SENSORY CELL/GLAND CELL COMPLEXES ASSOCIATED WITH THE PALLIAL TENTACLES OF THE BIVALVE *LIMA HIANS* (GMELIN), WITH A NOTE ON SPECIALIZED CILIA ON THE PALLIAL CURTAINS

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[Plates 1–10]

CONTENTS

The numerous brilliant orange tentacles with their characteristically ruffed appearance borne by the middle folds of the mantle margins of *Lima hians* possess at least three types of ciliated sensory receptor. The most commonly occurring type consists of a dense tuft of 35–40 stiff, non-motile cilia borne by a cluster of 4–6 primary sensory neurons; it is thought to function as a multidirectional mechanoreceptor. Each cluster of sensory neurons is invariably associated with a pair of gland cells which release a sticky acrid substance when the tentacles are autotomized. Associated with these sensory cell/gland cell complexes in some, but not all, cases is a monociliary receptor and an additional unpaired gland cell; the function of the gland cell is unknown. The monociliary receptor consists of a single, long, stiff kinocilium the base of which is surrounded by a corolla of nine short, club shaped stereocilia. A complex basal apparatus connects the basal body underlying the kinocilium with the stereocilia. It is suggested that this second type of receptor functions as a vibration receptor. The third type of receptor consists of 17–20 non-motile cilia arranged in a circle and borne by a single sensory neuron which, in its distal region, envelopes a gland cell; the latter probably secretes mucus. The receptor is thought to serve as a chemo- and/or mechanoreceptor.

Each of the epithelial cells covering the tentacles encloses a large, fluid filled vacuole with the cytoplasm and cell organelles restricted to a narrow zone underlying the plasma membrane. Each cell functions as a readily deformable constant volume unit capable of adjusting to the marked changes in form and volume which the tentacles may undergo.

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The distal regions of the outer faces of the enlarged inner folds (the pallial curtains) of the mantle margins bear dense patches of short (2 µm), stiff, non-motile cilia. The matrix of the apical regions of these cilia is electron dense and this matrix is interpreted as serving to reinforce and strengthen the apical region. The cilia are thought to function as an anti-slip device when the outer faces of the pallial curtains are opposed. It is also suggested that the electron dense material at the tips of the cilia may so bind the peripheral and central tubules in these regions that intrinsic movement of the cilia by the sliding of the peripheral tubules relative to one another is prevented, although limited passive bending of the cilia could still occur. A similar, but less extensive, electron dense matrix was observed at the tips of the stiff, non-motile, sensory cilia.

INTRODUCTION

Ciliary tufts associated with the ctenidial filaments of bivalves and suspected of having a sensory function have been noted by many workers (Atkins 1936; Owen 1974), but their location among the dense array of cilia covering the frontal faces of the gill filaments makes a study of the cells associated with them difficult. The mantle margins of the file shell, *Lima hians* (Gmelin), are notable for the presence of several hundred brilliant orange or yellow tentacles and it was suspected that they would possess ciliated sensory receptors more amenable to a detailed study. This proved to be so. The tentacles possess at least three types of ciliated sensory receptor and, moreover, the non-sensory epithelial cells and gland cells which, together with the sensory cells, cover the tentacles exhibit a number of unusual features.

During the course of this work it was noted that certain areas of the epithelium covering the outer faces of the greatly enlarged inner folds of the mantle margins bear dense patches of short modified cilia which appear to assist the folds in their function of controlling the entry and exit of water into and out of the mantle cavity.

MATERIALS AND METHODS

Living specimens of *L. hians* were obtained from the Marine Laboratory, Millport. The nerve supply to the pallial tentacles was demonstrated by the Schiff reaction described by Owen (1959). For light microscopy, tentacles and portions of the inner marginal folds were fixed either in cold formolsaline or a modified Bouin-Dubosq fixative (Atkins 1937). Sections of this material were subjected to a variety of general staining and histochemical methods details of which are noted in the text.

For transmission electron microscopy material was fixed either in 4 % glutaraldehyde made up in 3 % NaCl at pH 7.2 (cacodylate buffer) for 2 h and postfixed for 1 h in 1 % osmium tetroxide, or in 1 % osmium tetroxide in 3 % NaCl (pH 7.2) only, for 1 h. While initial fixation in glutaraldehyde provided a more complete and satisfactory preservation of the tissues, sections of material fixed in osmium tetroxide only proved more useful in determining the general disposition of the sensory cells and of the microtubules associated with the gland cells. Some of the more striking differences associated with the two methods of fixation are noted in the text. Following washing and dehydration the tissues were embedded in Araldite resin and sections were stained with alcoholic uranyl acetate (5 min) and lead citrate (5 min).

For scanning electron microscopy material was fixed in a 3:1 mixture of 4 % glutaraldehyde and 1 % osmium tetroxide (pH 7.2, cacodylate buffer). After washing and dehydration the tissues were transferred to amyl acetate and dried by the critical point method. The dried pieces were transferred to specimen stubs, given a thin coating of gold, and viewed in a Cambridge Stereoscan scanning electron microscope at accelerating voltages of 17–20 kV.

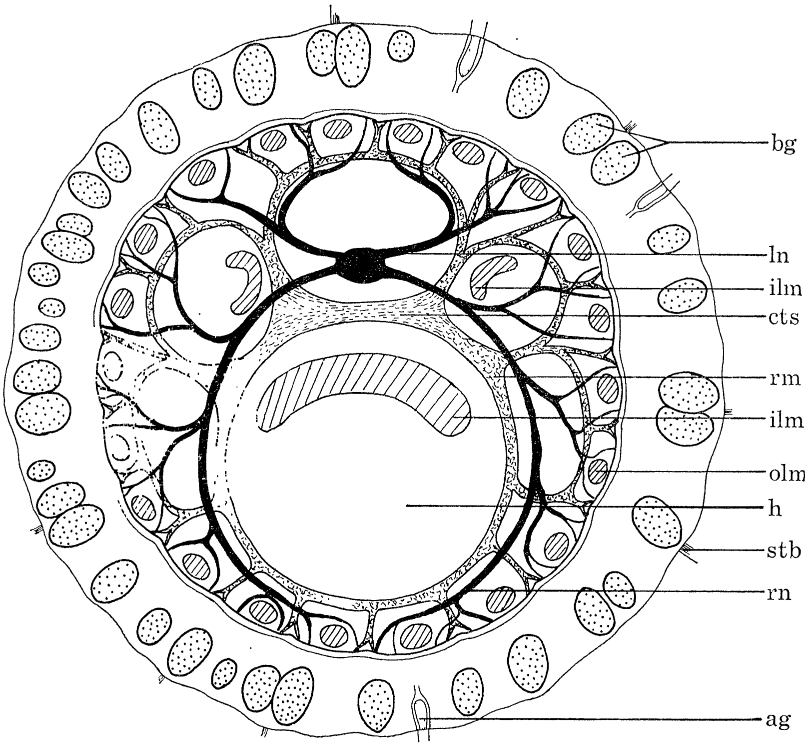

FIGURE 1. Diagrammatic transverse section of a pallial tentacle in the region of a glandular ruff to show the central haemocoele (h) and the disposition of nerves (ln, rn) and muscles (ilm, olm, rm); after Gilmour (1963).

