ULTRASTRUCTURE OF THE ANTENNAL SENSILLA OF *ACETES* (CRUSTACEA, DECAPODA, NATANTIA, SERGESTIDAE)

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[Plates 1–8]

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Many mesopelagic shrimps, including all Sergestidae and some Penaeidae, have long second antennae with similar patterns of setation. The morphology of the antenna and the ultrastructure of five types of antennal setae of the sergestid *Acetes sibogae australis* are described.

The basal portion of the antenna of *Acetes* is normally held at about right angles to the long axis of the body; the antenna has a right-angle bend about a third of the way along its length and its distal two-thirds trails parallel to the body as the animal swims.

Distal to the flexure each antennal segment bears a pair of type 1 setae, which bear lateral setules forming an almost closed tube on the medial side of the antenna. Although they have elaborate tracts leading from them, we believe that the type 1 setae are uninnervated.

Two kinds of type 2 setae project into the lumen of the tube formed by the type 1 setae; thick type 2B setae have abundant setules nearly occluding the lumen of the tube and occur only just beyond the flexure; thin type 2A setae have fewer setules and occur at widening intervals along the full length of the tube. Both kinds are innervated by four neurones, three of which bear a ciliary dendrite, one a paraciliary dendrite. These four dendrites lose their microtubular structure proximal to the setal base but the tubule containing their amorphous extensions is fastened to the base of the seta by an amorphous electron-dense material. Both kinds of type 2 setae have a well-developed scolopale and are almost certainly mechanoreceptors.

The proximal portion of the antenna bears four types of setae. Type 3 setae are paired, unadorned cylinders with a pore at the tip; although externally similar the type 3A setae are innervated by three dendrites and the type 3B by eight to ten. The dendrites of both 3A and 3B setae have a short ciliary segment and poorly developed scolopales. Type 3 setae are probably chemoreceptors.

A single setule-bearing type 4 seta occurs at the distal end of each segment of the basal third of the antenna closely associated with a pair of type 3 setae. Type 4 setae are innervated by three neurones each bearing a ciliary dendrite. These dendrites fuse distally and are attached to the wall of the seta at its base by dense amorphous material. Type 4's have a well-developed scolopale and are probably mechanoreceptors.

Type 5 setae are setule bearing, located on the posterior side of the antenna, and larger than the type 4's, but their internal structure is identical to that of the type 4's and they are also presumed mechanoreceptors.

There are four to seven pairs of sparsely setuled type 6 setae found only within the antennal flexure and paired, setule-bearing type 7 setae are located at the tip of the antenna. Both types are presumed mechanoreceptors but their ultrastructure was not investigated.

Literature on the ultrastructure of crustacean sensilla is summarized and compared with the results of the present study. Setal function and arrangement are then discussed in terms of the known behaviour and ecology of sergestids.

1. Introduction

Any naturalist on first seeing a sergestid with its antennae entire might ask what use such long and elaborate structures were to the animal. It was just such a question, and the uncertain answers which it elicited, that led to the present study.

In some genera of the Penaeidae and in the Sergestidae the antennal flagellum is very long, sometimes reaching three times the length of the animal's body. It is further specialized by having a flexure (or elbow) about one third of the way along its length. The segments proximal to the kink bear several types of small setae, while distal to the kink each segment bears a pair of long plumose setae which, together with the setae of adjacent segments, form an almost closed tube. Some of the segments distal to the flexure also bear a central seta which extends into the lumen of the tube formed by the lateral setae.

Foxton (1969) has provided an excellent brief survey of the taxonomic distribution and general morphology of the antennal specializations of the Penaeidea. In the present paper we have attempted to answer, at an ultrastructural level, some of the questions which he has posed about the anatomy of the various sorts of receptors which occur on the antennae. On the basis of Foxton's account we had expected to find only three types of setae; and while the three types he describes are indeed the most abundant, we have identified a total of seven types in *Acetes*. There are also small numbers of one or two further types which we have not examined. We have concentrated our efforts on the three setal types described by Foxton but have also included all information which we obtained on the other types of setae to provide a more complete picture of the sensory capabilities of the antennae of *Acetes*.

The most spectacular sergestid antennae occur on the larger midwater species. However, because of their great length these antennae are almost always entangled in the net or other animals of the catch and are broken off. Fortunately, members of the sergestid genus *Acetes* are found almost worldwide in shallow coastal waters where they can easily be captured in excellent condition. *Acetes* are relatively small (up to 4 cm) but they are hardy, euryhaline and, most important for this study, their antennal morphology is similar to that of the mesopelagic genera (Foxton 1969). In addition, they can be maintained for long periods in the laboratory, they display quite remarkable chemoreceptive abilities (Hamner & Hamner, in preparation), and in general they appear to be a favourable subject for the experimental analysis of the sensory capabilities of a planktonic animal. We have carried out the present study on the Australian species of *Acetes*, *A. sibogae*. This species was originally described as *Acetes australis* by Colefax (1940) but M. Omori (personal communication to D. J. G. Griffin) has recently stated that the Australian specimens should be regarded as a subspecies of *A. sibogae* Hansen. Because an animal's sensory capabilities can only be meaningfully evaluated in terms of the environment in which it lives, we have included below a brief summary of *Acetes* natural history.

2. Natural history of *Acetes*

Shrimps belonging to the genus *Acetes* are distributed worldwide in shallow water coastal areas with mud bottoms. They can tolerate quite low salinities and are often found in estuaries and backwaters in almost fresh water. Tropical species of *Acetes* apparently spawn year-round, while the spawning of temperate species is determined by temperature (Omori 1974). *Acetes* hatches as a nauplius and then passes through protozoeal, zoeal and post-larval stages. The most

complete descriptions of larval development are those of Menon (1933) for *A. erythraeus* Nobili and Morris (1948) for *A. sibogae* (as *A. australis*).

Growth rate, longevity and eventual size reached depend on temperature and the availability of food. Omori (1974, p. 283) has summarized the data for *A. japonicus* as follows:

'According to Ikematsu (1953) the summer generation of *Acetes japonicus* that hatches in May and June grows fast in the warmer season and spawns the winter generation between August and early October; the winter generation grows for a few months but obviously growth ceases in winter. They grow again in spring and spawning takes place after May. Sizes at maturity differ markedly between the two generations. The average body length of adults of the winter generation is more than 1.5 times that of the summer one. Both generations die after spawning and hence the life-span is nine to ten months for the winter generation, whereas it is two and half to three months in the summer generation (figure 17). Yasuda *et al.* (1953) even estimate... the life-span of the latter generation to be only twenty-five to fifty days.'

Gut contents of sergestids are usually well macerated and almost unidentifiable, but include copepods, unidentifiable crustacean remains and detritus (Le Reste 1970; Omori 1974).

Species of *Acetes* are extremely important in the trophic structure of the mangrove swamps of the Indo-west-Pacific and presumably form a significant part of the diet of juvenile fish found in these areas. Omori (1974, p. 294) has summarized records of the many fish species which feed on *Acetes*. In addition, *Acetes* is heavily fished for human consumption in Asia and eastern Africa, constituting about 25 % of the annual catch of shrimps in the Indo-west-Pacific region (Omori 1974, p. 305).

3. Materials and methods

Specimens of *Acetes sibogae* were collected by dipnetting and diving in Sydney Harbour and Port Hacking at various times during 1974 and 1975. We were unable to discover any sexual dimorphism with regard to either type or distribution of the antennal receptors so antennae from animals of both sexes were used in our morphological studies. Whole mount light microscopy was usually carried out on fresh material but in certain cases formalin-fixed material was used.

Obtaining adequate fixation for electron microscopy proved difficult and thirteen different fixatives were tried. None of these gave consistently good results but the best results were obtained when the osmolarity of the fixative vehicle was equal to or greater than that of seawater (Bone & Ryan 1972). Most of the figures are of material fixed in either:

(*a*) 4.5 % glutaraldehyde in seawater (2 h) followed by 1 % OsO_4 in seawater, or

(*b*) 5 % glutaraldehyde in seawater plus 5 % polyethylene glycol with the osmolarity then adjusted to 1130 mosmol/l with distilled water (2 h) followed by 1 part 2 % OsO_4 (in Millonigs buffer) plus 1 part seawater with added polyethylene glycol.

An antenna was cut off into the fixative of choice and was then cut into thirds. Each individual third was then cut up into varying lengths which were transferred to a porous specimen capsule (Reichardt Flo-through Specimen Capsule). The tissue remained in the capsule through dehydration and into propylene oxide, where it was washed out of the capsule before resin was added. Tissue was embedded in Spurrs and TAAB embedding media.

For light microscopy, material was sectioned at 0.5 or 1.0 μm and stained with toluidine blue. For transmission electron microscopy thin sections were stained with uranyl acetate and lead citrate and examined and photographed on a JEOL 100C electron microscope.

Antennae were fixed for scanning electron microscopy in 10 % formalin. They were then dehydrated through an acetone series, critical point dried, and viewed and photographed on a Hitachi HHS-2R scanning electron microscope or a JEOL 100B with ASID-SEM mode.

4. Terminology

Figure 1, and figures 2–11, plate 1, with the definitions given below, clarify the terminology to be used in this paper:

proximal	toward the body or basal with respect to the antenna
distal	toward the tip of the antenna
dorsal	upward with respect to the animal's body and to the antenna when it is held in the normal swimming position shown in plate 1
ventral	downward with respect to the animal's body and to the antenna when it is held in the normal swimming position shown in plate 1
anterior	the outer side of the antenna when it is held in the normal swimming position shown in plate 1
posterior	the inner side of the antenna when it is held in the normal swimming position shown in plate 1

There is no consistent terminology for some of the cells and intracellular structures of arthropod sensilla; wherever possible we have followed the usages of Whitear (1962), Mill & Lowe (1973) and Lowe, Mill & Knapp (1973). 'Scolopale' is here used as defined by Whitear (1962, p. 305): 'The scolopale itself is here defined as an agglomeration of fibrous material contained within a special enclave of the scolopale cell; it is therefore an intracellular organ.'

We refer to all of the antennal sensilla of *Acetes* as 'setae' although several types may not fulfil Thomas's (1970) definition of the term due either to lack of a pore at the tip or because (our type 3 setae) they do not arise from a moveable socket.

5. Observations on the biology of *Acetes sibogae australis*

In most years *Acetes* are uncommon in the area of Sydney, Australia (D. J. G. Griffin, personal communication) although occasionally (e.g. in August 1974) they appear in great abundance. They are then found in schools of a hundred or more, but at times of lesser abundance there may be only two or three animals swimming together. In schools of *Acetes* the antennae of neighbouring animals are almost touching; in general all animals face in the same direction and most swim with the body horizontal or with the head slightly down. The school moves slowly and frequently remains almost stationary. Only occasionally does an individual go shooting forward rapidly. However, the schools on which these observations were based were occasionally preyed on by a fish – the yellow tail (*Trachurus mccullochi*), and their behaviour may not have been typical of undisturbed schools.

Most animals hold their antennae out level with or slightly below the long axis of the body. The basal segment of the antenna usually forms an angle of about 90° with the body while the flagellum distal to the flexure streams backward parallel to the body. Many animals had antennae heavily coated with detritus, yet they were never seen to clean them. Frequently

animals were lacking the tips of their antennae as evidenced by the absence of the terminal setae. When kept in aquaria the animals, when disturbed, show a tail-flip escape response which propels them rapidly backwards. This frequently carries them above the surface of the water.

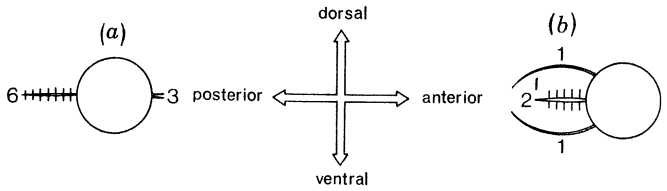

FIGURE 1. Diagrammatic representation of transverse sections of a left antenna viewed from the proximal end at the level of (*a*) the type 3 and type 6 setae (see figure 3) and (*b*) the type 1 and type 2 setae (see figure 2).

TABLE 1. BODY AND ANTENNAL DIMENSIONS OBTAINED FROM MEASUREMENTS OF TEN *ACETES*

portion of body	$\bar{x}$/mm	s
body length from tip of rostrum to tip of uropods	26.2	2.2
base of antenna to point of flexion	17.5	1.2
point of flexion to tip of antenna	39.3	4.4
length of entire antenna	56.8	5.3
length of antennal segments		
(*a*) near base of antenna	0.151	0.014
(*b*) just beyond point of flexion	0.084	0.004
(*c*) near tip of antenna	0.071	0.008

6. DISTRIBUTION AND EXTERNAL MORPHOLOGY OF THE ANTENNAL RECEPTORS

The structure of the antennae of *Acetes* has been discussed by several authors (see, for example, Kishinouye 1905; Burkenroad 1934; Colefax 1940) but as none of their descriptions is totally applicable to the specimens which we have examined we will review the gross

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DESCRIPTION OF PLATE 1

An *Acetes* with its antennae in the normal swimming position. Brackets and arrows show the distribution of the various setal types and the photographs show their external morphology. The setae in figures 2–7 are in their normal orientation with respect to the animal while those in figures 8–11 are turned through 90°.

FIGURE 2. A portion of the antenna distal to the flexure showing setal types 1, 2A and 2B.

FIGURE 3. The antennal flexure with type 6 setae proximally and the first of the type 1 setae distally.

FIGURE 4. The paired type 7 setae at the tip of the antenna.

FIGURE 5. Type 5 setae on the posterior side of the basal portion of the antenna.

FIGURE 6. Types 3 and 4 setae showing their most common distribution pattern.

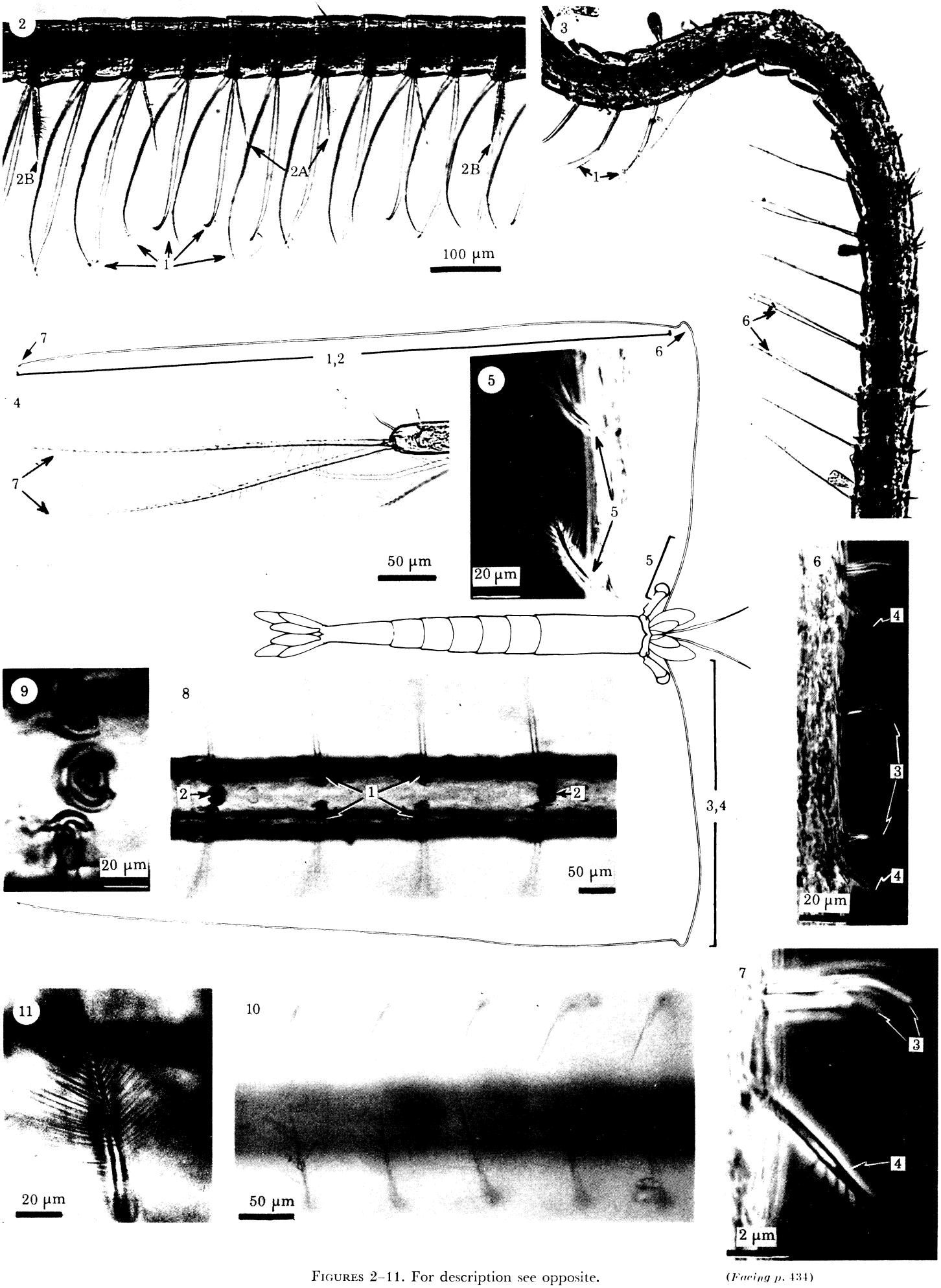
FIGURE 7. Type 3 and 4 setae at higher magnification.

FIGURE 8. A portion of the antenna distal to the flexure with the microscope focused on the bases of the type 1 and type 2 setae.

FIGURE 9. Bases of the type 1 and type 2 setae at higher magnification.

FIGURE 10. The same portion of the antenna shown in figure 8, this time with the microscope focused on the distal portion of the setae to show that the setae and their setules form an almost closed tube.

FIGURE 11. Higher magnification view of the distal portion of a type 1 seta to show the arrangement of the setules.



FIGURES 2–11. For description see opposite.

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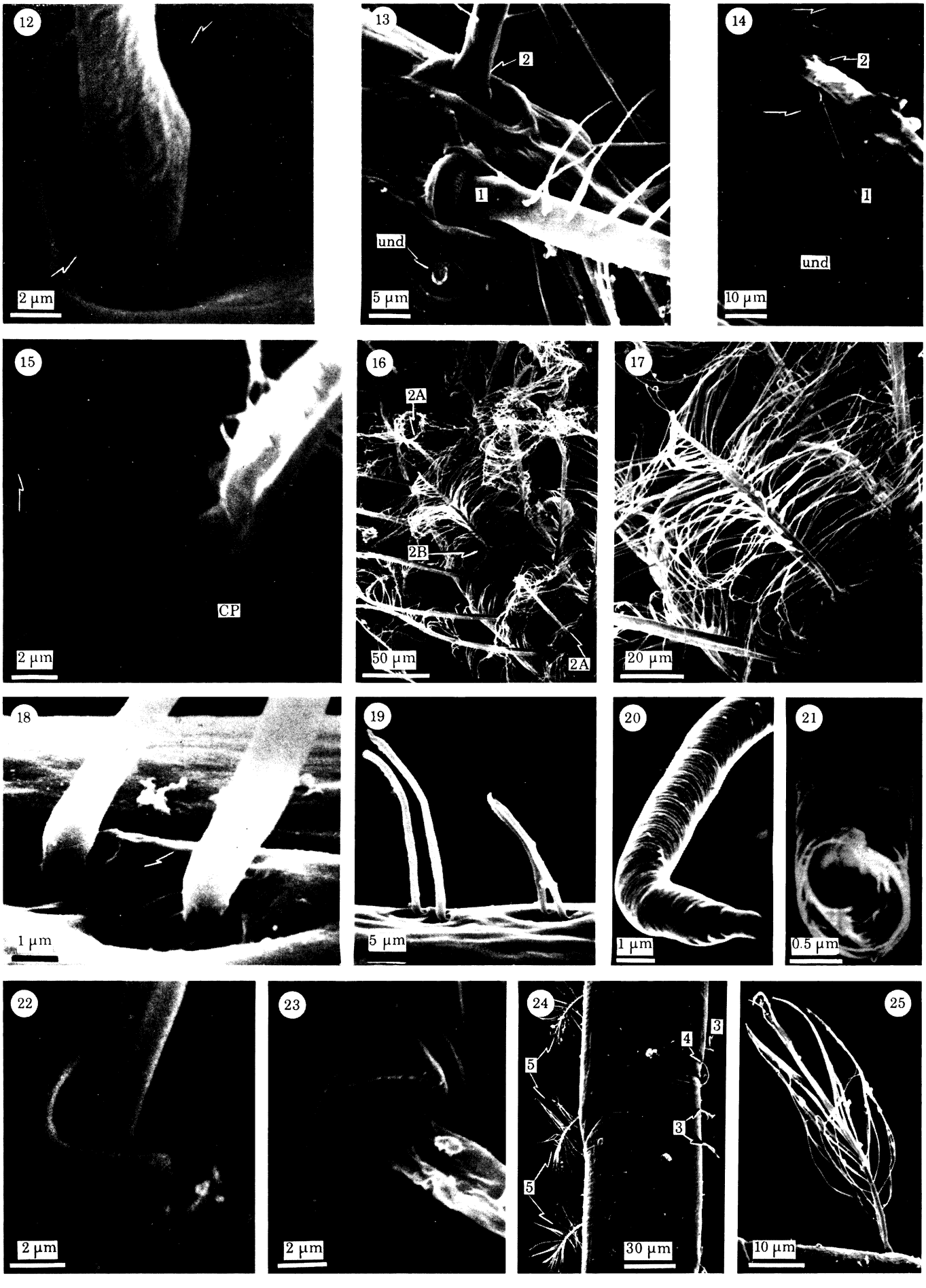


FIGURES 12–25. For description see opposite.

morphology here. An entire, undamaged antenna can be recognized by a pair of setae (type 7 setae, figure 4) at its tip, but only a small proportion of the populations of *Acetes* which we examined had the antennae entire. Body and antennal dimensions of ten *Acetes* with undamaged antennae are summarized in table 1.

The number of segments in 3 antennae with type 7 setae at their tips was 486, 539 and 632. Some of this variability may have been due to breakage earlier in the life of the animal followed by regeneration of the type 7 setae.

Plate 1 summarizes the setal types and their distribution on the antennae of *Acetes*. The terminology of Foxton (1969) has been retained for setal types 1–3. In *Acetes* there are two sorts of type 2 setae (here designated 2A and 2B, see figures 2, 16, 17, plates 1 and 2) and we have also found four additional types of setae which we have designated types 4–7.

The dimensions and external morphology of each of the setal types are discussed below:

Type 1 setae. Each segment distal to the elbow bears a pair of long plumed setae (figures 2, 8–11, plate 1) each of which is mounted in an apparently flexible membrane within a cuticular depression (figures 12–14, plate 2). These setae curve outward from the sides of the antenna and then bend rather abruptly inward and distally to form an almost closed arch (figures 2, 10). The setae bear fine lateral projections or setules which either overlap or come close to doing so (figures 10, 11), thus forming what is essentially a closed tube, which is medial to the antenna as the animal swims. This tube is elliptical in cross-section with a width of 0.16–0.21 mm, and a height of 0.17–0.24 mm (figure 1). Just distal to the elbow the setae which form the walls of the tube become progressively longer, thus forming a scoop-shaped aperture. The diameter of the tube also increases steadily for a short distance beyond the elbow. The setae reach their maximum length within a hundred segments distal to the elbow and then become progressively shorter towards the tip of the antenna where they may be as little as two-thirds of the maximum length.

Description of plate 2

Scanning electron micrographs of the various setal types on *Acetes* antennae.

FIGURE 12. Base of a type 1 seta, note mounting in flexible membrane (arrows).

FIGURE 13. Side view of the bases of a type 1 seta, a type 2 seta, and an undescribed type of seta (und).

FIGURE 14. Top view of the same three setal types shown in figure 13. Note paired pores (arrows) associated with the base of the type 2 seta.

FIGURE 15. Top view of the base of type 2 seta. Note associated pore (arrow) and cuticular plug (CP) in the proximal portion of the setal socket.

FIGURE 16. Relation between type 1 setae and the types 2A and 2B setae. The type 2B seta is larger, has many more setules, and more nearly fills the lumen of the tube formed by the type 1 setae than does the type 2A.

FIGURE 17. Enlargement of the type 2B seta shown in figure 16.

FIGURE 18. Bases of type 3 setae. These appear to be less flexibly mounted than the other setal types. There is a pore between the bases of the two setae (arrow).

FIGURE 19. Lower magnification view of type 3 setae.

FIGURES 20, 21. The type 3 setae have annulations along the shaft and an apparent pore at the tip.

FIGURE 22. Base of a type 4 seta.

FIGURE 23. Base of a type 5 seta showing that this setal type is mounted at a pronounced angle.

FIGURE 24. Type 3, 4 and 5 setae on a basal antennal segment.

FIGURE 25. Higher magnification of type 5 seta.

Type 2 setae. There are two distinct sorts of type 2 setae (figures 2, 16). Both sorts project from the antenna into the lumen of the tube formed by the type 1 setae. Type 2A are the smaller setae, which run from the elbow to the tip of the antenna; type 2B are larger setae which are limited to the area just distal to the elbow. Both sorts bear lateral setules, but those on type 2B setae are more abundant than those on the type 2A and more nearly fill the lumen of the tube (figures 16, 17, plate 2). Type 2 setae gradually increase in length distally from the elbow for about one-fifth the length of the flagellum after which they gradually decrease again, reaching 70 % of their maximal length about halfway along the flagellum and then remaining about the same height to the end of the antenna. The spacing of the central setae also increases distally (table 2).

TABLE 2. NUMBER OF SEGMENTS WITHOUT TYPE 2 SETAE AT VARIOUS POINTS ALONG THE LENGTH OF *ACETES* ANTENNAE

(Each number in the table is the average of the first ten intervals starting at seta 1, 100, 200, etc., with numbering of the setae starting from the first segment bearing a type 2 seta distal to the flexure.)

animal no.	from no. 1	from no. 100	from no. 200	from no. 300	from no. 400	from no. 500	from no. 600
2	1.4	2.0	5.5	6.4	5.7	4.3	—
4	1.3	3.2	4.7	4.4	5.1	—	—
5	1.5	2.0	3.4	4.5	3.8	4.3	3.4
$\bar{x}$	1.4	2.4	4.5	5.1	4.9	4.3	3.4
s	0.1	0.7	1.1	1.1	1.0	0	0

Type 2 setae are mounted on an apparently flexible membrane in a pit which contains a cuticular insert proximally (figures 9, 14, 15 and 17), the direction from which water would flow as the animal swims. There is a pore, which opens into a tubule, located in the cuticle on either side of each type 2 seta (figures 14 and 15).

Type 3 setae. Type 3 setae are most abundant on the portion of the antenna proximal to the flexure but their distribution within this area varies from animal to animal. The setae are paired unadorned cylinders which usually bend distally near their tips (figures 6 and 7, plate 1, figure 19, plate 2). The most common distribution of these setae is that shown in figure 6 with two pairs per segment. However, a few paired setae, similar at least in external morphology, are found on the anterior side of the antenna opposite the types 1 and 2 setae on the distal portion of the antenna. The length of the setae varies considerably, ranging up to 0.04 mm, and a great many are broken. Undamaged setae have pores at the tips (figures 20, 21, plate 2). There is also a single pore, which opens into a tubule, on the surface of the antenna between the members of each pair of type 3 setae (figure 18).

Type 4 setae. These are associated with the type 3 setae on the antennae proximal to the flexure. However, they differ from type 3 in that they always occur singly (figures 6 and 7); most commonly at the distal end of each antennal segment just distal to a pair of type 3 setae. They are also sometimes found lateral to the type 3 setae. Type 4 setae are basically rods 0.02–0.05 mm long with a relatively small number of setules. There is a single cuticular pore and tubule associated with each.

Type 5 setae. These have more setules and are generally larger than type 4's (figures 5, 24, 25). They are limited to the posterior side of the proximal third of the area between the antennal base and the elbow. They vary between 0.01–0.05 mm in length and point distally, with the

shaft of the seta forming an angle of 30–45° with the antenna. There is a single cuticular pore and tubule associated with each type 5 seta.

Paired *type* 6 *setae* are located on the four to seven segments just proximal to the antennal flexure (figure 3). The setae bear short sparse setules and vary in length between 0.17 and 0.34 mm with the longest pairs in the centre of the series.

A single pair of *type* 7 *setae* is located at the end of the antenna (figure 4), their length varies with that of the animal, but most fall in the range 0.3–0.6 mm. They bear setules which project from them in all directions.

7. Internal organization of the antenna

Transverse sections at various points along the length of the antenna are shown in plate 3. The centre of the antenna is occupied by a large posterior blood vessel (AM) and a smaller anterior blood vessel (unlabelled arrows in plate 3). The material contained in these vessels has a generally amorphous appearance, although structured bodies, presumed to be blood cells,

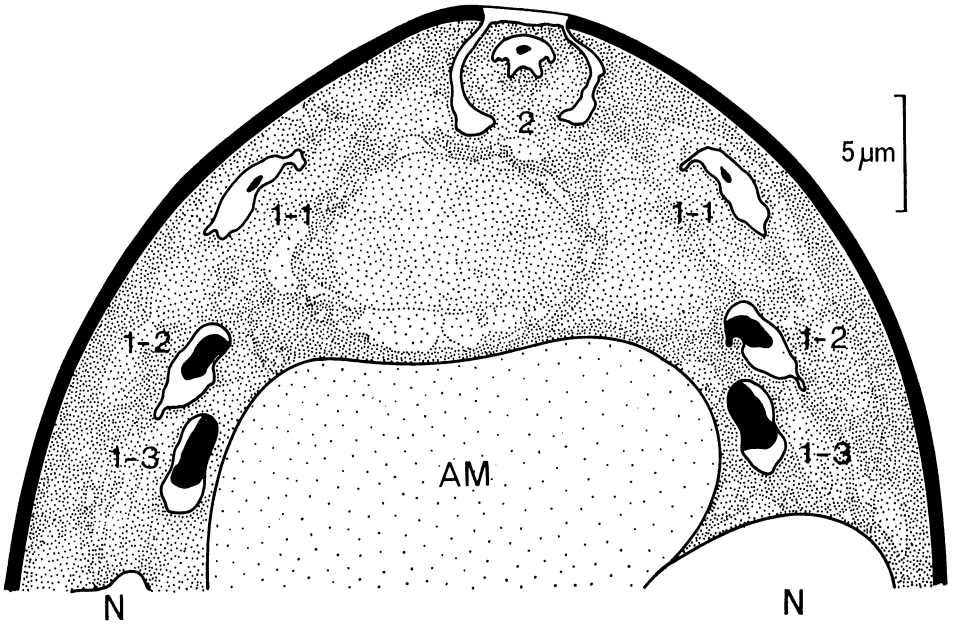


Figure 26. Tracing of a transverse section of an antenna to show how the tracts from the type 1 setae move deeper into the antenna.

Figures 41–46 show different sections from the same antenna. Note the bilateral symmetry of the tracts and the steadily increasing area occupied by insulating material as the tracts move deeper. The posterior side of the antenna is up.

1–1, tracts from type 1 setae at distal end of this segment.
1–2, tracts from type 1 setae on next segment distally.
1–3, tracts from type 1 setae on second segment distally.
2, base of type 2 seta on this segment.

are occasionally seen. There are a few scattered setae externally like types 3, 4 and 5 on the anterior side of the antenna distal to the elbow and another undescribed setal type (figures 13 and 14, plate 2) sometimes associated with the type 1 setae, but most of the setae in this area are the types 1 and 2 which are borne on the posterior side of the antenna. The somata of the neurons which innervate the type 2 setae lie approximately 100 μm proximal to the setae. From the somata the sensory neurons run anteriorly and proximally until they join the

antennal nerves which run the length of the antenna. There is a tract running downward from each type 1 seta which we originally thought, in agreement with Foxton (1969), contained one or more dendrites. However, we now believe the type 1 setae are uninnervated for the following reasons; (1) axon totals in electron micrographs of transverse sections of the basal portion of two antennae can be accounted for on the basis of axons of other setal types and are too low if the type 1 setae were innervated (this is assuming that the antennae sectioned were entire and had an average number of segments; if the antennae were not entire, and if the sensory axons degenerate rapidly, this may not be a valid argument), (2) the cellular extensions making up the tract neither penetrate the seta nor contact its wall, (3) the extensions do not contain a modified cilium, as do all other presumed receptors on the antenna. In spite of our conclusion that the contents of the tracts are non-neural, we have described them in considerable detail since we do not understand their function nor have we found a description of comparable structures in the literature. We shall call the cellular processes located within the tracts running to the setae 'type 1 processes'. The number of tracts from type 1 setae of more distal antennal segments in a given transverse section of the antenna varies with position on the antenna and between animals (figures 26, 29–31). The proportion of each tract occupied by type 1 processes steadily increases as the tract moves deeper into the antenna, while the area occupied by 'insulating material' steadily decreases (figure 26). In the distal portion of the antenna the antennal nerves are small but they gradually increase in size proximally as more and more axons are added to them until near the antennal flexure they occupy much of the dorsal and ventral portion of the antenna. In the basal third of the antenna these axons gradually become organized into bundles. Two of the dorsal bundles and a portion of another adjacent bundle (figure 27) consist mostly of very fine, tighty packed neurones of distinctive appearance. Such bundles are not found in sections of the antenna distal to the elbow and since neurones from the type 3 setae join these bundles, and are identical in appearance to the axons within them, we believe these consist of axons from type 3 setae.

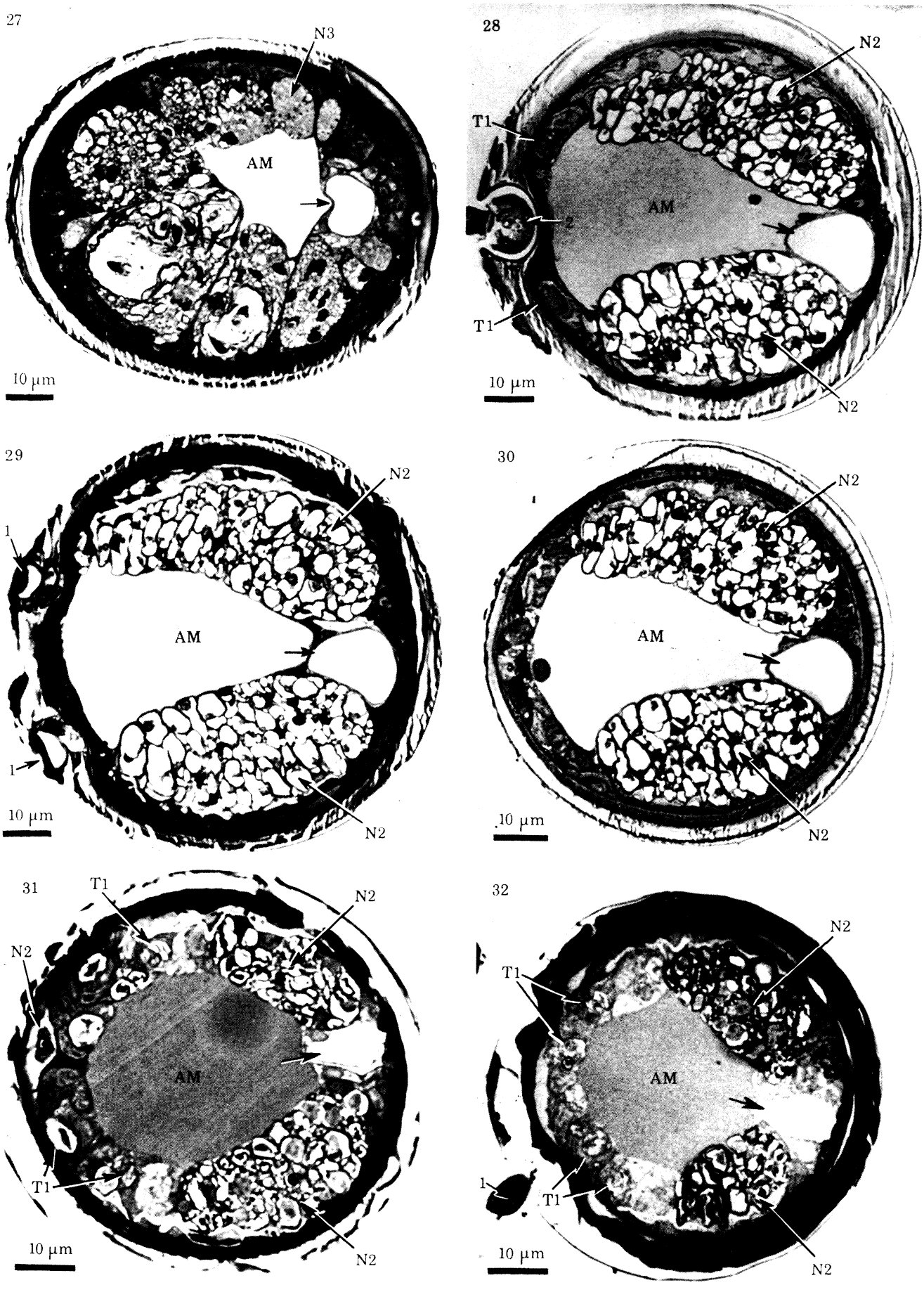
8. Ultrastructure of setal types 1–5

(*a*) *Type* 1 *setae*

Animals show one of three different morphologies in the tracts that lead proximally from the type 1 setae. We do not know the functional significance of these different morphologies nor have we any information on their possible correlation to such factors as age, sex, or position in the moult cycle. Animals were consistent in the morphology of the tracts from type 1 setae throughout the length of the antenna.

Description of plate 3

Representative transverse sections of the antenna moving from proximal (figure 27) to distal (figure 32). In figure 27 note the distinct bundling of the axons in the basal portion of the antenna and the appearance of three bundles of very fine axons (N 3) which are those from the type 3 setae. Figures 28–30 are all from the middle third of a single antenna in which the tracts from the type 1 setae (T 1) are uninsulated (see figure 48 for an electron micrograph of a tract from this same antenna). In the middle third of the antenna the axons from the type 2 setae (N 2) are gathered into two large nerves. Figure 31 is from the middle third of another antenna and shows type 1 and 2 tracts insulated with amorphous material. Figure 32 is from the distal third of an antenna again with amorphous insulating material. The proportion of the section occupied by the antennal nerves is less than in more proximal sections. Anterior is to the right and the anterior blood vessel is indicated by an unlabelled arrow.



FIGURES 27–32. For description see opposite.

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The type 1 setae are consistently hollow distal to a plug of electron-dense material which totally occludes their bases (figure 33A, C, E). From the hollow shaft of the seta arise setules which are strengthened basally by a dense cuticular anchor and by a hollow cuticular ridge (figure 33B, see also figures 71–74 for comparable supporting structures in type 2 setae). Just distal to the plug is a less-dense vacuolated area, while proximally the plug grades into a material resembling honeycomb (figure 33A, C, E).

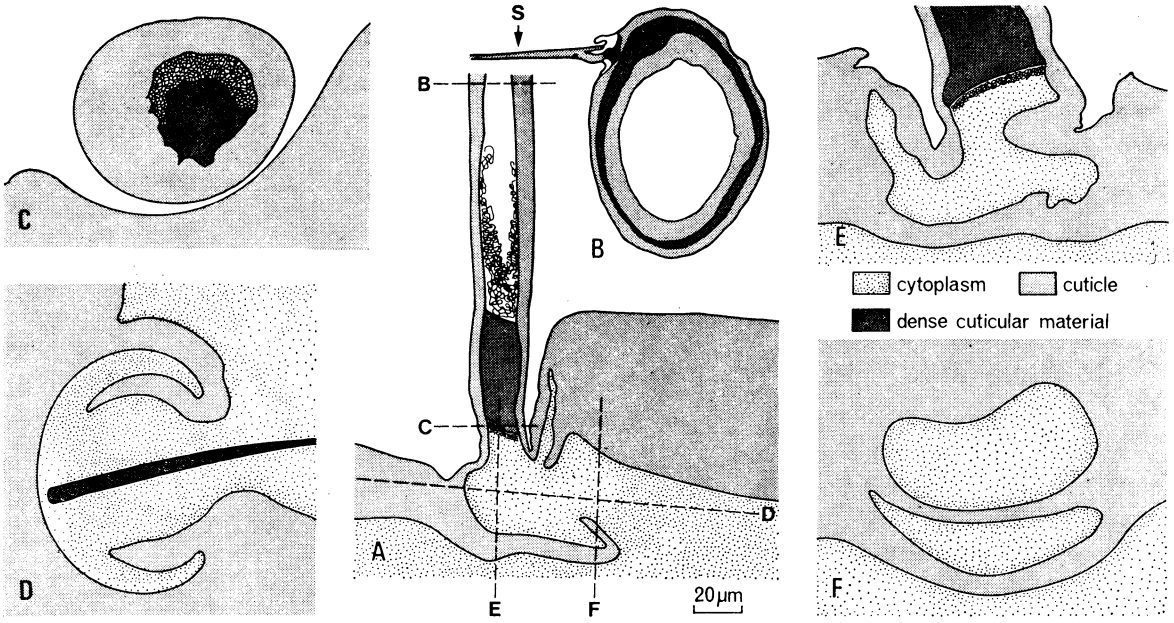


FIGURE 33. Various aspects of the anatomy of a type 1 seta and its base.

(A) Vertical longitudinal section of a type 1 seta and its base. Other parts of the figure are related to this as shown by the lines.

