THE FINE STRUCTURE OF THE INSECT EAR

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CONTENTS

A brief account is given of observations of the fine structure of the insect ear by light microscopy. The observations generally confirm those of previous workers. The electron microscope has revealed many new structures in the ganglion. Problems of the structure of the neuron and its sensory hair, the scolopale, and the relationships of the membranes of the neuron and the various accessory cells, all so little understood by light microscopy, can now be resolved.

The locust has a pair of ear drums, situated one on each side of the first abdominal segment. The auditory ganglion is attached to the inner surface of the drum and it contains about seventy bipolar sensory neurons. A sensory neuron, wrapped in a series of three satellite cells, together with an attachment cell, constitutes a *sensory unit* (sensillum). The sensory units lie inside the capsule of the ganglion and they are attached to the hypodermis of special processes of the drum.

The apex of the dendrite of each neuron bears a cilium that contains nine fibrils, orientated longitudinally and concentrically. A *root* (a rod-shaped structure) runs downwards from the base of the cilium within the dendrite, and splits repeatedly into thirty or more *rootlets*. Both root and rootlets have a cross-striation of pale and dark bands of different widths. The result is a periodicity which is polarized or asymmetrical. The upper part of the root terminates in nine concentric projections. It is these processes that actually touch the base of the cilium. They enclose a structure termed a *root apparatus*.

The distal part of the dendrite and the cilium project into a scolopale, the body of the cilium being contained in a wide extracellular compartment within the scolopale. The upper region of the cilium has a dilatation containing fibrous structures that are not present in the other parts of the cilium. The tip of the cilium projects into a channel in the scolopale cap. The cap, unlike the other components of the scolopale, is an extracellular structure.

By light microscopy the scolopale appears as a tubular structure with a narrow entrance and is sealed at the other end by the cap. Electron microscopy shows that the wall of the scolopale is composed of six or more concentric rods of fibrous material. At the entrance the rods lie close together around the dendrite. Near the cap the rods are also close together and become fused into a tube, into which the cap fits like a lid. In the central region the scolopale rods lie farther apart. The rods are intracellular structures of the scolopale cell (see below). In this central region only a thin layer of scolopale cell cytoplasm and membrane surrounds each rod so that the extracellular compartment around the cilium extends outwards between the columns of cytoplasm containing the scolopale rods.

There are three satellite cells. (*a*) The *Schwann cell*, whose processes encapsulate the cell body and axon of the bipolar neuron. (*b*) The *fibrous sheath-cell*, so-called because it contains fine fibrous material; it is wrapped round the basal region of the dendrite. (*c*) The *scolopale cell*, which is wrapped round the upper region of the dendrite, round the extracellular compartment containing the cilium, and contains the scolopale rods in the inner region of its cytoplasm. Finally, the scolopale cell is linked to the hypodermis of the drum by the *attachment cell*.

The auditory nerve carries the axons of the bipolar cells from the ganglion to the central nervous system. Each of these axons has a separate sheath composed of interlocking folds of a Schwann cell. A second group of afferent axons, probably originating from hair receptors of the drum, are also found in the auditory nerve. They do not have individual sheaths, but run in bundles within folds of the Schwann cell.

1. Introduction

Sensory units (sensilla), consisting of bipolar neurons, each with its dendrite projecting into a tubular structure called a scolopale and having various accessory cells, occur commonly in insects. In relatively few species, however, are these units aggregated and attached to a tympanic membrane to form an ear (see Pumphrey 1940). As long ago as 1826 Müller described the structure of a tympanic organ of an acridiid and since then there have been several important and detailed studies of the insect ear made by light microscopy (e.g. Schwabe 1906; Vogel 1923; Eggers 1928; Hers 1938). These papers are now unfortunately relatively inaccessible, so in addition to the electron-microscope study, a brief light-microscope account with related photomicrographs has been included; all past workers appear to have relied on line drawings for illustrations.

Various physiological studies have been made on the insect ear, but little is known about the actual transducer mechanism involved. Electron microscopy will, no doubt, play an important role in the ultimate solution of this problem. Most attention has been given to the study of the electrical changes generated in response to sound stimuli, by recording from the auditory nerve. This and other features of the acoustic physiology of insects have been adequately reviewed by Pumphrey (1940, 1950), who has pointed out that the insect ear is a displacement receptor in contrast to the mammalian organ, which is a pressure receptor. It is probably not capable of frequency discrimination, for insects appear to rely on amplitude modulation for the transmission of information (see also, Wever & Bray 1933; Pumphrey & Rawdon-Smith 1936*a*, *b*, 1939; Haskell 1956*a*, *b*; Roeder & Treat 1957).

The light-microscope observations reported here for the most part confirm the studies of previous workers. The electron microscope has revealed surprisingly complicated structures in the sensory unit, which could not possibly have been visualized with the limited resolution of the light microscope. The dendrite of each neuron is now seen to have at its tip a cilium,* containing longitudinally oriented fibrils (Gray & Pumphrey 1958). The base

* The term cilium is used throughout this paper although the fine structure of this process differs in certain respects from that of motile cilia (see § 9, p. 88).

of the cilium is connected to an extensive rooting system, whose branches have a marked cross-striation of dense and pale bands and reach far down within the dendrite cytoplasm. The cilium and the distal portion of the dendrite to which it is attached, are inserted into a scolopale. This is now seen to be a tube, whose walls are formed by six or more concentrically arranged intracellular rods of fibrous material. The tip of the cilium lies within a canal in the scolopale cap, an extracellular structure which closes off the distal end of the scolopale. More types of satellite cells can be recognized than was possible with the light microscope and the method of attachment of the sensory unit to the drum becomes clear. Finally, two distinct groups of axons can be distinguished in the auditory nerve, which are in some ways comparable to myelinated and unmyelinated axons of vertebrates.

2. Material and methods

Investigations were confined to the adult female locust (*Locusta migratoria migratorioides*) supplied by the Anti-Locust Research Centre, London. The tympanic membrane is situated on the first abdominal segment (see below), and the auditory ganglion (Müller's organ) is attached to its inner surface. A locust was decapitated, the abdomen bisected longitudinally and the air sacs round the inner surfaces of the drums opened to expose the ganglia.

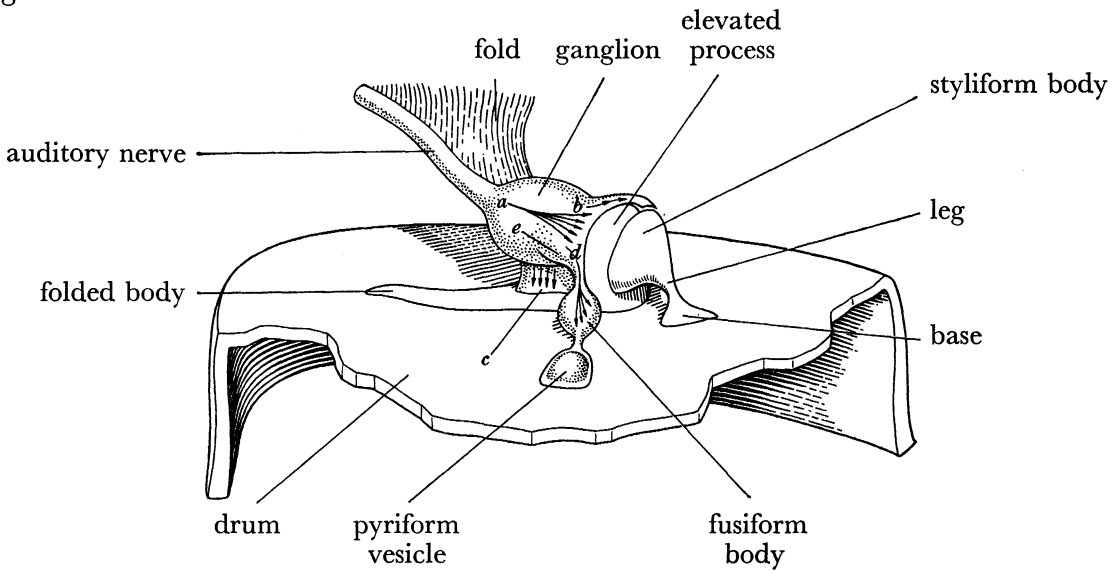


Figure 1. A diagram to show the method of attachment of the auditory ganglion to the inner surface of the ear-drum of the locust.

Light microscopy

Ganglia were fixed *in situ* with Bouin's fluid, immersed in fresh fixative for 24 h, embedded in carbowax, sectioned serially in different planes at 8 to 10 μ and stained in haematoxylin and eosin (see Gray, 1958 for carbowax method on small objects). Also ganglia were examined with phase-contrast microscopy after gentle teasing and mounting in mammalian Ringer.

Electron microscopy

The delicate air-sac epithelium, which forms the wall of the ganglion, was removed from its surface with fine needles and ice-cold fixative was dripped on to the ganglion. It was

either 1 % OsO_4 or 0·6 % $KMnO_4$ (Luft 1956) in mammalian Ringer, buffered at pH 7·4 with veronal acetate. The drum with the attached ganglion was then removed and placed in fresh fixative for 4 h.

The fixed material was washed in distilled water and dehydrated in ethanol. The osmic-fixed ganglia were then 'stained' for 3 h with 1 % phosphotungstic acid in absolute ethanol. The materials were embedded in Araldite (Glauert & Glauert 1958). Sections were viewed with a Siemens Elmiskop 1 *b* electron microscope.

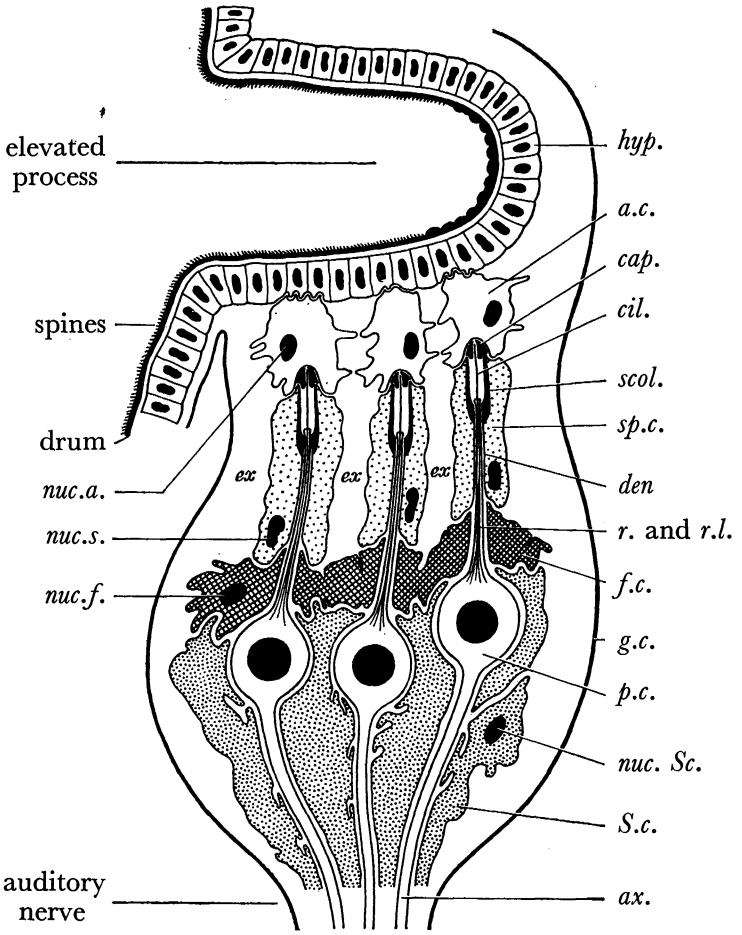


FIGURE 2. A diagrammatic section through the auditory ganglion to show the arrangement and method of attachment of three sensory units (sensilla). Each sensory unit contains a neuron and satellite cells. The ganglion contains 60 to 80 units. For key to abbreviations see p. 94.

3. THE SENSORY UNIT (SENSILLUM)

In this section, a general account of the sensory unit as seen by light and electron microscopy is given.

The bipolar neurons have large round nuclei (figure 2, and figure 10, plate 5) and their perikarya are enclosed in numerous folds of *Schwann cells*, which also enclose the axons running centrally from the bases of the perikarya. Each Schwann cell folds round several cell bodies and their axons. Only the nuclei of these Schwann cells are distinguishable in the light micrograph (figure 10).

The dendrites are from 80 to 100 μ long. The dendrite base is enclosed, together with those of neighbouring dendrites, in a satellite cell referred to as the *fibrous sheath-cell*. The nucleus of the latter is oval and smaller than the neuron nuclei.

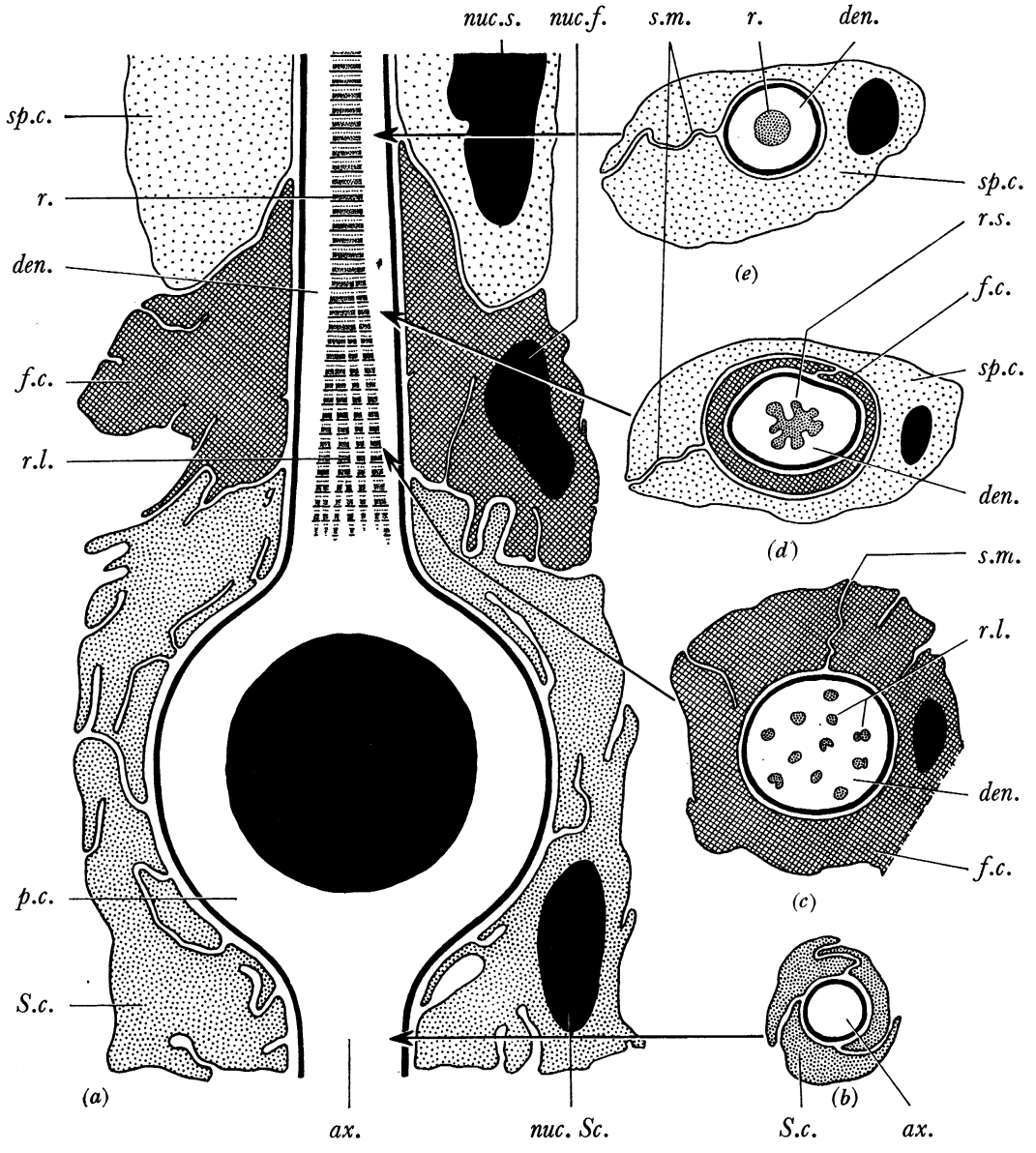


FIGURE 3. Diagrammatic longitudinal section through the basal region of a sensory unit (left). Transverse sections at various levels are shown on the right. Various cytoplasmic inclusions, for example, mitochondria, endoplasmic reticulum and dendrite tubules have been omitted. The upper region of the unit is shown in figure 4. For key to abbreviations see p. 94.

The remaining distal region of the dendrite is enclosed in still another type of satellite cell—the *scolopale cell*. The nuclei of these cells lie in the proximal region of the cytoplasm, are irregular in outline, and are the smallest of the types of nuclei in the ganglion.

The scolopale (figures 2, 10 and inset figure 10), except for its cap, lies in the cytoplasm of the scolopale cell. By light microscopy the scolopale appears as a tube, narrower

proximally than distally. Electron microscopy (§7) shows that the wall is, in fact, composed of several concentric rods. The distal region of the dendrite with a cilium at its tip, is inserted into an extracellular cavity within the scolopale cell, which are both tubular.

The tips of the scolopale cells are in contact with the *attachment cells*. The nuclei of these resemble those of the fibrous sheath-cells in shape and size. The attachment cells are in 'contact' with each other by finger-like processes and with the hypodermal layer of the drum by folds.

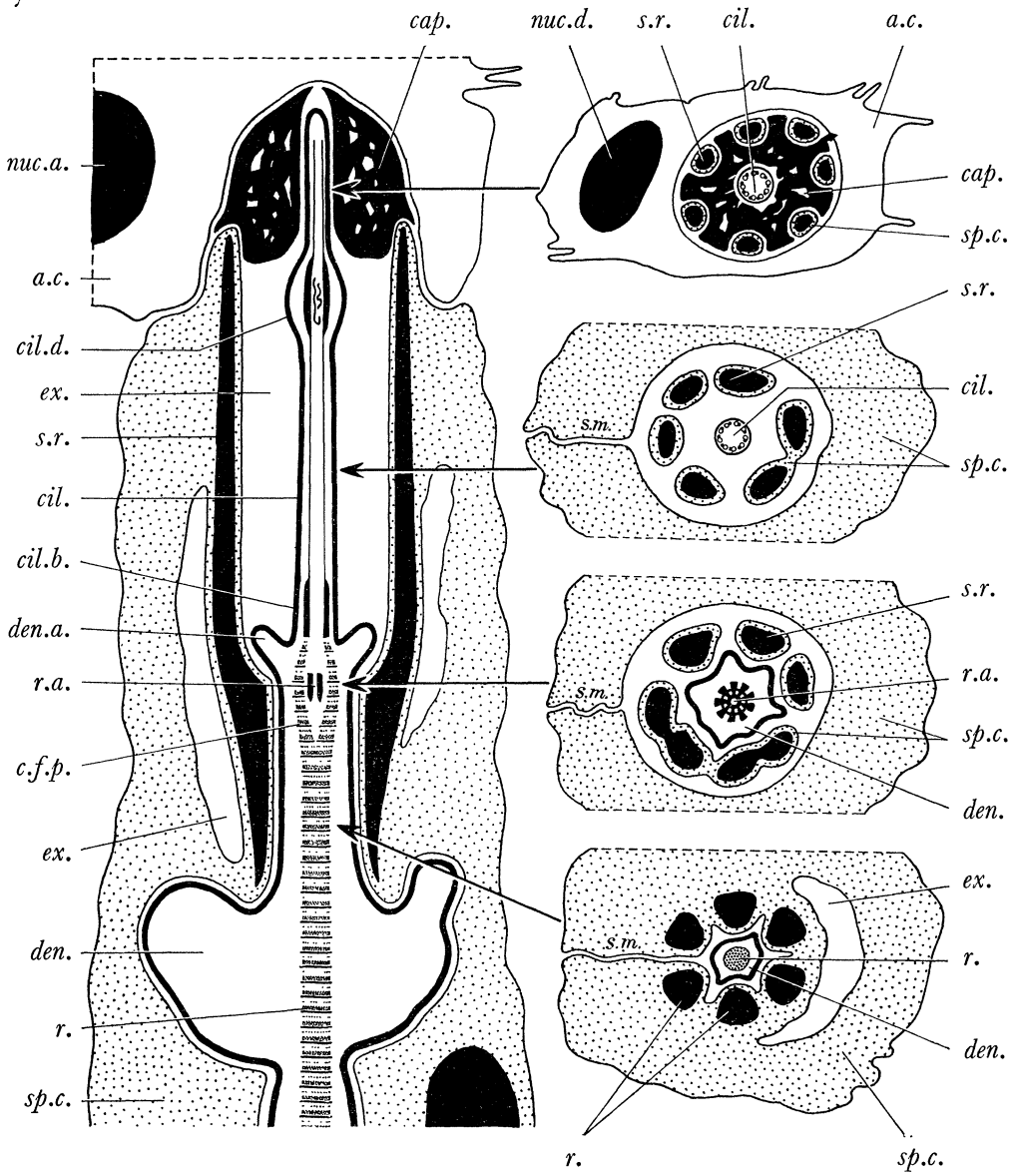


FIGURE 4. The upper region of the sensory unit (see figure 3). For key to abbreviations see p. 94.

A high-power light micrograph of the scolopale is shown in figure 10 (inset). The vacuole at its entrance is regarded as an artifact (see § 7). The axial fibre within the dendrite is shown by electron microscopy to be the root of the cilium situated at the apex of the dendrite. The root splits into rootlets in the basal region of the dendrite. The cilium is just discernible by light microscopy in the upper region of the scolopale. Electron microscopy shows that its tip lies within a channel in the scolopale cap (figure 5*a*).

4. General structure of the ear and method of attachment of the ganglion to the drum

The external appearance of the right ear, situated on the first abdominal segment, is shown in figure 7, plate 4. It is covered by the wings except during flight. The drum is pear-shaped, about 2·5 mm long and 1·5 mm at its widest. It lies in a recess, partly

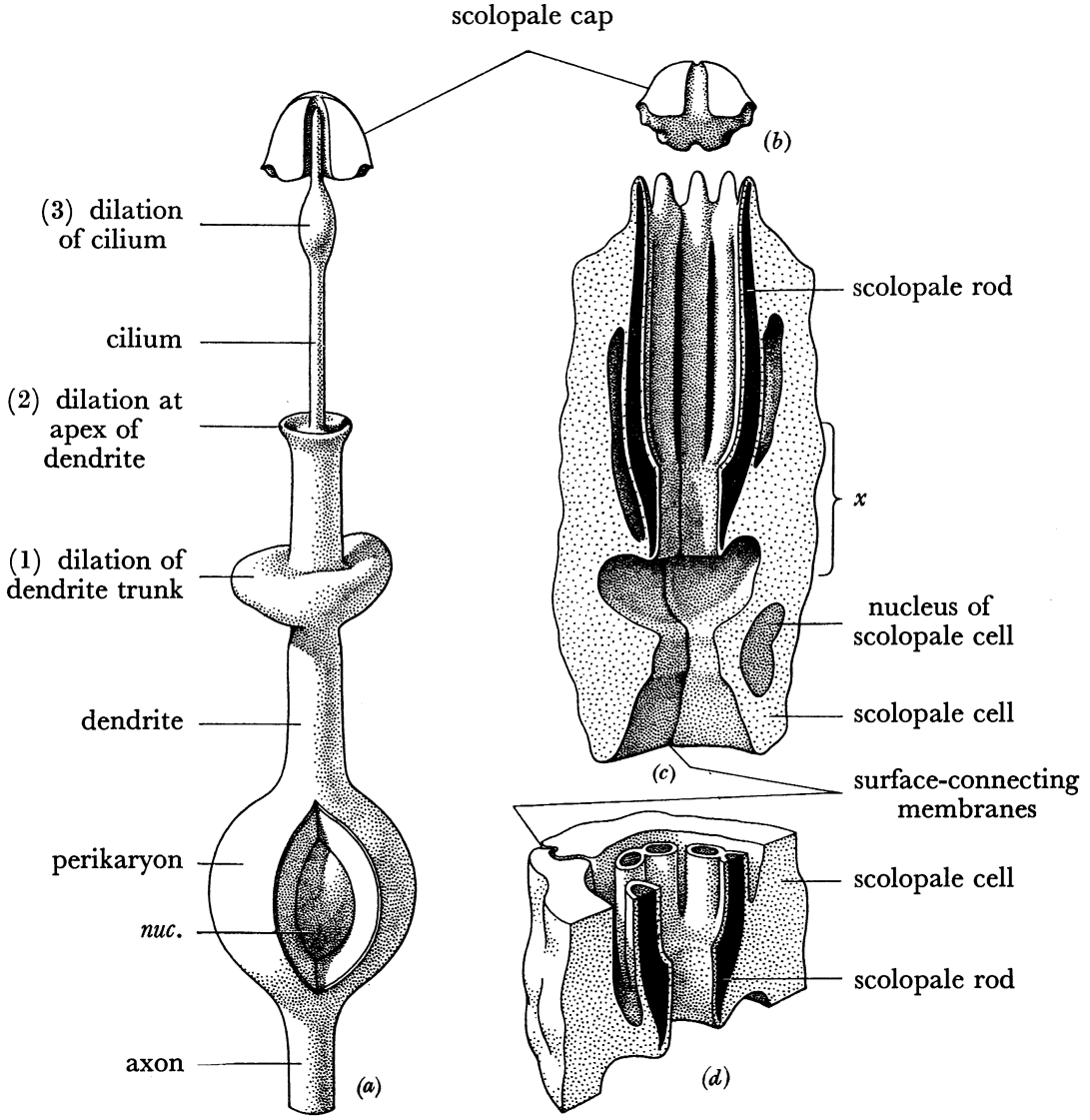


Figure 5. (*a*) Cell body and dendrite of the sensory neuron with satellite cells removed. (*b*) The scolopale cap—an extracellular structure. (*c*) The scolopale cell sectioned longitudinally. (*d*) A portion of the scolopale cell section shown in (*c*)—region *x*.

surrounded by a thickened exoskeletal rim forming a sort of external auditory meatus (Pumphrey & Rawdon-Smith 1936*b*). A flap, reminiscent of the human tragus, projects backwards and completes the wall of the recess. A spiracle leading into the air sac situated internal to the drum, lies anteriorly beneath the flap. The spiracle is perhaps analogous to the mammalian Eustachian tube (see Pumphrey 1940).