THE PALLIAL TENTACLES

Two significant features of the mantle margins of *L. hians* are the numerous brightly coloured tentacles and the well developed pallial curtains formed by the enlarged inner marginal folds. The pallial tentacles arise from the middle fold of the mantle margin with the longest tentacles when fully extended reaching an overall length of 7 to 8 cm; they can contract to 1 to 2 cm in length. The general morphology and musculature of the tentacles has been described by Gilmour (1963, 1967). The internal cavity of each tentacle is an extension of the pallial haemocoele (figure 1, h) and movements of the tentacles result from variations in hydrostatic pressure controlled by numerous transverse septa and the activity of longitudinally [olm, ilm) and radially (rm) arranged muscle fibres; there are no circular muscles. With the exception of a short basal region each tentacle has a ruffed or annulated appearance (figure 2, plate 1), the ruffs coinciding with zones of gland cells which occur at regular intervals along the length of the tentacle. A branch of the circum-pallial nerve extends along the length of each tentacle (figure 3, plate 1; ln) and, at the level of each zone of gland cells, gives rise to a number of radial nerves (figure 1, rn) which branch repeatedly as they approach the basement lamina underlying the covering epithelium. This epithelium consists of peculiar vacuolated cells interspersed in the regions of the ruffs by what, for convenience, are here termed sensory cell/gland cell complexes.

(*a*) *The epithelial cell*

Under the light microscope (Gilmour 1967) the tentacles appear to be covered by a regular cuboidal to columnar epithelium. Sections of the epithelium viewed under the scanning (figure 10, plate 3) and transmission (figures 4, 5, plate 1) electron microscopes, however, show numerous large and apparently empty spaces (v) and give an initial impression of poorly fixed material. Repeated observations on both fresh and fixed material confirm, however, that each epithelial cell encloses a large, fluid filled, membrane bound vacuole (figure 9, v) with the cytoplasm and cell organelles confined to a thin peripheral zone underlying the plasma membrane. The nucleus is situated basally and surrounded by a thin zone of cytoplasm containing ribosomes, mitochondria and glycogen granules. Strands of cytoplasm extend towards the basal membrane which together with the lateral plasma membrane is underlain by a layer of cytoplasm rarely more than 0.1 μm thick. The apical plasma membrane is modified to form a dense array of microvilli (figure 7, plate 2; mv) and is underlain by a somewhat thicker zone of cytoplasm some 0.2 μm in depth. This apical zone of cytoplasm includes mitochondria and numerous electron dense, membrane bound spheres up to 0.15 μm in diameter; they are presumed to be pigment granules (pg) responsible for the orange colouration of the tentacles in living specimens. Adjoining cells are linked by way of well developed septate desmosomes (sd) and near these junctions are numerous small dictyosomes. The epithelium rests on a well developed fibrous basal lamina (figure 40, plate 9; bl). The shape and dimensions of the vacuolated epithelial cells show considerable variation not only in different regions of the tentacles but also correlated with the extension and contraction of the tentacles. In the regions of the glandular ruffs the individual cells may vary from 35 to 80 μm in height, being taller and narrower in contracted tentacles; between the ruffs they vary from 10 to 25 μm in height.

Sections of material fixed in glutaraldehyde followed by post-fixation in osmium tetroxide, when compared with sections of material fixed in osmium tetroxide only, show a number of differences. In the former, the pigment granules (figure 7, plate 2; pg) are represented by electron dense spheres but in material fixed in osmium tetroxide only (figure 8, pg) the content of these spheres is poorly preserved and the apical zone of cytoplasm is filled with apparently empty membrane bound vacuoles. The orange pigment in the tentacles and mantle margins of *L. hians* has been identified as a xanthophyllic carotenoid (Fischer, Kon & Thompson 1956), a hydroxy hydrocarbon, and such pigments are frequently associated with lipids. Thus the

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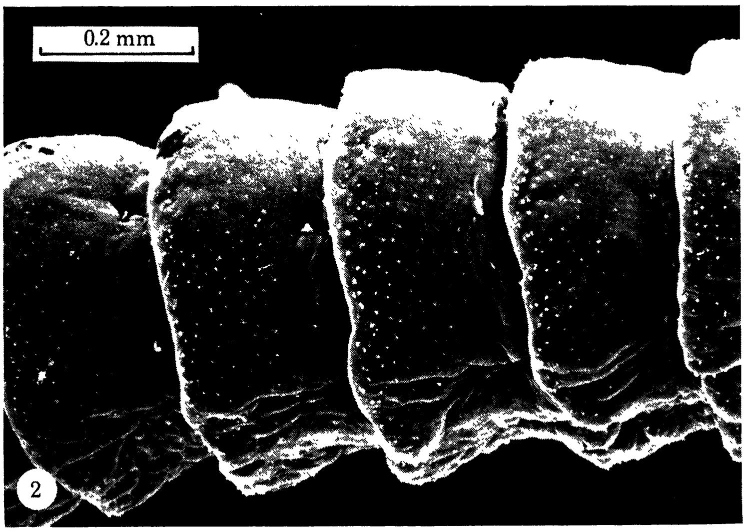
Description of plate 1

FIGURE 2. Scanning electron micrograph of a portion of a pallial tentacle showing the ruffed appearance and the numerous ciliary tufts associated with each ruff.

FIGURE 3. Whole mount of a portion of a pallial tentacle treated with Schiff reagent (Owen 1959) to demonstrate the longitudinal nerve (ln) and the radial nerves extending to each glandular ruff.

FIGURE 4. Low-power electron micrograph of a section through the epithelium of a pallial tentacle in the region of a glandular ruff showing the vacuolated epithelial cells (v) and the sensory cells associated with a type B ciliary tuft (stb); fixative osmium tetroxide.

FIGURE 5. Low-power electron micrograph of a section through the epithelium of a pallial tentacle in a plane more or less parallel to the surface of the tentacle and showing the vacuolated epithelial cells (v), and the paired gland cells (bg) and sensory cells (scb) which comprise a type B sensory cell/gland cell complex; fixative osmium tetroxide.



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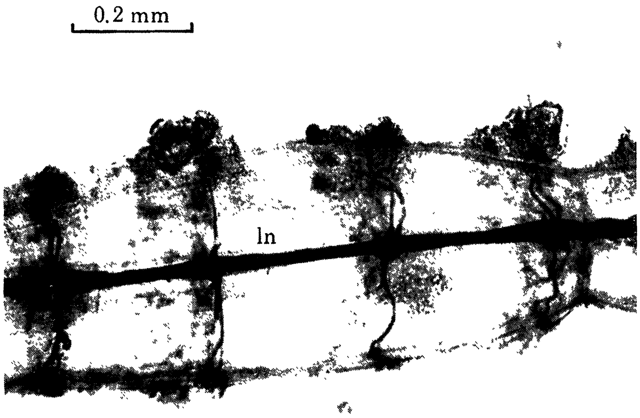

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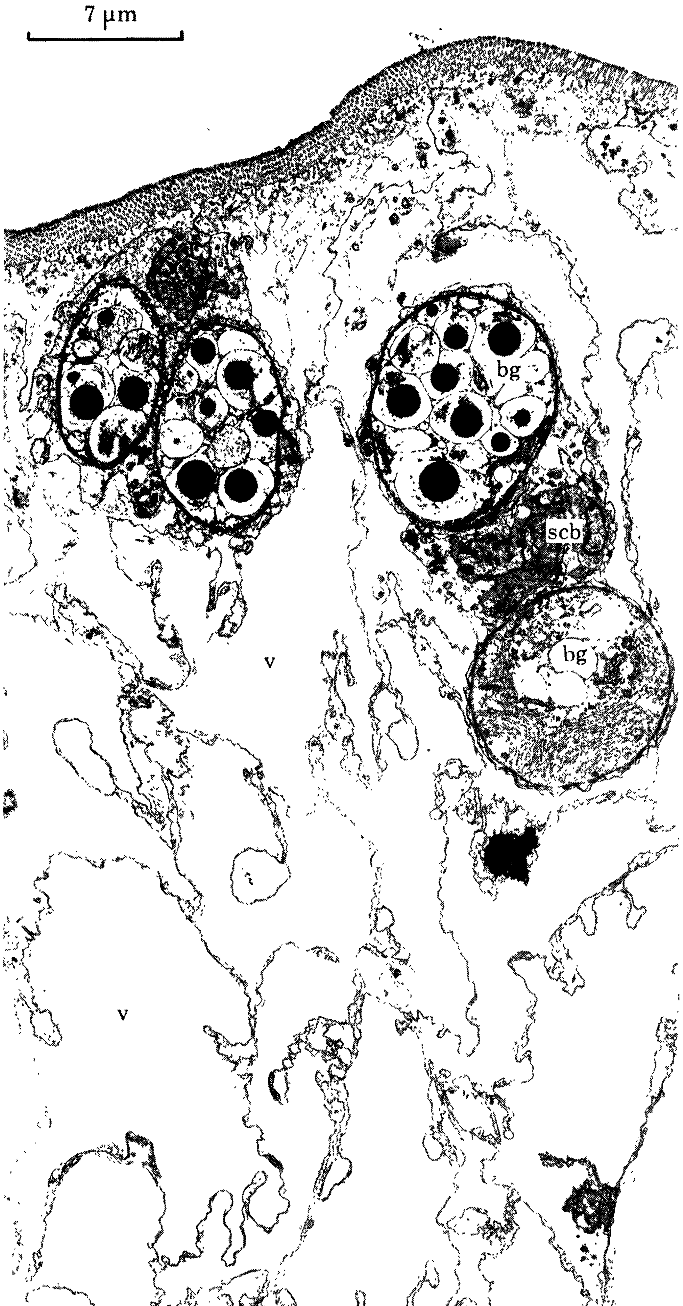

