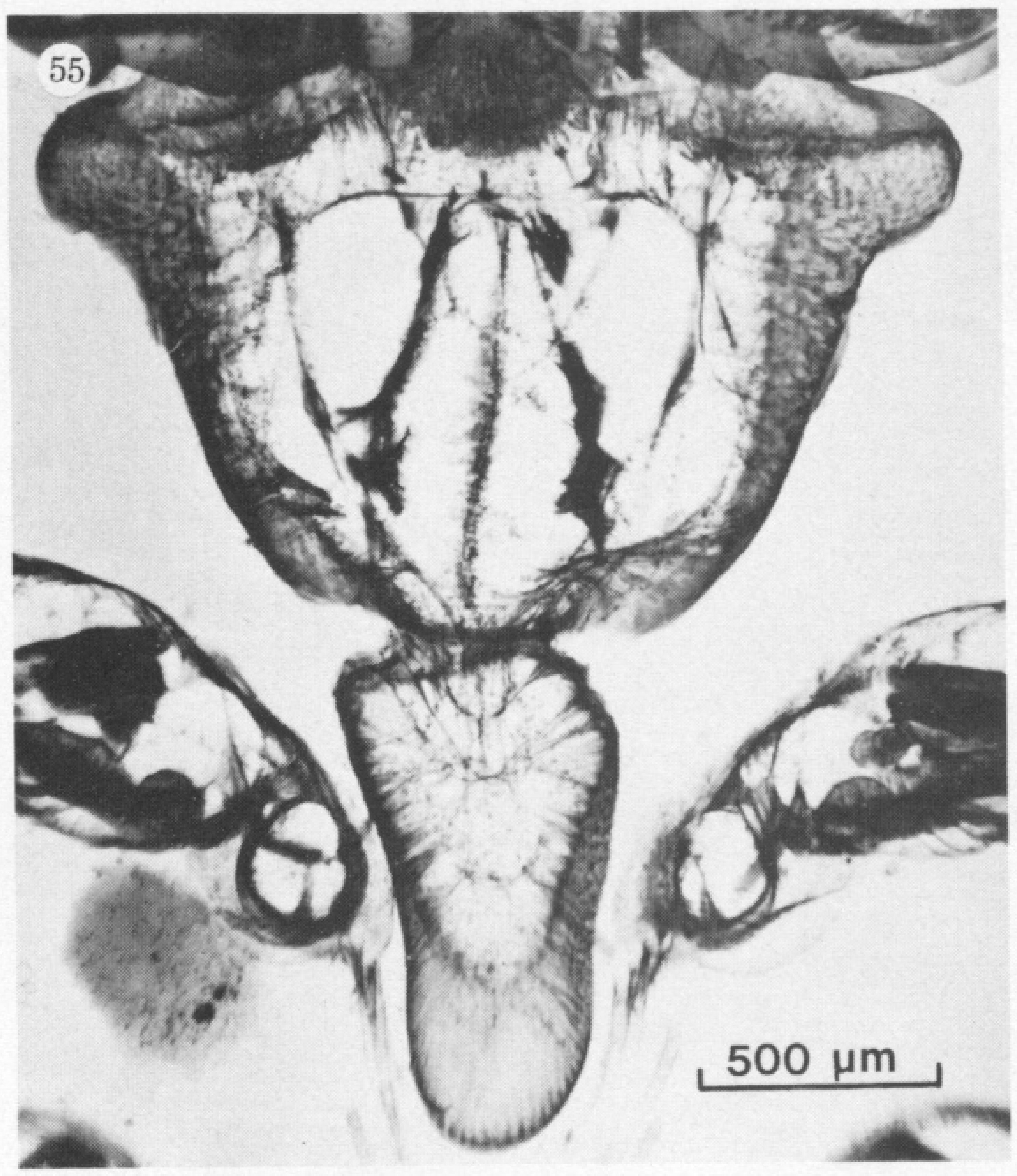

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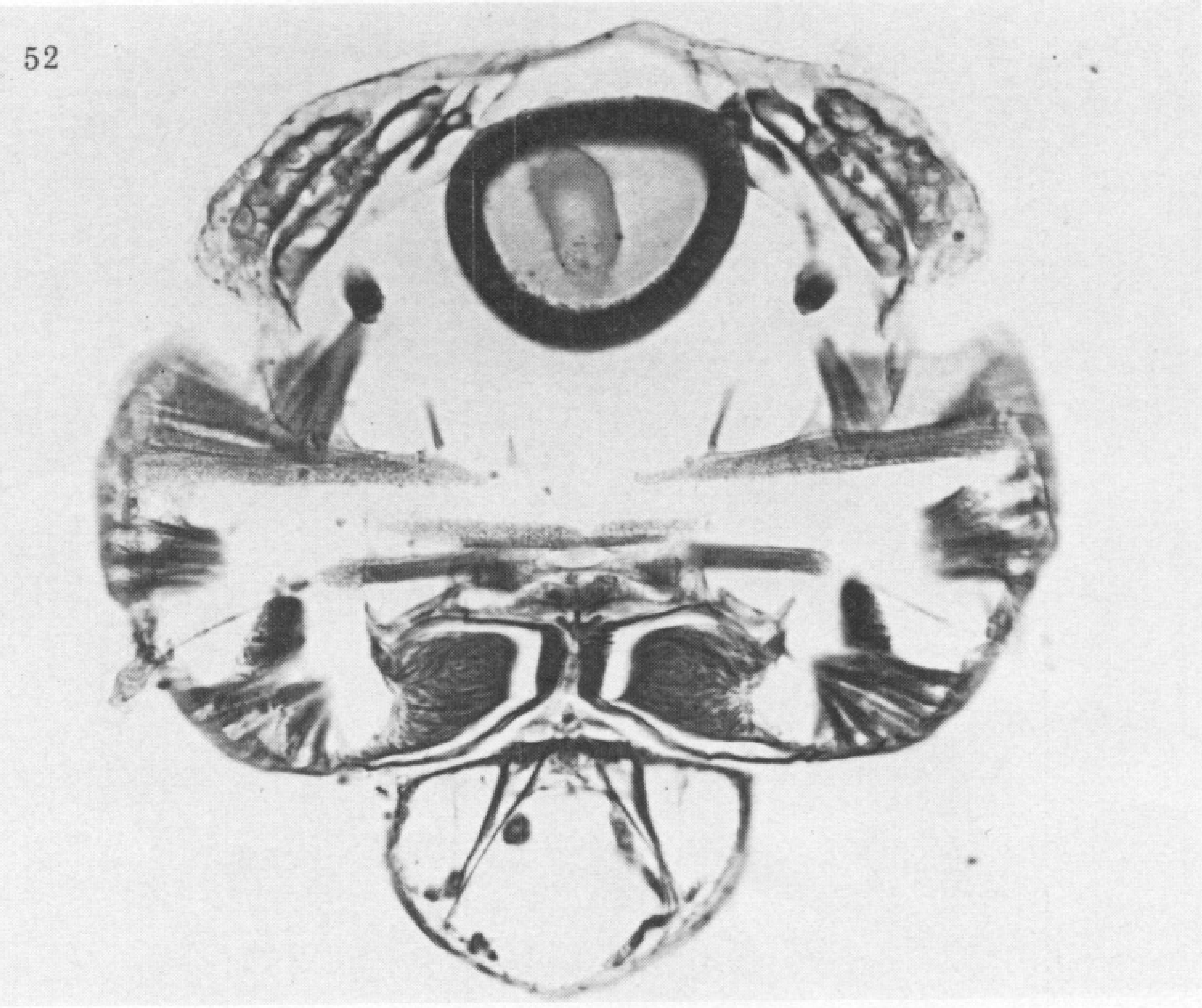

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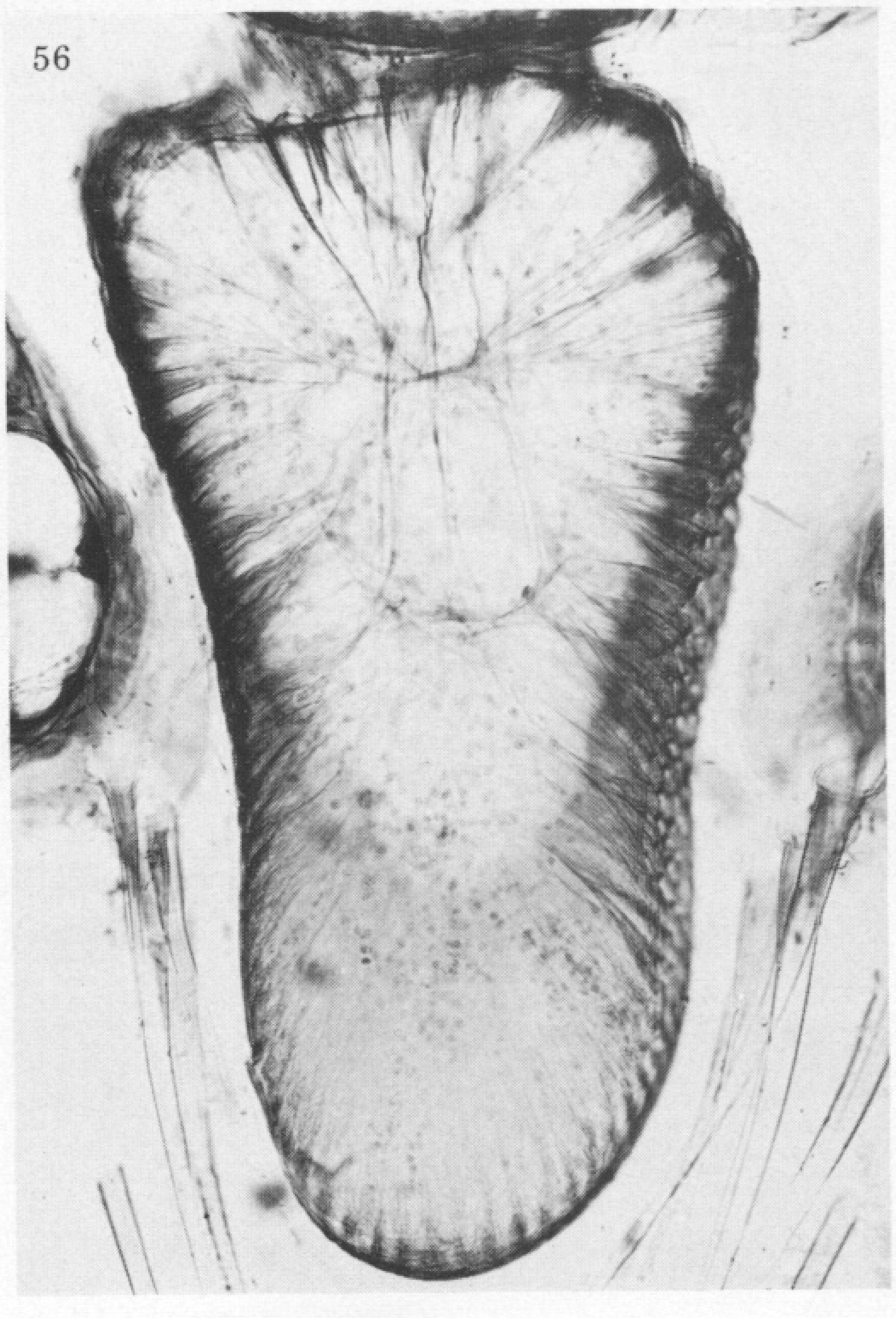

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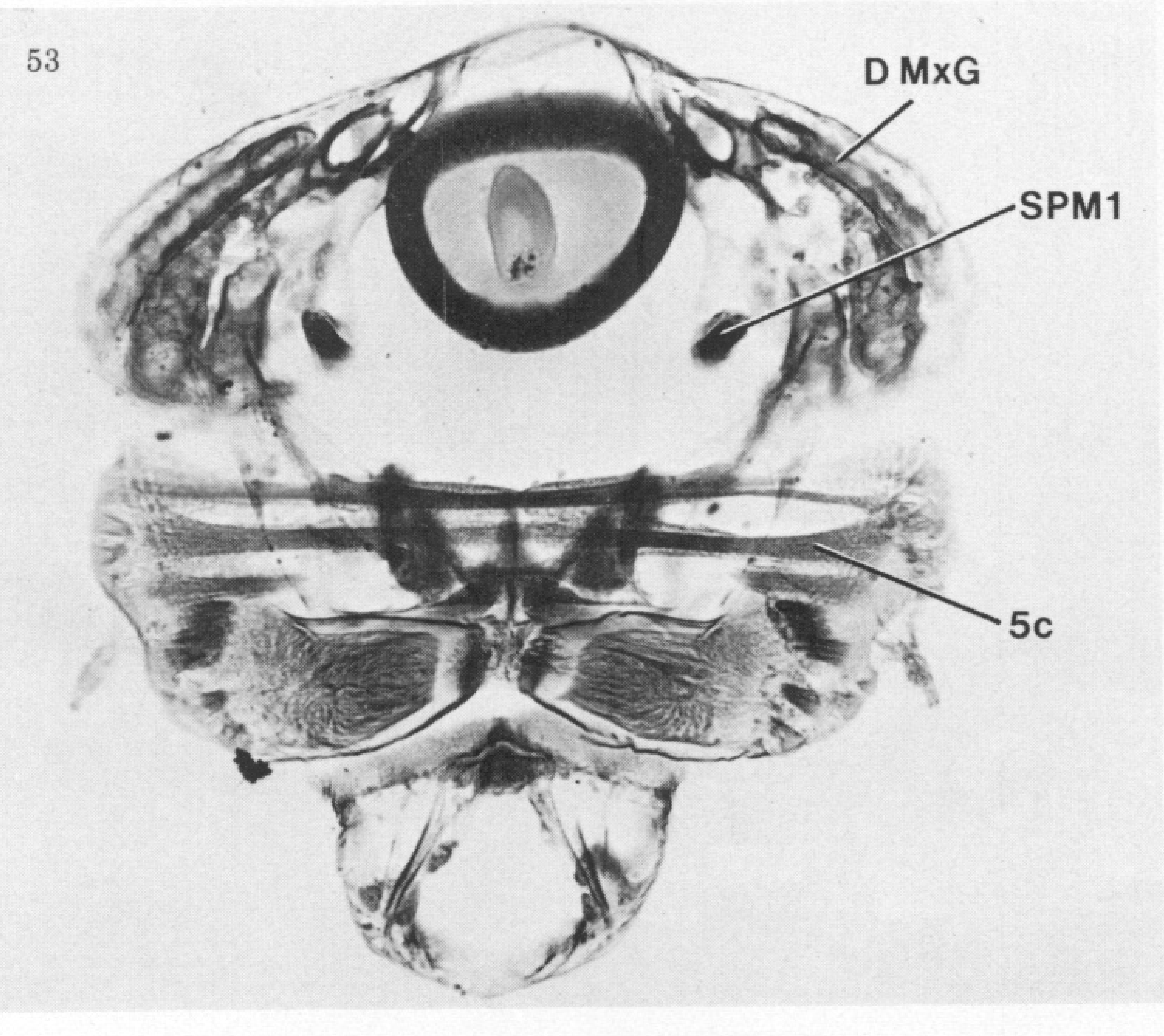

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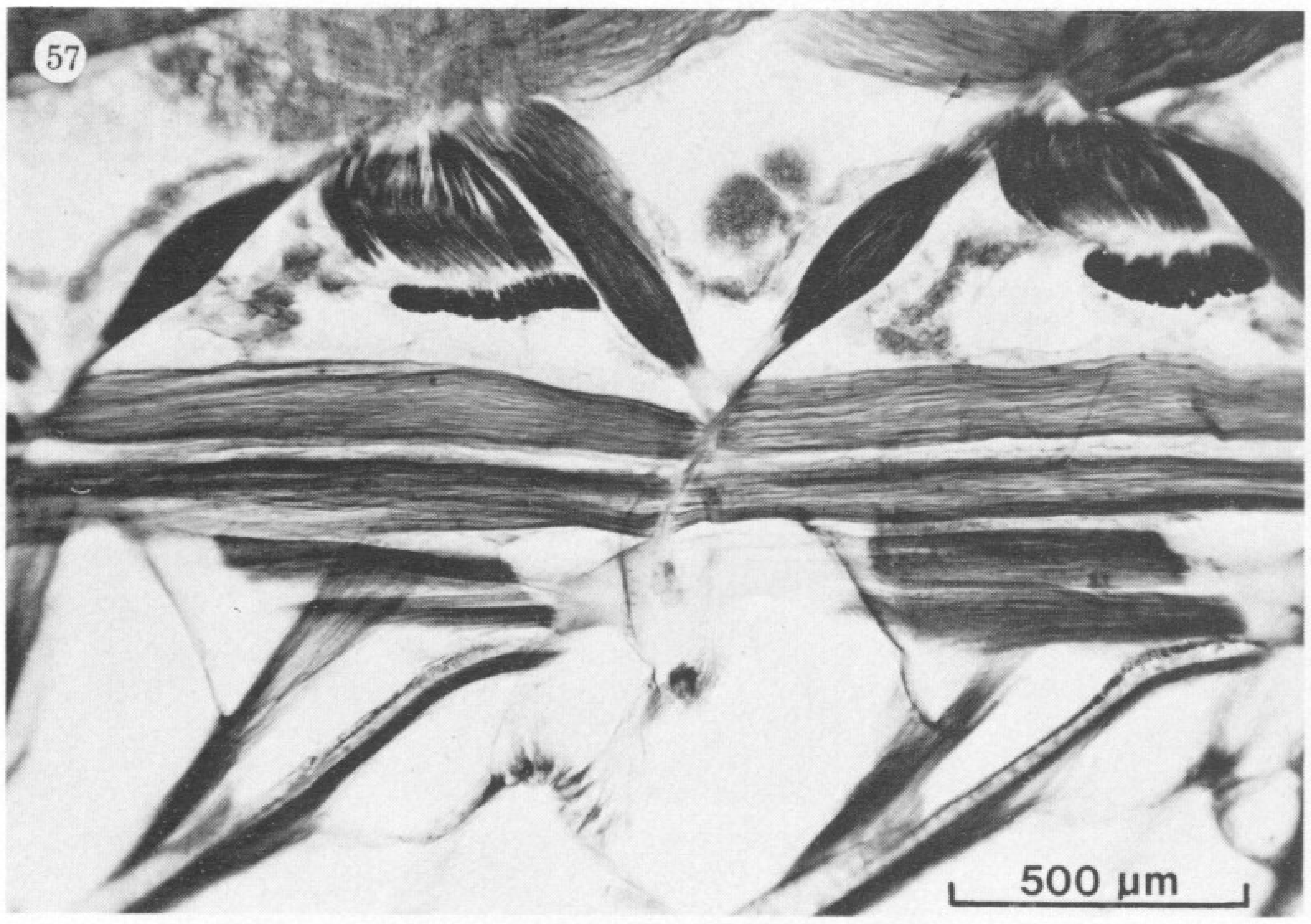

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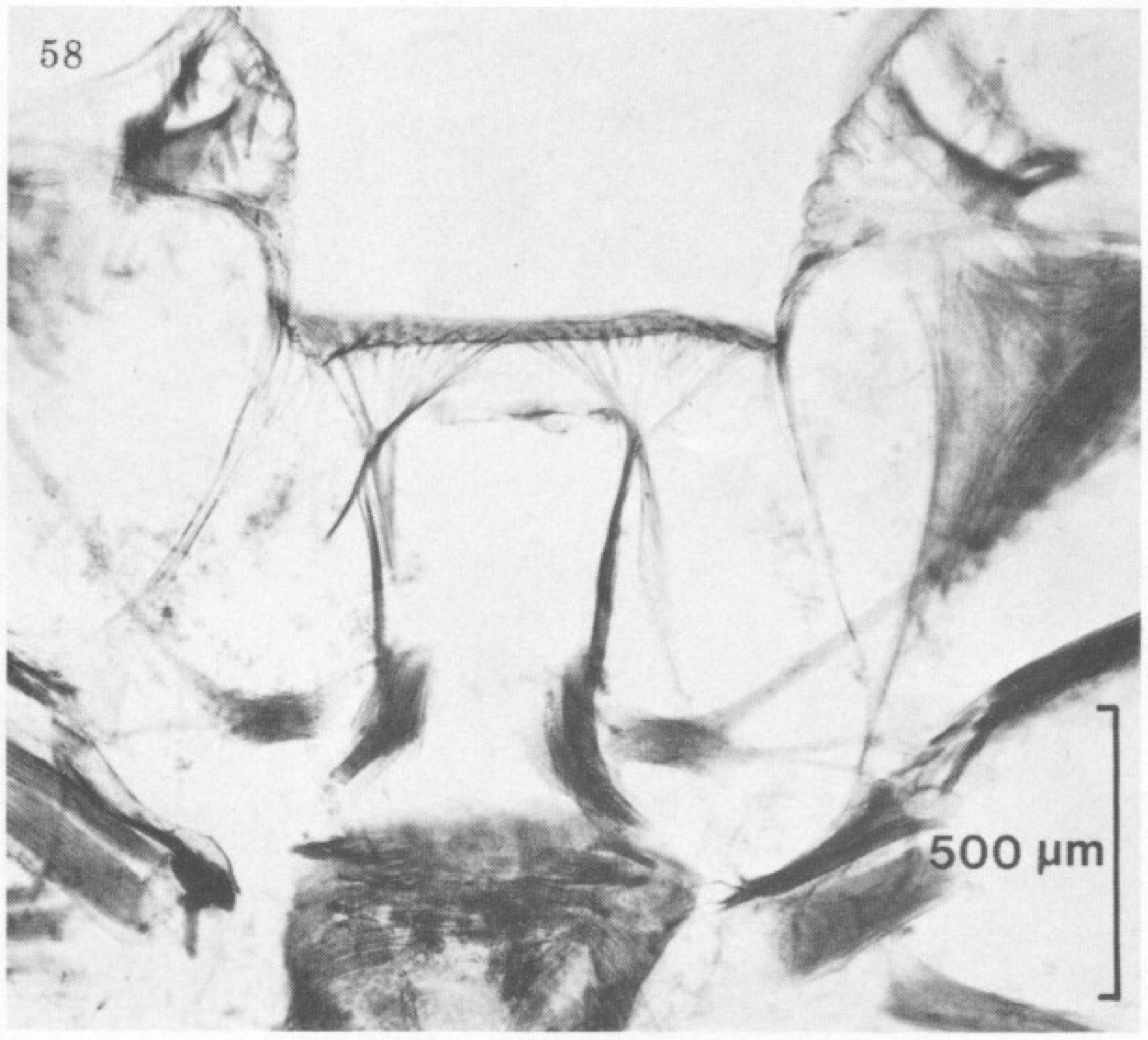

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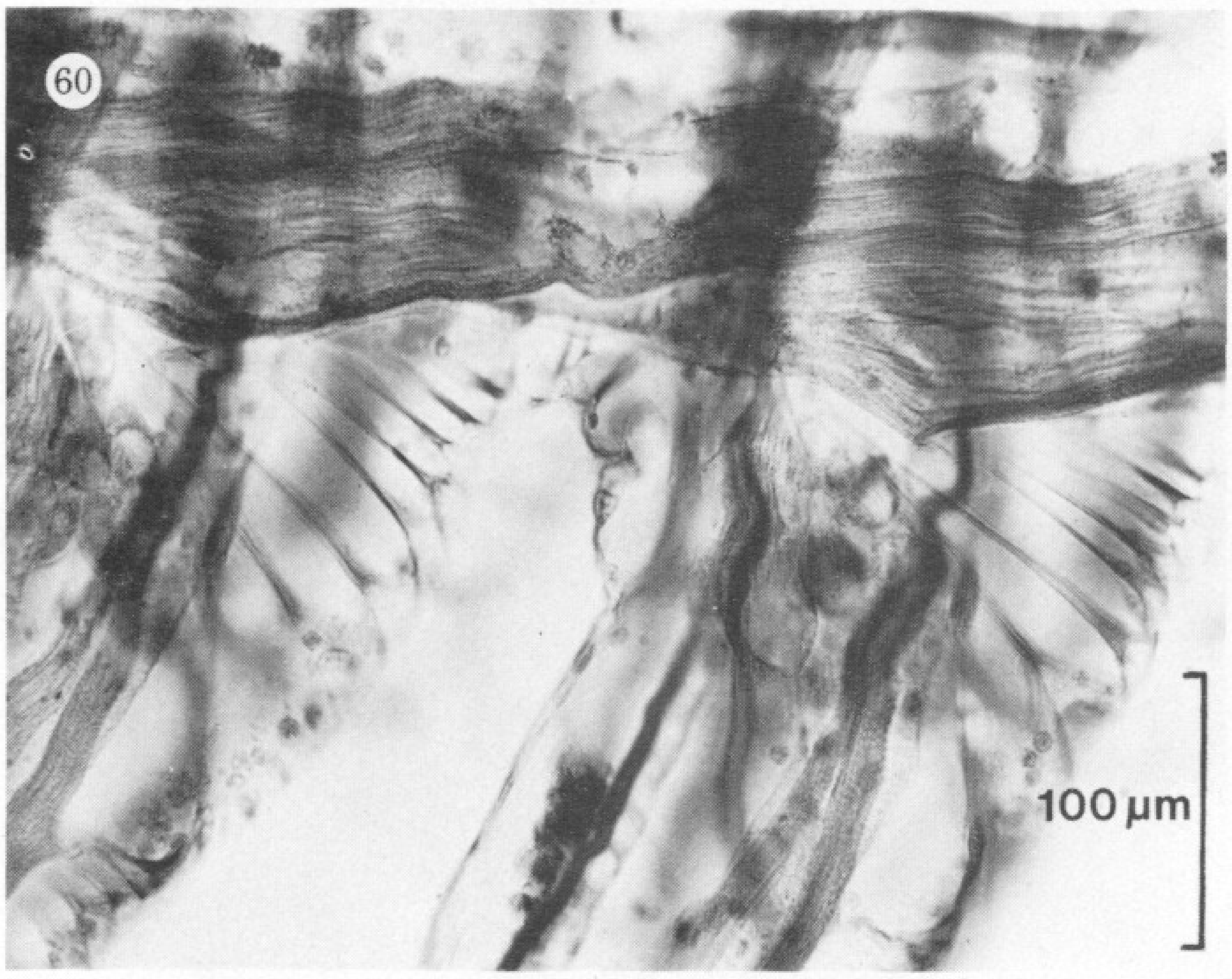

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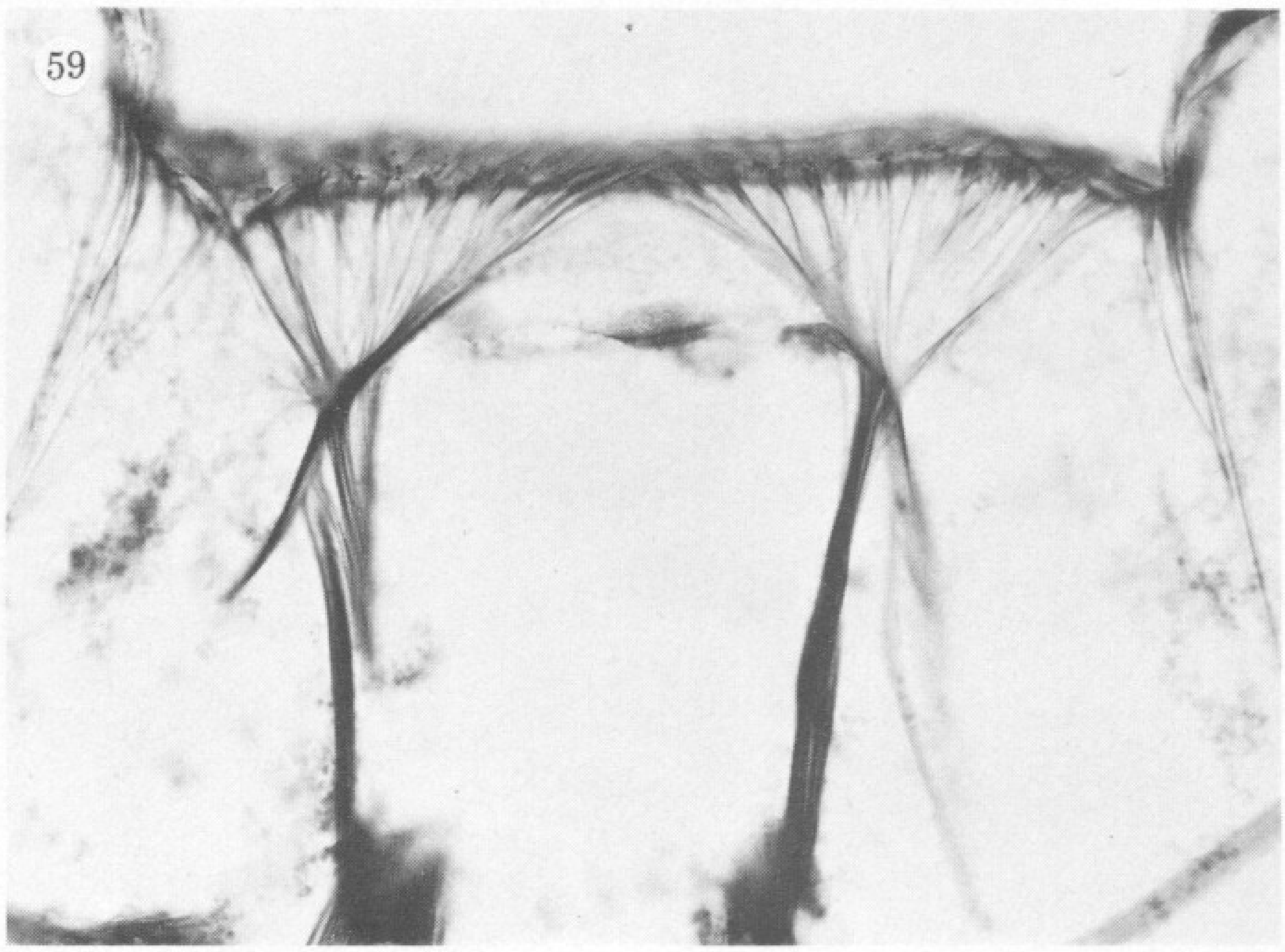

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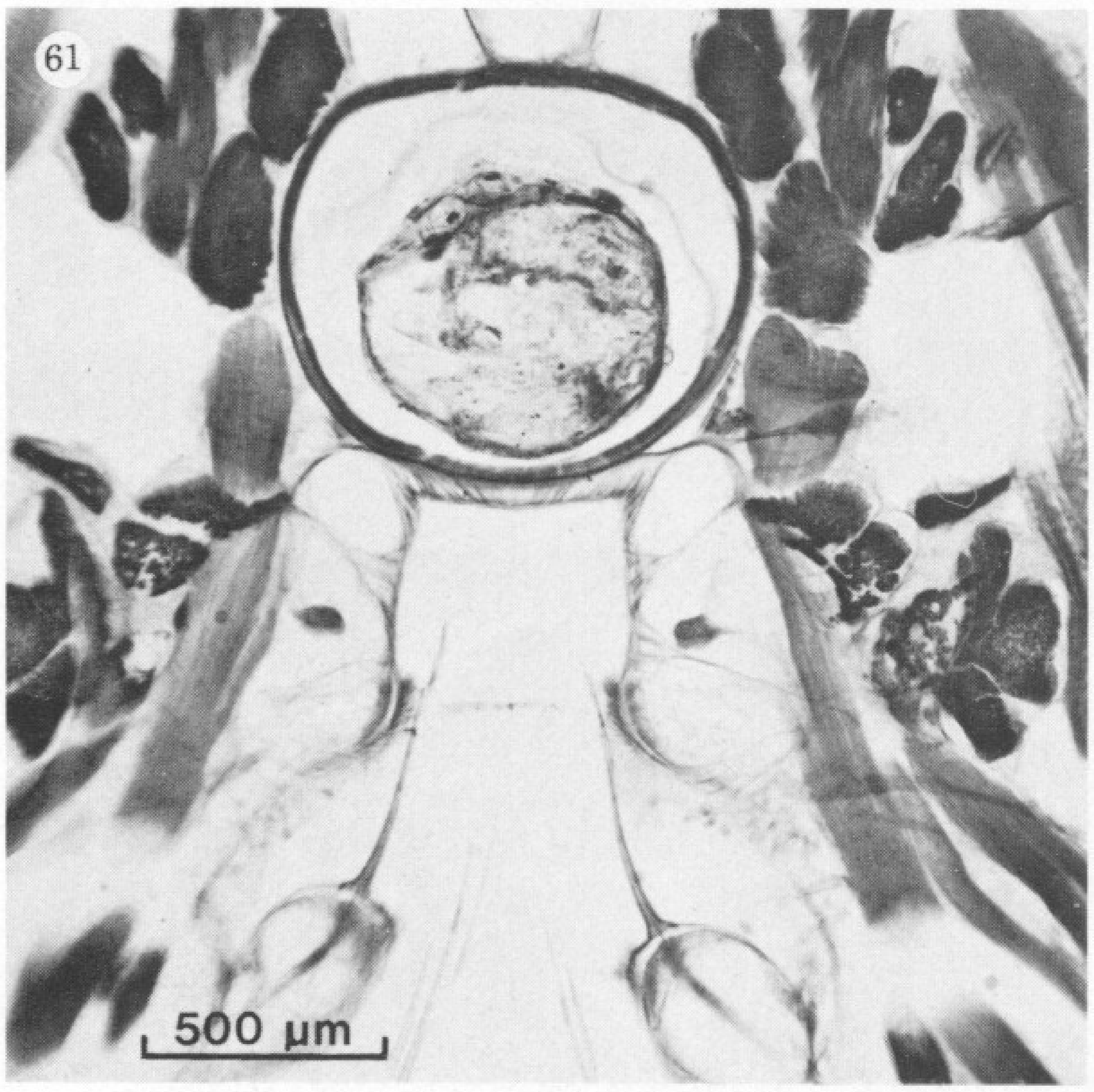