(B) Cross-section of a seta distal to the plug showing bracing at the base of the setule (S).

(C) Cross-section at the level of the plug. Note that the base of the hair is totally occluded.

(D) Horizontal longitudinal section of hair base. Note dense strand of unknown composition crossing the base. This was seldom seen in light micrographs and not in any of our series of electron micrographs.

(E) Vertical transverse section of hair base.

(F) Vertical transverse section of hair base proximal to E.

Scale applies only to (*a*), other portions of figure not to scale. All parts of this figure are tracings from micrographs.

The bases of type 1 setae are mounted in a membrane within a cuticular socket (figures 12–14, plate 2) which is entered by way of a proximal channel (figure 33A, D). In a few of our light microscope sections a dark thread crosses the socket to apparently attach at the base of the seta (figure 33D). However, in none of our EM sections, which include series in all three planes, were we able to locate a connection to the base of the seta. In all of these series the central type 1 process enters the setal base accompanied by a variable number of wrapping processes and both sorts of processes become steadily smaller without any apparent specializations or connections to the setal base (figures 35, 36, 41, 42, plate 4).

The three distinct morphological types of tracts leading from type 1 setae are those without any insulating material (figures 28–30, 48, 49), those with amorphous insulating material (figures 35–40) and those with highly ordered lamellated insulating material (figures 41–47). However, the structure of the type 1 process is identical in all three types of tracts (figure 34). The insulating material is an extracellular substance deeply invaginated into the complex cells

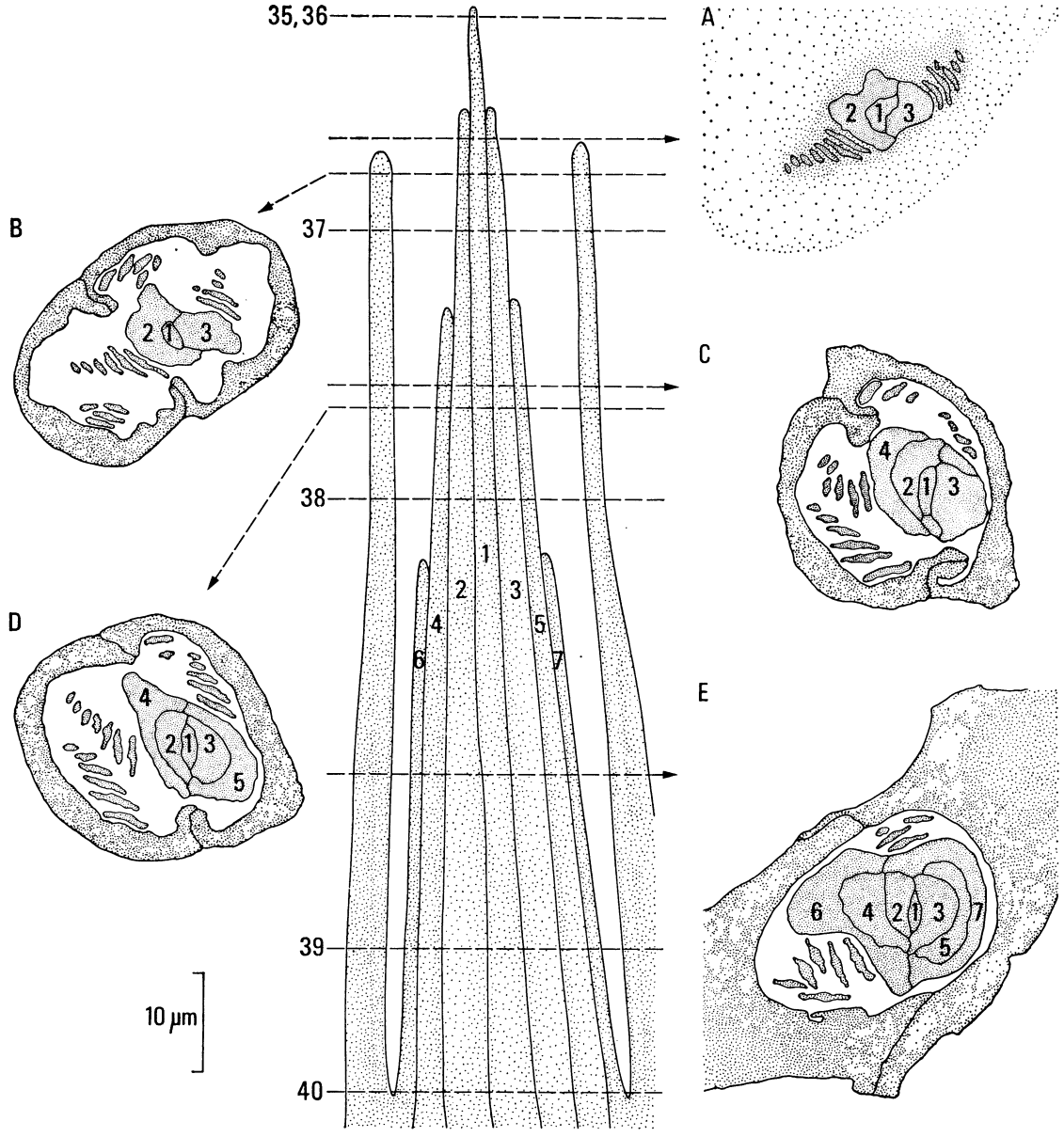
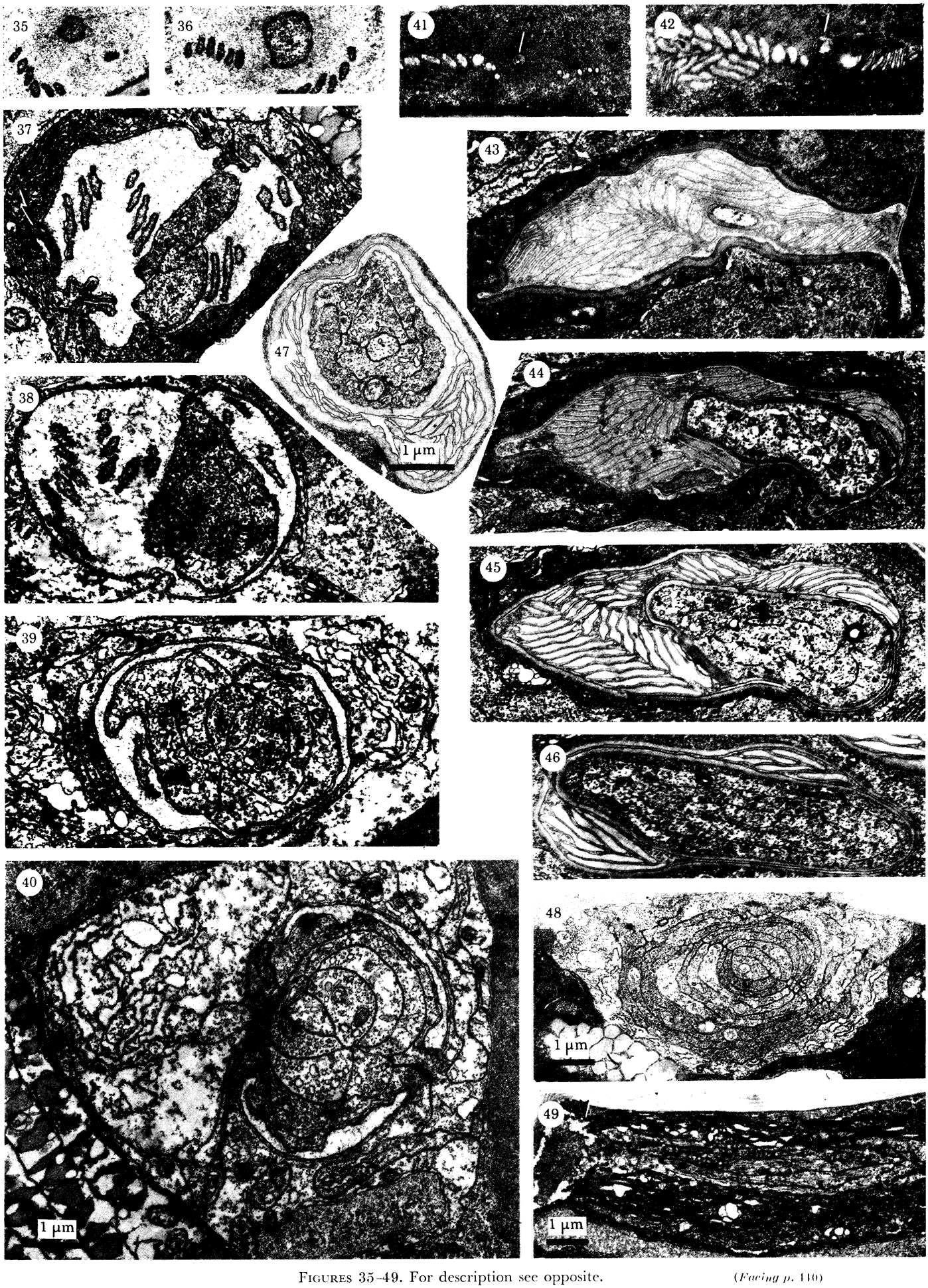


FIGURE 34. Schematic longitudinal section of type 1 tract insulated with amorphous material. The small protrusions penetrating the insulating material from the wall of the cylinder (see A–E) have been omitted from the longitudinal section for clarity. A–E are tracings from a series of transverse sections of a single tract. The numbers within the tract show how the tract grows by progressive addition of lamellae to the outside. Labelled lines show approximate positions of figures 35–40. Scale applies only to longitudinal section.

DESCRIPTION OF PLATE 4

Ultrastructure of type 1 tracts; consult figure 34 for further information and locations of some sections. Figures 35–40 show progressively more proximal areas of type 1 tracts with amorphous insulation. Figures 35, 36 and 40 are representative sections while figures 37–39 are from a single tract. In figure 37 note that the lamellae within the amorphous material appear to originate from the walls of the cylinder surrounding the amorphous material (arrow). Figure 40 shows that the outer lamellae originate from the cells that form the walls of the cylinder. Figures 41–46 are from progressively more proximal areas of type 1 tracts with lamellar insulation. Arrows in figures 41 and 42 mark the central type 1 process. Figures 41–43 are representative sections while figures 44–46 are from a single tract. The areas within the lamellae are poorly preserved, but the figures serve to show the degree of development of the lamellar insulating material along the length ot the tract and the increasing area of the tract occupied by the type 1 process proximally. Figure 47 is a section of a tract with adequate preservation of the tissue within the lamellar sheath. The similarity in the pattern of material within the insulation to that shown in figure 38 is apparent. Figure 48 is a cross-section of an uninsulated tract from the antenna shown in figures 28–30. Figure 49 is a vertical longitudinal section of an uninsulated type 1 tract showing how the type 1 processes end (arrow) with no apparent extension into the hair base. Scale in figure 40 applies to figures 35–46.



FIGURES 35–49. For description see opposite.

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which constitute the type 1 process. The small islands of tissue within the amorphous material originate from the walls of the cylinder which holds the amorphous material (figure 37) and presumably remain attached to the wall at their bases. There are no cytological differences between the central type 1 process and the other processes which enfold it. All contain microtubules and mitochondria. The tracts from the type 1 setae of each segment end symmetrically immediately adjacent to the antennal nerves on the dorsal and ventral sides of the antenna. The outermost lamella on either side of the type 1 process clearly originates from the cell which forms the wall at that side of the tract (figure 40). We have not been able to trace the remaining segments of the type 1 process to their nuclei due to the complexity of the area at the base of the tract. However, there are four additional nuclei in the area. There are no apparent extensions joining the antennal nerve from the type 1 process and for the reasons listed above we believe the cells forming the process are non-neural.

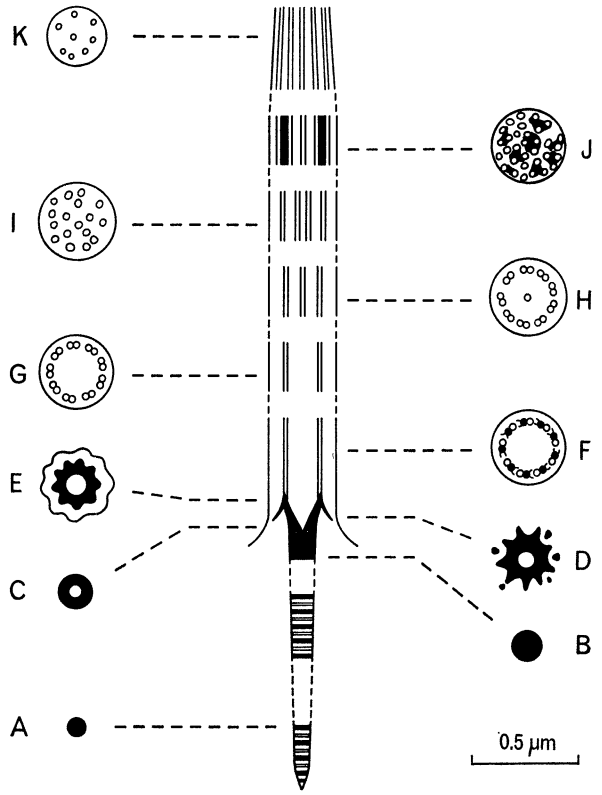


FIGURE 50. Schematic diagram of ciliary structure of type 2 dendrites. This is an idealized reconstruction as the different cilia go through these stages at differing distances along their lengths. The basal portion of the cilium is not unusual (A–E). A, B and C subfibres, set at an angle around the open centre of the cilium, were occasionally recognizable at about level E. However, they were completely embedded in the dense black material of the ciliary base and we did not find evidence for a well developed basal body such as has been described in insects (Gaffal & Bassemir 1974; Young 1973). Near the base of the cilium each doublet consists of a hollow tubule plus a solid tubule with arms (F). Further up the cilium (G) each doublet consists of two hollow tubules without arms. Continuing distally single tubules begin to be added centrally (H) and the doublet organization is gradually lost until there is an apparently random pattern of microtubules (I). Beyond this the cilia no longer behave uniformly since all except the largest continue distally with randomly arranged microtubules until they begin to lose their tubules and get smaller as they approach their ends. The tubules in the large cilium, however, begin to clump, usually into groups of three, which are held together by electron dense material (J). Further distally the electron dense material disappears and the cilium becomes smaller and the tubules fewer (K). Broken lines between (F) and (J) indicate omission of approximately 5 μm each.

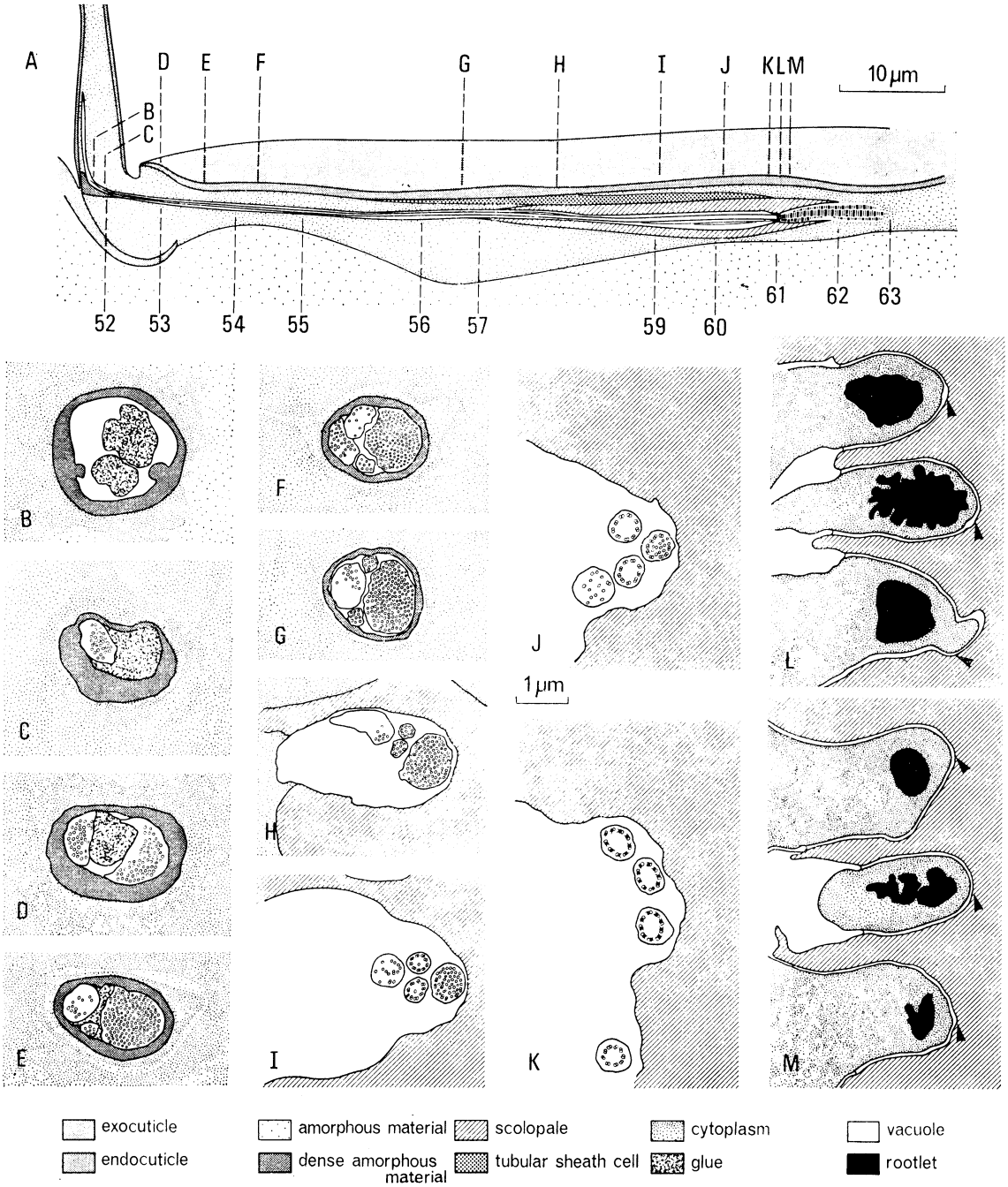


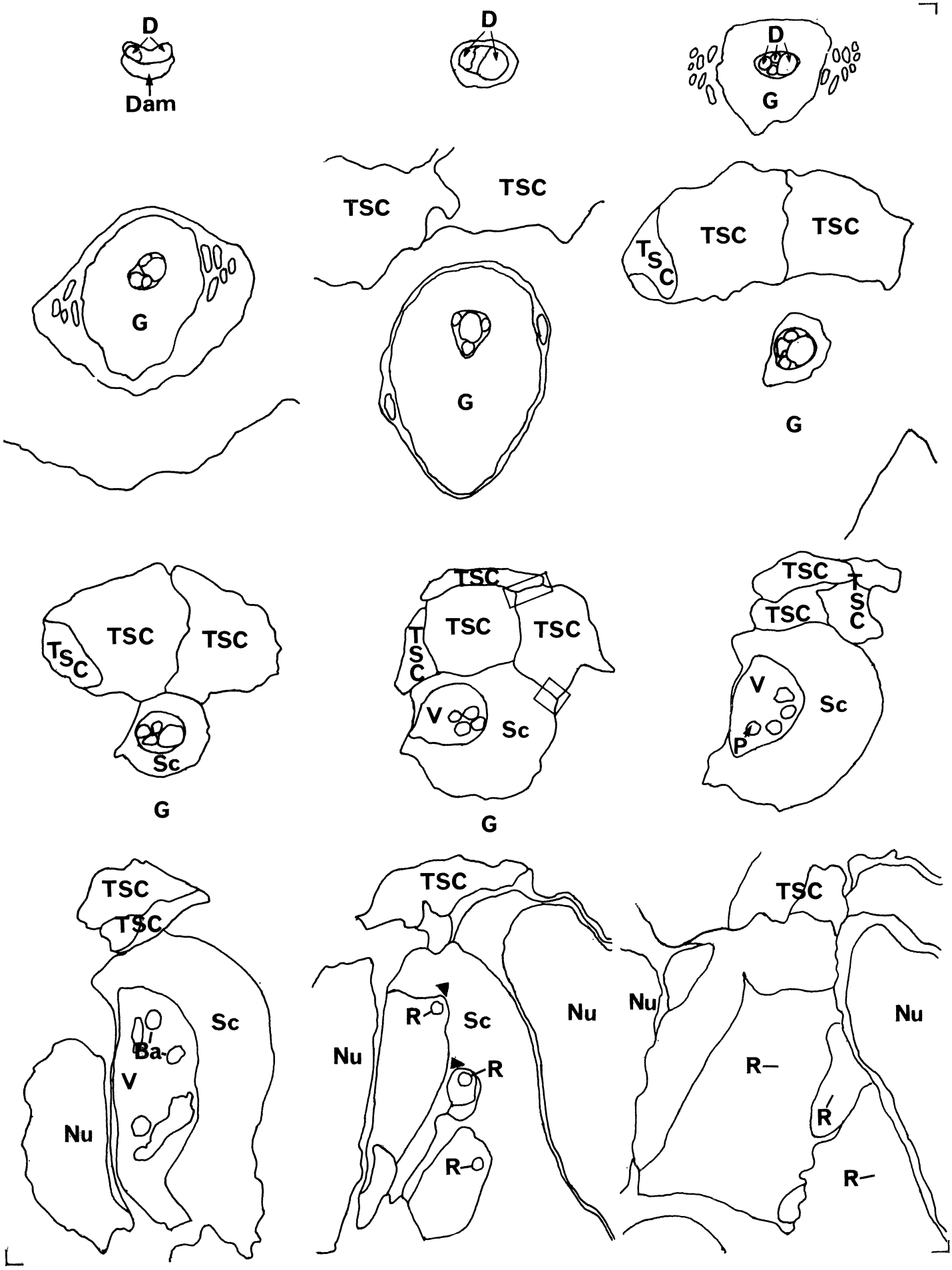
FIGURE 51. A schematic drawing of a type 2 seta modified from an actual longitudinal section. The transverse sections are tracings of the series from which figures 52 and 53 were taken. Their position on the longitudinal section is indicated by the appropriate letters. Numbered lines show the location of the sections in plate 5. Note the complete consistency in the pattern shown by the four dendrites in this figure and in plate 5. Desmosomes between the dendrites and the scolopale cell in L and M are labelled with arrows.

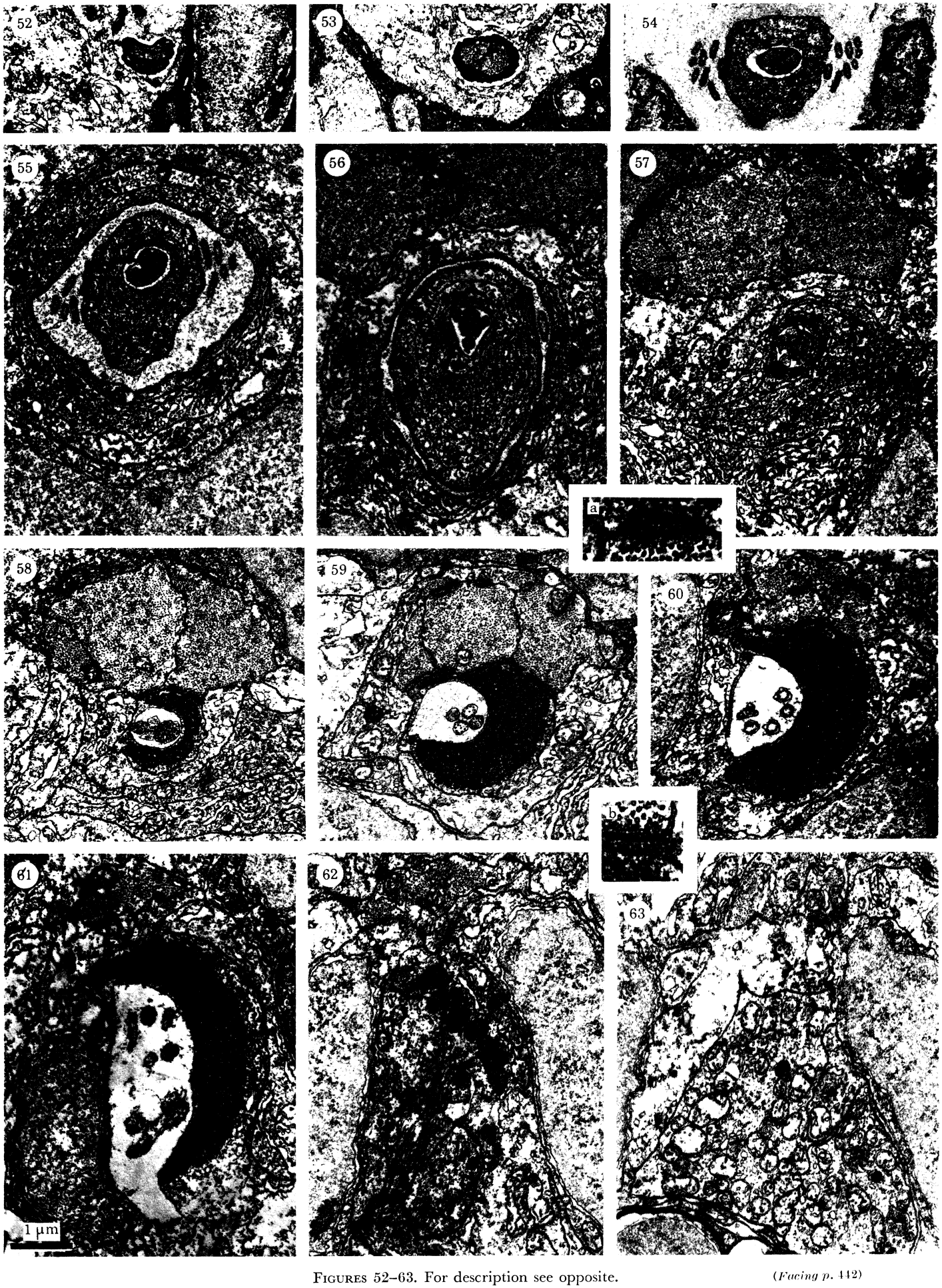
DESCRIPTION OF PLATE 5

Transverse sections of innervation of type 2A seta. Refer to figure 51 for the location of the sections. Figures 54–63 are a series from a single seta while figures 52 and 53, from another series, are included to fill in missing portions of the longer series. See text for details. The insets show desmosomes between tubular sheath cells (*a*) and between the scolopale cell and a tubular sheath cell (*b*). Desmosomes between dendrites and the scolopale cell in figure 62 are marked by arrows.

Scale in figure 61 applies to entire plate.

Overlay for plate 5





FIGURES 52–63. For description see opposite.

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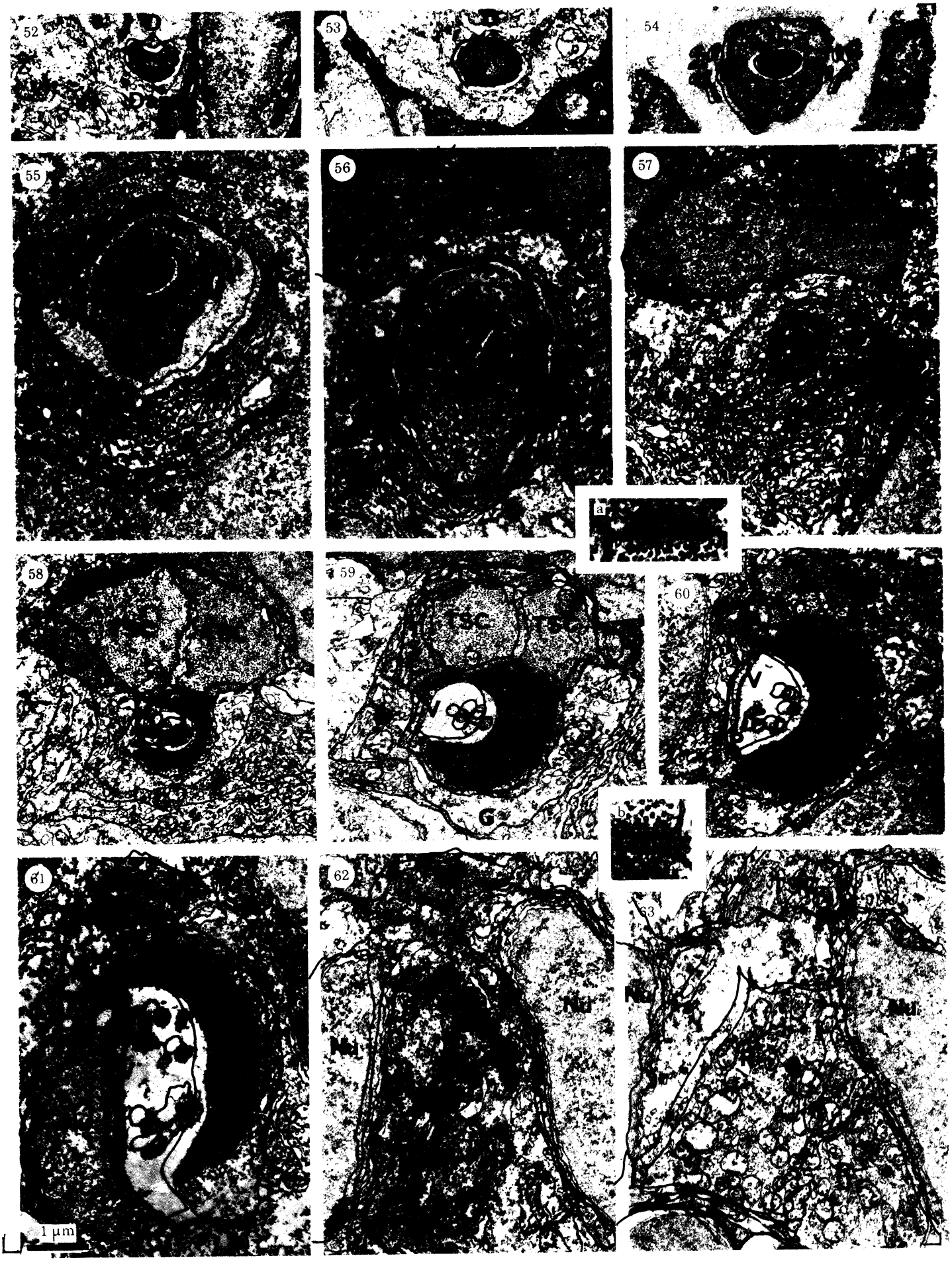
52
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57
a
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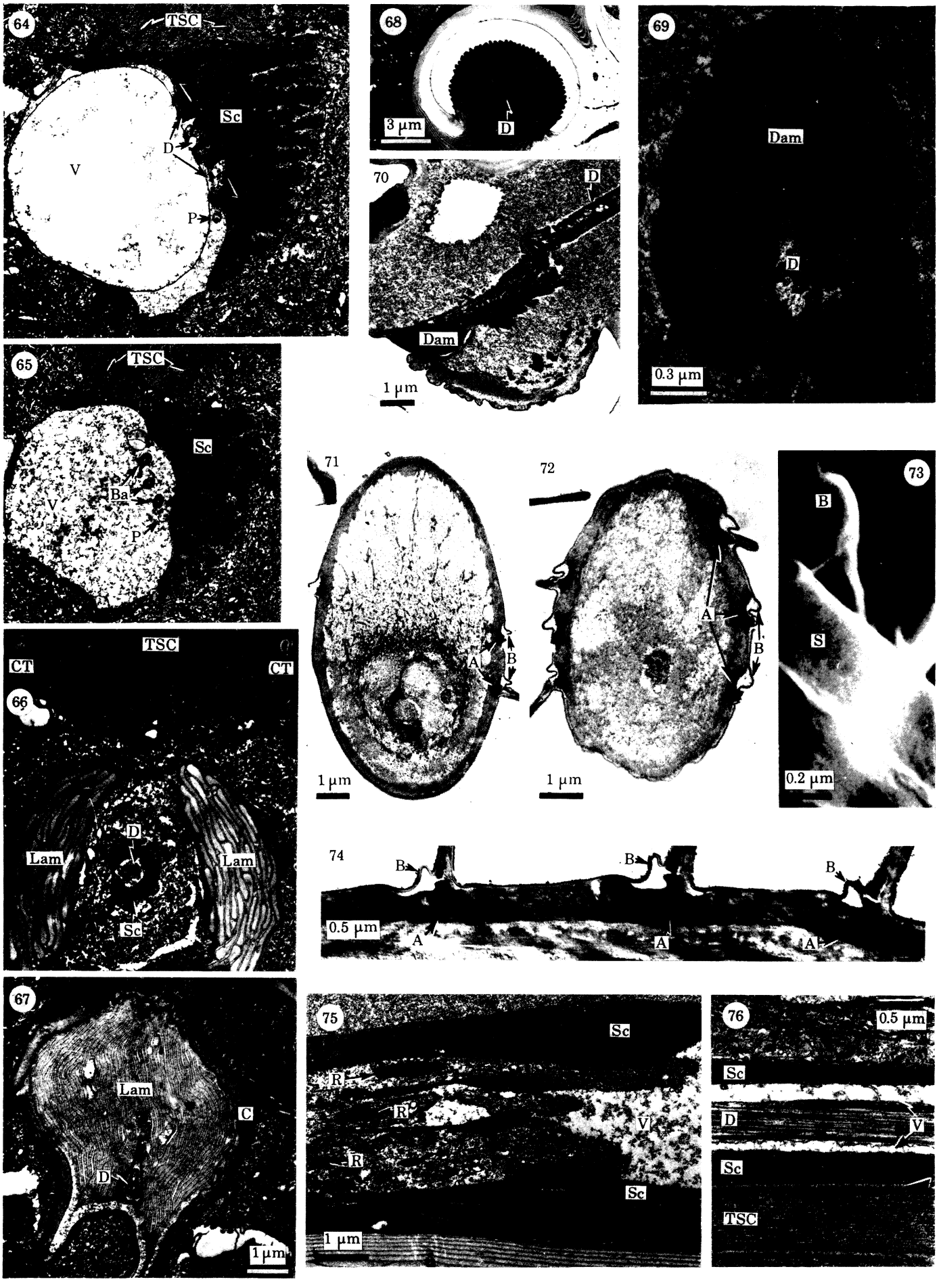
1 μm



FIGURES 64–76. For description see opposite.

As can be seen from figures 41–46 and especially in figure 47 the type 1 processes wrapped by highly structured insulating material are arranged in the same way as those wrapped in amorphous insulating material. The nature of the lamellated insulation and the origin of its highly ordered structure are unknown.

(*b*) *Type 2 setae*

Based on external morphology there are two distinct sorts of type 2 setae (2A, 2B) but there is no correlated difference in internal morphology. However, type 2 setae do show the same range of differences in insulating material as type 1 setae, from no insulating material to a highly developed lamellated insulation. Within an antenna, the type and degree of insulation are consistent for both type 1 and type 2 setae. The various cells associated with the type 2 setae are described below.

(i) *The setae*

Type 2 setae, in contrast to type 1, are solid but their internal consistency is not uniform, as can be seen in figures 71 and 72. The setules are solid and all show basal specializations consisting of a high-density rootlet or anchor (A) and a hollow cuticular fold or buttress (B), partially surrounding the base of each setule (figures 71–74). This cuticular fold is on the side of the base from which water comes if it flows through the tube as the animal swims.

The distal ends of the dendrites, which are enclosed in a tubule, cross the base of the seta and are attached to the distal wall of the base, in what appears to be a firm mechanical linkage, by a dense black amorphous material (Dam, figures 69–70). The tubule containing the dendritic extensions then continues distally in association with the wall of the seta.

(ii) *Sensory neurones*

There are four sensory neurones per seta, three of which bear a ciliary dendrite (figures 60–65). The fourth bears a dendrite which lacks a rootlet and either contains unordered micro-

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Description of plate 6

Type 2 setae.

Figures 64–67. Transverse sections of a large type 2 (2B) seta to show similarity of dendritic structure to other type 2 setae (figure 51, plate 5) in spite of a quite different overall appearance caused by the presence of the lamellated sheath. Desmosomes between dendrites and the scolopale cell in figure 64 are marked by unlabelled arrows. The scale in figure 67 applies to all of these figures.

Figure 68. Horizontal longitudinal section of the base of a type 2 seta showing the tip of the dendrite enclosed in dense amorphous material.

Figure 69. Higher magnification of the dendrite tip of figure 68.

Figure 70. Vertical longitudinal section of the base of a type 2 seta showing the relation between the dendrite and the dense amorphous material.

Figures 71 and 72. Transverse sections of a type 2 seta showing structural modifications of the bases of the setules which may strengthen their resistance to water flow. These are a dense anchor (A) and a hollow cuticular buttress (B) partially surrounding the base of the setule.

Figure 73. Scanning electron micrograh showing the buttress partially surrounding the base of a setule.

Figure 74. Longitudinal section of type 2 seta again showing structural modifications of the setule bases.

Figure 75. Longitudinal section of the three ciliary dendrites, each containing a rootlet, which innervate a type 2 seta.

Figure 76. Vertical longitudinal section of tubular sheath cell, scolopale and dendrite. Note desmosome between scolopale cell and tubular sheath cell (arrow).

tubules or, in some cases, none. The somata of the sensory cells stand out clearly from the surrounding cells because their cytoplasm is much less dense and they are packed with mitochondria. The somata of the two outer ciliary dendrites are 10–12 μm in diameter and are usually found side by side beneath the setae on the next-most-proximal segment approximately 100 μm away from the seta which they innervate. The soma of the central ciliary dendrite is slightly further proximal, and the soma of the paraciliary dendrite must lie still further proximally although it has not been located. The ciliary rootlets (R) are found distal to the neurone nuclei and have a periodicity of 80 nm (shown in l.s. in figure 75 and in t.s. in figures 62–64). Desmosomes attach the dendrites to the scolopale cell at the level of the ciliary bases (arrows figures 62, 64). The cilia are borne on projections (figures 61 and 75) and the internal structure of a cilium at various points along its length is summarized in figure 50. There is an obvious asymmetry in the scolopale cell (Sc, plate 5) and this is paralleled by a consistent asymmetry in the ciliary structures, with the dorsal and ventral cilia the first to lose their 9 + 0 organization. In our three EM series of this region the paracilium (P) has both the fewest and least organized microtubules. The central cilium, which is most deeply enveloped in the scolopale cell, expands distally and is consistently the largest (see figure 51 and plate 5) while the dorsal and ventral cilia are smaller. As they approach the base of the seta the cilia end one by one in a rather featureless material which Whitear (1962) has termed 'glue'. From our material it appears that the small dorsal and ventral cilia end first and usually only a single cilium remains at the setal base. As the cilium in its tubule approaches the distal wall of the seta it is tightly surrounded by amorphous electron dense material which links it to the wall (Dam, figures 52, 68–70).

Proximal to the cell bodies the axons move dorsally or ventrally and more deeply into the antenna until they reach the larger blood vessel. They then continue dorsally or ventrally along the margin of the blood vessel to join either the dorsal or ventral antennal nerve.

(iii) *The scolopale cell*

The scolopale cell (Sc), which surrounds the extracellular space containing the dendrites (D), has the form of a hollow sleeve of varying internal diameter. Both the scolopale cell and the scolopale itself, which consists of a mass of dense filaments, are asymmetrical with their thickest portions lying ventrally.

The nucleus of the scolopale cell lies proximal to the scolopale, which ends at the level of the ciliary rootlets (figure 51A). The cytoplasm of the scolopale cell appears more dense than that of the sensory cells and contains numerous mitochondria. The scolopale reaches its maximum dimensions along the proximal portion of the vacuole (V) containing the dendrites. Further distally the scolopale and the extracellular space which it surrounds shrink steadily and the scolopale ends about 30 μm beyond the ciliary basal bodies. The scolopale cell forms a characteristic thickened (desmosome-like) junction at all its points of contact with the tubular sheath cells (figures 58–60, 76).

(iv) *The tubular sheath cells*

The tubular sheath cells (TSC) are readily recognized by their microtubule-packed cytoplasm (figures 56–66, 76); the only other prominent organelles are a few scattered mitochondria. There are three such cells contacting the scolopale cell and lying between it and the nearest wall of the antenna, and at least one more between these cells and the cuticle. As previously mentioned, all three cells form desmosomes where they abut the scolopale cell and, in some cases,

where they contact each other. The microtubules of the tubular sheath cells run parallel to the long axis of the scolopale cell. Their nuclei lie distally just beneath the cuticle near the point where the dendrites break out into the subcuticular space before reaching the base of the seta. The only prominent organelles in these cells other than microtubules are a few scattered mitochondria.

(v) *Glial cells*

Glial cells (G) are the only other cell type intimately associated with the sensory cells. They are complex with many projections (plate 5) and we have not been able to establish the exact number of cells involved. The glial wrapping reaches its maximum complexity near the distal end of the scolopale; the wrapping pattern is simpler both proximally and distally.

(vi) *Comparison of uninsulated and insulated type 2 setae*

Figures 64–67 are transverse sections of a type 2B seta taken from the same series of sections as the type 1 setae shown in figures 41–46 and a similar degree of lamellar insulation (Lam) is apparent in both cases. Although there is a superficial difference from the amorphously insulated type 2 seta shown in plate 5, a detailed comparison of figures 64–67 with comparable areas in plate 5 reveals all of the same cell types arranged in essentially the same ways; the only difference being that the insulation is lamellar in one case and amorphous in the other.