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FIGURES 2–5. For description see opposite.

FIGURES 6–8. For description see opposite.

difference in preservation could be due to the nature of either the lipid or of the pigment. A second difference concerns the appearance of the apical plasma membrane and associated microvilli. In material fixed in osmium tetroxide only, numerous invaginations suggestive of an active process of pinocytosis occur between the bases of the microvilli (figure 8, plate 2); the glycocalyx associated with the plasma membrane presents a granular appearance. When glutaraldehyde is included in the fixation process, the microvilli appear to be branched near their origin from the cell (figure 7) and there are no invaginations of the membrane between the microvilli; the glycocalyx, particularly between the tips of the microvilli, has a pronounced fibrous appearance.

(*b*) *Sensory cell/gland cell complexes*

Tentacles examined in the scanning electron microscope show numerous tufts of cilia projecting from the surface in the regions of the glandular ruffs (figure 2, plate 1). At low magnifications all the tufts appear to be similar but further examination shows that they can be subdivided into one or other of two main types. In one, the tufts consist of 17 to 20 cilia arranged round the periphery of a central depression which is devoid of microvilli (figure 15, plate 3) and which as sections examined in the transmission electron microscope reveal, represents the opening of a gland cell (figure 17, plate 4; ag). The second and more numerous type of tuft consists of some 35 to 40 cilia arranged in a dense cluster and, in tentacles detached from the animal prior to fixation, there is usually present on each side of such tufts a circular pit representing the site of an 'exploded' gland cell (figure 13, plate 3). Thus the tentacles possess at least two types of sensory cell/gland cell complex and for convenience the former will be referred to as a type A complex and the latter, with its paired gland cells, as a type B complex.

(i) *Type A complex*

Figures 16 and 18 (plate 4) are electron micrographs of sections through a type A sensory complex, the former in a plane more or less parallel to the surface of the tentacle and the latter at right angles to the surface. It is apparent that the ring of cilia seen in scanning electron micrographs (figure 15, plate 3) arises from a single cell shaped like a wine glass (figure 9 sca). The cytoplasm forming the 'wall' of the bowl is some 0.2 μm thick, except near its base where it bulges to accommodate a crescent shaped nucleus. The bowl envelopes a single gland cell some 16 μm tall by 4 μm in diameter (figure 17, plate 4; ag). Basal to the bowl the ciliated cell tapers to form a narrow 'stem' which extends towards the basal lamina (figure 18, sca). The cilia, together with a small number of microvilli, arise from the circular rim of the cell at the surface of the tentacle (figures 16, 17). Each ciliary shaft is approximately 5 μm in length

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DESCRIPTION OF PLATE 2

FIGURE 6. Electron micrograph of a section through the basal region of the epithelium showing a cluster of neurons (ax) and associated sheath cells (ss); fixative osmium tetroxide.

FIGURE 7. A section through the apical region of the epithelium showing the narrow zone of cytoplasm with its contained pigment granules (pg) which bounds the cell vacuole (v); fixative glutaraldehyde followed by osmium tetroxide.

FIGURE 8. An enlargement of the area marked in figure 11 (plate 3) to show the apical region of a monociliated sensory cell (mcr) and the modified basal apparatus underlying the kinocilium and the stereocilia (sc). Compare the appearance of the pigment granules (pg), apical plasma membrane and microvilli with that in figure 7; fixative osmium tetroxide.

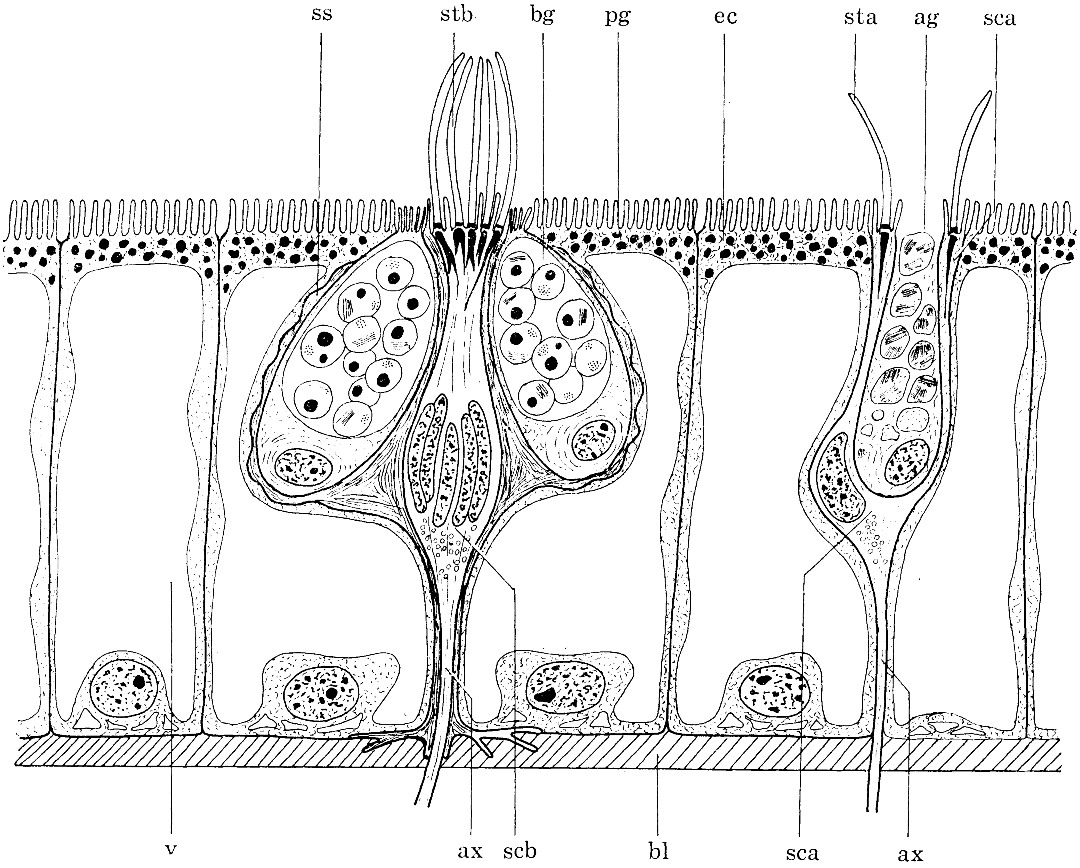


FIGURE 9. A diagrammatic representation of the main elements comprising the epithelium in the region of the glandular ruffs of the pallial tentacles. They include vacuolated epithelial cells (ec), type B ciliary tufts (stb) with associated sensory neurons (scb) and paired gland cells (bg), and type A ciliary tufts (sta) arising from a single sensory neuron (sca) which in the distal region envelopes a single gland cell (ag).