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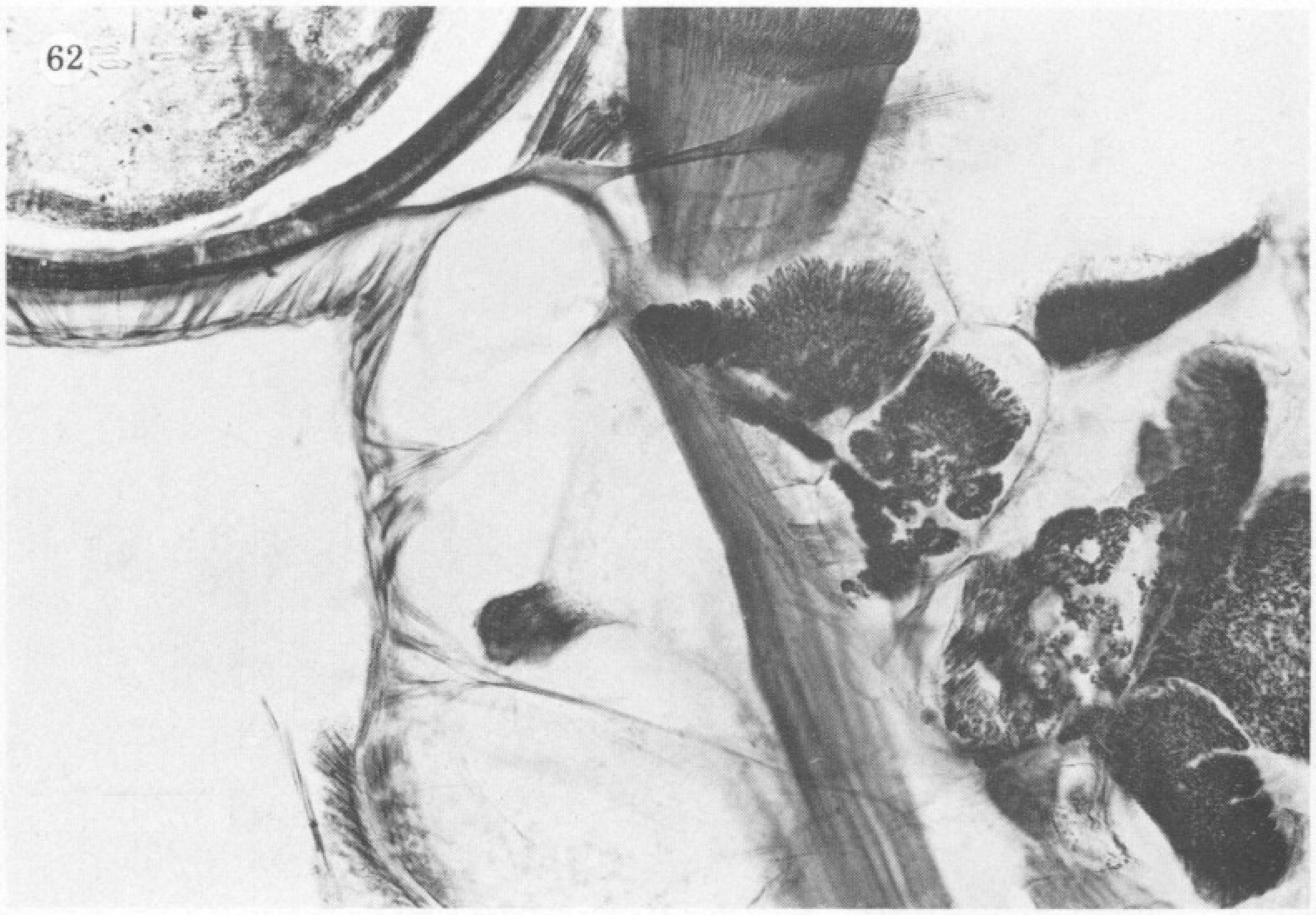

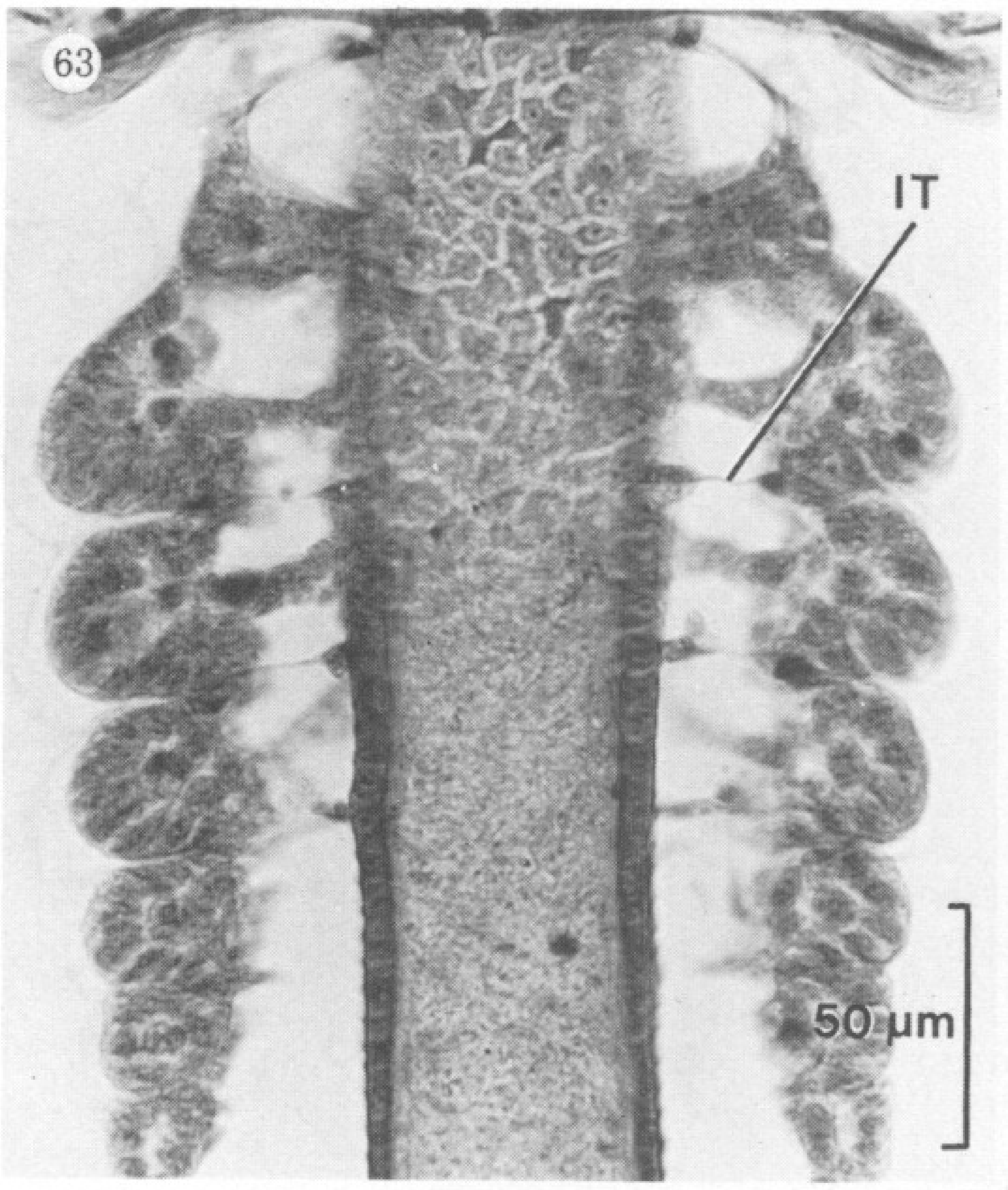
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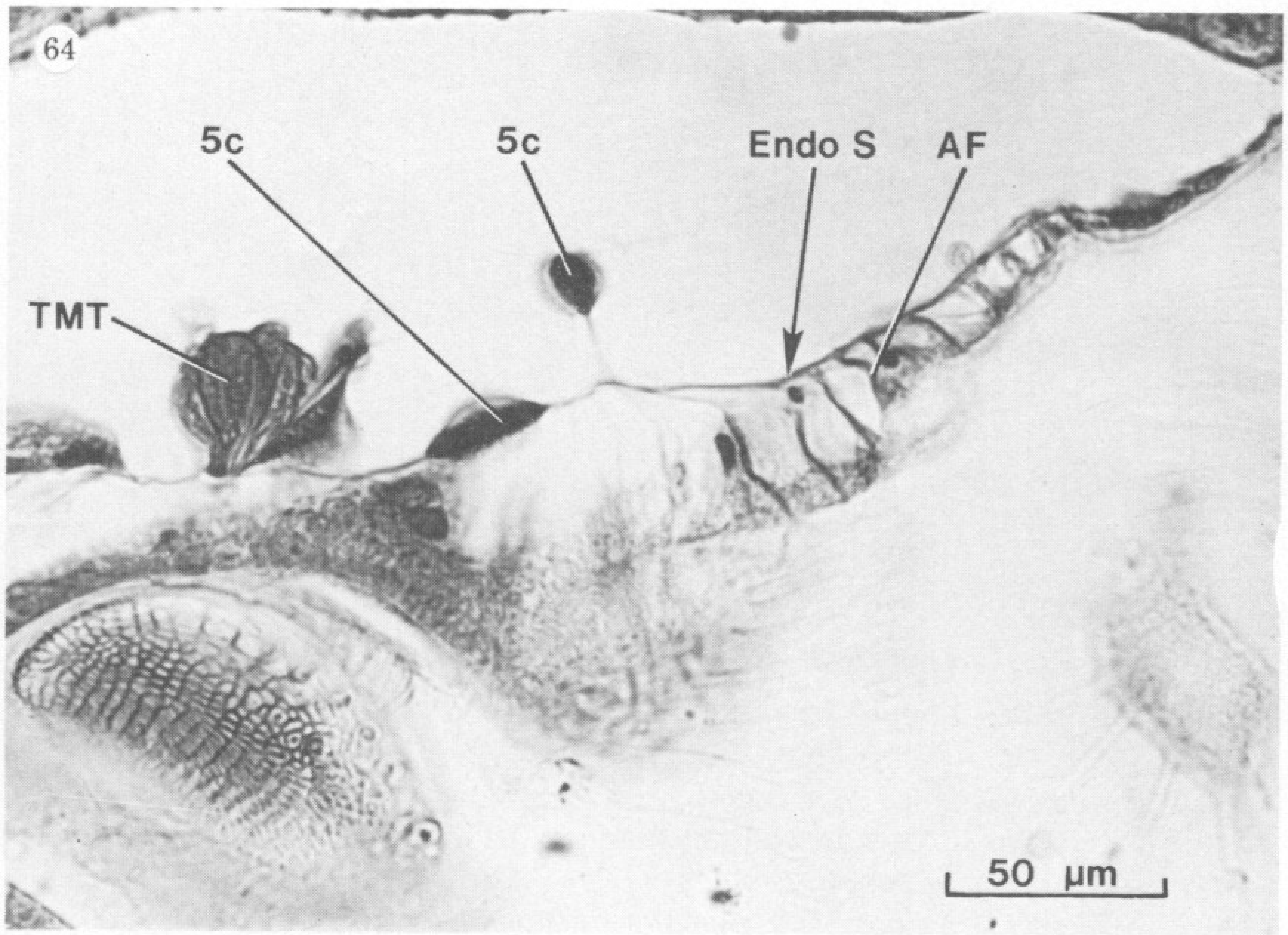
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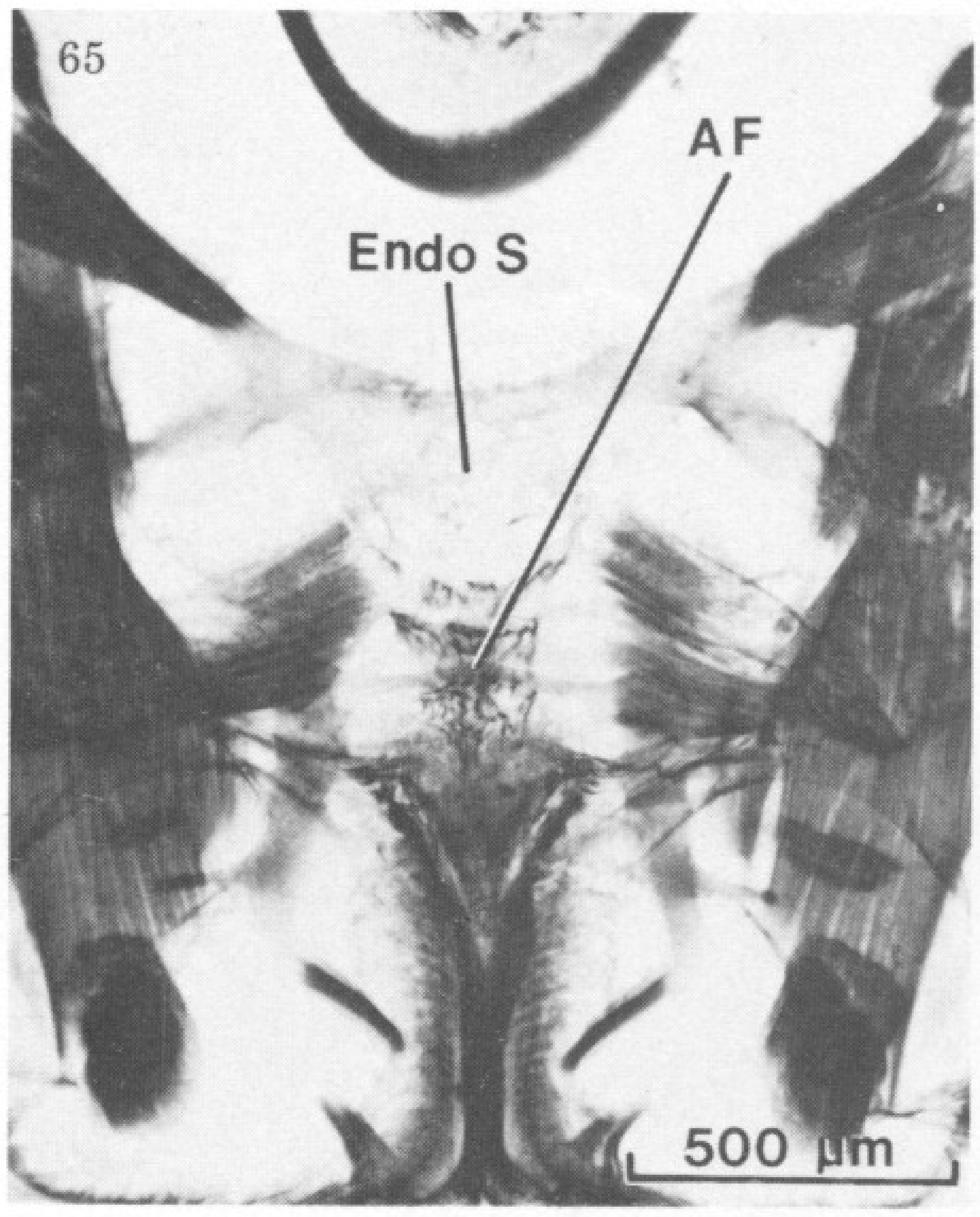
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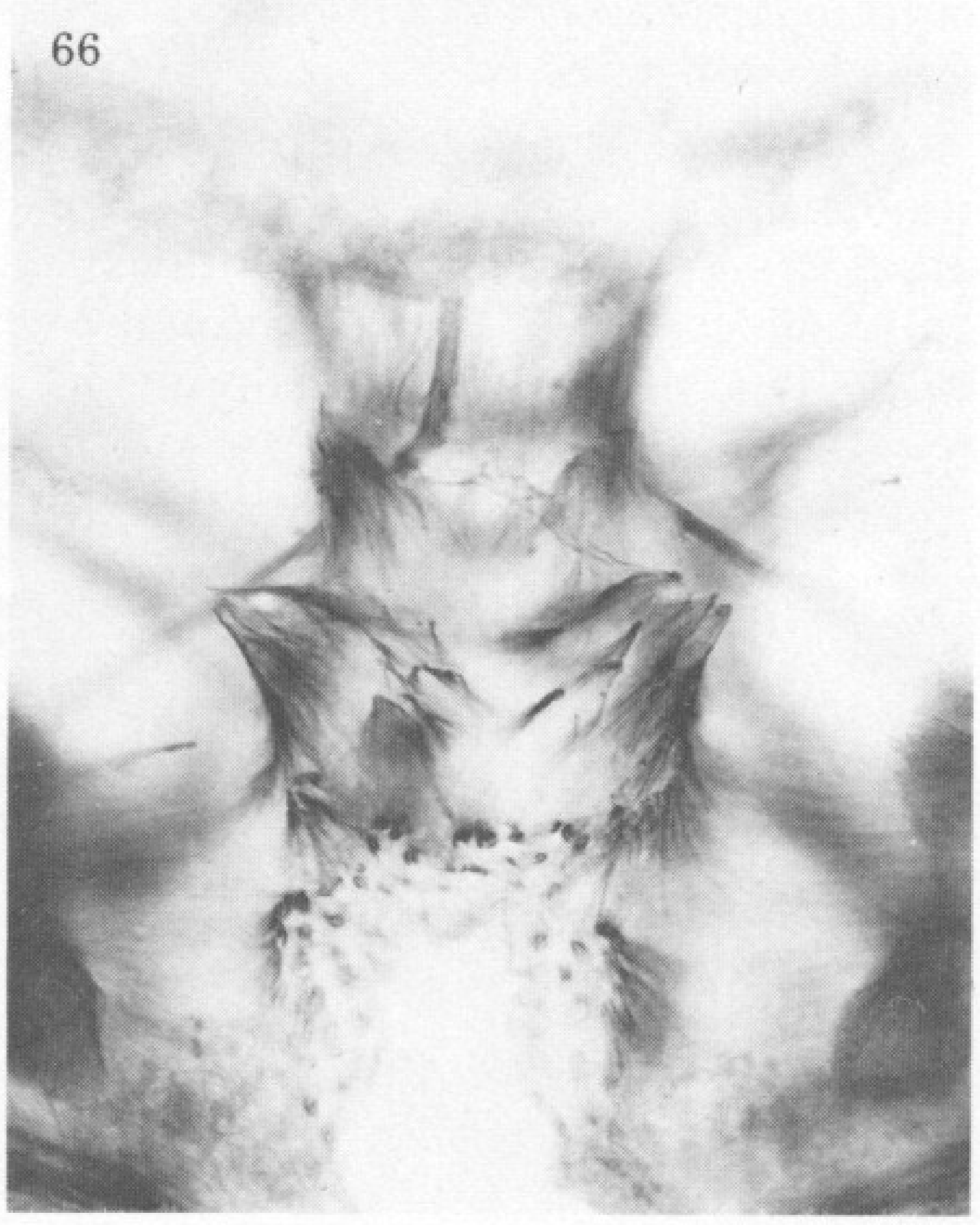
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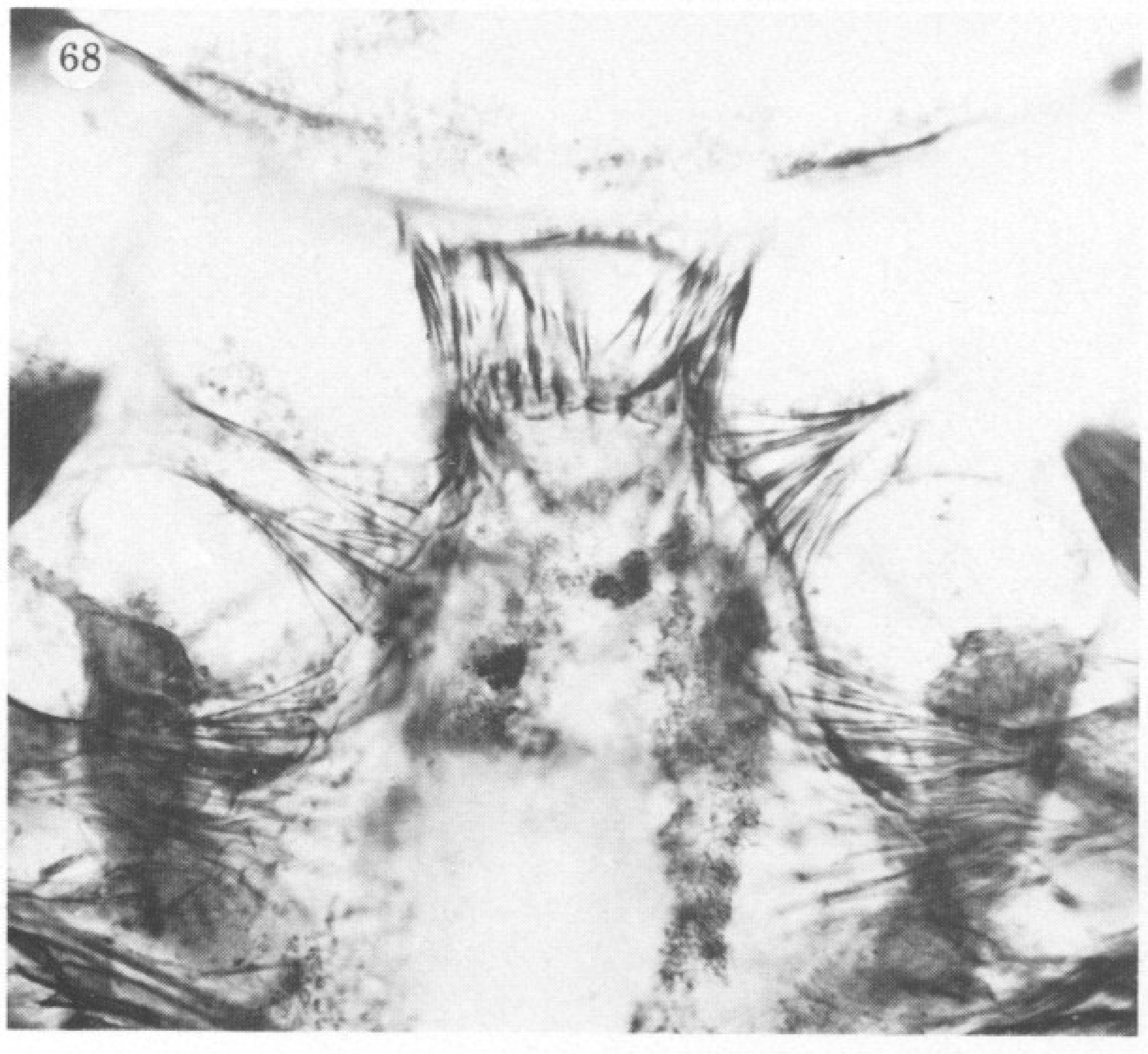
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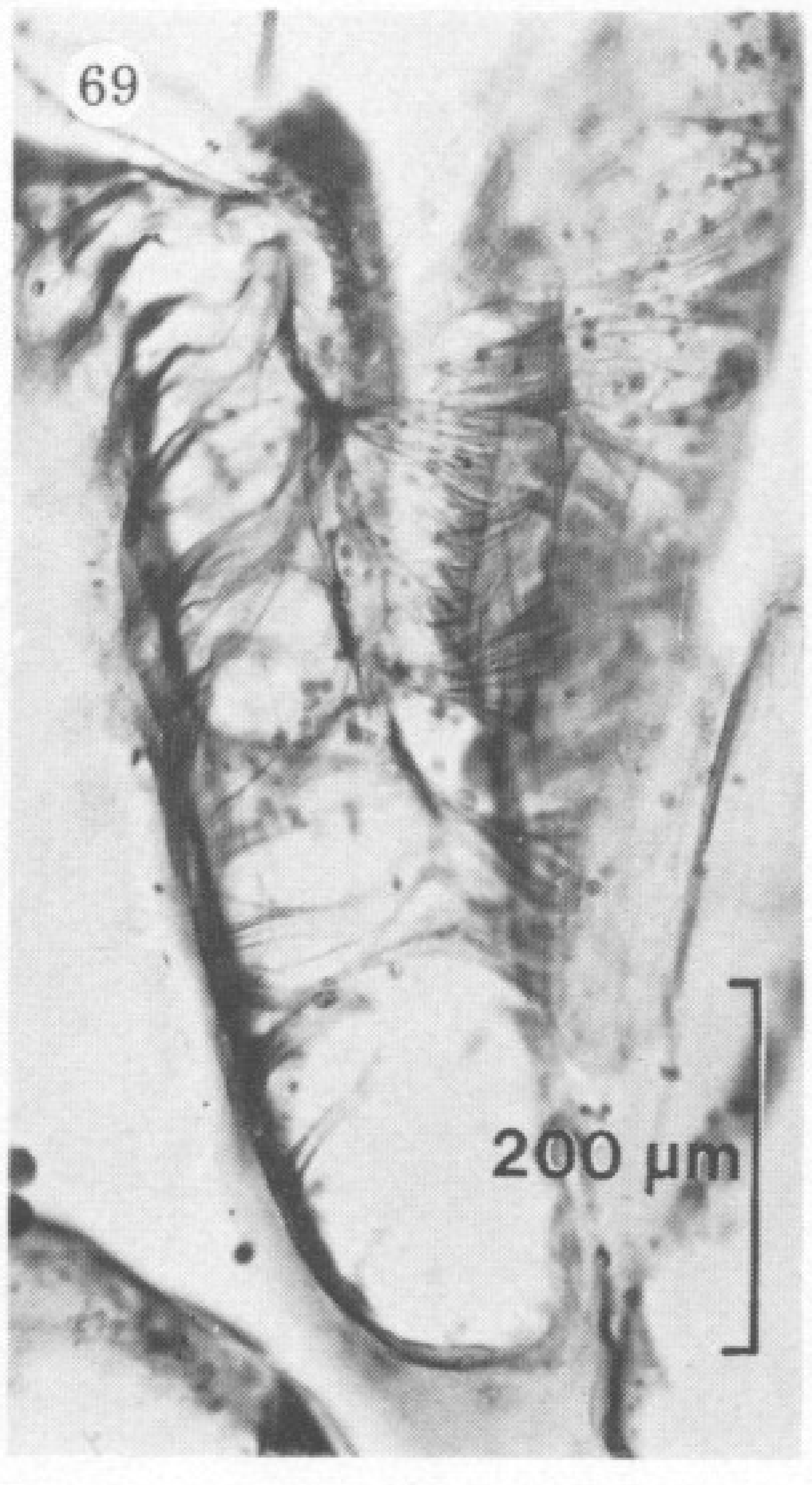
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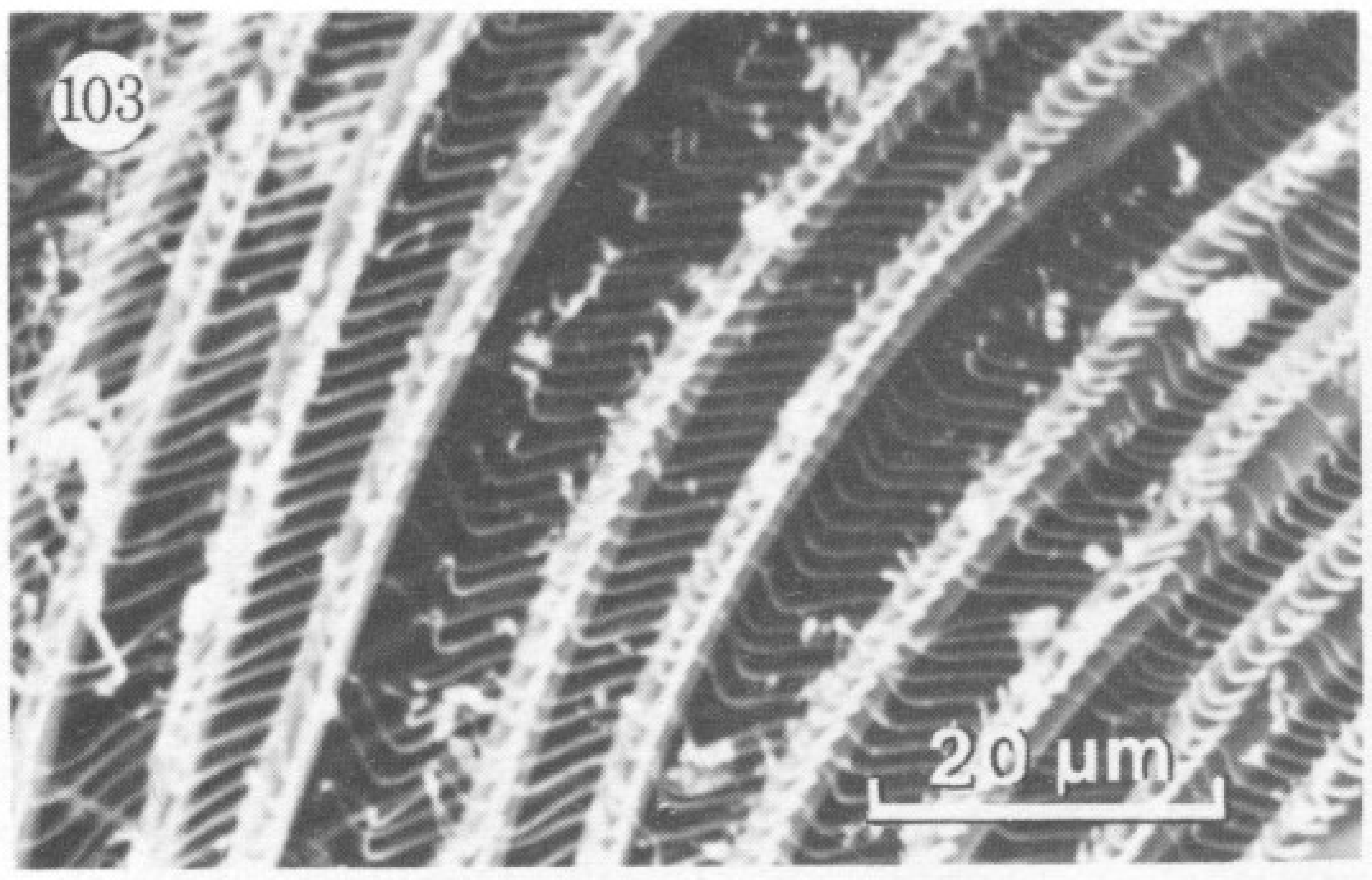