The ganglion, attached to the inner surface of the drum, is shown in figure 1 and figure 6, plate 4. The drum itself is a sheet of exoskeleton for the most part 2 to 3 μ thick, but it increases to four times this thickness where the ganglion is attached. The external surface of the drum is covered by spines (figure 2 and figure 10, plate 5) 1 to 2 μ long. The hypodermal layer of columnar epithelium continues over the inner surface, and the relations are similar to those of the general exoskeleton (see Wigglesworth 1953).

The ganglion (figures 1, 6) is about 250 μ long and 150 μ at its broadest. Its capsule is formed from two layers of cells. The outer is the flattened epithelium of the air sac. This surrounds the ganglion, continues over the inner surface of the drum and also forms the fold containing the auditory nerve. The ultrastructure of this epithelium appears similar to that of tracheal walls in general (see Locke 1957) and will not be considered further. The inner layer of cells immediately surrounds the mass of sensory units, and a basement membrane 0·1 μ thick separates the two layers.

The sensory units of the ganglion are attached in four groups to four specialized regions of the drum (terminology of Albrecht 1953). The first is the *elevated process* (figures 1, 6 and 10). This is an invagination about 100 μ deep. Its wall is much thicker than that of the rest of the drum and it has a number of non-spinous convex projections in its deepest region.

The second region of attachment is the *folded body*, a thickened region of the drum, extending for about 100 μ from the base of the elevated process.

The third is the *styliform body*. It has a flattened concave surface, curved around and applied to the elevated process. Like the elevated process, it stands perpendicular to the drum surface and is supported by a narrow leg continuous with a base, which is a thickened region of the drum. Figure 10 shows the leg and the concave body in section. The styliform body is separated from the elevated process by hypodermal layers.

The fourth region of attachment is the *pyriform vesicle*. This is a thickening of the drum exoskeleton. It lies about 250 μ from the orifice of the elevated process.

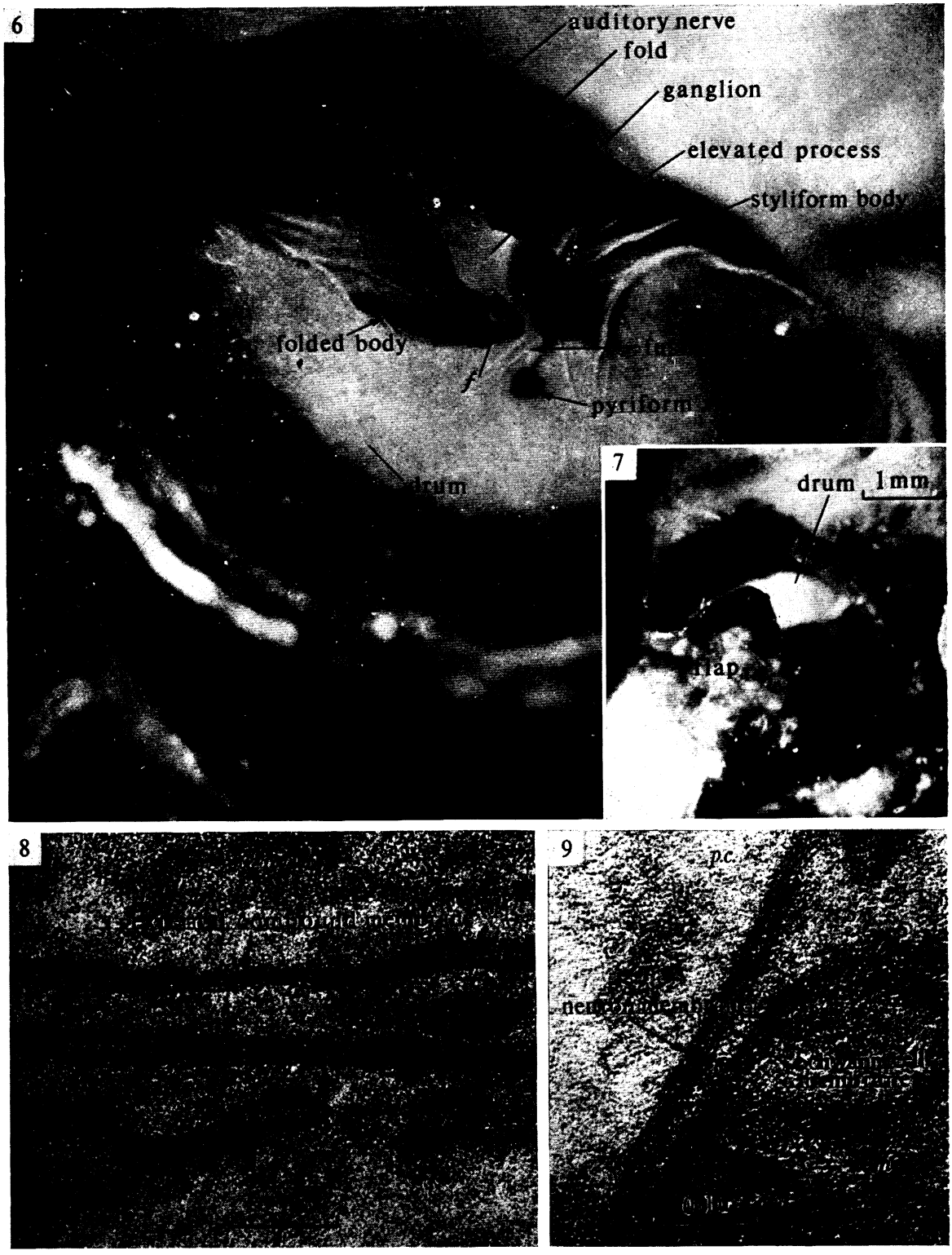
Each of the four attachment processes is simply a modification of the drum exoskeleton and is covered internally by hypodermis. It is to this cellular layer of each process that the sensory units are attached by the so-called attachment cells.

The four groups total from 60 to 80 sensory units. About 35 are attached to the elevated process (arrows *a*, figure 1); about 12 to the styliform body (arrow *b*); about 10 to the folded body (arrows *c*: they are in a projection of the capsule of the ganglion, *f*, figure 6); about 8 are attached to the pyriform vesicle (arrows *d*).

The scolopale and attachment cells of the sensory units connected to the pyriform vesicle form a swelling—the fusiform body (figures 1, 6). The bipolar cell bodies of these units form a swelling (figure 1, *e*) on the middle of the ganglion.

The scolopales of the sensory units of groups (*a*), (*c*) and (*d*) are orientated in three mutually perpendicular planes. The fourth group (*b*), attached to the styliform body, is orientated in the same plane as group (*a*).

A similar total number of units has been reported by Pumphrey & Rawdon-Smith (1936*b*) although they only distinguished three groups. Presumably they included (*a*) and (*c*) in one group.



All material OsO_4 fixed, phosphotungstic acid stained except figures 8, 9 and 14 ($KMnO_4$ fixed).

FIGURE 6. The auditory ganglion attached to the inner surface of the ear-drum of the locust. The air sac has been dissected away. Micrograph of fresh material taken by reflected light.

FIGURE 7. Lateral view of the ear-drum, which is situated on the first abdominal segment.

FIGURE 8. The membranes of Schwann-cell processes that are wrapped round the neuron cell body. The gap is closed (arrow) to form an external compound membrane ($KMnO_4$ fixed).

FIGURE 9. A portion of a Schwann-cell fold apposed to the neuron cell membrane. Details of the membranes are shown clearly after fixation with $KMnO_4$.

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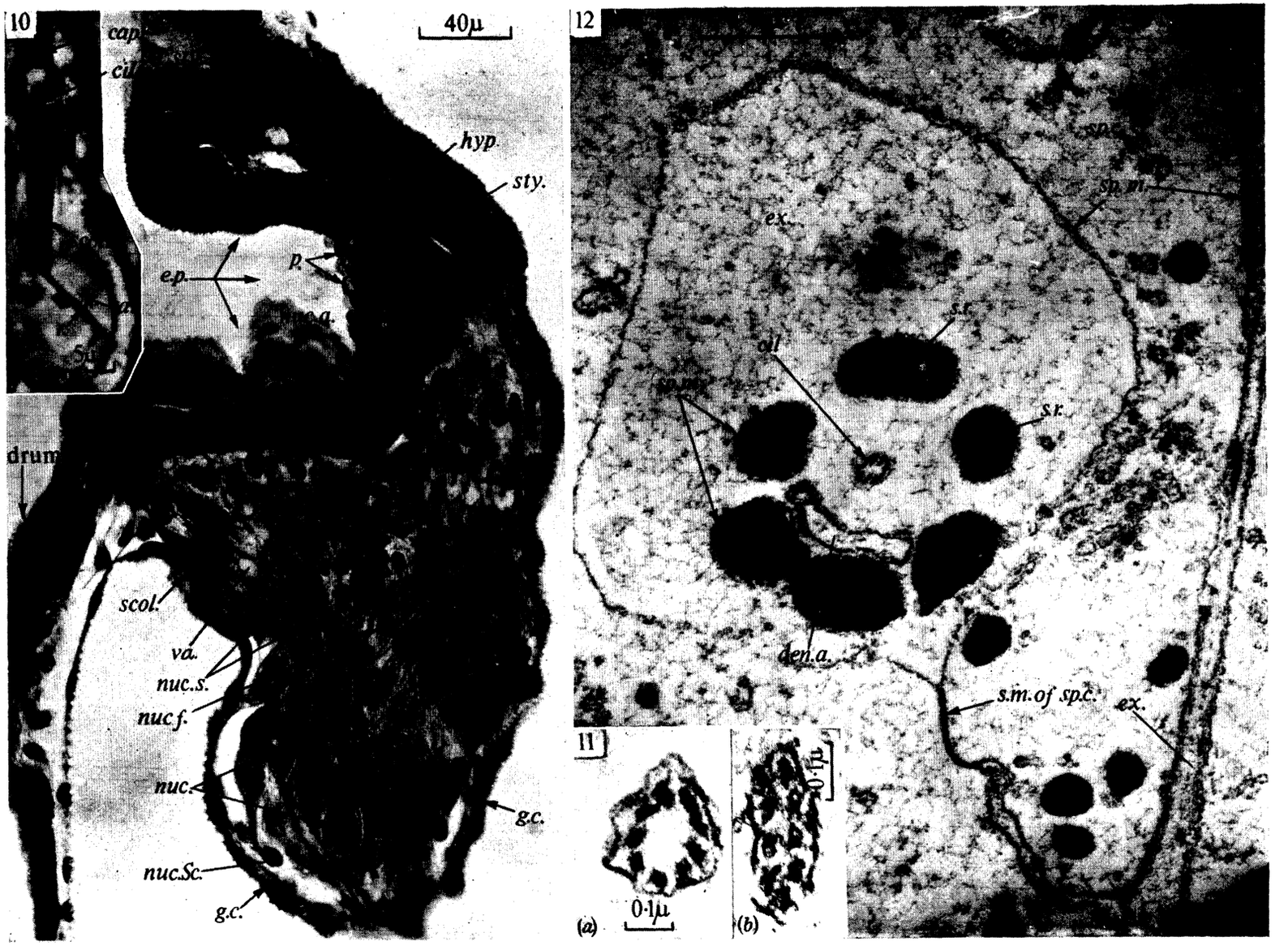

FIGURE 10. Light-micrograph of a cross-section of the auditory ganglion attached to the drum. *Inset* a scolopale (both sections stained with haematoxylin and eosin).

FIGURE 11. Cross-sections of the cilium (see figure 12). (*a*) most commonly observed section, where the nine filaments are presumed to be cut obliquely, (*b*) filaments here presumed to be cut perfectly transversely. The composite structure of each filament can be seen. The flattened profile of the cilium might be an artifact.

FIGURE 12. Transverse section through the lower region of the cilium. Six rods form the scolopale wall in this region.

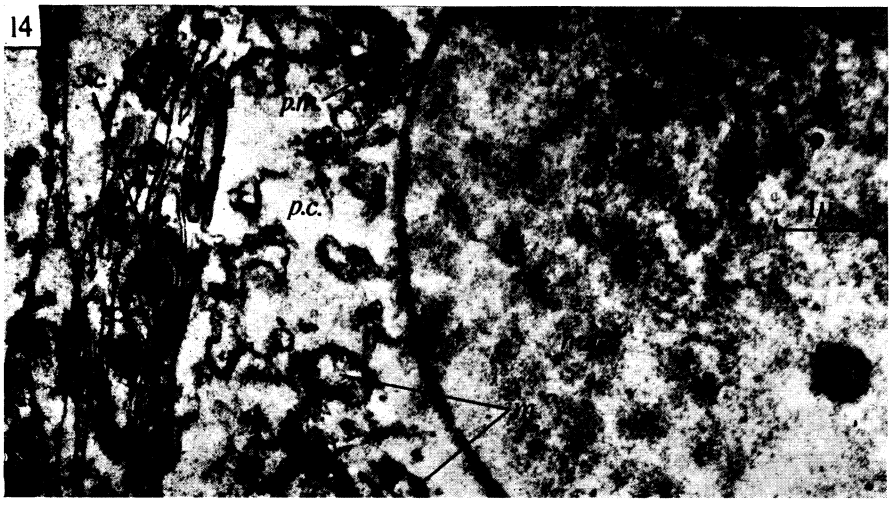

FIGURE 13. The basal region of the dendrite of the sensory neuron. The dendrite is sheathed in the processes of satellite cells.

FIGURE 14. Portion of the cell body of the sensory neuron, showing the capsule formed by folds of the Schwann cell ($KMnO_4$ fixed).

FIGURE 15. Double membrane systems with associated vesicles found frequently in the perikaryal cytoplasm of the neuron together with clusters of small granules.

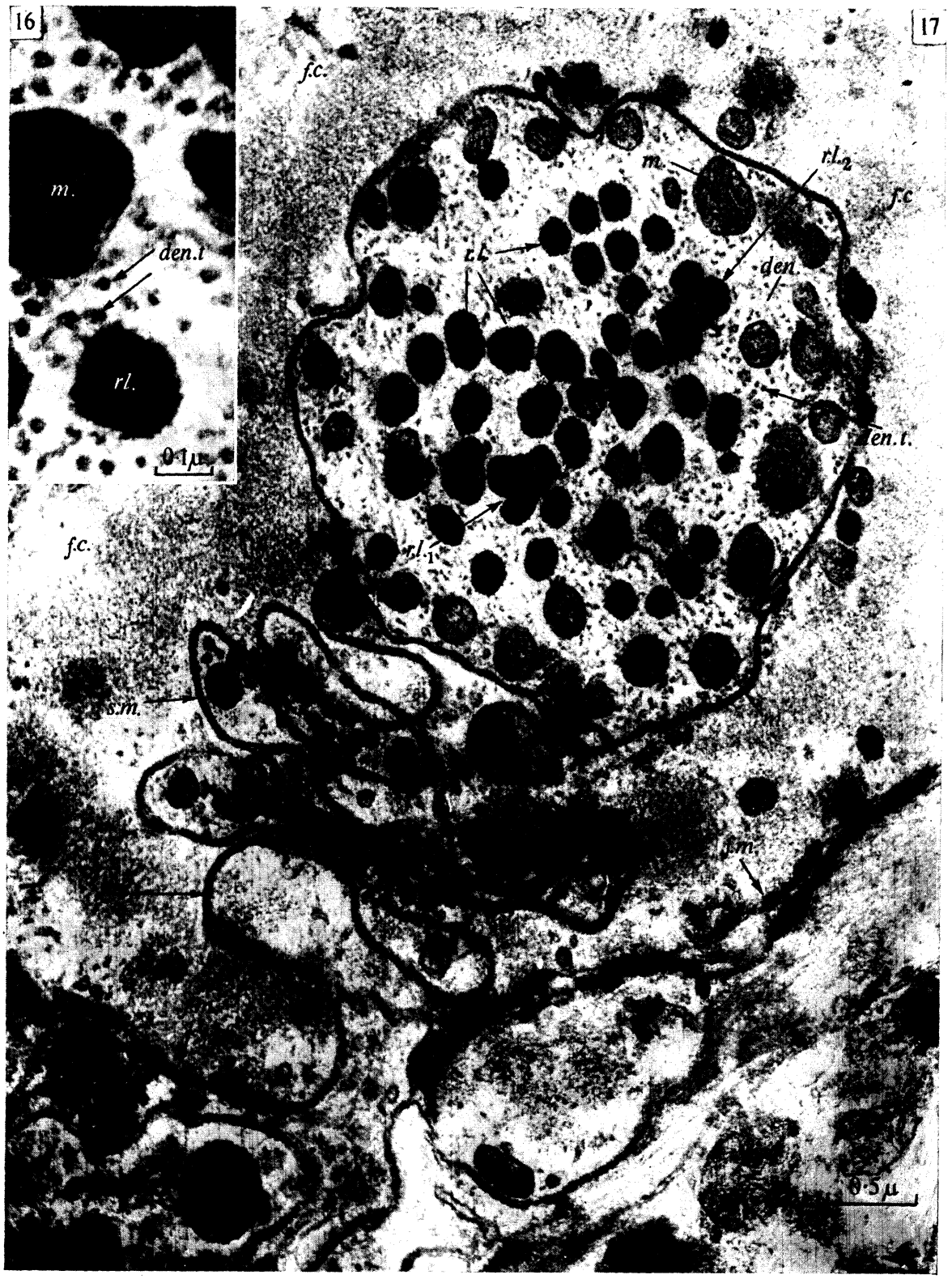

FIGURE 16. Portion of dendrite in transverse section (see figure 17).

FIGURE 17. Transverse section through the dendrite, showing rootlets, mitochondria and tubules. The dendrite is wrapped in the fibrous sheath-cell at this level.

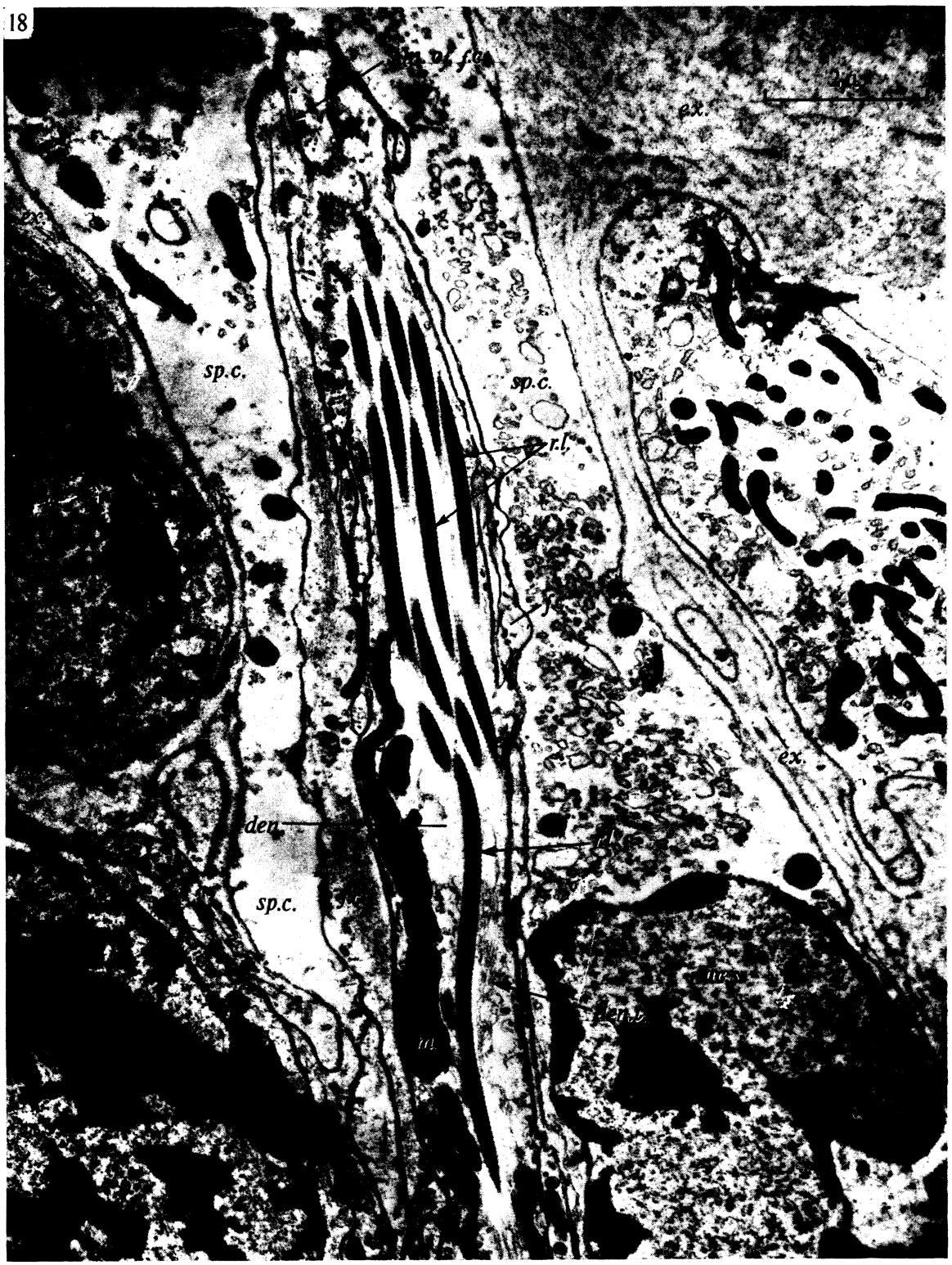

FIGURE 18. Longitudinal section of basal region of dendrite showing rootlets, mitochondria and tubules. The dendrite in this region is encased in the fibrous sheath-cell, around which is the scolopale cell.

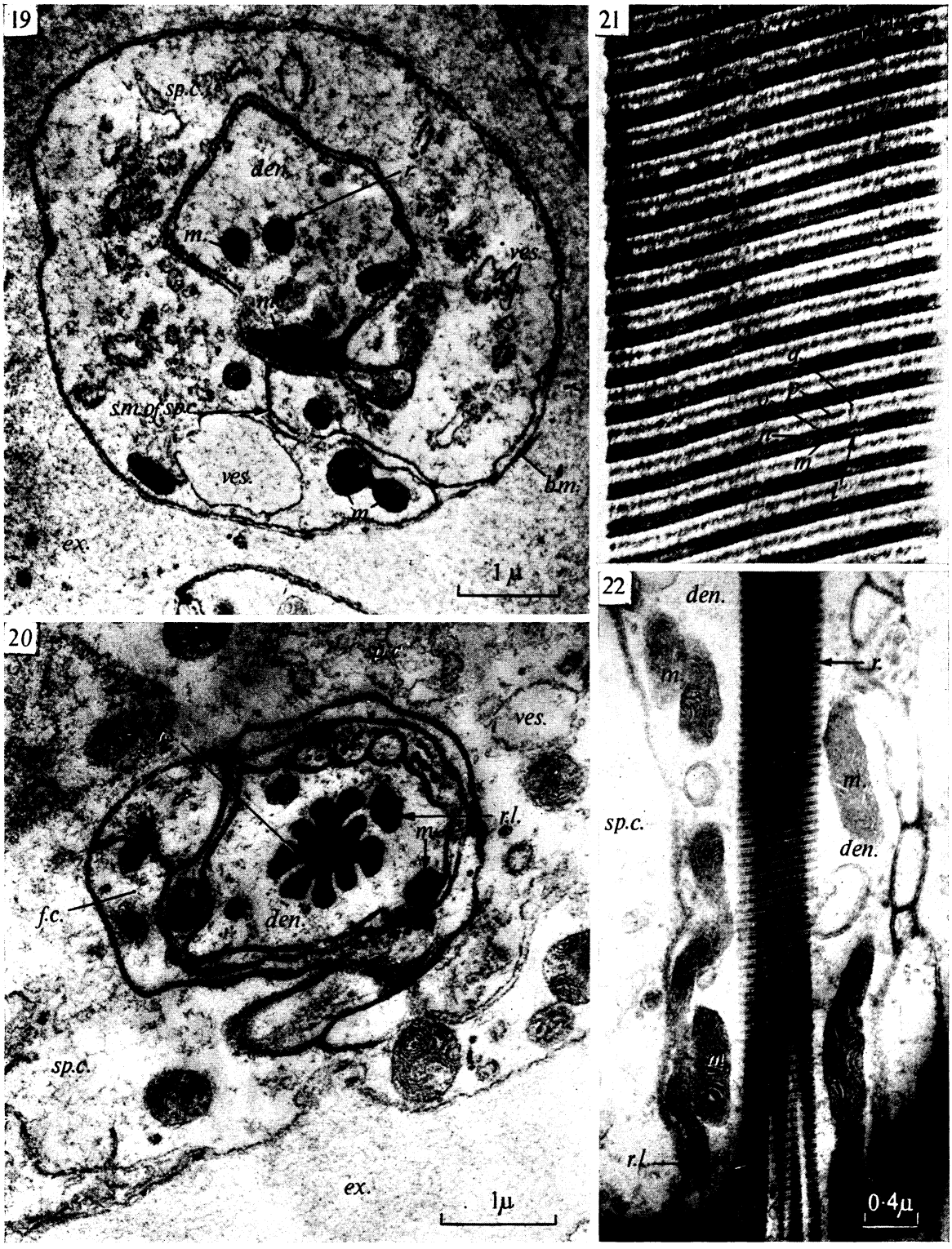

FIGURE 19. Cross-section of the dendrite in the root region. At this level the dendrite is enclosed in the scolopale cell only (see figure 21).

FIGURE 20. Cross-section of dendrite in the region where the root branches into rootlets (see figure 22).

FIGURE 21. Longitudinal section of the root at high magnification (see figure 19).

FIGURE 22. Longitudinal section of the root within the dendrite, where the root divides into rootlets.