(vii) *Cuticular tubules*

A pair of pores, one on either side, is associated with each type 2 seta (figures 14, 15) and from these pores a pair of tubules accompanies the dendrites downward (see, for example, figure 66, CT). In cross-section these tubules consistently show a thin outer tube (i.d. 0.39–0.55 μm) separated by a space from a thick inner tube (i.d. 0.25–0.45 μm). These tubes are similar to cuticle in appearance. In a few cases microtubules are present within the tubules, but more frequently the tubules are empty or have amorphous contents.

(*c*) *Type 3 setae*

There are no apparent external differences between the members of each pair of type 3 setae, but on the basis of internal morphology they are of two distinct sorts which are always paired with each other and are always consistent with respect to their relative positions. The dorsal seta (type 3A) always contains three dendrites, while the ventral seta (type 3B) usually contains about ten dendrites. The nerve bundles of both types of setae are contained in parallel cuticular tubes with the ten dendrite type (3B) always entering its tube first. Dendrites do penetrate the type 3 setae, but we do not know where they end due to poor fixation within the setae. The neurones innervating type 3 setae are occasionally selectively labelled with small black dots (figure 85). These dark bodies may normally occur within the cells or may be, for example, a lead precipitate resulting from some chemical constituent of the neurones, but they appear to be specific to neural tissue.

Associated with each pair of type 3 setae is a cuticular tubule identical to the pair described in association with the type 2 setae (figures 77–84). This tubule usually starts downward from the surface between the type 3 setae (figures 18, 77–79) but as it passes deeper into the antenna it becomes progressively more closely associated with the dendrites from the type 3A seta (figures 81–84).

(i) *Type 3A setae*

Proximally from the setal base, the dendrites, which are enclosed in a tube of cuticle, travel inward through the cuticle, then parallel to and just beneath it for 16–17 μm before moving deeper into the antenna for about a further 15 μm (figures 77A–D, 78, 79) still within the tube of cuticle. On emerging from the tube the three dendrites become wrapped in microtubule-containing cells (figures 77E, F, 80). Continuing proximally, two of the dendrites pass through

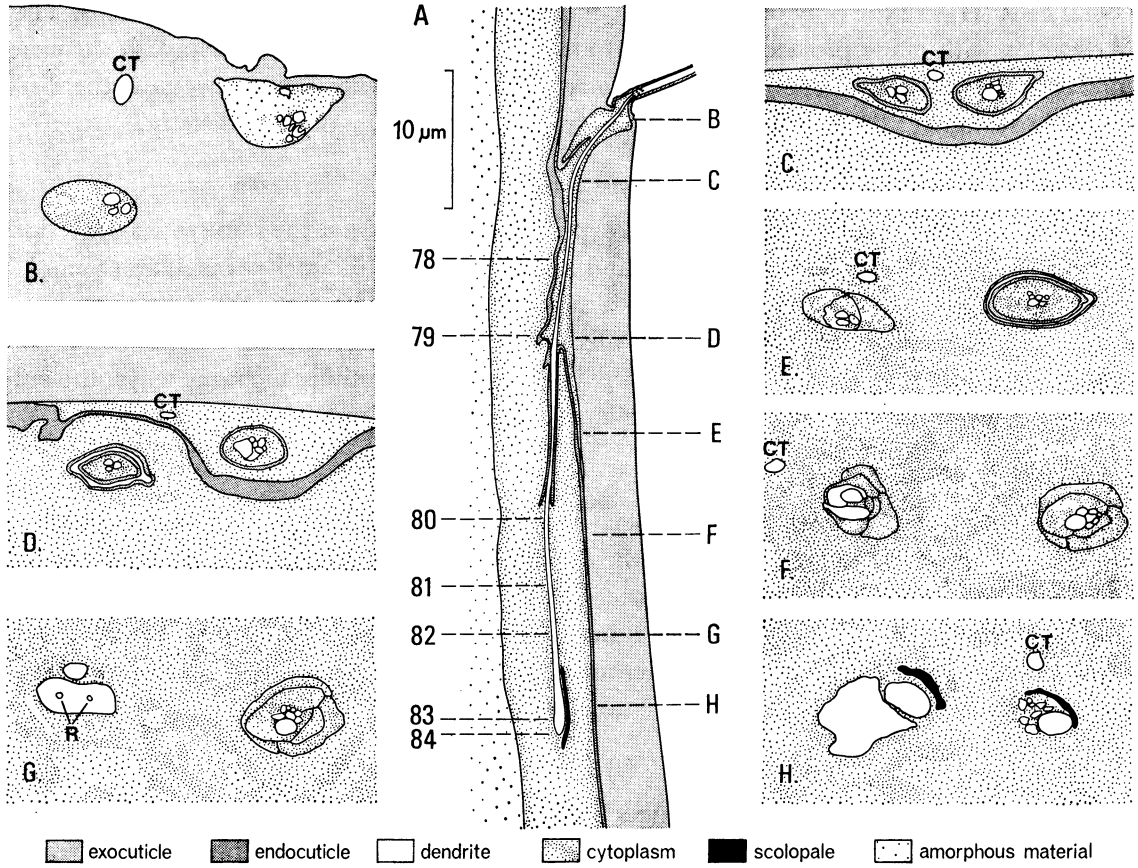


FIGURE 77. Diagram of innervation of type 3 setae showing the location of the sections in plate 7.

(*a*) Schematic longitudinal section of type 3 seta modified from a micrograph of a longitudinal section. In general structure longitudinal sections of the two sorts of type 3 setae are very similar, but for purposes of relating to the transverse sections this is assumed to be a longitudinal section of a type 3B (10 dendrite) seta.

(*b–h*) Tracings of transverse sections of type 3 setae at the levels shown. Apparent variability in number of type 3B dendrites is probably a fixation artefact.

DESCRIPTION OF PLATE 7

Type 3 setae.

FIGURES 78–84. Representative sections of the innervation of type 3 setae. See figure 77 for location of the sections and text for discussion. Scale in figure 83 applies to all of these figures.

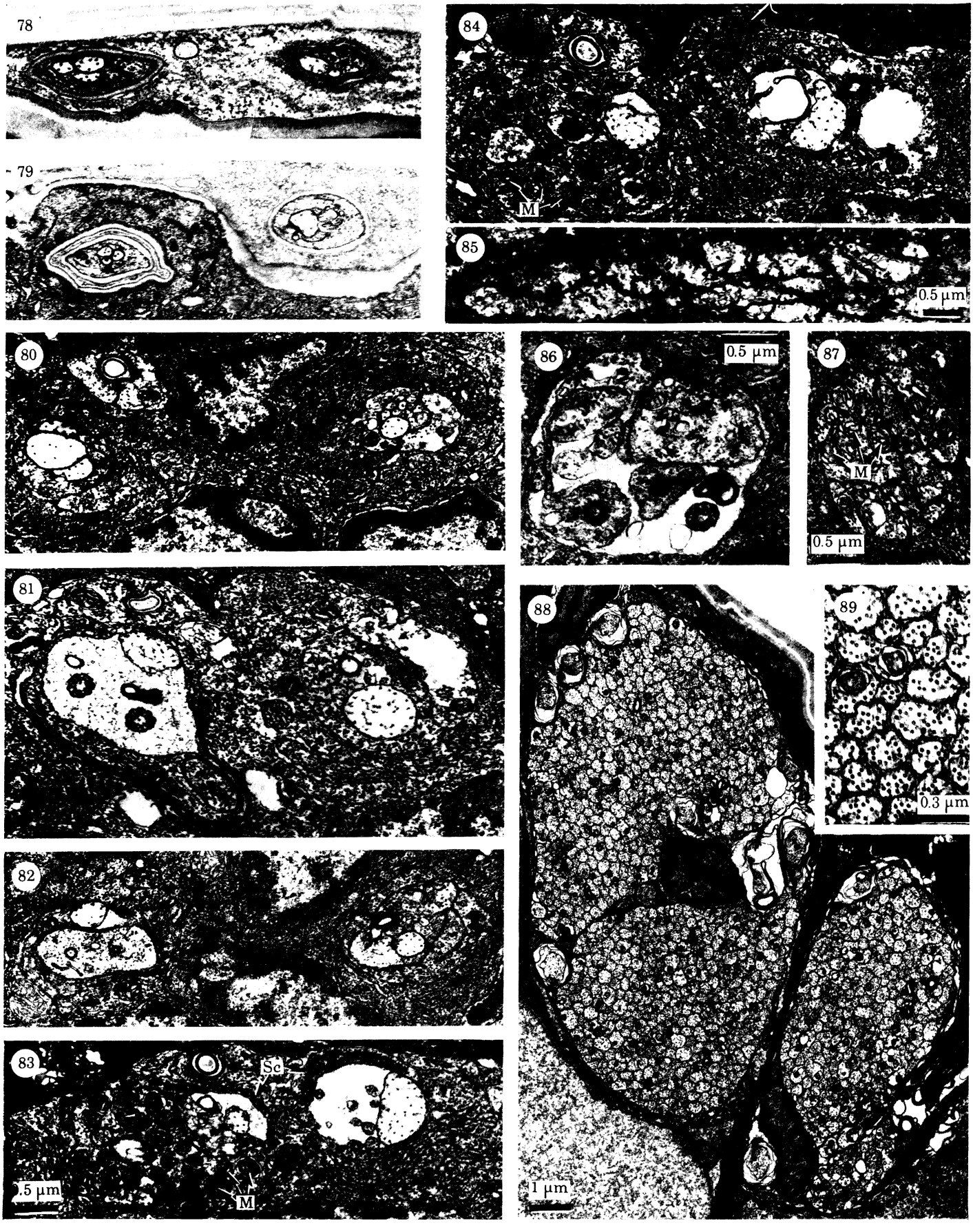
FIGURE 85. Selective 'labelling' of axons with black deposits.

FIGURE 86. The ciliary portion of type 3B dendrites.

FIGURE 87. A bundle of eight axons from a type 3B seta.

FIGURE 88. Bundles consisting almost entirely of type 3 axons.

FIGURE 89. Higher magnification view of type 3 axons. Note abundant microtubules.



FIGURES 78–89. For description see opposite.

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a short ciliary portion (figure 81) within a vacuole and then appear to enter a single cell (figures 77G, 82). The ciliary rootlets are not particularly well developed (figure 82); just further proximally is a region packed with mitochondria (figures 83, 84). The third dendrite, which is within a vacuole surrounded by the scolopale cell, continues proximally beyond the first two (figures 83, 84) before passing through a ciliary stage. There are probably two axons leading proximally to the bundle of type 3 axons, but in a few cases there appear to be three or more.

(ii) *Type 3B setae*

The dendrites of the type 3B setae are less consistent in their number and arrangement than those from the type 3A setae. One type 3B dendrite (rather empty but for sparse microtubules)

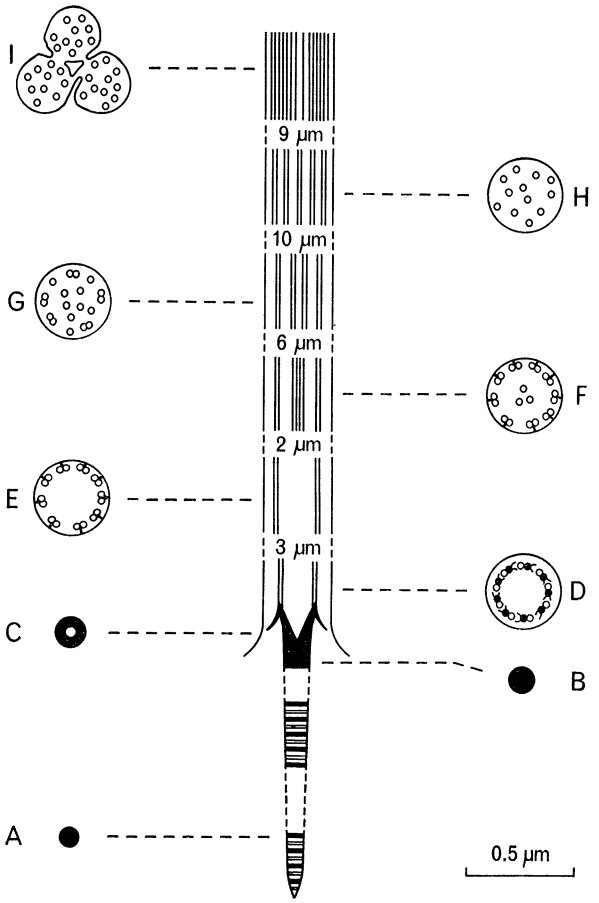


FIGURE 90. Schematic diagram of internal structure of dendrites innervating type 4 setae. Longitudinal portions of the cilium associated with the transverse sections are not to scale. The transverse sections are separated by approximately the distances shown on the figure. The main differences between the structures shown here and those shown in figure 50 are the connection of the doublet tubules to the wall of the cilium (E, F) and the fusion of the cilia near their tips (I).

is much larger than the 7–9 others (figures 77–84). Some of the apparent variation in the number of small dendrites in our material may be an artefact of poor fixation, but there also appears to be genuine variation. The type 3B dendrites follow the same route as those innervating the type 3A setae: they first (figures 78, 79) travel 15–20 μm just beneath the cuticle enclosed in a cuticular tube and then leave the cuticle and move deeper into the antenna for approximately another 15 μm still within the tube. On emerging from the tube they are wrapped in

microtubule-containing glial cells (figure 80). Each dendrite, including the large one, passes through a ciliary stage (figure 86). At this level the dendrites are within a vacuole which is partially surrounded by a thin layer of dense scolopale material (figure 83). The scolopale cell forms a thickened junction with an adjacent microtubule-containing cell (figure 84, arrow) similar to that formed with the tubular sheath cells of the type 2 setae. Proximally the vacuole ends in 8–10 cells bearing ciliary rootlets (figure 86) beyond which the cells are filled with

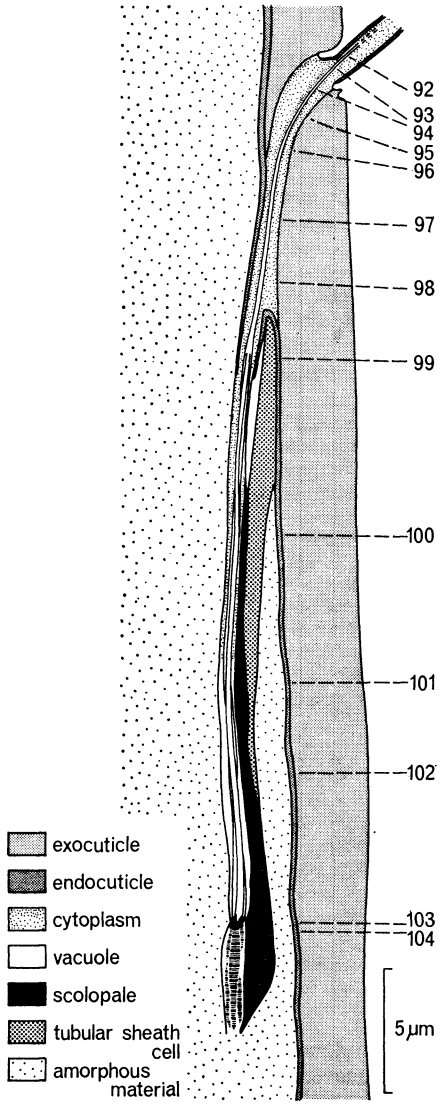
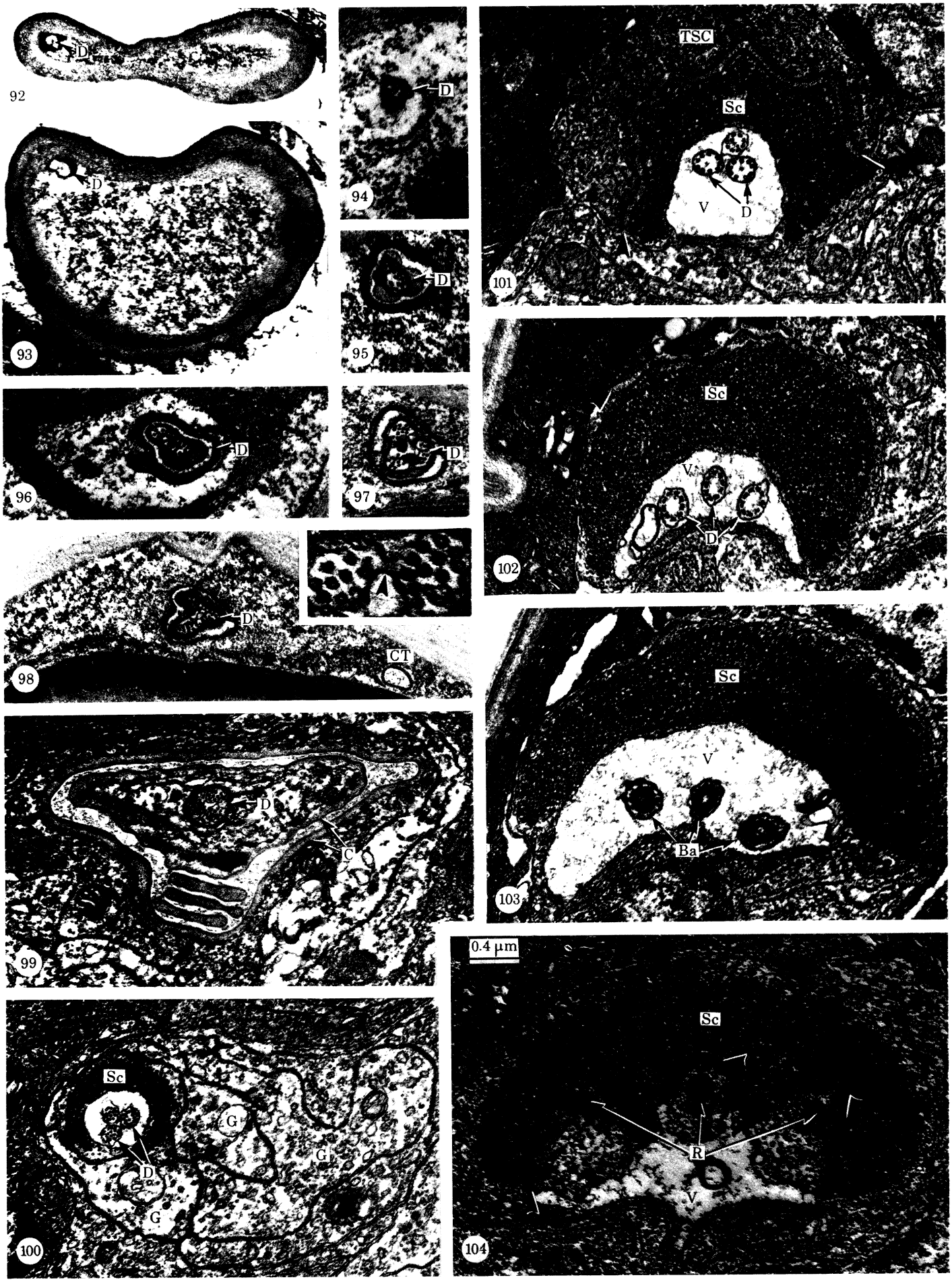


FIGURE 91. Schematic longitudinal section of innervation of a type 4 seta reconstructed from longitudinal and transverse sections. Numbered lines show the location of corresponding transverse sections in plate 8.

DESCRIPTION OF PLATE 8

Representative transverse sections of a type 4 seta and its innervation. See figure 91 for location of these sections and text for discussion. Figures 92–94 are from one series, figures 95, 102, 103 from another and figures 96–101, and 104 from another. Inset in figure 98 shows a cytoplasmic bridge (arrow) connecting two dendrites. Arrows in figure 104 mark desmosomes between dendrites and the scolopale cell. Scale in figure 104 applies to the entire plate.



FIGURES 92–104. For description see opposite.

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mitochondria. After reaching their cell bodies the bundles of 8–10 axons (figure 87) travel proximally and postero-dorsally to join the bundles of type 3 axons (figures 88, 89).

(*d*) *Type* 4 *setae*

There is normally a type 4 seta closely associated with the paired type 3 setae at the distal end of each antennal segment. A longitudinal section of a type 4 seta is shown in figure 91 which also serves as a guide to plate 8. Near their bases the type 4 setae are flattened in transverse section (figure 92) and contain an extension of the dendrites which innervate the seta. As in the case of the type 2 setae this dendritic extension is surrounded by dense amorphous material which appears to connect it to the wall of the seta (figures 92–96). Proximal to the setal base there is a single dendrite containing microtubules and surrounded by dense amorphous material (figure 95). Continuing proximally and still within the cuticle, there are two fused microtubule-filled dendrites (figure 96) which become three, at first still connected (figures 97, 98) but later separating, though all still contained within a single cuticular tube (figure 99). The three dendrites then leave the tube and are enclosed within a vacuole (figure 100) that steadily increases in size proximally and which is surrounded by a scolopale cell. Both the vacuole and the scolopale cell which surrounds it continue to increase in size and the scolopale cell forms a desmosomal junction with an adjoining microtubule-filled cell comparable to that formed between the scolopale cell and the tubular sheath cell of the type 2 setae (figure 101). The internal ciliary structure of all three dendrites is relatively uniform and is summarized in figure 90. Toward the base of the vacuole the dendrites change from a triangular to a linear array and then pass into typical basal body and rootlet structure. At the rootlet level, the intracellular vacuole has almost disappeared (figure 104) and the dendrites are attached to the scolopale cell by desmosomes (arrows). Further proximally, the scolopale material becomes reduced to three separate areas immediately adjacent to the ciliary rootlets. Each of the cilia is borne on a separate cell and the neurones travel postero-ventrally to join the ventral antennal nerve. The type 4 setae are accompanied by a cuticular tubule (figure 98) similar to that described in association with the types 2 and 3 setae.

(*e*) *Type* 5 *setae*

Judging from a single series of sections a type 5 seta has three ciliary dendrites and differs little from a type 4 except that the relative size of the vacuole contained in the scolopale cell of the type 5 is less than that of the type 4. The type 5 seta is accompanied by a cuticular tubule similar to those described in connection with setal types 2, 3 and 4.

9. Discussion

(*a*) *Previous related studies*

As can be seen from table 3, which summarizes ultrastructural studies on crustacean sensilla, knowledge of these receptors is rudimentary compared to what is known about cuticular receptors of insects (McIver 1975). Only two types of crustacean sensilla have been studied in sufficient detail in more than one species to allow meaningful comparison and generalization: aesthetasc hairs on the antennules of decapods and the PD organ (a proprioceptor that monitors movement and position of the propodite-dactylopodite joint) of the crabs *Carcinus* and *Cancer*.

There is also a dearth of information on the electrophysiological responses of identified crustacean sensilla. Even for the frequently-investigated aesthetasc hairs of crustaceans little is known about responses of individual hairs, nor has it ever been unequivocally established that the chemoreceptive responses recorded from the antennule nerve arise from the aesthetasc hairs, although this seems likely (Ache 1972; Ache & Case 1969; Ameyaw-Akumfi & Hazlett 1975; Fuzessery & Childress 1975; Hodgson 1958; Laverack 1964; Shepheard 1974). Only in the proprioceptors of crab walking legs (see Mill & Lowe (1973) and Lowe, Mill & Knapp (1973) for a summary of previous anatomical and physiological work) and in the thread hairs of *Scylla* (Dunn 1975; Silvey, Dunn & Sandeman 1976) have structural studies and electrophysiology combined to give adequate knowledge of the behaviour of individual sensilla. Therefore, we must base most of our discussion on anatomy alone and it is, of necessity, speculative.

(*b*) *Setal types and their postulated functions*

We found no evidence for innervation or a receptive function for *type* 1 *setae* and so provisionally assume they are not receptors; the significance of their elaborate structures remains unexplained. Their sole function may be to protect the type 2 setae.

Setal types 2, 4 *and* 5 are almost certainly mechanoreceptors because their dendrites are linked to the setal wall at its base, as in insect mechanoreceptors, and the ciliary portions of their dendrites are well developed as are their scolopales. Also, they are mounted in a flexible membrane and they have abundant setules which would make them more efficient in picking up nearby waterborne vibrations. If stretching of the dendrites is the effective stimulus the type 2 setae would have a null point of least stretch in the erect position against the proximal cuticular plug. Any water flowing through the tube formed by the type 1 setae would lead to bending of the type 2's distally. The tube begins at the flexure where internal water flow would first be possible, and the type 1 setae forming the walls of the tube gradually increase in length distal to the flexure, causing the entrance to the tube to resemble a scoop. Further specializations possibly related to monitoring water flow are the presence of type 2B hairs, which almost completely occlude the tube, only on the portion of the antenna just distal to the flexure where flow would presumably be strongest, and the much greater density of both sorts of type 2 setae in the same region compared to their density further distally on the antenna. However, if the function of the type 2 setae is to monitor water flow the positioning of the tube entrance partially behind the proximal portion of the antenna (as the antenna is normally held during swimming) is difficult to explain, as is the rapid increase in diameter of the tube a short distance distal to its entrance. Preliminary experiments have established that the type 2 setae do bend when water flows past the antennae, but the extent and significance of this effect when an animal is swimming is unknown.

Type 2 setae would also presumably respond to sources of vibration, such as other animals, in the near field. A vibrating glass sphere placed in the water induces waves in the antenna (preliminary observations) which might move the setae relative to the antenna, thus exciting the setal receptors. Taylor (1975) found that vibratory stimuli caused a travelling wave in the antennal flagellum of the crayfish and has classified the mechanoreceptors found there into four groups on the basis of their electrophysiological responses. He concluded: '...it appears quite probable that the flagellum is primarily used as a frequency analyzer for the detection and analysis of small waterborne vibrations'.

An interesting analogy can be drawn between the antennal receptor system of sergestids and

TABLE 3. SUMMARY OF INNERVATION OF CRUSTACEAN SENSILLA WHICH HAVE BEEN INVESTIGATED ULTRASTRUCTURALLY

organism	part of organism	type of sensillum – suspected function	innervation of sensillum	investigator
Subclass Copepoda				
Cyclops scutifer Sars	basal portion of antenna	seta – presumed mechanoreceptor	2 ciliary dendrites	Strickler & Bal (1973)
Calanus finmarchicus	frontal organ (area between anterior cuticle and brain)	unit 2 – presumed chemoreceptor monitoring internal environment	'a few large dendrites ending in branching cilia'	Elofsson (1971)
Euchaeta norvegica				
Chiridius armatus		unit 3 – presumed chemoreceptor monitoring external environment	'*c.* 17 dendrites ending with cilia at the cuticle'	Elofsson (1971)
Diaptomus pallidus	mouthparts	type I – presumed chemoreceptor	1 or 2 ciliary dendrites and sometimes a smaller non-ciliary dendrite	Friedman & Strickler (1975)
	type 1 sensilla mainly on mandibles			
	type 2 sensilla on first and second maxillae and on mandibular palps	type II – presumed chemoreceptor	1–5 dendrites, 1 or 2 of which are ciliary; the others with an unstructured array of doublet microtubules	Friedman & Strickler (1975)
Gladioferens pectinatus (Brady)	mandibles (antennae, labrum, labium and maxillipeds)	type 1 – presumed chemoreceptor	1–5 non-ciliary neurones	Ong (1969)
		type 2 – presumed mechanoreceptor	1–5 ciliary neurones	Ong (1969)
		type 3 – presumed mechanoreceptor and chemoreceptor	1–5 ciliary and non-ciliary neurones	Ong (1969)
Subclass Cirripedia				
Elminius modestus	operculum	hair – presumed chemoreceptor	2 microtubule-containing dendrites	Foster & Nott (1969)
Subclass Malacostraca				
Order Decapoda				
S. O. Natantia				
Acetes sibogae	antennae	type 2 seta – presumed mechanoreceptor	4 neurones giving rise to 3 ciliary dendrites and 1 paraciliary dendrite	this study
	antennae	type 3a seta – presumed chemoreceptor	2 or 3 neurones giving rise to 3 ciliary dendrites	this study
	antennae	type 3b seta – presumed chemoreceptor	8–10 neurones each with a ciliary dendrite	this study
	antennae	type 4 seta – presumed mechanoreceptor	3 neurones each with a ciliary dendrite	this study
	antennae	type 5 seta – presumed mechanoreceptor	3 neurones each with a ciliary dendrite	this study
S.O. Reptantia				
Astacus leptodactylus Esch.	5th walking leg	cuticular stress detectors	1 or 2 neurones with ciliary dendrites (when 2 always heterodynal)	Moulins & Clarac (1972)
Astacus fluviatilis	statocyst	hair of statocyst crescent – gravity receptor	3 neurones each with a ciliary dendrite	Schöne & Steinbrecht (1968)
Panulirus argus	antennule	aesthetasc hair	*ca.* 350 neurones each with a ciliary dendrite	Laverack & Ardill (1965)
Panulirus interruptus	antennule	aesthetasc hair	*ca.* 350 neurones, each with a dendrite containing 2 cilia	Ghiradella *et al.* (1968)
Pagurus hirsutiusculus	antennule	aesthetasc hair	*ca.* 400 neurones, each with a dendrite containing 2 cilia	Ghiradella *et al.* (1968)
Coenobita compressus	antennule	aesthetasc hair	*ca.* 100 neurones, each with a dendrite containing 2 cilia	Ghiradella *et al.* (1968)
Cancer productus	antennule	aesthetasc hair	*ca.* 100 neurones, each with a dendrite containing 2 cilia	Ghiradella *et al.* (1968)
Paragrapsus gaimardii	antennule	aesthetasc hair	*ca.* 130 neurones, each with a dendrite containing 2 cilia	Snow (1973)
Scylla serrata	statocyst	thread hair – gravity sensor via angular acceleration	2 neurones each with a single cilium/dendrite	Dunn (1975)
Carcinus maenas	CB, MC, CP and PD organs of walking legs	span respectively coxopodite – basipodite joint, meropodite – carpopodite joint, carpopodite – propodite joint and propodite – dactylopodite joint	CB isodynal with 2 neurones each with a ciliary dendrite; MC, CP and PD heterodynal with 2 neurones, one ciliary and the other paraciliary	Whitear (1962)
Cancer pagurus	PD chordotonal organ of walking leg	spans propodite – dactylopodite joint and monitors:		Mill & Lowe (1973)
		(1) elongation – elongation sensitive movement cells (e.s.m. cs)	2 neurones; 1 with a ciliary dendrite, the other with a paraciliary dendrite	Mill & Lowe (1973)
		(2) relaxation – relaxation sensitive movement cells (r.s.m. cs)	2 neurones; 1 with a ciliary dendrite, the other with a paraciliary dendrite	Mill & Lowe (1973)
		(3) position – position sensitive cells	2 neurones; 1 with a ciliary dendrite, the other with a paraciliary dendrite	Lowe, Mill & Knapp (1973)

the lateral line of fishes in that both systems have ciliated mechanoreceptors attached to structures (type 2 setae in sergestids, the cupula in fishes) that occlude, or partially occlude, a tube which is in direct contact with the water through which the animal is swimming.

The dendrites of the type 4 and 5 setae are attached to the setal wall in the same manner as those of type 2 setae and probably function similarly to provide information on movements in the near field. The cytoplasmic bridges connecting the type 4 dendrites near where they reach the seta are unusual, but their functional significance is unknown.

The characteristic feature of arthropod cuticular mechanoreceptors is supposedly an accumulation of microtubules (tubular body) in the distal region of the dendrite (McIver 1975), but of the crustacean sensilla and proprioceptors investigated (table 3) only an antennal seta of the copepod *Cyclops scutifer* (Strickler & Bal 1973) contained such a structure. The type 4 and 5 setae of *Acetes* are similar to the statocyst hairs of *Astacus* described by Schöne & Steinbrecht (1968) and in neither animal is there anything resembling a tubular body near the tips of the dendrites. In type 2 setae the dendrite most deeply embedded in the scolopale cell, which enlarges to a size considerably greater than the other dendrites, shows a structure somewhat resembling a tubular body in that the microtubules are connected by electron-dense material for a portion of their length. However, the microtubules in the other dendrites lack such linkages. The one characteristic of all presumed crustacean mechanoreceptors and proprioceptors, that is lacking in presumed chemoreceptors, is a well-developed scolopale.

Spike initiation in crustacean bipolar sensory cells is dendritic (Mendelson 1963, 1966; Mellon 1963) but the exact site of transduction and production of the generator potential remains unknown. For insect mechanoreceptors it is believed that the tubular body at the tip of the dendrite is involved in the transduction process (see McIver (1975) for references) and that compression of this body is the effective stimulus (Thurm 1965; Chapman & Duckrow 1975). That compression of the dendrite tip could also be the effective stimulus for *Acetes* sensilla is apparent from figure 70, which shows the dendrite tip thrown into a series of sharp folds and bends.

However, Young (1970) and Mill & Lowe (1973) have suggested longitudinal stretch as the adequate stimulus in chordotonal organs in the legs of cockroaches and crabs, respectively, and these organs have structural similarities to the sensilla of *Acetes*. If stretch is the effective stimulus in *Acetes* it is presumably necessary for the dendrites to stretch or move relative to the surrounding structures. There are well-developed desmosomes between the dendrites and scolopales at the level of the rootlets in all of the presumed mechanoreceptors of *Acetes*, as is the case in *Astacus* (Schöne & Steinbrecht 1968) and *Cancer* (Mill & Lowe 1973). These desmosomes could serve to anchor the dendrites basally, while the desmosomes between the scolopale cell and the tubular sheath cells, which are packed with microtubules and end just beneath the cuticle, would presumably provide a relatively rigid support for the scolopale cell and help to prevent it from moving as the dendrites are stretched.

The effect of the ridge partially surrounding the bases of the setules of type 2 setae is not known because its dimensions and those of the setule base are so small. The ridge might either have the effect of carrying water smoothly upward and past the setule base, or the gap between the ridge and the setule base may be sufficient to create an area of turbulent flow in front of the setule. The dense anchor at the base of the setule presumably serves to strengthen it against water flow.

Although their ultrastructure was not investigated their position and morphology suggest

that *type* 6 *and* 7 *setae* are also mechanoreceptors. The type 6 setae, located within the flexure of the antenna, may monitor the degree of bending of the elbow either by strains imposed on their bases or, in the case of extreme bends, by directly contacting the flagellum. Type 7 setae have setules coming off in all directions and appear to be mounted so that they could be sensitive to vibrations coming from any direction.

Type 3 *setae* appear to be chemoreceptors. Their apparently inflexible mounting and lack of setules argues against their being mechanoreceptors. Also, the eight to ten dendrites of the type 3B seta would be unusual for arthropod mechanoreceptors which are generally characterized by only one or two neurones innervating each seta (Slifer 1970; McIver 1975), while chemoreceptors normally have more. The very short ciliary segment compared to other setal types is another characteristic of arthropod chemoreceptors (Slifer 1970). Finally, the neurones from the type 3 setae differ from those of the presumed mechanoreceptors in that they are all uniformly small, packed with microtubules, and form relatively pure bundles leading out of the antenna. While none of these arguments is convincing by itself, combined, they lead us to believe that the type 3 setae are chemoreceptors.

Although type 3 setae have a pore at their tip we doubt whether this is a significant indicator in judging the function of a seta. Ghiradella, Case & Cronshaw (1968) have examined the aesthetascs (which are believed to have a chemoreceptive function) of four species of decapods without finding terminal pores, while pores have been found in many setae which are almost certainly mechanoreceptors (Thomas 1971; Snow 1974). One interesting feature shared by the aesthetasc hairs of *Pagurus alaskensis* (Snow 1974) and type 3 setae is the large number of both with broken tips even in freshly collected animals.

The function of the pores and cuticular tubules associated with each of the setal types 2–5 is unknown. These tubules usually appeared empty or contained a small amount of unstructured material, although a few enclosed a microtubule-containing structure similar to a dendrite. Such structures were usually found in tubules lying just beneath the cuticle. In longitudinal sections of the antenna it is apparent that the tubules descend to just above the amorphous material, but we have been unable to identify their endings. In *Acetes* the tubules are straight and lack the cavity which Snow (1974) suggests exist below the pores on the antennule of the hermit crab *Pagurus alaskensis*.

One feature of all the setal types of *Acetes*, except type 3B, was the constant number and arrangement of the innervating dendrites. This constancy was especially apparent in the innervation of the type 2 setae where the pattern of change in ciliary structure, swelling of the innermost dendrite, and other changes are consistently repeated from one seta to another. Presumably this regularity in structure has a functional significance and, once correlated structural and functional studies have been carried out on more crustacean setae, it may be possible: (*a*) to predict with greater certainty to what stimuli a seta reacts solely from its external morphology and pattern of innervation and (*b*) to design experiments to better test theories of the significance of certain structural features of the dendrites.

(*c*) *Ecological considerations*

Most genera of sergestid shrimps, other than *Acetes*, *Peisos* and *Lucifer*, perform diurnal vertical migrations and Omori (1974) has suggested that the abundant fine setae on the antennae might serve to slow sinking. However, the antennae are certainly not designed solely to minimize sinking and the arrangement of type 1 and type 2 setae suggests additional functions.

Shallow water species of sergestids are omnivores, but deeper-living species are, of necessity, carnivores, feeding mainly on copepods and euphausiids (Renfro & Pearcy 1966; Judkins & Fleminger 1972; Omori 1974). Omori has observed two methods of prey capture by *Sergia lucens* in the laboratory. In the first method the sergestid swims directly into the prey and encloses it with a net formed by the third maxillipeds and first to third periopods. In the second method the prey is apparently sensed at a distance several times the body length of the sergestid and circled rapidly several times. This circling creates a vortex in which the prey is trapped and it is then easily captured by the second maxillipeds.

Many diurnally migrating sergestids live at depths where light, other than that produced by bioluminescence, is either dim or absent, and, in addition, most feed most actively at night (Omori 1974). Therefore they presumably locate their prey either chemically or by mechanoreception and the latter would appear to us more likely, although Hamner & Hamner (in preparation) have established that *Acetes* has a remarkable ability for following chemical trails. The two long linear arrays of type 2 setae on the antennae at a distance from the animal's body could provide an accurate means of prey localization as well as playing a rôle in schooling and in escape from predators. *Acetes*, which live in shallow water at relatively high light levels, are probably less dependent on mechanoreceptive location of prey organisms than their deep water relatives because of the greater availability of detritus, but they presumably still use their mechanoreceptive ability in schooling and during the night when they feed most actively (Le Reste 1970; Omori 1974). Other functions which the antennae might serve are: (1) to monitor swimming speedndi via beng of the type 2 setae; and (2) to filter food from the water. The antennae are not specialized for this latter function but a small amount of food might be obtained by the animal if antennae which have become loaded with detritus are cleaned by the mouthparts.

The antennular chemoreceptors of *Acetes* are important in tracking chemical trails such as would be created by falling detritus (Hamner & Hamner, in preparation), but antennal chemoreceptors may also play a rôle by greatly increasing the area sampled and by increasing the accuracy with which scent trails are followed. The close association of setae of types 3 and 4 is particularly interesting in this respect and suggests that the message from the antenna to the brain is, 'you have run into something that is edible/not edible' rather than just 'you have run into something'.

Another rôle antennal chemoreceptors might play is in the location of potential mates. There is at present no evidence for sex pheromones in pelagic decapods. However, such pheromones have been demonstrated in the crab *Portunus* (Ryan 1966), the lobster *Homarus* (Atema & Engstrom 1971) and the crayfish *Procambarus* (Ameyaw-Akumfi & Hazlett 1975) and pheromones could play an even more important rôle in the dim light or darkness of the deep ocean.

Fuzessery & Childress (1975) have investigated the chemoreceptive ability of the bathypelagic mysid *Gnathophausia ingens* and found a behavioural response threshold to a mixture of amino acids of 10^{-10} to 10^{-11} M. The behavioural responses evoked included: (1) circular movements of anterior endopodites over the mouth, (2) unconcerted endopodite extension, (3) concerted extension of the endopodites perpendicular to the body, and (4) arching of the abdomen ventrally. This behaviour would increase the chances of the animal touching anything nearby. An electrophysiological threshold to the amino acid mixture was established as 6×10^{-8} M for the dactyls and 5×10^{-7} M for the antennae.

Far more impressive chemoreceptive behaviour has been demonstrated by *Acetes*, which can

accurately follow the chemical trail left by falling food particles and locate them the equivalent of 20 m away (Hamner & Hamner, in preparation). Also, *Acetes* is an excellent experimental animal since it is tolerant of temperature and salinity changes and will survive for months in the laboratory. Because of these attributes we believe it will prove to be an adequate subject for a thorough investigation of the sensory capabilities of a planktonic crustacean.