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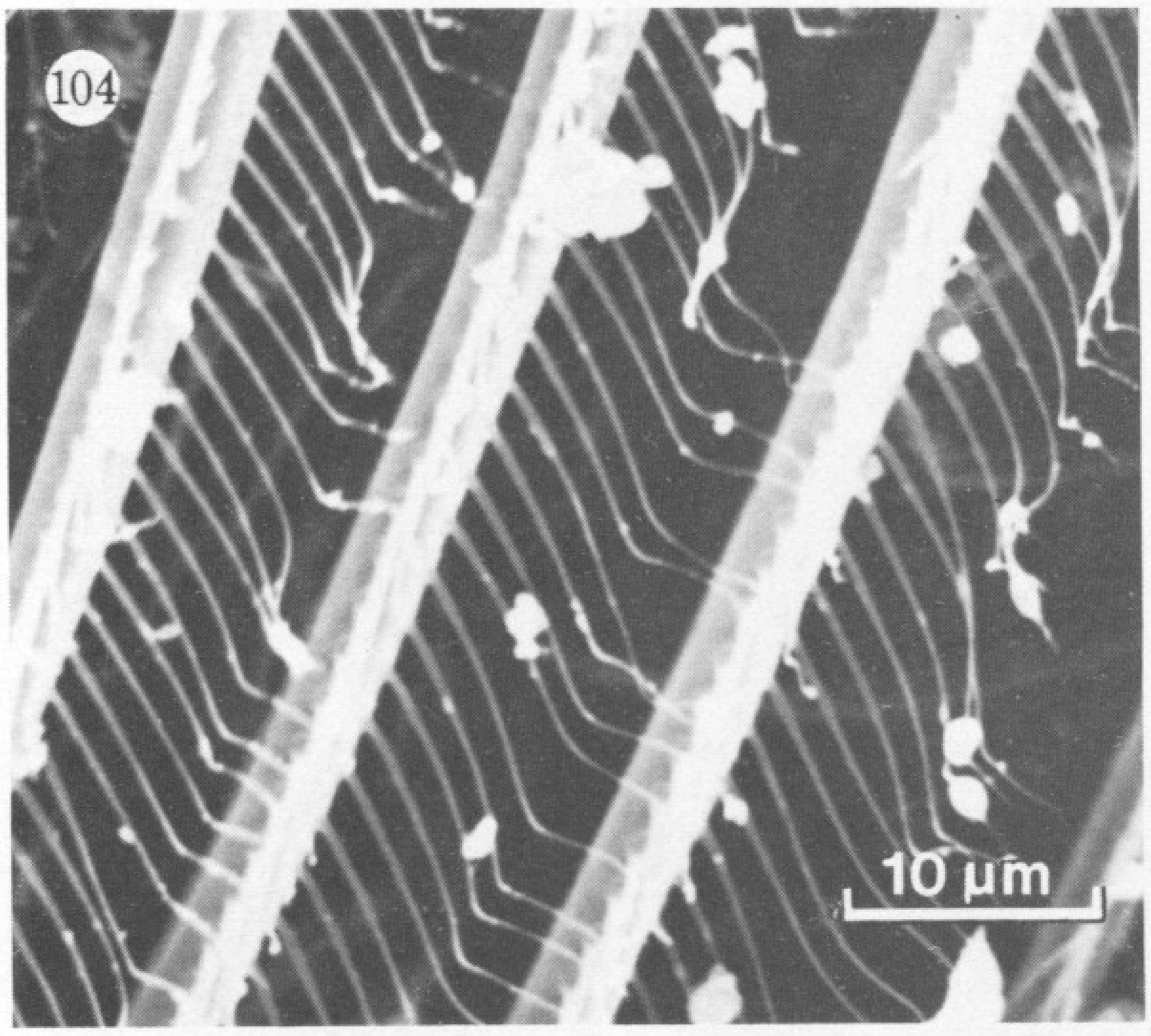
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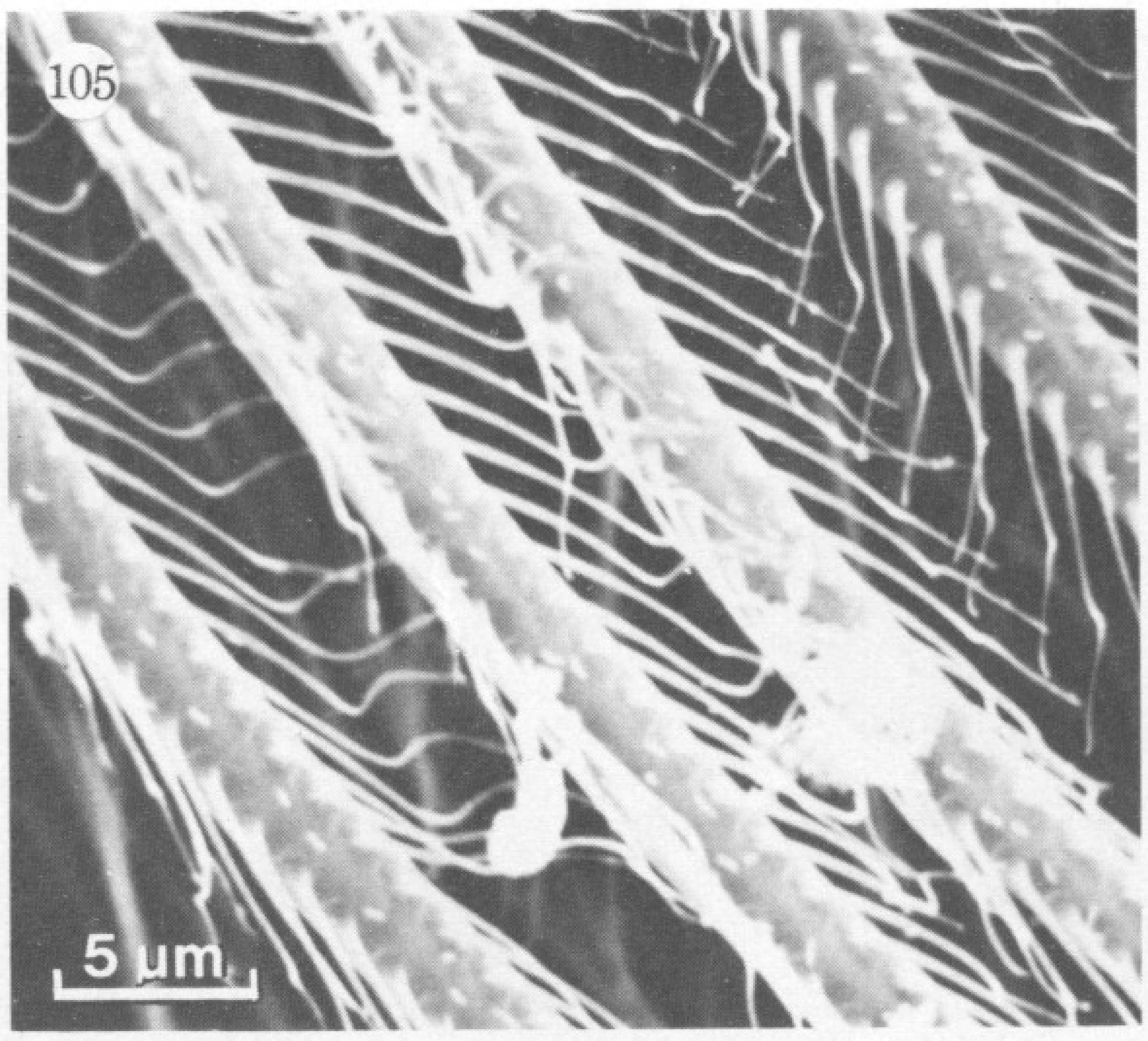
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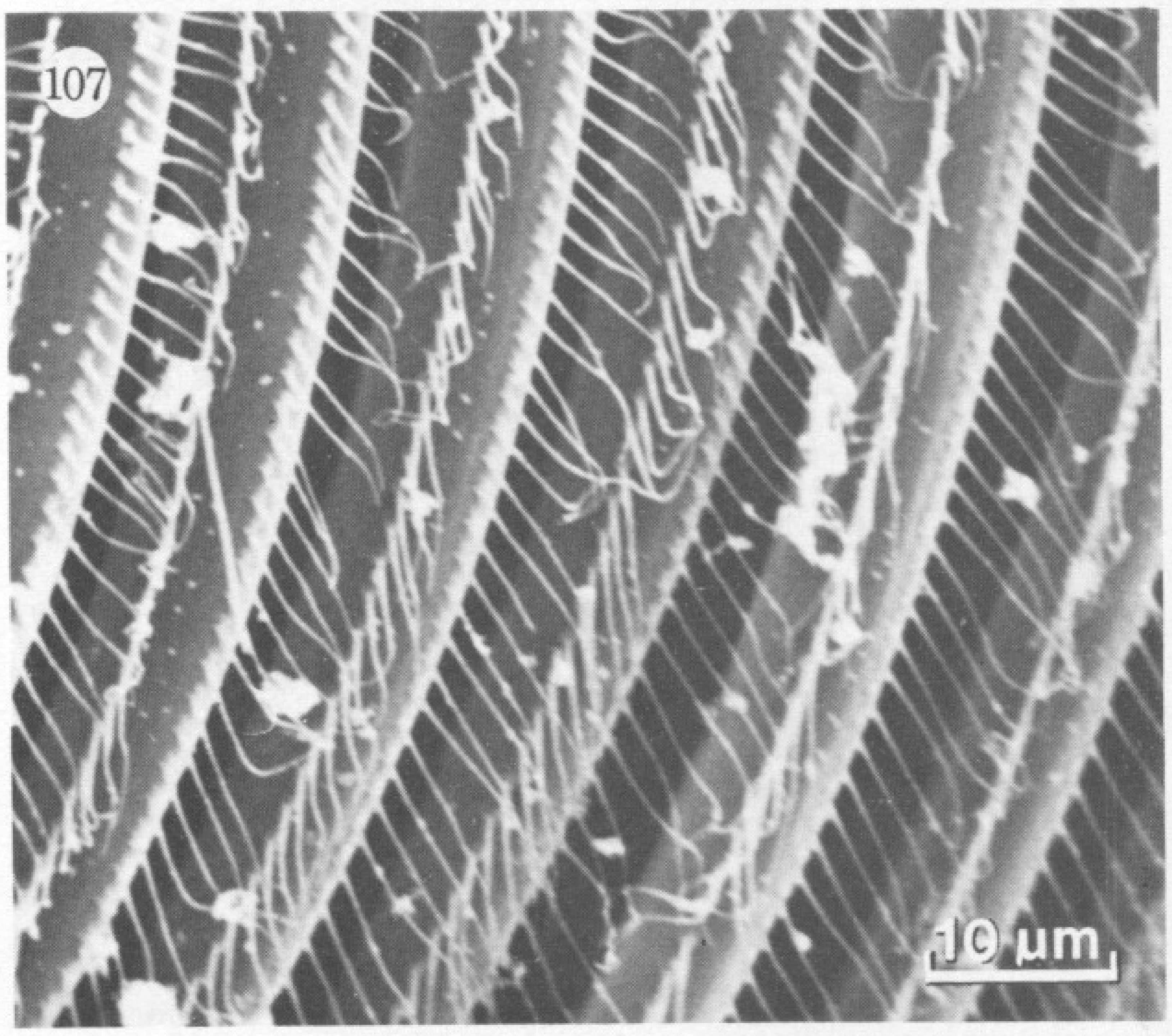
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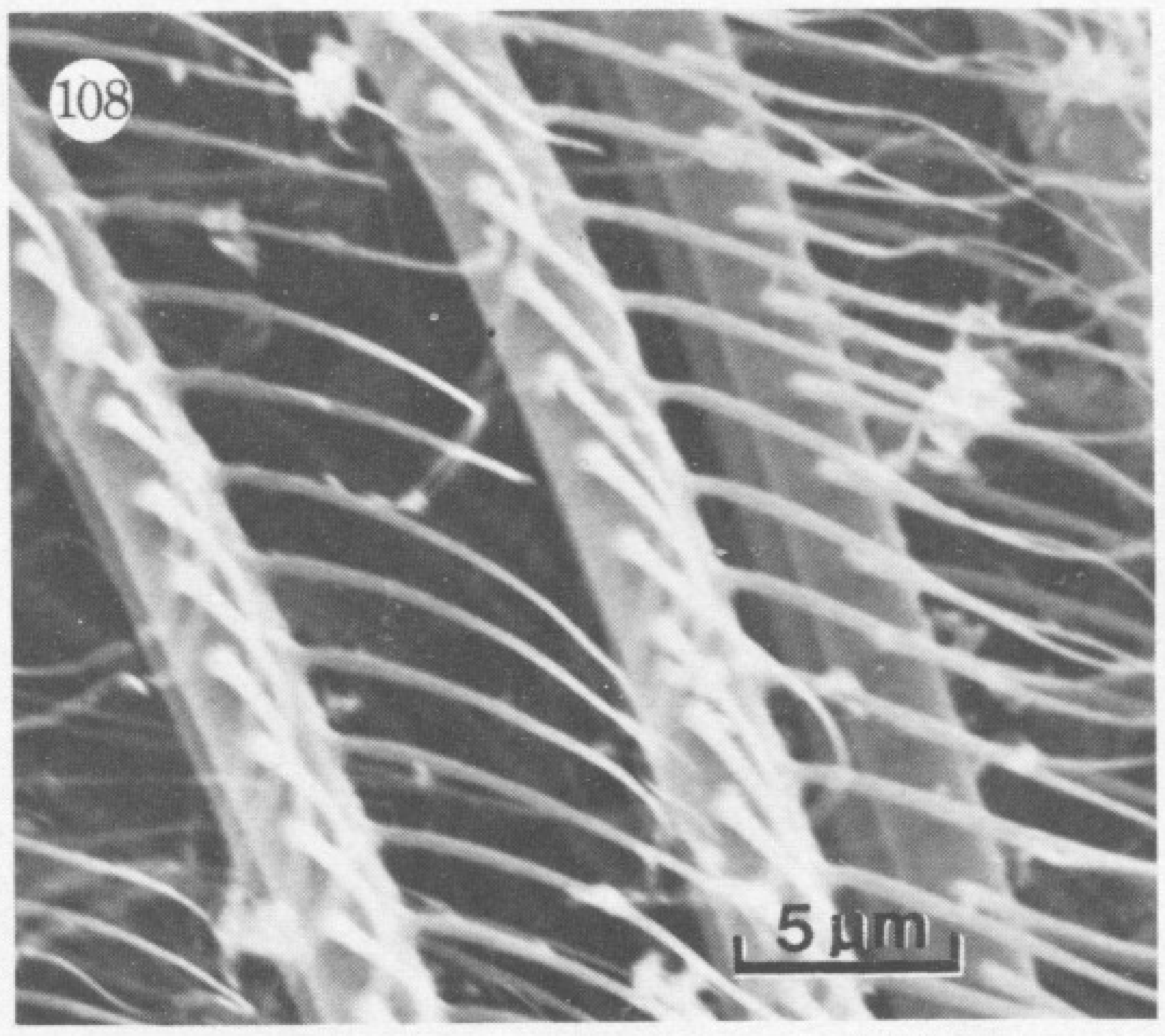
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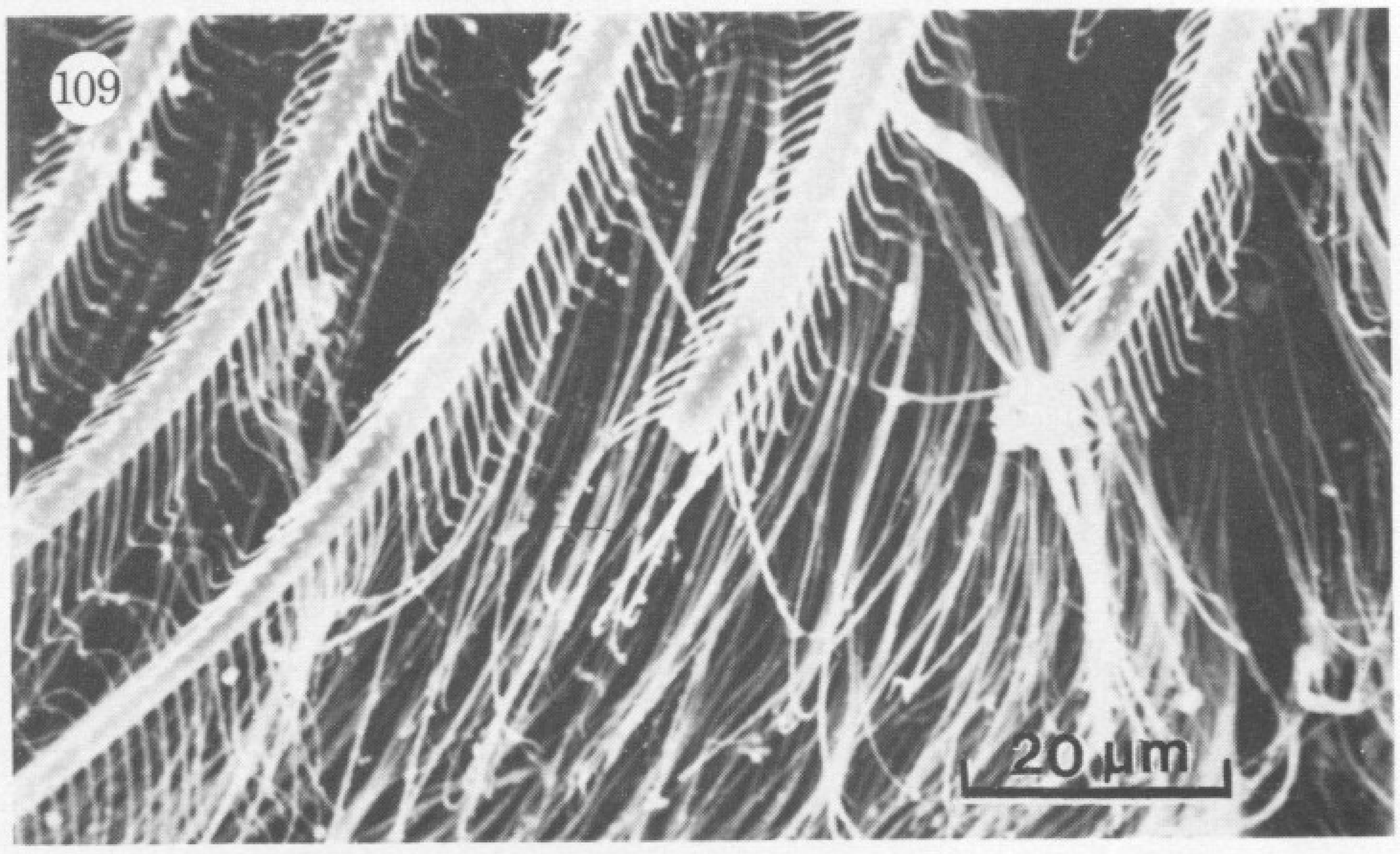
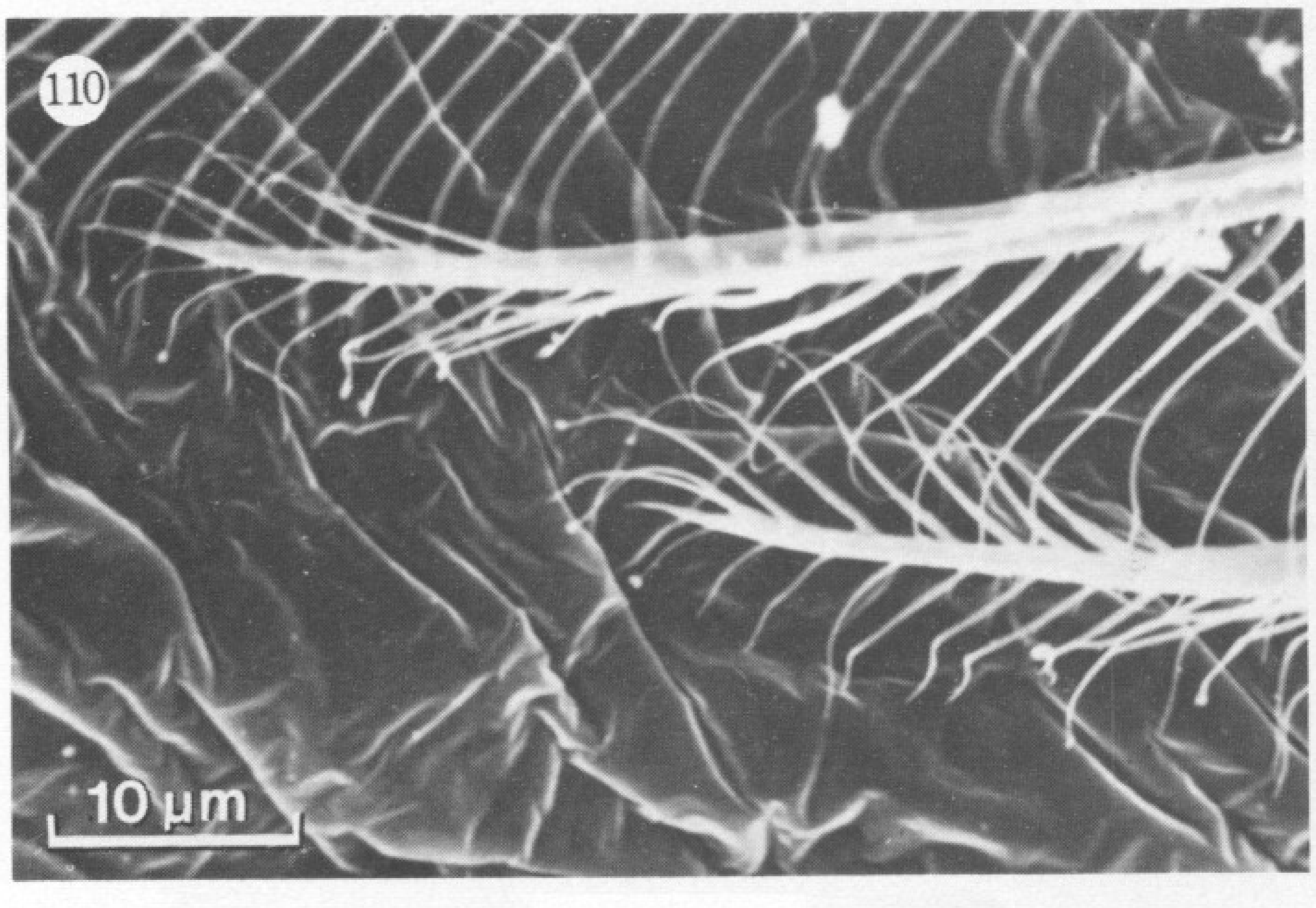
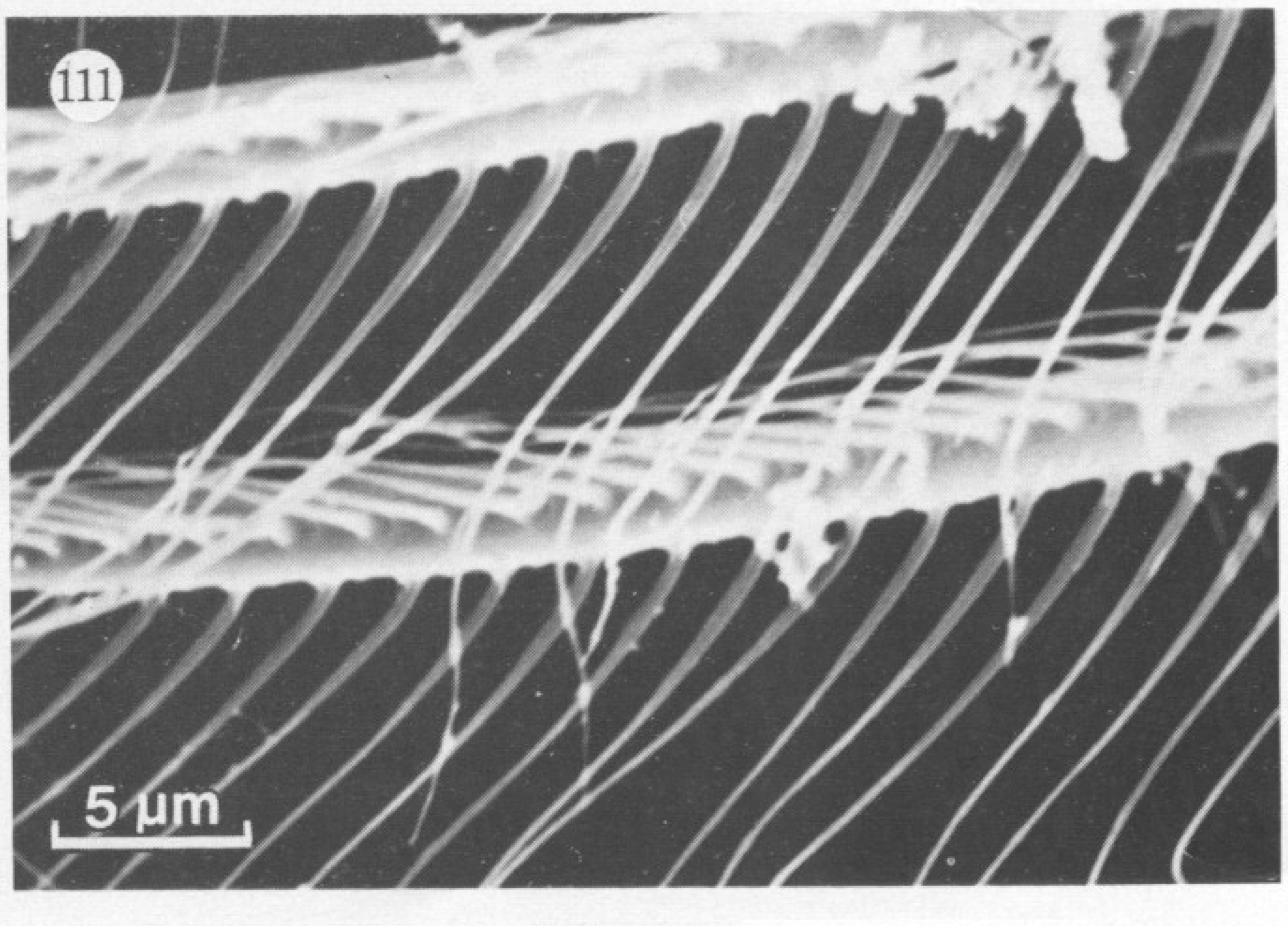
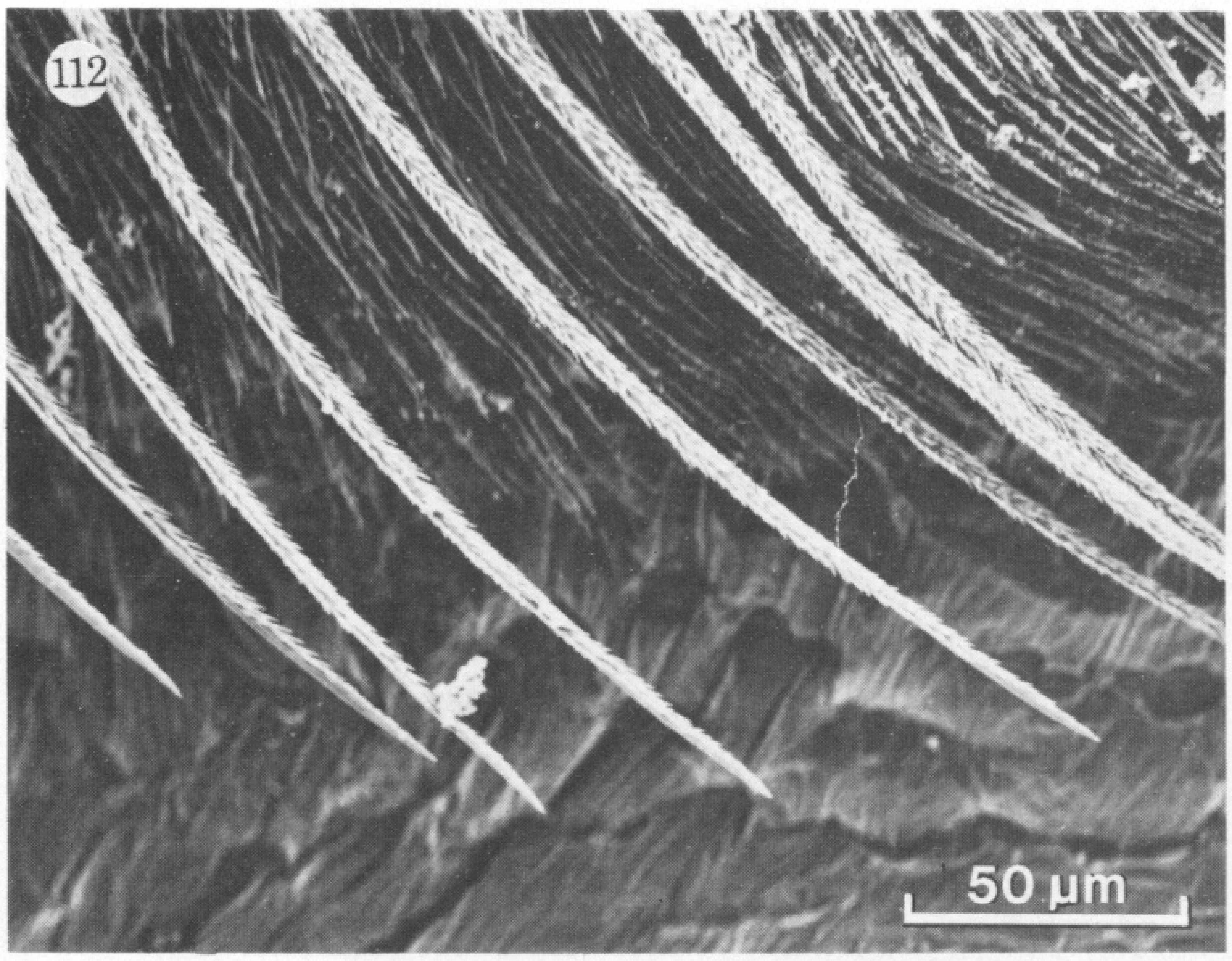
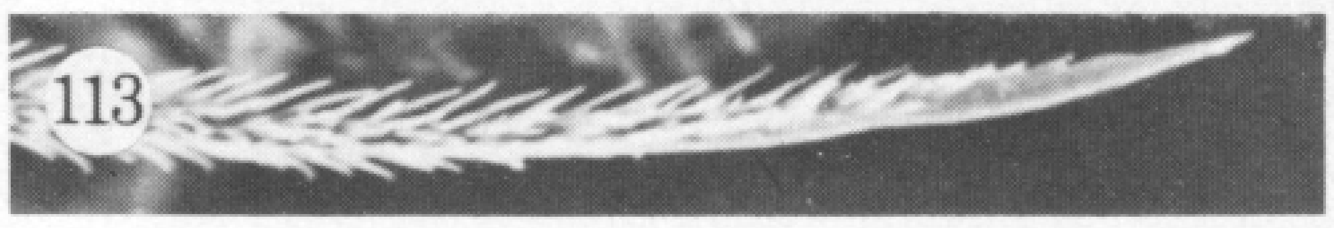