DESCRIPTION OF PLATE 3

FIGURE 10. Stereoscan electron micrograph of a glandular region of a pallial tentacle in which the epithelium has been torn to reveal the vacuolated nature of the epithelial cells and a type B sensory complex (stb) with its associated gland cells (bg).

FIGURE 11. Transverse section of a pallial tentacle to show a type B sensory cell/gland cell complex. The inset marked is shown in greater detail in figure 8 (plate 2); fixative osmium tetroxide.

FIGURE 12. Low-power stereoscan electron micrograph of the glandular region of a pallial tentacle showing the ciliated sensory tufts.

FIGURE 13. Stereoscan electron micrograph of a type B sensory complex comprising a tuft of 35–40 cilia with on each side the circular depressions marking the openings of 'exploded' gland cells.

FIGURE 14. A type B sensory tuft as in figure 13, but in this case associated with a single long kinocilium.

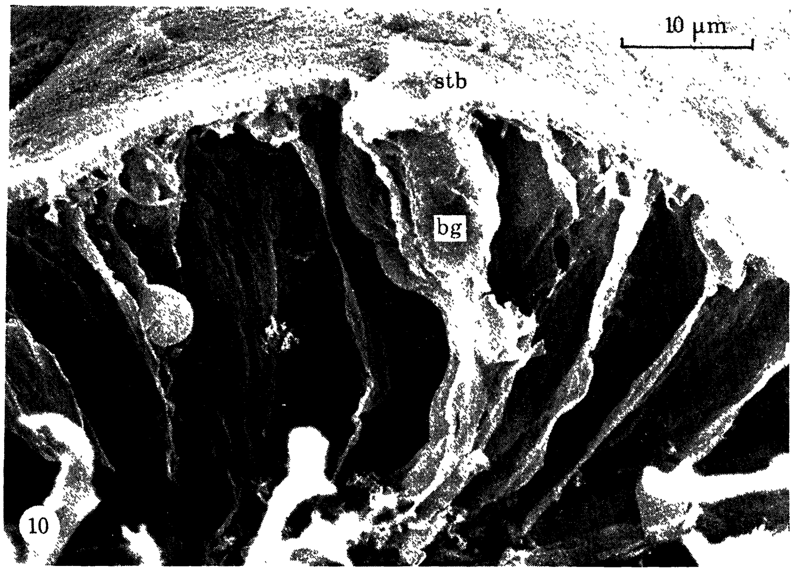
FIGURE 15. A type A sensory tuft; the area within the circle of cilia represents the opening of a gland cell.

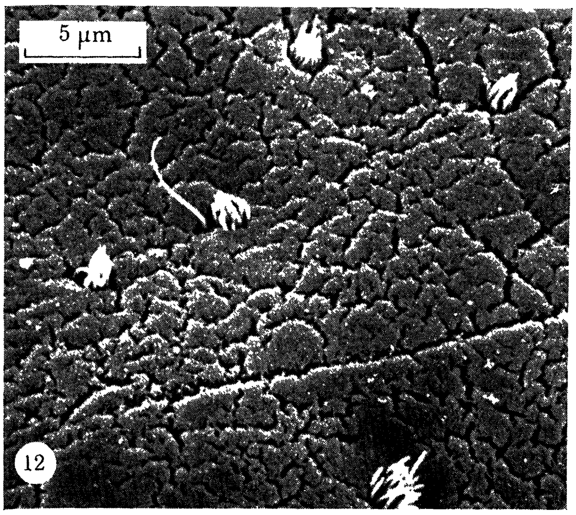
DESCRIPTION OF PLATE 4

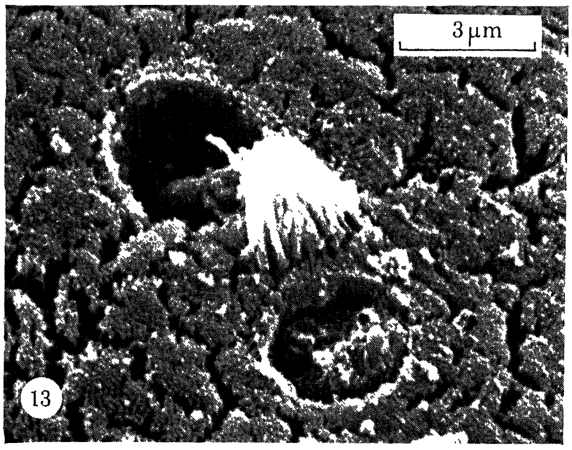
FIGURE 16. A section through the distal region of a type A complex in the plane of the line XY in figure 17. The cilia arise from a single sensory cell which encircles a gland cell (ag); fixative osmium tetroxide.

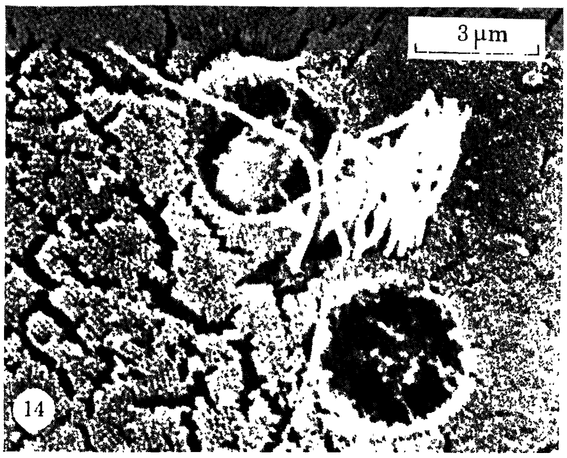
FIGURE 17. A transverse section of a pallial tentacle showing the components of a type A sensory cell/gland cell complex. The line XY represents the plane of the section in figure 16; fixative osmium tetroxide.

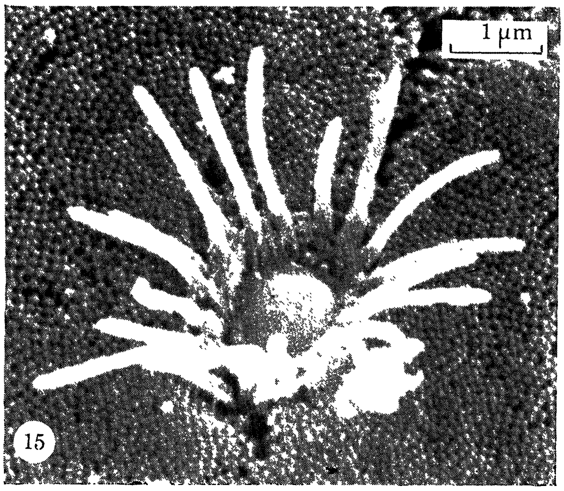
FIGURE 18. A section through a type A sensory cell/gland cell complex showing the extension of the sensory cell (sca) towards the basal lamina; fixative osmium tetroxide.





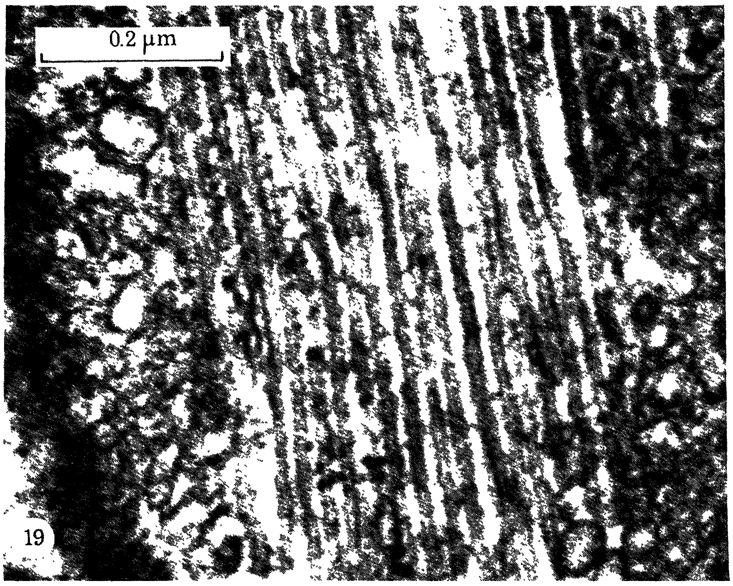






FIGURES 10–15. For description see opposite.