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Note added in Proof, 25 *October* 1976

Between submission and publication of this paper several highly relevant works have been published. These include many of the contributions in the following book:

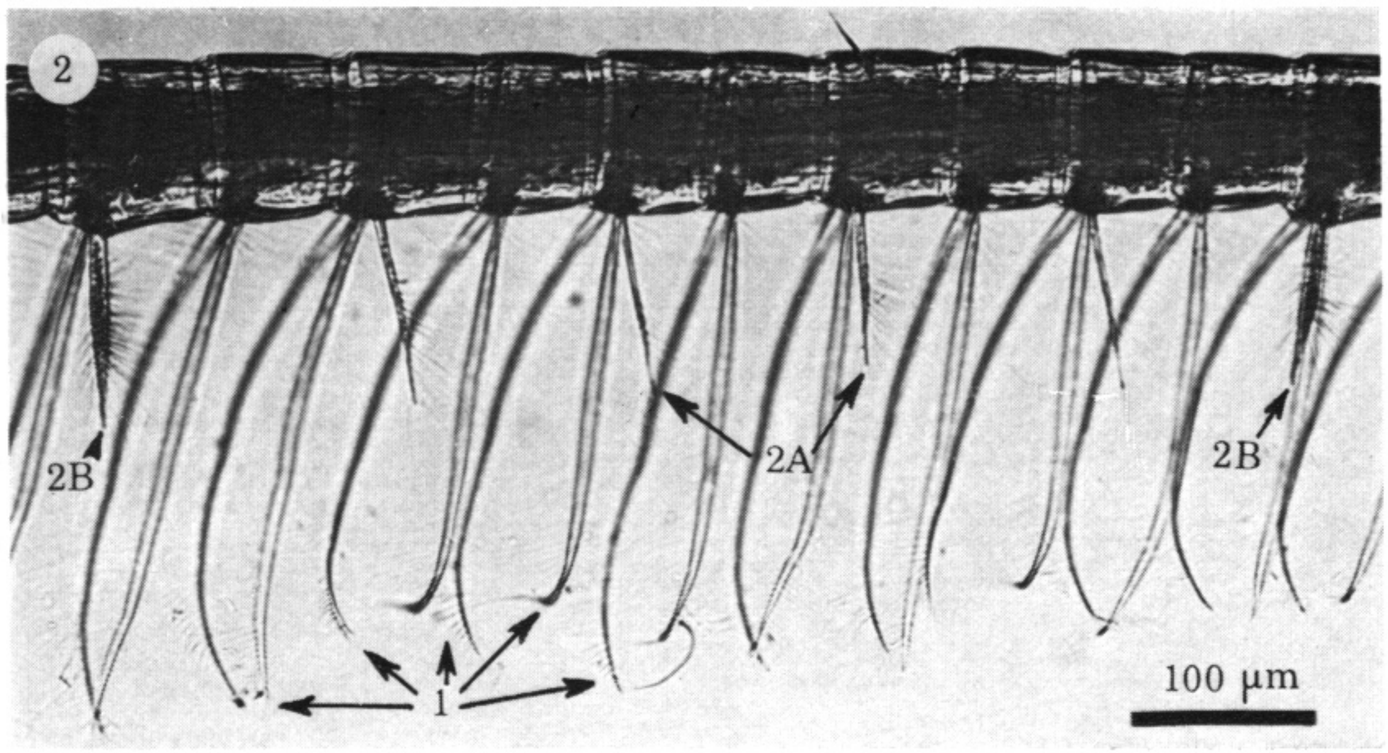
Mill, P. J. (ed) 1976 *Structure and function of proprioceptors in the invertebrates*. London: Chapman & Hall,

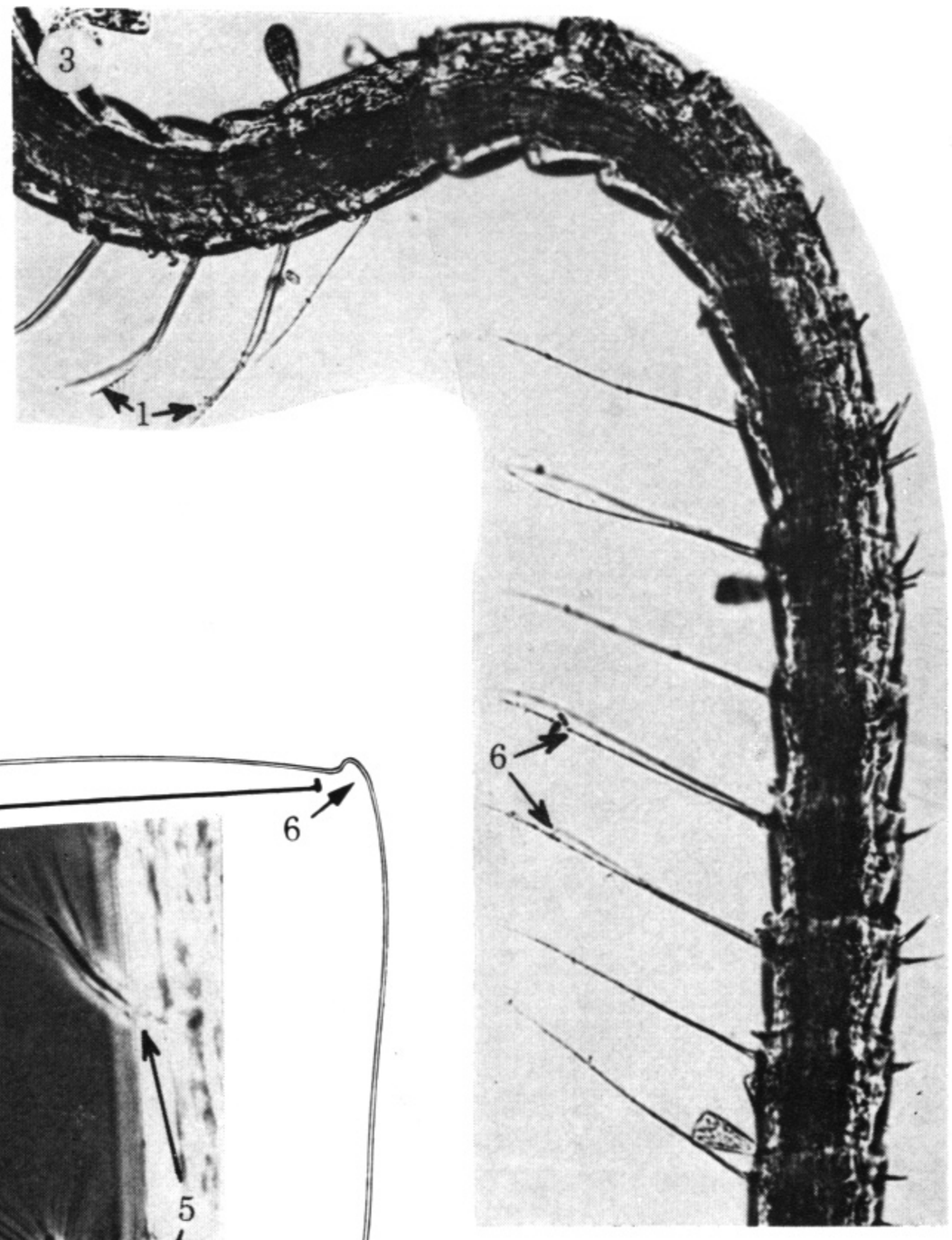
and a major work on *Acetes*:

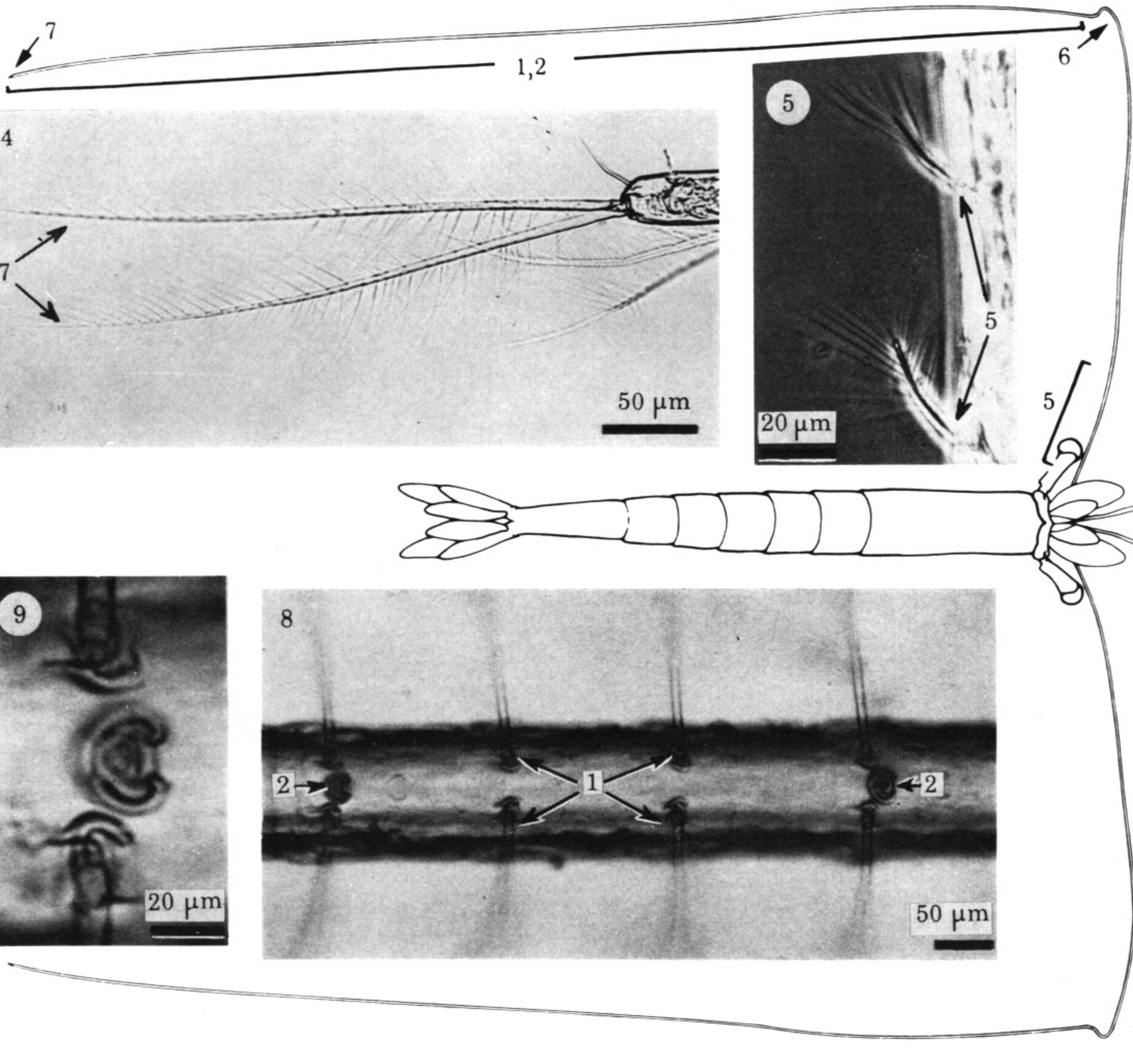
Omori, M. 1975 The systematics, biogeography, and fishery of epipelagic shrimps of the genus *Acetes* (Crustacea, Decapoda, Sergestidae). *Bull. Ocean Res. Ins., Univ. Tokyo, no.* 7, pp. 1–91.

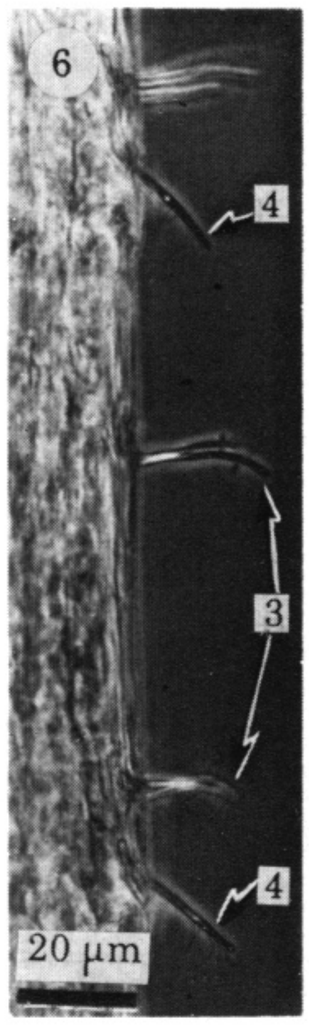
Explanation of abbreviations

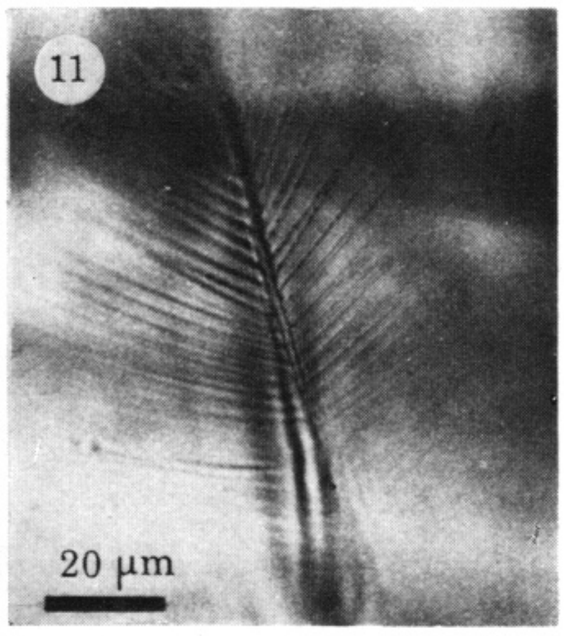
1	type 1 seta
2A	type 2A seta
2B	type 2B seta
3	type 3 seta
4	type 4 seta
5	type 5 seta
6	type 6 seta
7	type 7 seta
A	anchor
AM	amorphous material within antennal blood vessels
B	buttress
Ba	basal region of cilium
C	cuticle
CP	cuticular plug
CT	cuticular tubule
D	dendrite
Dam	dense amorphous material connecting dendrite-containing tubule to setal wall
G	glia
Lam	lamellae
M	mitochondrion
N	neurones
N2	axons from type 2 setae
N3	axons from type 3 setae
Nu	nucleus
P	paracilium
R	rootlet
S	seta
Sc	scolopale
T 1	tract from type 1 seta
TSC	tubular sheath cell
und	undescribed setal type
V	vacuole

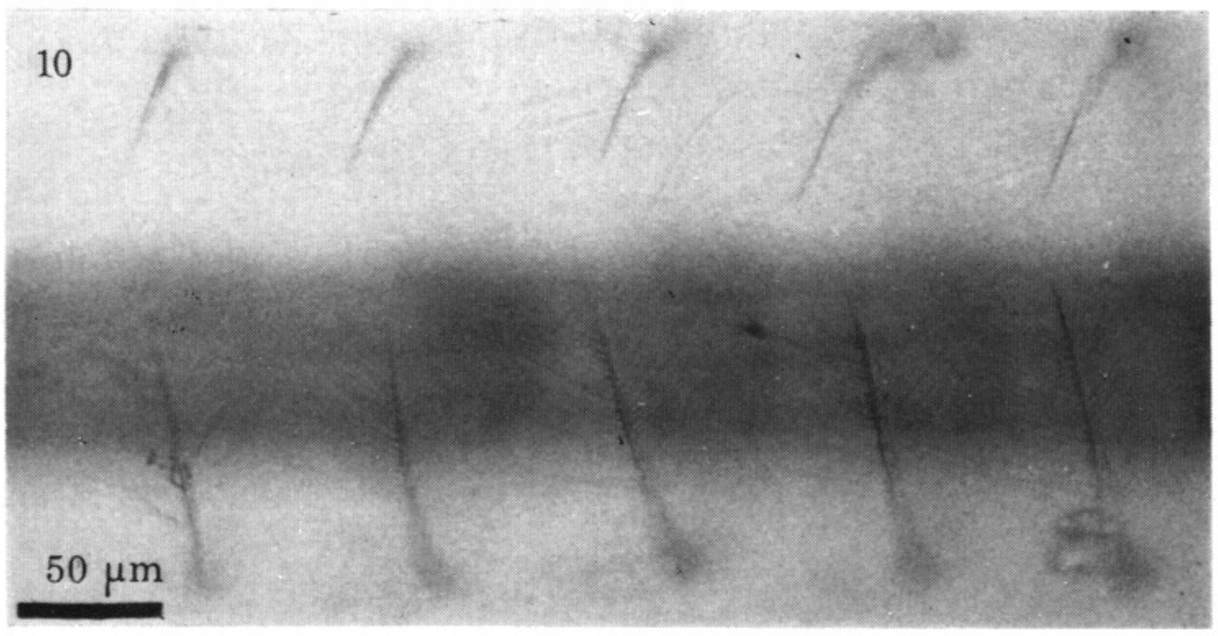


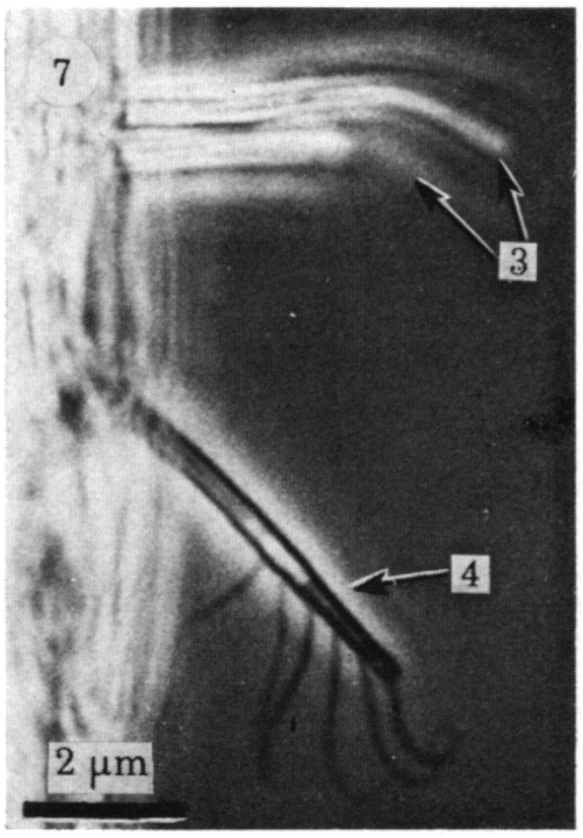




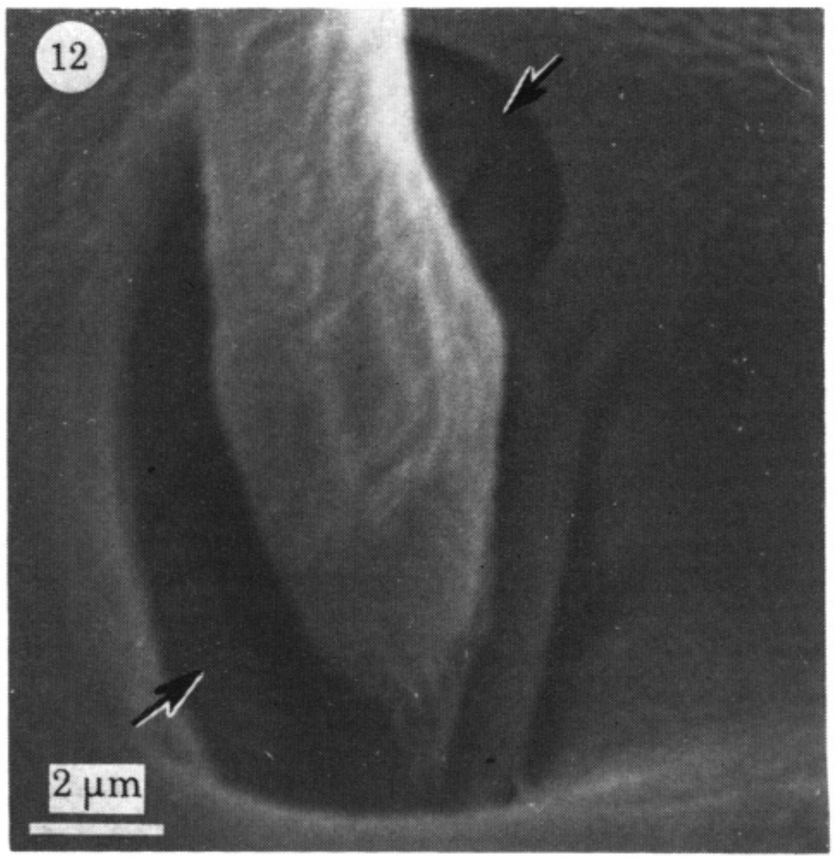


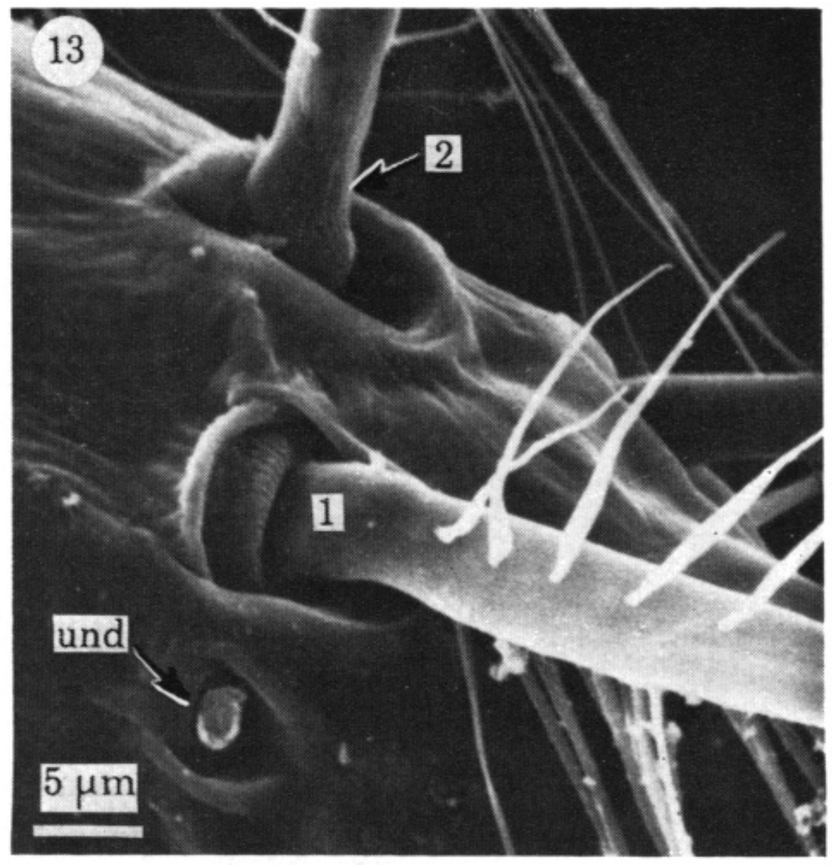


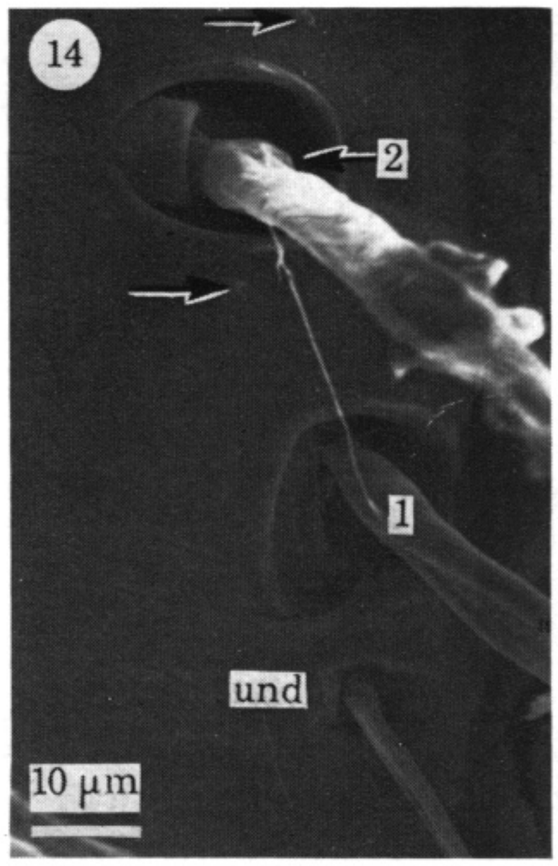


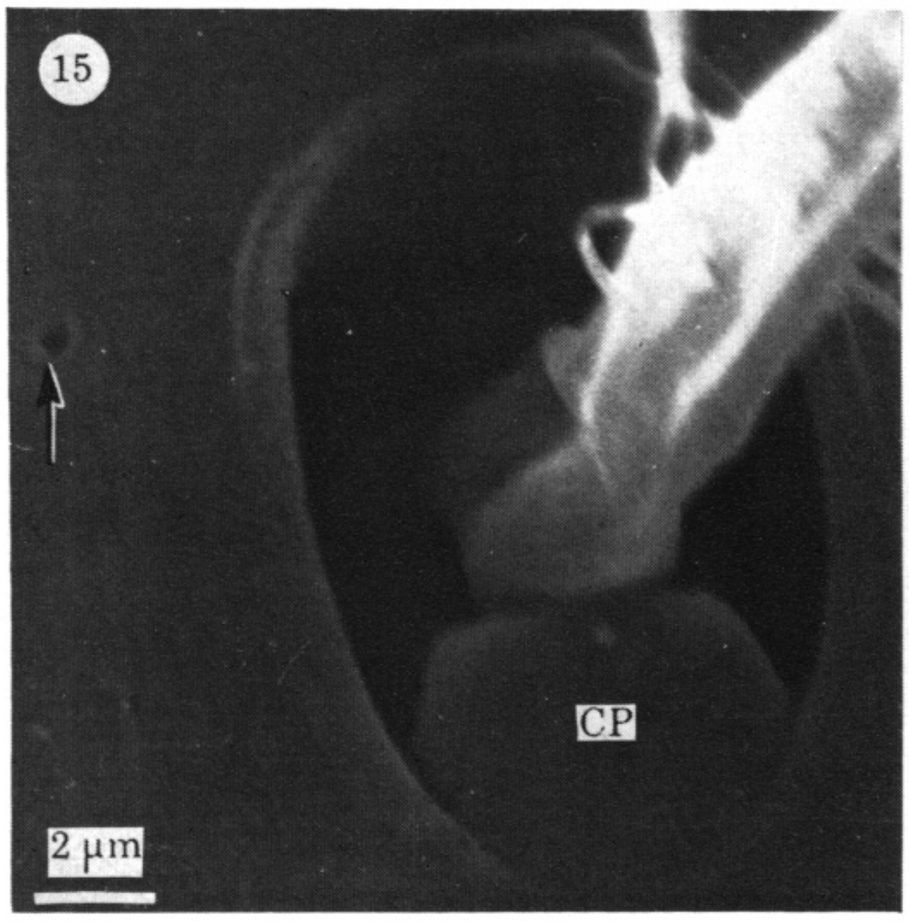


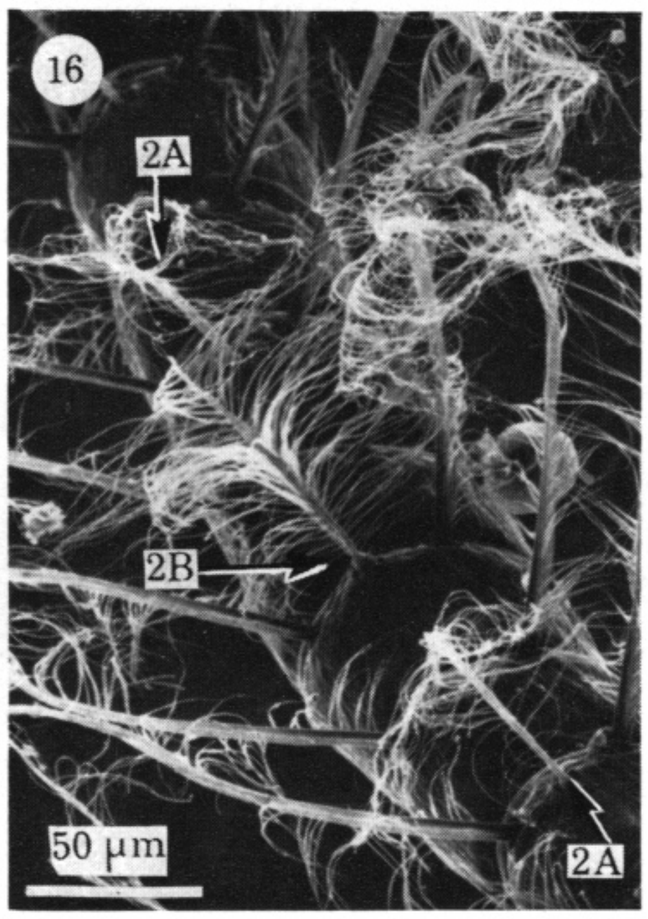
FIGURES 2–11. For description see opposite.