109

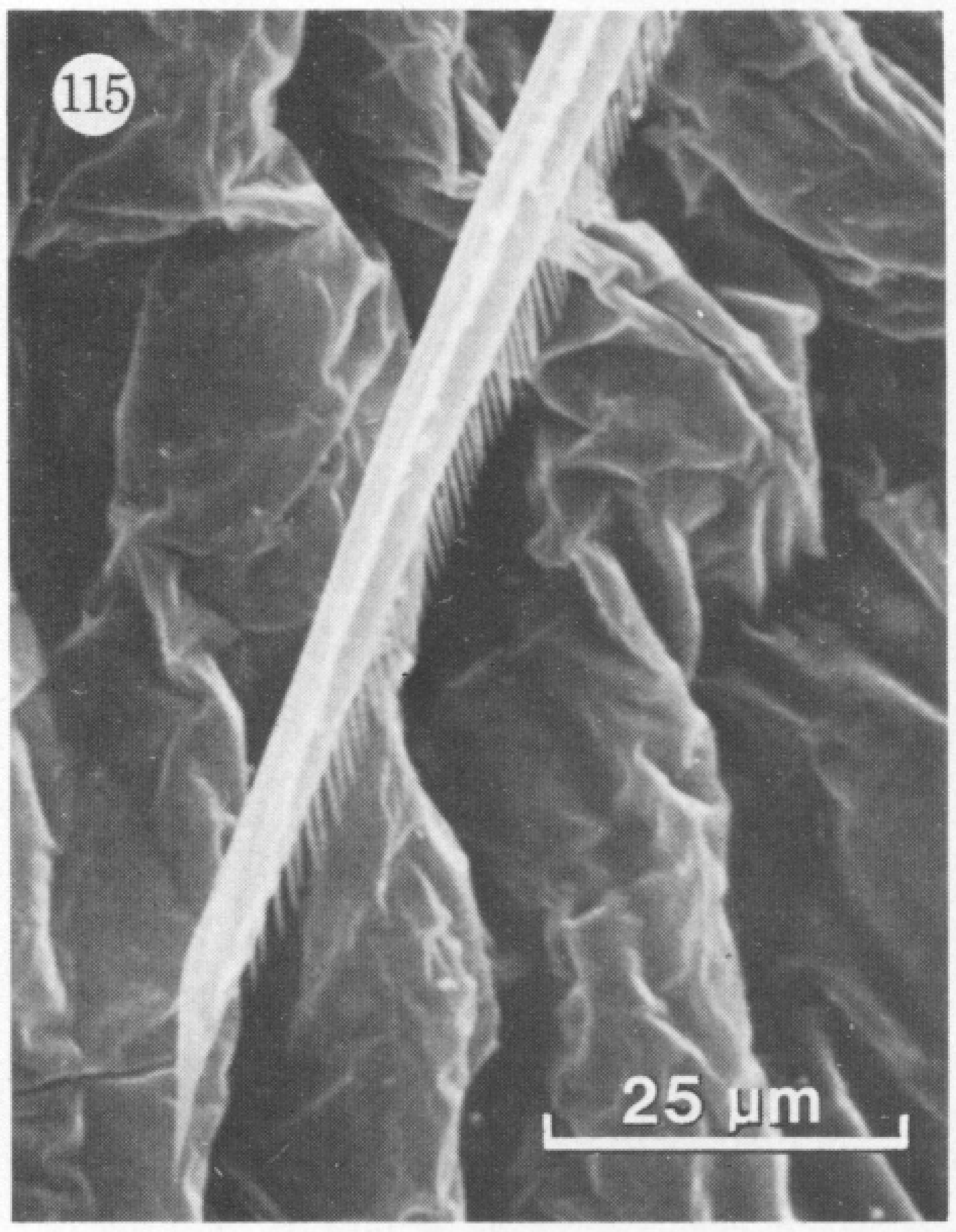

110

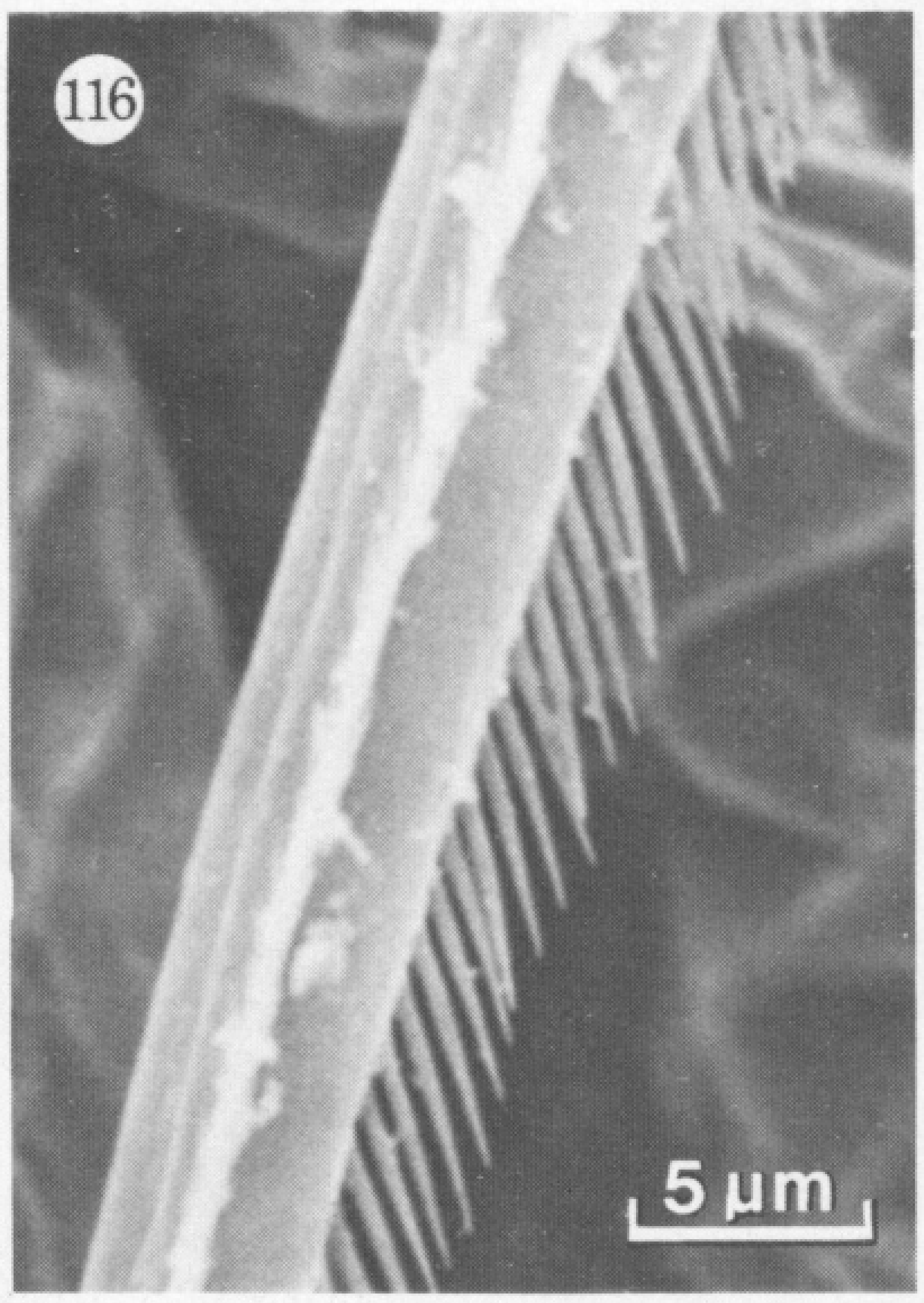

111

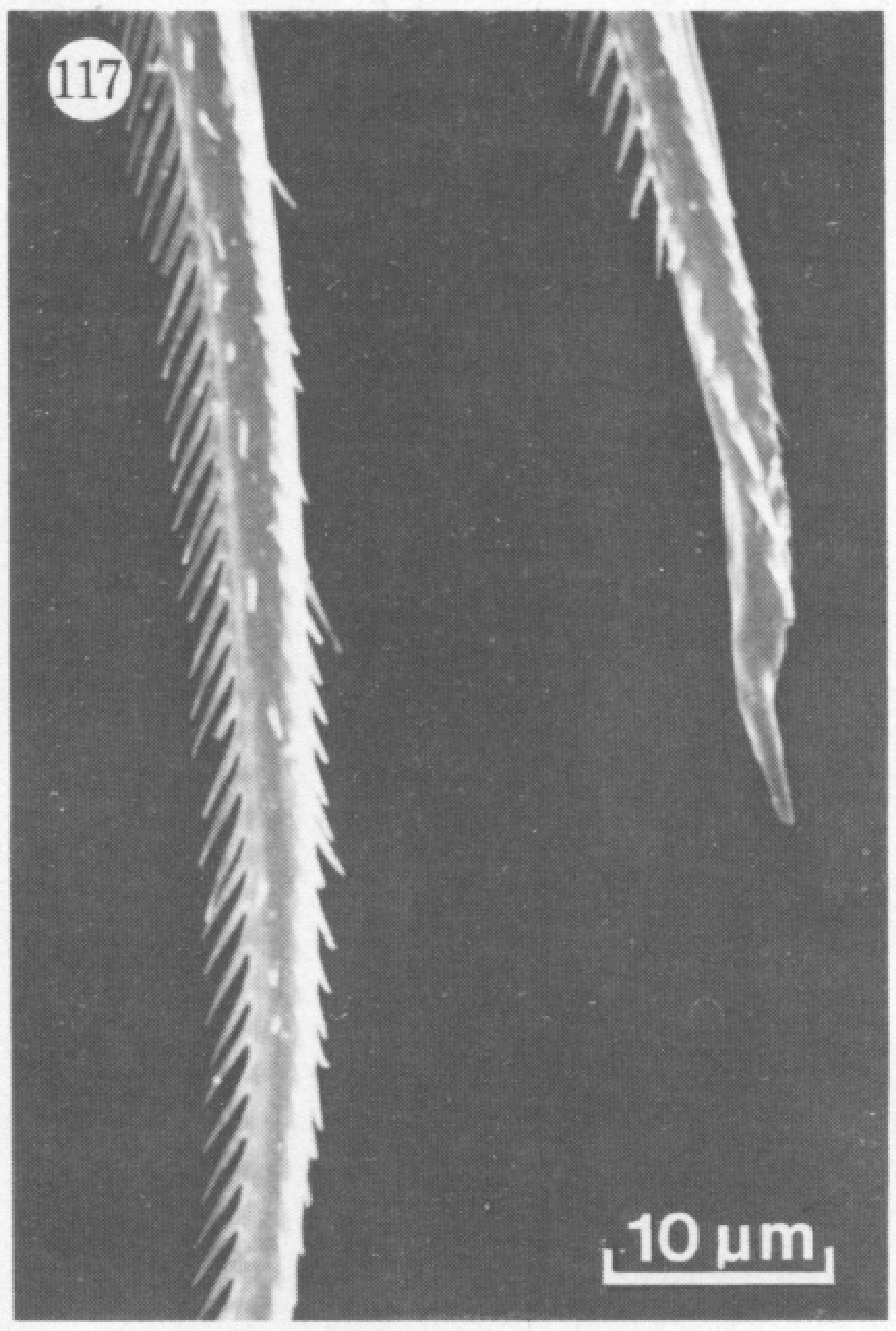

112
50 µm

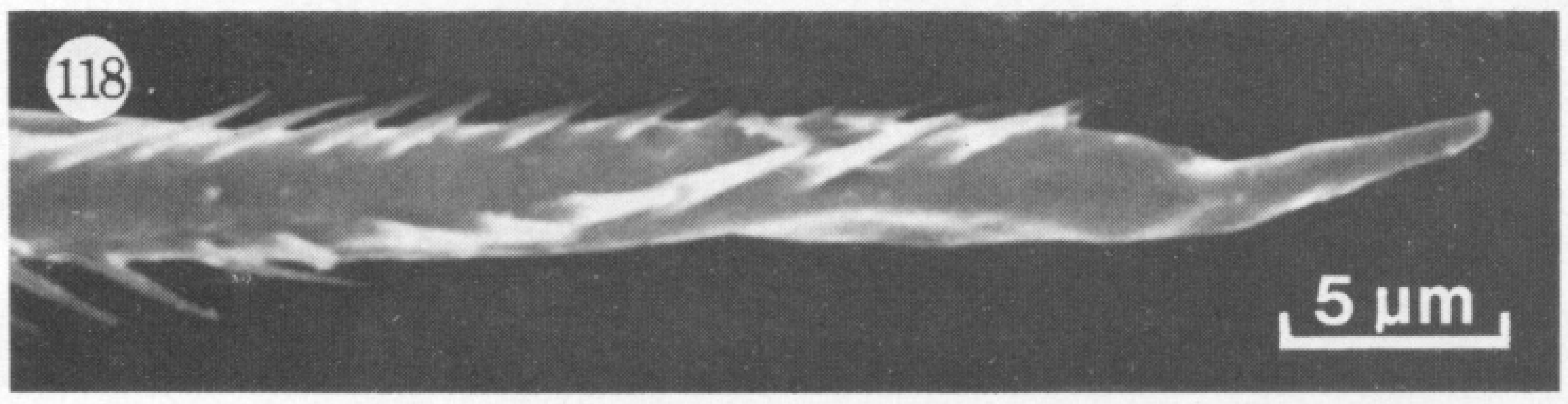

113

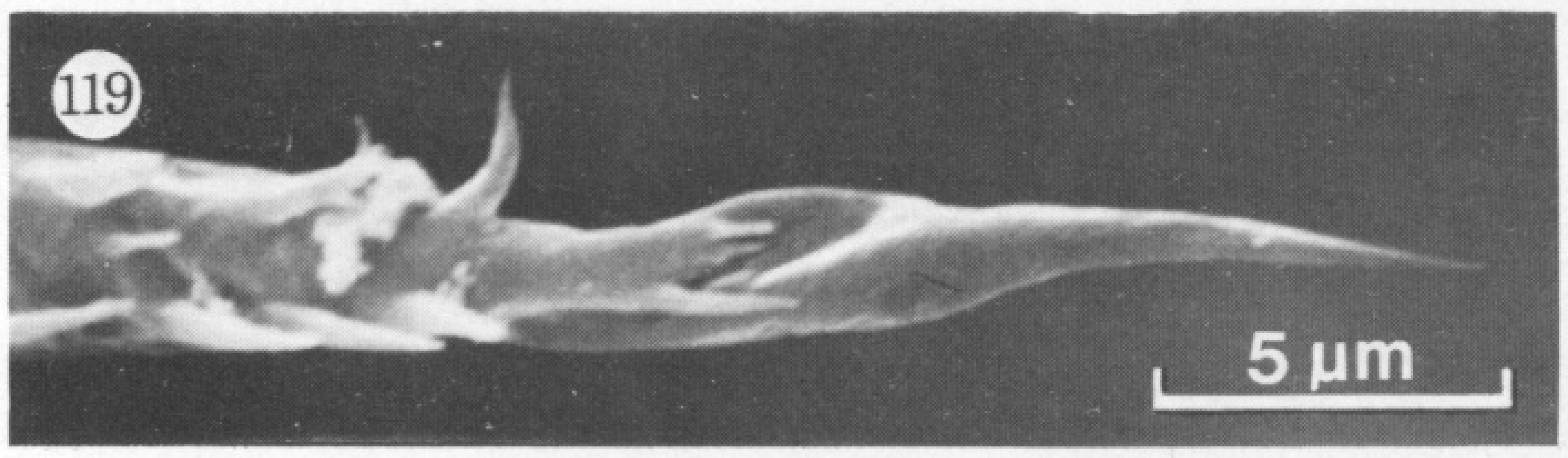

114
25 µm

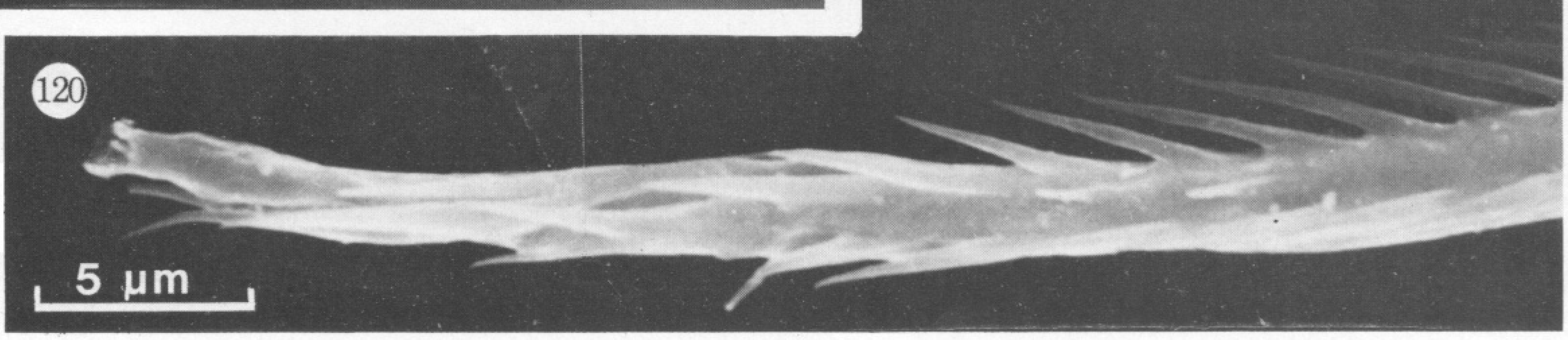

115
25 µm

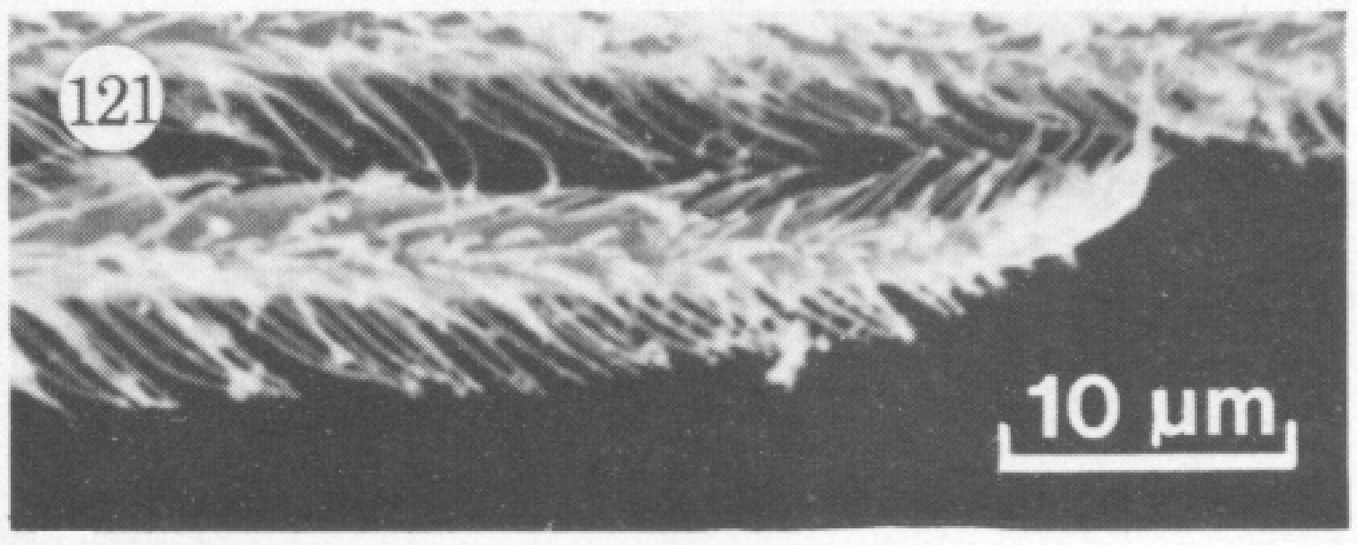

116
5 µm


117
10 µm

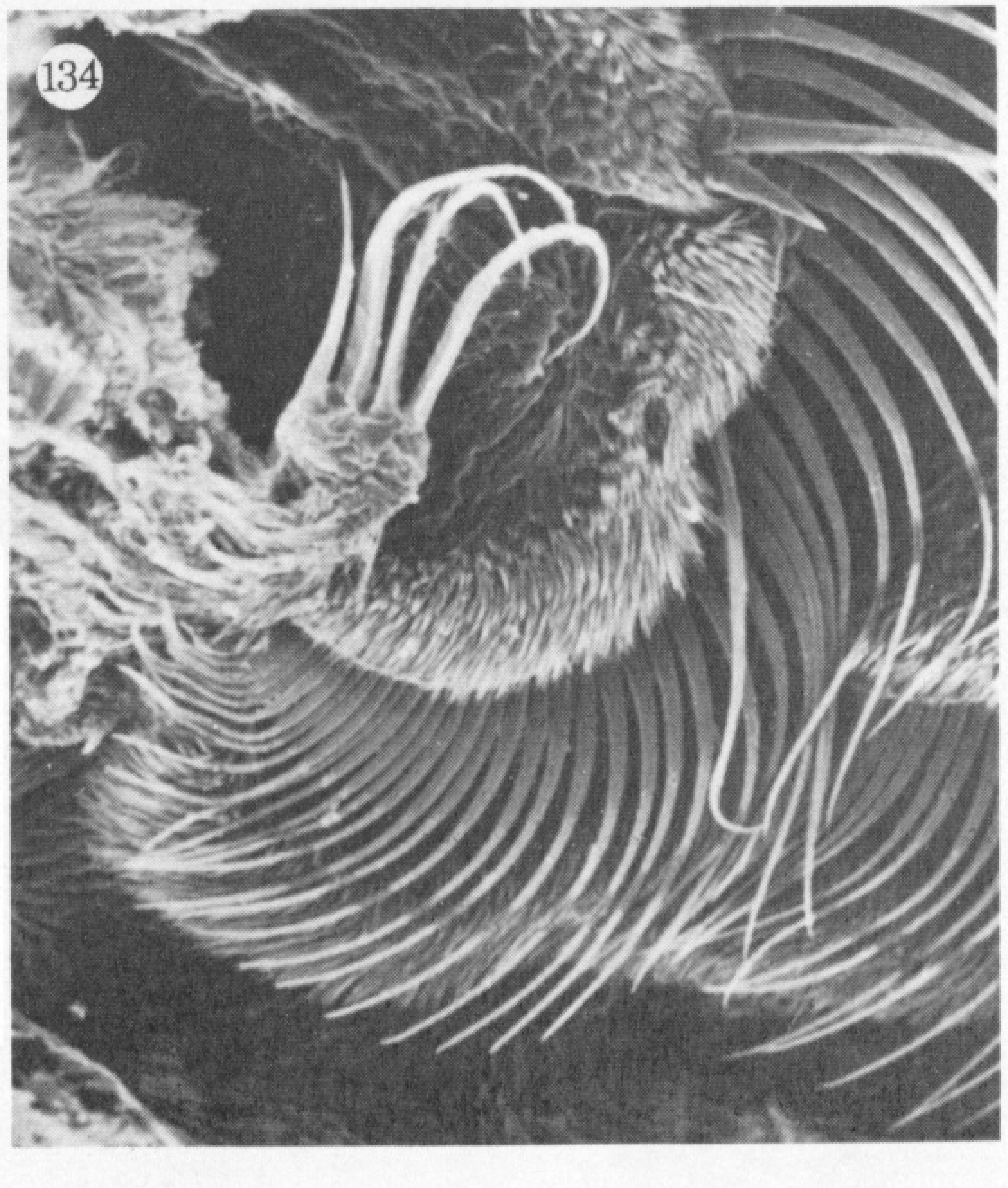

118
5 µm


119
5 µm

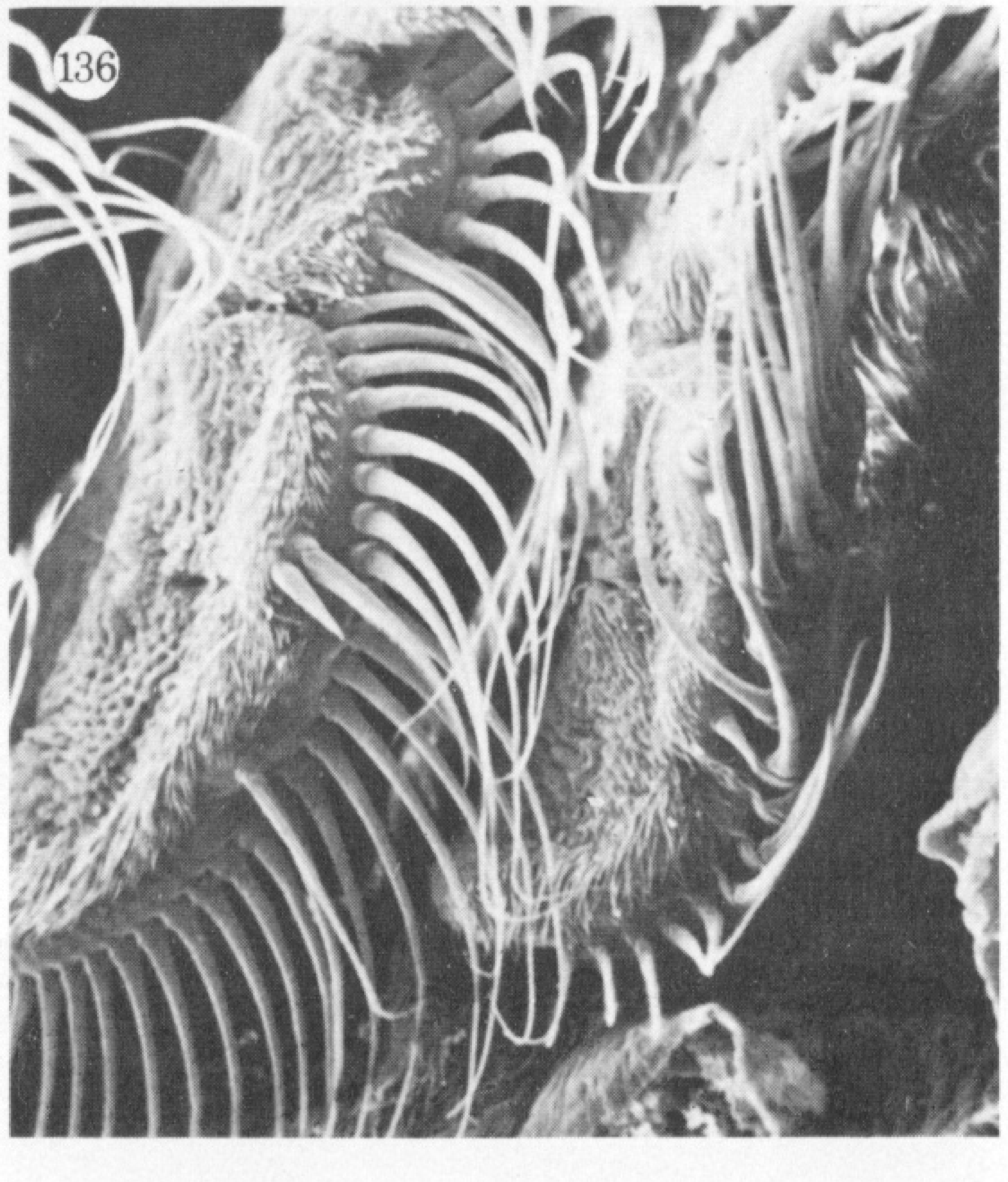

120
5 µm

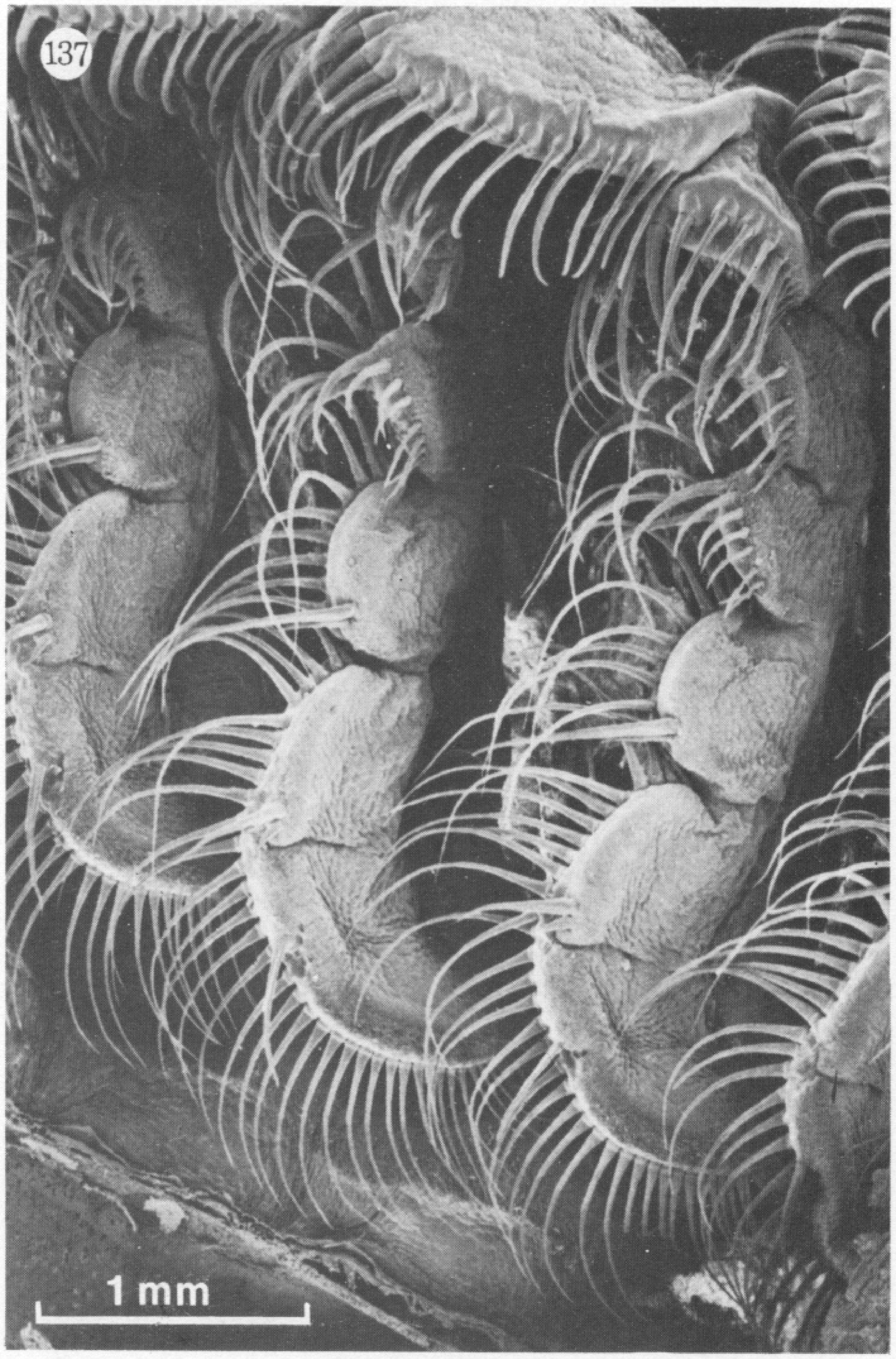

121
10 µm