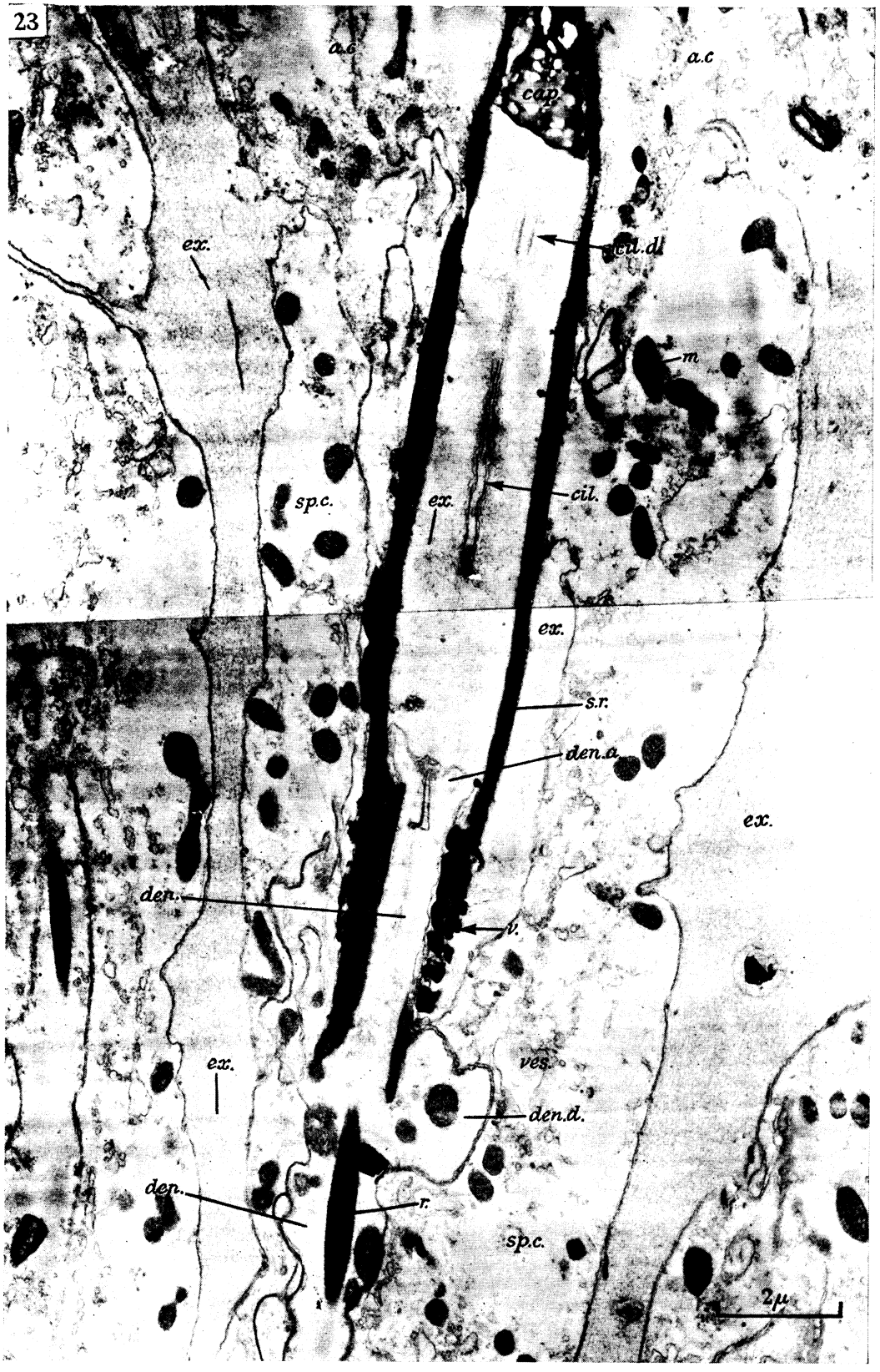

FIGURE 23. Longitudinal section through a scolopale lying within the inner part of the scolopale cell. The attachment cell and scolopale cap are seen above. The apex of the dendrite lies within the lower part of the scolopale. Part of the cilium is seen lying in an extracellular compartment within the scolopale cell. Some of the fibrils of the cilium appear in the section.

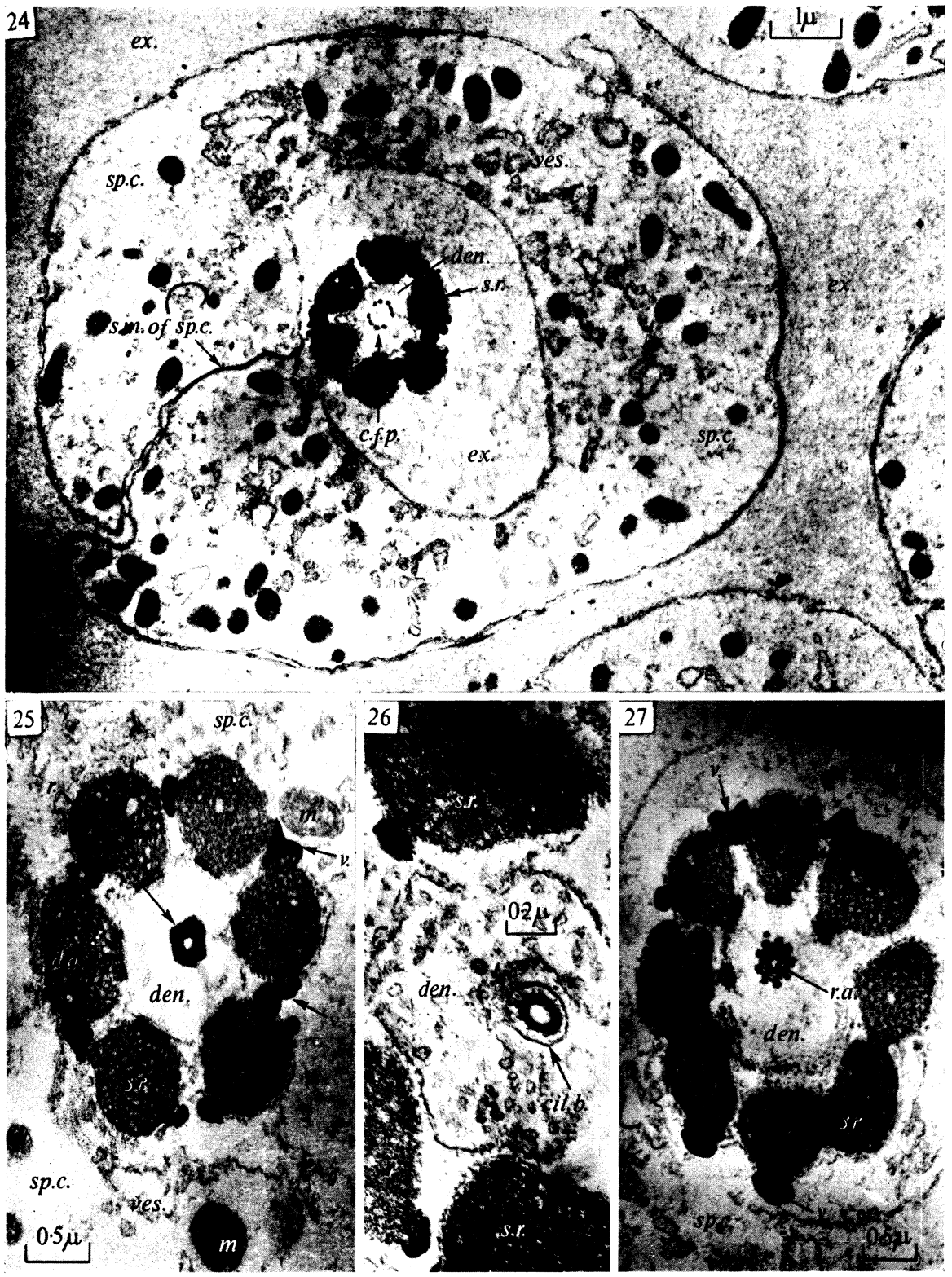

FIGURE 24. Transverse section of the dendrite showing the nine concentric finger processes which project from the apex of the root. The basal regions of the scolopale rods (within the scolopale cell) surround the dendrite.

FIGURE 25. Transverse section through the dendrite in the region where the root becomes hollow. The tubular wall splits into nine finger processes (figure 24).

FIGURE 26. Transverse section through the base of the cilium. It contains a tubular structure (dense ring) from which arise the nine fibrils of the cilium. Part of the apical dilatation of the dendrite, which contains vesicles, is shown in the section.

FIGURE 27. Transverse section through the dendrite at the level of the root apparatus.

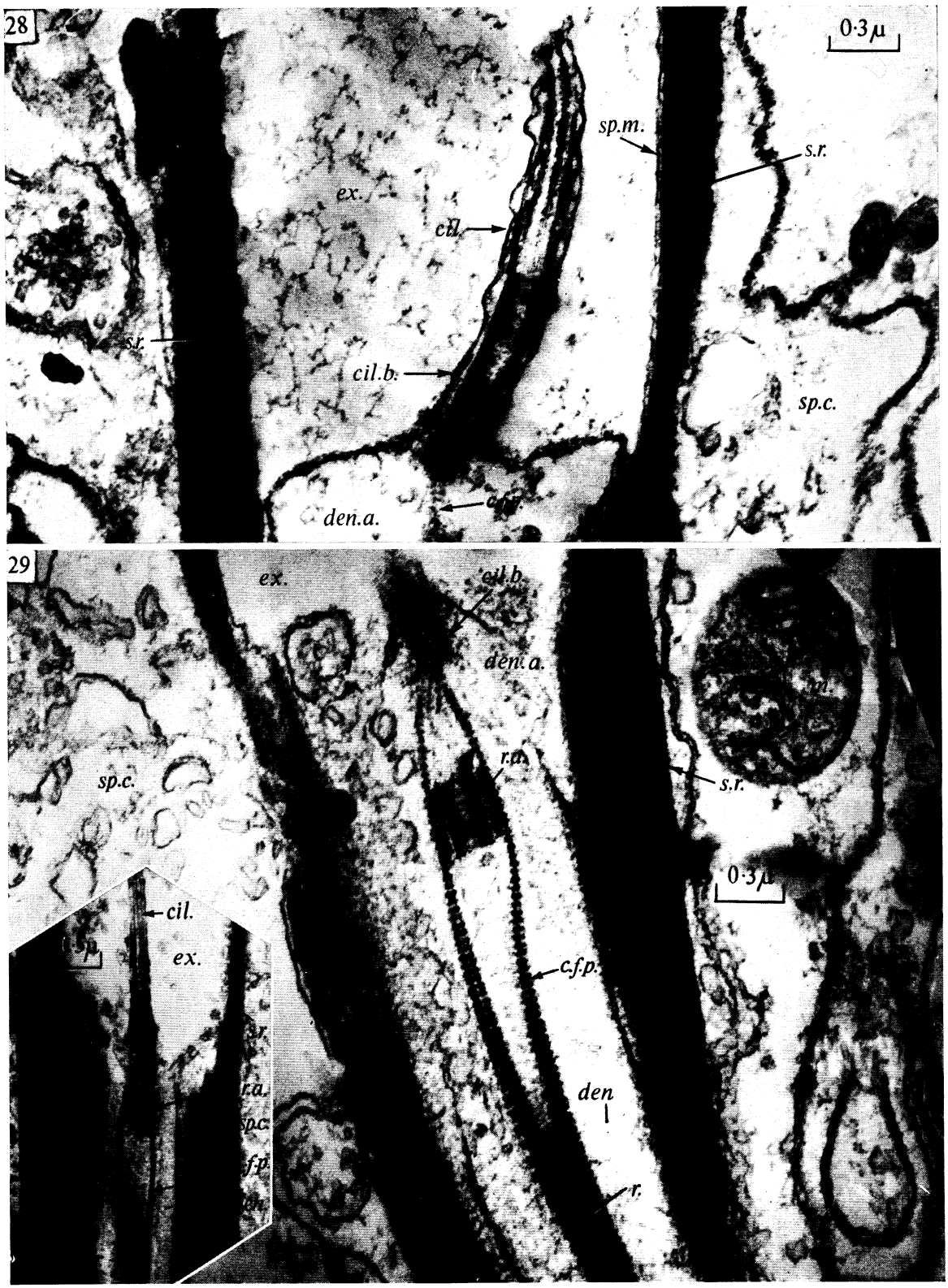

FIGURE 28. Longitudinal section of the apex of the dendrite, showing the base of the cilium arising from it. The cilium lies in an extracellular compartment.

FIGURE 29. Longitudinal section through the apex of the dendrite (the downward continuation of figure 28). The root is seen splitting to enclose the root apparatus. The processes of the root contact the tubular structure in the base of the cilium. *Inset.* A low-power micrograph to show the relationship of root and cilium in the same preparation (see figures 28, 29).

FIGURE 30. The scolopale cap has a central channel. Into it projects the cilium. The dilated region of the cilium is also shown. *Inset.* Section through the cleft between apposed processes of the scolopale cell. It shows a 'honeycomb' structure of extracellular material (see figure 31, inset).

FIGURE 31. Transverse section through the dilatation of the cilium. The cilium lies in an extracellular compartment that is surrounded by the scolopale cell. The scolopale cell contains the scolopale (formed by partly fused rods at this level) and around the scolopale cell in this region is the attachment cell. *Inset.* Cross-striations of extracellular material between apposed processes of the scolopale cell. This is a section perpendicular to that of figure 31 (inset). A thin section through the 'honeycomb' of extracellular material would have this appearance.

FIGURE 32. Longitudinal section through the dilatation of the cilium. The scolopale cap lies above.

FIGURE 33. Transverse section through the scolopale cap. The cilium with its nine fibrils is seen in the central channel.

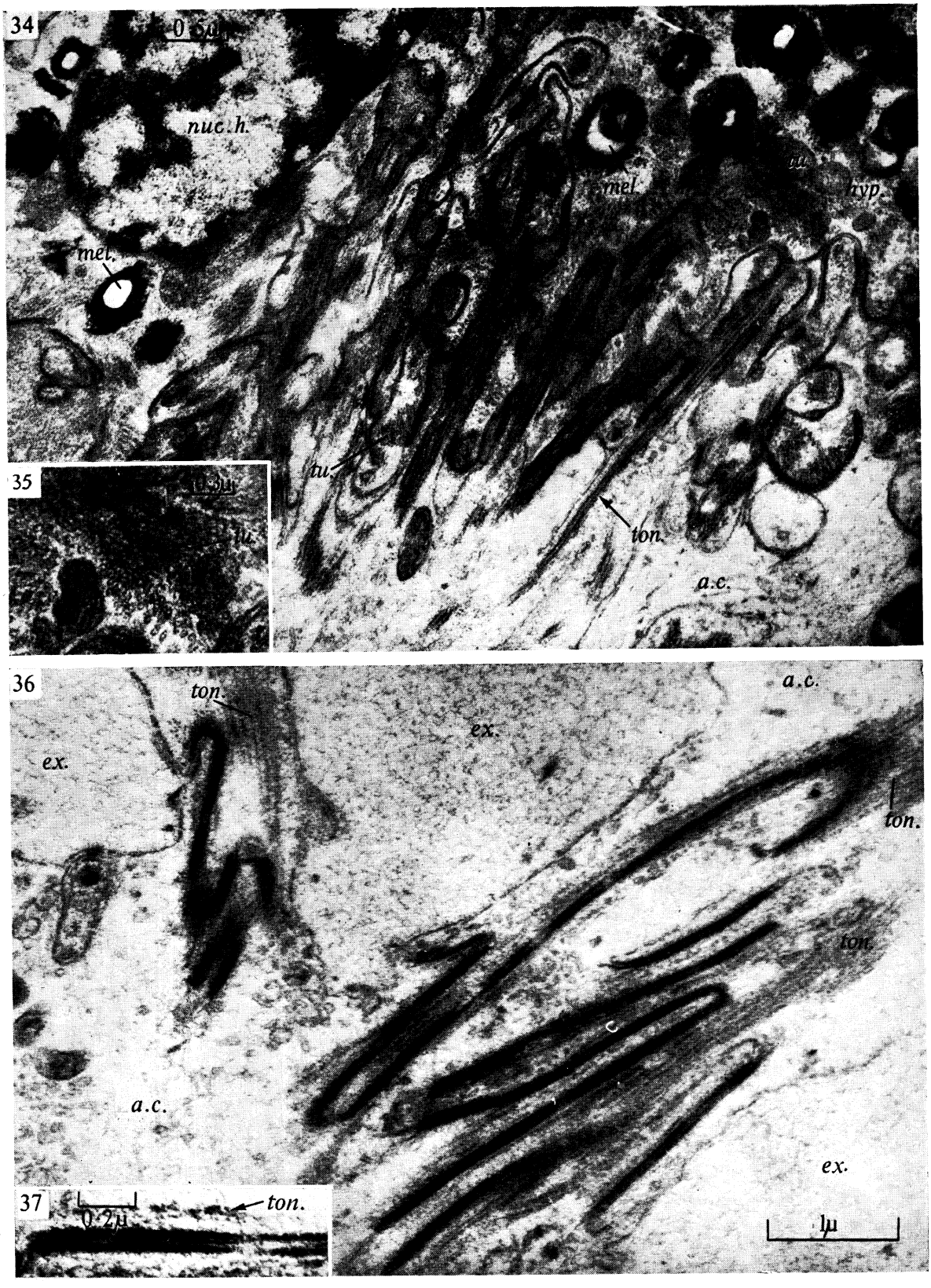

FIGURE 34. Above, a hypodermal cell of the drum with pigment granules, tubules and a nucleus. Below, the attachment cell. The cells are connected to each other by folded, thickened membranes.

FIGURE 35. The tubules of the hypodermal cell (figure 34) seen at higher magnification.

FIGURE 36. Two connecting regions, formed by folded membranes, are seen between two attachment cells. The apposed membranes have thickened regions and tonofibrils (see figure 37).

FIGURE 37. Section of thickened regions of apposed membranes of the attachment cells. A third thinner line of extracellular material appears between the membranes. Tonofibrils lie in the adjacent cytoplasm.

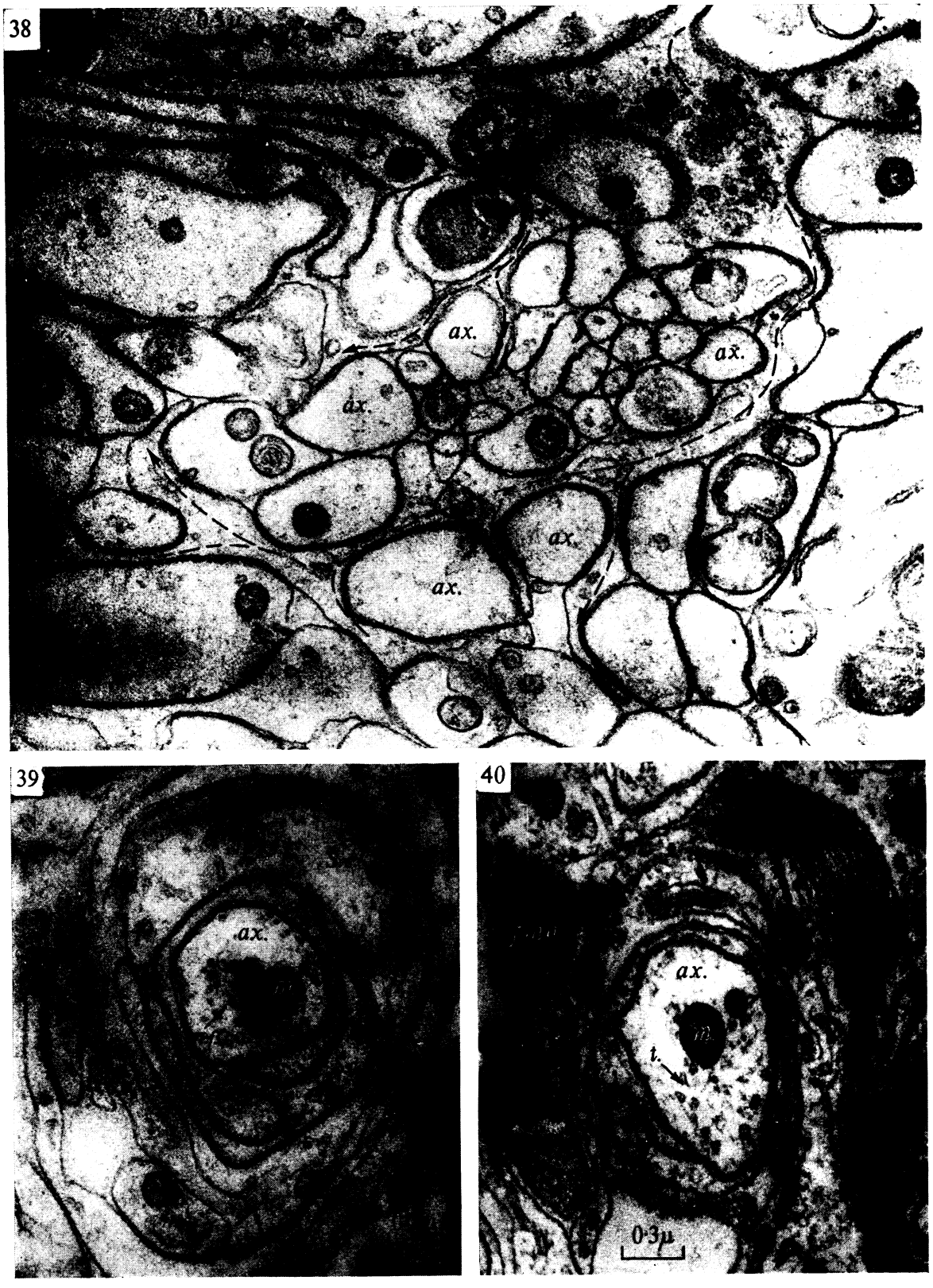

FIGURE 38. Group of extraganglionic axons found in the auditory nerve. The axons lie in bundles that are enclosed in Schwann cell folds (broken lines).

FIGURE 39. An auditory axon. It has its own sheath of Schwann-cell folds.

FIGURE 40. An auditory axon with its sheath of Schwann cell folds. Sheets of extracellular material lie around the outer part of the sheath.

5. The neuron perikaryon

The cytoplasm of the bipolar neuron contains numerous mitochondria (figures 13 and 14, plate 6), which are spherical, elongated or branched. A prominent feature of the cytoplasm is the presence of numerous configurations, each consisting of parallel paired membranes with associated ring profiles (figures 13 and 15, plate 6). Often a group of the latter appears, apparently without this association ($p.m._1$ and $p.m._2$). Probably in such cases the plane of section is through the margin of such a system. There are three or four and sometimes more pairs of parallel membranes in each configuration. They have no granules associated with their cytoplasmic surfaces. These systems are, of course, reminiscent of dictysomes, Golgi bodies or agranular reticulum (see Dalton & Felix 1957; Palay & Palade 1955). The endoplasmic reticulum appears as isolated tubular profiles associated with fine granules (presumably ribonucleoprotein particles). The granules also form rosettes (figure 15) and are distributed in clumps throughout the cytoplasm of the perikaryon (figure 13) (see Palay & Palade 1955).

The perikaryon is surrounded by a capsule of numerous folds of a satellite cell (figures 2, 3 and 14). Since these folds appear to be processes of the same cells that form folds round the axons (§ 8), they are here termed Schwann-cell folds.

The folds continue for a short distance to enclose the base of the dendrite (as far as *g*, figures 3, 13). In this region they are sandwiched in between the lowest processes of the second satellite cell (the fibrous sheath-cell—see below) and the dendrite. The more distal part of the dendrite becomes directly opposed to the fibrous sheath-cell.

Details of the surface membranes of the neuron and Schwann processes

These membranes have also been observed after fixation with $KMnO_4$ and results confirm the observations of Robertson (1958, 1959), who has described the unit membrane configuration present at cell surfaces in vertebrate material, and interpreted it in terms of molecular orientation. In this insect material the surface membrane of the perikaryon (figure 9, plate 4) has the unit structure consisting of two parallel dense lines, each 20 Å thick and a clear intervening layer 35 Å thick. The Schwann membrane has a similar structure. Between these opposed membranes is an extracellular region 100 Å wide.

Three Schwann cell folds, which form part of the neuron capsule (figure 14, plate 6) are shown in figure 8, plate 4. Occasionally the extracellular region between them (100 Å gap) is absent and the unit membranes of the opposed processes appear as three dense lines. Such a relationship has been described in peripheral nerve in vertebrates by Robertson (1958, 1959) and he has termed it an external compound membrane.

In osmium-fixed material the cell boundary is usually observed as a single dense line. According to Robertson (1959), its position corresponds with the inner (cytoplasmic) of the two dense lines of the unit membrane revealed by $KMnO_4$ fixation.

6. The basal region of the dendrite

The basal region of the dendrite is about 2 μ in diameter and is roughly circular in cross-section (figure 17, plate 7). The cilium at the apex of the dendrite (see below) sends down a root within the dendrite and in this basal region it splits repeatedly into rootlets (often into as many as thirty or forty) (figures 3, 4). The rootlets are shown in micrographs

in figure 17 in transverse section and in figure 18, plate 8 in longitudinal section. They bear a marked cross-striation similar to the parent root (see § 7). Since the rootlets subdivide, configurations $r.l._1$ and $r.l._2$ (figure 17) would be expected. Elongated mitochondria occur frequently in this region of the dendrite, together with numerous dendrite tubules (figures 16 to 18) (see Palay 1956; Gray 1959*b*, *c*).

This rootlet region of the dendrite is surrounded by processes of the second satellite cell, the fibrous sheath-cell (figure 2, 3); so-called because its cytoplasm contains fine fibrous material (figures 17, 18; Gray 1959*a*). The processes surrounding the dendrite become opposed (figures 3, 17) to form a surface-connecting membrane, the extracellular cleft about 200 Å across, bounded by the apposed surface membranes of the fibrous sheath-cell (see Robertson 1959). Three or more dendrites may be enclosed in folds of the same fibrous sheath-cell. A large number of deep indentations are characteristic of the surface of this cell (see Gray 1959*a*).

It is of particular interest that the fibrous sheath-cell has numerous extracellular collagen-like fibrils in association with its outer boundaries. Their description and further details of this cell have been given in a separate paper (Gray 1959*a*).

7. The distal region of the dendrite

(*a*) *Dendrite region outside scolopale-bearing region of scolopale cell*

As the distance along the dendrite from the nucleus increases, the rootlets join and finally form a single root (figures 2 to 4). The overall length of the root and rootlets is 80 to 100 μ. In this region the dendrite tubules are absent and mitochondria become less numerous. Figure 22, plate 9 (longitudinal section) and figure 20, plate 9 (cross-section) show the region where the root splits into first-order rootlets. One rootlet has already become separated and the root appears round and solid in cross-section (figures 19, 4). Its cross-striation is seen in figure 22 and at higher magnification in figure 21. It consists of units repeating at approximately 700 Å. A period consists of a thin dense line (*l*) followed by a less dense band (*m*), a dense band (*n*) thicker than (*l*), a pale band (*o*), a dense band (*p*) and a pale band (*q*). Thus the striations are polarized, i.e. asymmetric and the polarization is always in the same direction. The order in the direction from nucleus to dendrite extremity is *l*, *m*, *n*, *o*, *p*, *q*, *l*, *m*, *n*, *o*, *p*, *q*, etc.

Before entering the scolopale region of the scolopale cell, the dendrite narrows and then widens again into a cup-shaped dilation (figure 4; figure 5*a*, (1); figure 23, plate 10). This dilation corresponds in position with, but appears smaller than, the vacuole (§ 3) seen with the light microscope (see Gray & Pumphrey 1958). Possibly the dilation increases in diameter during fixation with Bouin's fluid for light microscopy, resulting in an apparent vacuole.