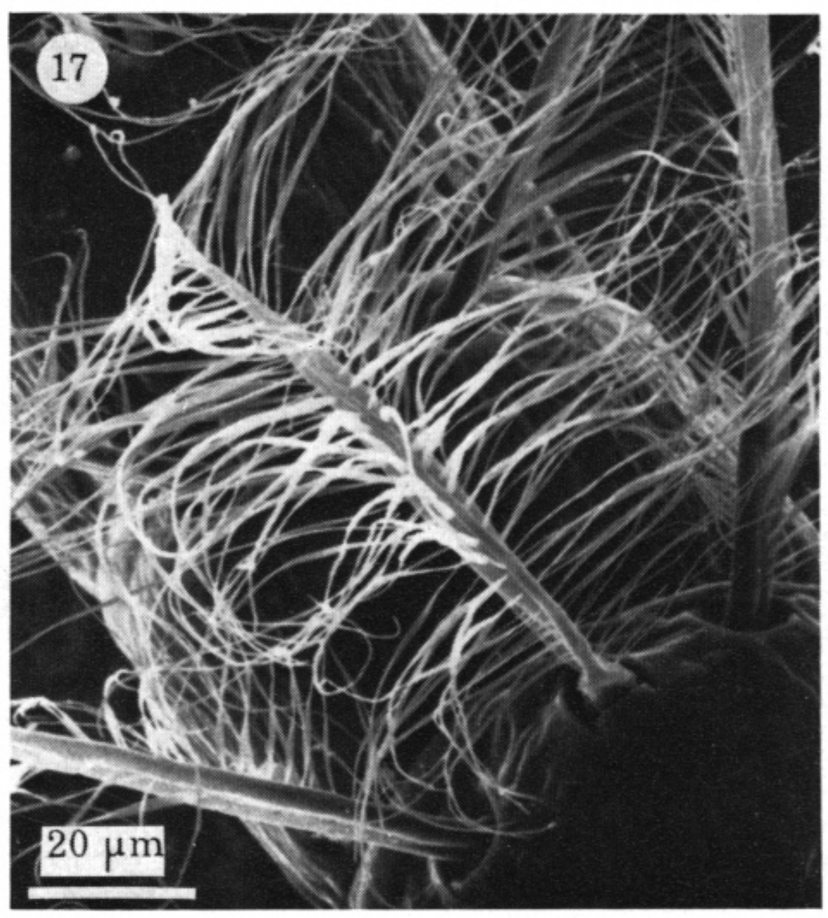


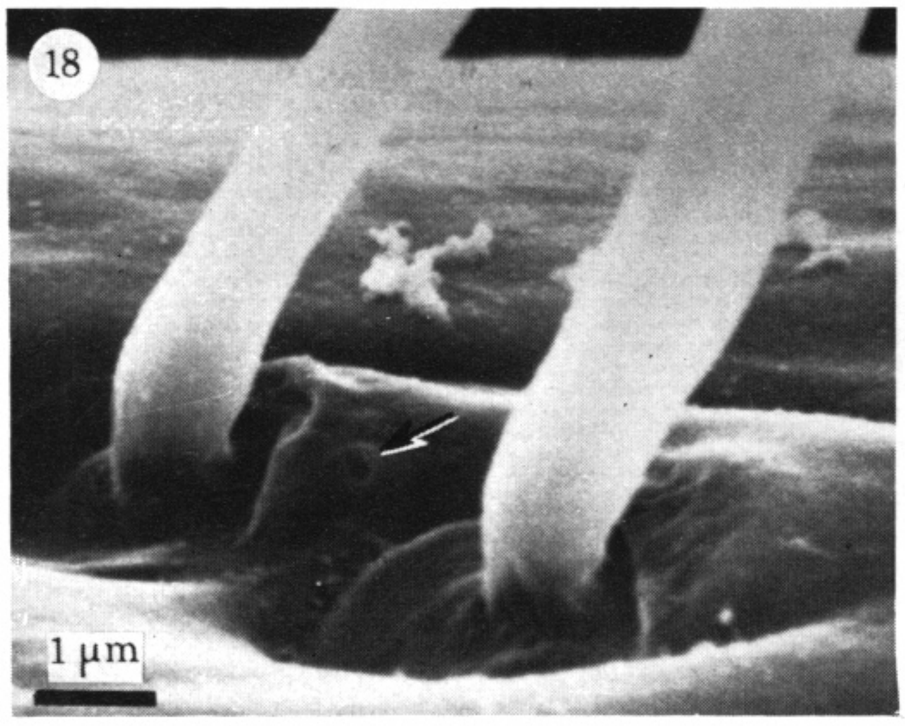


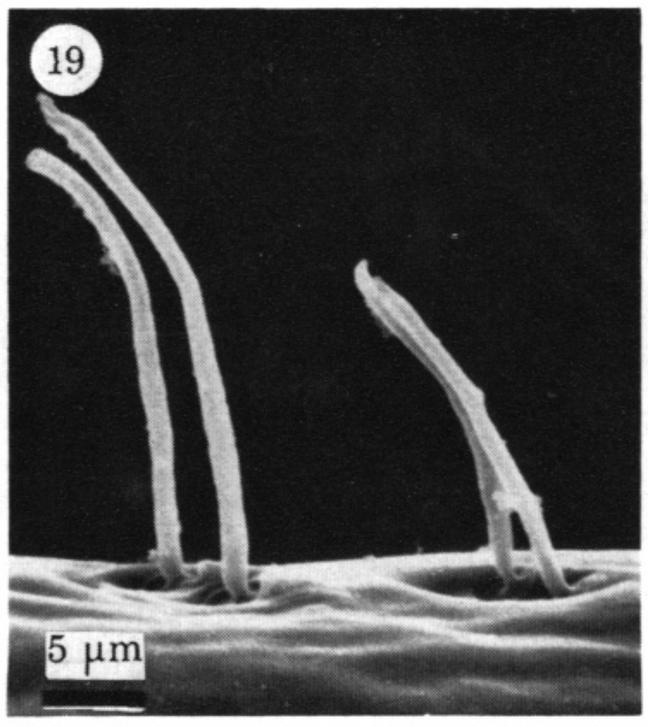


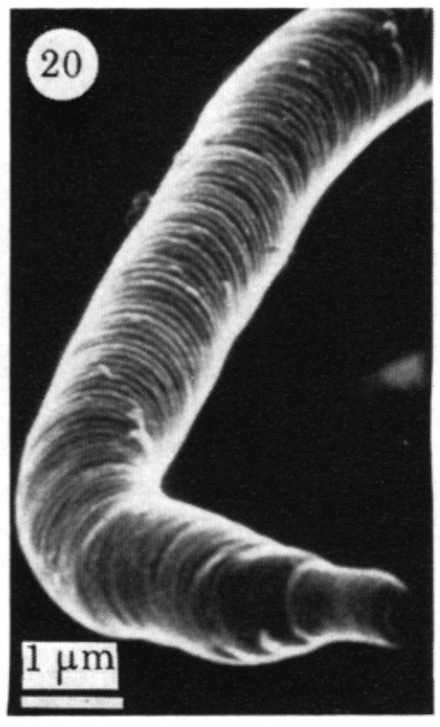


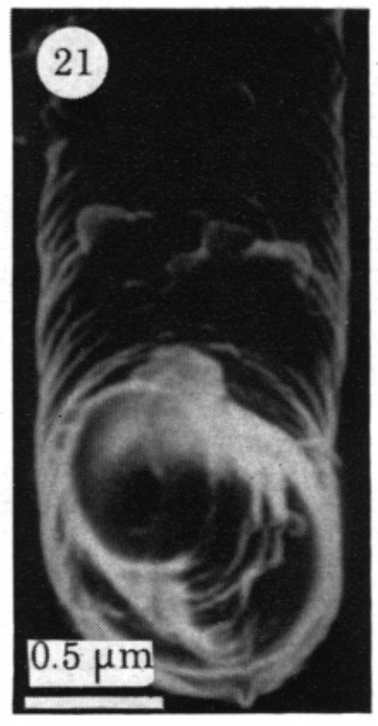


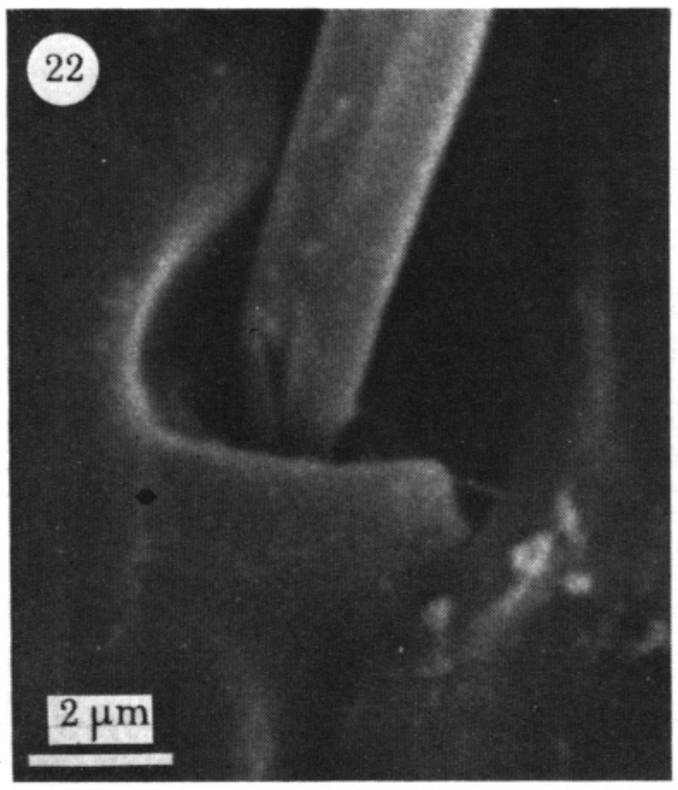


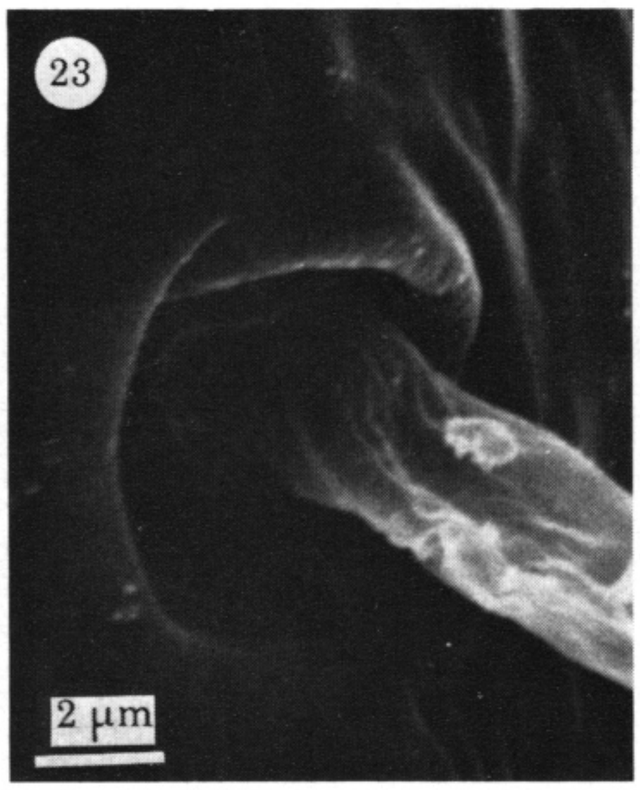


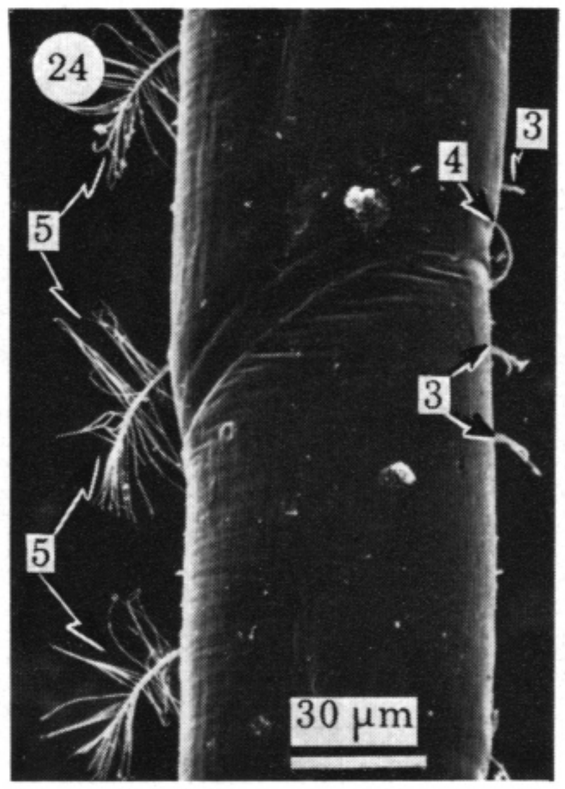


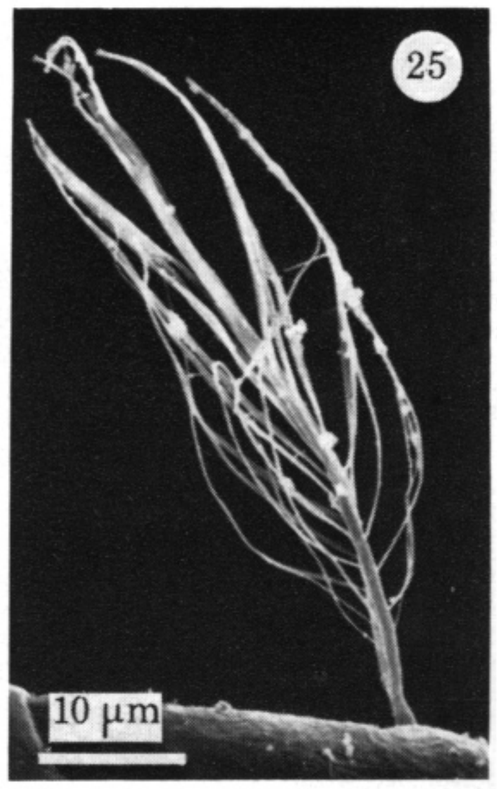




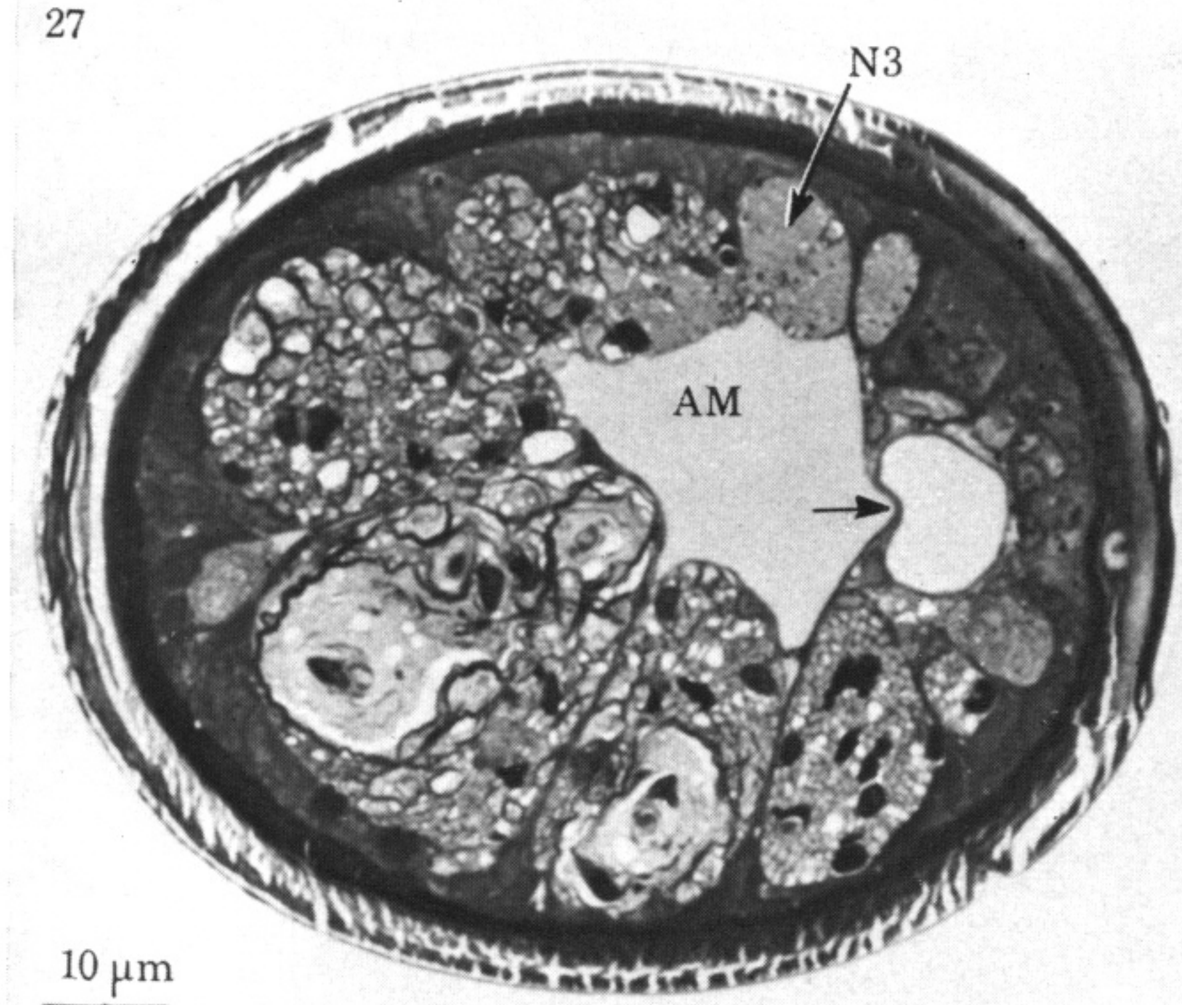


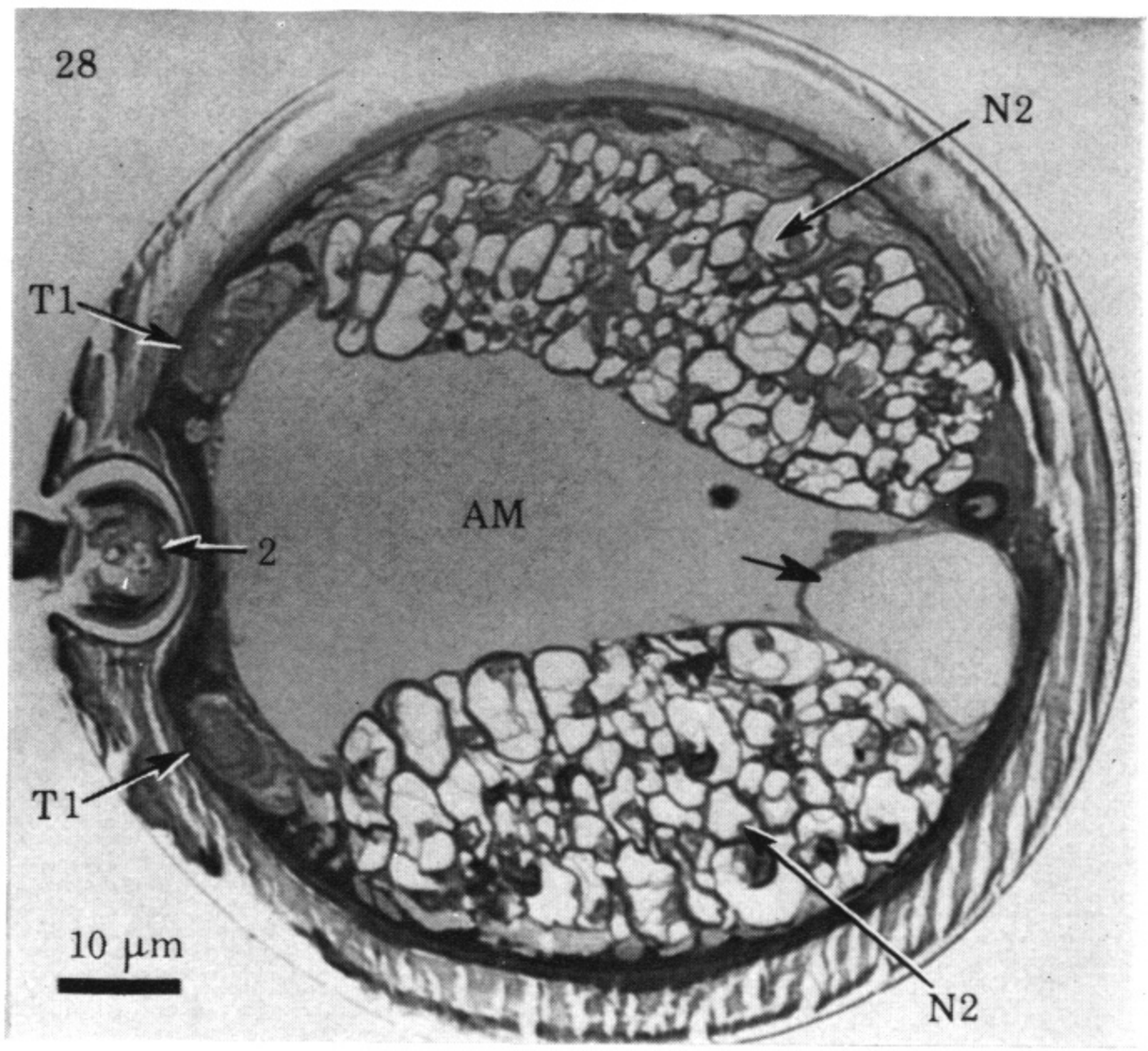


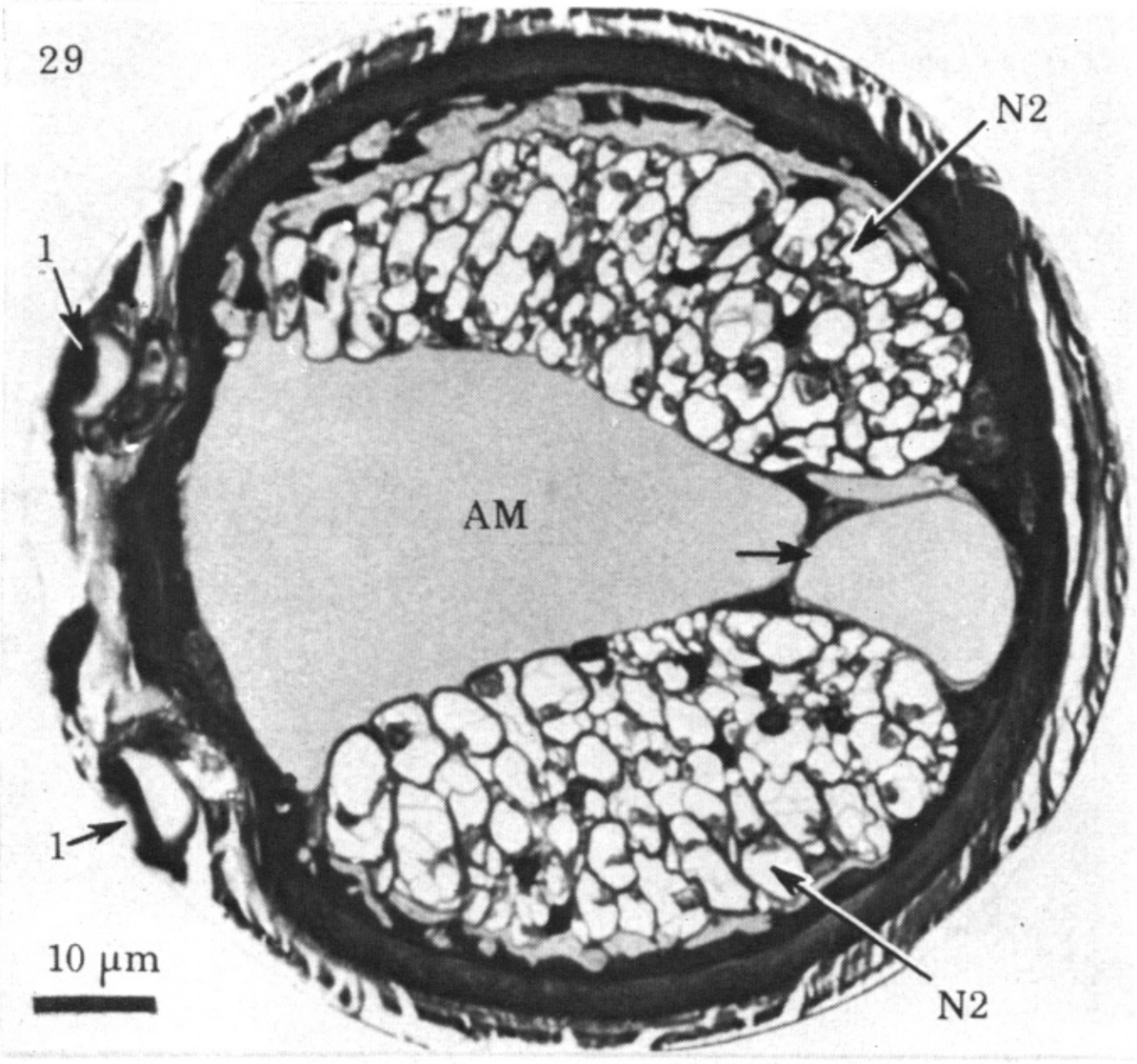


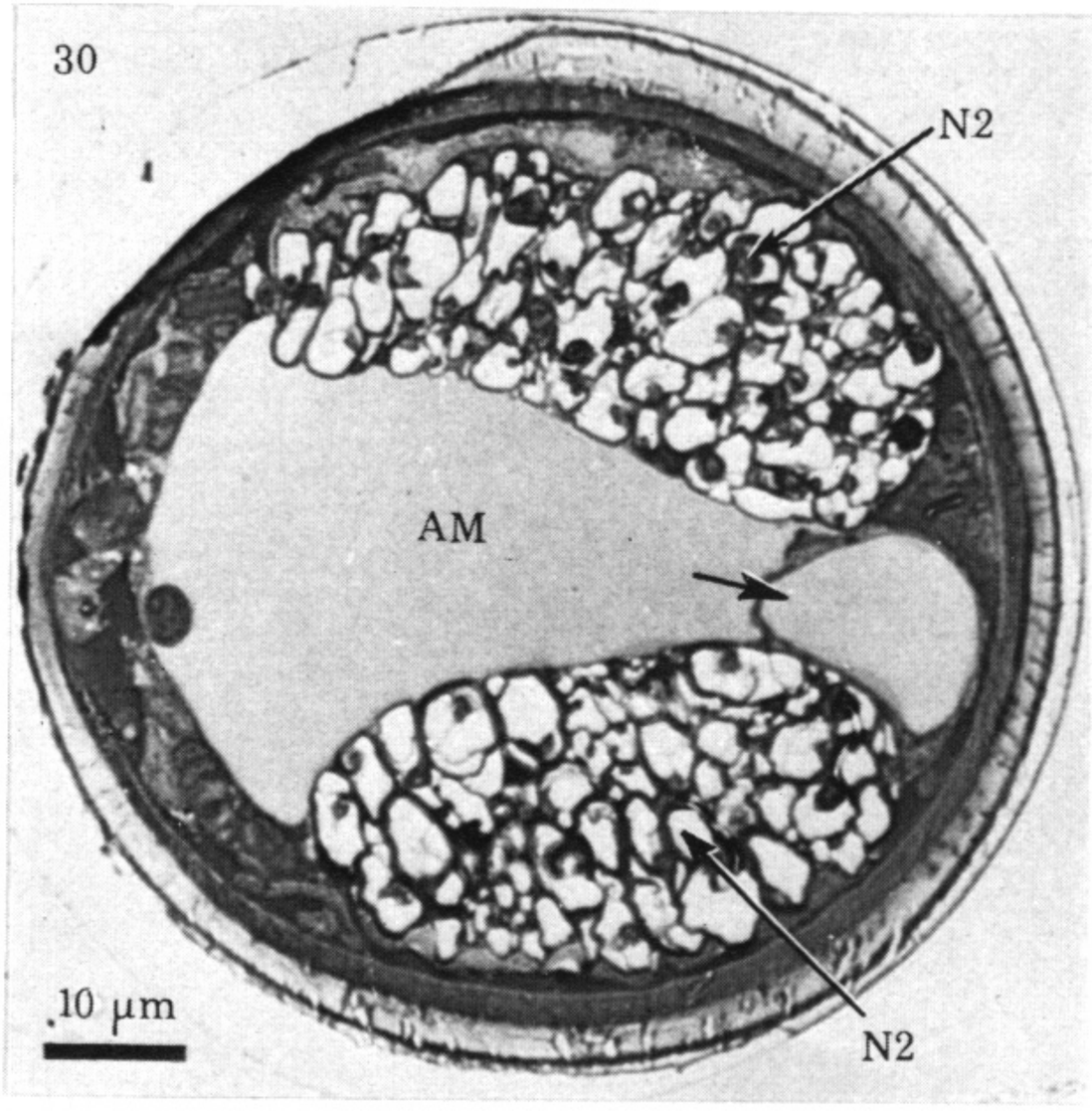


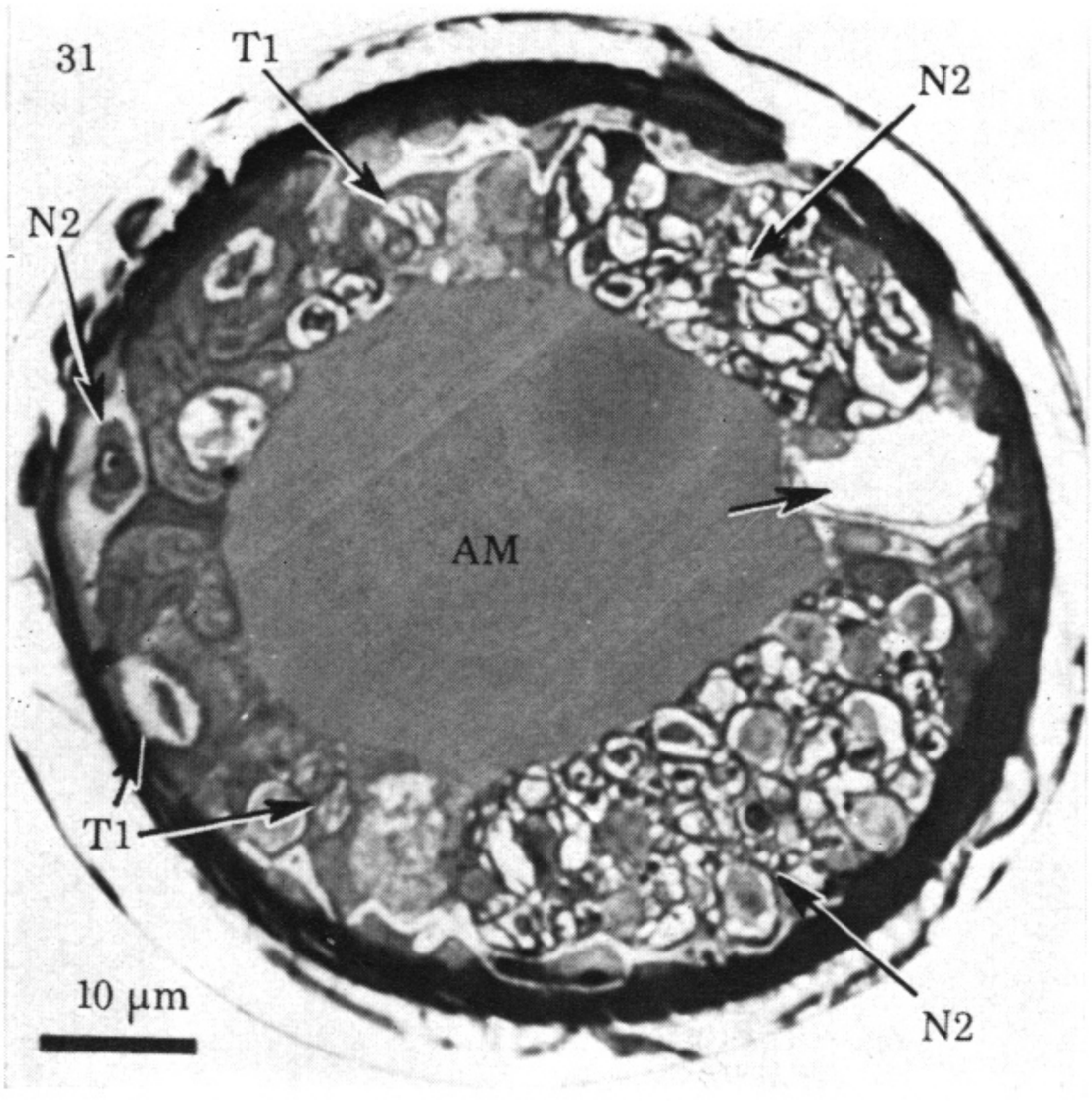
FIGURES 12–25. For description see opposite.

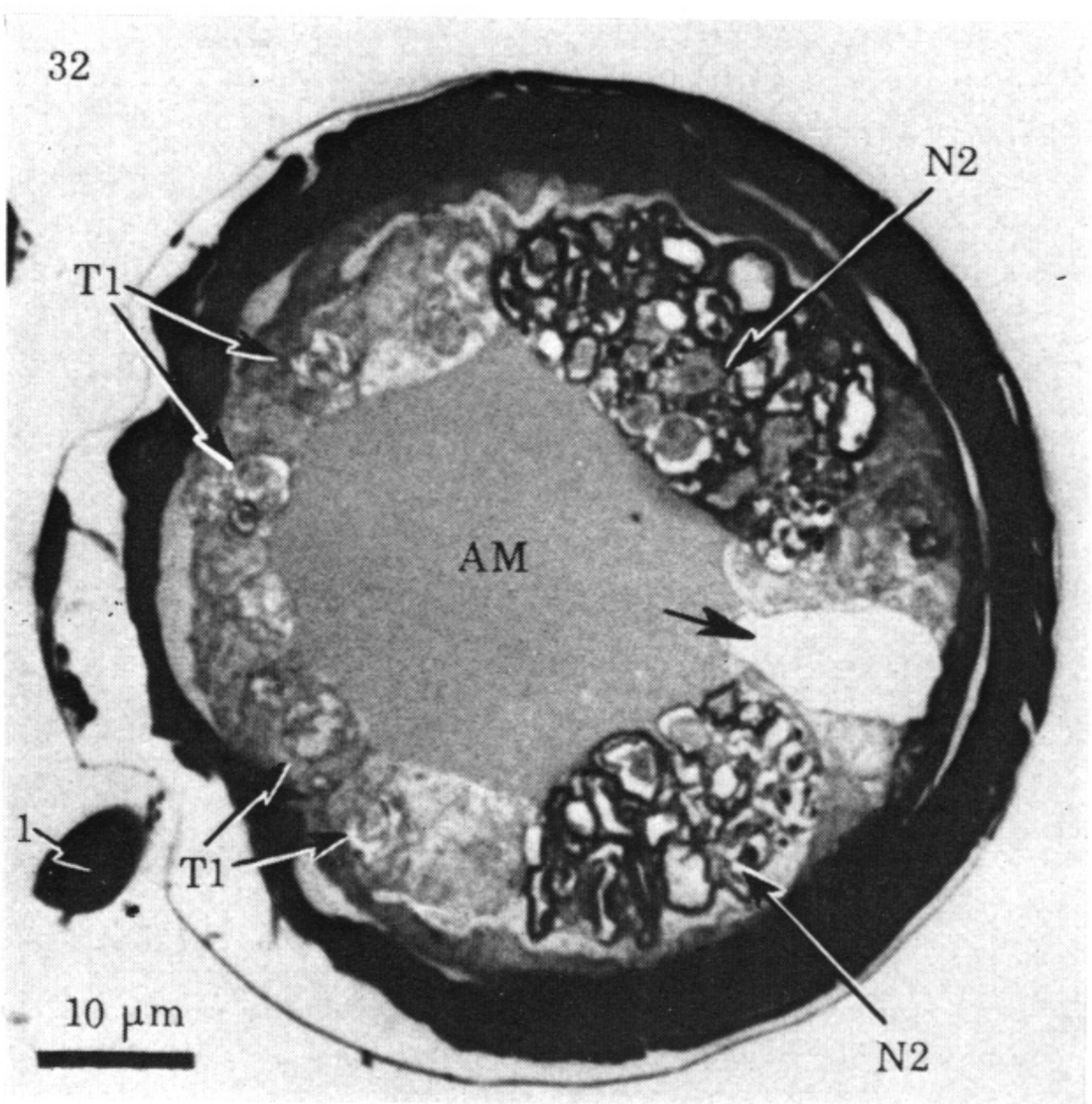




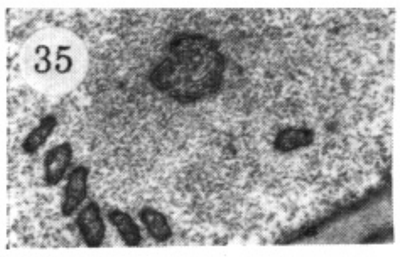


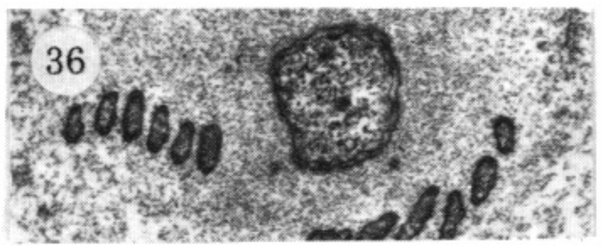


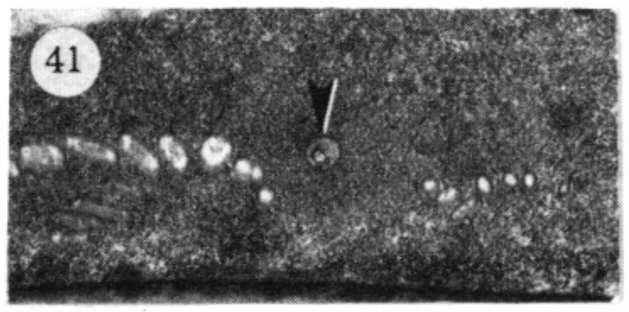


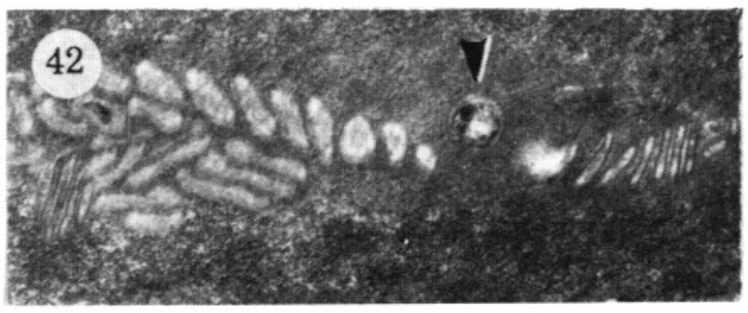


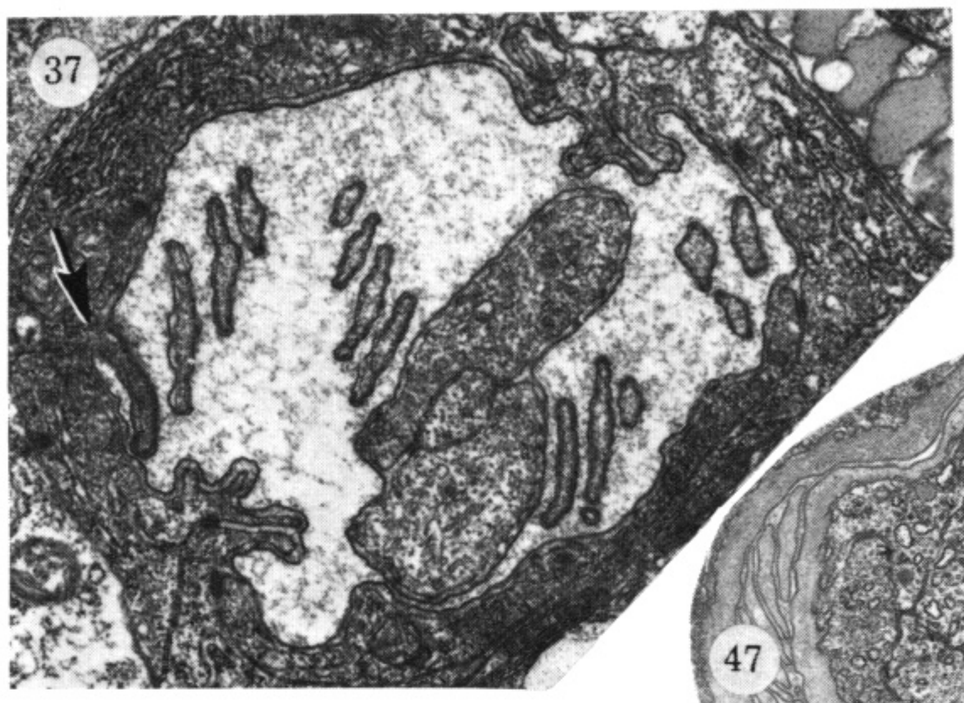
FIGURES 27–32. For description see opposite.