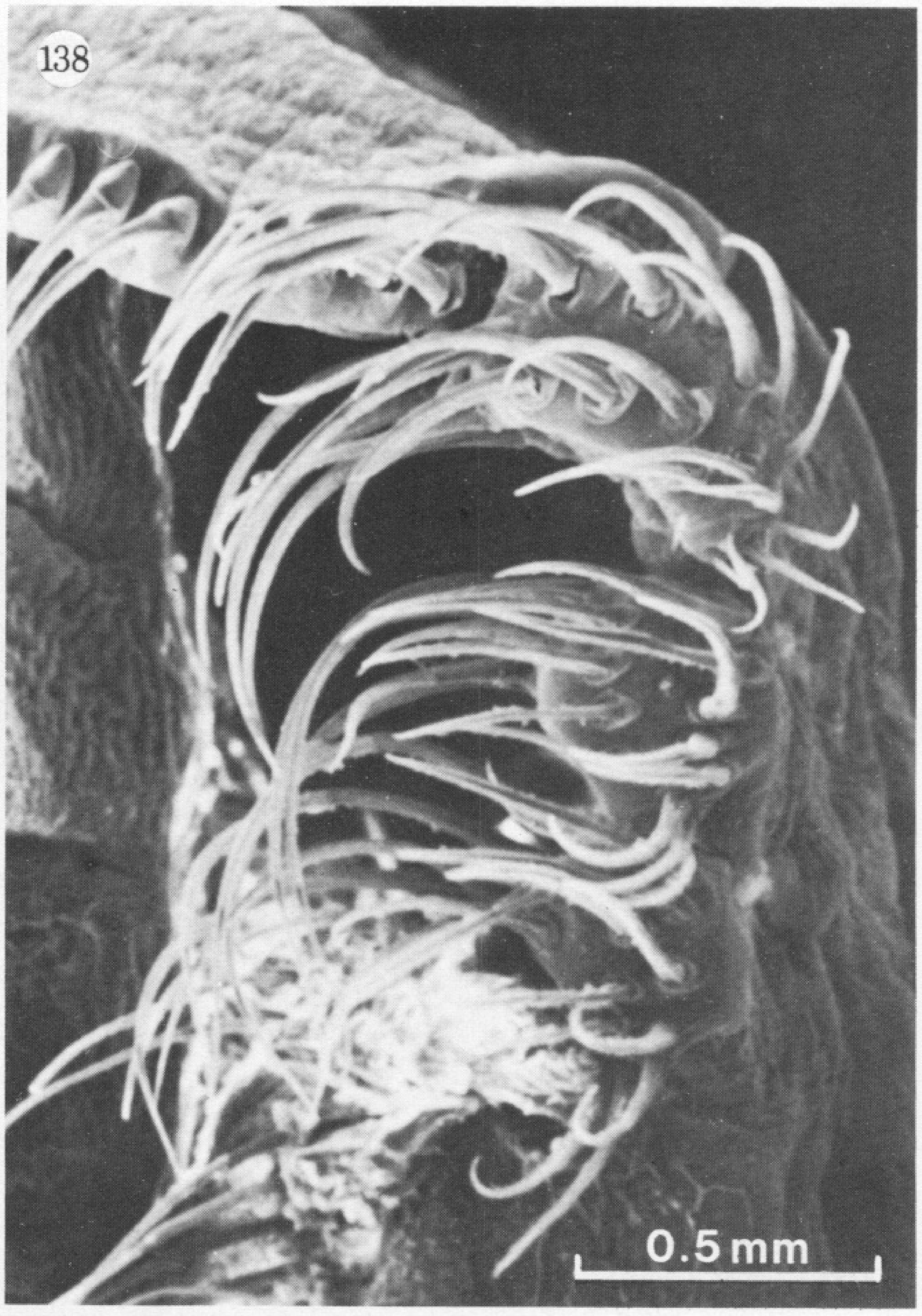

133
500 µm

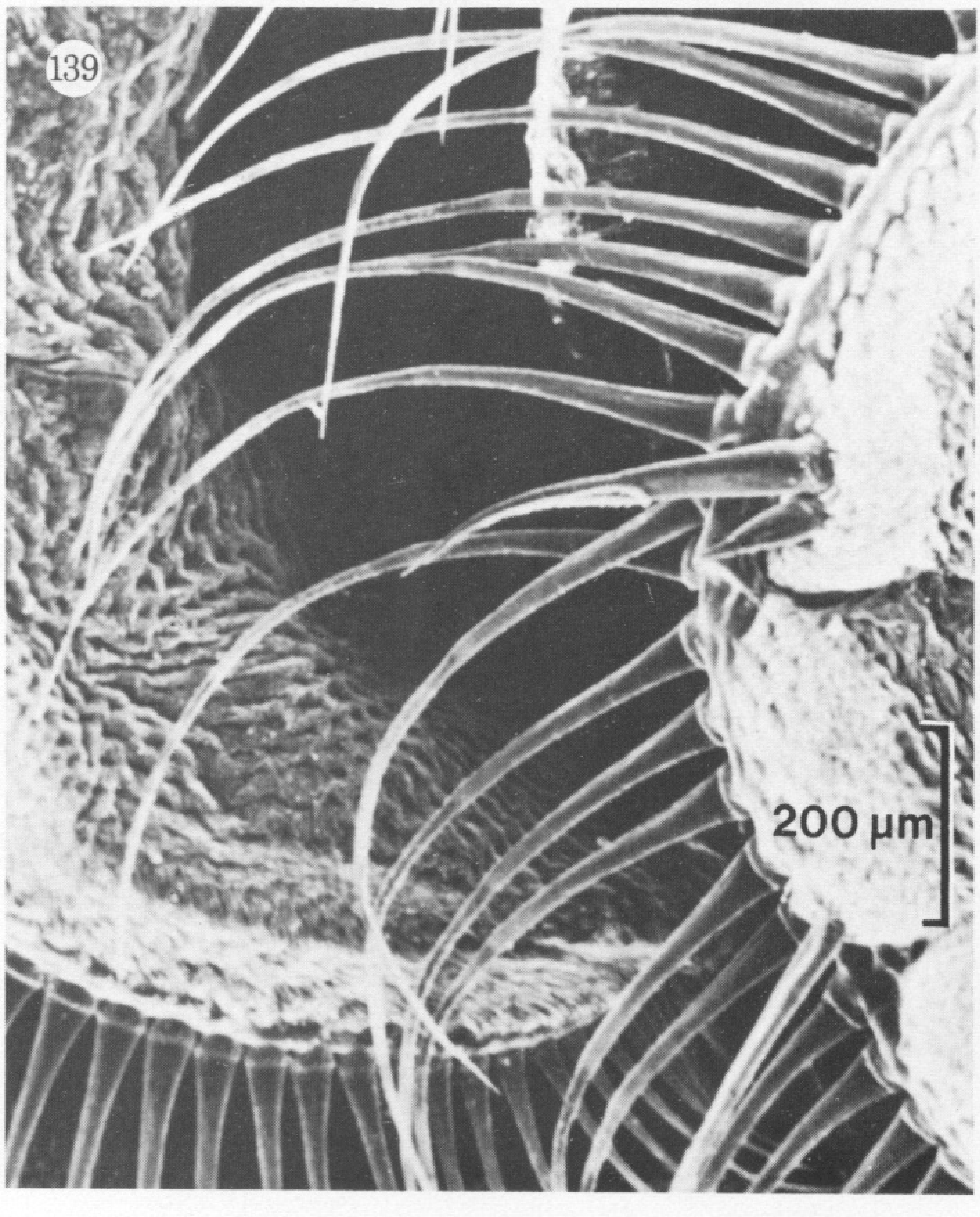

134

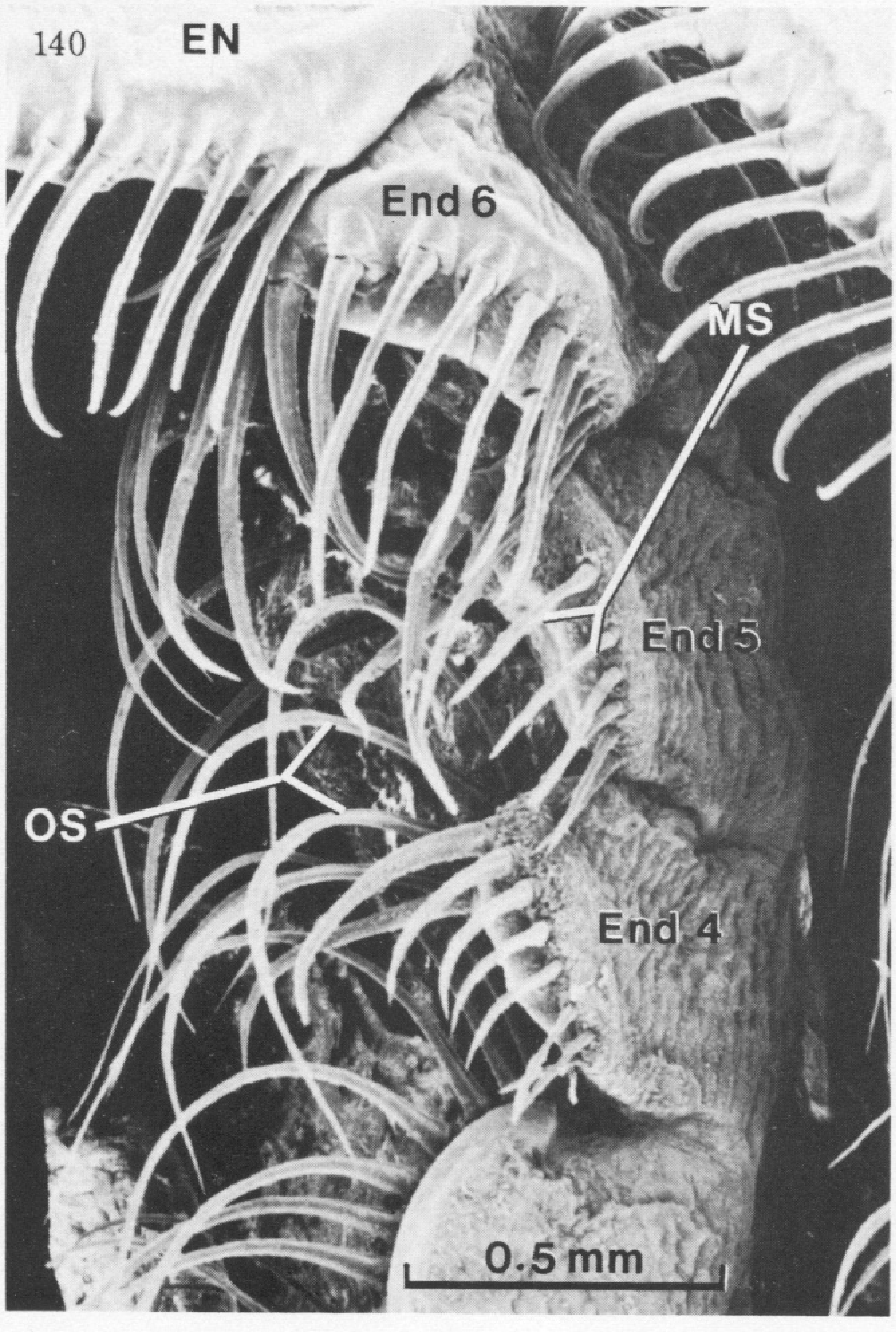

135

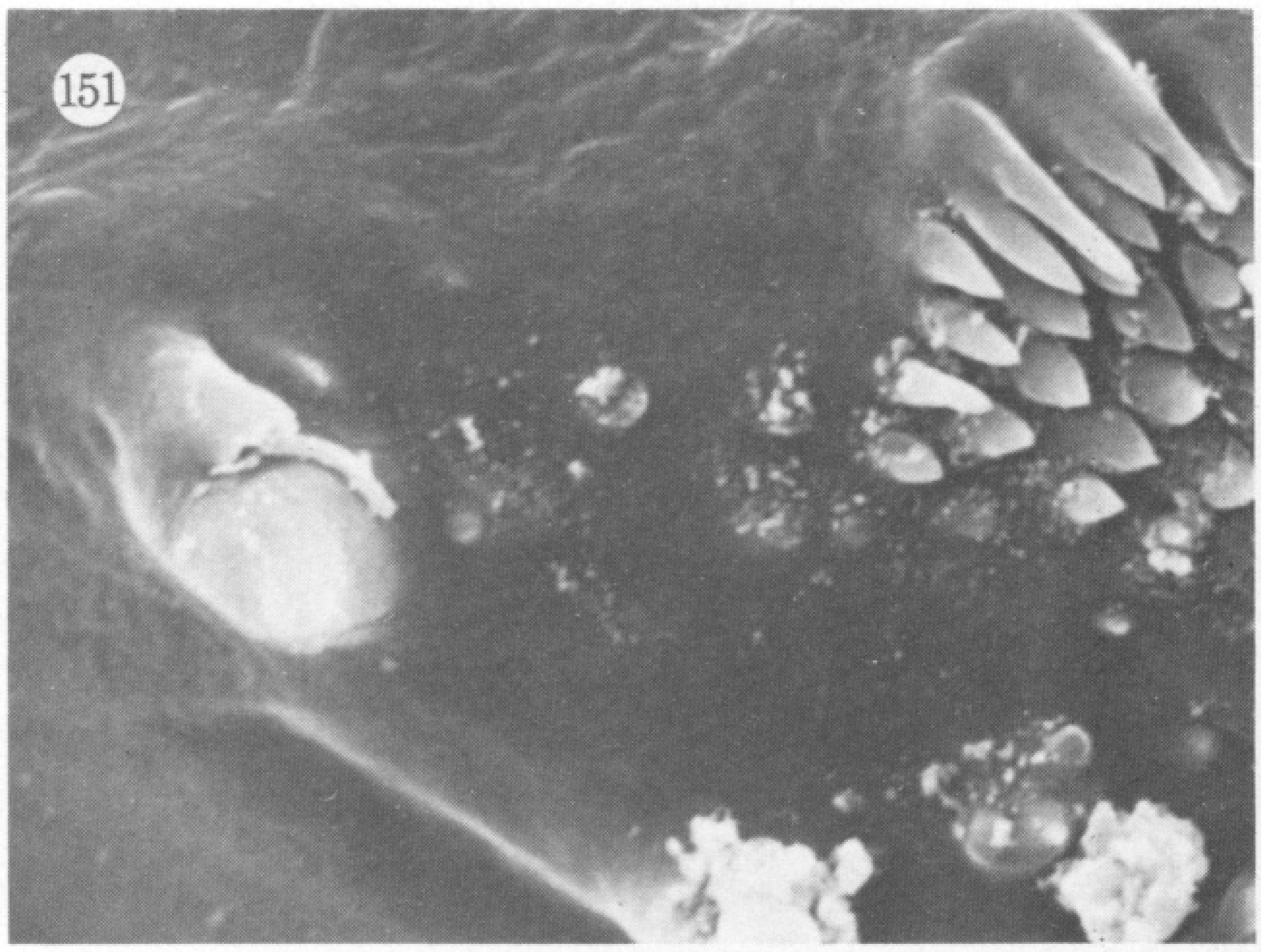

136

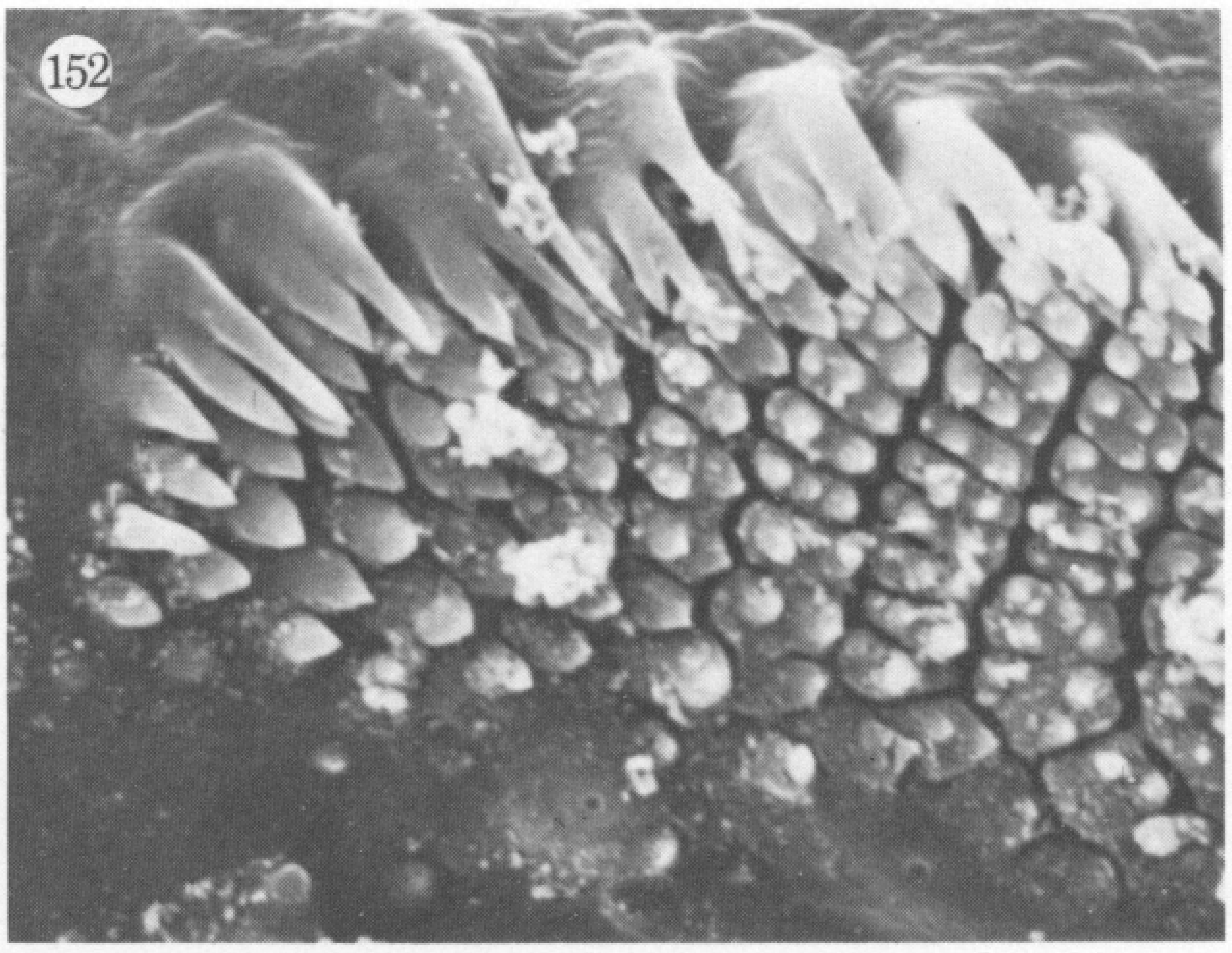

137
1 mm

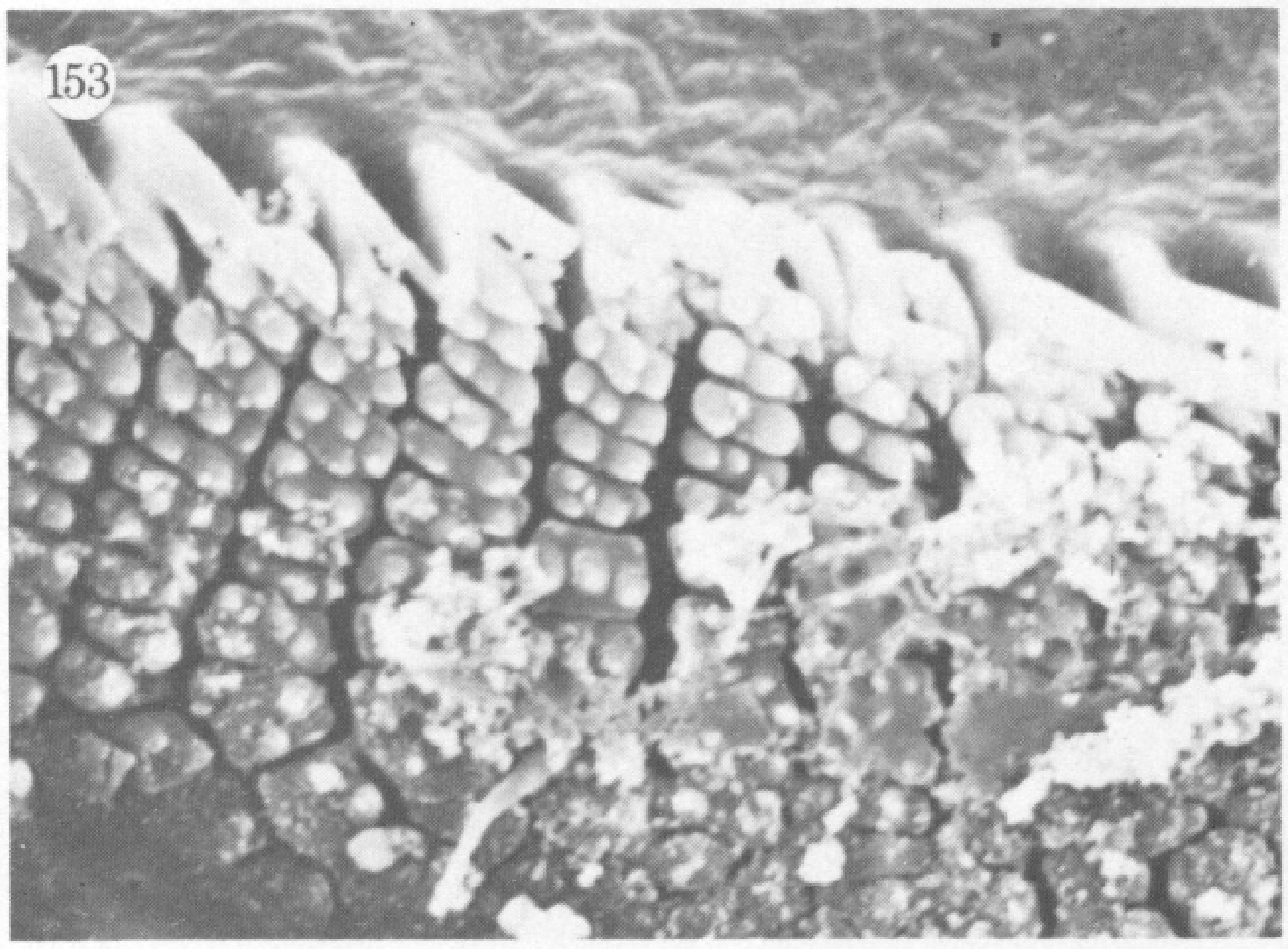

138
0.5 mm

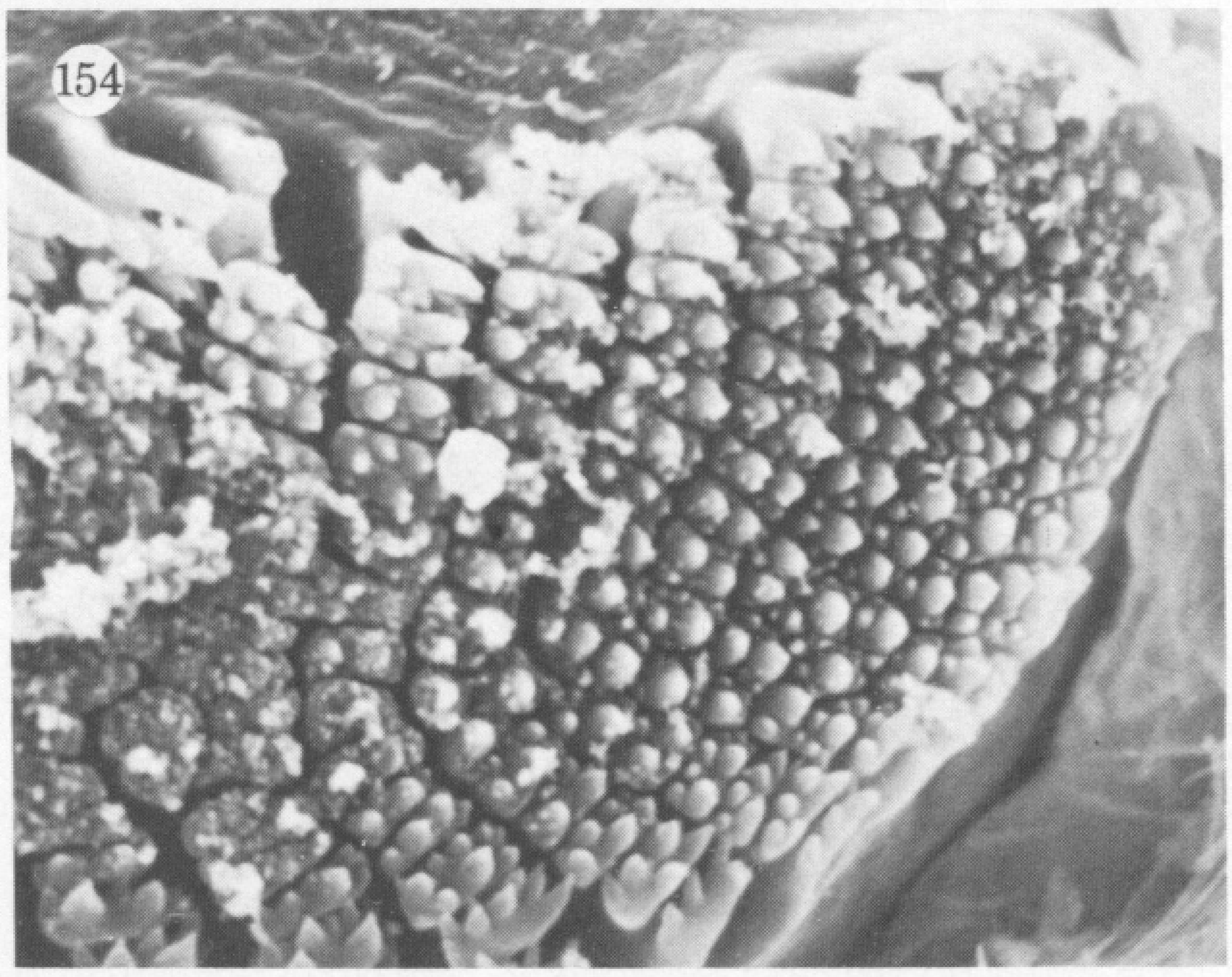

139
200 µm

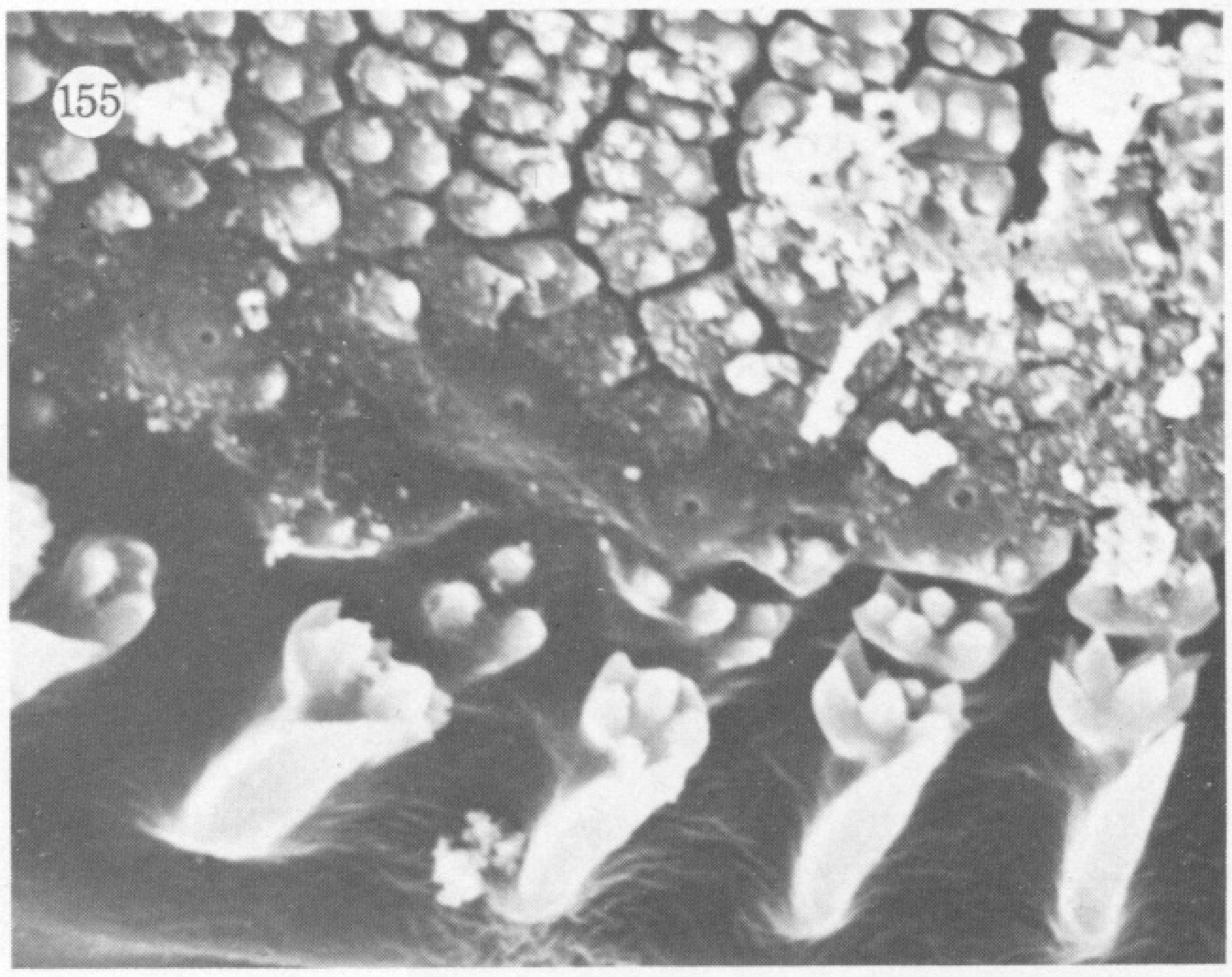

140
EN
End 6
MS
End 5
OS
End 4
0.5 mm

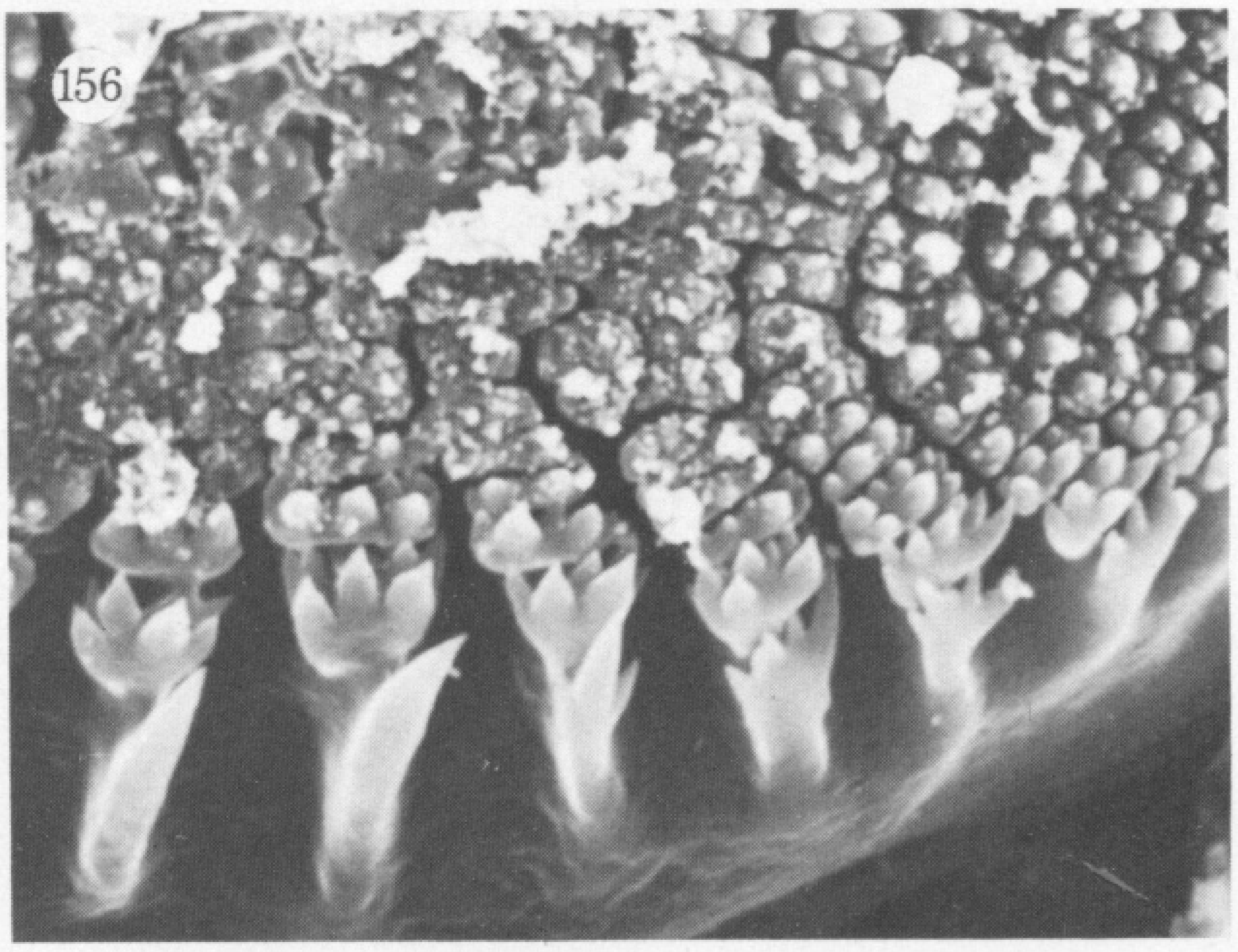

151

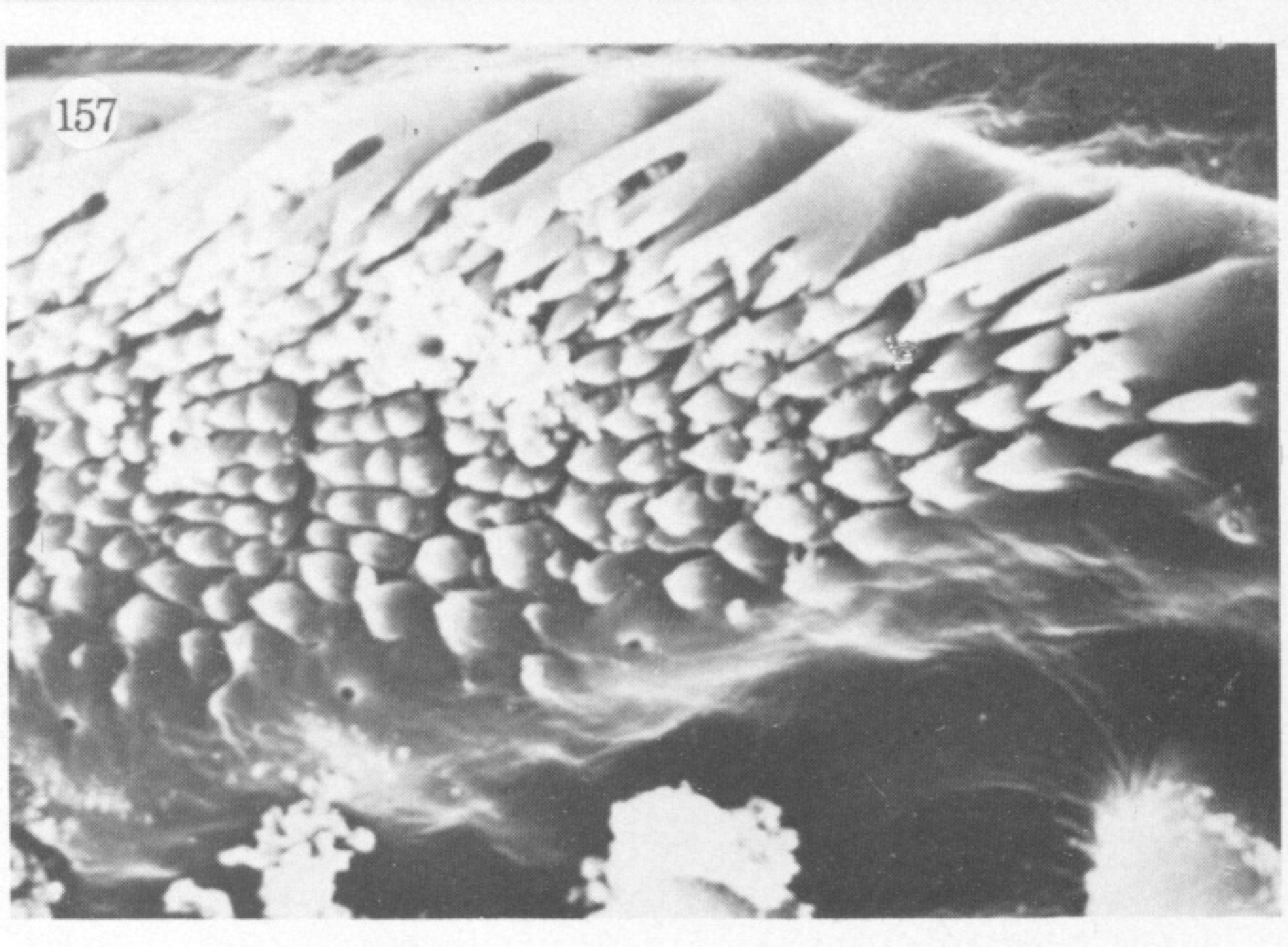

152