FIGURES 16–18. For description see p. 50.



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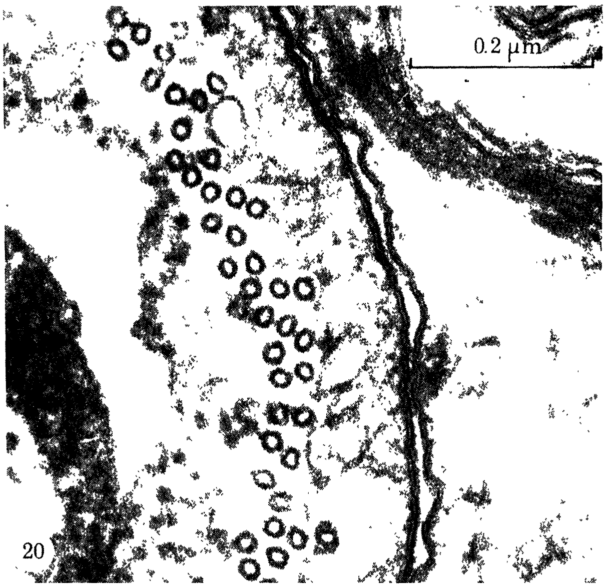

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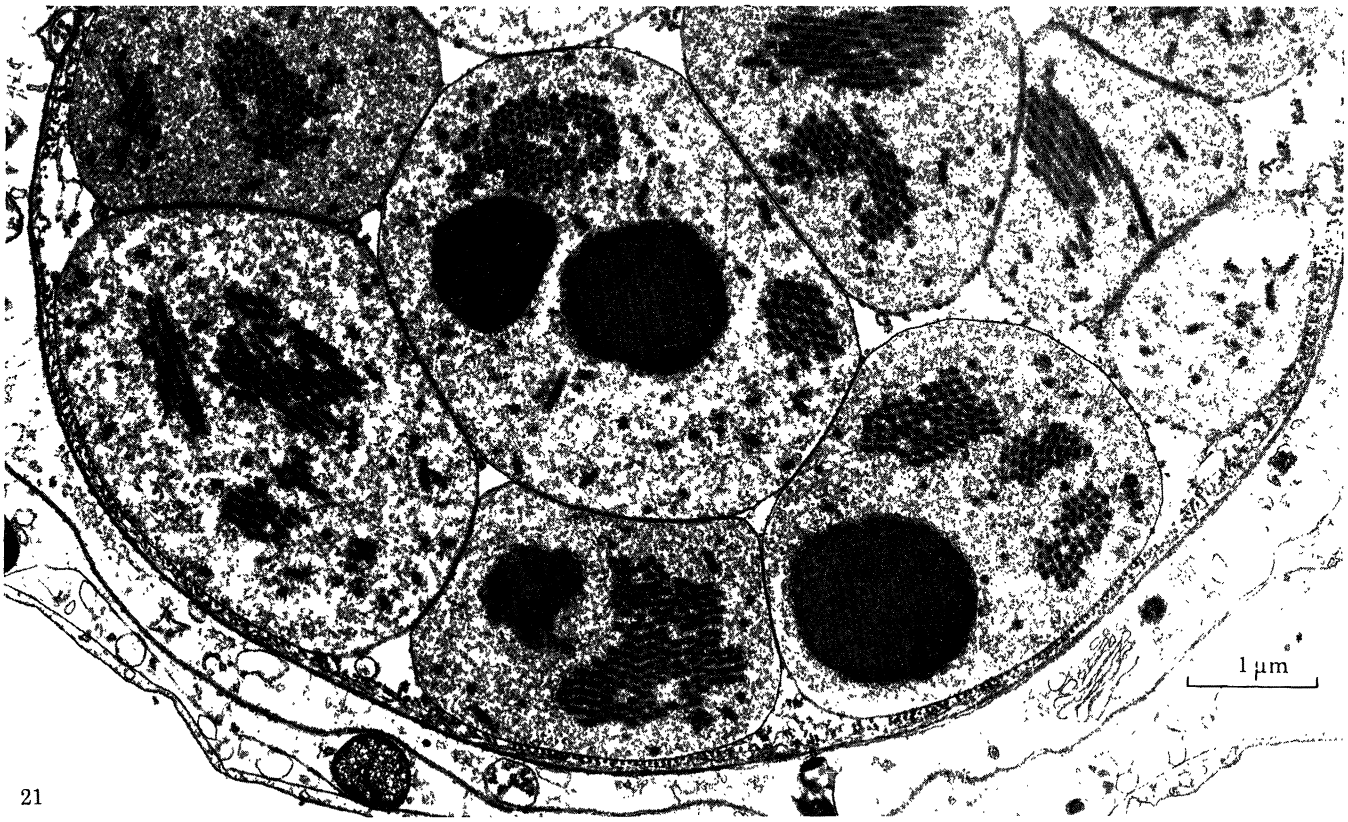

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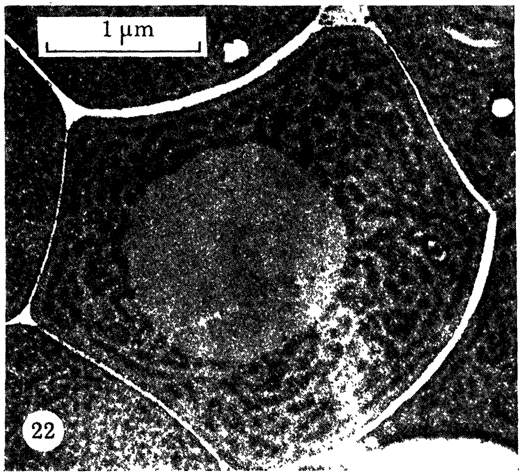

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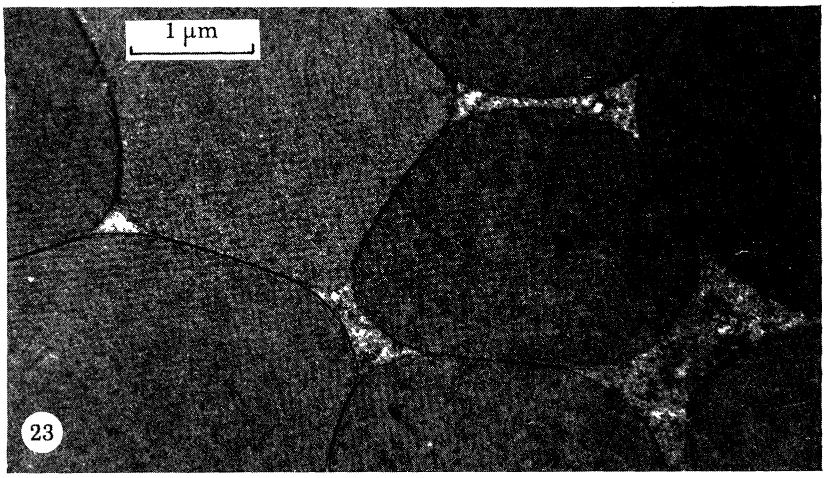