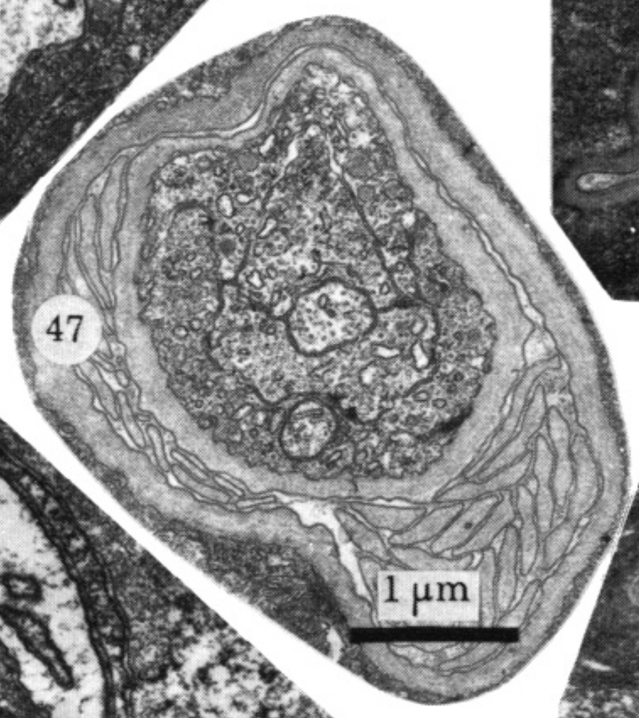


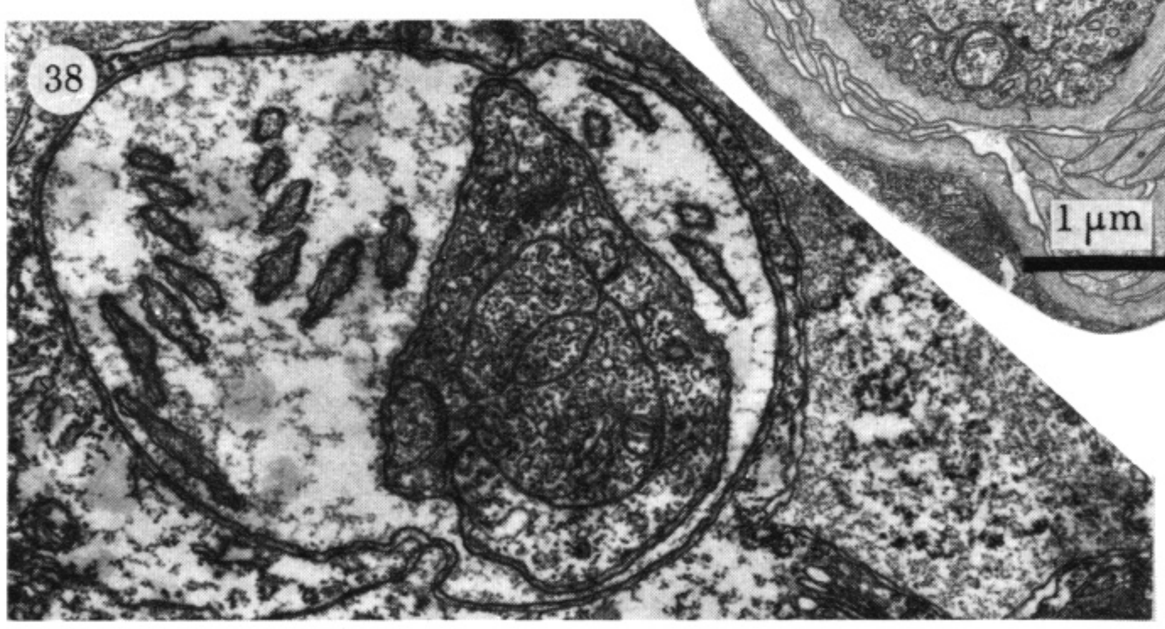


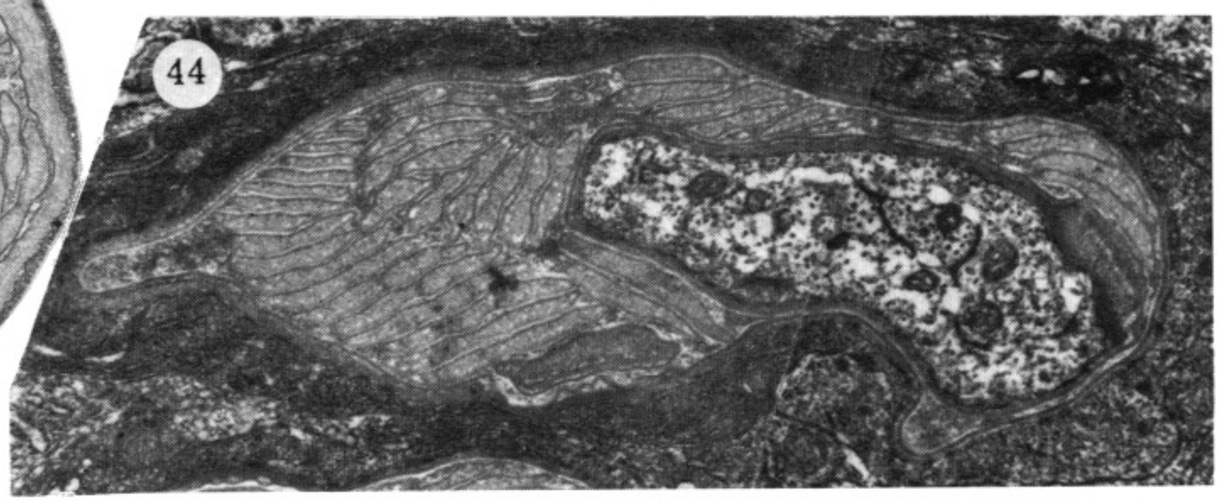


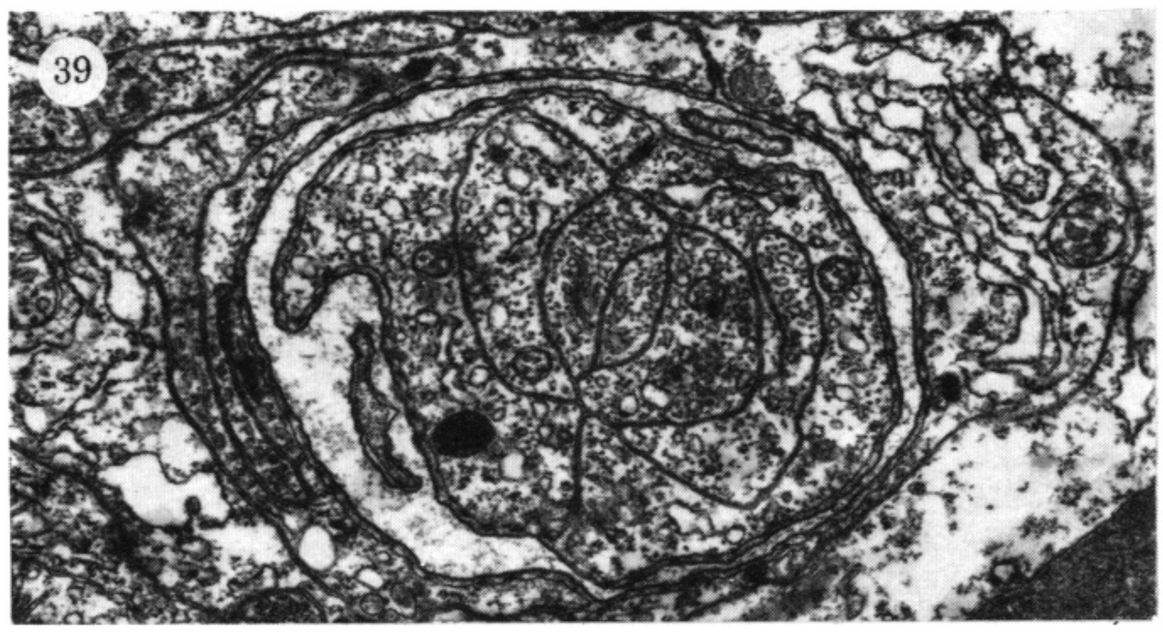


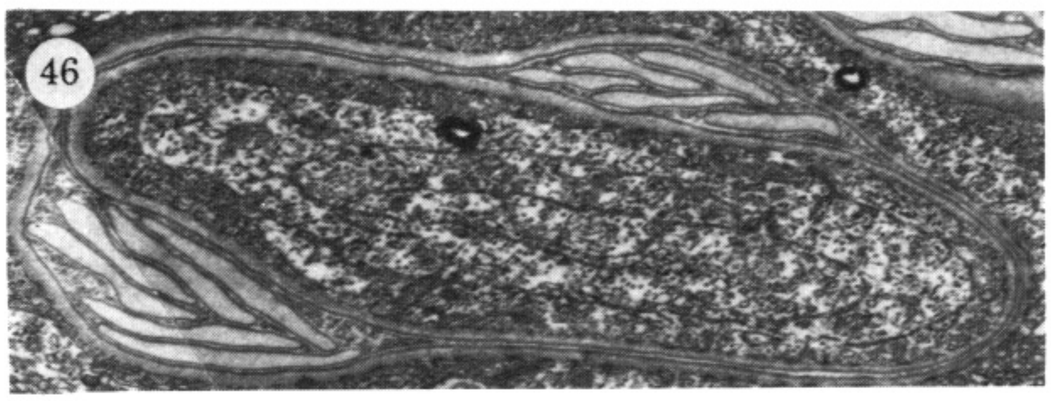


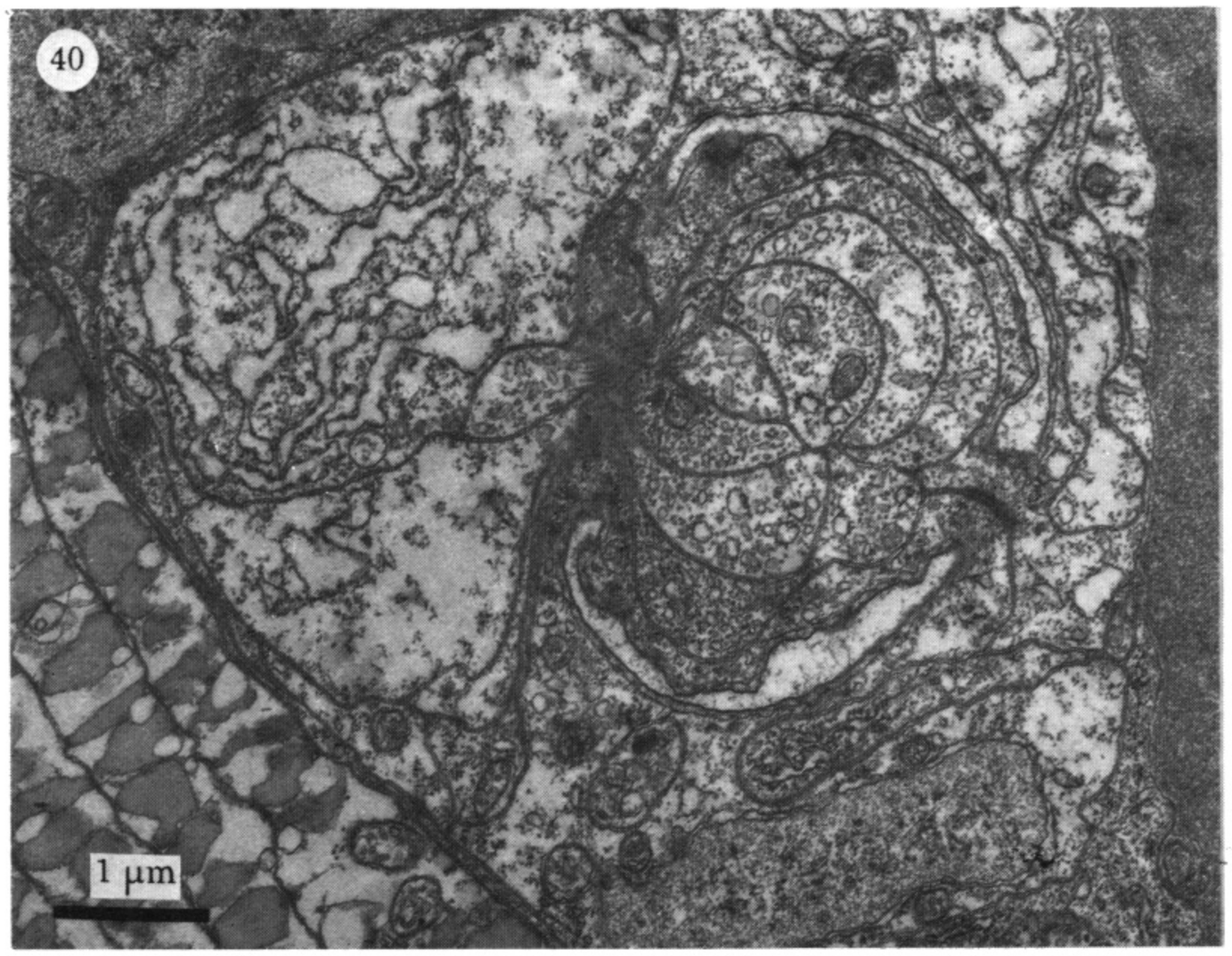


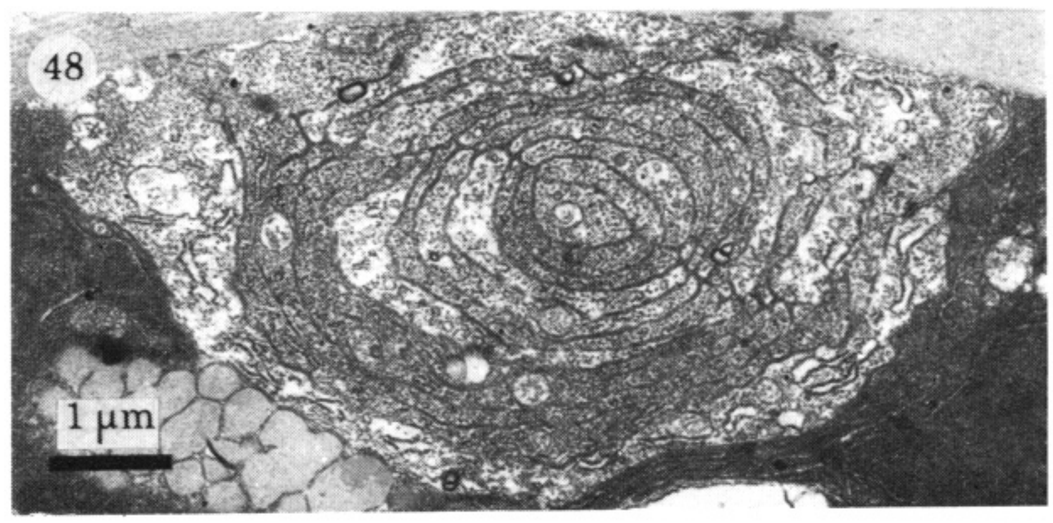


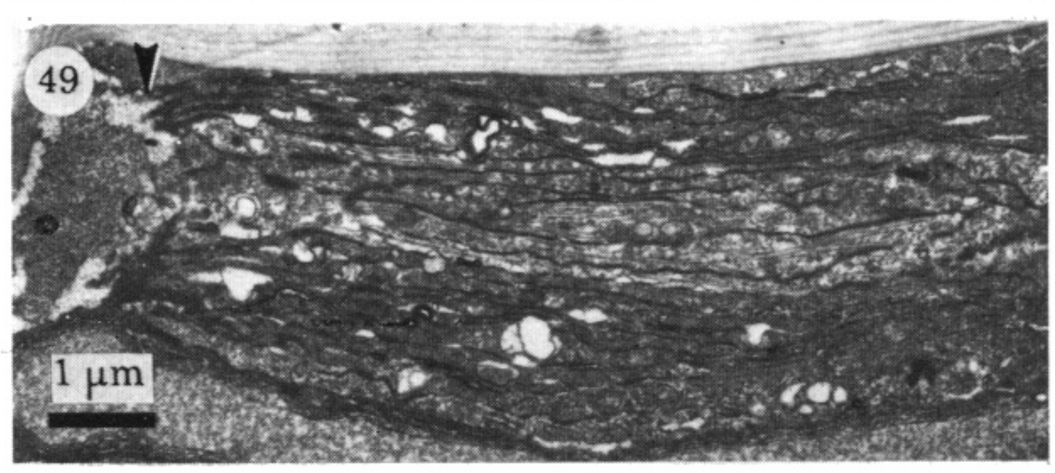




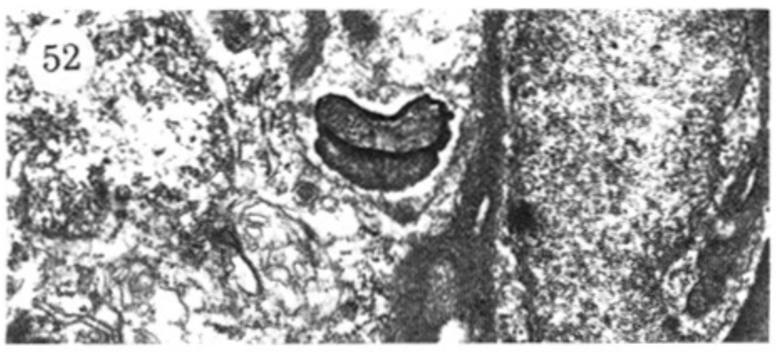


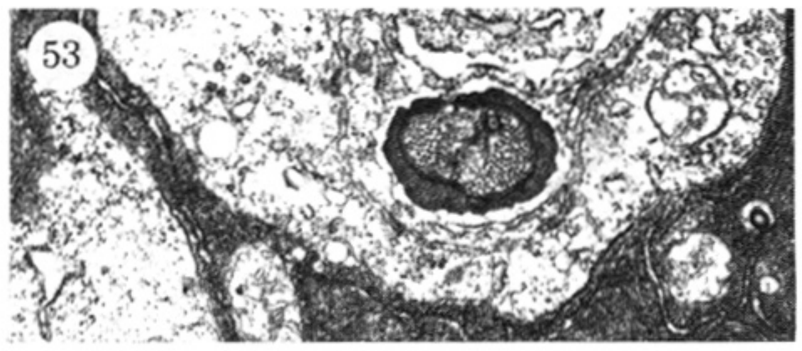


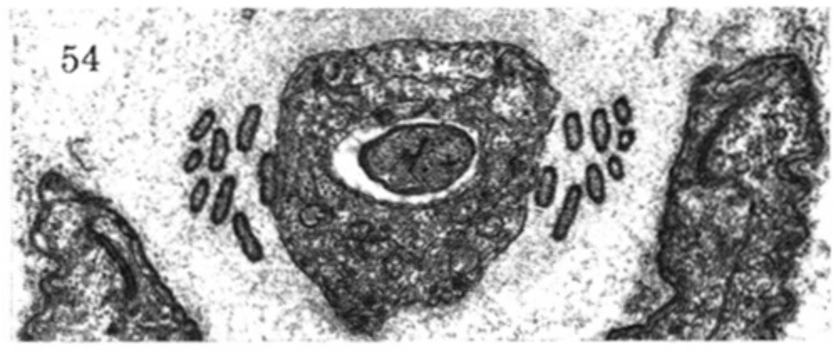


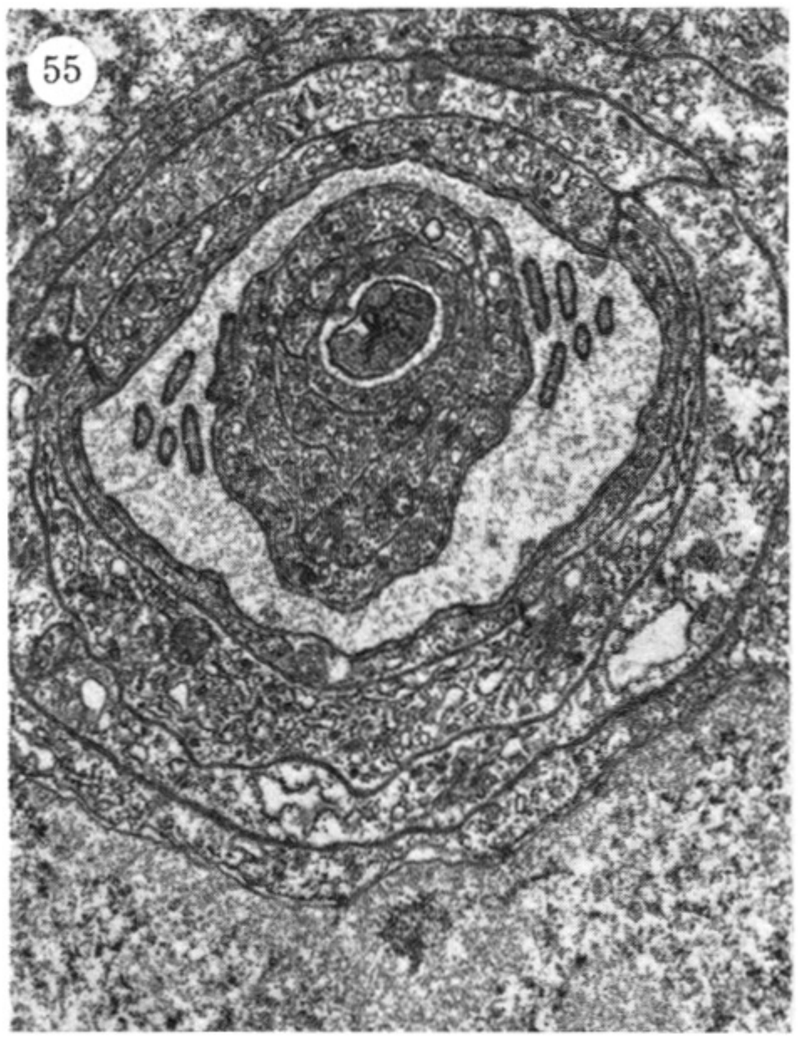


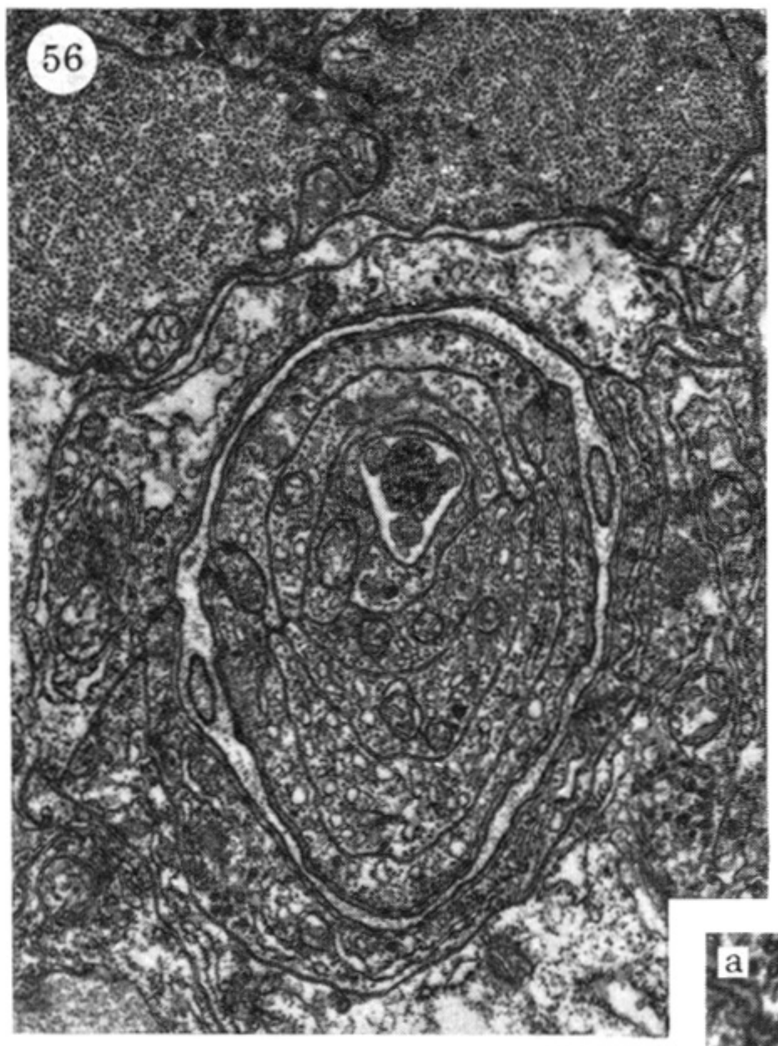
FIGURES 35–49. For description see opposite.

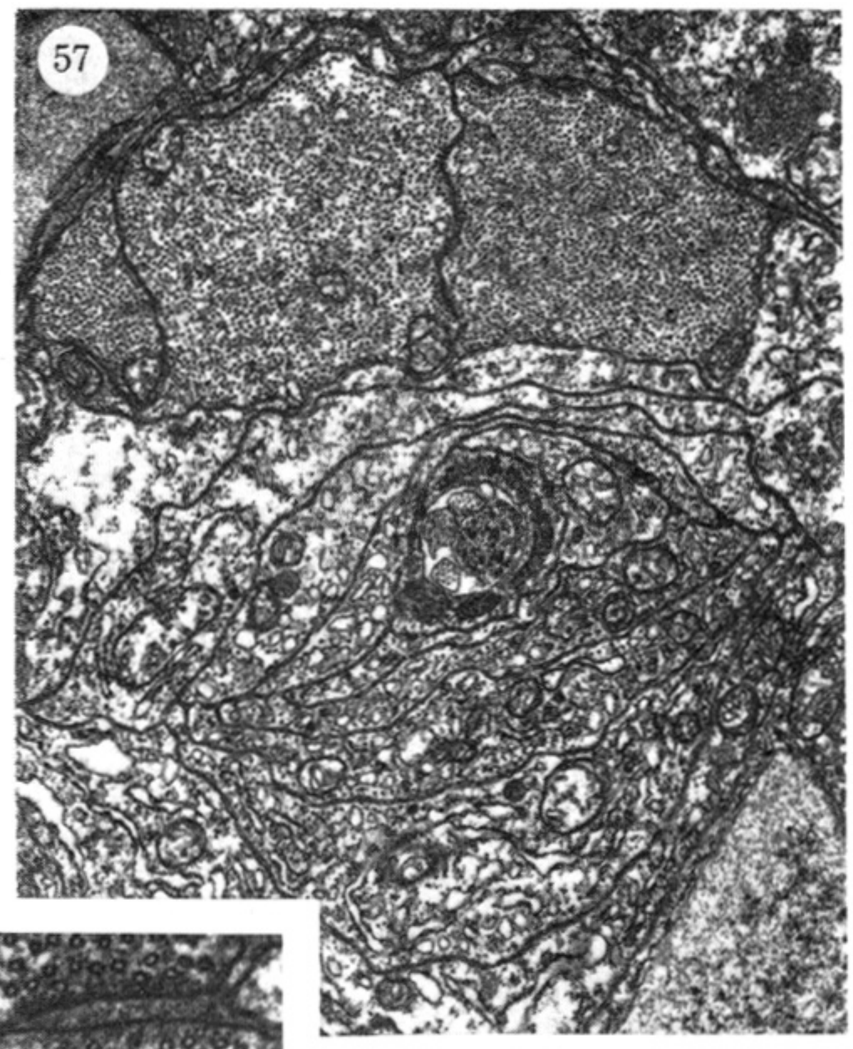


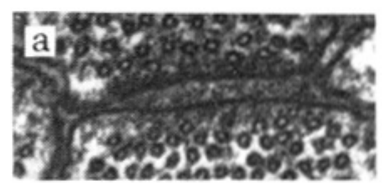


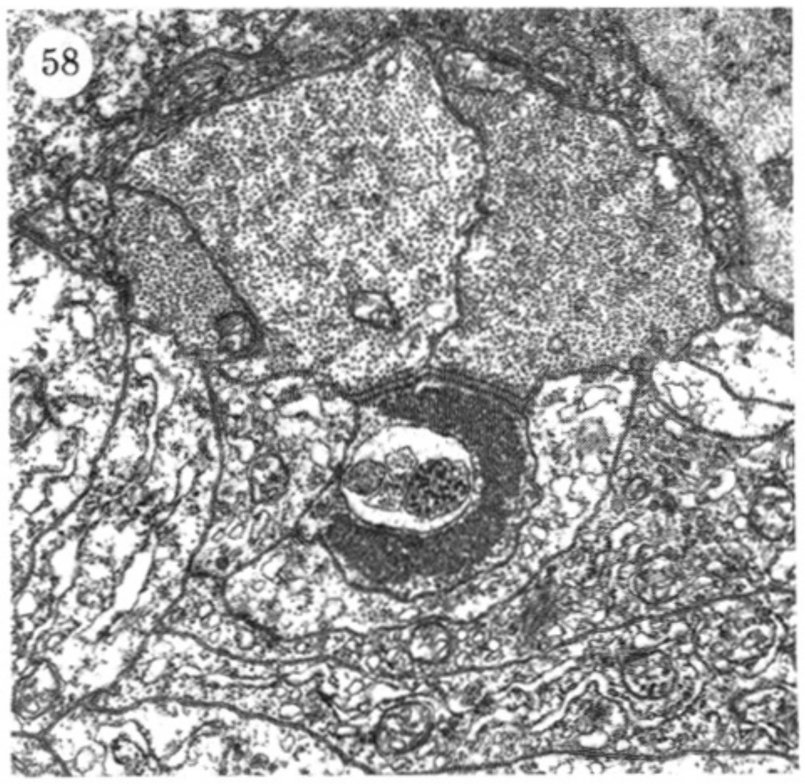


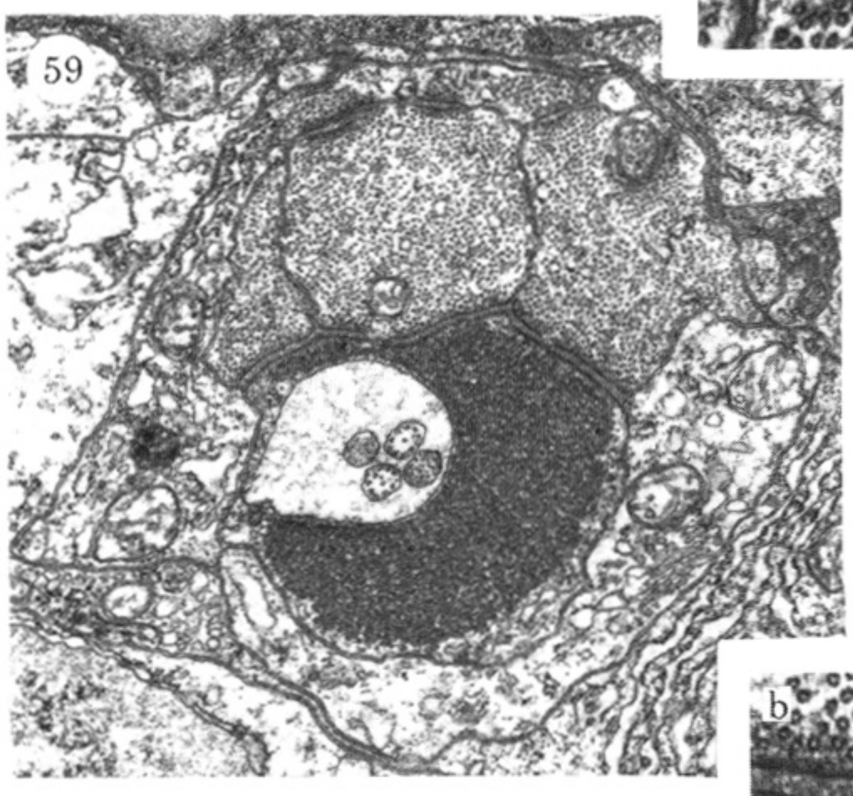


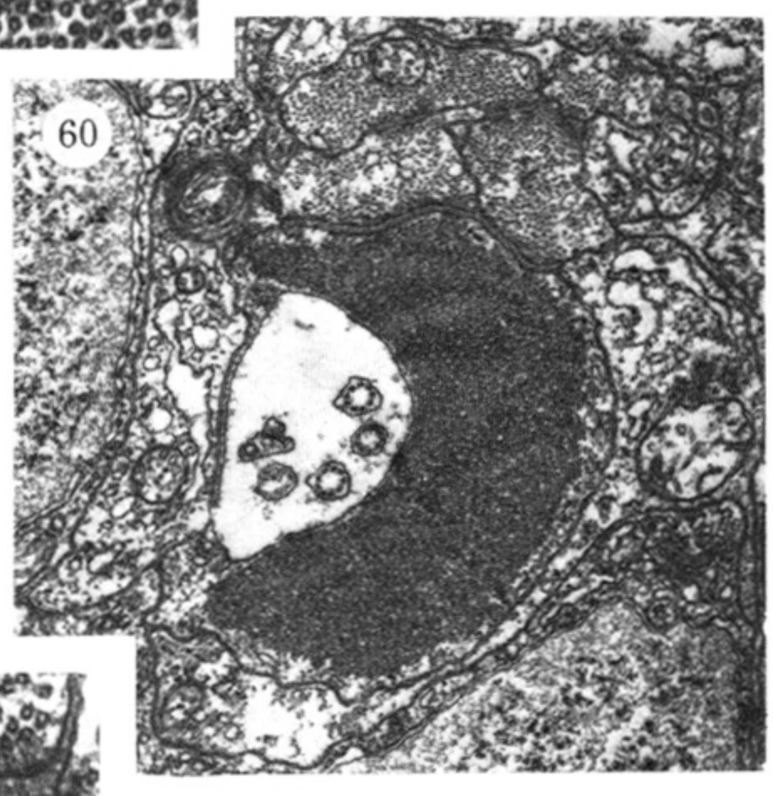


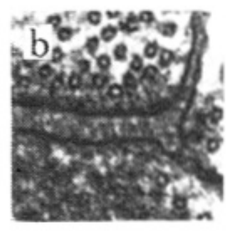


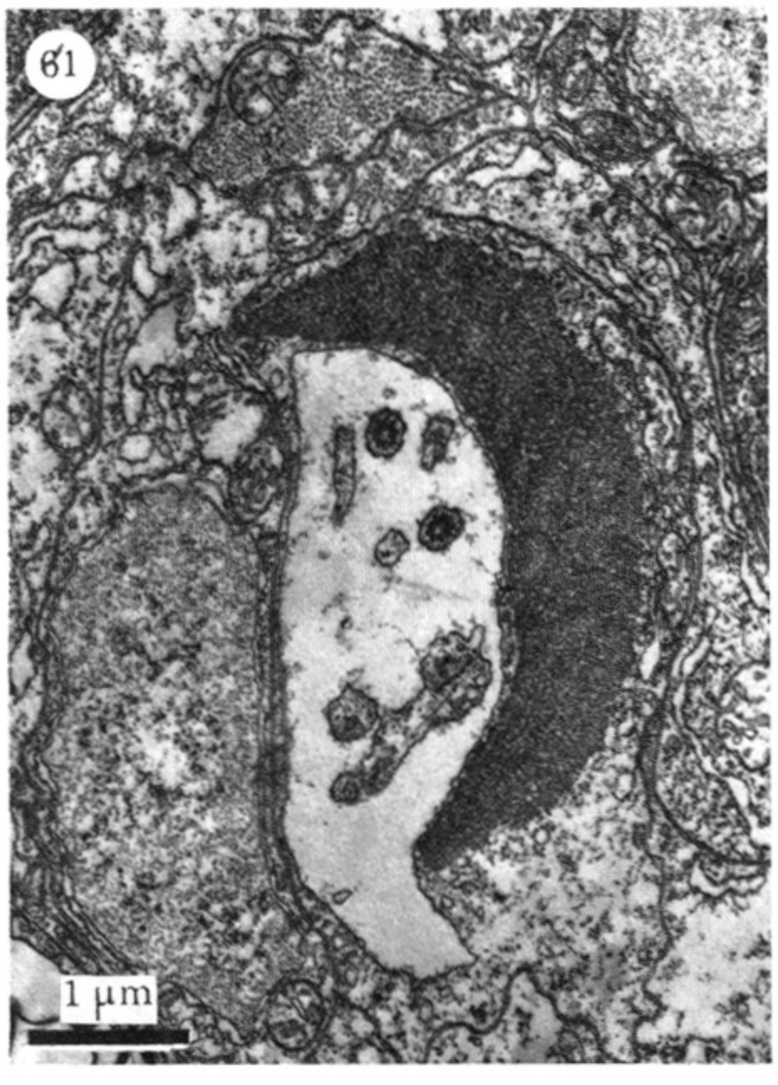


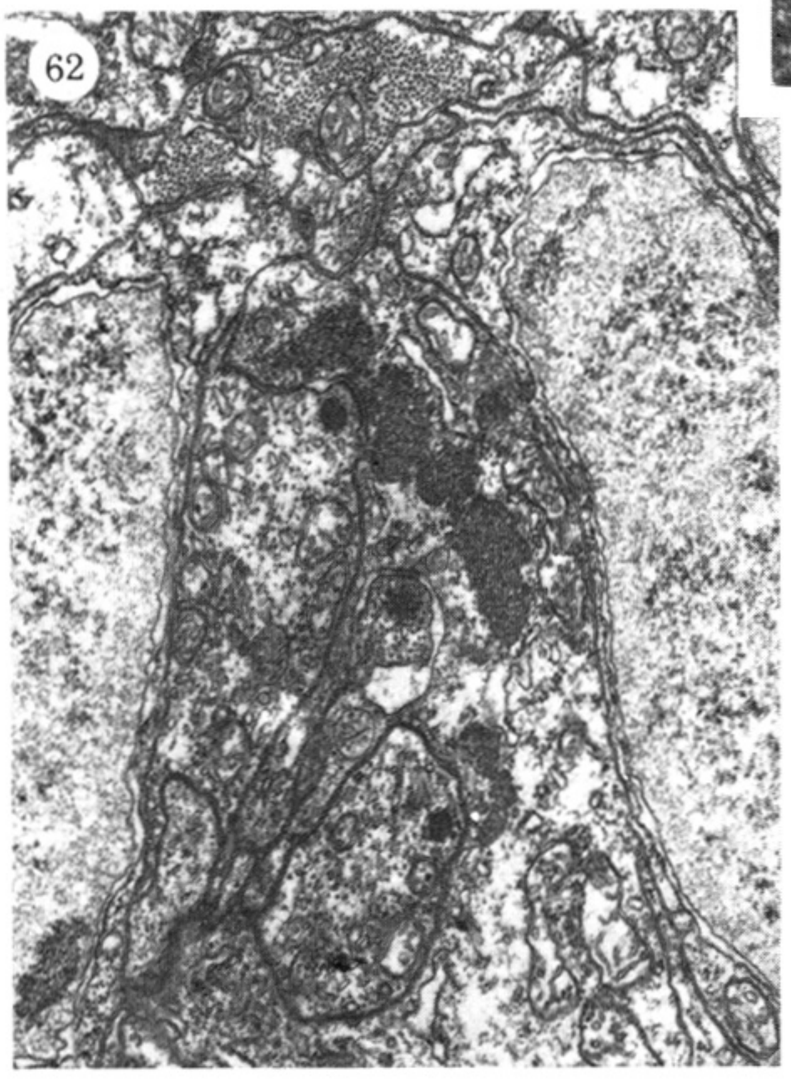


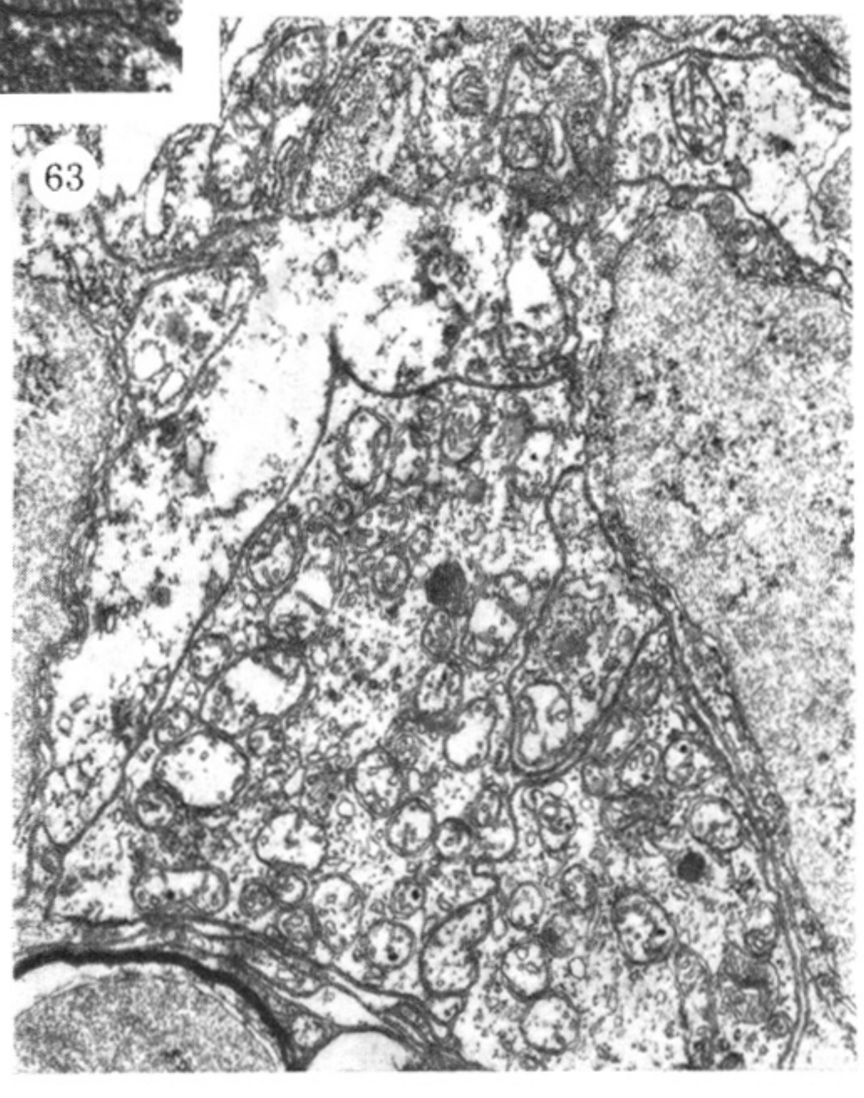




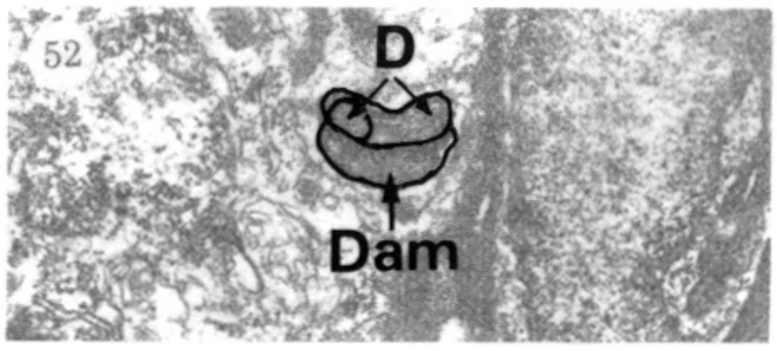


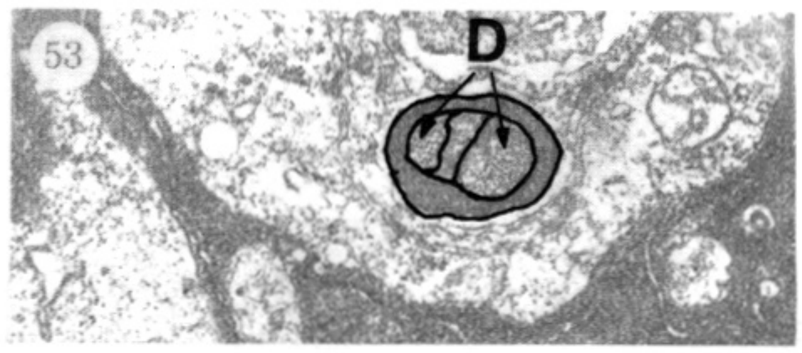


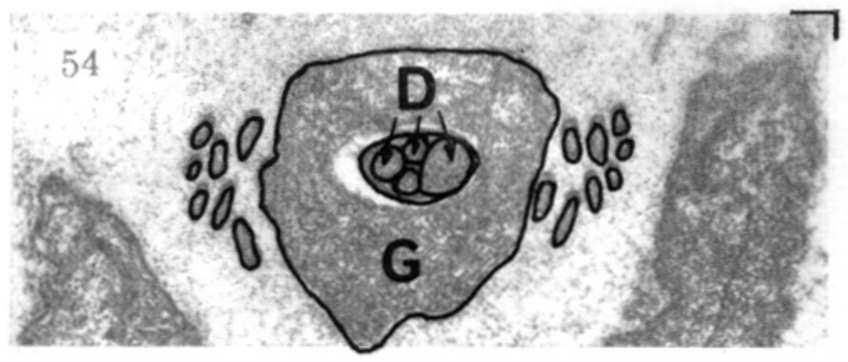


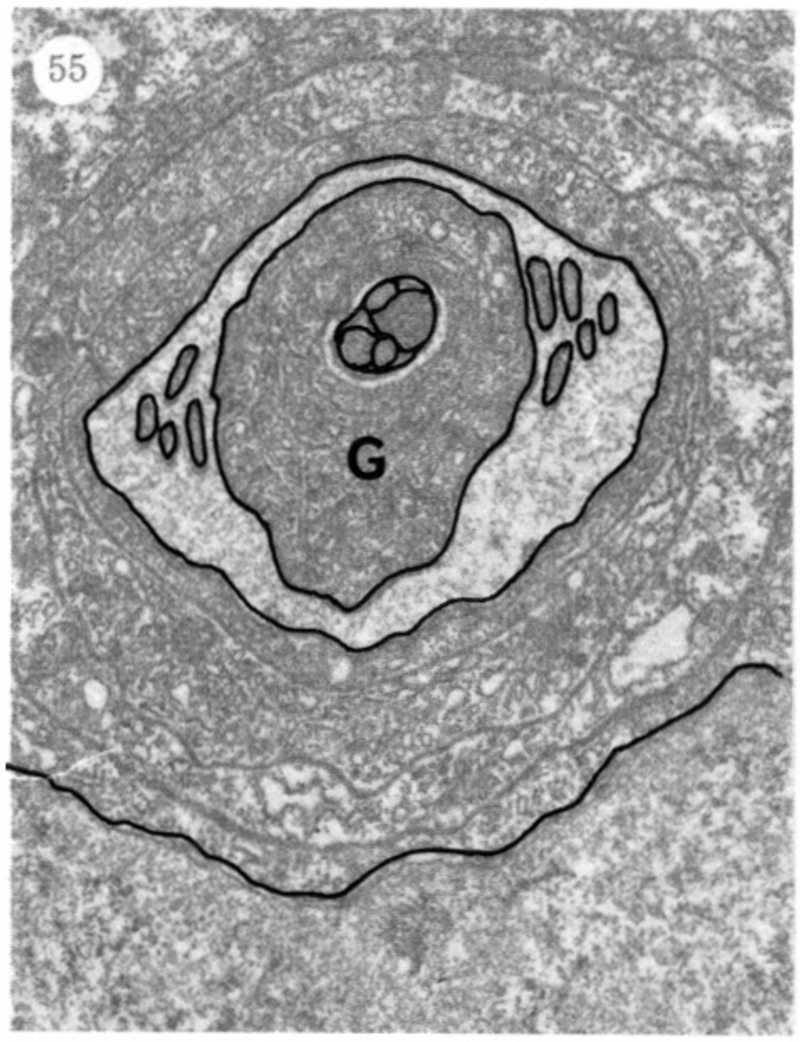


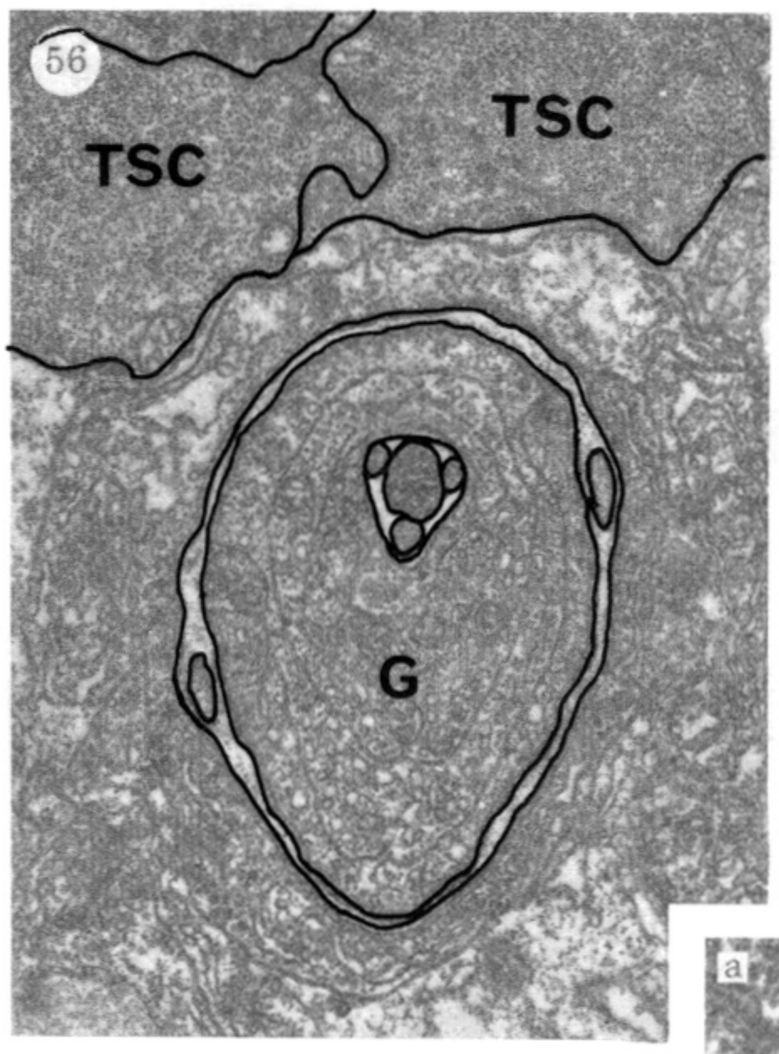
FIGURES 52–63. For description see opposite.