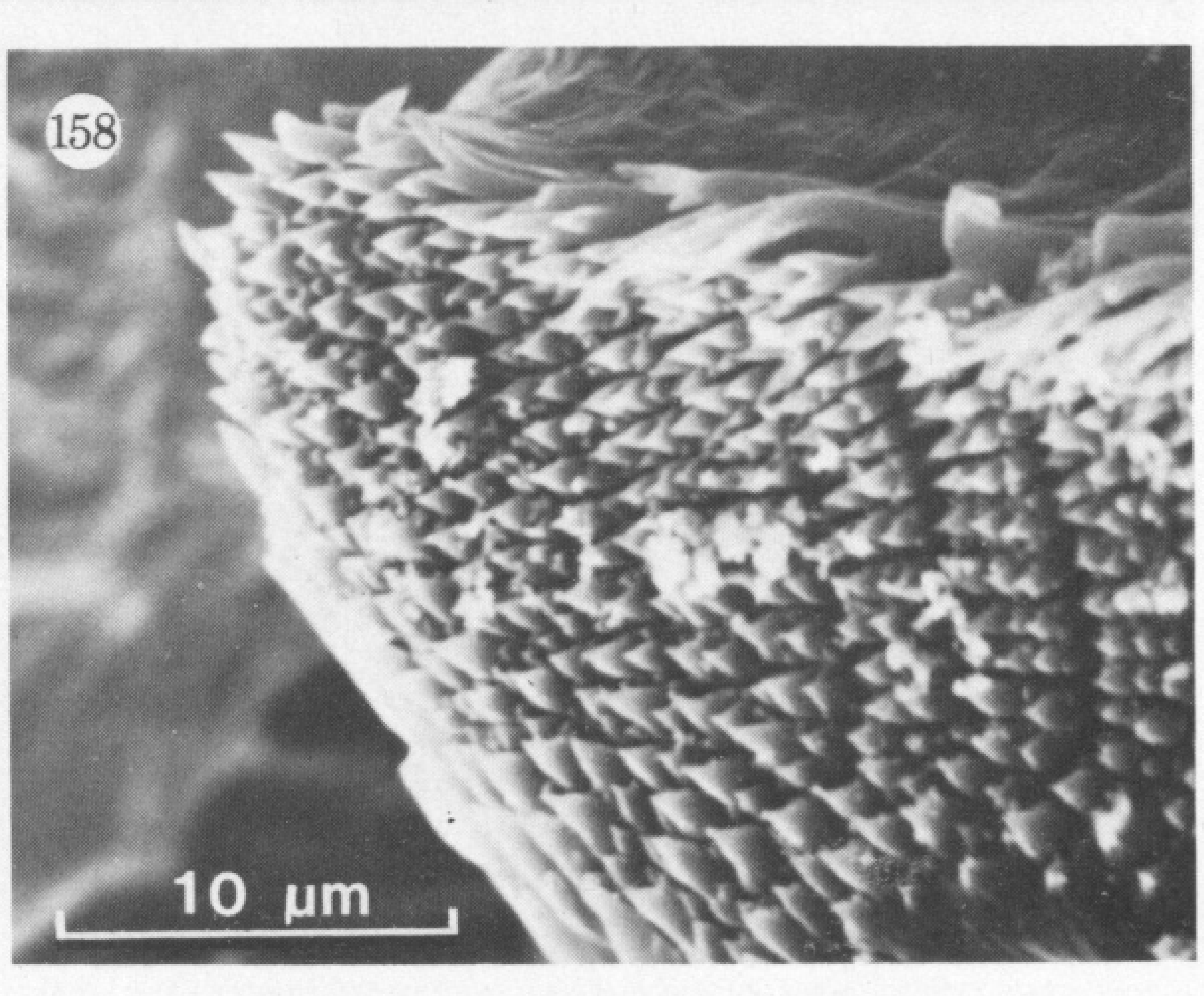

153

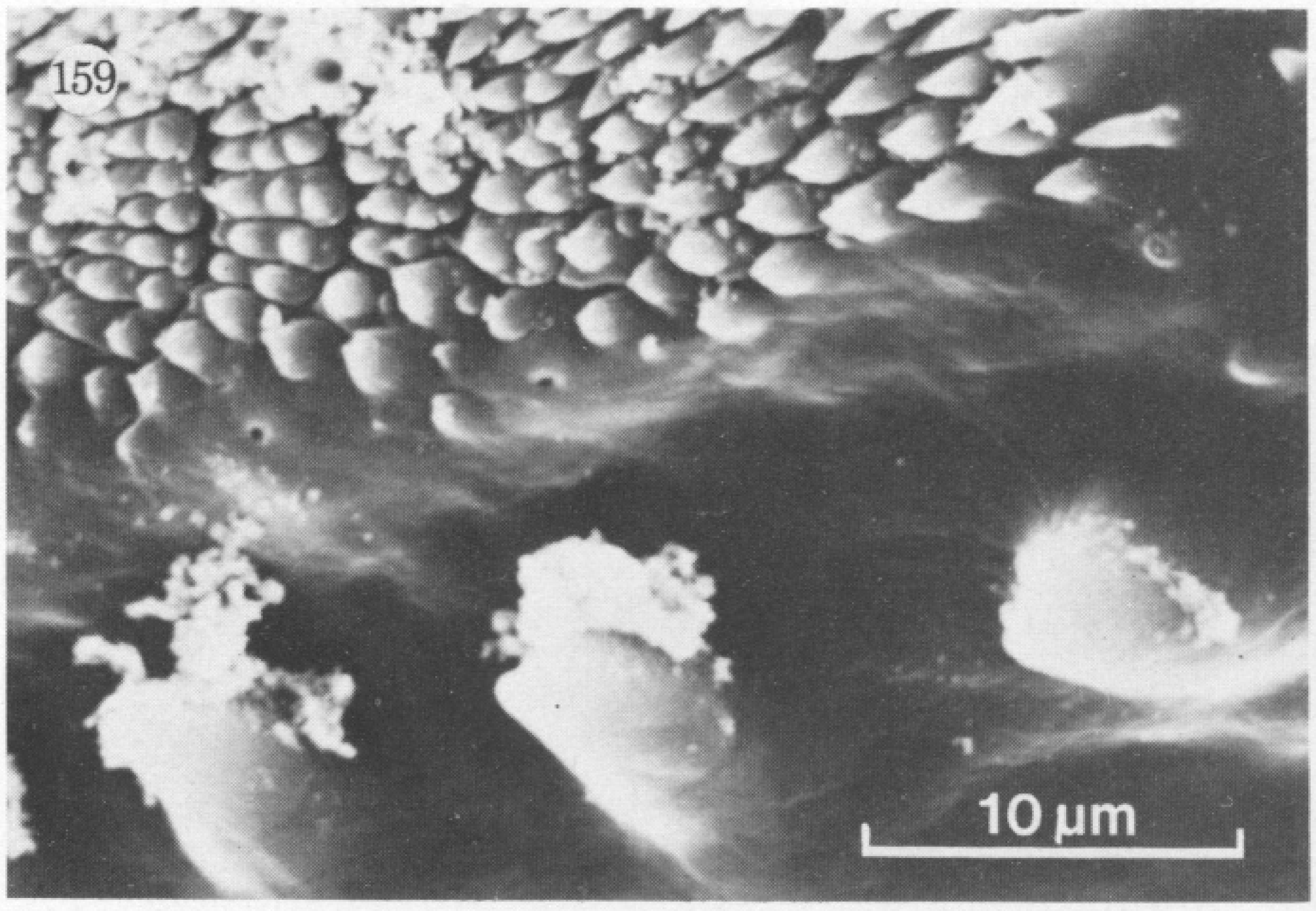

154

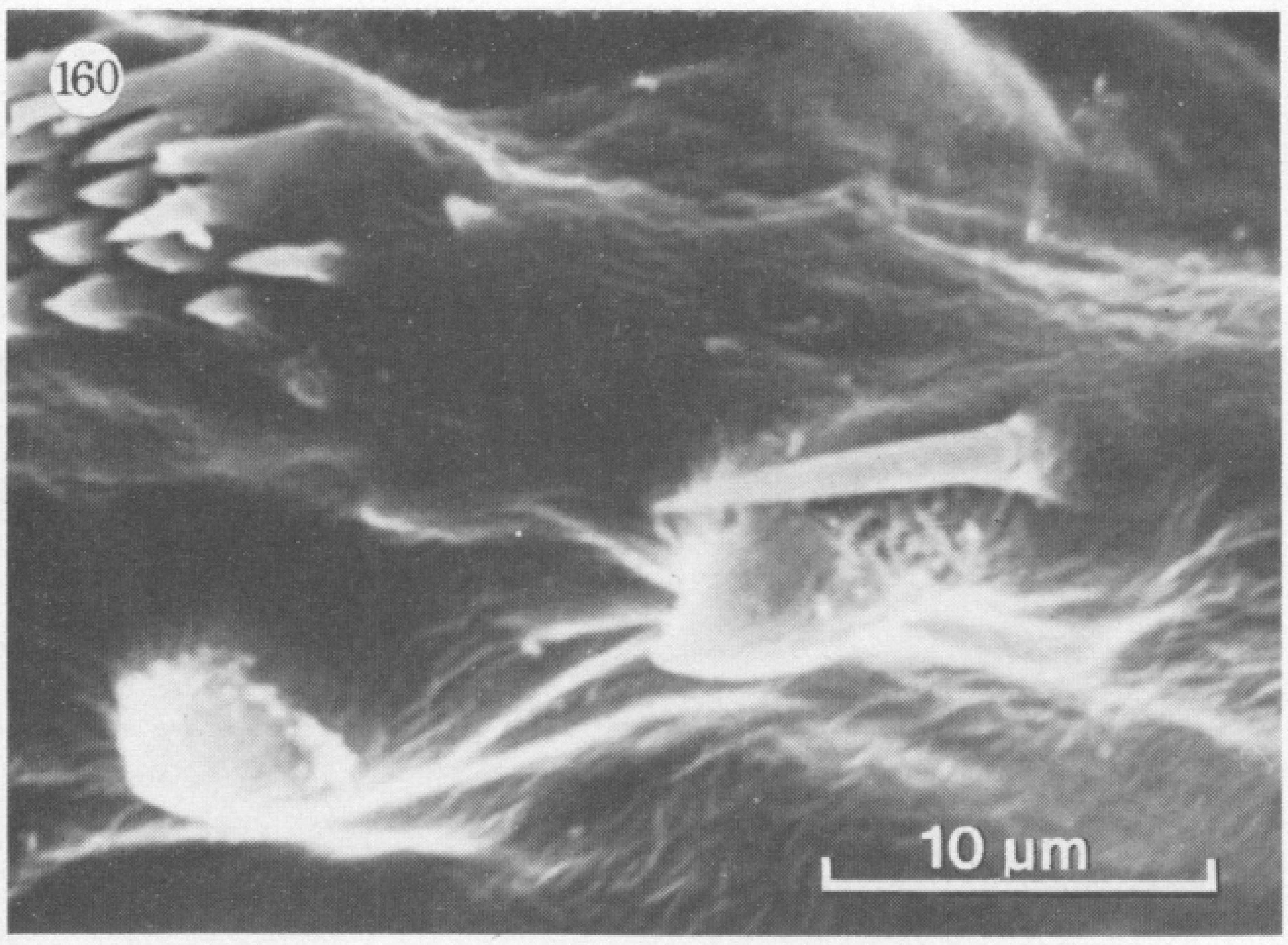

155

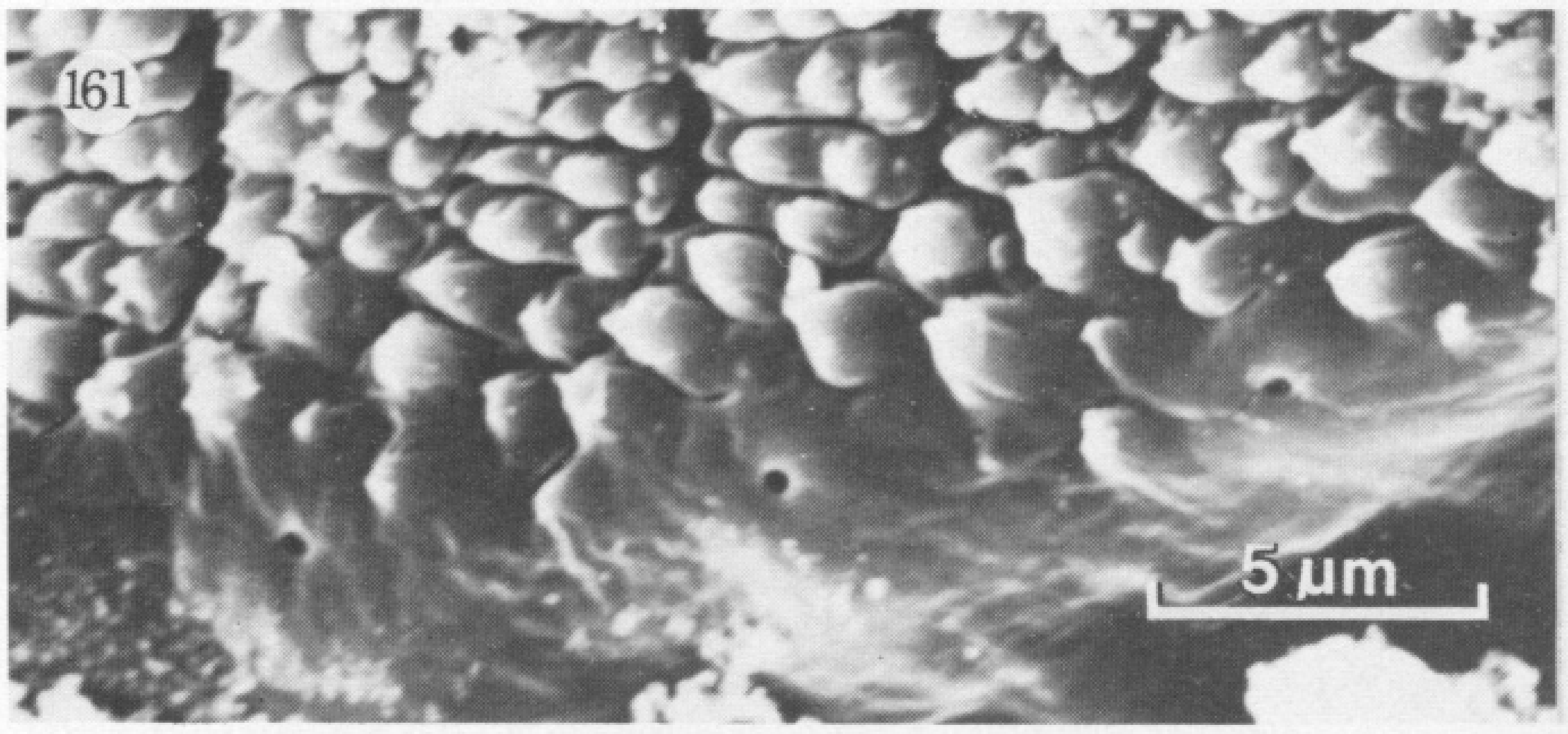

156

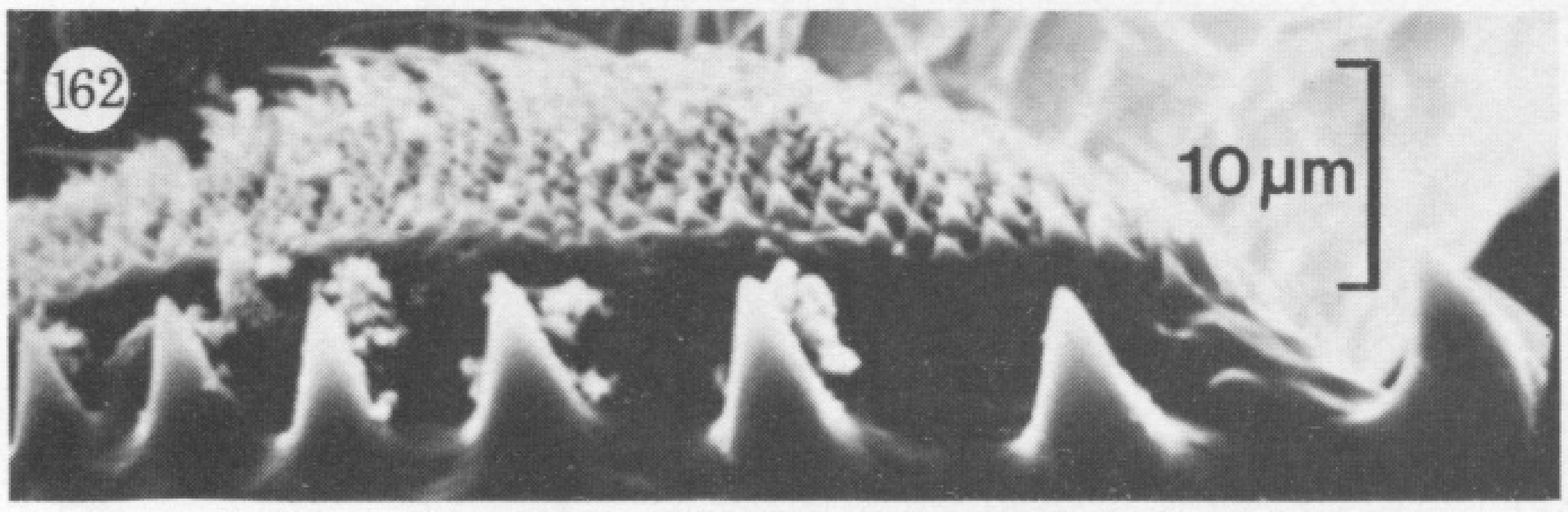

157

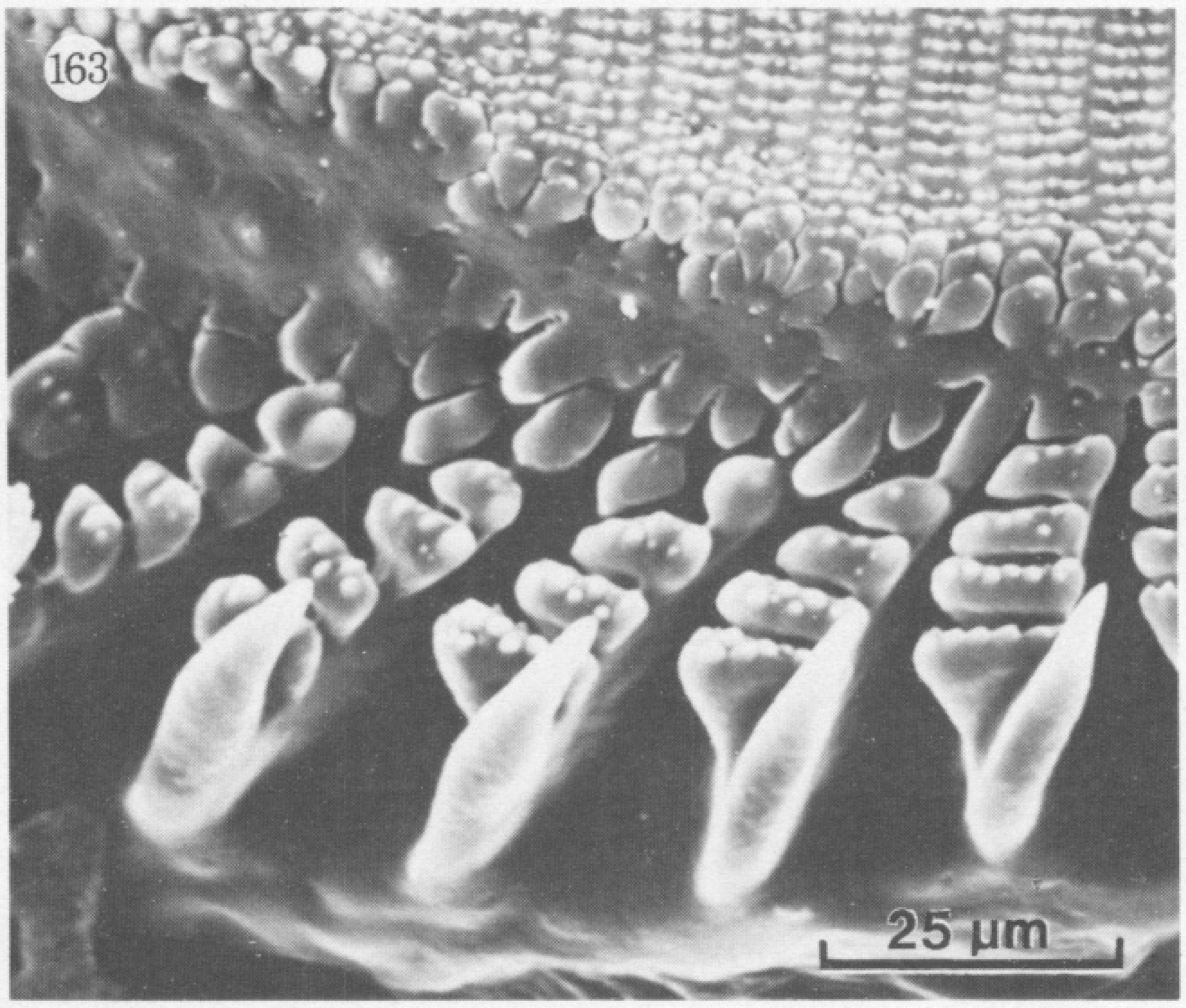

158
10 µm

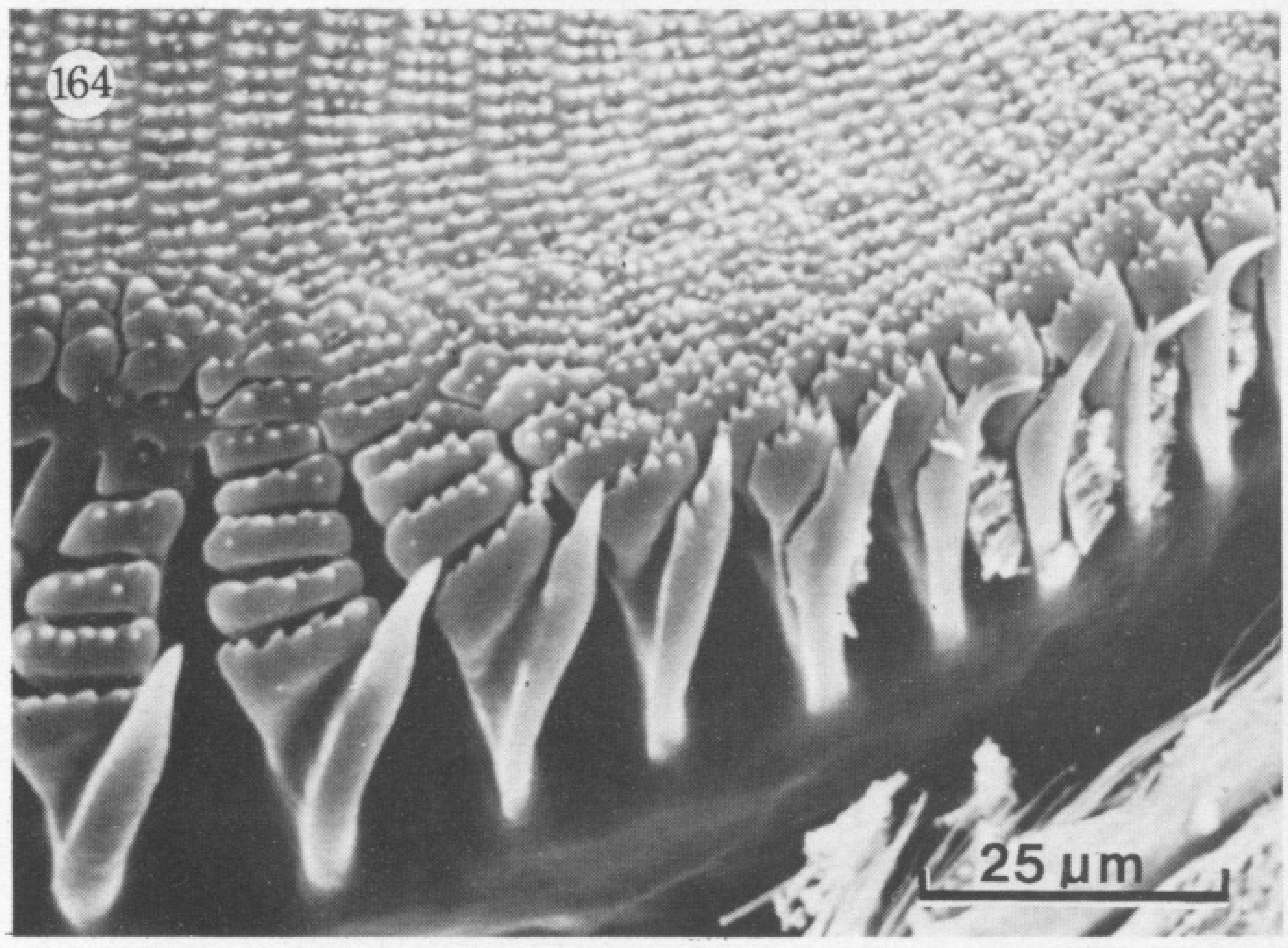

159

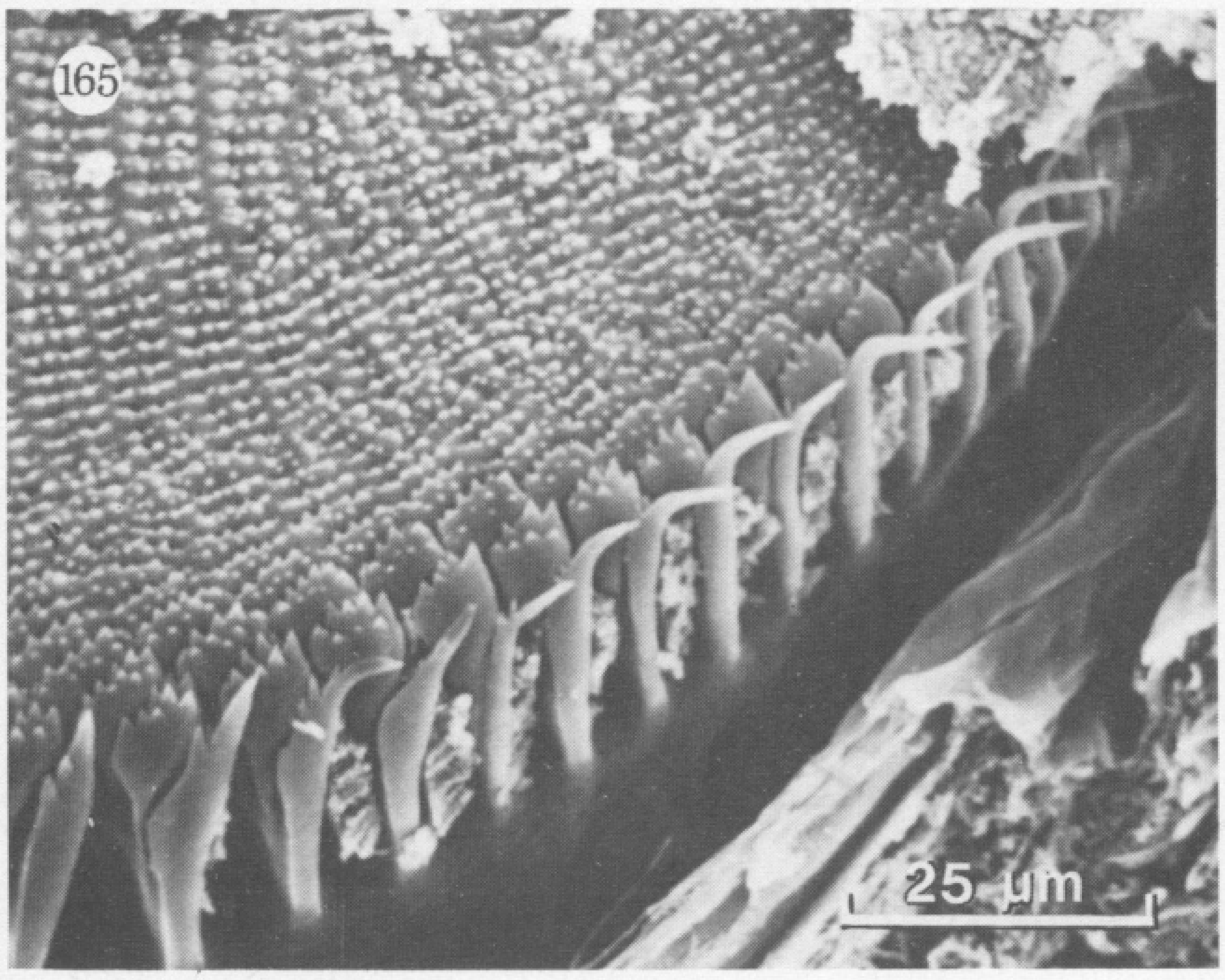

160

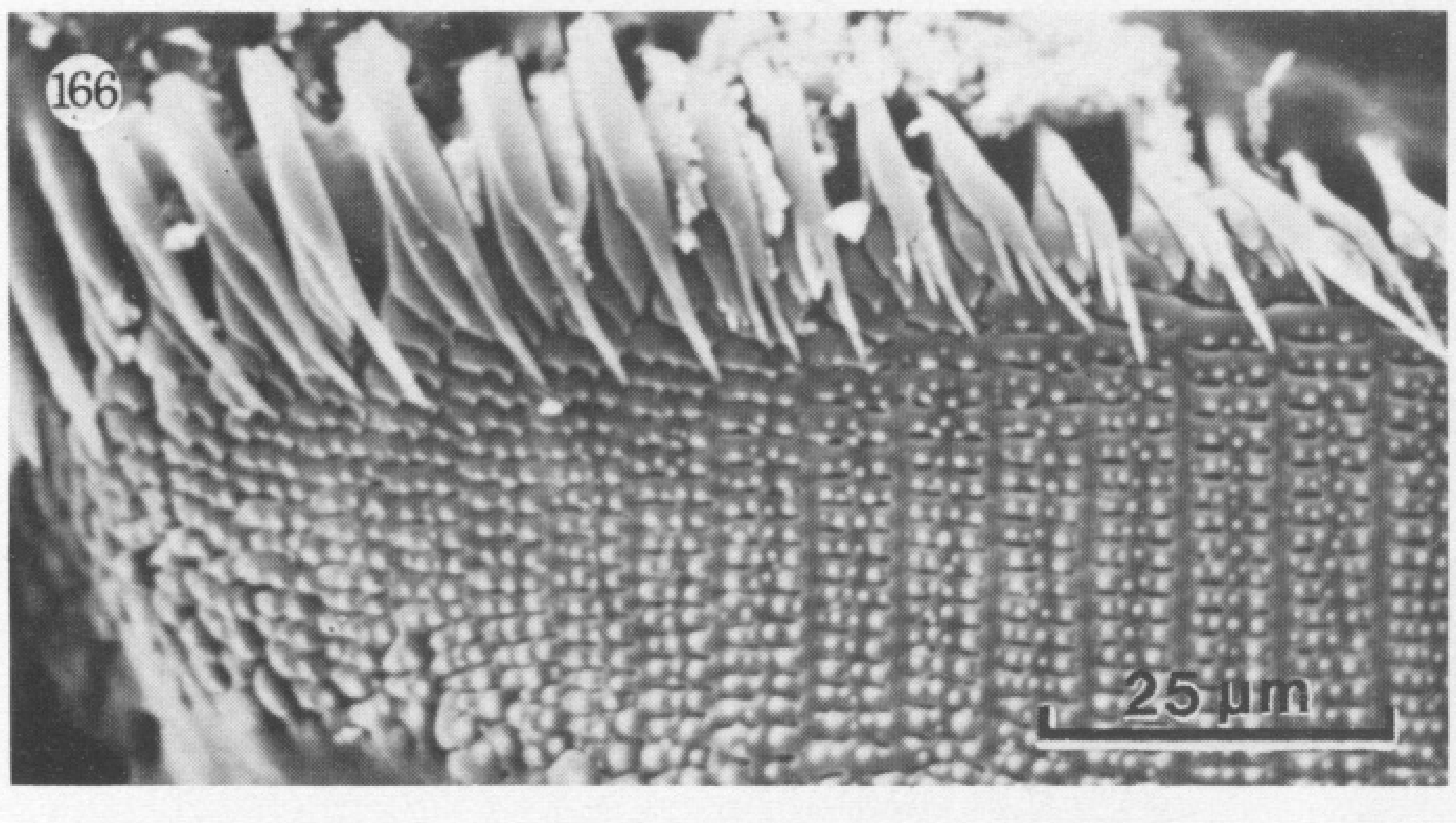

161

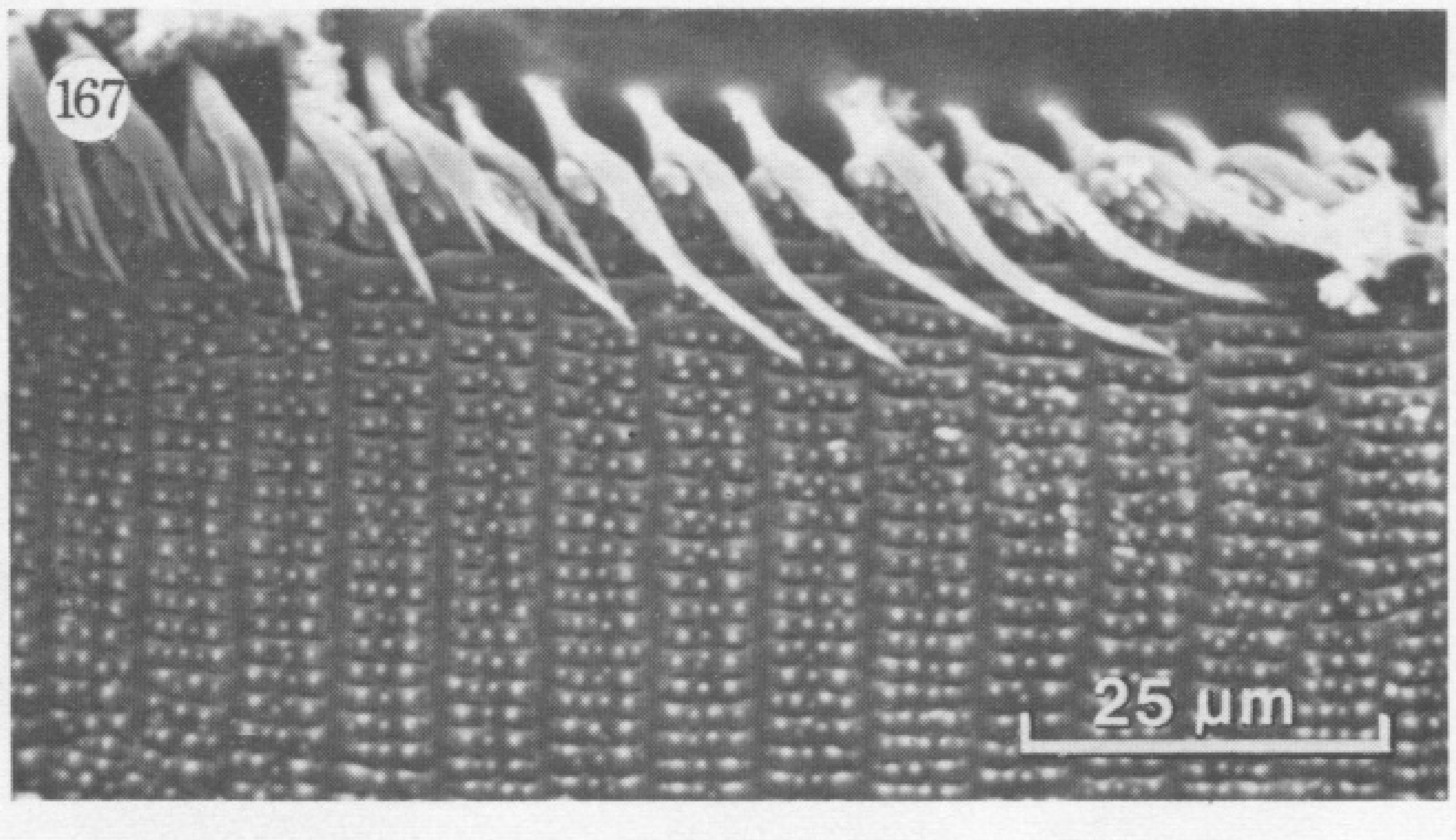

162

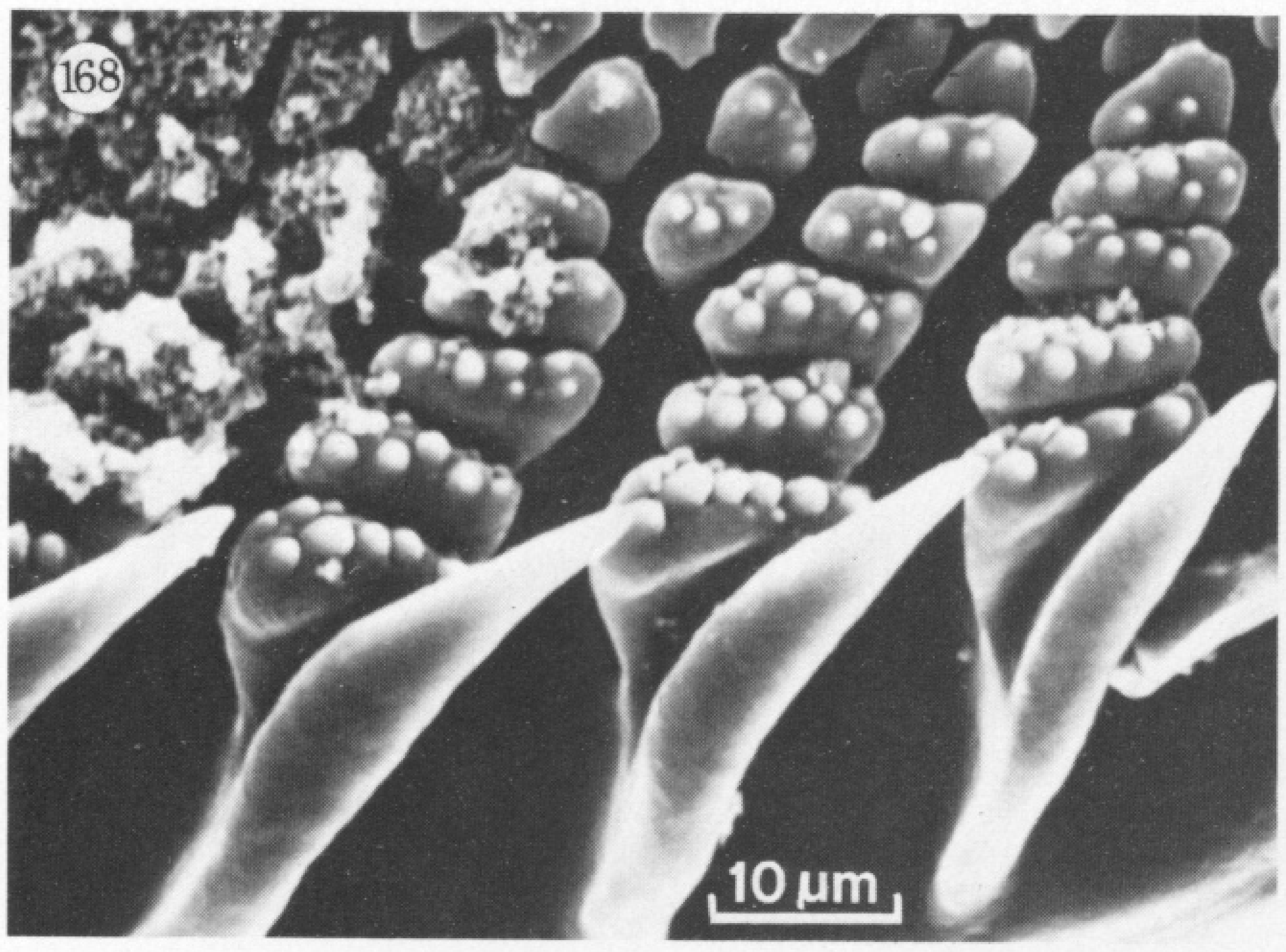

163

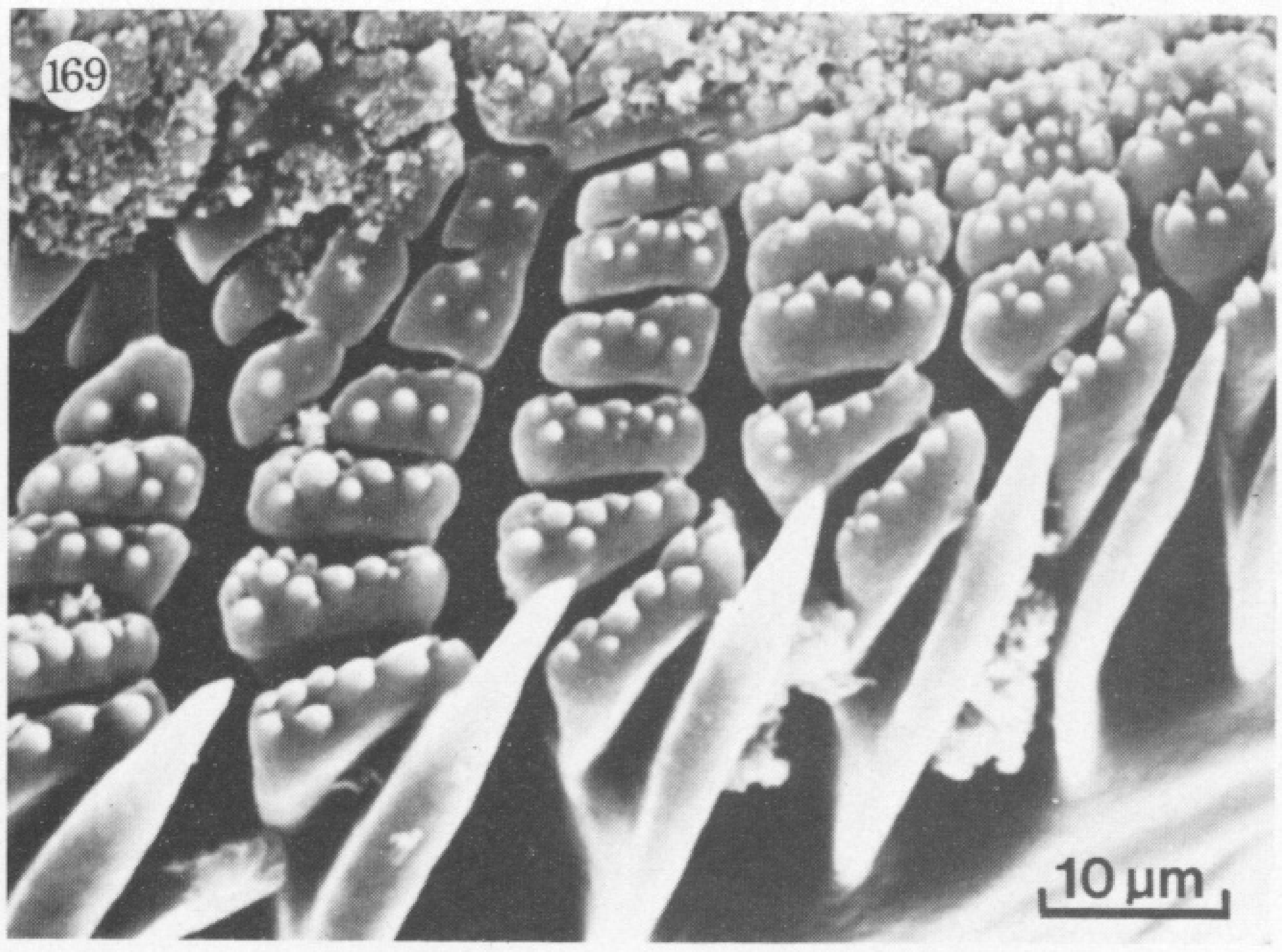