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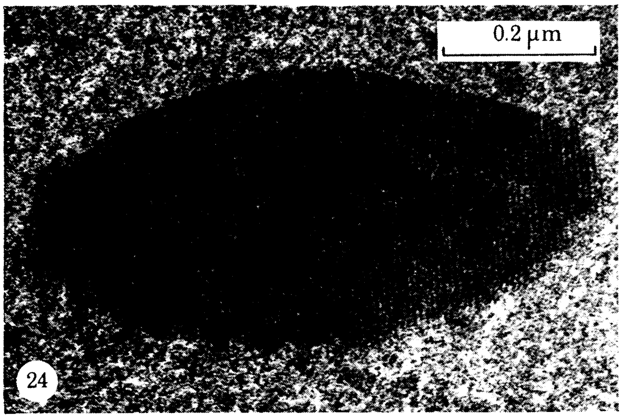
Figures 19–23. For description see p. 51.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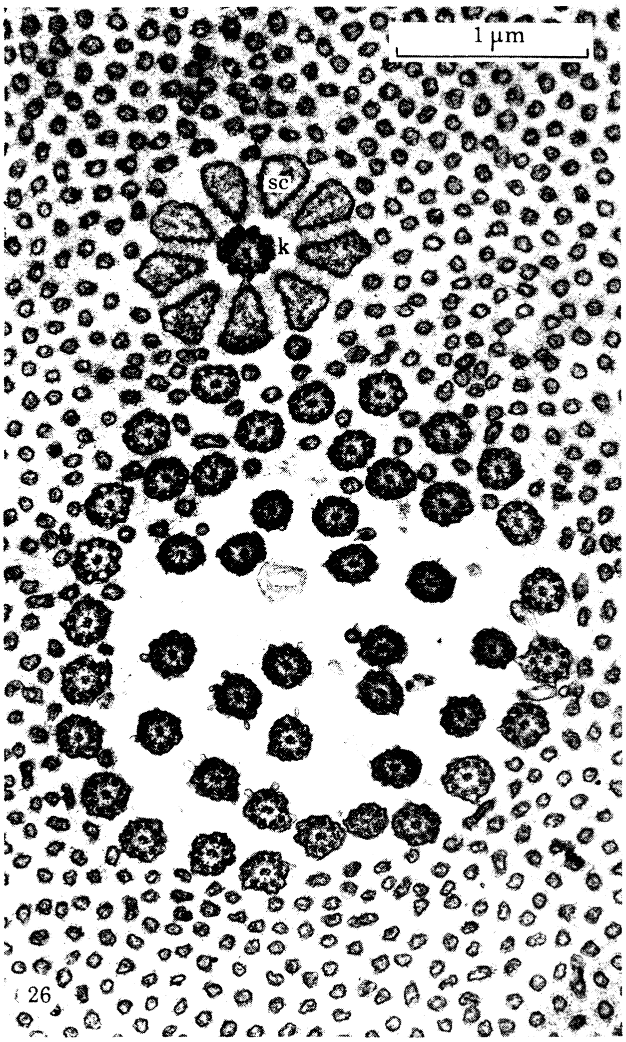
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FIGURES 24–28. For description see opposite.

and contains the normal 9 + 2 complement of fibrils; well developed rootlets extend from the basal bodies into the cytoplasm. The basal feet (figure 16, bf), one of which extends laterally from each basal body, are centrifugally arranged. The cytoplasm forming the bowl of the cell contains mitochondria and numerous microtubules while basal to the nucleus, that is where the cell tapers to form the 'stem' (figure 18, sca), the cytoplasm is filled with numerous small dense-core vesicles which appear to arise from the Golgi bodies situated in this region. It was not possible to trace the cell to the basal lamina underlying the epithelium and thus to determine whether, as in the type B sensory cells, the cell penetrates the lamina to join the underlying nerve trunks. There is little doubt, however, that this type A ciliated cell is a sensory cell and probably a primary sensory cell since despite careful examination no synapses could be identified in the basal regions of the epithelium.

The type A gland cell which lies within the cup formed by the ciliated sensory cell consists of a basal region, containing the nucleus (figure 17, n) and perinuclear cytoplasm, and a distal region filled with secretory spheres (sp) and occupying some two thirds of the total volume of the cell. The perinuclear cytoplasm is filled with a well developed granular endoplasmic reticulum and a number of active Golgi bodies. The latter appear to give rise to the secretory spheres which in the basal region are filled with a diffuse granular material. Distally, the secretory spheres are somewhat larger, show an increased electron density, and include regions of electron dense fibrous material. The opening of the gland cell at the surface of the tentacle lies within the circle of cilia and is capped by a thin membrane devoid of microvilli.

(ii) *Type B complex*

As already noted, type B sensory complexes are characterized in scanning electron micrographs by tufts of 35 to 40 cilia which in suitably treated material frequently have on each side a circular pit representing the site of an 'exploded' gland cell (figure 13, plate 3). Sections of the tentacles show that unlike the type A ciliary tufts these dense tufts of cilia are borne by a compact cluster of 4 to 6 cells (figures 29, 30, plate 7) and each cluster of such cells is invariably associated with a pair of gland cells (figure 5, plate 1; bg) to form what can be termed the basic type B complex shown diagrammatically in figure 9. Two further structures are,

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DESCRIPTION OF PLATE 5

FIGURES 19 and 20. Longitudinal and transverse sections through the microtubules present in the 'wall', i.e. the peripheral cytoplasm underlying the lateral plasma membrane, of the paired type B gland cells; fixative osmium tetroxide.

FIGURE 21. Transverse section through a region of a mature type B paired gland cell showing the complex nature of the contained secretory spheres; fixative glutaraldehyde followed by osmium tetroxide.

FIGURES 22 and 23. Electron micrographs representing early stages in the maturation of the secretory spheres in a paired, type B gland cell; fixative glutaraldehyde followed by osmium tetroxide.

DESCRIPTION OF PLATE 6

FIGURES 24 and 25. Further stages in the maturation of the secretory spheres in the paired type B gland cells; fixative glutaraldehyde followed by osmium tetroxide.

FIGURE 26. Electron micrograph of a section through a type B sensory tuft and associated kinocilium (k) and stereocilia (sc) in a plane parallel to the surface of the tentacle; fixative glutaraldehyde followed by osmium tetroxide.

FIGURE 27. Transverse section of a pallial tentacle showing the distal region of an unpaired gland cell; fixative osmium tetroxide.

FIGURE 28. The cell body region of the unpaired gland cell shown in figure 27; fixative osmium tetroxide.

however, occasionally although not invariably associated with type B complexes. In approximately 1 in 10 of the complexes there is located to one side of the tuft of cilia a single long cilium the base of which is surrounded by a characteristic arrangement of modified microvilli or stereocilia (figure 14, plate 3). The second feature, in this case associated with approximately 1 in 4 of the complexes, is a single unpaired gland cell (figure 29, plate 7; ug) with an appearance and disposition distinct from that of the paired gland cells. The relationships of these various elements which may comprise a type B complex are shown in figure 30 and also in a simplified diagrammatic form in figure 38. The cluster of cells (scb) bearing the dense tuft of cilia occupy a more or less central position. Of the four quadrants around this position, two, one on each side, are invariably occupied by the paired gland cells (bg) and the remaining two by the unpaired gland cell (ug) and the cell bearing the single long cilium (mcr) when either or both of these are present. It will be noted that while the cell bearing the single cilium abuts directly on to the cluster of cells bearing the ciliary tuft, the paired and unpaired gland cells are separated from the cluster by intervening epithelial cells.

As described below, the ciliated cells are primary sensory neurons and as such extend through the basal lamina (figure 40, plate 9; ax). The paired gland cells, on the other hand, do not make contact with the basal lamina underlying the epithelium (figure 11, plate 3). Both gland cells and sensory cells are, however, invested by sheath cells which are attached to the basement lamina by well developed hemidesmosomes (figure 9); the cytoplasm of these sheath cells is filled with a dense feltwork of fibrils (figure 6, plate 2; ss).