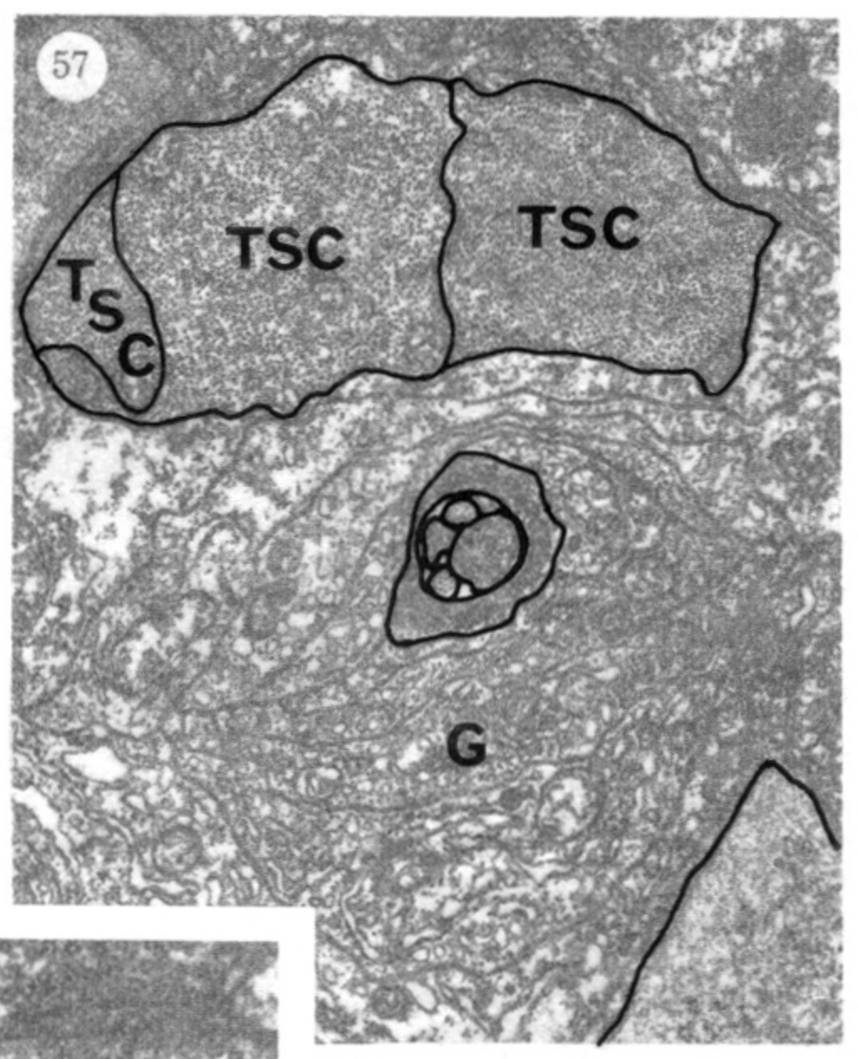


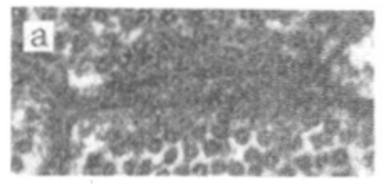


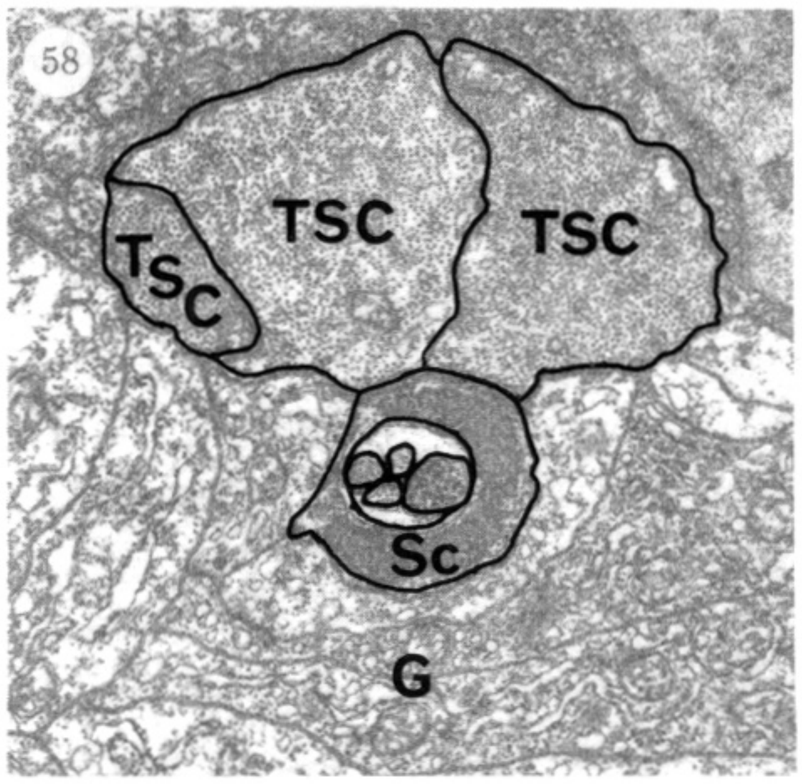


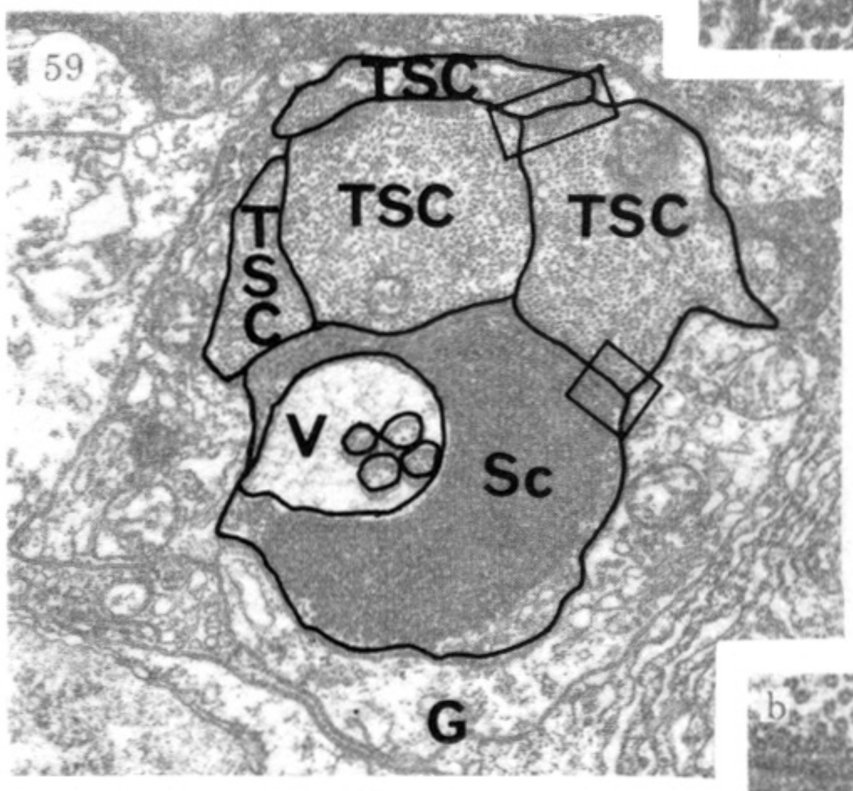


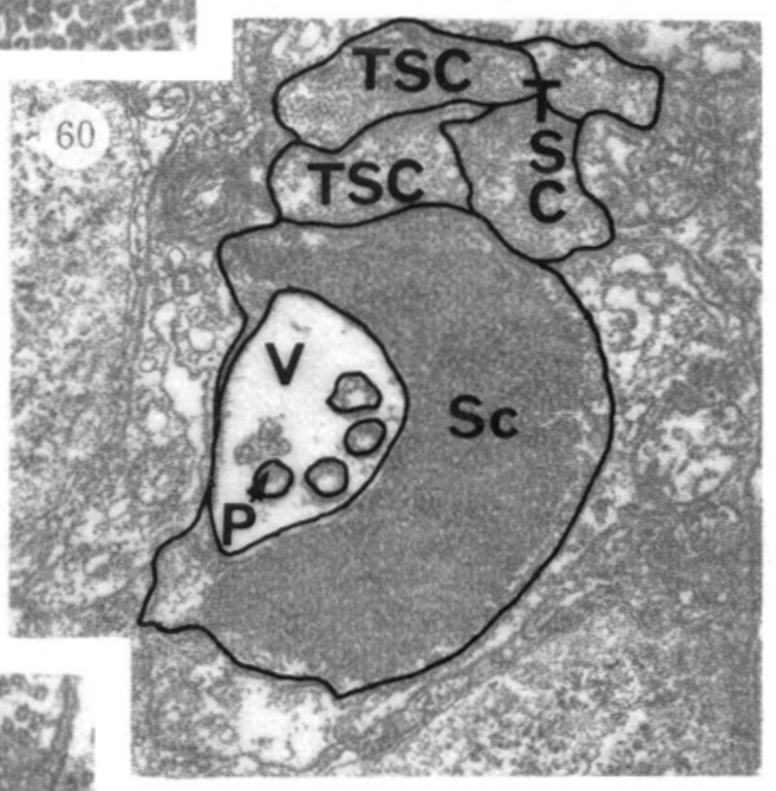


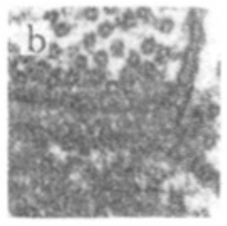


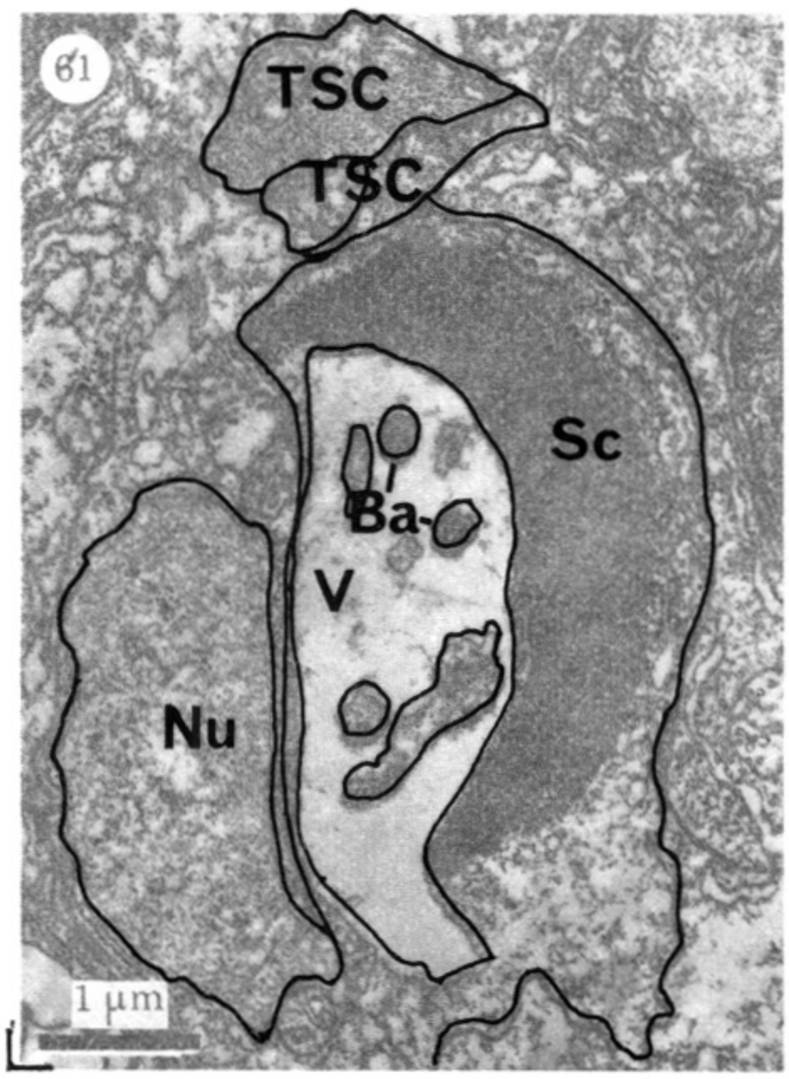


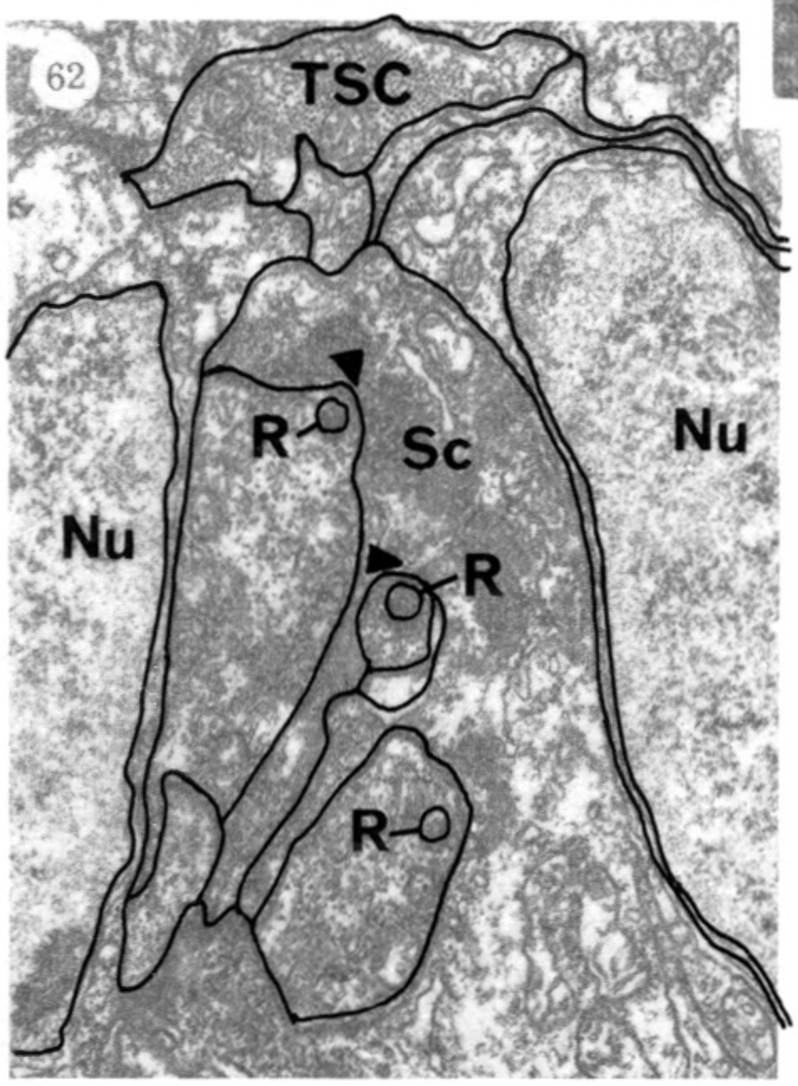


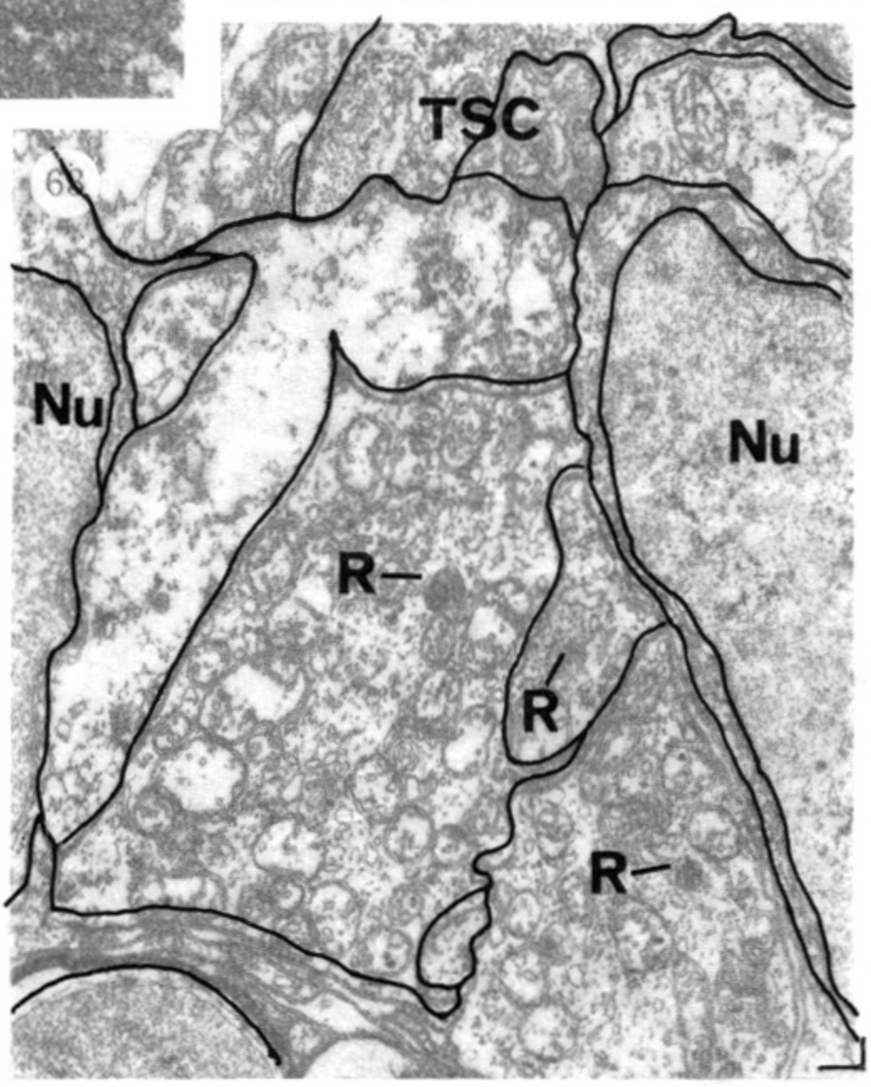




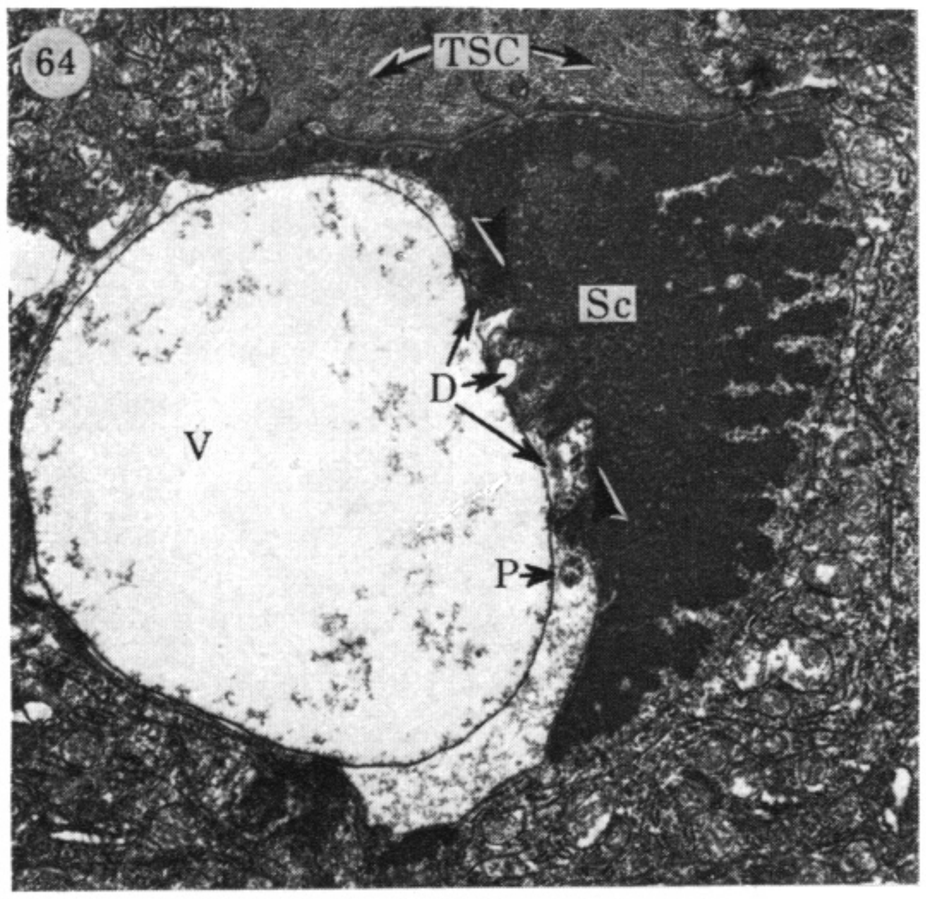


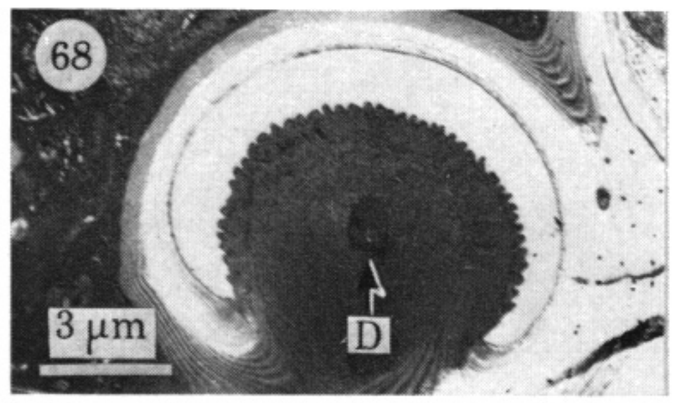


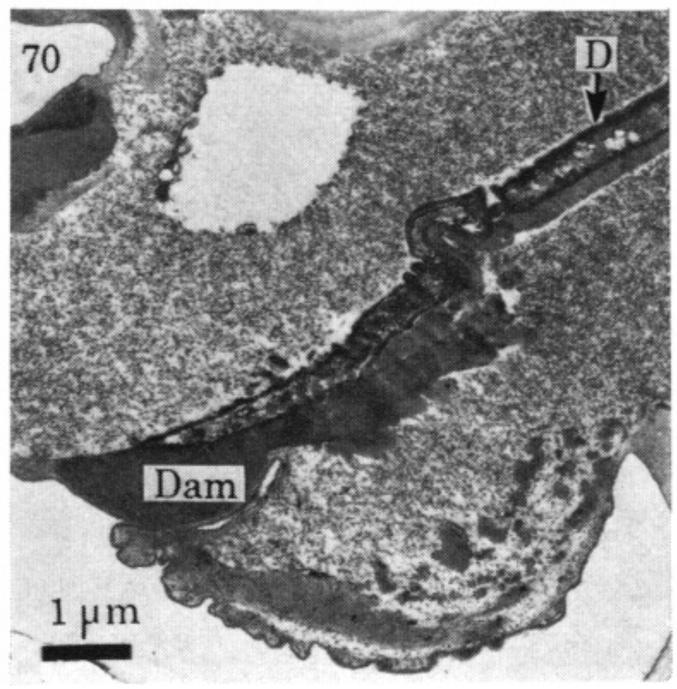


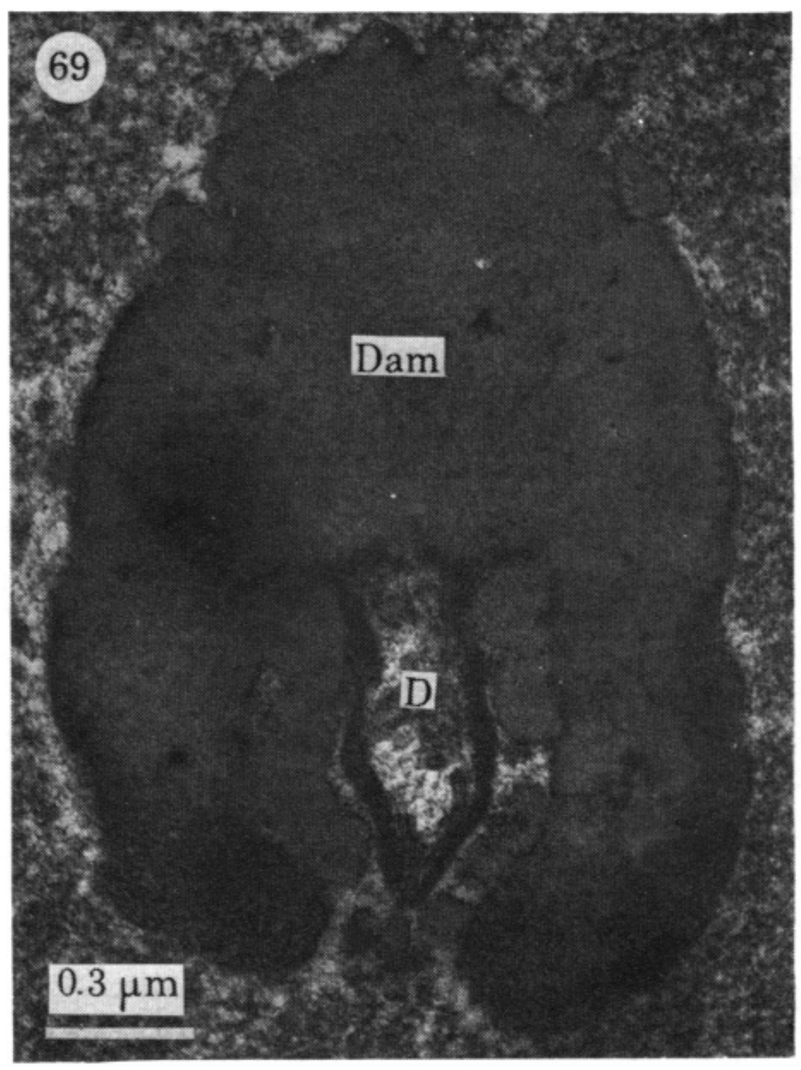


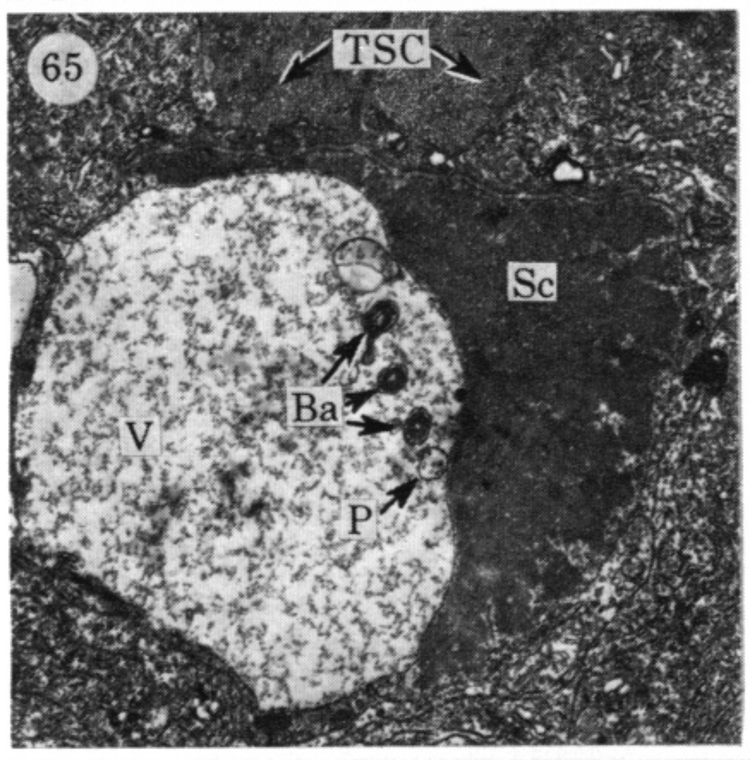
FIGURES 52–63. For description see opposite.

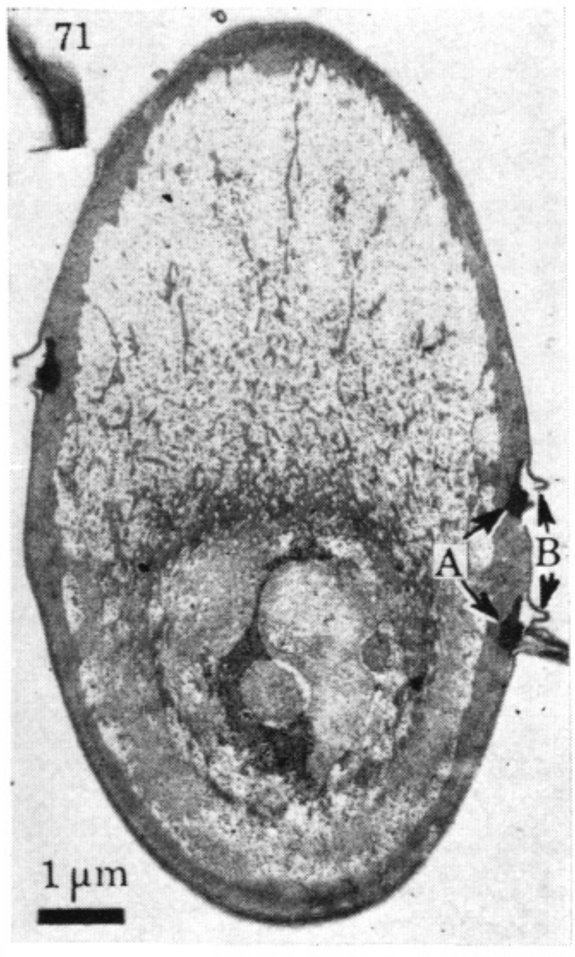


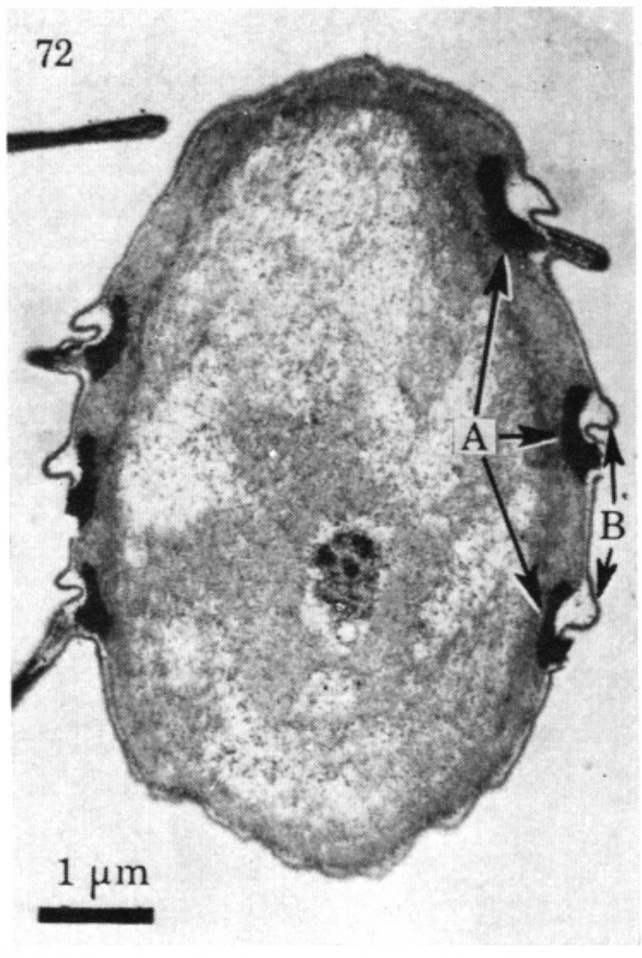


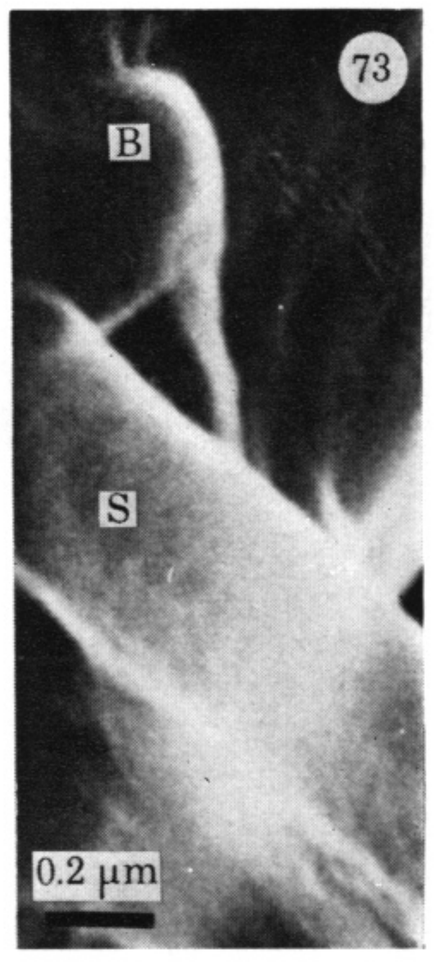


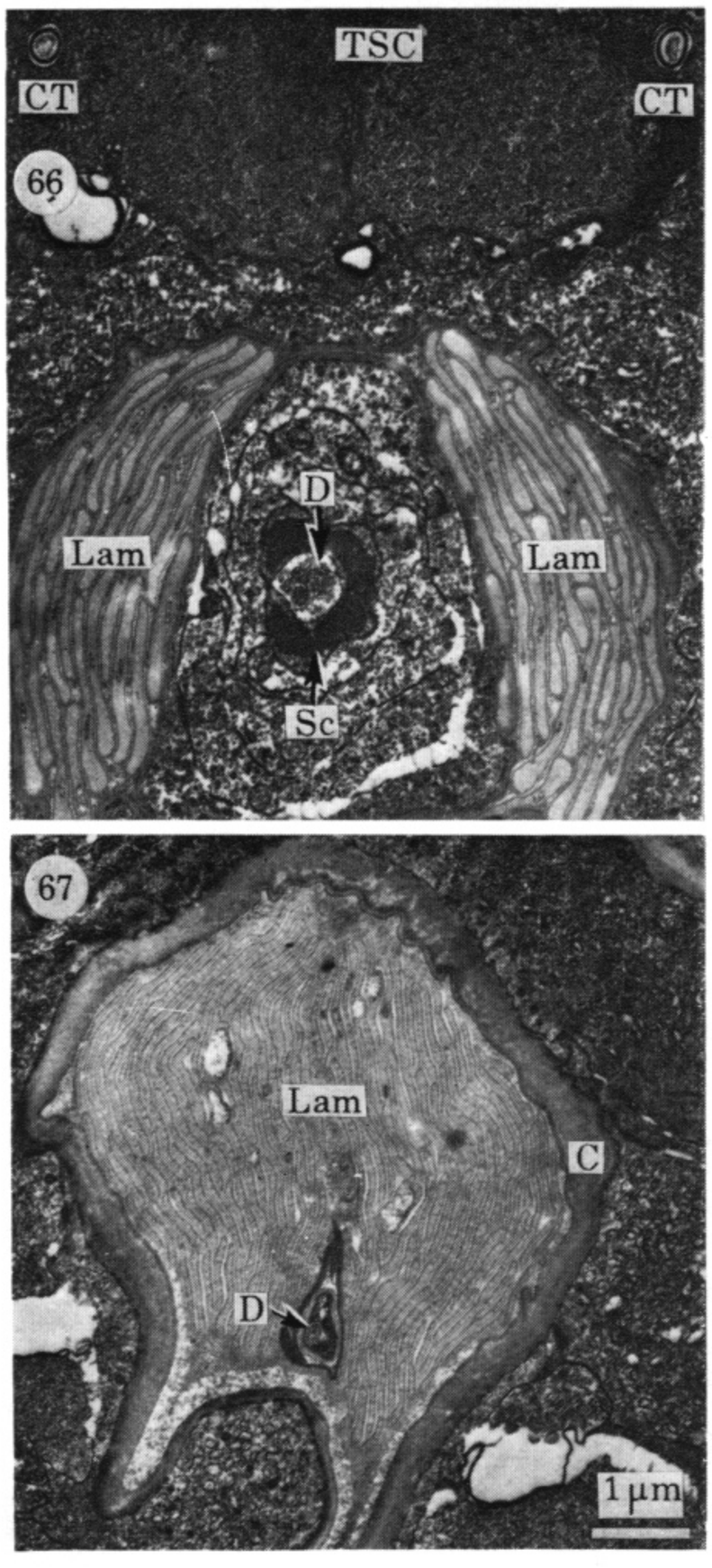


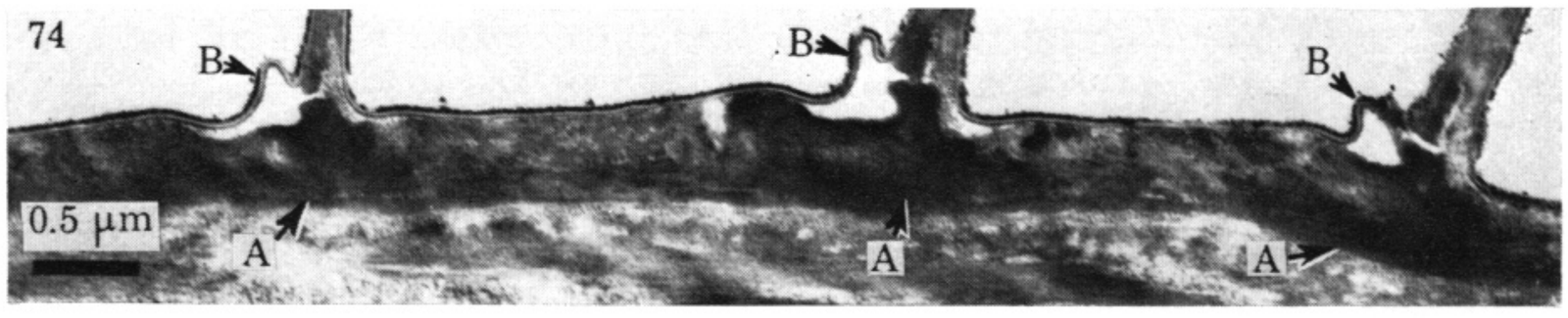


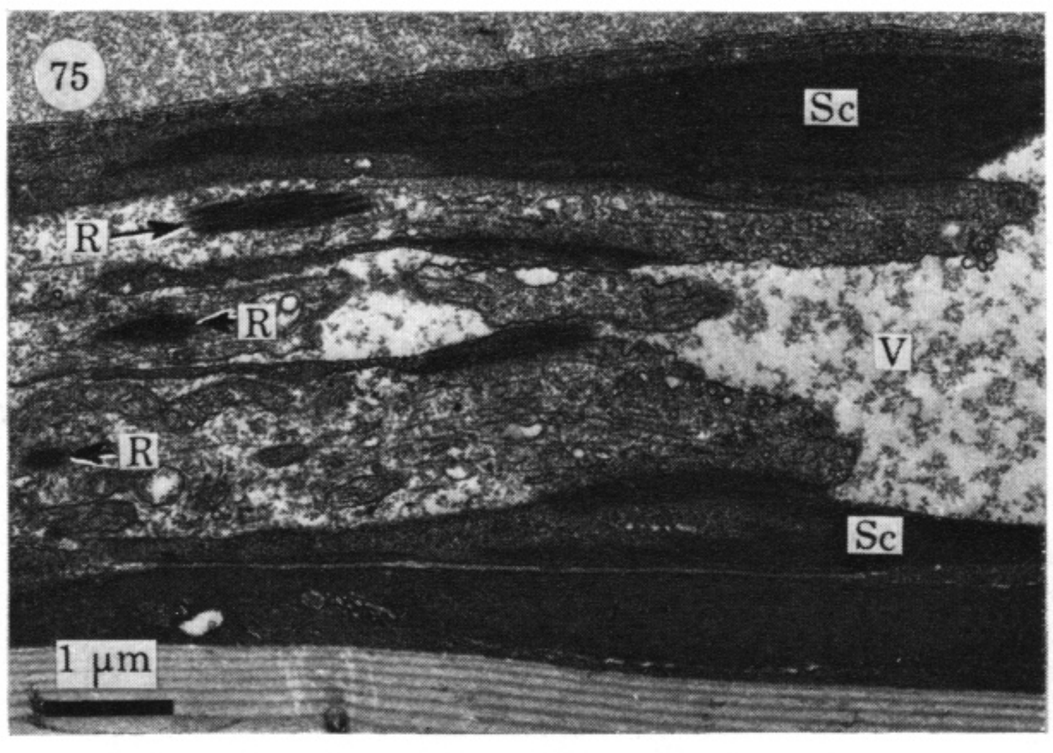


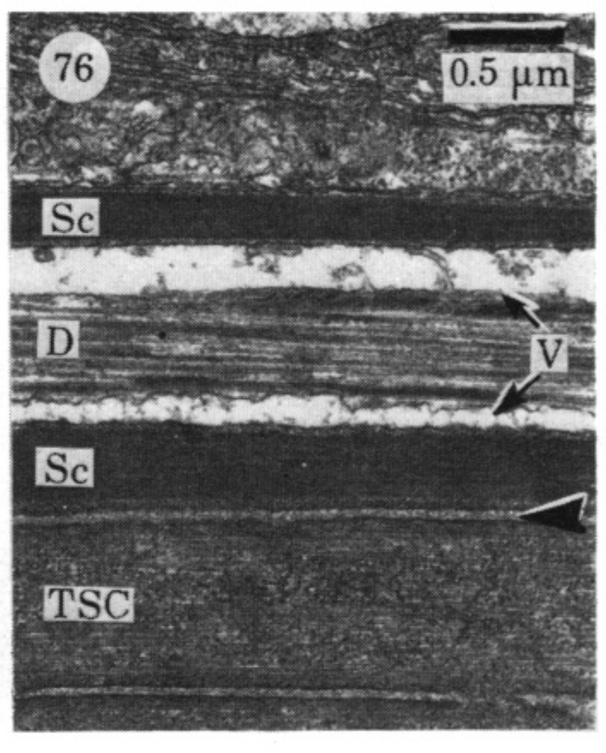




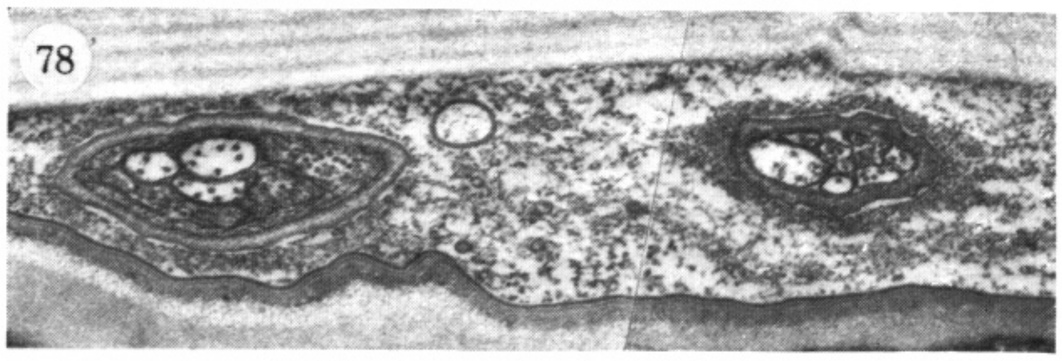


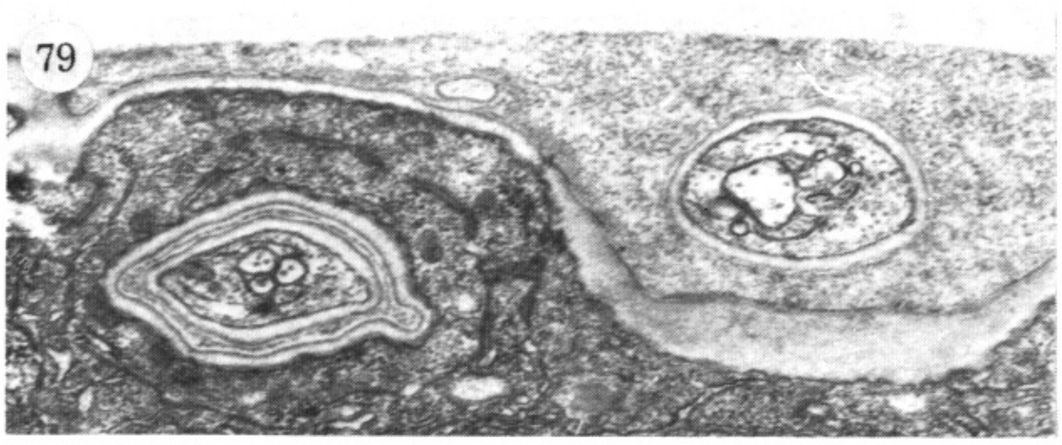


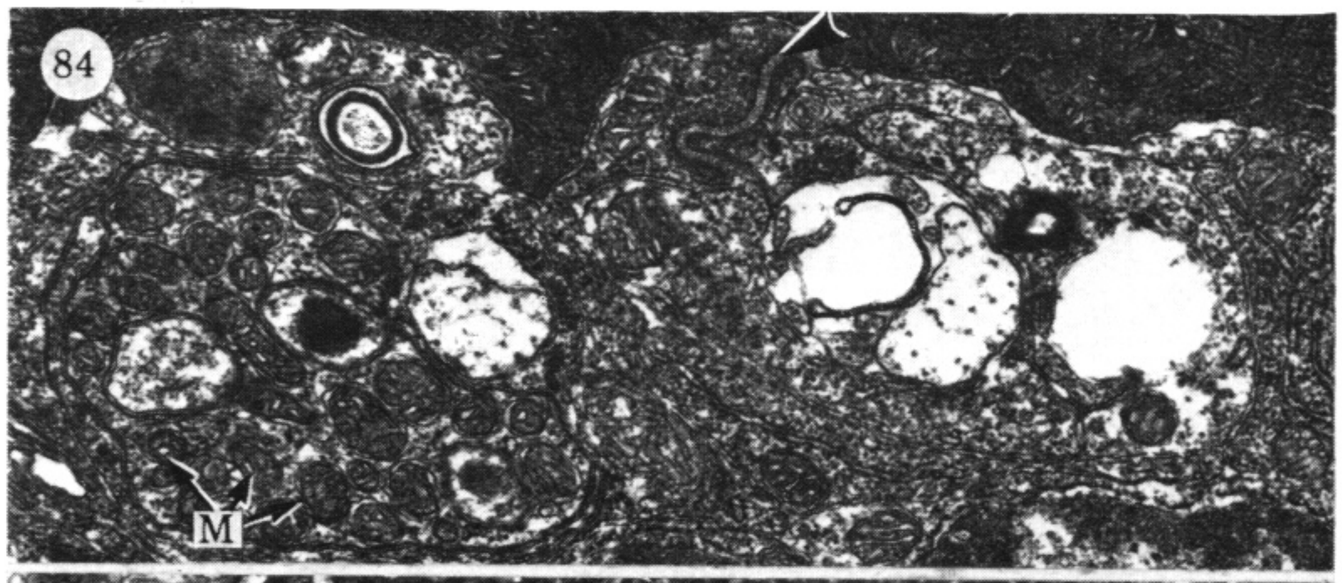


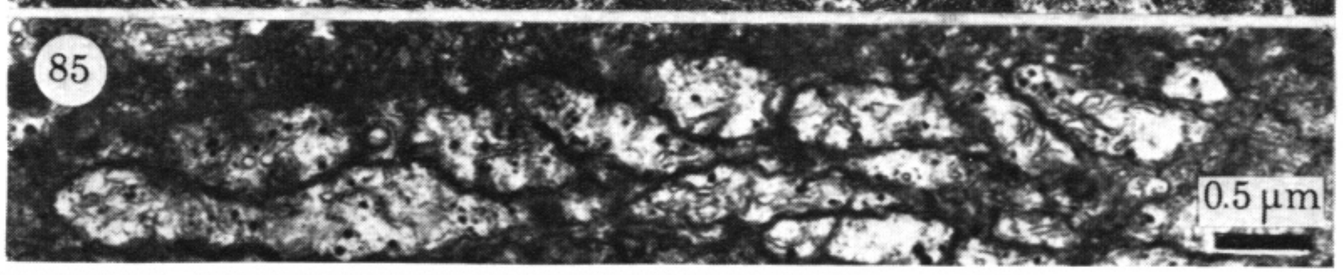


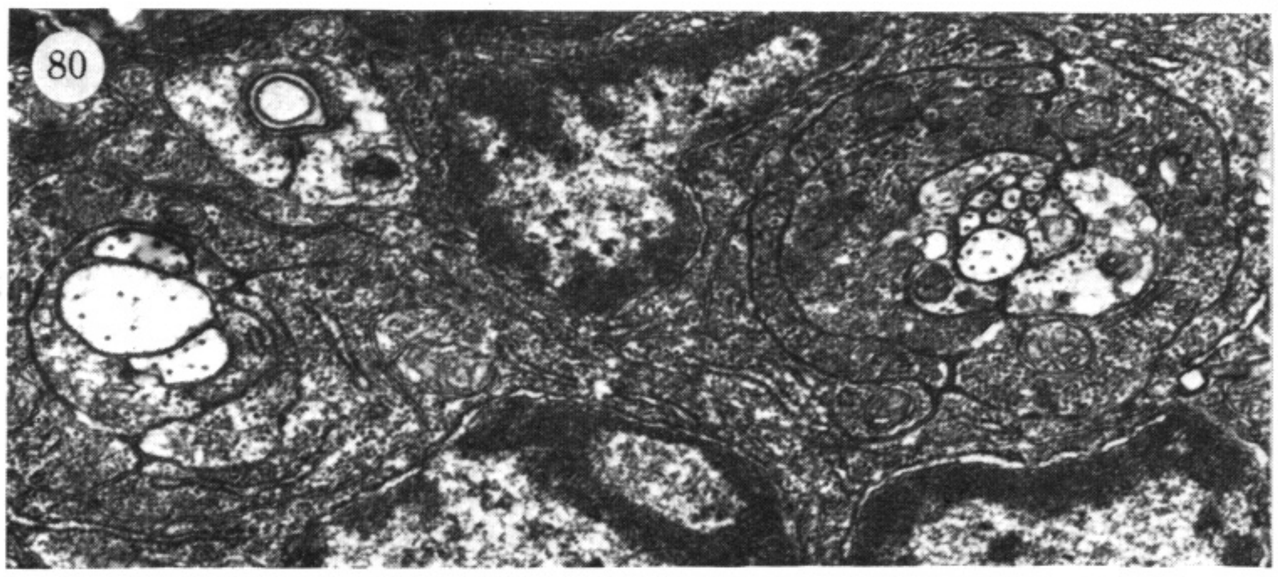
FIGURES 64–76. For description see opposite.