In this region a third satellite cell, the scolopale cell, surrounds the dendrite (figures 2, 4, 19 and 23). This is so-called because it contains the scolopale (except its cap) intracellularly in its upper region. This upper region will be described in the next section.

The cytoplasm of the scolopale cell has a 'clear' appearance, having few mitochondria and numerous vesicles. The nucleus is situated in its proximal region (figures 2, 18). The surface-connecting membrane running out from the extracellular region around the dendrite (meso, see Robertson 1959) is shown in figure 19. At high magnifications certain

densities along these mesos are seen to consist of bands of material crossing the extracellular gap (figure 24, *s.m.* enlarged in figure 31, inset). Figure 30 (inset) shows a fortunate section presumed to be perpendicular to the previous one, i.e. passing through the extracellular gap and parallel to the surface membranes. The apposed walls of the cell are thus seen to have a honeycomb of hexagonal compartments formed from extracellular material sandwiched between them. This material also occurs in the mesos of the fibrous sheath-cell and between the apposed membranes of the fibrous sheath-cell and scolopale cell. Fernández-Morán (1958) described cross-striations between paired membranes in insect material similar in certain respects to those described here. He observed that the membranes extended from the lumina of tracheae and considered them ultratracheoles, although he was not able to show that they were tubular in nature. The structures described here in the locust are clearly not tubules but extracellular clefts and they are in communication with extracellular material around the sensilla. Tracheoles are absent from the auditory ganglion of the locust (Gray 1959*a*).

An extensive extracellular zone (figures 2, 18, 19 and 23) separates the scolopale cell of one sensory unit from that of another. Unlike the satellite cells mentioned above, where neighbouring dendrites are enclosed in folds originating from the same cell, only one dendrite is enclosed in a scolopale cell.

(*b*) *The part of the dendrite within the scolopale-bearing region of the scolopale cell*

Within the scolopale cell the dendrite narrows again and runs upwards for about 5 μ (figures 4, 5 and 23) and forms a second saucer-shaped dilation at its apex (figure 5*a* (2)), which follows the curvature of the scolopale cell membrane. A cilium projects from the centre of the dilation. The section of figure 23 is slightly oblique, the upper part of the cilium appearing, but not its base. The cilium is considered in detail below.

Within the scolopale cell the root continues upwards in the dendrite cytoplasm. At first it remains solid (figures 4, 29 and inset). Then it becomes hollow (figure 25, plate 11), and finally the tubular wall becomes divided into nine concentric finger processes (figures 4, 24 (cross-section) and 29 (longitudinal section)).

The finger processes surround and are applied to an inner structure, the root apparatus (figures 4, 29 and inset in longitudinal section; figure 27 in cross-section). In figure 27 sections of the nine fingers appear as 'cogs' that form the outermost parts of the 'spokes'. The spokes apparently pass through an outer tube and make contact with an inner denser tube. The fingers continue upwards away from this structure, come together and contact the base of the cilium. In figure 28, plate 12 the cilium base is shown, but because of the plane of section, only a faint shadow (*c.f.p.*) represents one of the contacting fingers. The complete relationship of these structures is shown in figure 29 (inset).

The surface membrane and cytoplasm of the cilium are continuous with those of the dendrite (figure 28). The cilium (apart from the dilated region mentioned below) is about 0·15 to 0·2 μ in diameter. Its basal region contains a tube (figures 4, 28 and 26 in transverse section), extending for about 1·3 μ up the cilium. It is actually the base of this tube that is in contact with the nine finger processes (see previous paragraph). From the upper margin of this tube arise nine concentric fibrils (figures 4, 12 and 11*a*, *b*) and these continue upwards through the cytoplasm of the cilium.

The fibrils are usually sectioned obliquely (figure 11 *a*). Such micrographs are vague and only indicate that each fibril is a compound structure. One fortunate section (figure 11 *b*) assumed to be normal to the axes of the fibrils, shows that each fibril is in fact a double structure, a rod and a tube. The rod lies parallel to and in contact with the tube. The diameter of the rod can be seen to be slightly less than that of the tubular component. Small processes can be seen projecting from the rod. Normally a section of such a cilium appears roughly circular (figure 11 *a*). The flattened profile seen in figure 11 *b* might represent an artifact.

Towards its tip, the cilium dilates (figures 4, 5 *a*, 23 and 30) and here each of the nine fibrils appears flattened (figure 32, longitudinal section, and figure 31 in cross-section, plate 13). In figure 31 dense spots appear in the peripheral region of each flattened filament. Presumably each represents the rod and the flattened processes are sections of expansions of the tube (*x*, figure 32). Also in this region in the centre of the nine fibrils, three densities appear in cross-sections (figure 31). These appear to be sections of a twisted or coiled filament or filaments (figure 32, *y*). Finally, at its apex, the cilium constricts and regains its shape; this terminal region lies in a canal in the scolopale cap (figures 30, 33). Cross sections in this region (figure 33, plate 13) show that only the nine concentric fibrils are present as in the region below the dilation.

(*c*) *The scolopale and its relationship to the dendrite*

With the light microscope the scolopale appears as a tube (§ 3) closed at one end with a cap; it is impossible to tell whether it is part of the dendrite, part of the satellite cell enclosing the dendrite in this region, or an extracellular structure.

With the electron microscope the wall of the scolopale is seen to consist of several distinct rods arranged concentrically around the tip of the dendrite and its cilium. These columns occur intracellularly near the inner border of the scolopale cell, (the most distal of the satellite cells). The scolopale cap, on the other hand, is an extracellular structure.

At its base the scolopale consists of five, six or seven rods (figures 4, 5, 25 and 27) of fibrous material. The surface-connecting membrane of the scolopale cell, leading to the dendrite, has been observed to run between two of the columns. Towards the cap, the scolopale columns often branch either completely into two separate branches or partially, the two branches remaining in contact. Thus more and smaller profiles of columns appear in cross-sections of the upper regions of the scolopale (figure 31). The terminal region of the dendrite is surrounded by the scolopale cell with its columns and the membranes of these two cells, as far as the outer surface of the final cup-shaped dilation of the dendrite, are closely opposed (figures 4, 5 *a* (2) and 23). This is shown in transverse section in figure 25. The dendrite membrane shows thickenings opposite the scolopale rods. These might represent regions of firm attachment between dendrite and scolopale cell. The thin cilium, on the other hand, has an extensive extracellular space surrounding it and limited externally by the inner surface of the scolopale cell (figures 23, 28 and 31). The nature of the material contained in this space is not known.

The extracellular region around the cilium at its dilation is shown in cross-section in figure 31. In the lower region of the cilium the situation becomes more complicated. Here each scolopale rod is contained in only a small amount of cytoplasm of the scolopale cell.

In other words, the scolopale cell itself forms columns of cytoplasm with surface membranes and each column contains a scolopale rod. Thus the extracellular region around the cilium continues outwards between the columns and surrounds them (figures 4, 5, 12 and 23).

Usually, as described above, the wide extracellular compartment around the cilium continues right up to the scolopale cap. On one occasion, however, the upper half of the cilium dilation was observed to be surrounded closely by an inwardly projecting process of the scolopale cell. It is not known how frequently this alternative arrangement occurs.

Between the basal regions of the scolopale rods dense extracellular bodies occur, which usually appear V-shaped in cross-section (*v*, figures 25, 27; figure 23 in longitudinal section).

(*d*) *The scolopale cap and attachment cell*

The scolopale cap (figures 4, 5 and 23) is dome-shaped and fits into a rim of scolopale cell cytoplasm containing the upper parts of the scolopale rods, which are partly fused in this region. The cap contains a central channel housing the terminal region of the cilium and is composed of extremely electron-dense material containing numerous cracks, crevices and clear spaces (figure 33 in transverse section; figure 30 in longitudinal section). These might be fixation artifacts. The scolopale columns inside processes of the scolopale cell fit into cavities in the margin of the cap.

The scolopale cap is extracellular and its upper region is contained in a depression in the attachment cell (figures 2, 4). The membrane of the lower region of the attachment cell is opposed to and overlaps the upper part of the scolopale sheath-cell (figures 4, 23 and 31).

The attachment cells are in contact with one another in certain regions by interdigitating processes crossing the ground substance (figure 2). Two contacting regions are shown in figure 36. The opposed membranes often have several folds and in certain regions they appear dense and thickened and a third less-dense line of extracellular material is situated between them (figure 37, enlarged portion). Groups of tonofibrils lie in the cytoplasm near these dense regions of the membranes. Such thickenings are probably regions of especially firm attachment. They are similar to those described by Odland (1958) and others in mammalian epidermis.

The membranes of the attachment cells are also opposed to the hypodermal cells of the various regions of the drum (figures 2, 34). Here also dense regions with an intervening third line appear, together with tonofibrils. The upper cell (figure 34) is of the hypodermis and contains melanin granules and numerous bundles of fine tubules (enlarged portion figure 35).

Branches of the tracheal system occur occasionally in the ground substance near the hypodermis and attachment cells. However, they are absent from the body of the ganglion. This peculiarity has been discussed in a separate paper (Gray 1959*a*).

8. The auditory nerve

The auditory nerve (figures 1, 6) is a thin branch of the tergal nerve, which connects with the third thoracic ganglion (see Albrecht 1953). It leaves the base of the ganglion and runs in a fold of the air sac (§ 4). In this region it has a diameter of 20 to 25 μ. It has a two-layered sheath similar to that of the ganglion capsule (§ 3).

The auditory nerve contains two distinct groups of fibres; the axons of the auditory bipolar neurons and a second group that are extraganglionic in origin.

(*a*) *Auditory axons*

There are approximately 70 to 80 of these afferent fibres (diameters 0·3 to 1·5 μ) corresponding with the number of neuron cell bodies in the ganglion. The axons (figures 3, 39, 40) contain groups of mitochondria, tubules (200 Å in diameter) and neurofilaments, and are ensheathed in interlocking Schwann-cell folds. Sometimes folds of extracellular fibrous material (figure 40, plate 15) appear between the Schwann-cell processes.

The Schwann processes are usually separated from each other and from the axon by extracellular regions 200 Å or more across. However, at certain points apposed membranes of Schwann folds are in intimate contact so that the extracellular channels are closed at these regions. Similar situations were described in the Schwann-cell processes that encapsulate the neuron perikaryon (see § 5 for details).

(*b*) *The extraganglionic axons*

The fibres of this second group originate largely from a fine nerve that runs through the base of the auditory ganglion and enters the auditory nerve at its origin. These fibres are apparently the afferents of groups of hair and other receptors situated largely on the folded body (figure 1: 'rinnenförmiges Körperschen' of Schwabe 1906; Pumphrey & Rawdon-Smith 1936). These receptors have bipolar cells, but no scolopales.

The axons (figure 38, plate 15) lie together in bundles that are separated by Schwann-cell processes (the broken lines show two such processes). It is not always easy to distinguish between axon and Schwann processes. The more rounded profiles are presumably sections of axons, but this criterion cannot be applied for oblique sections and no doubt Schwann-cell processes occasionally appear round in section. It is therefore difficult to estimate the number and diameters of these axons. There are possibly more than sixty in this group with diameters ranging from 0·1 to 1·0 μ.

9. Discussion

In view of the reputed absence of cilia from insects and indeed from arthropods in general, it was surprising to find at the tip of a dendrite of a sensory cell in the locust ear the structure here described. By electron microscopy the typical motile cilium is now known to contain a column of concentric fibrils, usually connected via a basal body to a rooting system consisting of a banded fibre or fibres (see Fawcett & Porter 1954; Bradfield 1955; Sjöstrand 1956; Fawcett 1958; Roth 1958; Afzelius 1959; Cleland & Rothschild 1959). Since the locust hair has these essential features, it has been referred to as a cilium in this study. However, the hair has certain structural differences from the motile cilium and as yet there is no evidence for motility in any stage of ontogeny.

The typical motile cilium, common to both the animal and plant kingdoms, has a column of nine fibrils arranged concentrically around two axial fibrils. Each of the nine is a double tube (a figure eight in cross-section); each of the axial fibrils is a single tube. Recently Afzelius (1959) has described asymmetry in the doublets of the sperm tail, one tubular component of the fibril having a smaller diameter than the other. Also spurs were

observed projecting from the doublets. The insect hair has the peripheral nine fibrils composed of doublets with spurs. Also one component of the doublet has a smaller diameter, but, however, it appears as a rod, the larger one only appearing tubular. Axial fibrils appear to be absent, except in the dilated region near the cap of the scolopale. Here a coiled or twisted fibril (or fibrils?) is found in an axial position, but its nature is not fully understood at present. It does not resemble the two axial fibrils of motile cilia. Typical motile cilia apparently have no dilation along their lengths.

A variety of sensory hairs of vertebrates has been studied by various workers and several types have been shown to conform to the ciliary ultra-structure. For example, the hairs of the bipolar neurons of the olfactory epithelium have it (de Lorenzo 1957); so has one of the numerous hairs of each sensory cell of the crista and macula—the kinocilium (Wersäll 1956). Even the vertebrate rods and cones have certain ciliary affinities for the connecting stalk between the outer and inner segments contains fibrils, although in this case there are two concentric groups, each of nine fibrils, with no axial ones (see Sjöstrand 1956). Cilia-like structures are apparently absent from the neuro-epithelial cells of the taste buds. De Lorenzo (1958) considered their apical 'hairs' to be light-microscopic artifacts.

Few sensory cells of invertebrates have so far received examination by electron microscopy. The sensory cells of the arthropod compound eyes (see Fernández-Morán 1958) and those of cephalopod molluscs (Wolken 1958) do not appear to be derivatives of cilia. However, retinal cells of the lamellibranch mollusc *Pecten* have recently been reported to have a ciliary structure (Miller 1958). Nine dense loci can be observed in transverse sections, some of which appear double: the axial pair appear to be absent as in the locust.

Basal bodies (corpuscles) are a common feature of motile cilia (see Fawcett & Porter 1954; Bradfield 1955). At a corresponding position in the locust sensory cell, a complicated structure is seen enclosed by nine finger-like processes, which form the terminal region of the root. Here it has been termed simply the root apparatus since its function is entirely unknown: it bears no resemblance to the basal bodies of motile cilia so far described.

A root system is common to many invertebrate and vertebrate motile cilia (Fawcett & Porter 1954; Bradfield 1955; Fawcett 1958; Roth 1958), but with the exception of the rods and cones (Sjöstrand 1956) and the present study in the locust, it appears not to be a feature of other sensory cells with cilia-like processes. In the motile cilia, the root or roots are connected to the basal corpuscle, rather than directly to the base of the cilium as in the locust. The root of the comb-plate cilia of the Ctenophore *Pleurobrachia* shows a special resemblance to that of the locust in that it also divides into many finer rootlets (Bradfield 1955).

In all cases where roots related to cilia (motile or otherwise) have been described, they have been observed to have cross-striations (see Fawcett & Porter 1954; Bradfield 1955) with a periodicity of 500 to 700 Å, differing in different species: in the locust organ it is 650 to 700 Å. High resolution micrographs of the roots of the motile cilia of members of the phyla Annelida, Mollusca and Bryozoa show a polarized macroperiod of five bands in their cross-striations (Fawcett 1958), so the arrangement is quite different from that of the root of the locust.

The functions of these various structures remain obscure and a new series of questions now requires an answer. Movements from the drum are presumably transmitted via the

attachment cell. The scolopale cap is presumably attached rigidly to the rest of the scolopale. The base of the scolopale is in turn closely apposed around the distal part of the dendrite. The body of the cilium, in contrast, projects through an extracellular compartment within the scolopale and is thus not constricted by it. It is clearly important to determine the nature of the material in this compartment. The tip of the cilium, on the other hand, projects into a narrow channel in the scolopale cap. It is not possible to decide which of these various structures move in respect to one another simply by examination of the electron micrographs. Nor has examination of the surface membrane of the dendrite and its cilium revealed any specialization that might elucidate the problem of the transducer mechanism. An apparently structureless extracellular region, 200 to 300 Å wide, is present everywhere around the surface membrane of the dendrite, separating it from the satellite cell. A much wider extracellular compartment lies around the cilium. Extracellular channels (surface connecting membranes or mesos) link these compartments with the extracellular region outside the satellite cells. These various compartments are no doubt important for ionic current flow. Whether the 'honeycomb' of extracellular material situated in the cleft of the meso has any effect on diffusion through these channels is not known.

The role of the ciliary fibrils, root apparatus and root system also remains obscure at present, especially since the chemical composition of these structures is not known. Various suggestions concerning function have been made for these structures where they occur in motile cilia (see J. Gray 1955, 1958; Bradfield 1955; Roth 1958; Afzelius 1959; Cleland & Rothschild 1959), but of course they might not be the same in receptor cells.

Each ganglion contains about 70 of these sensory units and since the units are attached in mutually perpendicular groups to special processes of the drum, it seems likely that they transmit different sorts of information. There is no doubt that amplitude discrimination is possible, but there is no evidence for frequency discrimination. Location of the direction of sound occurs, but how accurate it is and in what respects it involves a differential response of the sensory units is not known with certainty (see Pumphrey 1940). Clearly electrical recordings from single sensory cells or their axons are needed to elucidate this point.

Axons of various invertebrates have been studied with the electron microscope. The Schwann-cell sheath has been described as a single fold in some species, or in others as several interlocking folds similar to that of the locust (see Schmitt & Geren 1954; Edwards, Ruska & de Harven 1957; Hess 1958*a*, *b*). Hama (1959) has described a spiral in the earthworm formed by the Schwann cell and the extracellular gap between adjacent turns was observed to be closed by intimate contact of the membranes. True (compact) myelin has been reported in crustaceans (McAlear, Milburn & Chapman 1958). In this case the extracellular compartments of the spiral are closed as in the earthworm and in addition the cytoplasm is excluded from the process so that the membranes are also in contact along their cytoplasmic surfaces (Geren 1954; Robertson 1959). The nature of the sheath and the location of extracellular pathways to the axon for ionic current flow, are of course of fundamental importance in an understanding of nerve conduction (see Schmitt 1958; Robertson 1959). In the sheath of the auditory axon and perikaryal capsule of the locust ganglion the cytoplasm is retained in the Schwann folds and the extracellular gaps between them are only closed at certain points.

A second group of axons of extraganglionic origin occurs in the auditory nerve. These axons differ from those described above in that they are not enclosed in separate sheaths, but lie about 200 Å apart with their membranes in direct apposition. Hess (1958*a*) found a similar arrangement in cockroach nerve. In vertebrates, unmyelinated fibres of the olfactory nerve and dorsal roots (Gasser 1958) and also those of developing peripheral nerves, are similarly arranged (Peters & Muir 1958; Robertson 1959). However, in vertebrates myelinated and unmyelinated fibres are associated with different Schwann cells, whereas in insects the Schwann folds of both types of axon are derived from the same cell (see Hess 1956).

The auditory nerve probably contains only these two groups of axons, both being afferent. The surfaces of the cell bodies and dendrites of the ganglion cells have been carefully studied, and there is no evidence for efferent endings comparable with those of hair cells of vertebrate ears (Rasmussen 1946).

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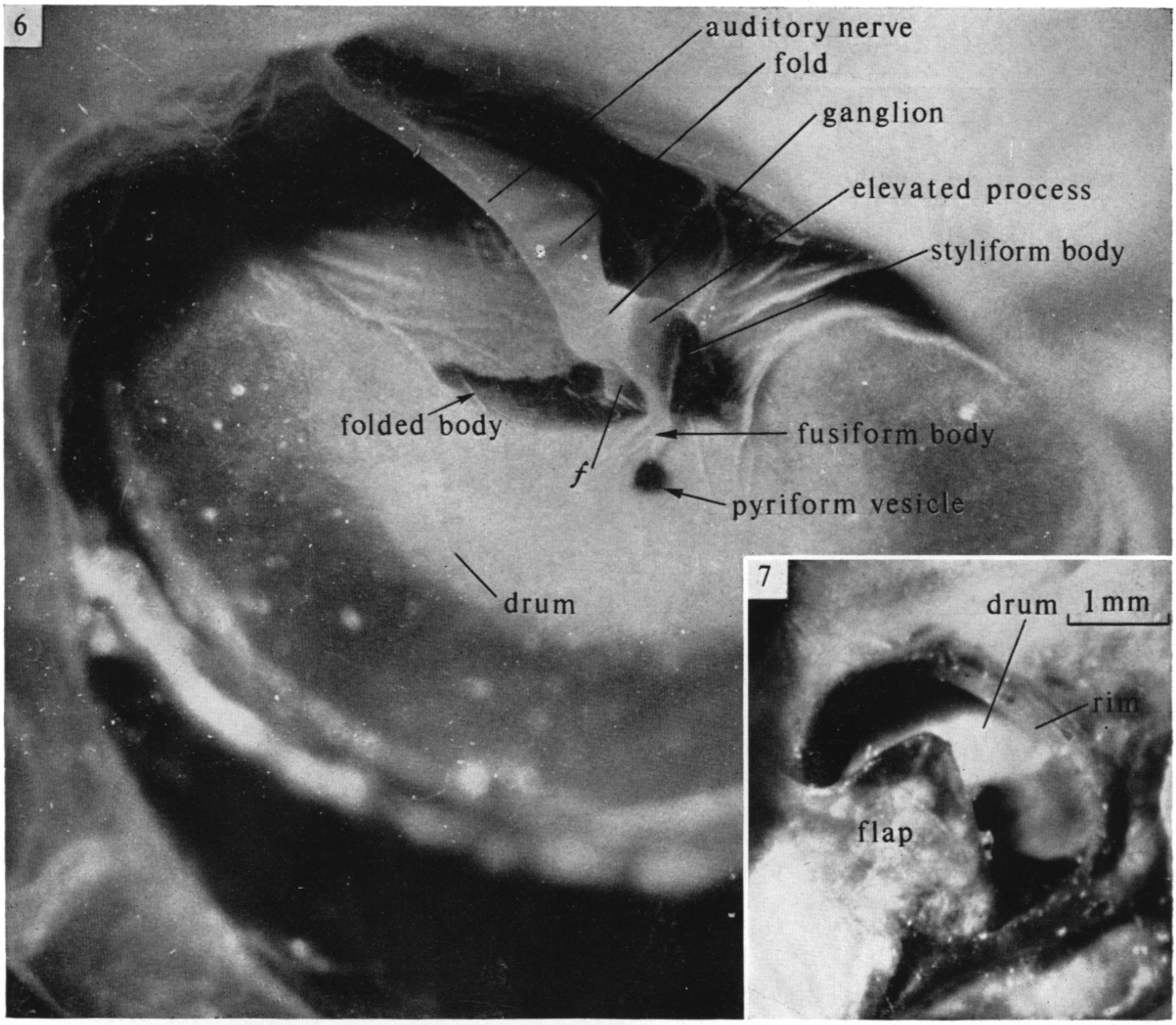
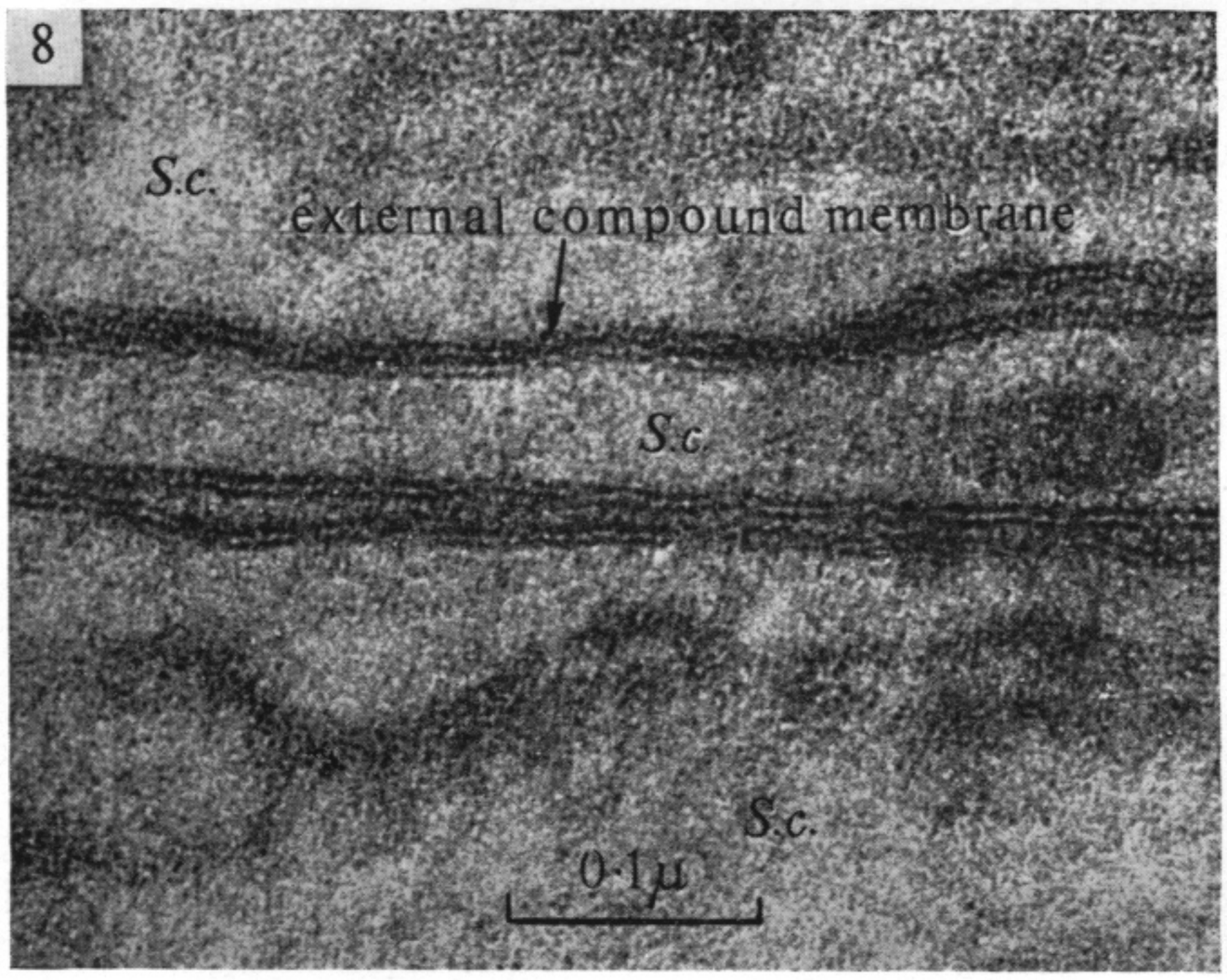
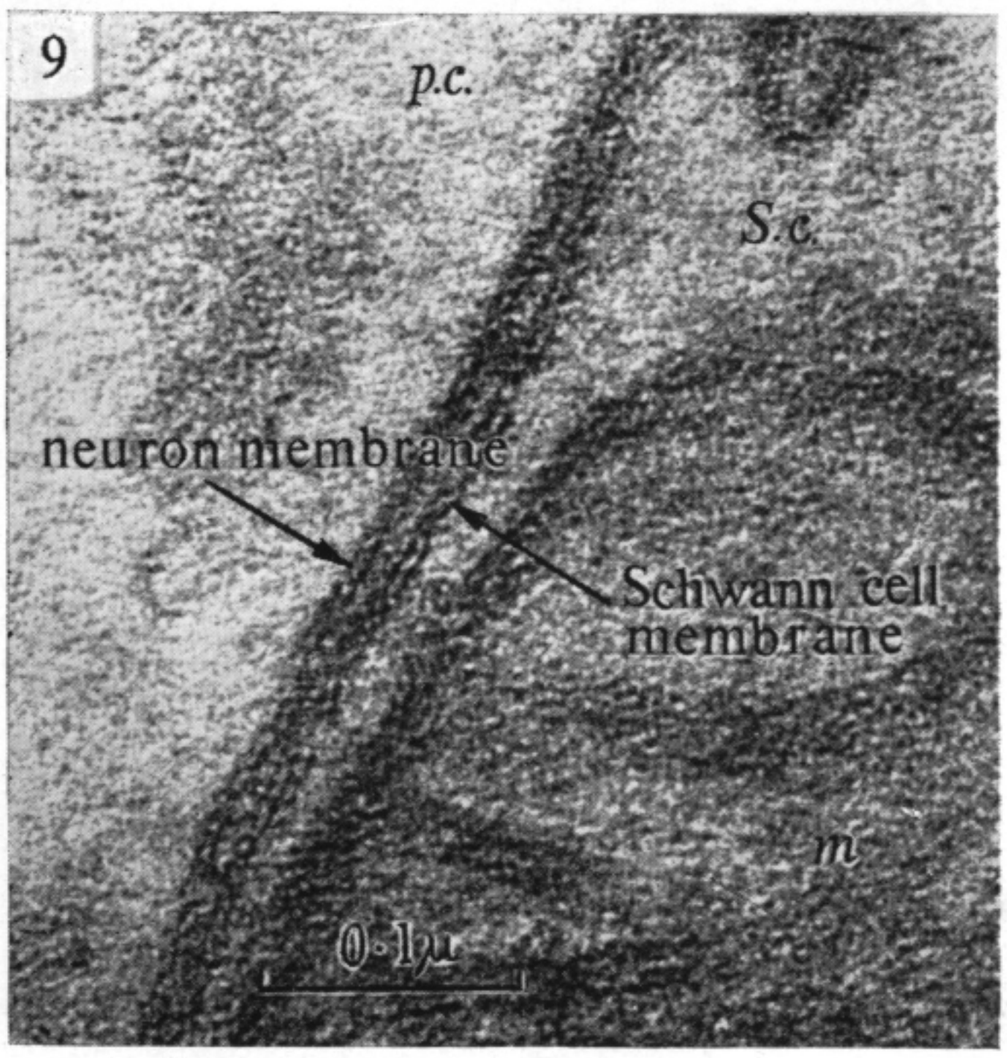
Key to abbreviations used on the figures