The paired gland cells (figure 5, plate 1; bg) occurring on each side of a cluster of ciliated sensory cells (scb) are ovoid in form, measure some 50 μm by 15 μm, and since they do not reach the basement lamina give the impression of being suspended from the surface of the tentacle (figure 11, plate 3). The basal quarter of the cell is occupied by the nucleus (n) and an extensive endoplasmic reticulum which frequently appears to be poorly preserved and to be undergoing disintegration. The remainder of the cell is filled with large (up to 4 μm in diameter) membrane bound spheres (sp). Enclosing this latter region of the gland cell and immediately underlying the lateral plasma membrane and narrow zone of vesiculated cytoplasm is a well developed system of microtubules most clearly seen in material fixed in osmium tetroxide only (figures 19, 20, plate 5). The tubules extend in the long axis of the cell from the region of the basal perinuclear cytoplasm to the subapical region near the septate desmosomes linking the gland cells to the adjoining epithelial cells. In this later region, the plasma membrane of the gland cell, accompanied by that of the adjoining epithelial cells, forms numerous button-like invaginations (figure 30, plate 7; figure 38, b). Over the apex of the gland cells the plasma membrane is intact and bears microvilli which are shorter and narrower than those borne by the adjoining epithelial cells; the gland does not open to the exterior.

The paired gland cells and their contents are clearly visible in material processed for light microscopy. In the majority the contained spheres show a faint yellow tinge in unstained material, give a positive Schmorl's reaction and are partially positive to mercury bromphenol blue; in the latter case the positive reaction is restricted to a small spherical region within each secretory sphere. A small number of paired gland cells contain spheres which give negative results with the above tests but react positively when treated with periodic acid – Schiff (p.a.s.). Under the transmission electron microscope the secretory spheres in the majority of gland cells have the appearance shown in figure 21 (plate 5). Each sphere contains one or more electron dense nucleoids and numerous rod-shaped structures occasionally dispersed throughout the matrix of the sphere but more frequently grouped into well defined clusters. In material fixed in osmium tetroxide only (figure 11, plate 3; sp) the general matrix of the spheres is poorly preserved. It is presumably the nucleoids of the spheres which react positively with bromphenol blue. Occasionally, the spheres in the gland cells present the appearance shown in figure 22 (plate 5). They lack both nucleoids and rod-like structures and the general matrix exhibits a reticulate pattern of electron dense material against a moderately electron dense background. Glands of this type are believed to represent those which react positively with p.a.s.

Despite the marked differences in appearance and staining properties the above descriptions almost certainly represent different stages of the one gland type with the more numerous form, in which the secretory spheres contain nucleoids and rod-like structures, representing the mature stage. This conclusion is based not only on the general morphology and disposition of the glands but also the occasional occurrence of glands which appear to represent stages intermediate between these two forms. The sequence is interpreted as follows. The reticulate electron dense material in the p.a.s. positive spheres (figure 22, plate 5) increases until the whole sphere presents a homogeneous moderately electron dense appearance (figure 23); this is accompanied by the loss of the p.a.s. positive reaction. Rod-like structures, initially dispersed haphazardly throughout the matrix appear to 'condense' within these spheres (figure 25, plate 6) as does also an electron dense nucleoid which at first exhibits a pronounced crystalline structure (figure 24). Finally, the rod-like structures group into well defined clusters and the crystalline structure of the nucleoid is lost or obscured (figure 21, plate 5).

The unpaired gland cell occasionally associated with type B sensory cell/gland cell complexes consists of a cell body which projects below the level of the paired gland cells and a long narrow neck which extends distally to open at the surface of the tentacle. The cell body which, like that of the paired gland cells, does not make contact with the basal lamina, contains the nucleus (figure 28, plate 6; n), a well developed endoplasmic reticulum and a large and apparently active Golgi apparatus (ga). Also present are numerous membrane bound spheres which, apart from some variation in the region of the Golgi apparatus, tend to be uniformly electron dense. The long neck of this unpaired gland cell is filled with similar electron dense spheres (figure 27) the contents of which appear to be released at the surface of the tentacle.

As already noted, the type B ciliary tufts are borne by clusters of 4 to 6 cells. At the surface of the tentacle each cluster of such cells forms a characteristic pattern which shows little variation. As shown diagrammatically in plan view (figure 38, scb), the outlines of one or two centrally placed cells are surrounded by two semi-circular cells which in turn are almost enclosed within a single cell, the whole forming a compact unit which bears the 35 to 40 cilia forming the tuft (figure 4, plate 1; stb). The cilia are some 5 μm in length, possess the normal $9+2$ complement of fibrils, and well developed rootlets which extend deep into the cytoplasm of the cells. Of particular interest is the orientation of the two central fibrils and of the basal feet, one of which projects laterally from the basal capsule of each cilium (figure 29, plate 7; bf). Each basal foot tends to project outward along a line radiating from the centre of the cluster of ciliated cells. If it is assumed that the cilia are motile this suggests that the effective stroke of each cilium comprising the tuft lies in a plane which radiates from the centre of the tuft. This conclusion is also supported by the orientation of the two central fibrils in the shaft of each cilium.

The configuration of the ciliated cells described above applies only at the surface of the tentacle and although the cells remain grouped together it is quickly lost as they penetrate the epithelium. The nuclei of the cells lie in the mid-region of the epithelium (figures 4 and 5, plate 1; figure 9) between the bases of the paired gland cells. Distal to the nucleus the cytoplasm of each cell contains a well defined Golgi apparatus, numerous small membrane bound vesicles, occasional multivesicular bodies and one or more electron dense lipo-fuchsin granules. Basal to the nucleus the cytoplasm contains numerous small membrane bound vesicles many containing dense contents. In the basal region of the epithelium each cell tapers to form an axon some 0.2 μm in diameter containing well defined microtubules. Clusters of 4 to 6 such axons invested by sheath cells extend to the base of the epithelium (figure 6, plate 2). The sheath cells are firmly attached to the basement lamina by way of hemidesmosomes while the axons penetrate the basal lamina (figure 40, plate 9) to join the radial nerves which arise from the longitudinal nerve extending the length of each tentacle.

The general features, that is the position of the nucleus, the presence of numerous small vesicles and of microtubules etc., of the cell which bears the single long cilium occasionally associated with type B ciliary tufts are essentially similar to those already described for the type B sensory cells. The major differences lie in the complexity of the basal apparatus which underlies the ciliary shaft and the presence of a ring or corolla of short microvilli or stereocilia which arise from the apical surface of the cell (figure 8, plate 2; sc) and surround the base of the cilium or kinocilium (figure 26, plate 6; k). The kinocilium is some 10–15 μm in length and, in the living tentacle, can be seen to project stiffly from the surface; the shaft appears to possess the normal $9+2$ complement of tubules. This is expressed with some hesitation since sections through the distal regions of the kinocilium were not obtained. The description given below is based on a fortunate series of transverse sections obtained through the basal regions of the kinocilium and the apical regions of the underlying cell, a selection of which are shown in figures 31–36 (plate 8); figure 37 is a diagrammatic representation based on these sections.