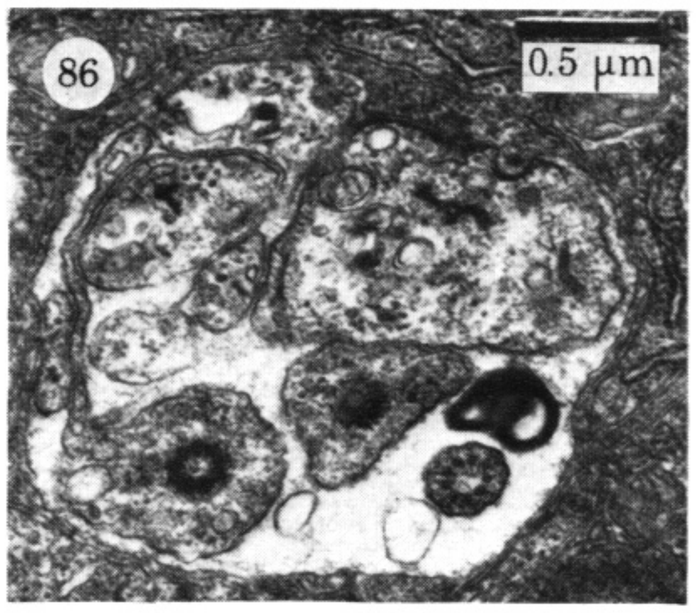


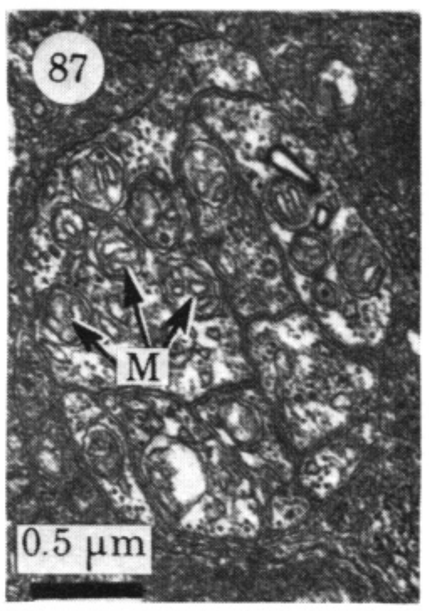


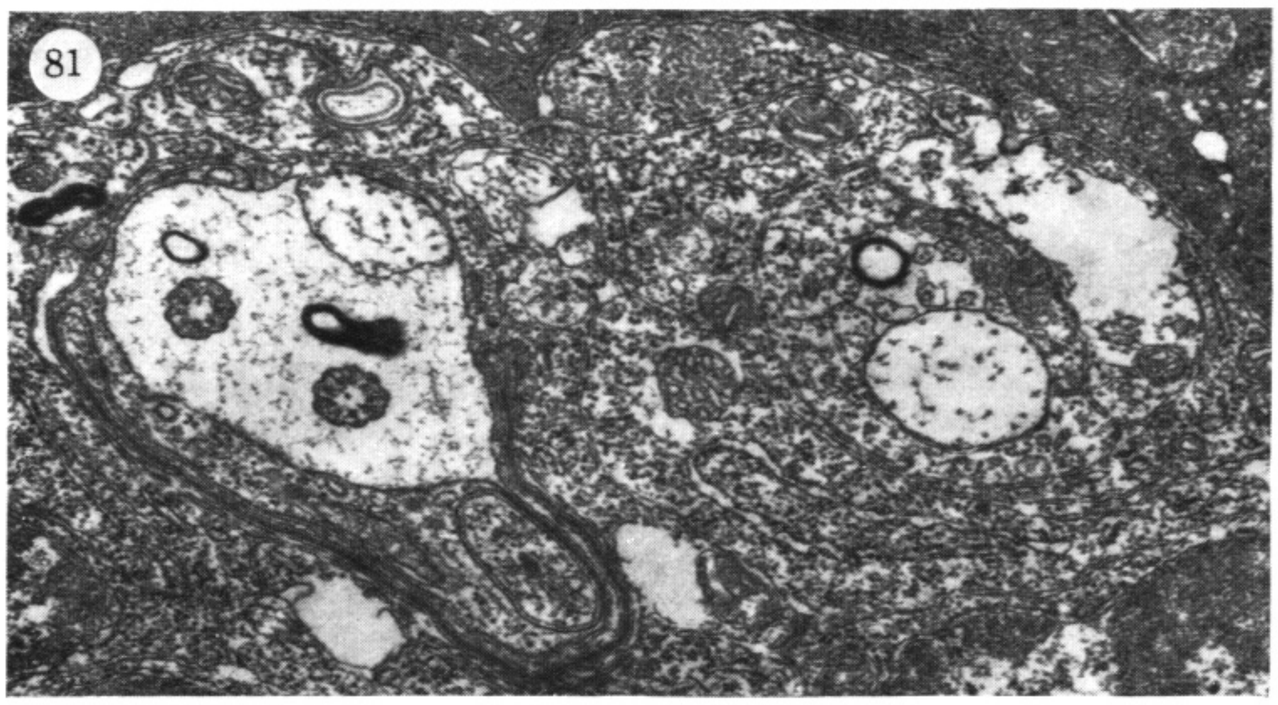


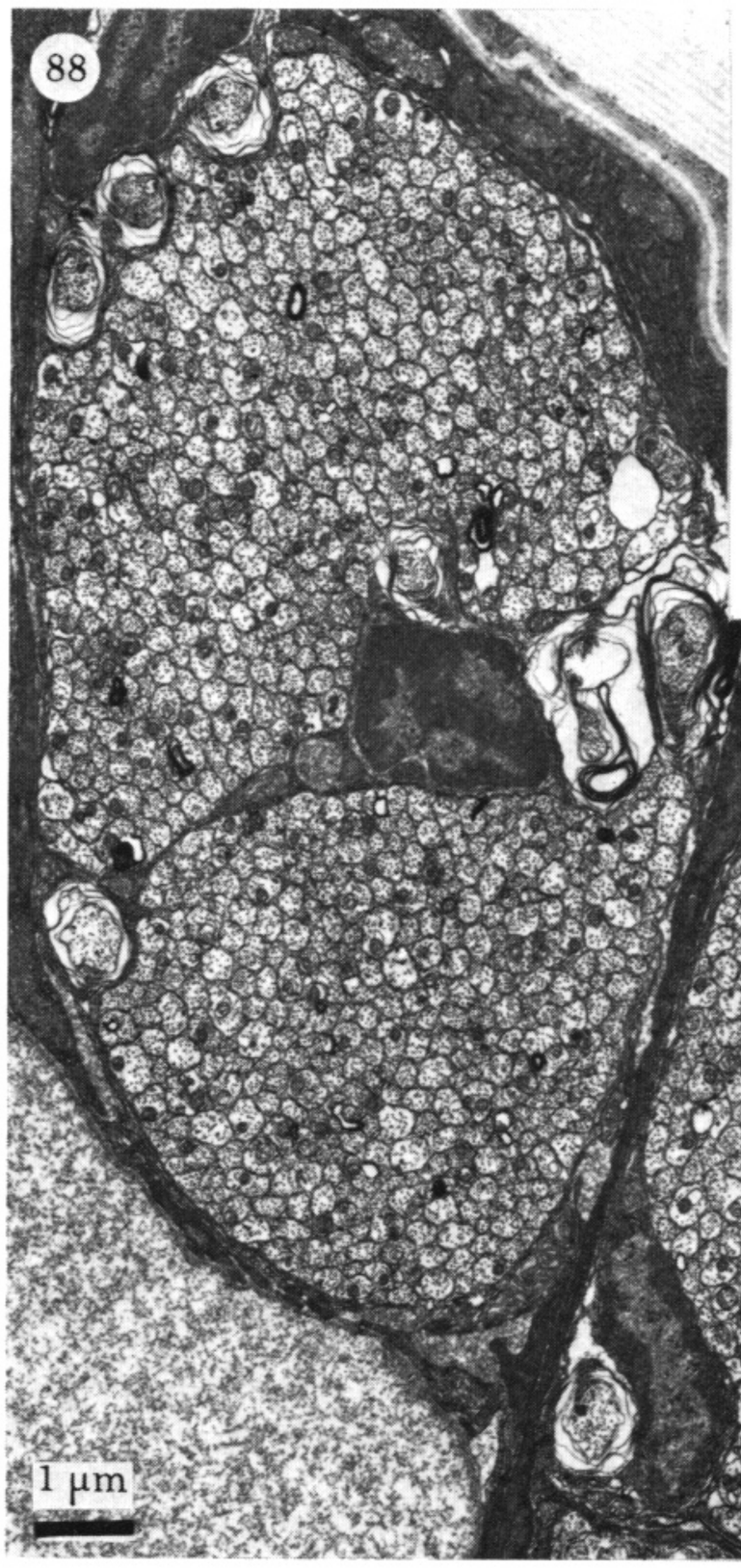


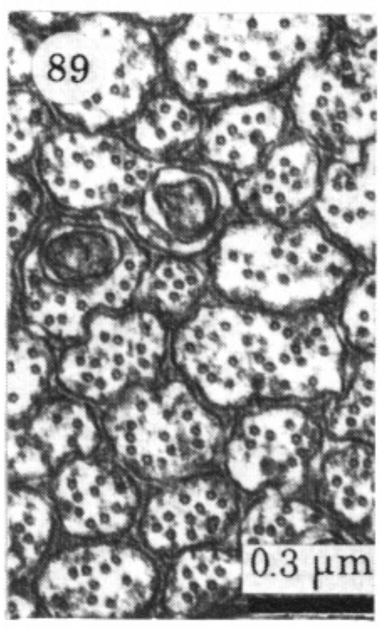


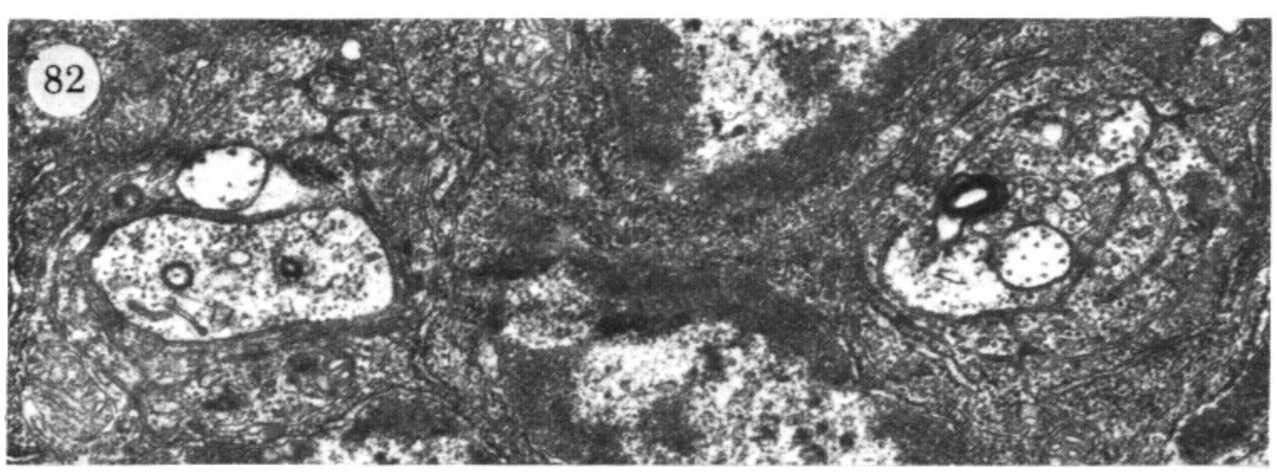


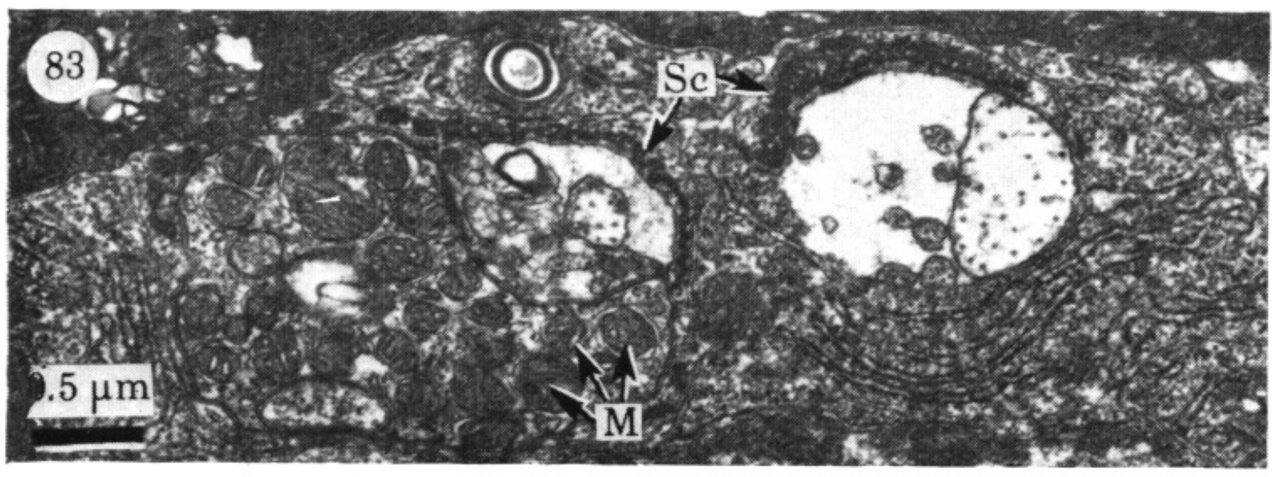


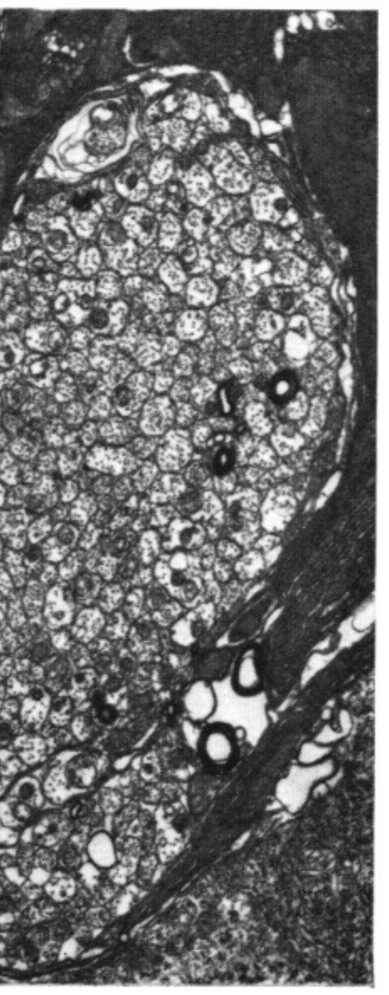




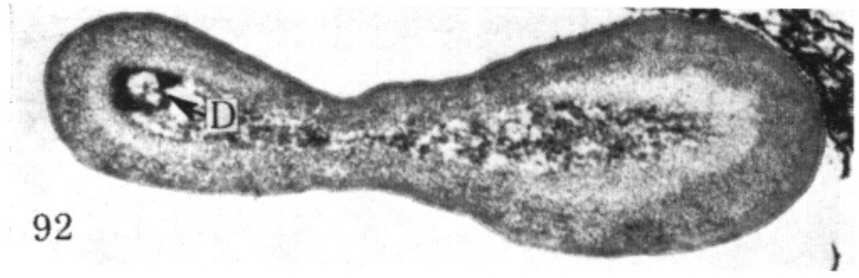


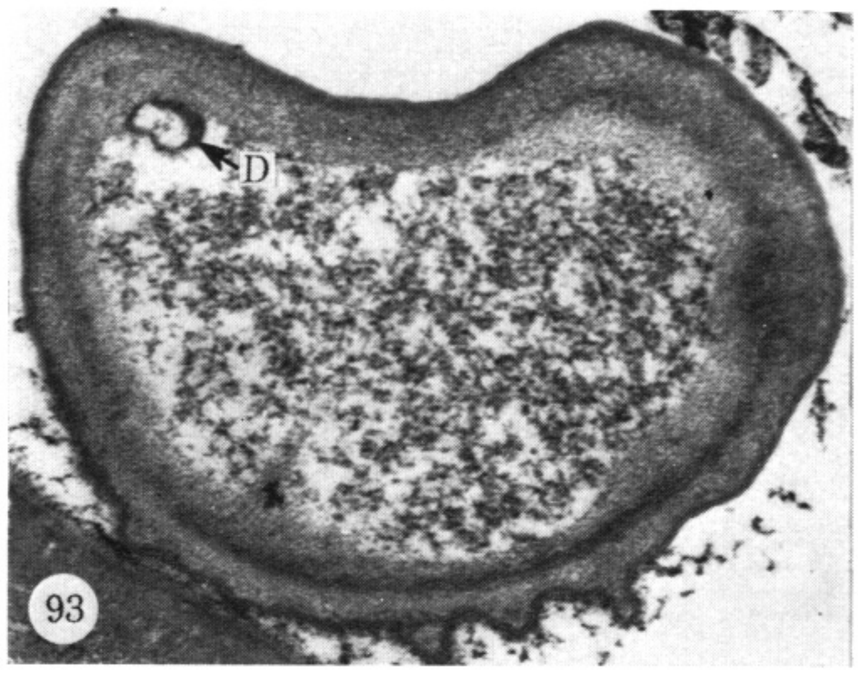


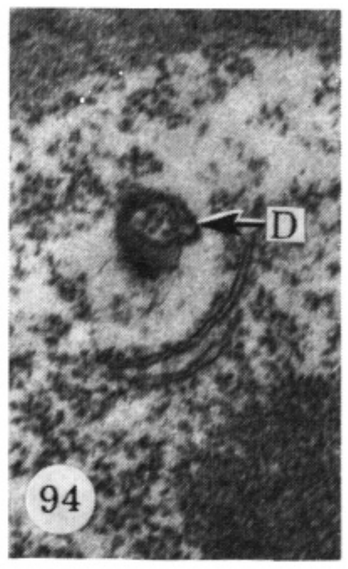


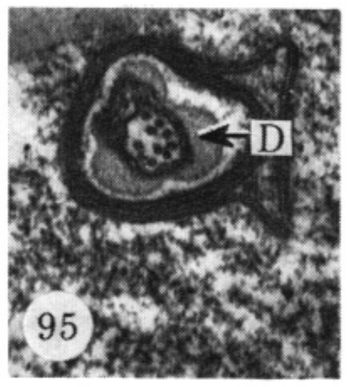


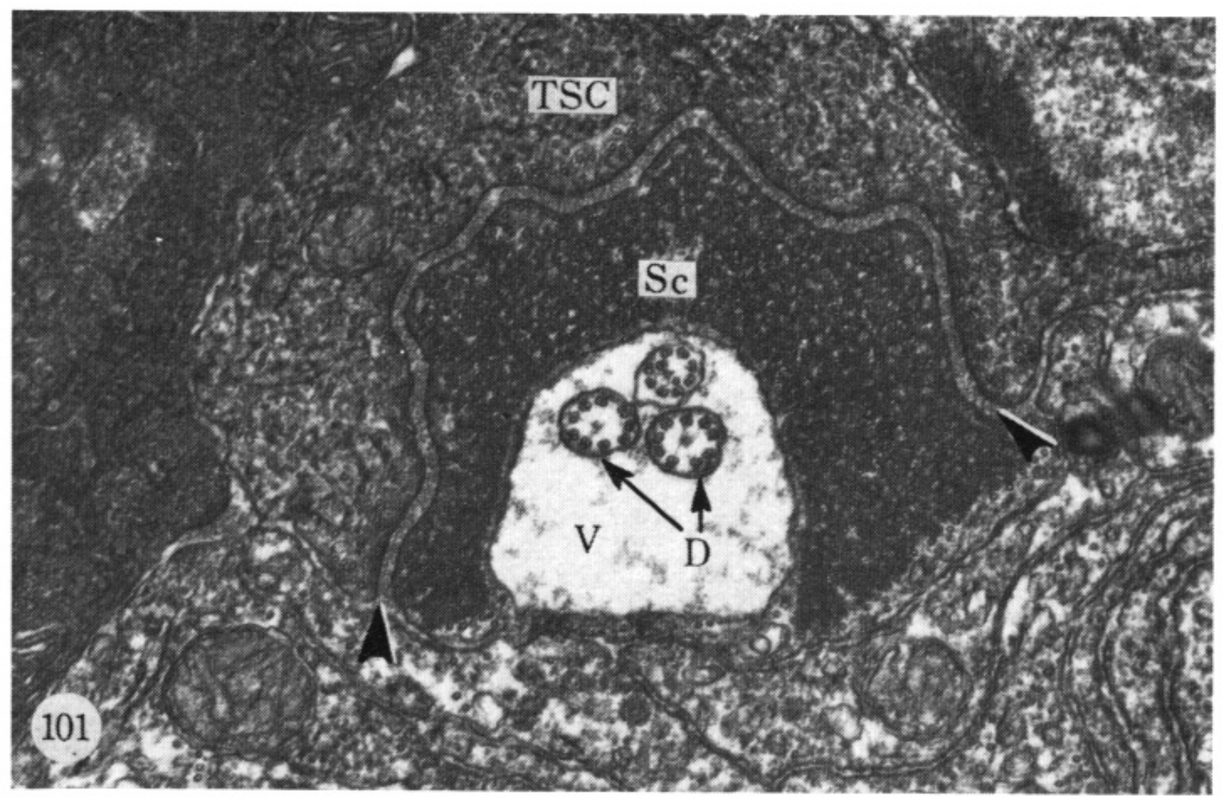
FIGURES 78–89. For description see opposite.

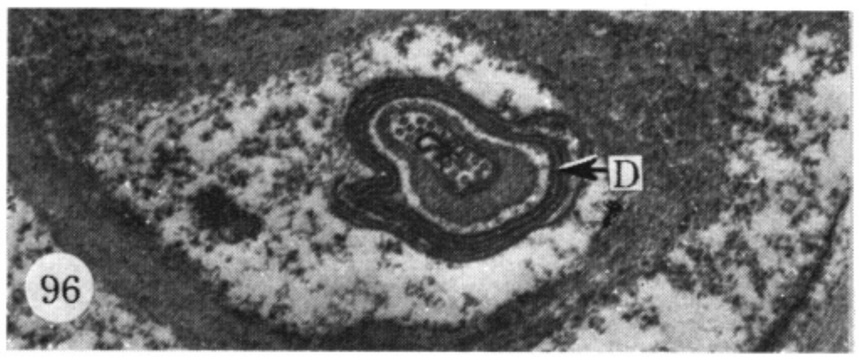


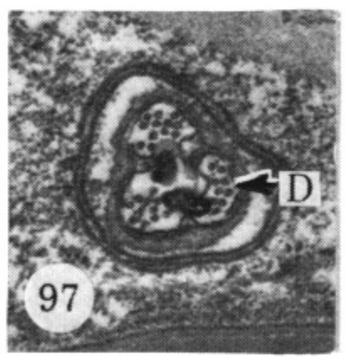


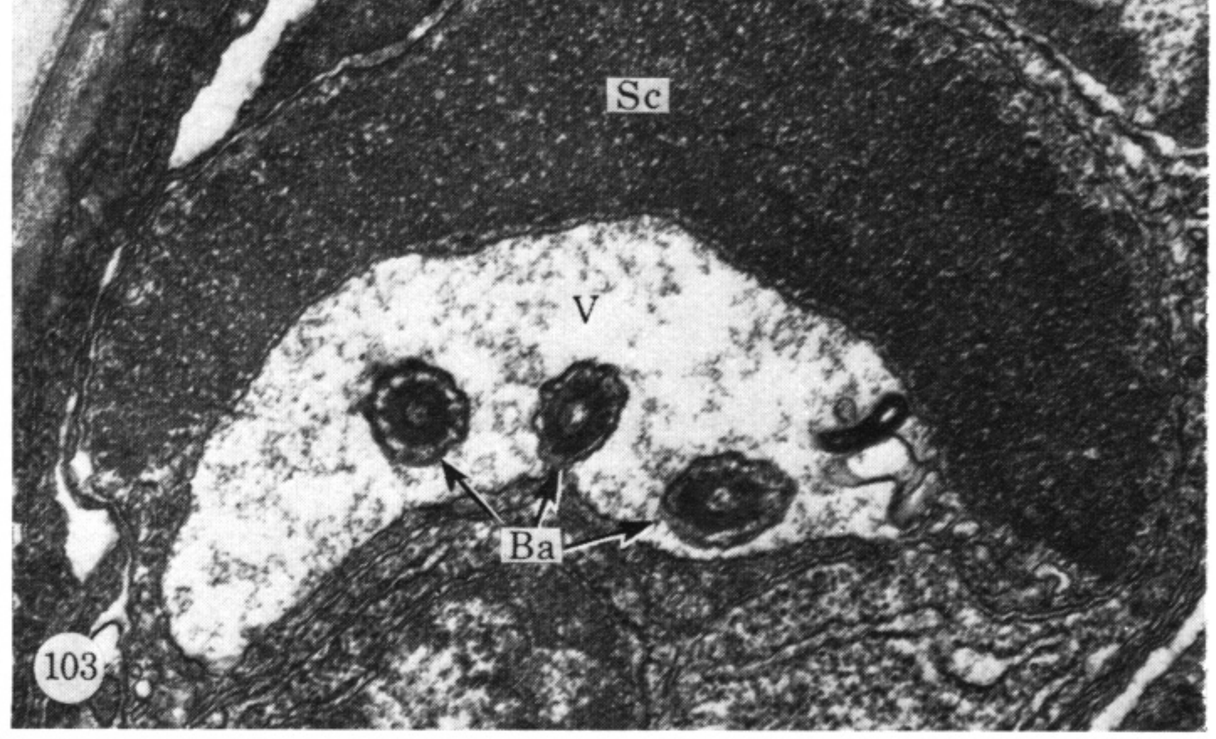


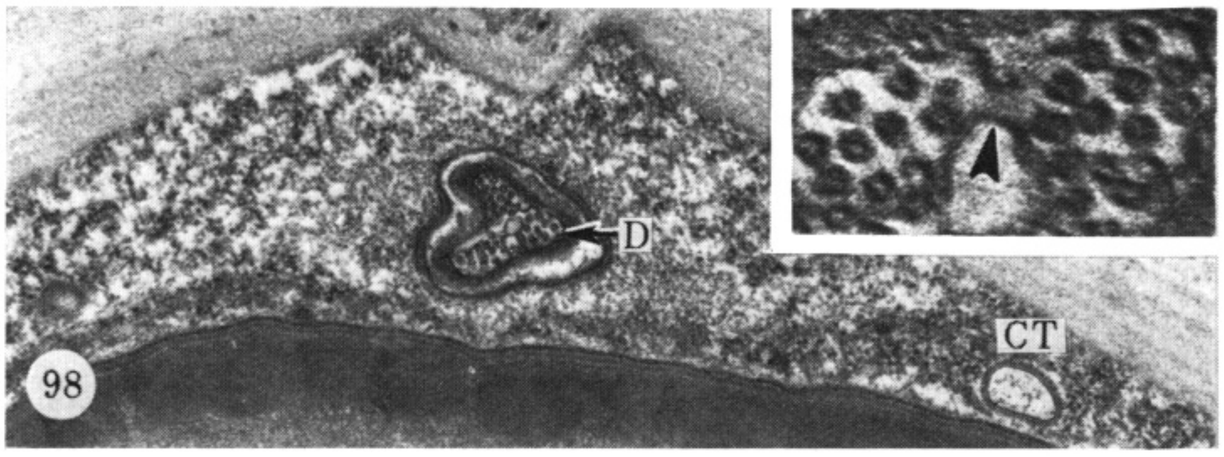


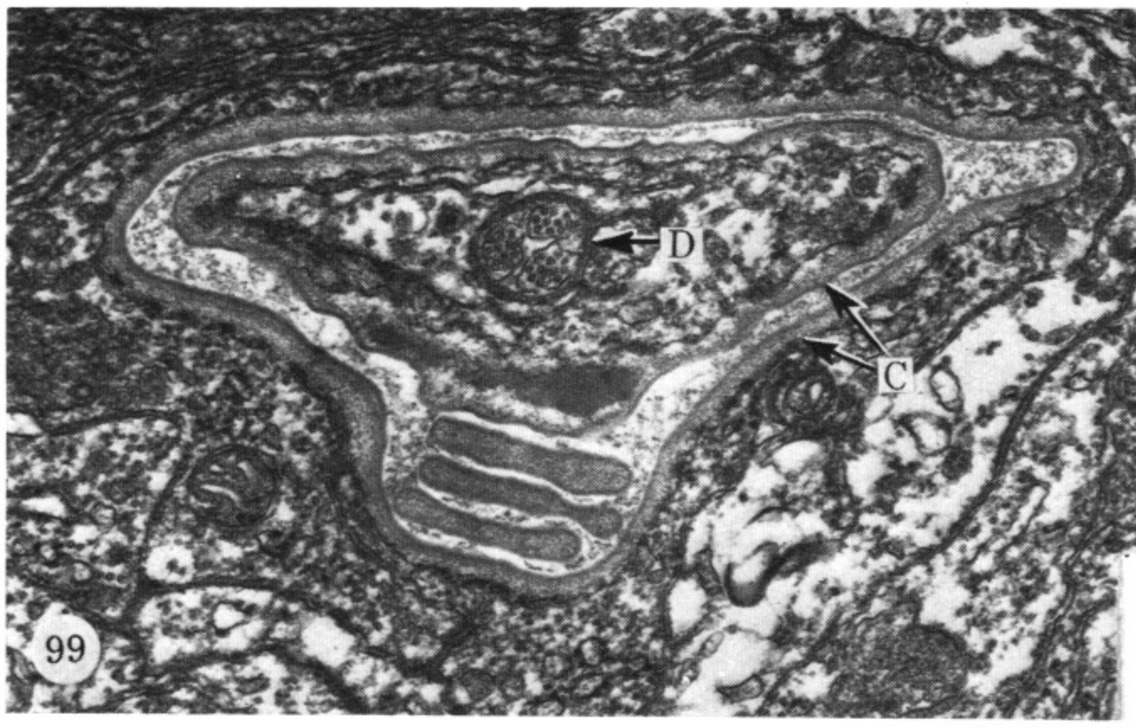


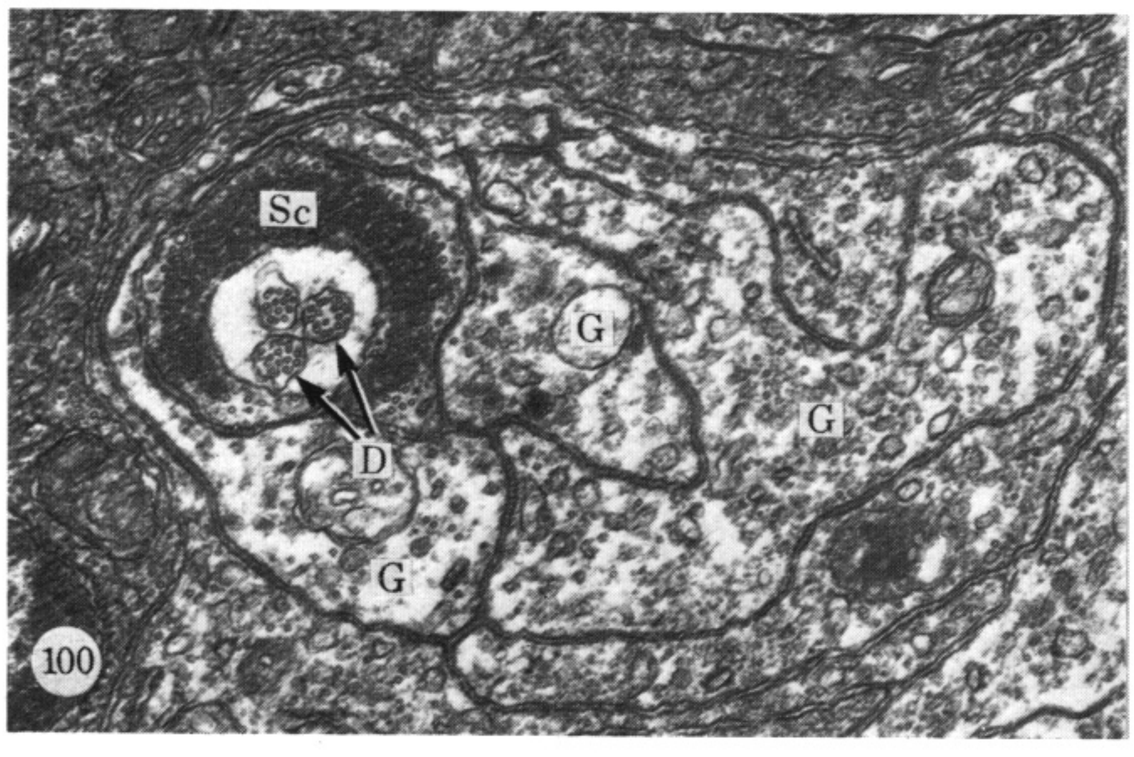


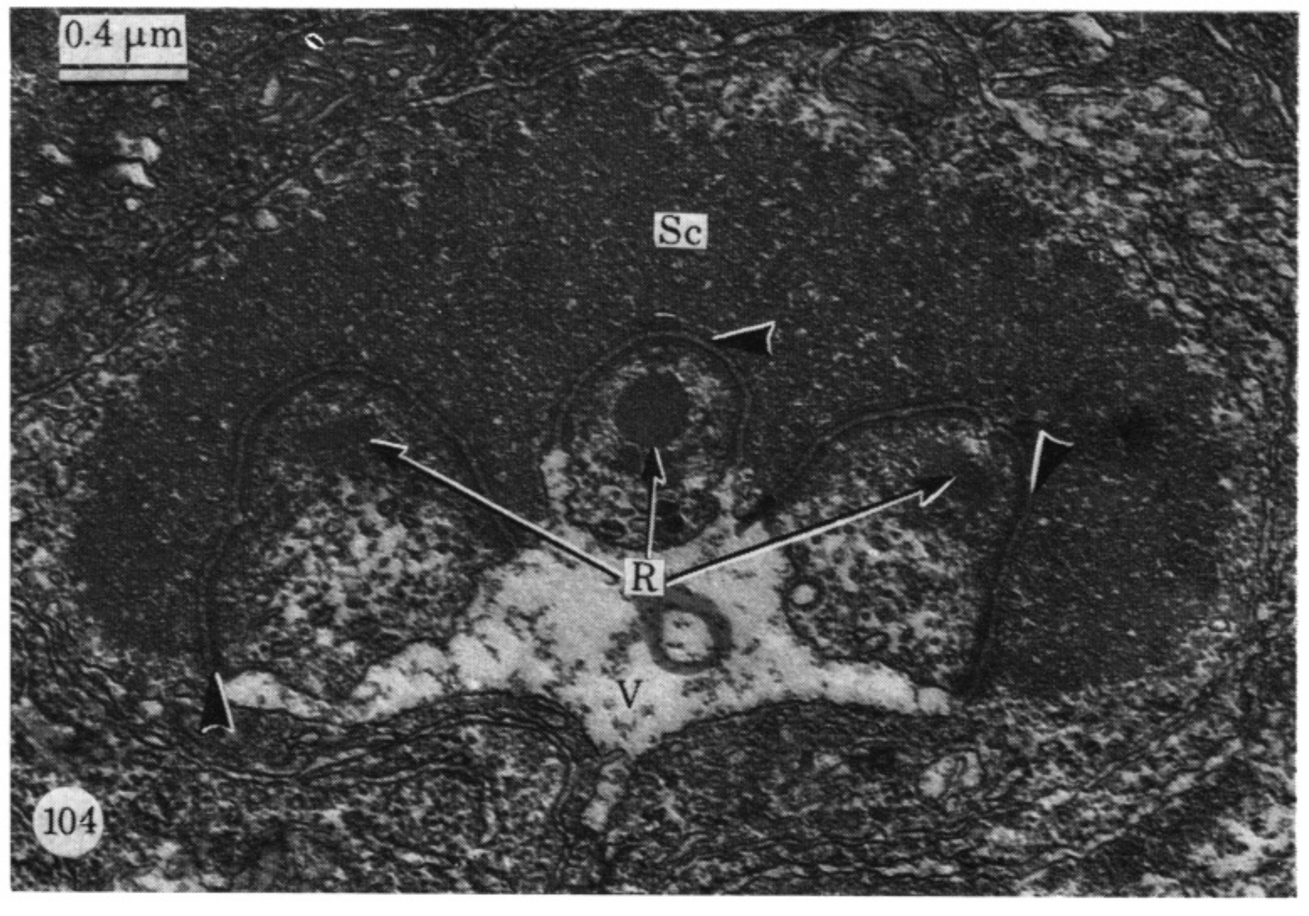












FIGURES 92–104. For description see opposite.