a.c attachment cell
ax. axon
b.m. basement membrane
cap. scolopale cap
c.f.p. concentric finger processes of apex of root
cil. cilium
cil.b. base of cilium
cil.d. dilatation of cilium
d.a. thickened regions of membranes of dendrite and scolopale cell
den. dendrite
den.a. dendrite apex
den.d. dendrite dilatation
den.t. dendrite tubules
e.p. elevated process
e.r. endoplasmic reticulum
ex. extracellular region
f.c. fibrous sheath-cell
f.m. surface membrane of fibrous sheath-cell
f.ma. fibrous material in axon sheath
g.c. capsule of ganglion
gr. granules of the endoplasmic reticulum
hyp. hypodermis
l.sty. leg of styliform body
m. mitochondrion(a)
mel. melanin granules
n. bipolar auditory neurons
n.f. neurofilaments
nuc. nucleus of bipolar neuron
nuc.a. nucleus of attachment cell
nuc.f. nucleus of fibrous sheath-cell
nuc.h. nucleus of hypodermal cell
nuc.s. nucleus of scolopale cell
nuc.Sc. nucleus of Schwann cell
p. convex projections of elevated process
p.c. cytoplasm of neuron perikaryon
p.m. paired membrane systems of neuron cytoplasm
r. root of the cilium inside the dendrite
r.a. root apparatus
r.l. rootlets of the cilium inside the dendrite
r.s. region where the root splits into rootlets
S.c. Schwann-cell folds
scol. scolopale
sp.c. scolopale cell
sp.m. scolopale cell membrane
s.r. scolopale rods (columns), which form the wall of the scolopale
s.m. surface-connecting membrane (i.e. the apposed membranes where a cell meets itself after wrapping round a structure)
sty. styliform body
ton. tonofibrils
t. tubules of axon
tu. tubules of hypodermal cell
v. V-shaped dense bodies
va. 'vacuole' seen at entrance of scolopale by light microscopy
ves. vesicles of scolopale cell

For other letters, see text.







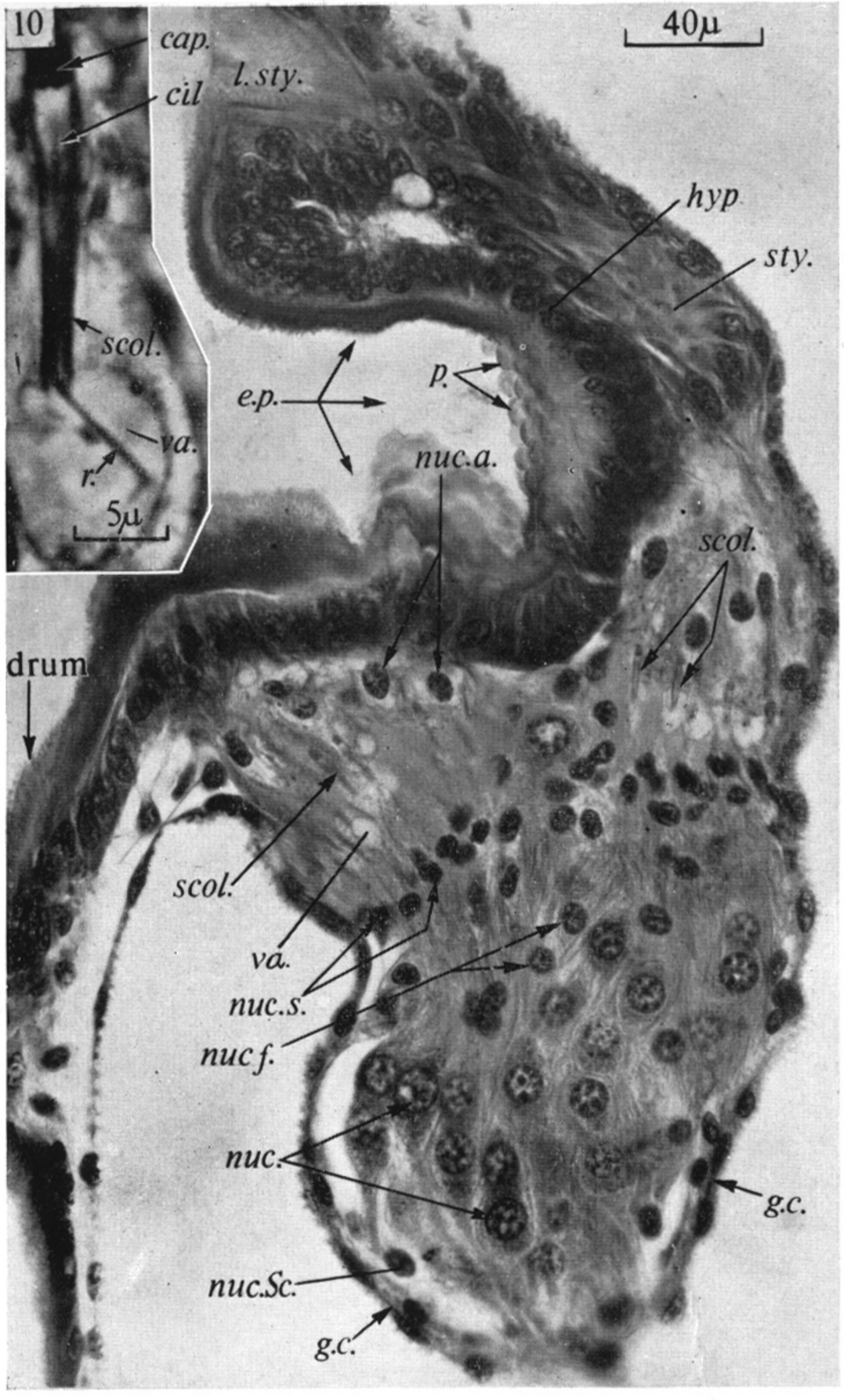
All material OsO_4 fixed, phosphotungstic acid stained except figures 8, 9 and 14 ($KMnO_4$ fixed).

FIGURE 6. The auditory ganglion attached to the inner surface of the ear-drum of the locust. The air sac has been dissected away. Micrograph of fresh material taken by reflected light.

FIGURE 7. Lateral view of the ear-drum, which is situated on the first abdominal segment.

FIGURE 8. The membranes of Schwann-cell processes that are wrapped round the neuron cell body. The gap is closed (arrow) to form an external compound membrane ($KMnO_4$ fixed).

FIGURE 9. A portion of a Schwann-cell fold apposed to the neuron cell membrane. Details of the membranes are shown clearly after fixation with $KMnO_4$.



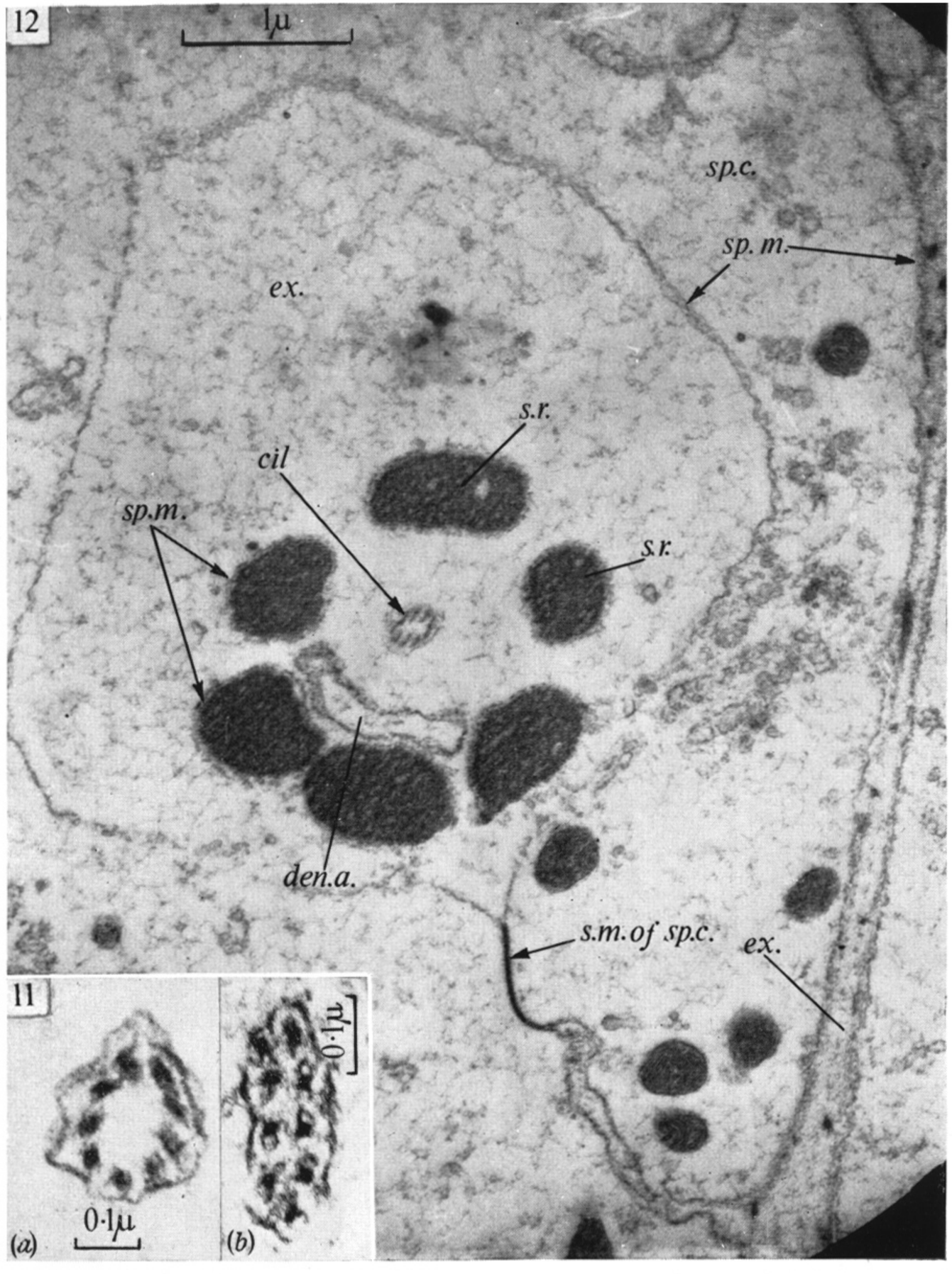


FIGURE 10. Light-micrograph of a cross-section of the auditory ganglion attached to the drum. *Inset* a scolopale (both sections stained with haematoxylin and eosin).

FIGURE 11. Cross-sections of the cilium (see figure 12). (*a*) most commonly observed section, where the nine filaments are presumed to be cut obliquely, (*b*) filaments here presumed to be cut perfectly transversely. The composite structure of each filament can be seen. The flattened profile of the cilium might be an artifact.

FIGURE 12. Transverse section through the lower region of the cilium. Six rods form the scolopale wall in this region.

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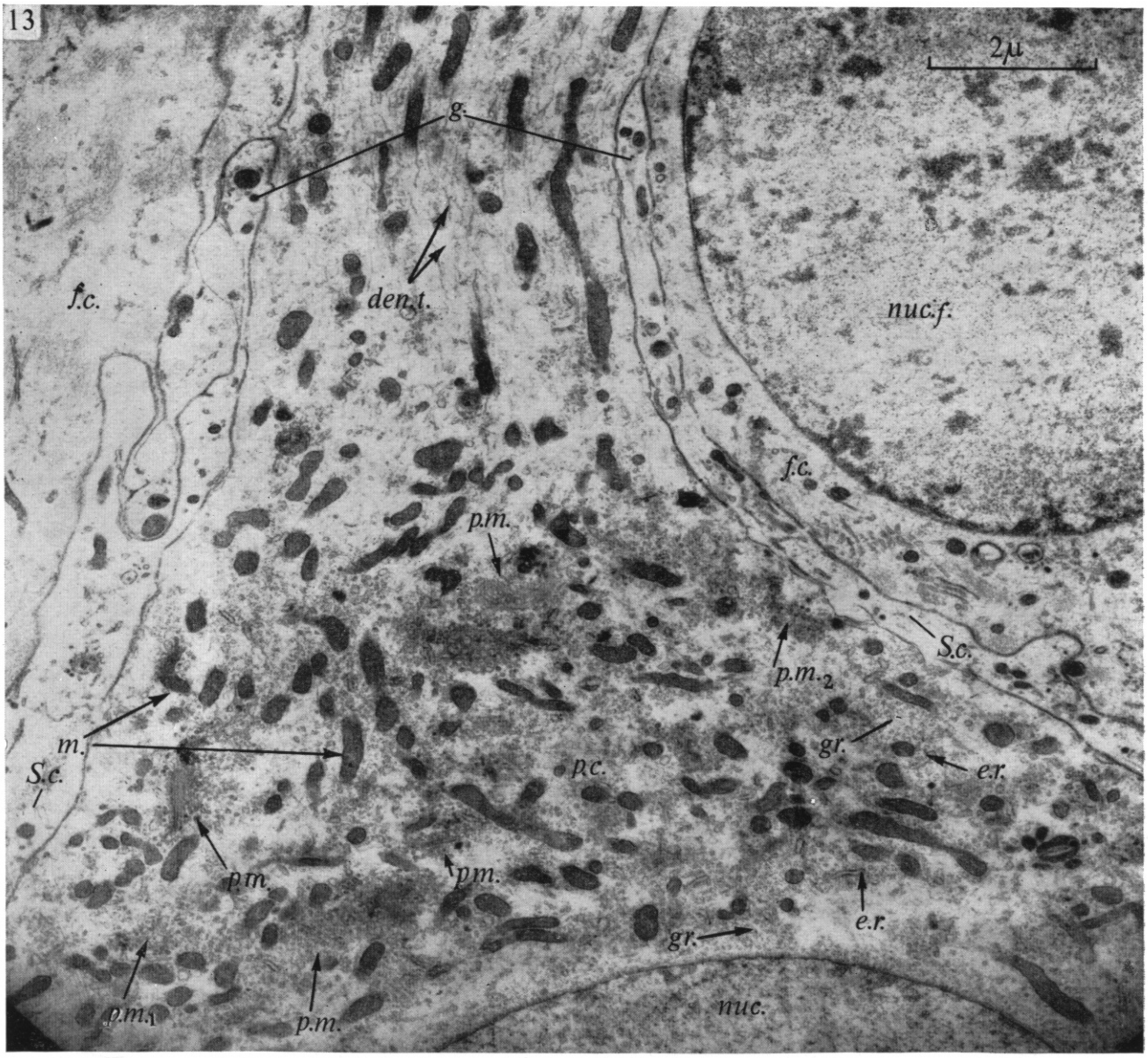

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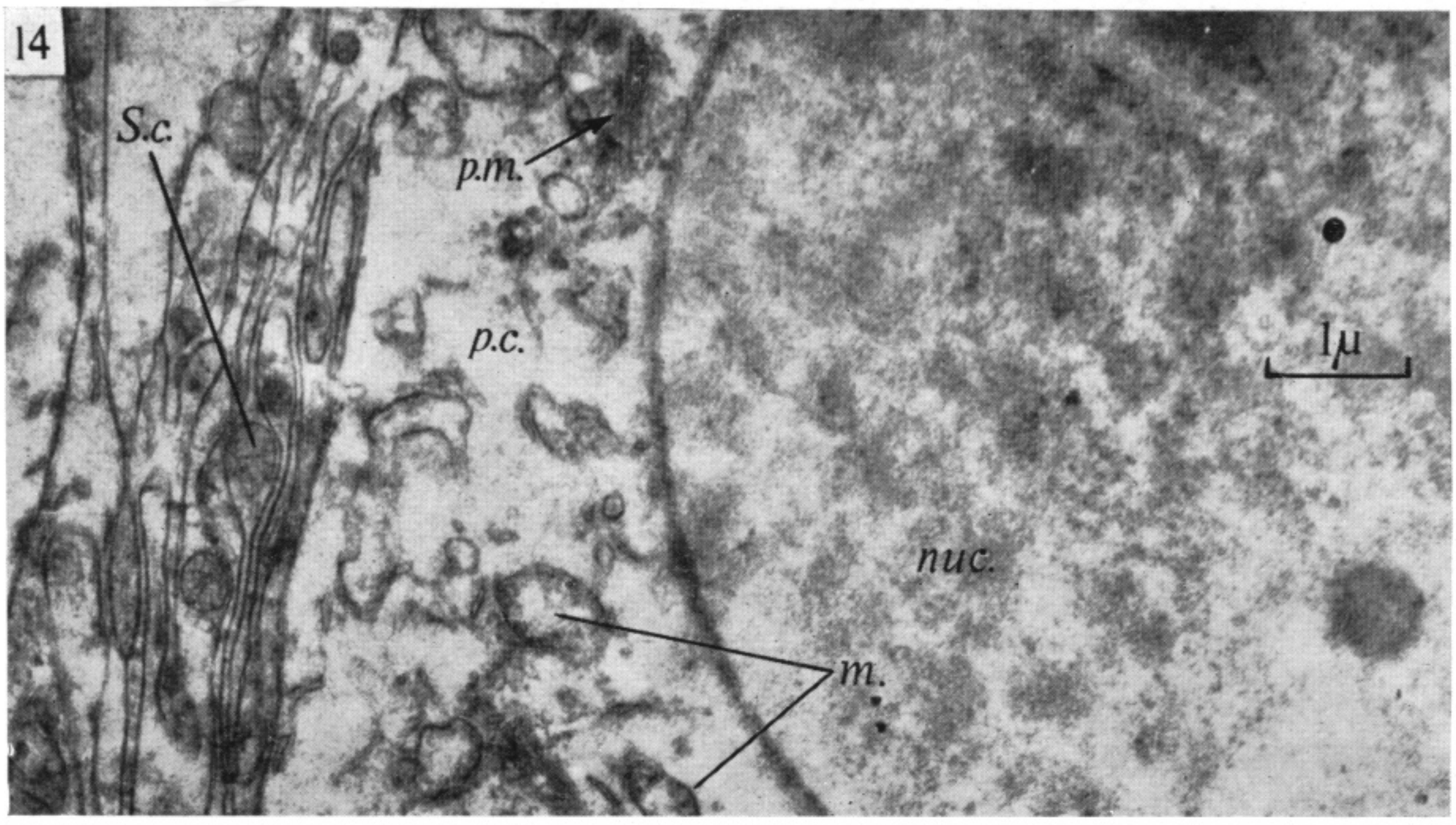

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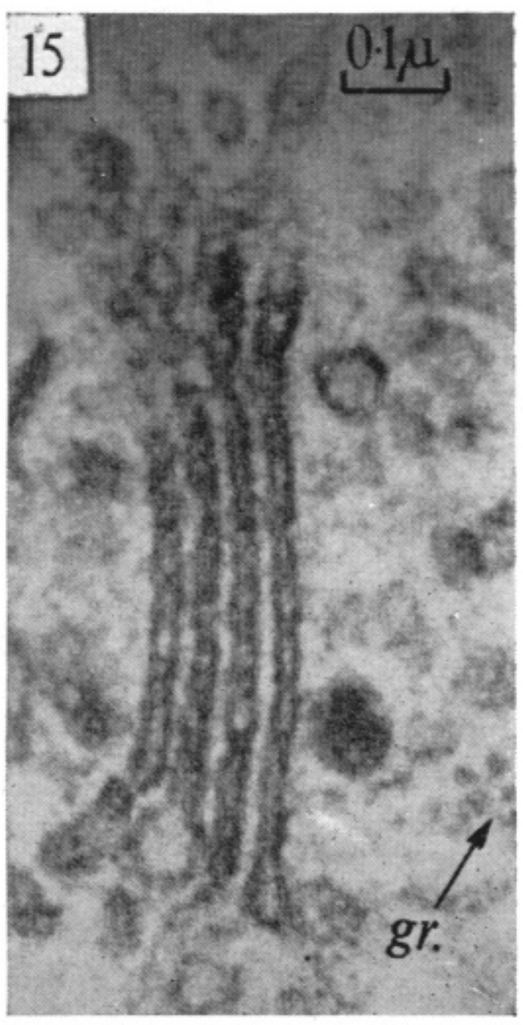
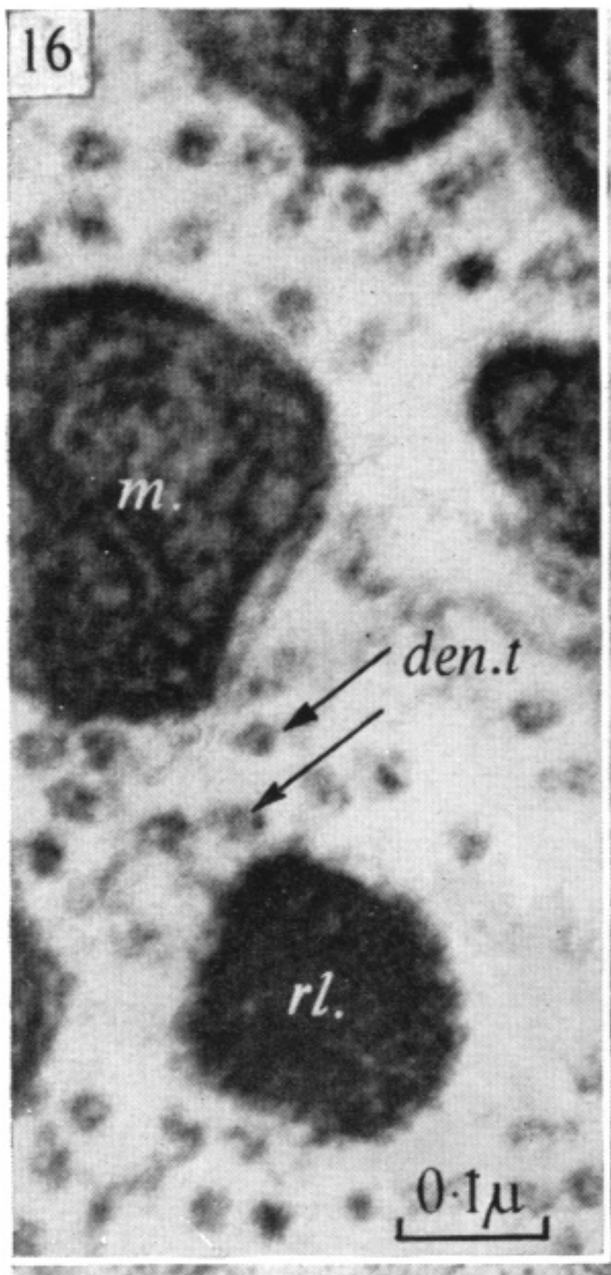


FIGURE 13. The basal region of the dendrite of the sensory neuron. The dendrite is sheathed in the processes of satellite cells.

FIGURE 14. Portion of the cell body of the sensory neuron, showing the capsule formed by folds of the Schwann cell ($KMnO_4$ fixed).

FIGURE 15. Double membrane systems with associated vesicles found frequently in the perikaryal cytoplasm of the neuron together with clusters of small granules.