164

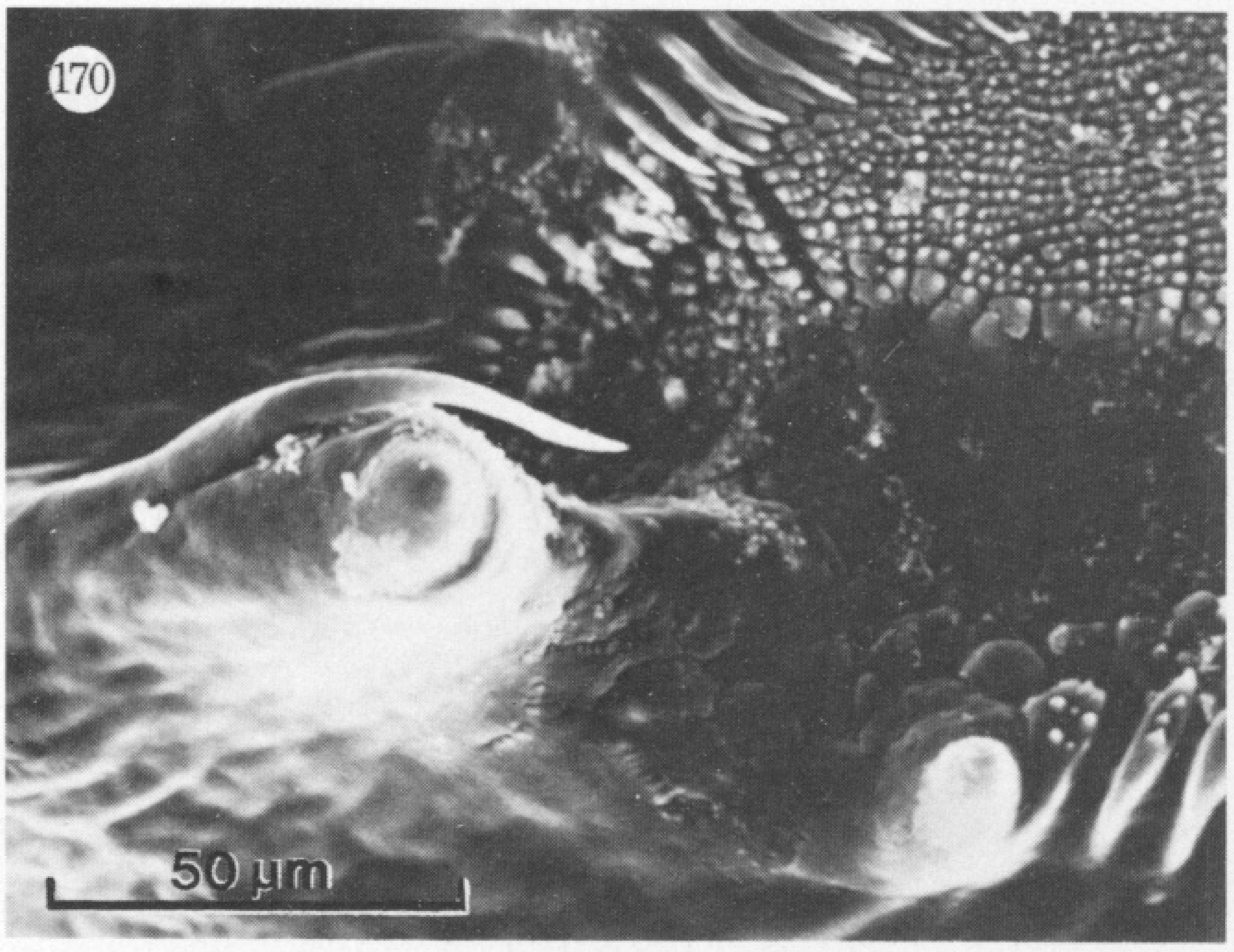

165

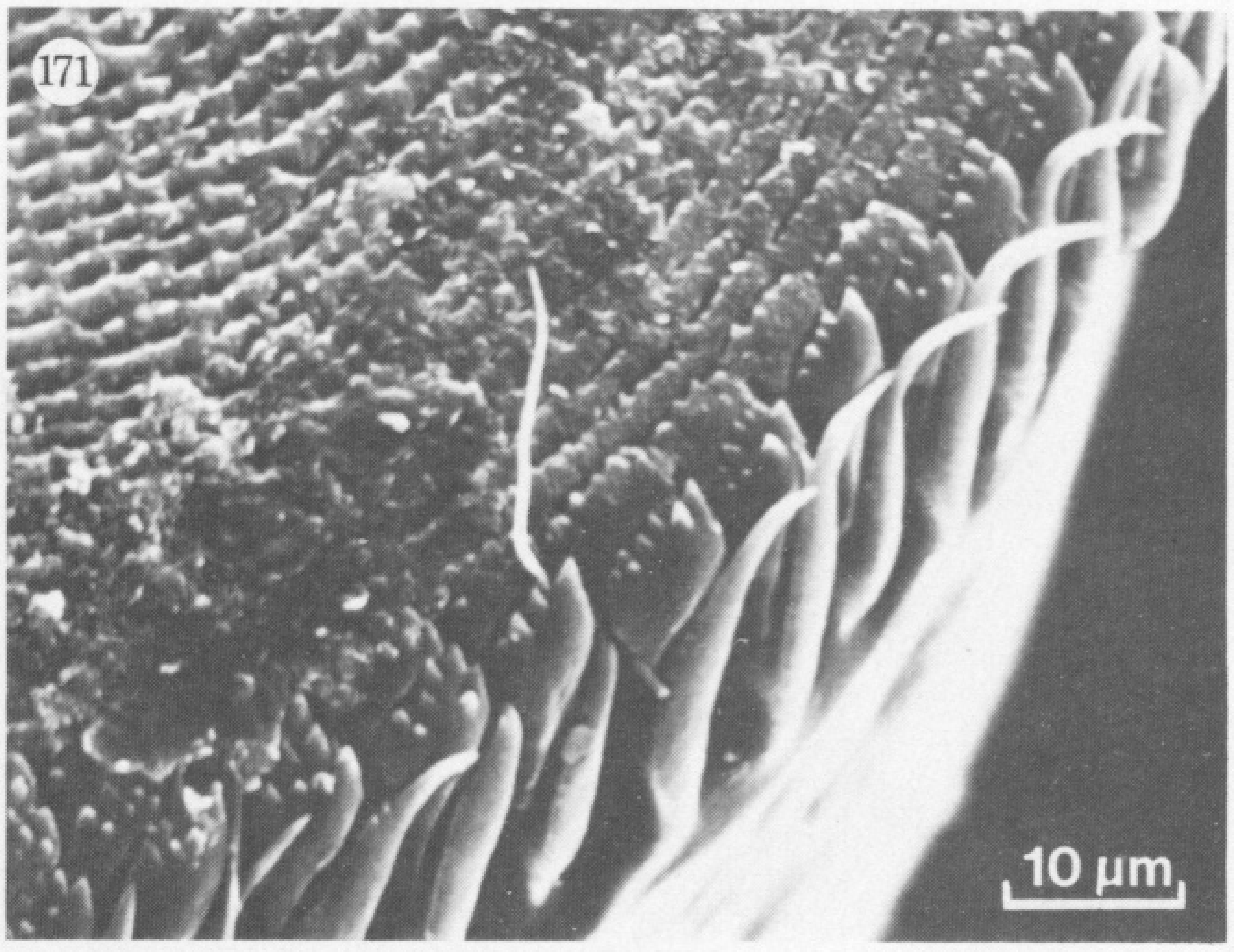

166

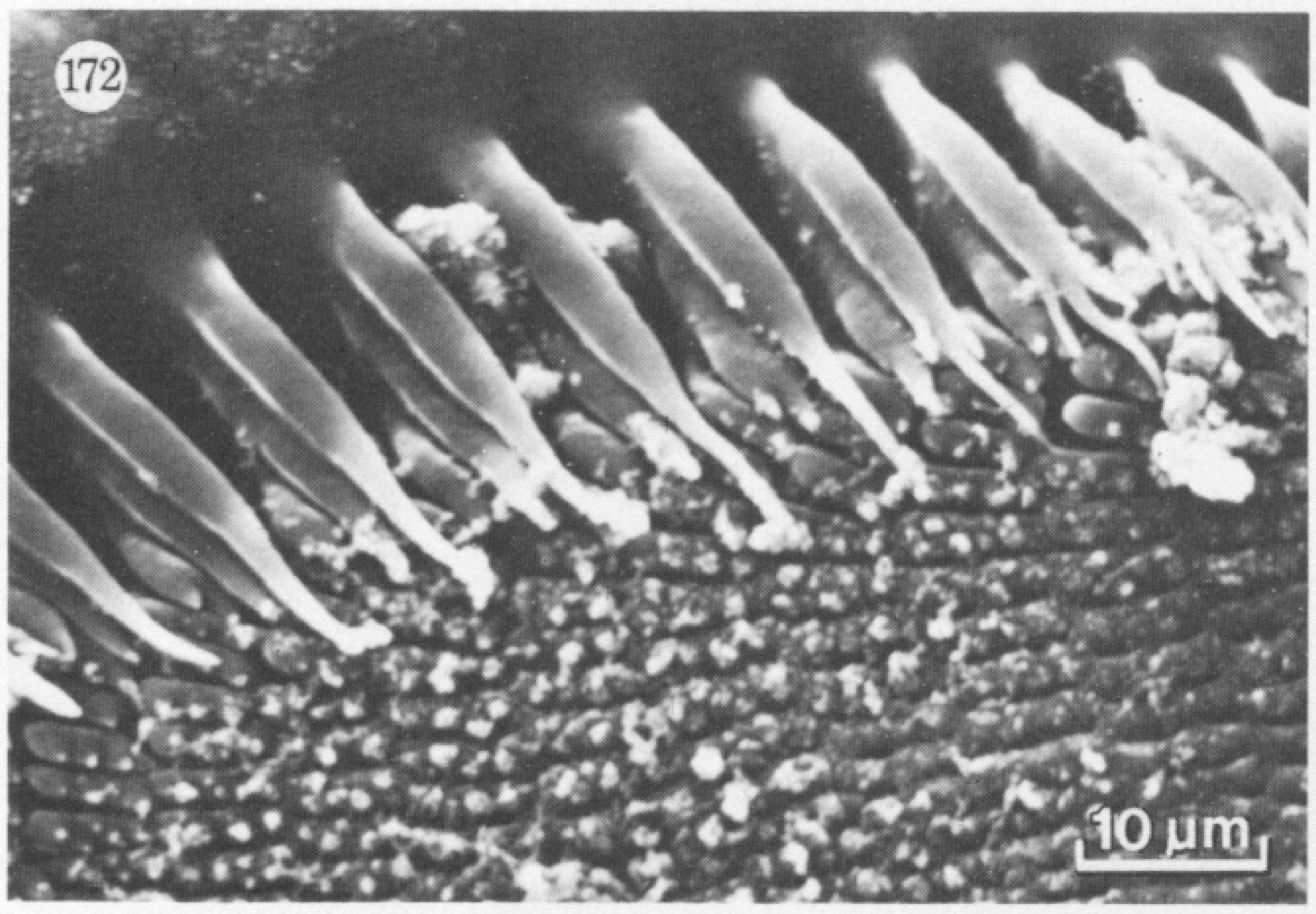

167

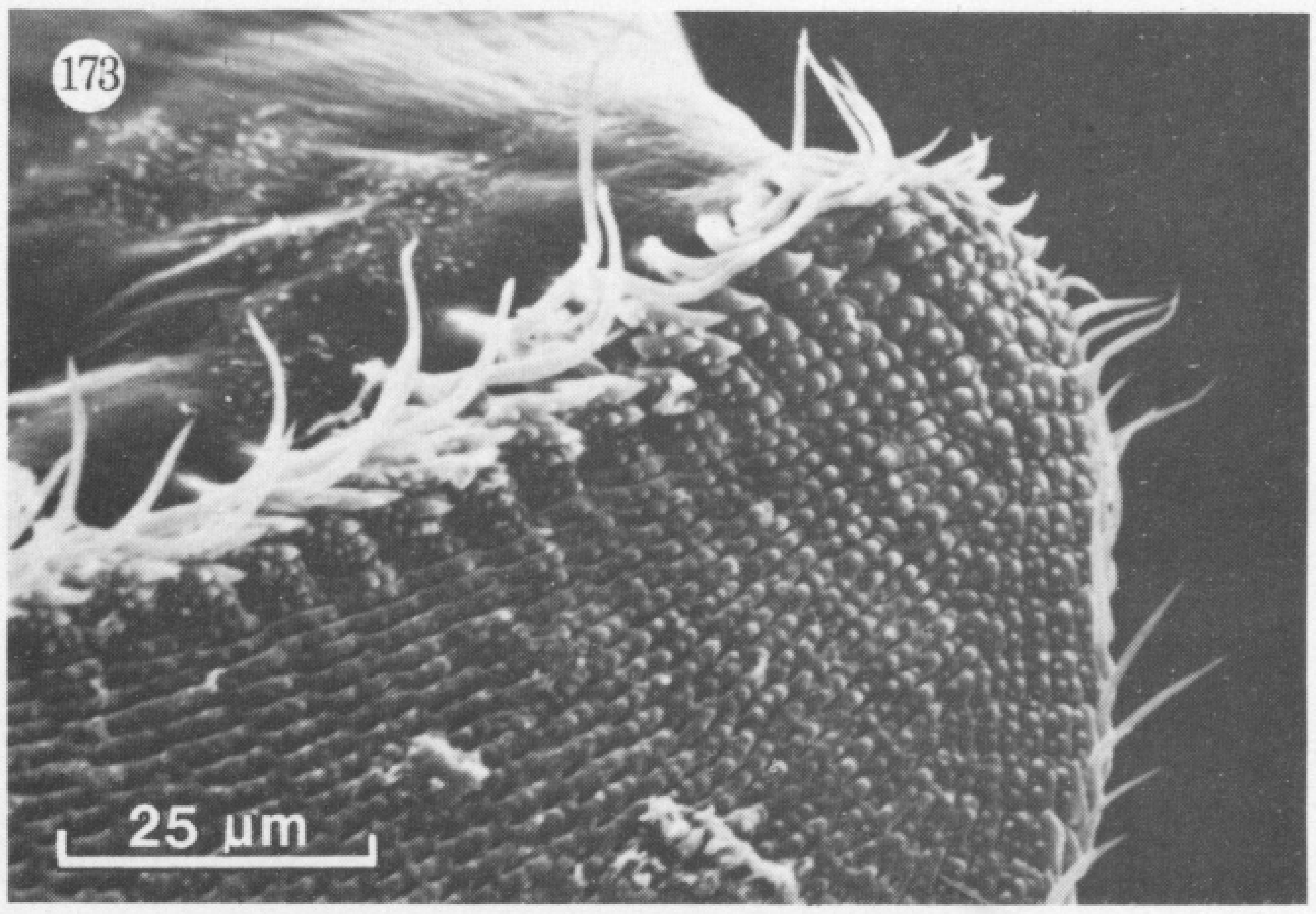

168
10 µm

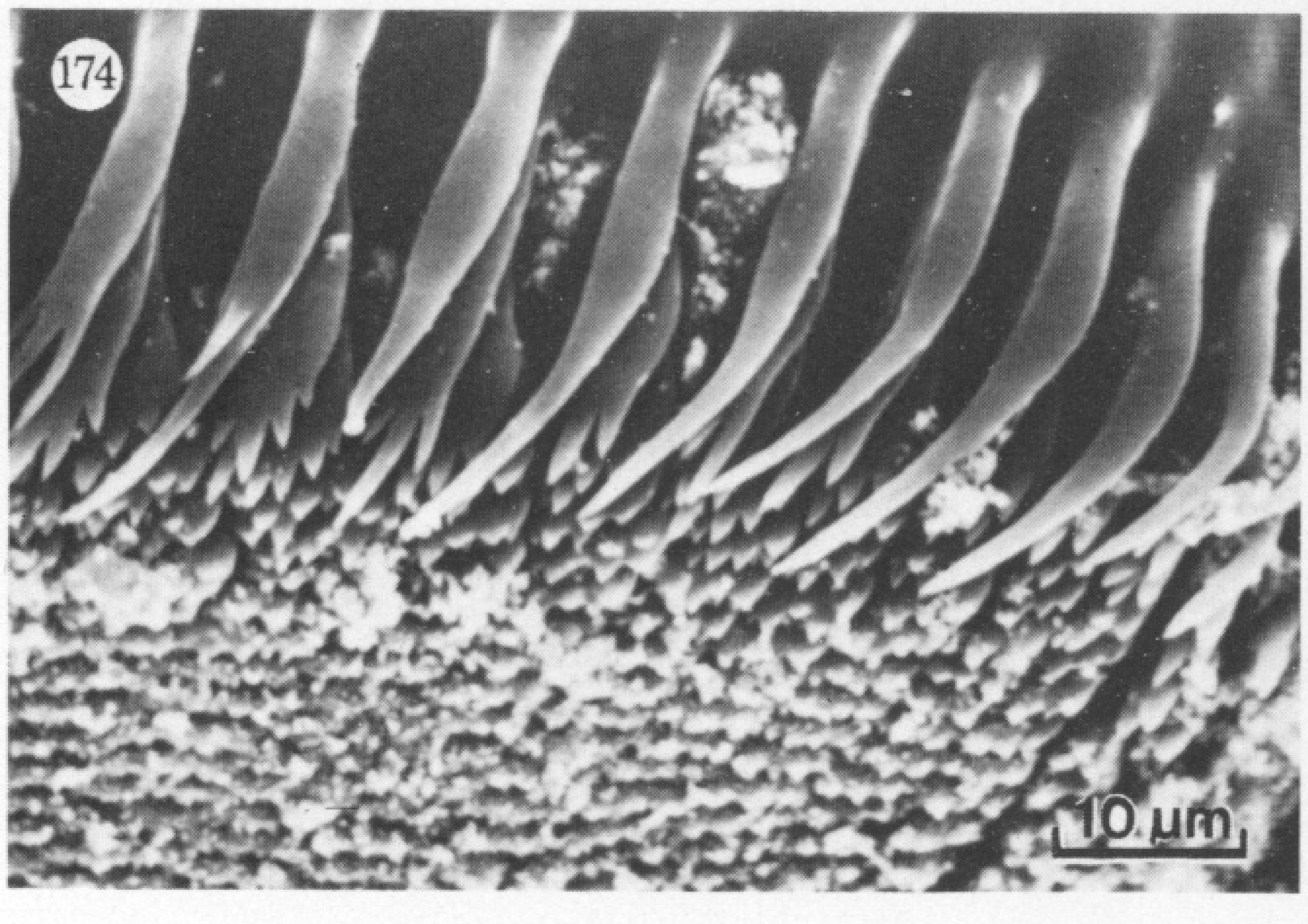

169
10 µm

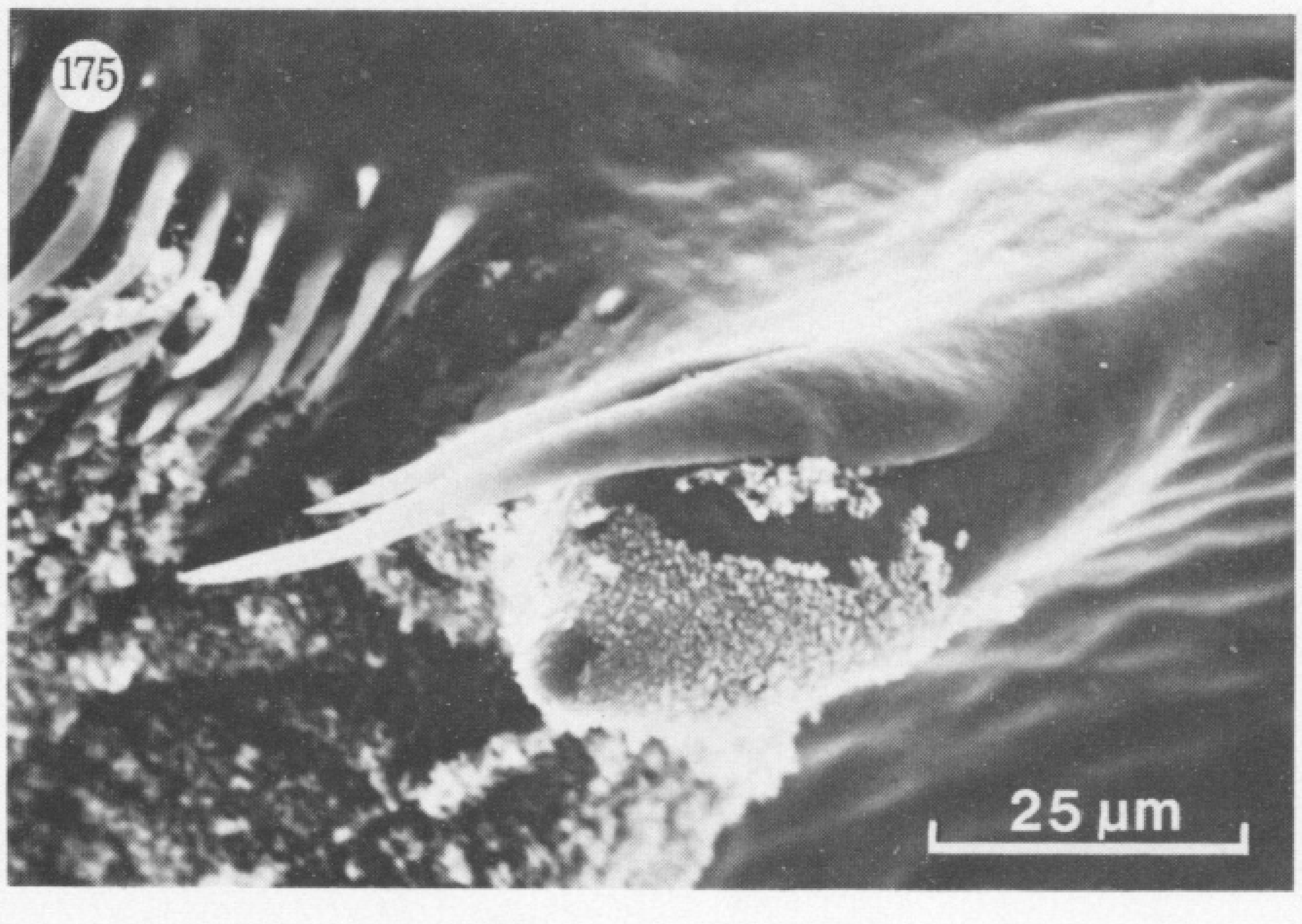

170
50 µm

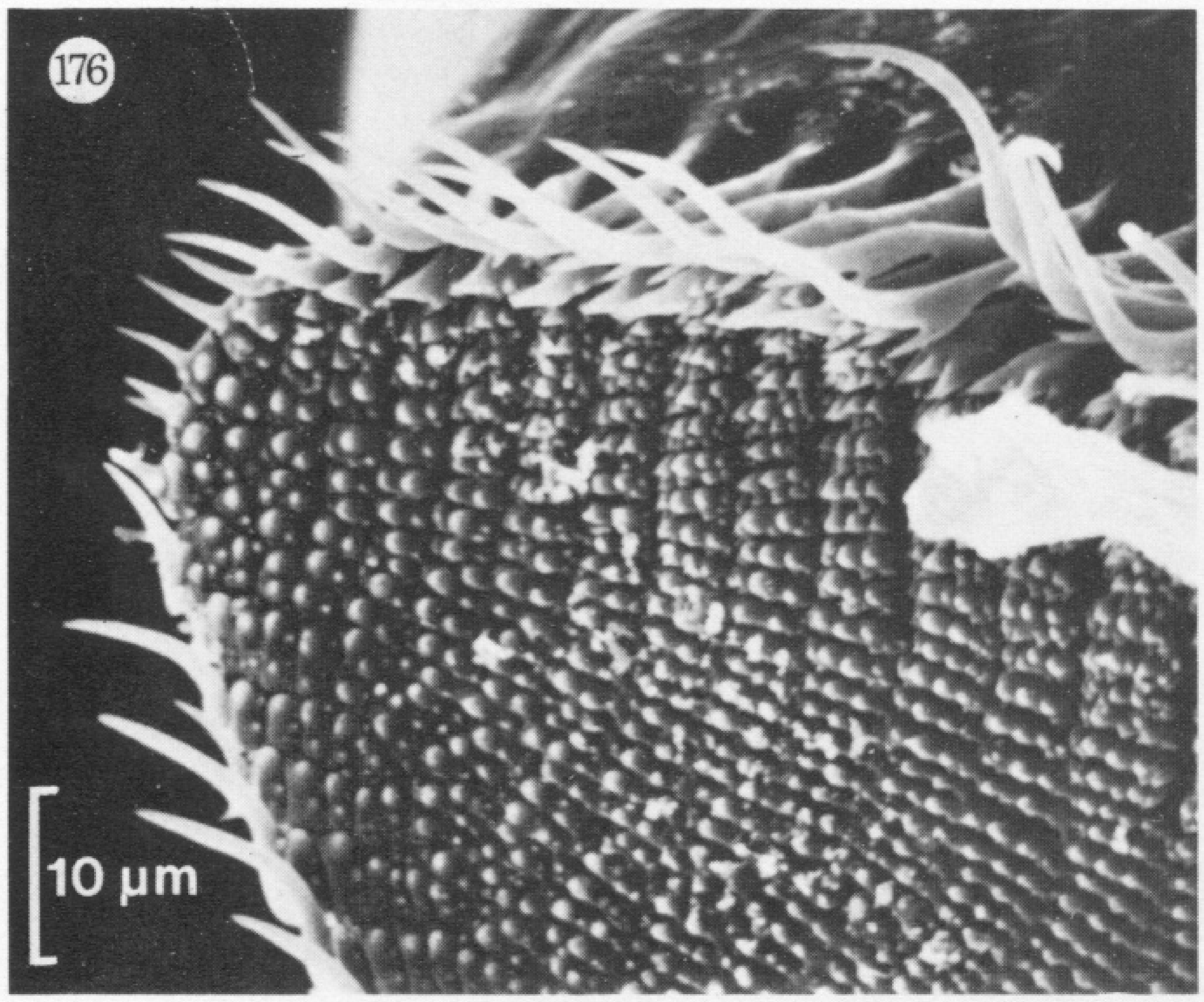

171
10 µm

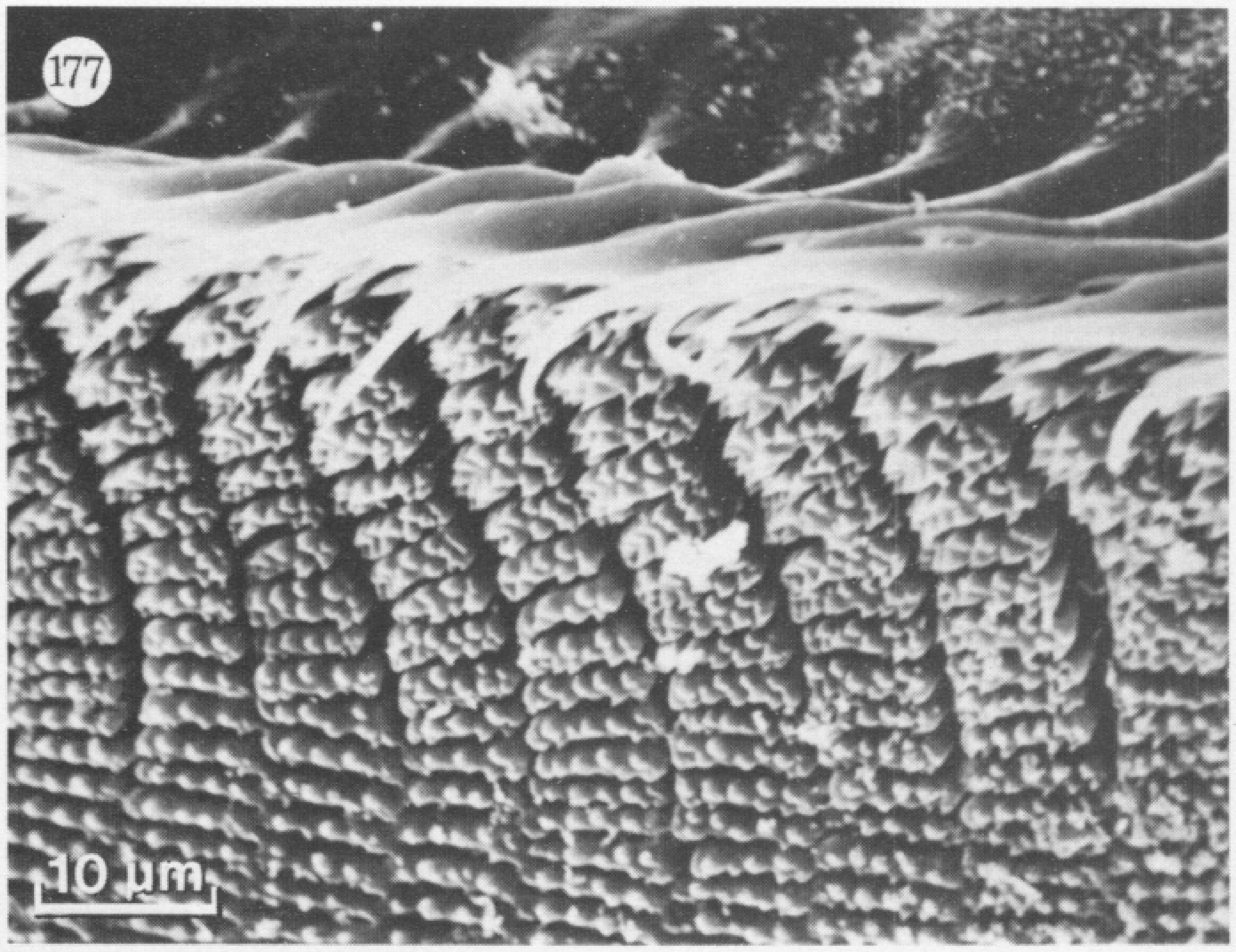

172
10 µm

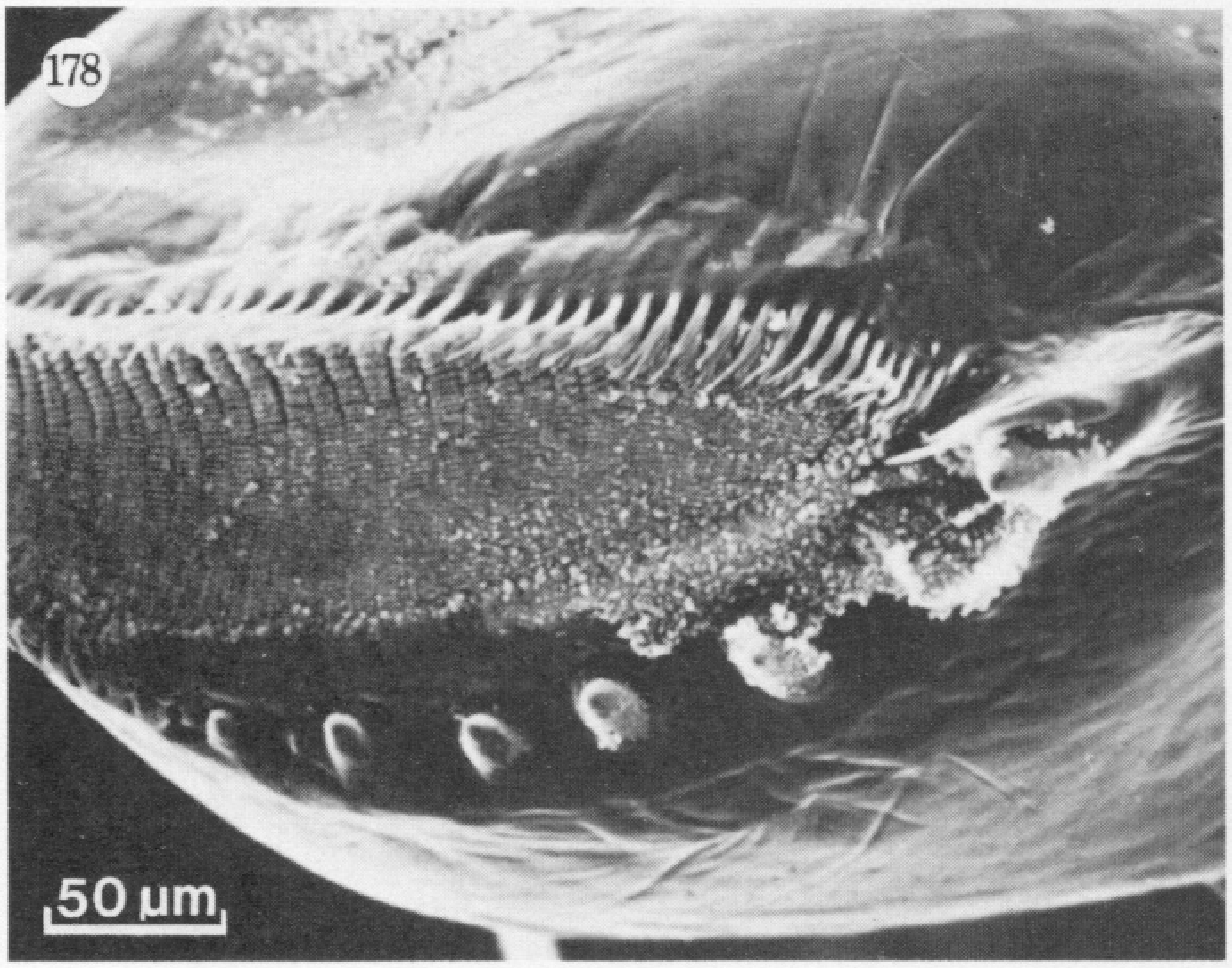

173
25 µm


174
10 µm


175
25 µm


176