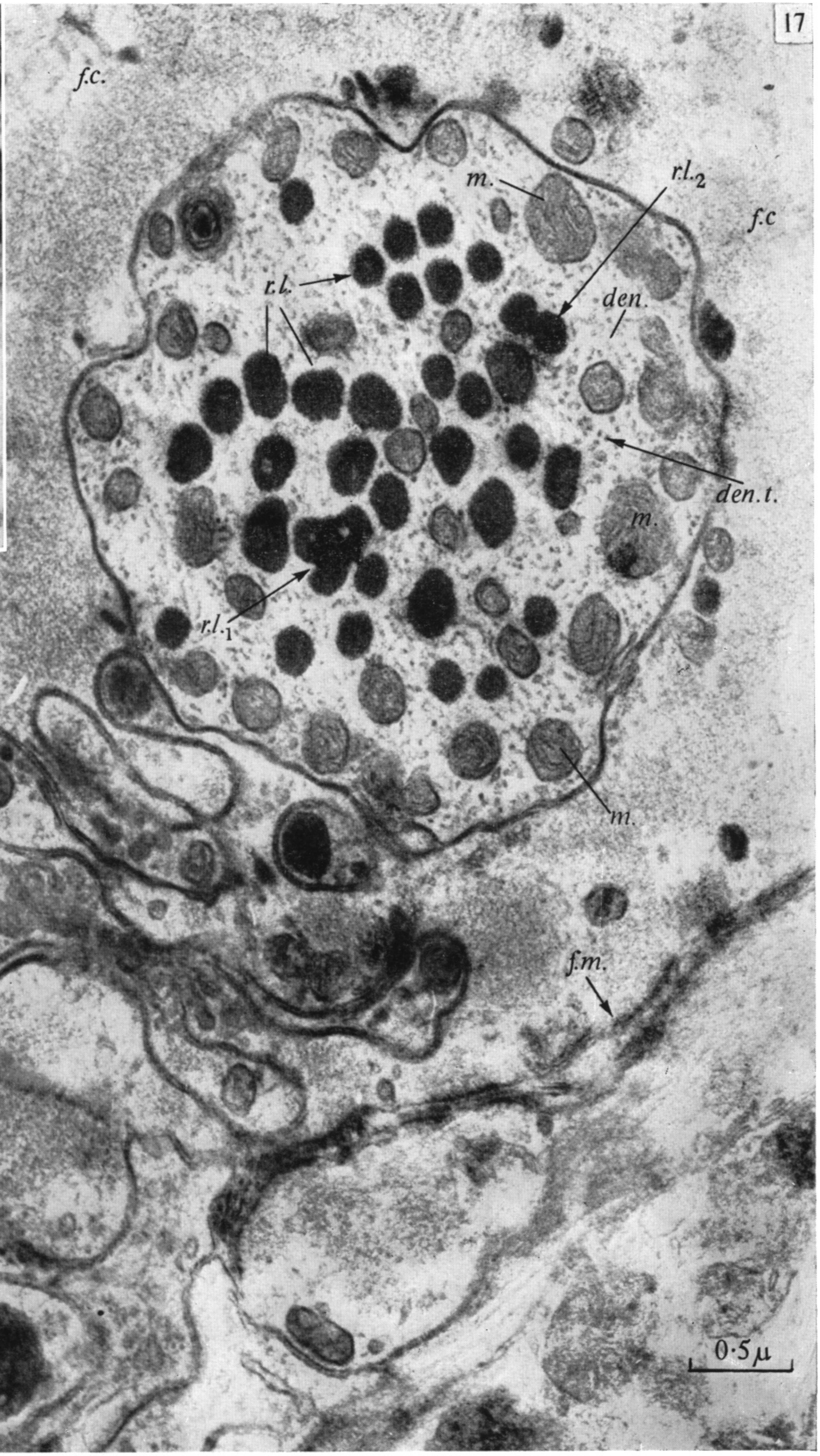


FIGURE 16. Portion of dendrite in transverse section (see figure 17).

FIGURE 17. Transverse section through the dendrite, showing rootlets, mitochondria and tubules. The dendrite is wrapped in the fibrous sheath-cell at this level.

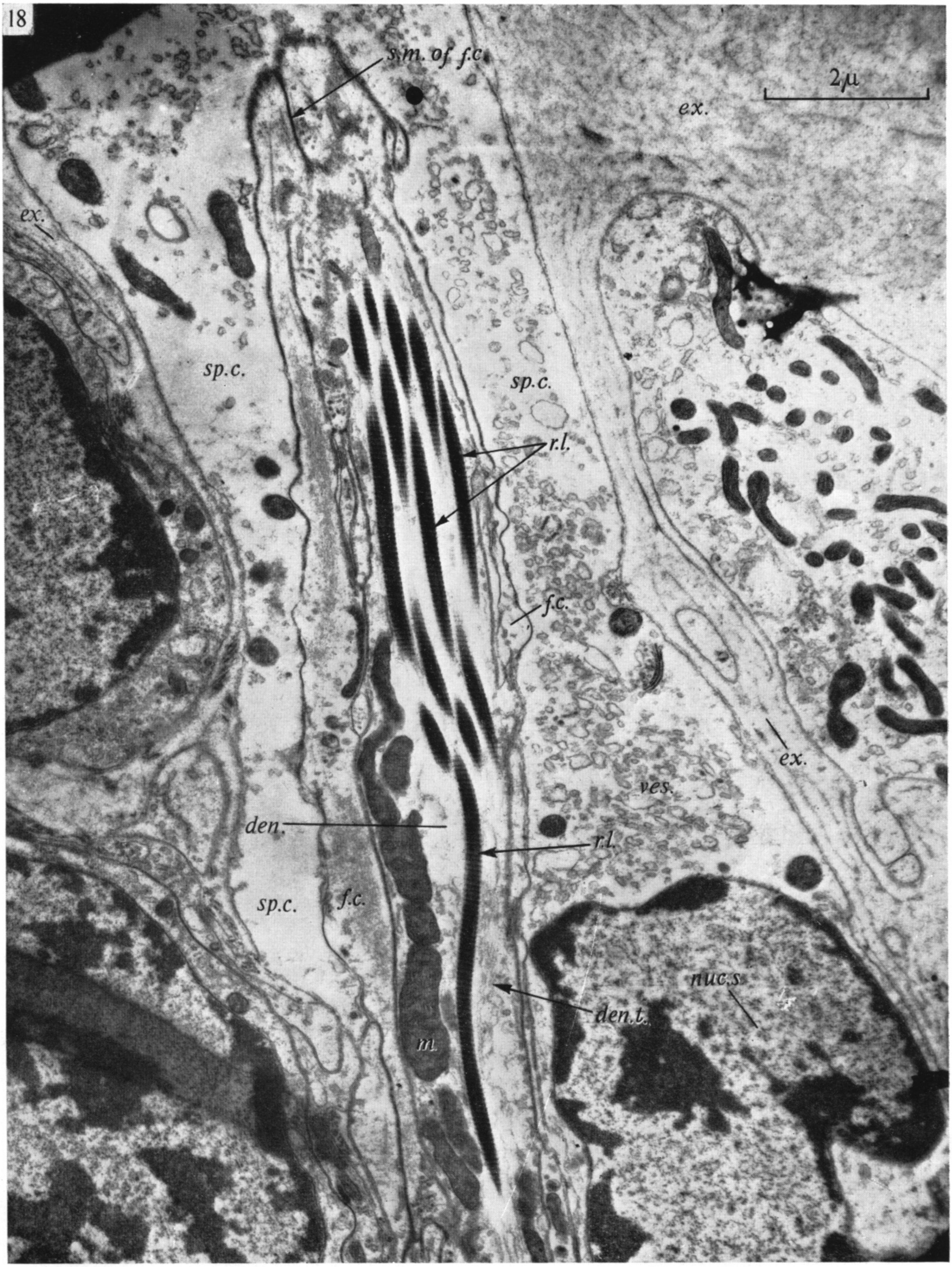
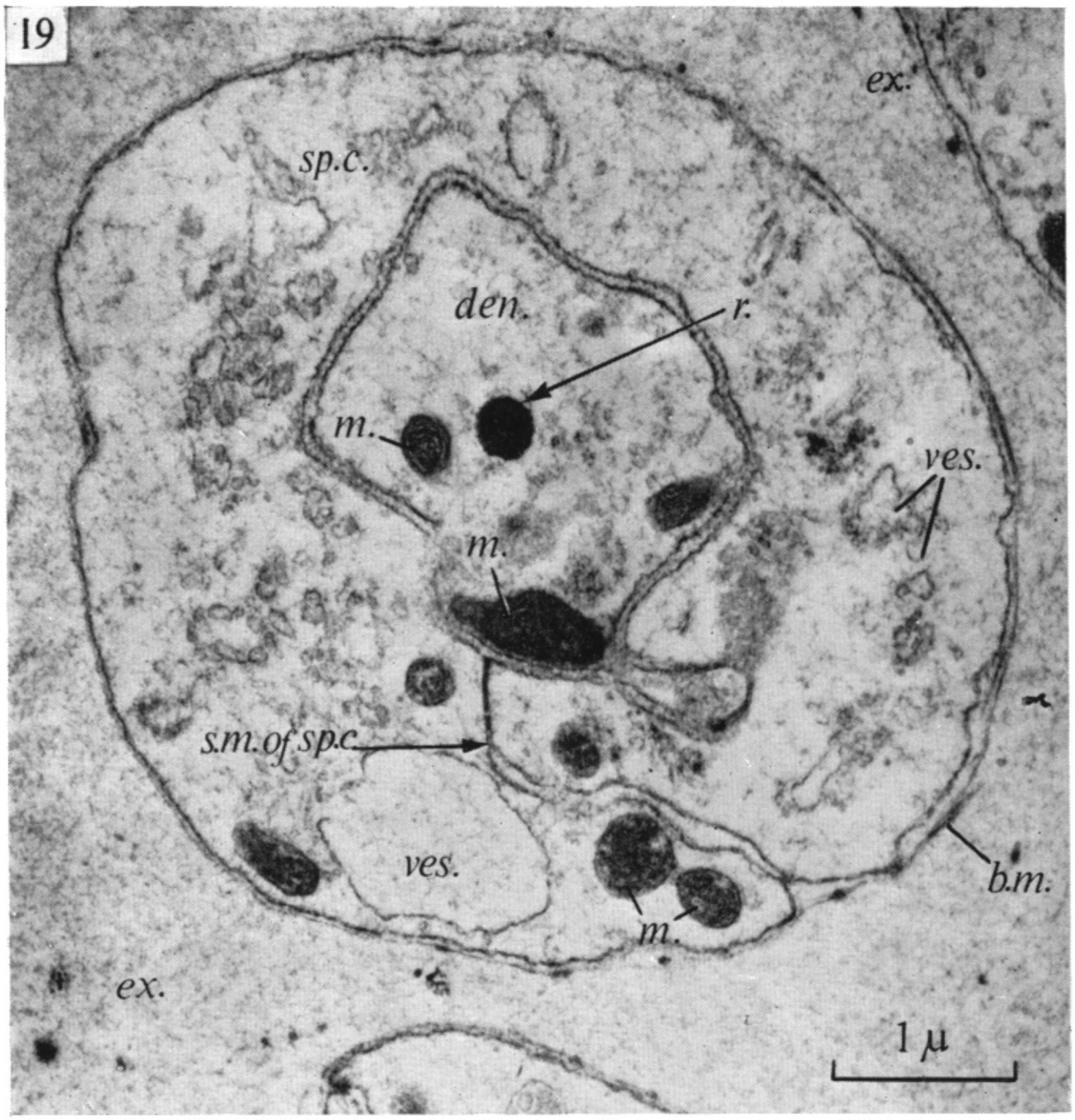
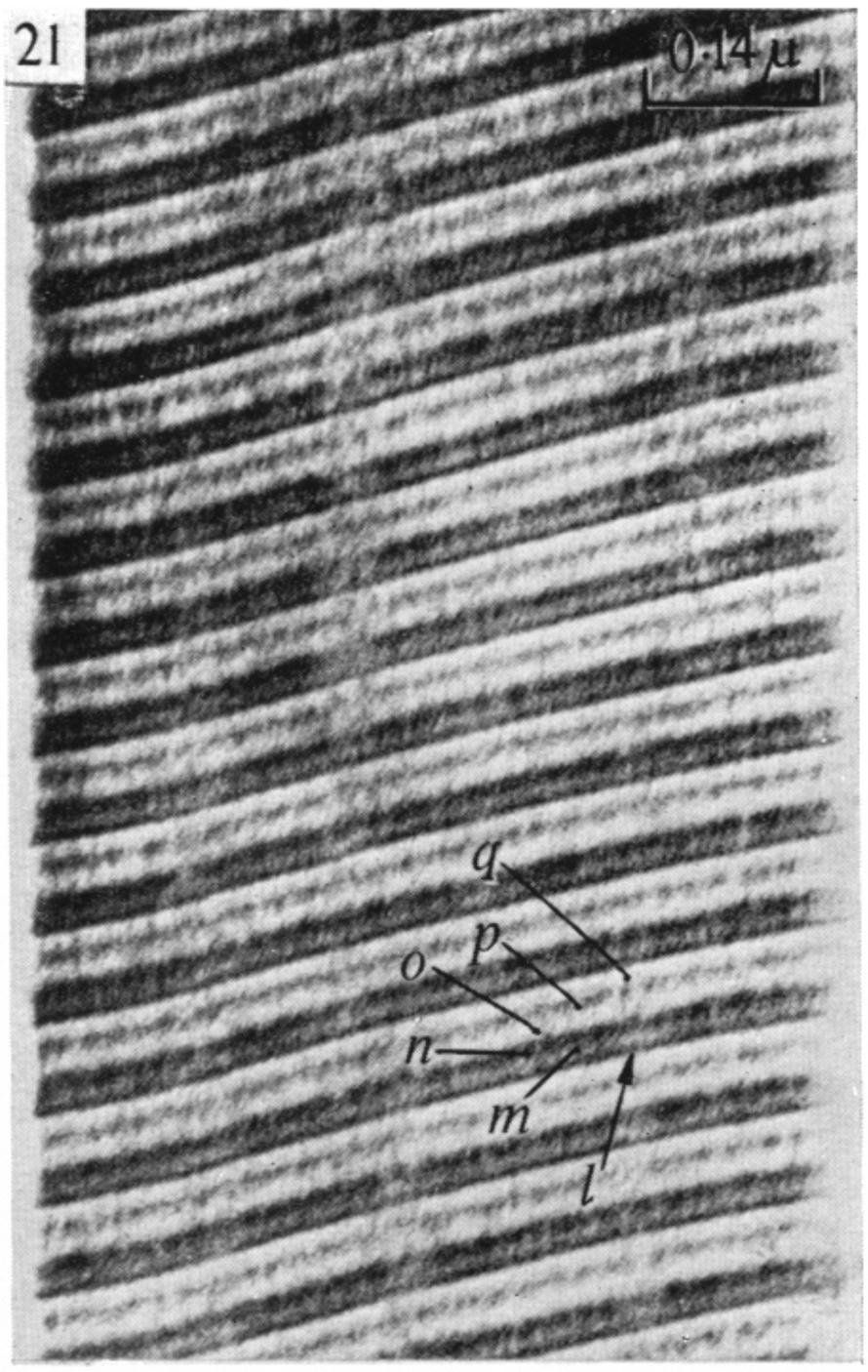
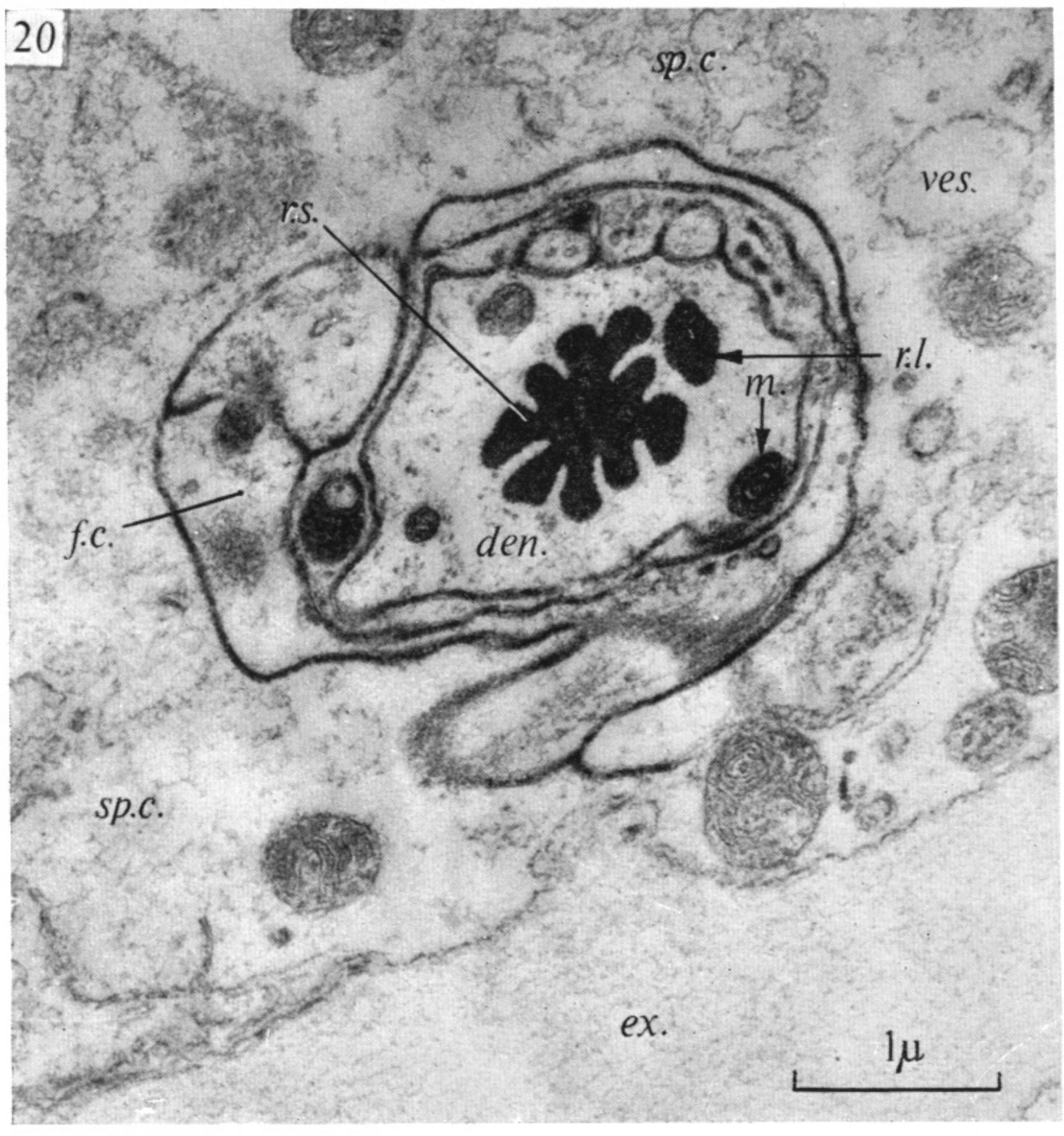


FIGURE 18. Longitudinal section of basal region of dendrite showing rootlets, mitochondria and tubules. The dendrite in this region is encased in the fibrous sheath-cell, around which is the scolopale cell.







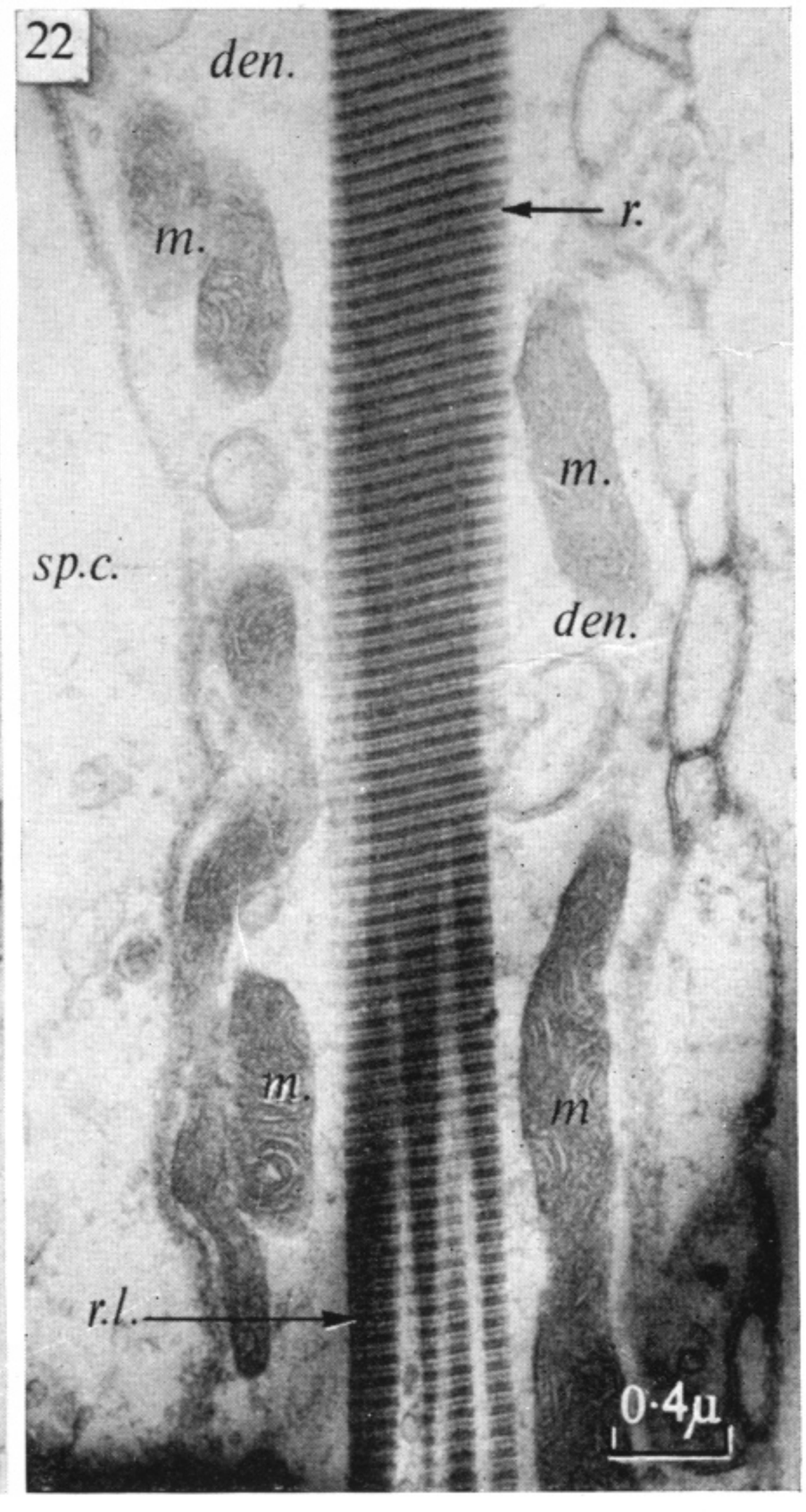


FIGURE 19. Cross-section of the dendrite in the root region. At this level the dendrite is enclosed in the scolopale cell only (see figure 21).

FIGURE 20. Cross-section of dendrite in the region where the root branches into rootlets (see figure 22).

FIGURE 21. Longitudinal section of the root at high magnification (see figure 19).

FIGURE 22. Longitudinal section of the root within the dendrite, where the root divides into rootlets.