177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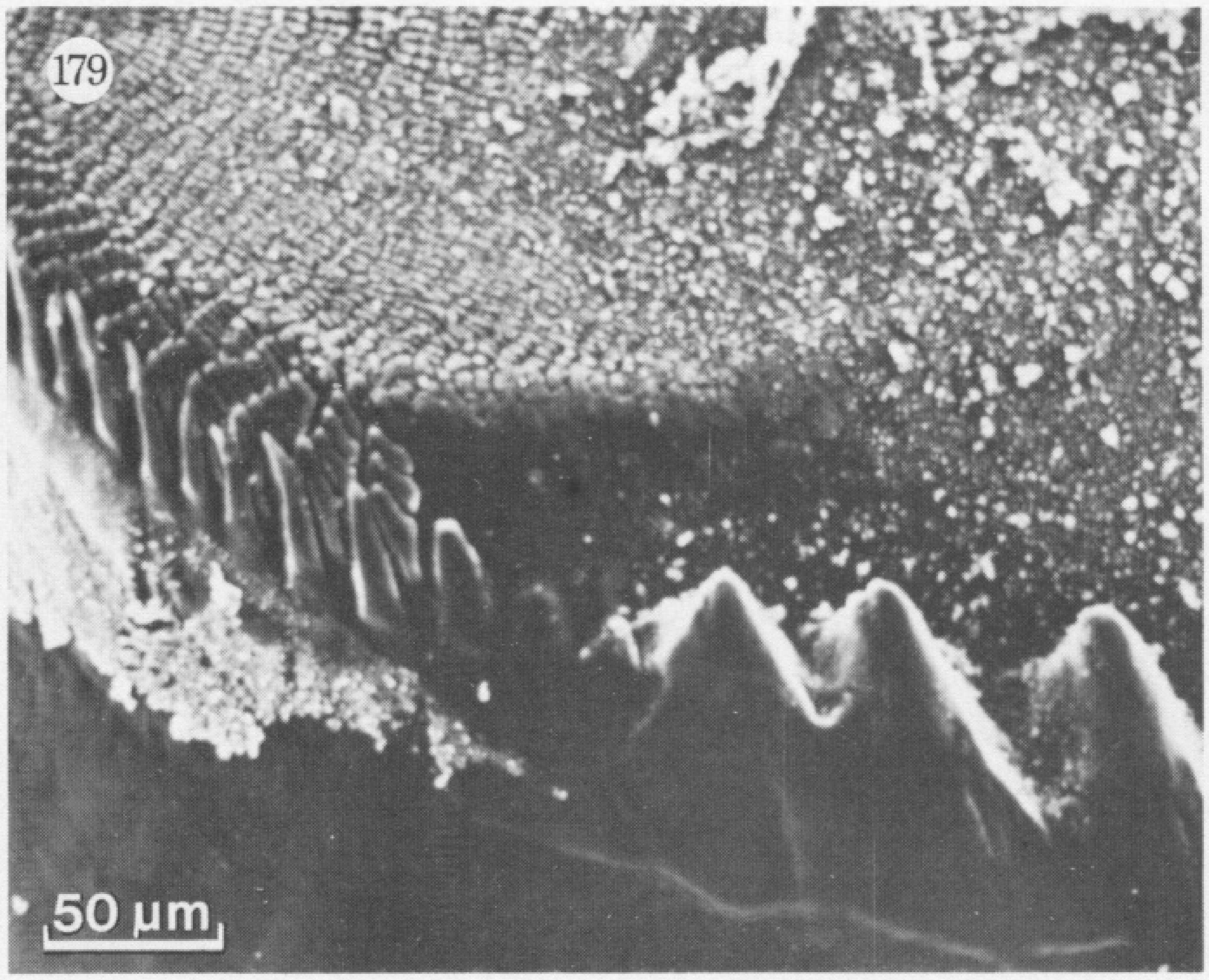
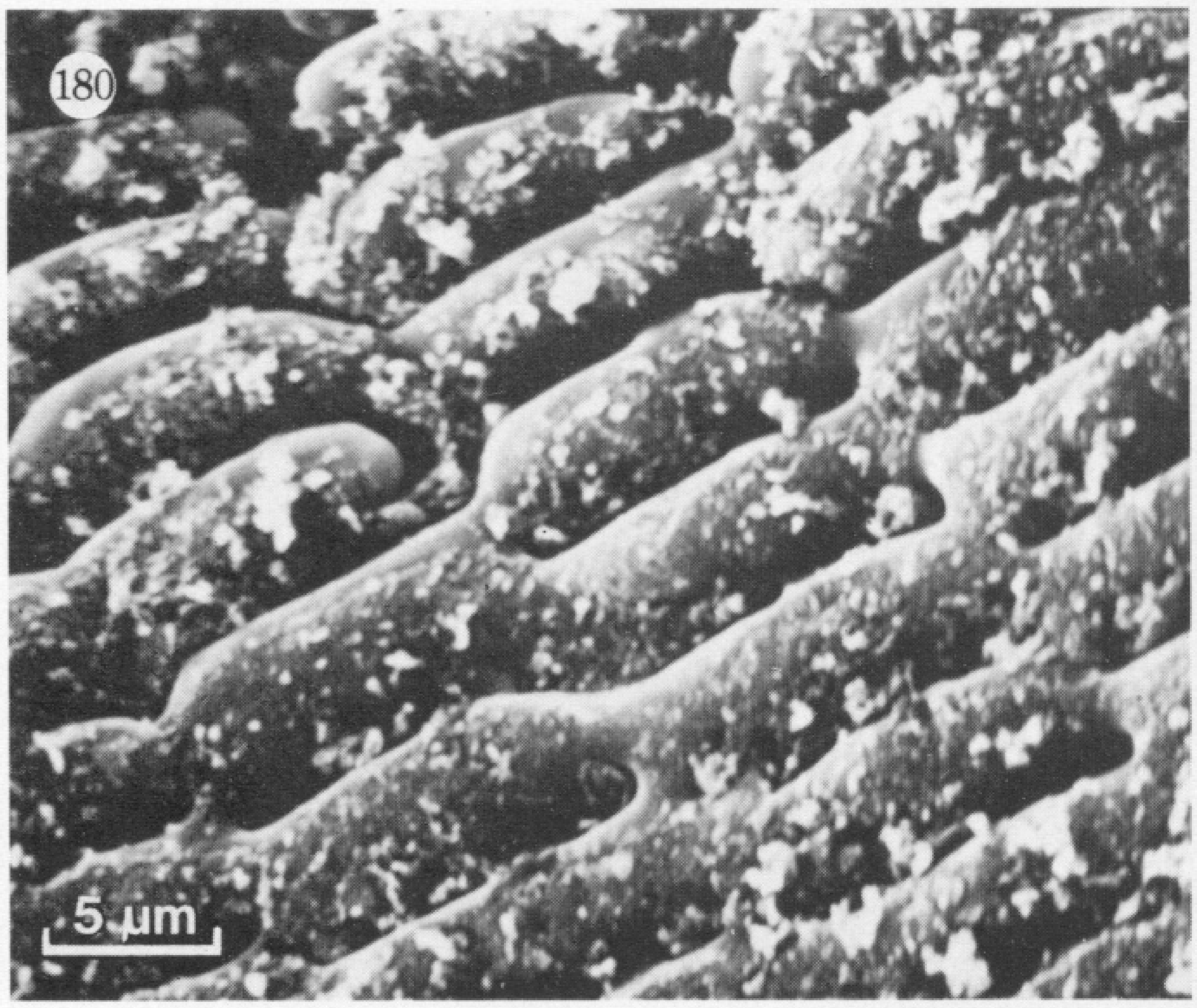

179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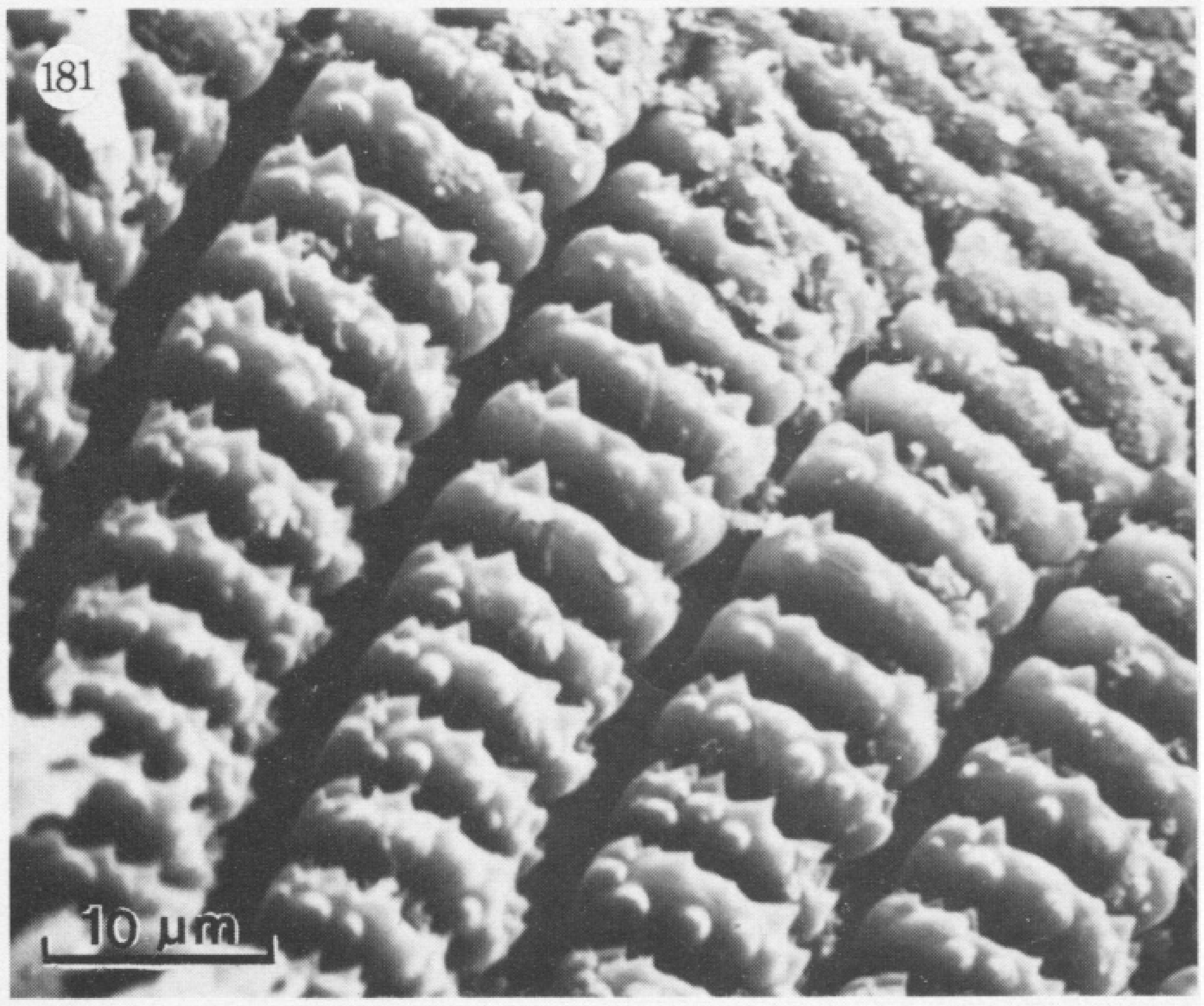
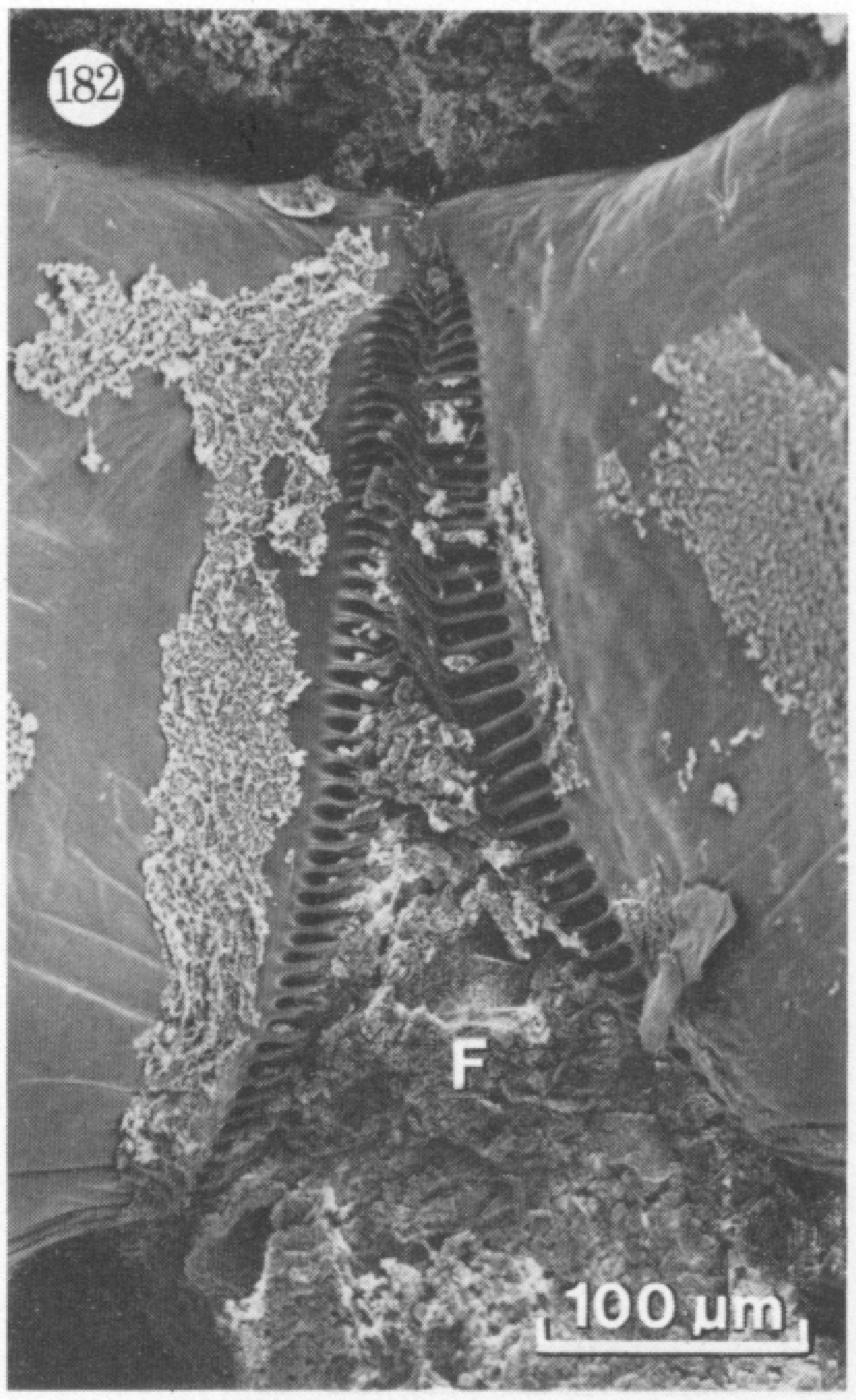
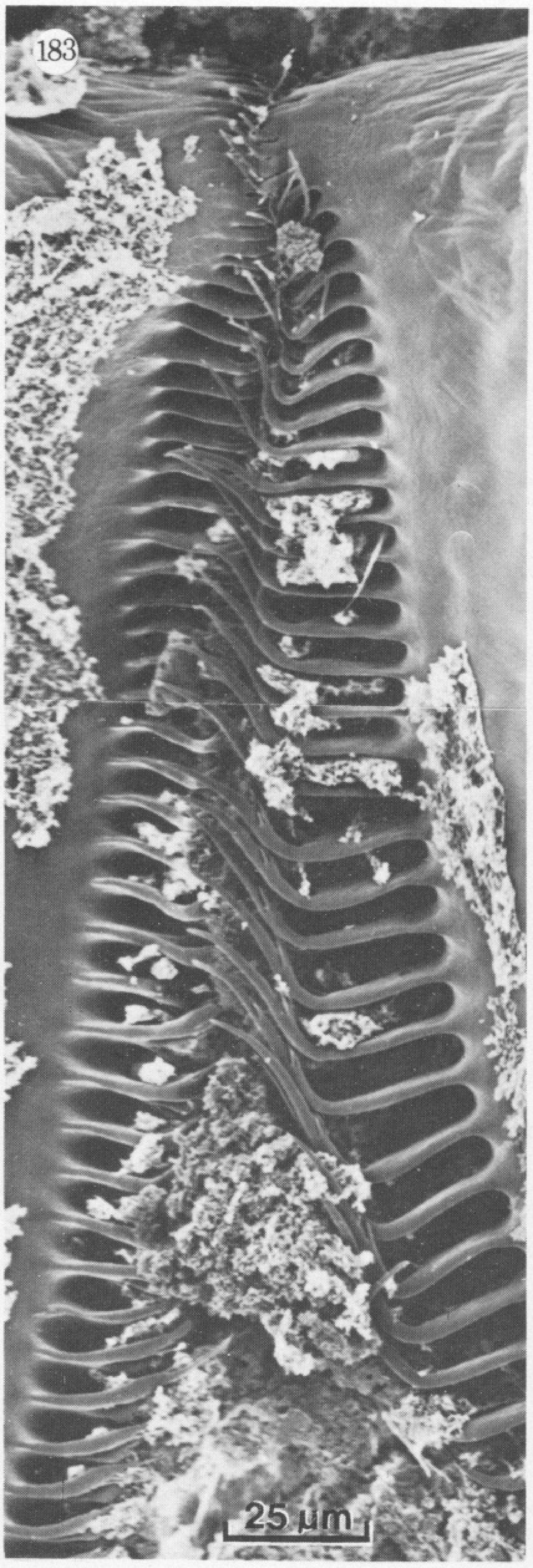
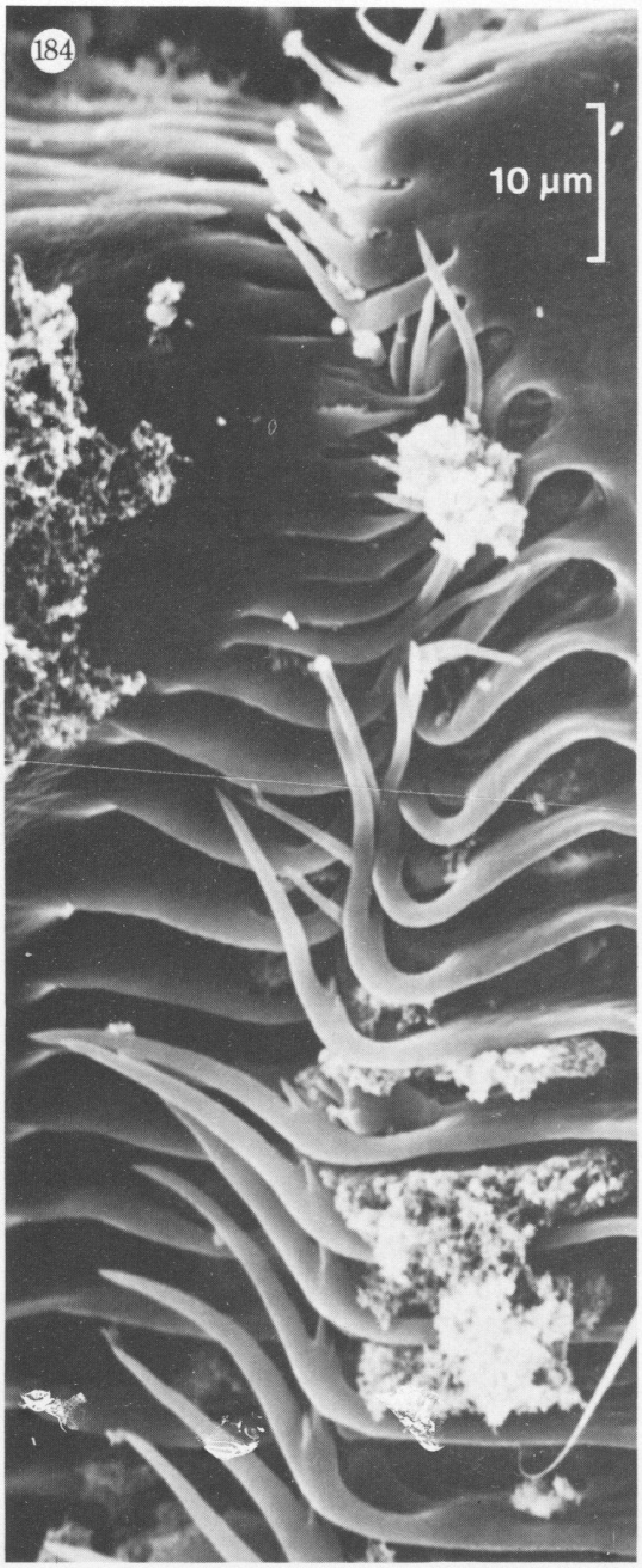
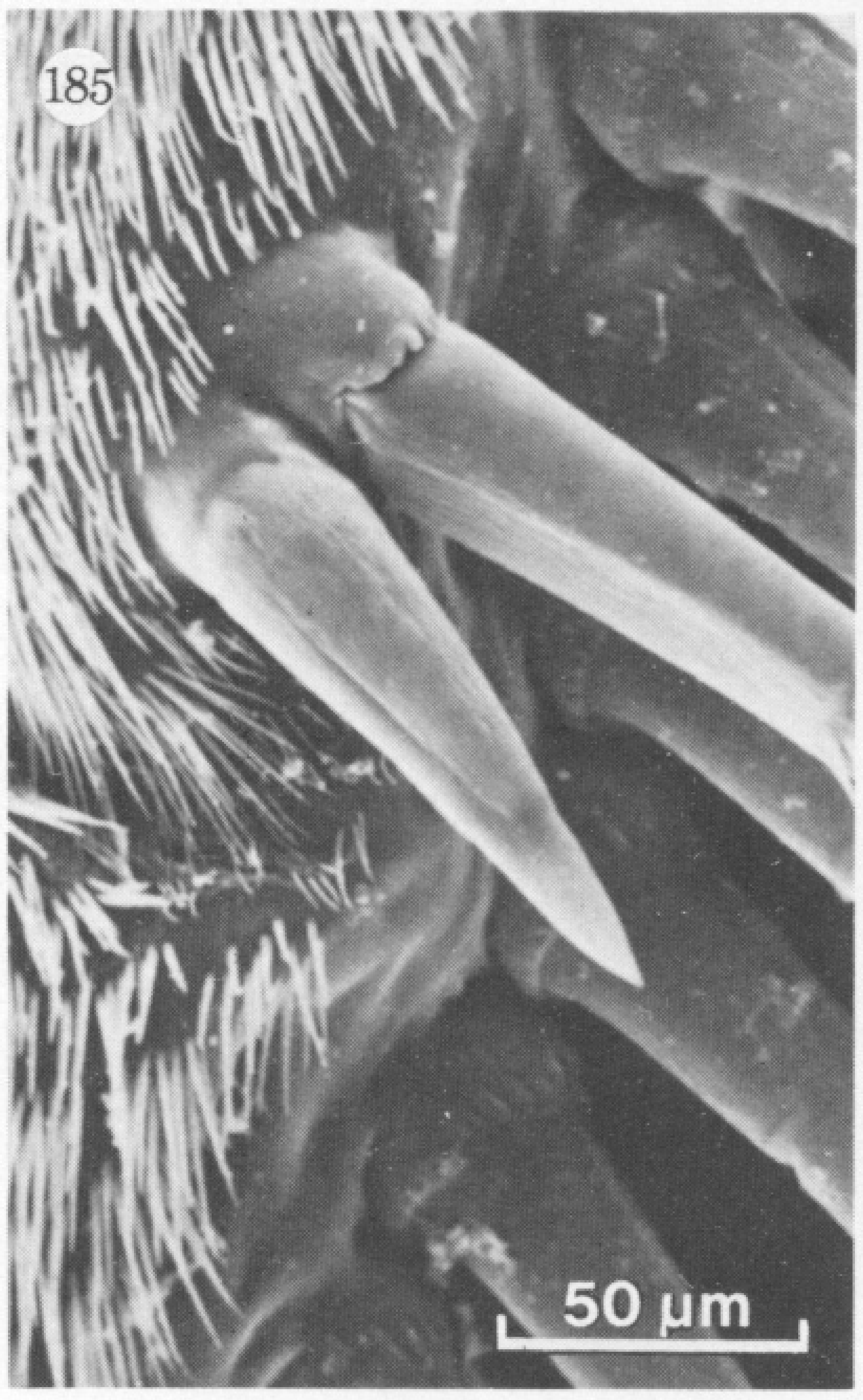
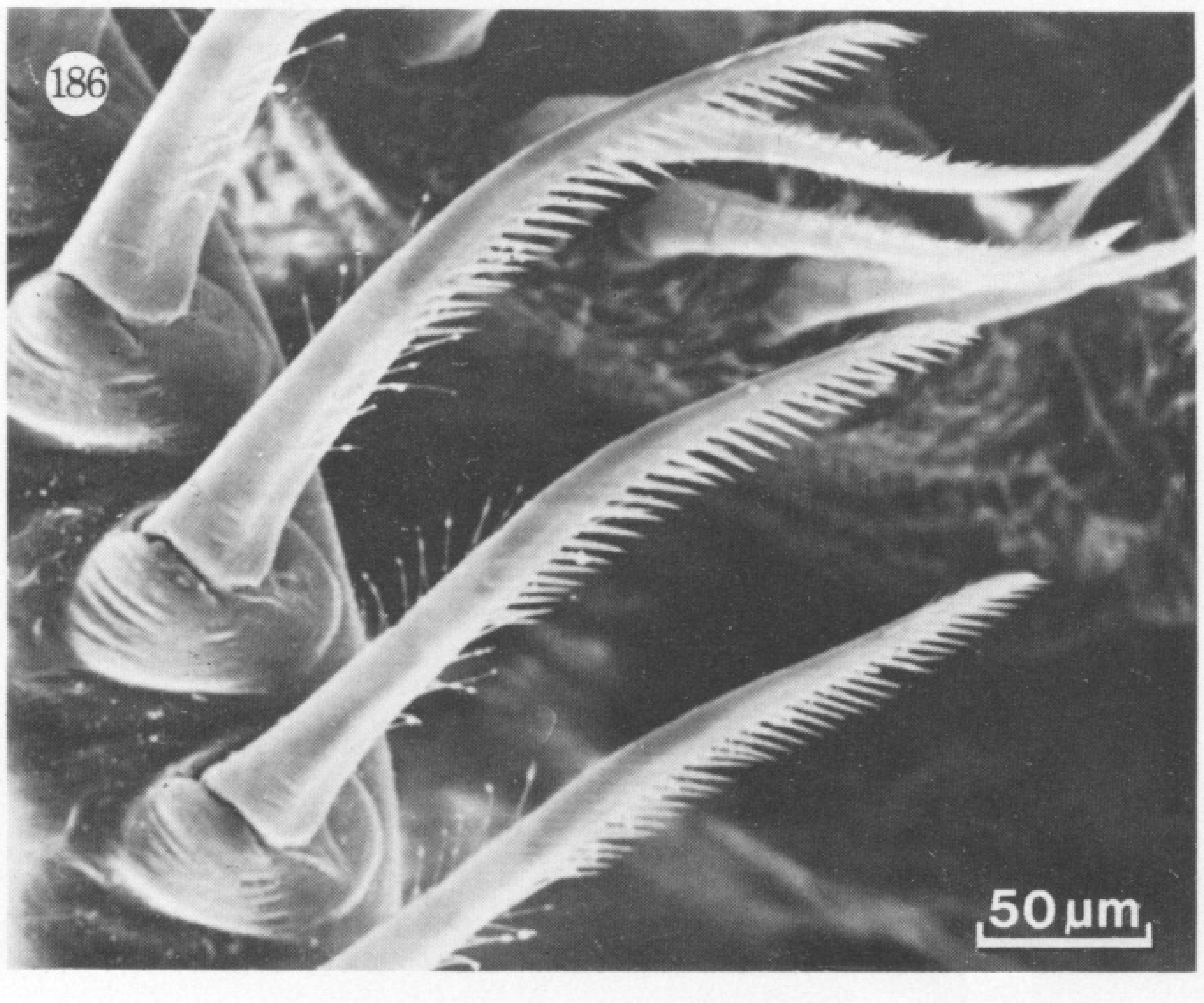

181

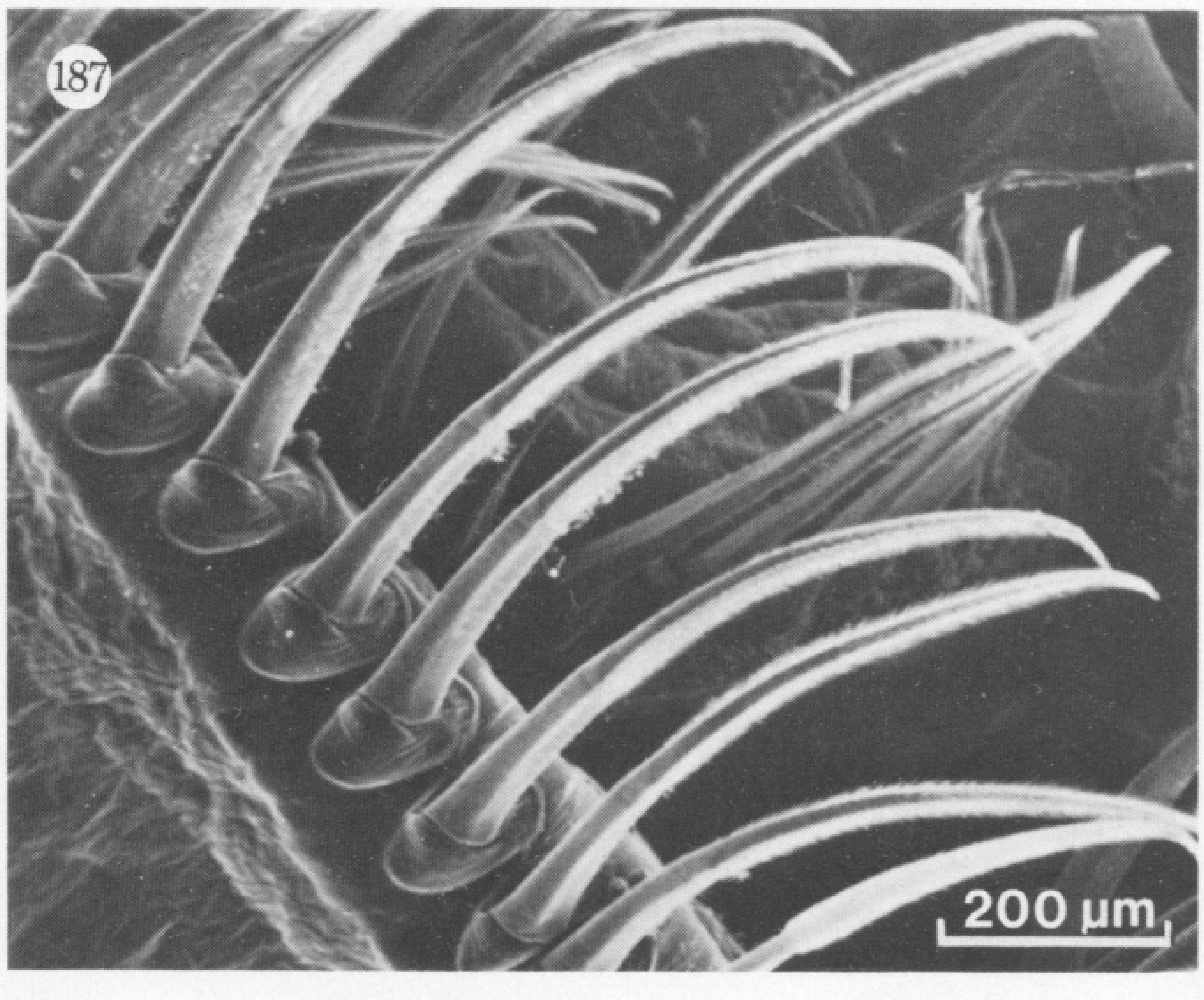

182
F
100 µm


183
25 µm


184
10 µm


185
50 µm


186
50 µm


187
200 µm