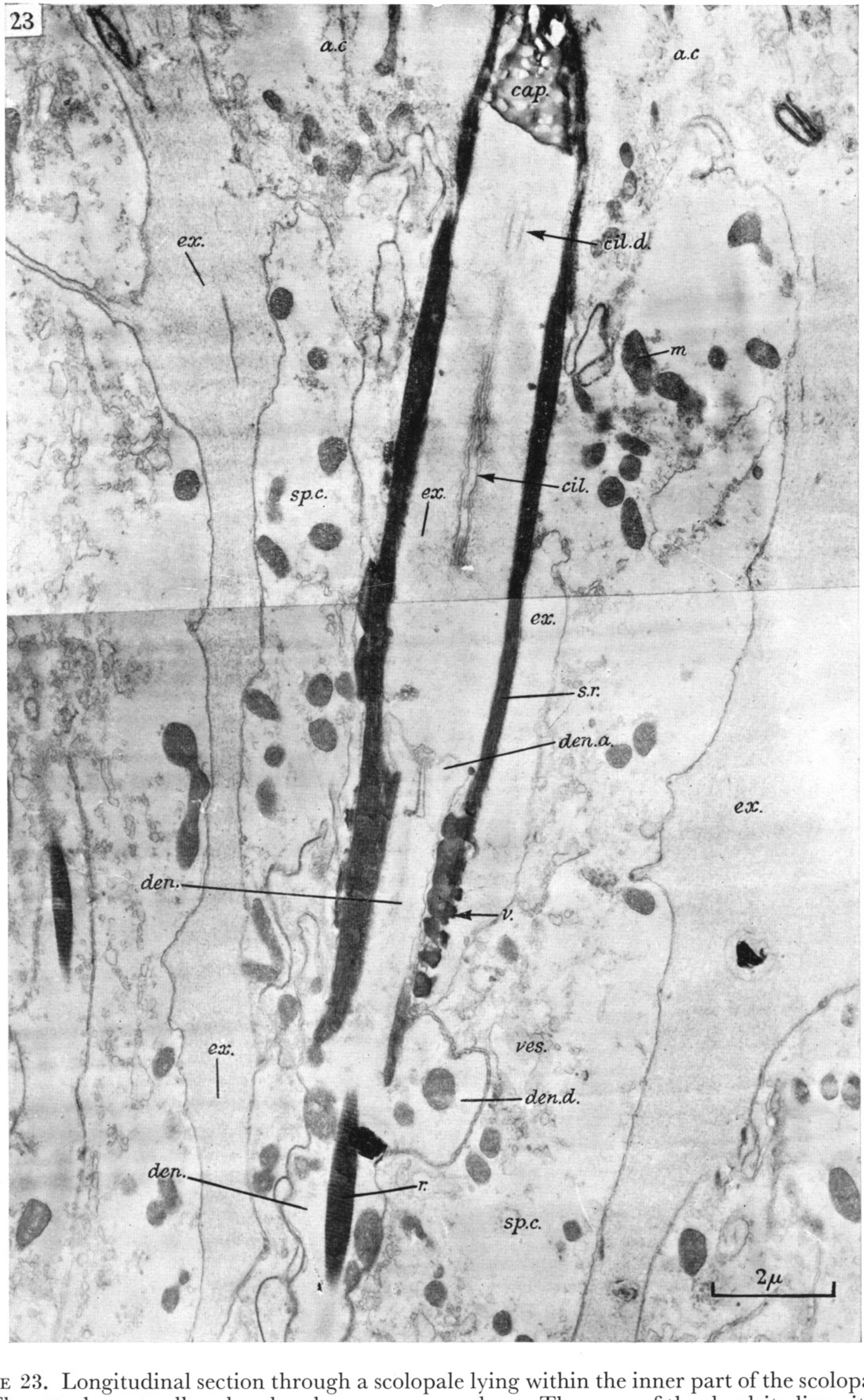
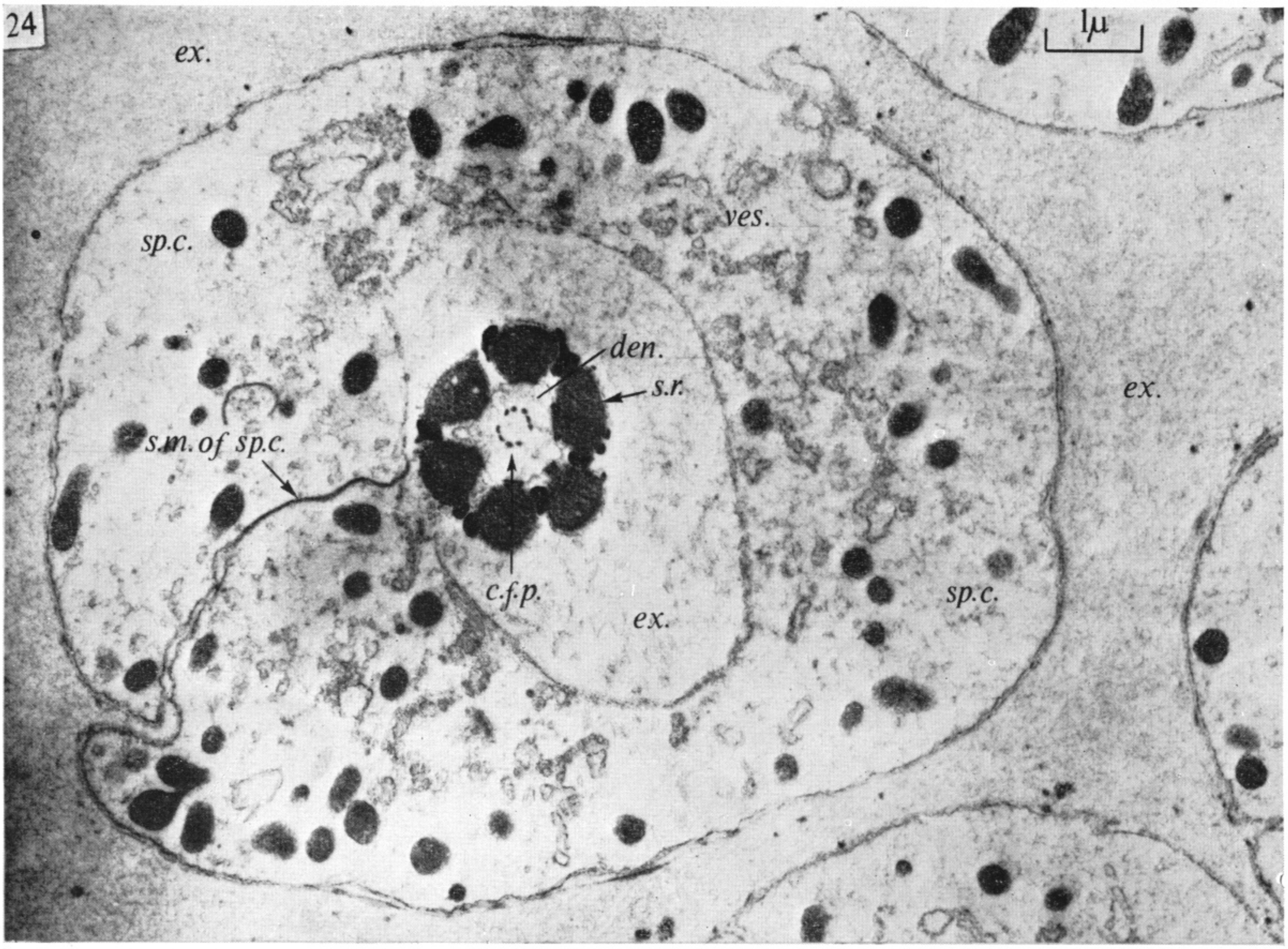
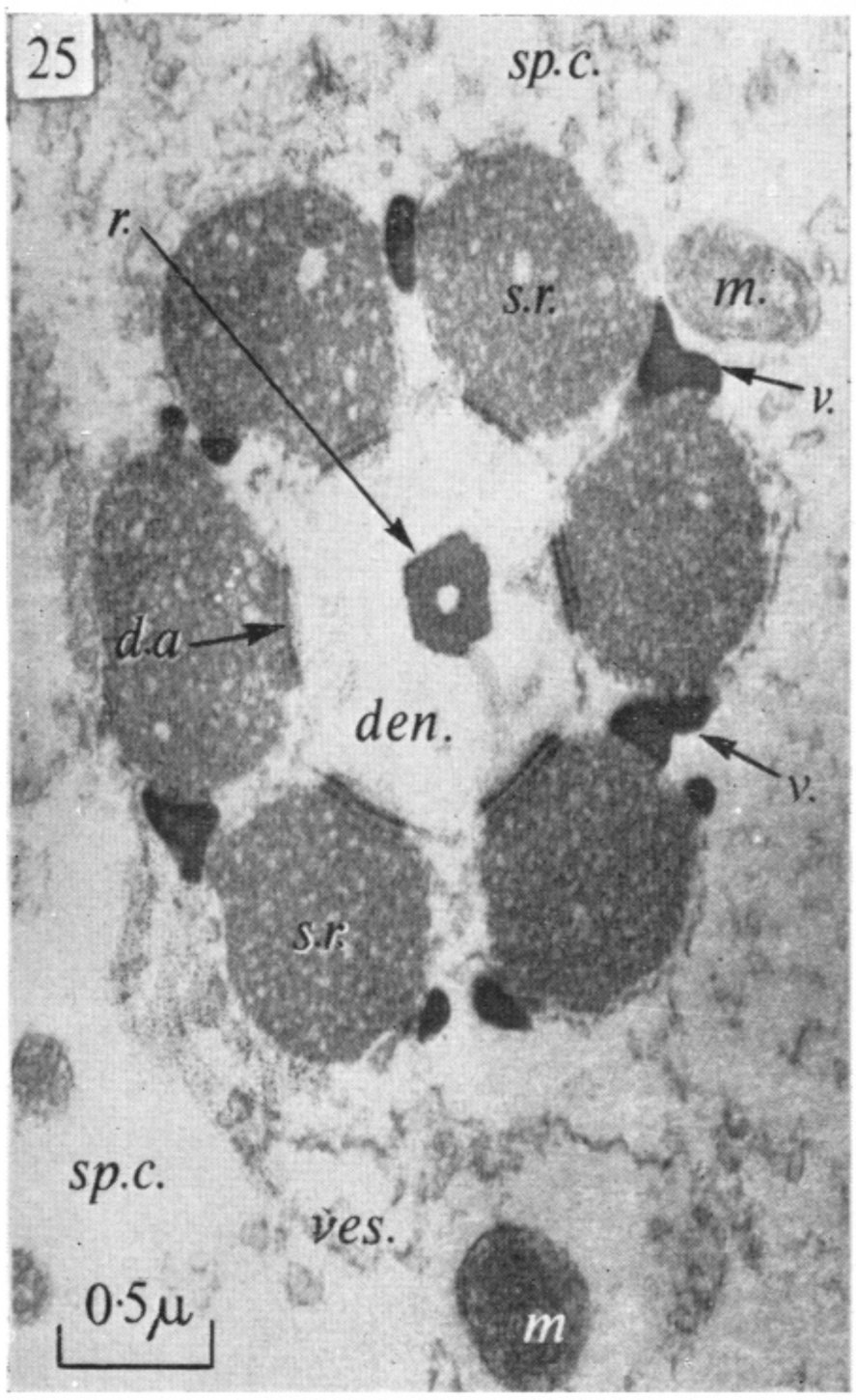
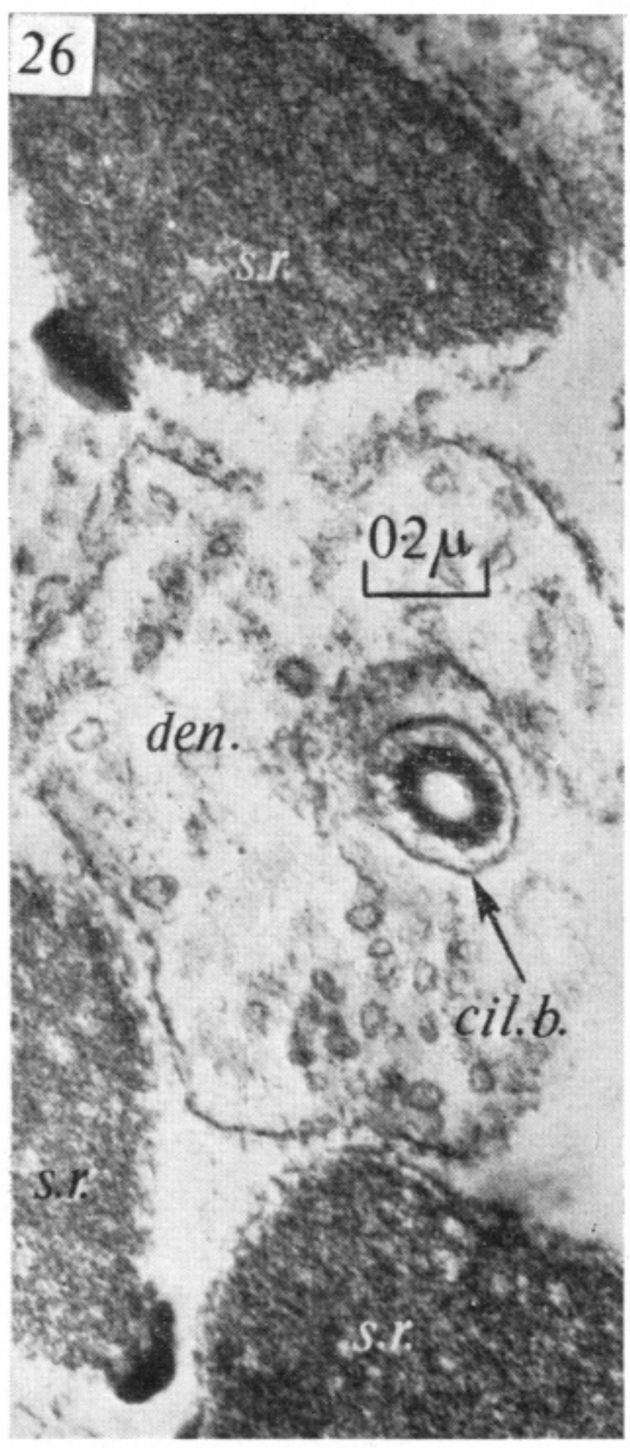


FIGURE 23. Longitudinal section through a scolopale lying within the inner part of the scolopale cell. The attachment cell and scolopale cap are seen above. The apex of the dendrite lies within the lower part of the scolopale. Part of the cilium is seen lying in an extracellular compartment within the scolopale cell. Some of the fibrils of the cilium appear in the section.







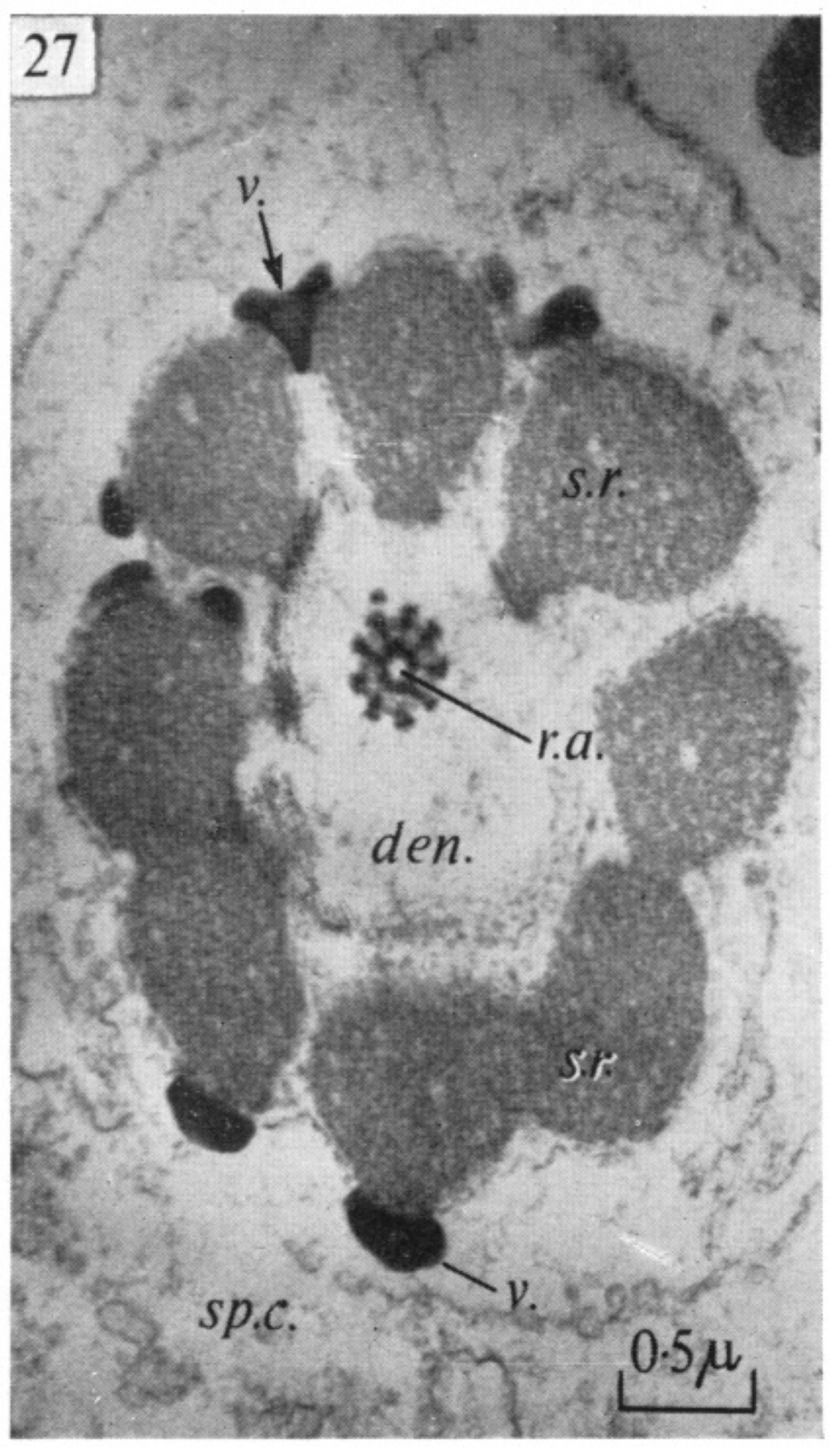
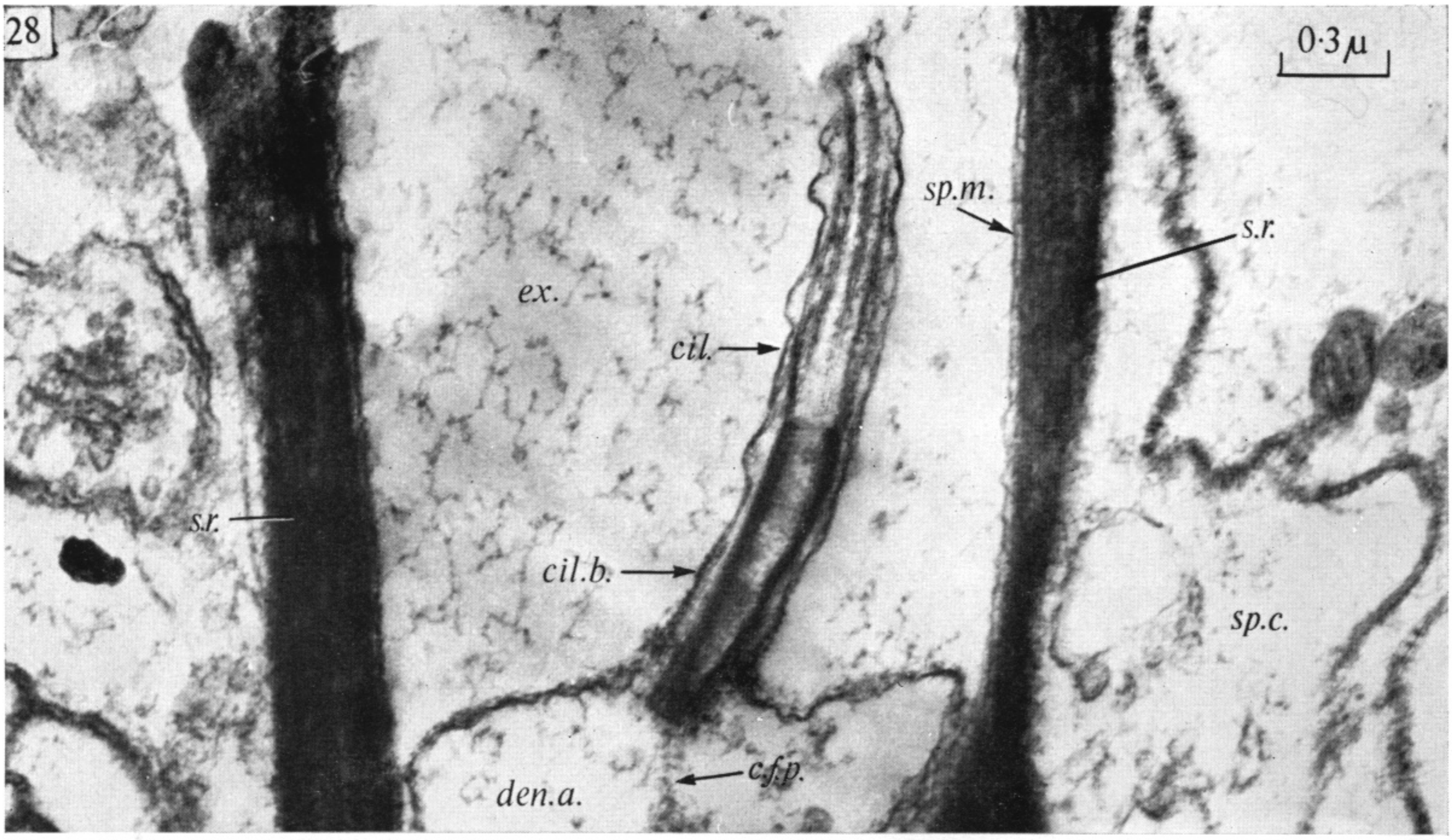


FIGURE 24. Transverse section of the dendrite showing the nine concentric finger processes which project from the apex of the root. The basal regions of the scolopale rods (within the scolopale cell) surround the dendrite.

FIGURE 25. Transverse section through the dendrite in the region where the root becomes hollow. The tubular wall splits into nine finger processes (figure 24).

FIGURE 26. Transverse section through the base of the cilium. It contains a tubular structure (dense ring) from which arise the nine fibrils of the cilium. Part of the apical dilatation of the dendrite, which contains vesicles, is shown in the section.

FIGURE 27. Transverse section through the dendrite at the level of the root apparatus.



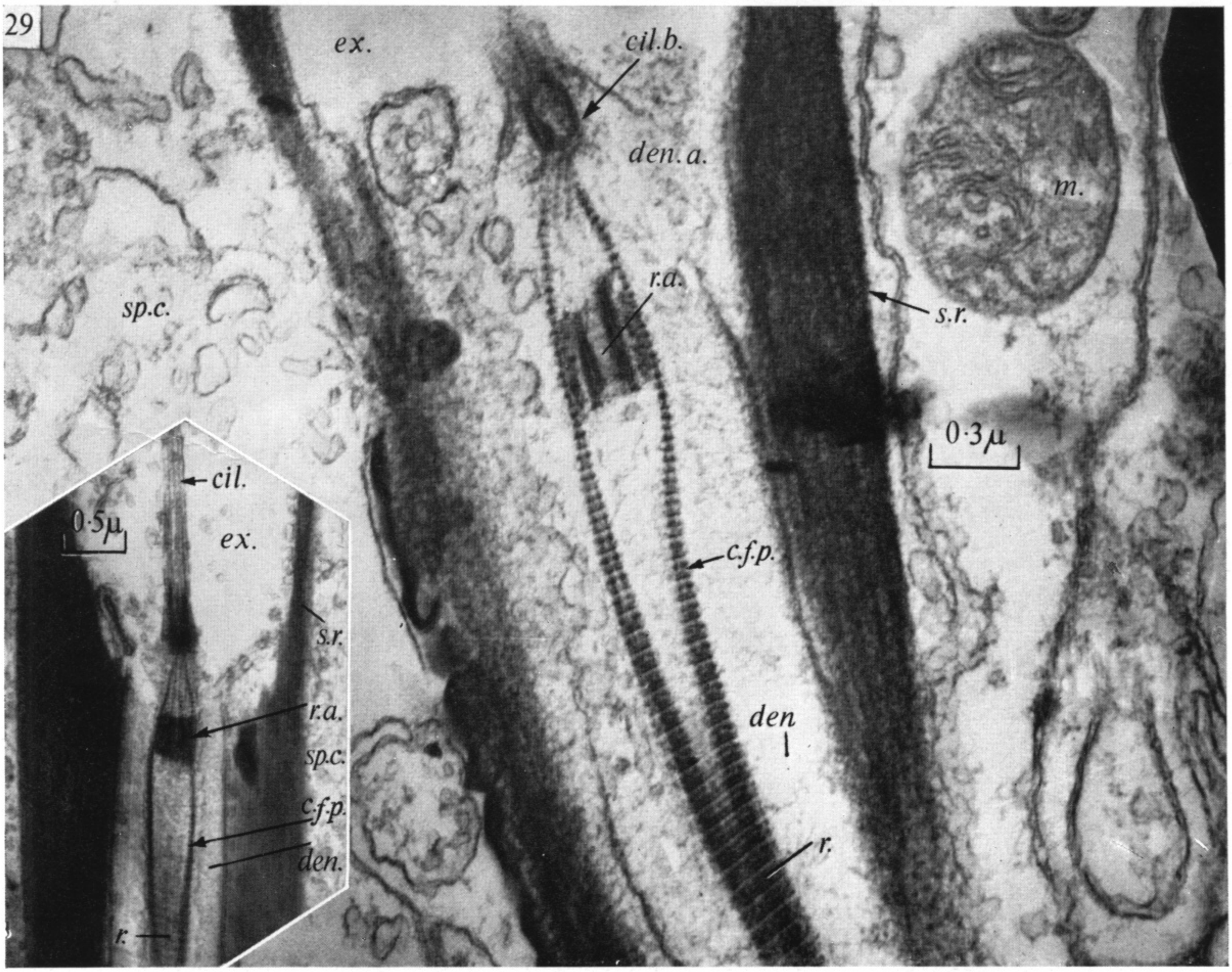
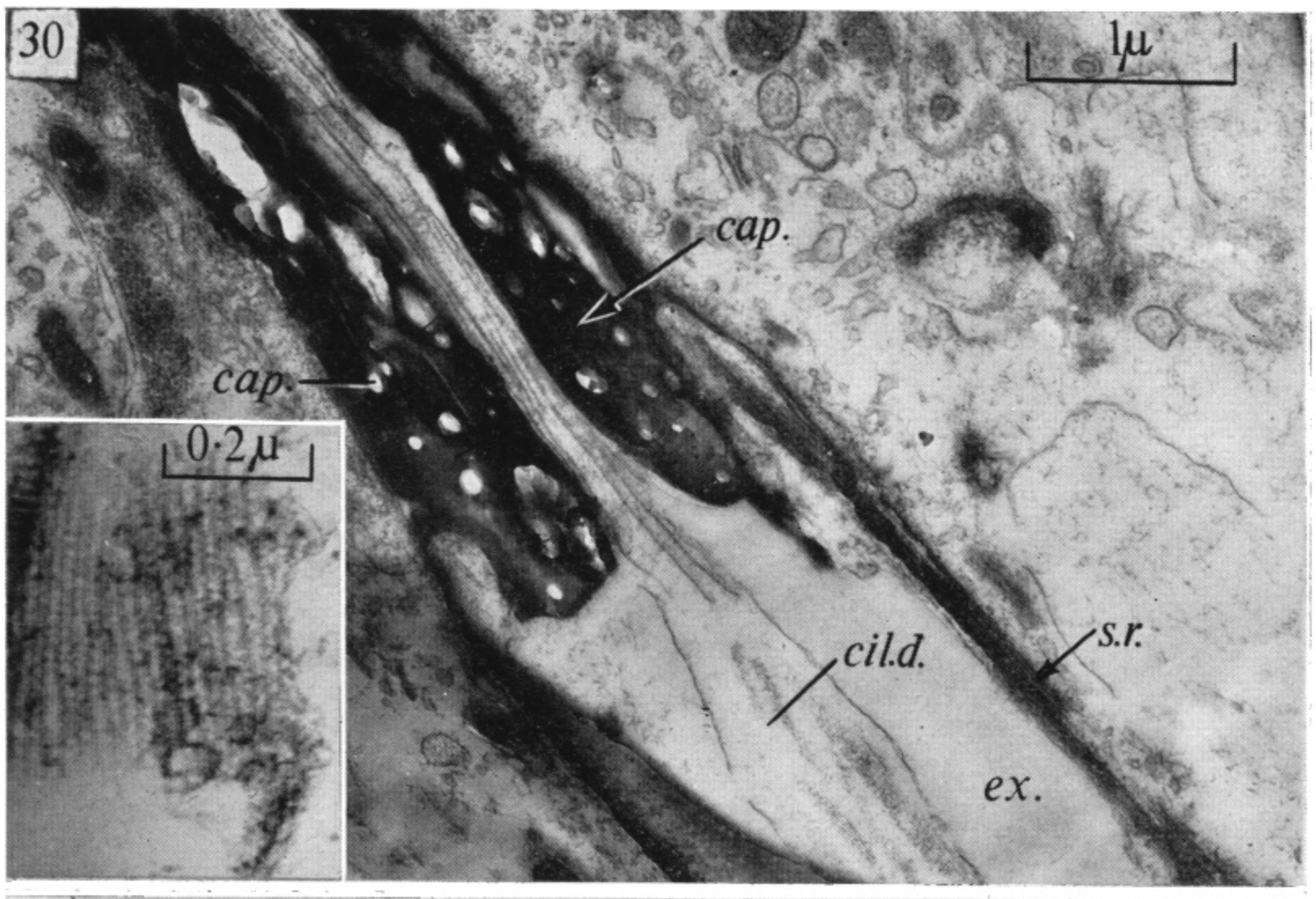
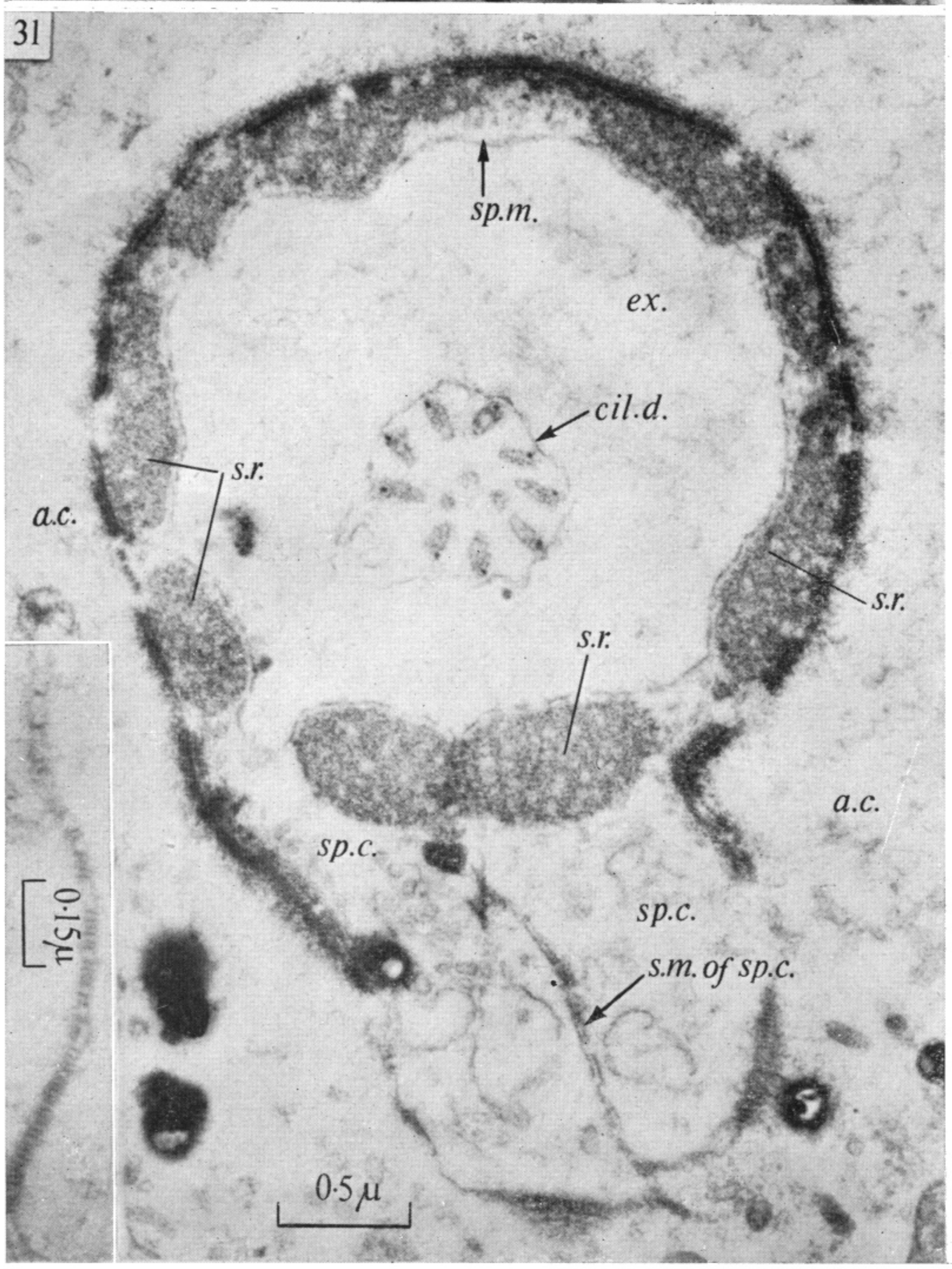
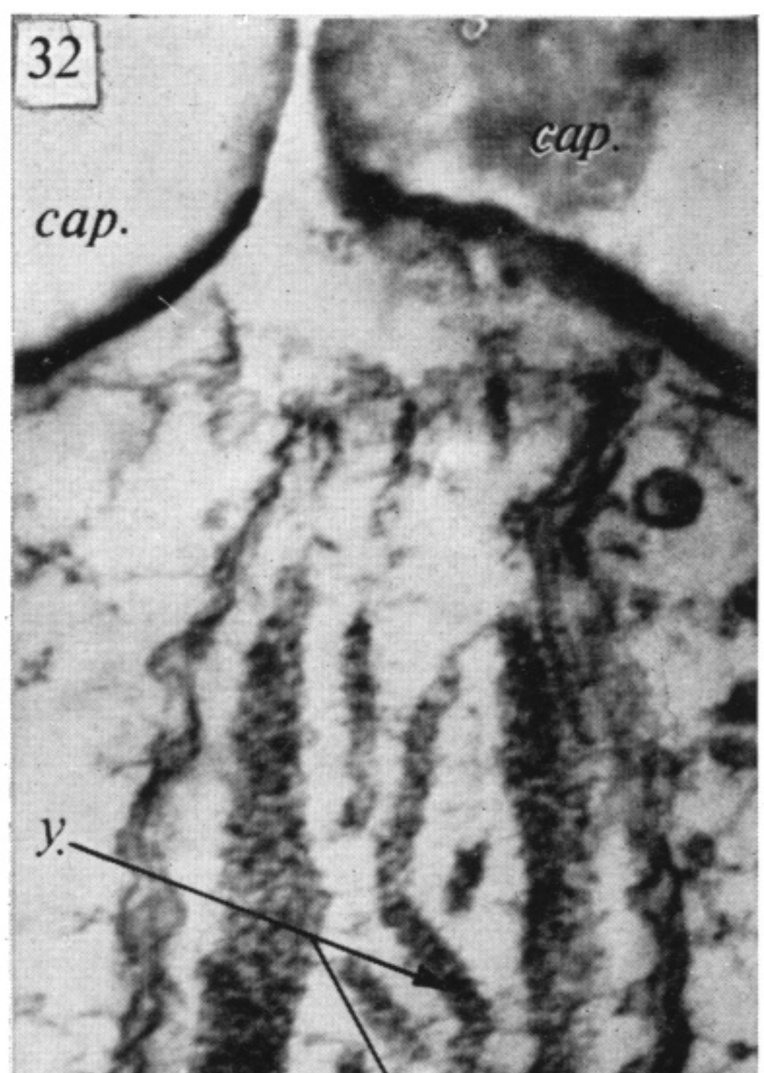


FIGURE 28. Longitudinal section of the apex of the dendrite, showing the base of the cilium arising from it. The cilium lies in an extracellular compartment.

FIGURE 29. Longitudinal section through the apex of the dendrite (the downward continuation of figure 28). The root is seen splitting to enclose the root apparatus. The processes of the root contact the tubular structure in the base of the cilium. *Inset.* A low-power micrograph to show the relationship of root and cilium in the same preparation (see figures 28, 29).







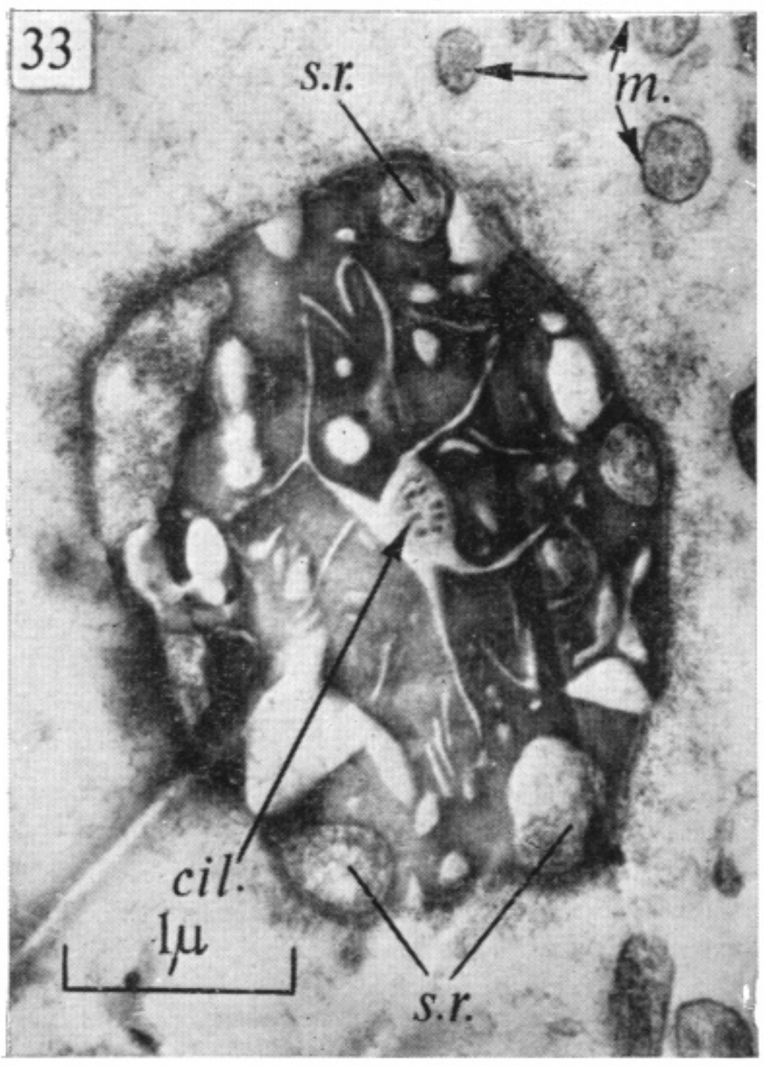
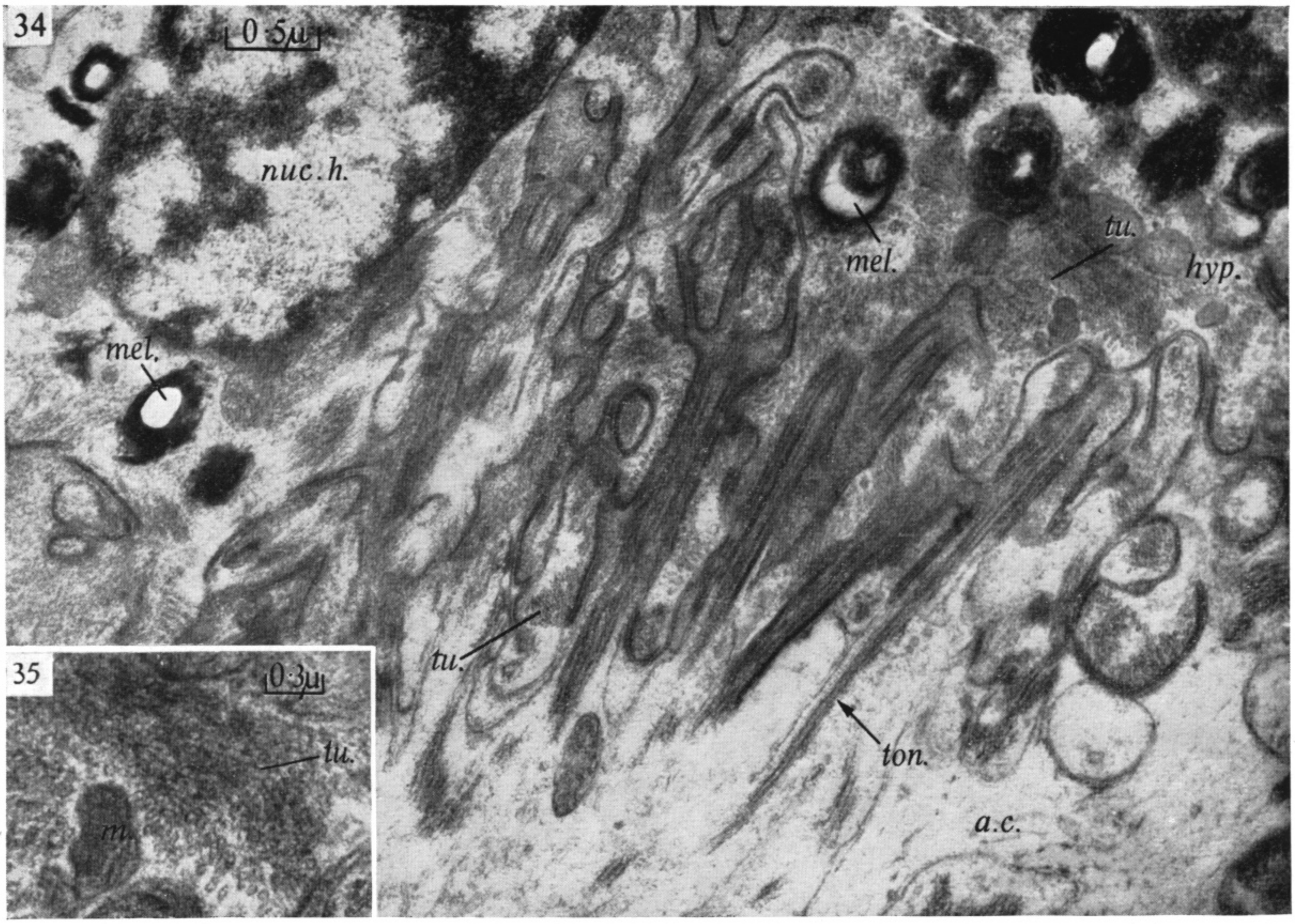


FIGURE 30. The scolopale cap has a central channel. Into it projects the cilium. The dilated region of the cilium is also shown. *Inset.* Section through the cleft between apposed processes of the scolopale cell. It shows a 'honeycomb' structure of extracellular material (see figure 31, inset).

FIGURE 31. Transverse section through the dilatation of the cilium. The cilium lies in an extracellular compartment that is surrounded by the scolopale cell. The scolopale cell contains the scolopale (formed by partly fused rods at this level) and around the scolopale cell in this region is the attachment cell. *Inset.* Cross-striations of extracellular material between apposed processes of the scolopale cell. This is a section perpendicular to that of figure 31 (inset). A thin section through the 'honeycomb' of extracellular material would have this appearance.

FIGURE 32. Longitudinal section through the dilatation of the cilium. The scolopale cap lies above.

FIGURE 33. Transverse section through the scolopale cap. The cilium with its nine fibrils is seen in the central channel.



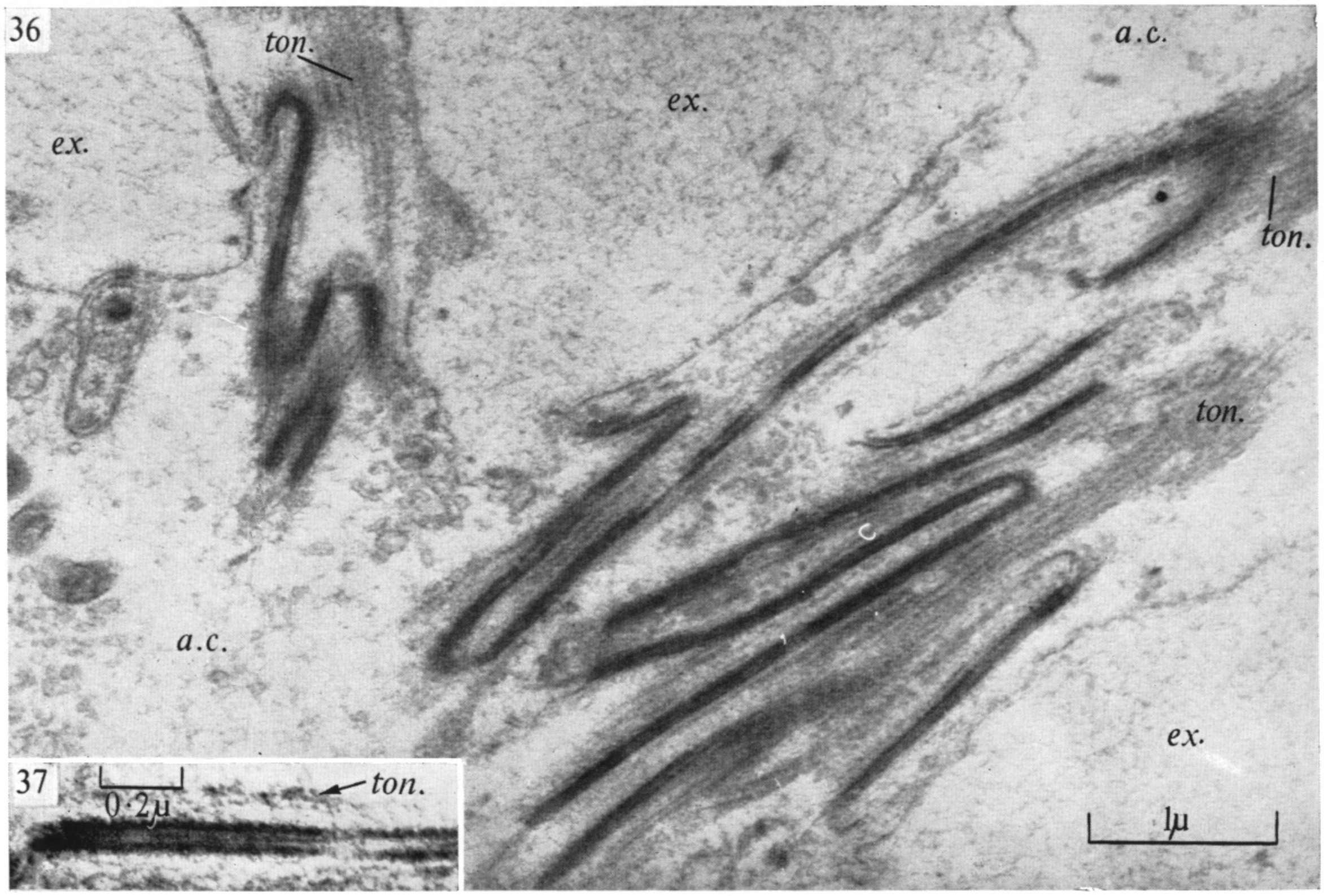
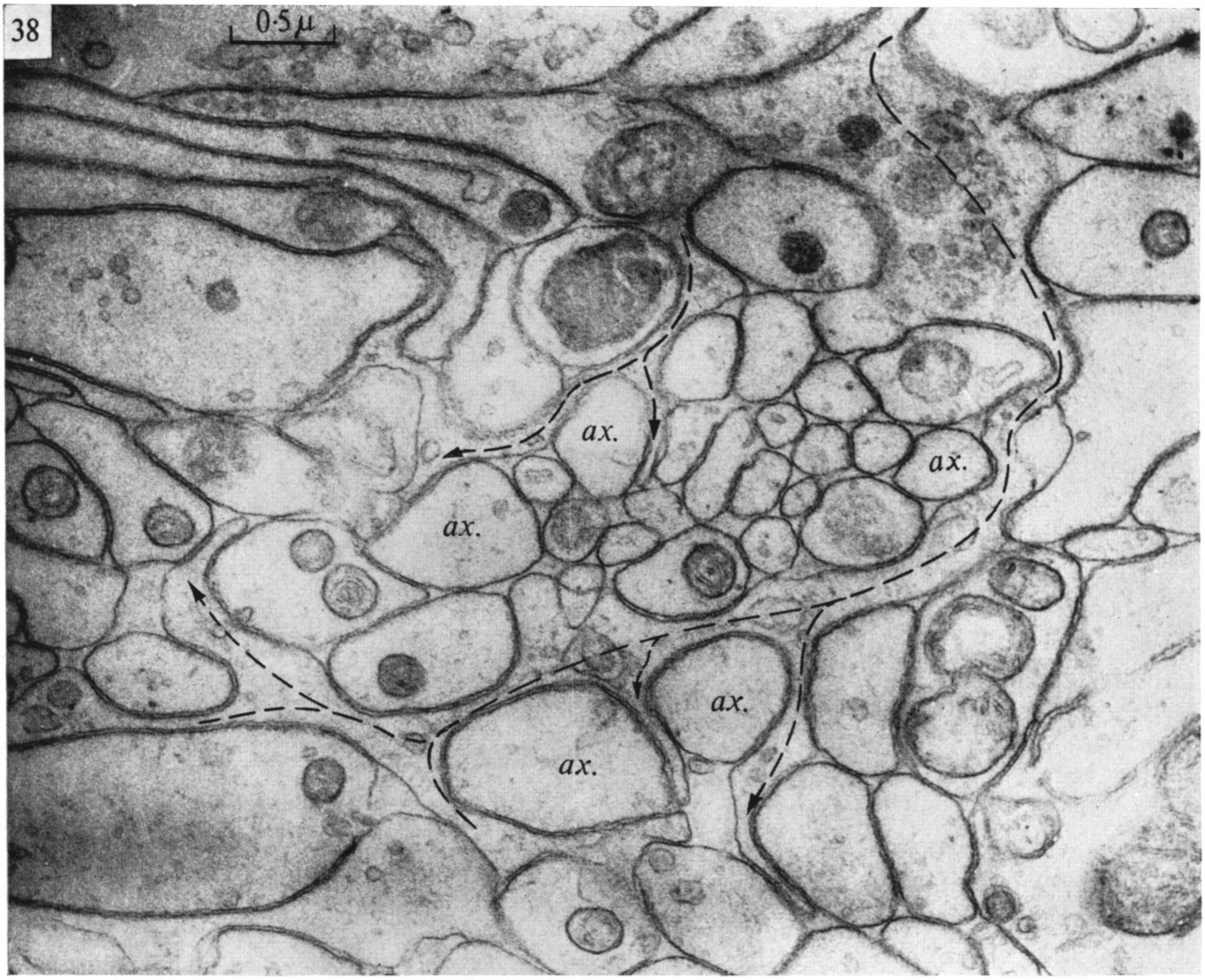


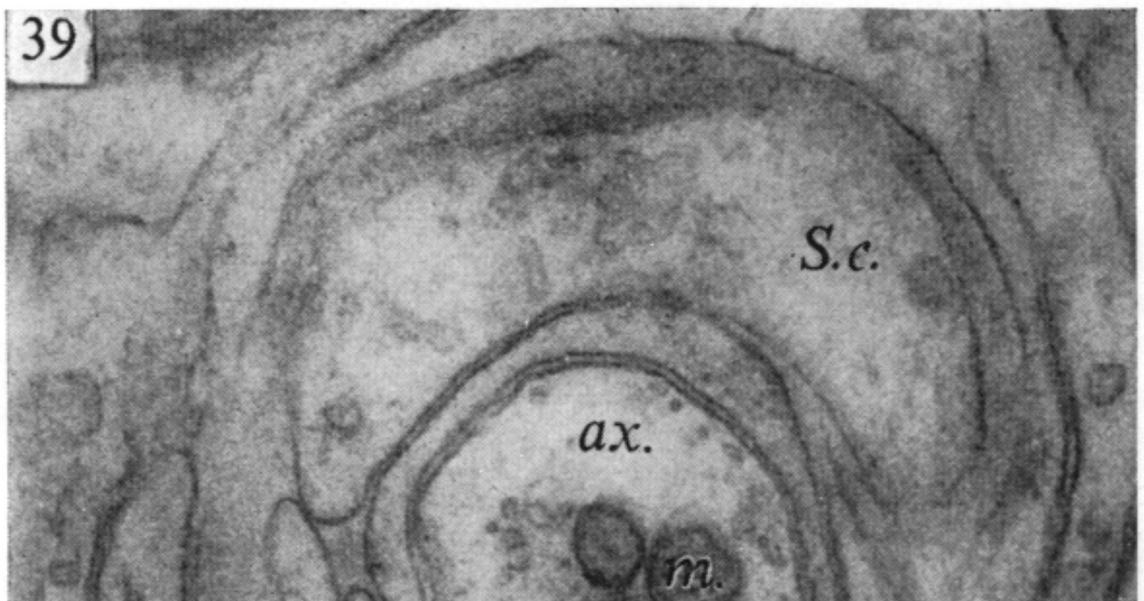
FIGURE 34. Above, a hypodermal cell of the drum with pigment granules, tubules and a nucleus. Below, the attachment cell. The cells are connected to each other by folded, thickened membranes.

FIGURE 35. The tubules of the hypodermal cell (figure 34) seen at higher magnification.

FIGURE 36. Two connecting regions, formed by folded membranes, are seen between two attachment cells. The apposed membranes have thickened regions and tonofibrils (see figure 37).

FIGURE 37. Section of thickened regions of apposed membranes of the attachment cells. A third thinner line of extracellular material appears between the membranes. Tonofibrils lie in the adjacent cytoplasm.





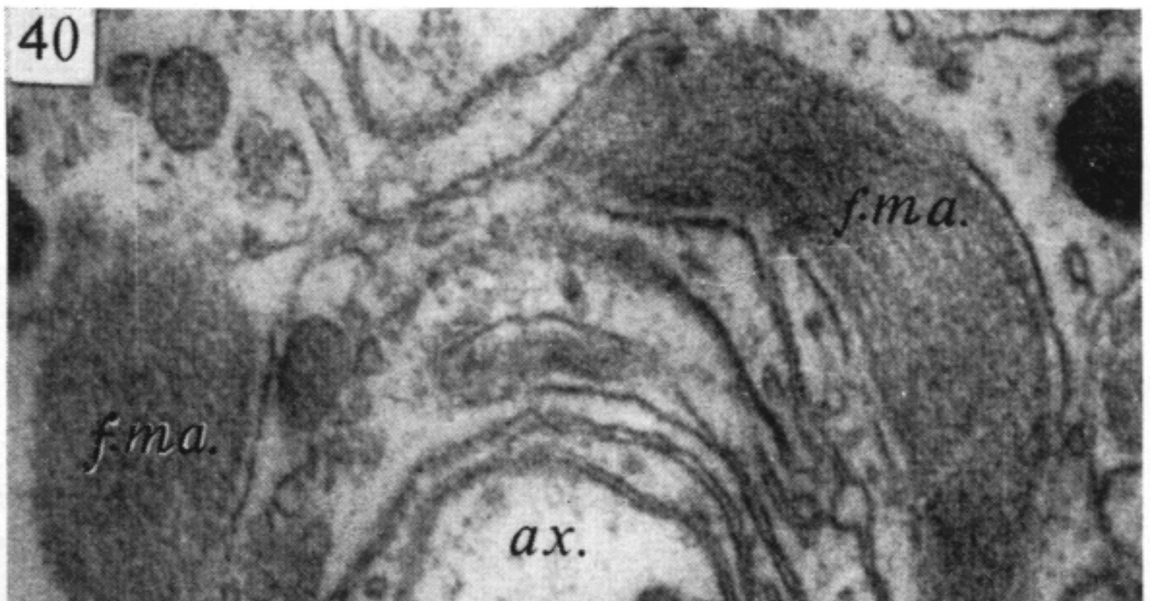


FIGURE 38. Group of extraganglionic axons found in the auditory nerve. The axons lie in bundles that are enclosed in Schwann cell folds (broken lines).

FIGURE 39. An auditory axon. It has its own sheath of Schwann-cell folds.

FIGURE 40. An auditory axon with its sheath of Schwann cell folds. Sheets of extracellular material lie around the outer part of the sheath.