Well developed rootlets extend into the cytoplasm of the cell (figure 8, plate 2). They arise not from the basal body underlying the kinocilium but from a short cylinder of fibrous material which encircles the basal body (figure 31, plate 8). The basal body (figure 32) possesses the typical arrangement of triplets and gives rise to nine radiating spokes which extend outward to the upper margin of the surrounding fibrous cylinder (figure 33). Here the spokes bifurcate

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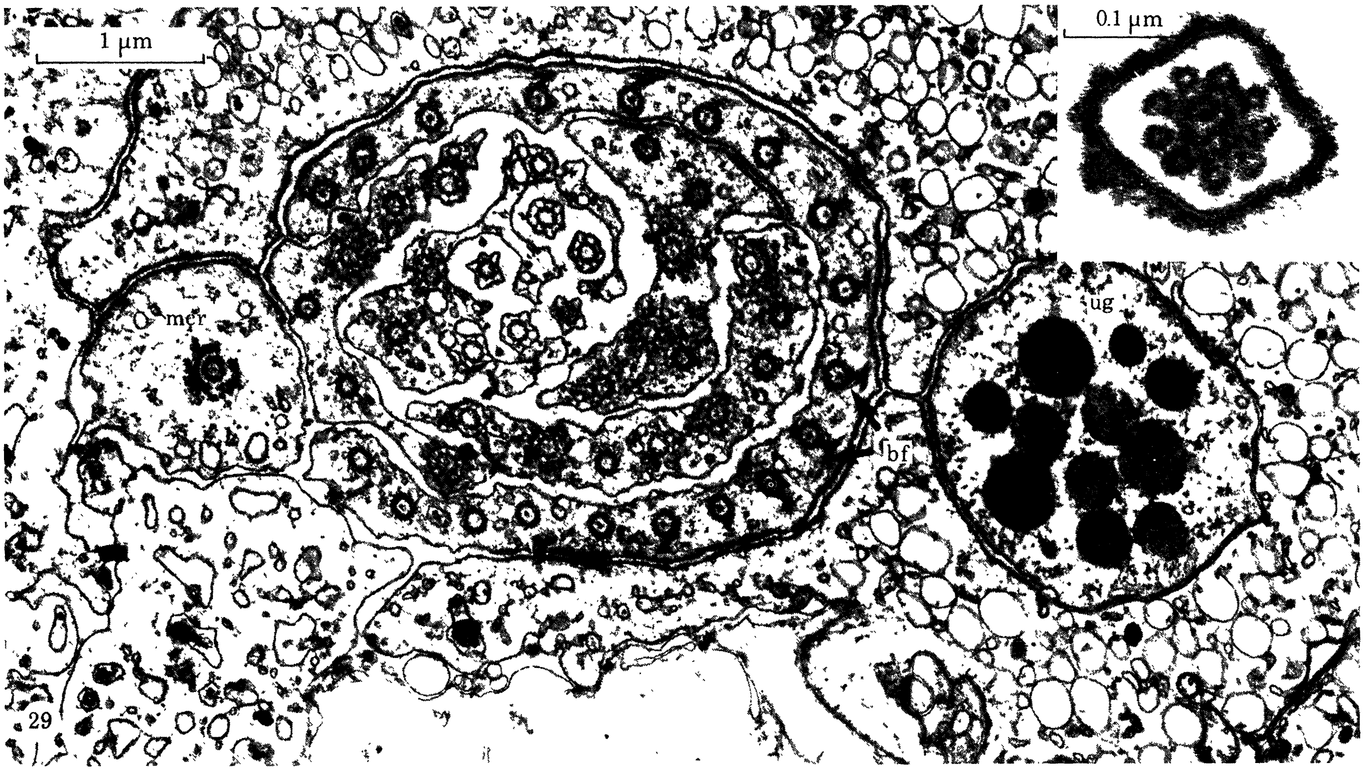
DESCRIPTION OF PLATE 7

FIGURE 29. Section in a plane parallel to the surface of the tentacle through a type B complex showing the orientation of the basal feet (bf), and the positions of the monociliary sensory cell (mcr) and unpaired gland cell (ug). Inset: a transverse section through the distal tip of one of the cilia in a type B sensory tuft. Fixative: osmium tetroxide.

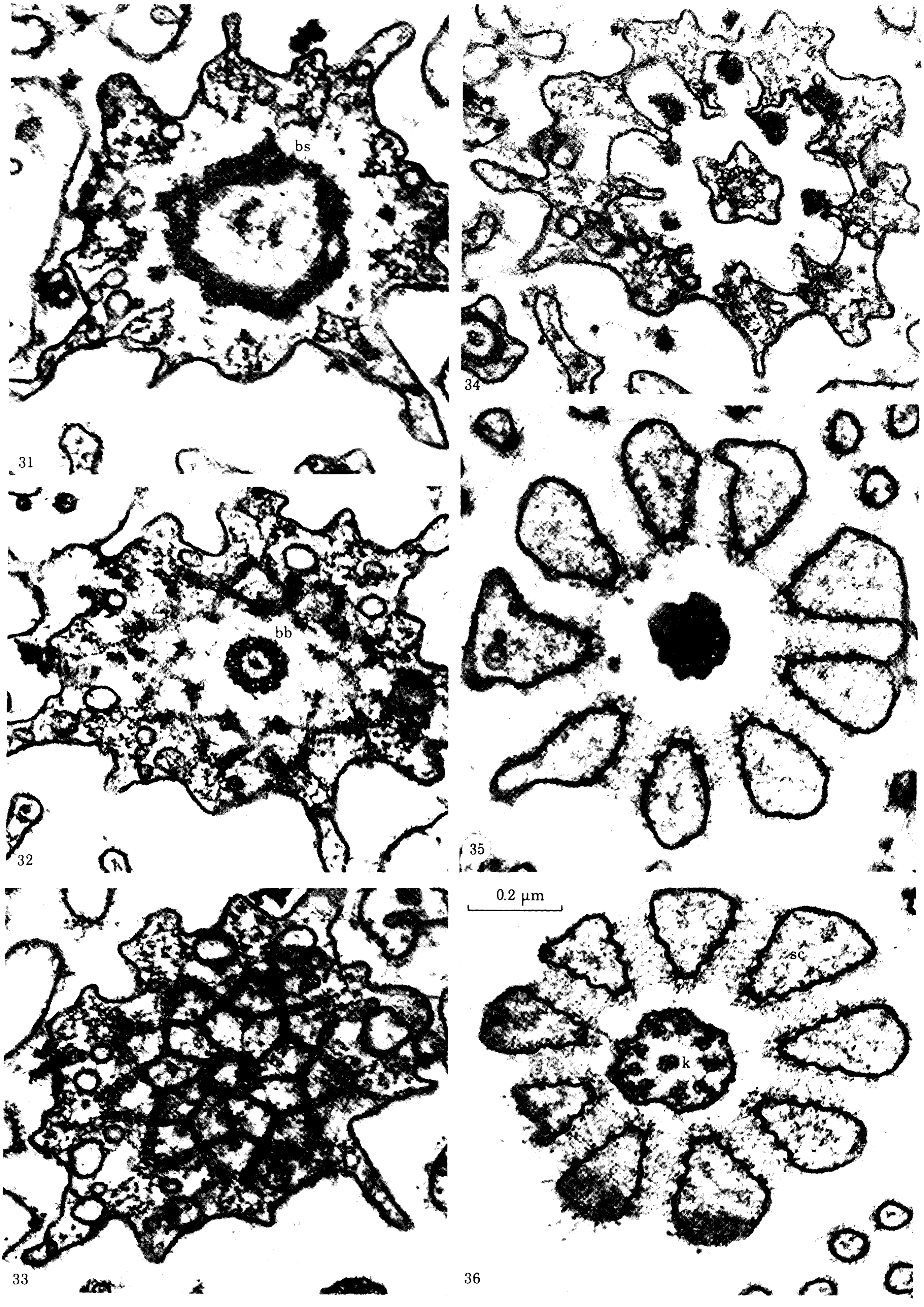
FIGURE 30. A similar section to that shown in figure 29 but at a slightly lower (i.e. basal) level and showing all the elements which may comprise a type B complex. These are: (i) the cluster of sensory neurons (scb) which bear the non-motile cilia, (ii) a single sensory neuron (mcr) which bears the kinocilium and nine stereocilia, (iii) paired gland cells (bg) and (iv) an unpaired gland cell (ug); fixative: glutaraldehyde followed by osmium tetroxide.

DESCRIPTION OF PLATE 8

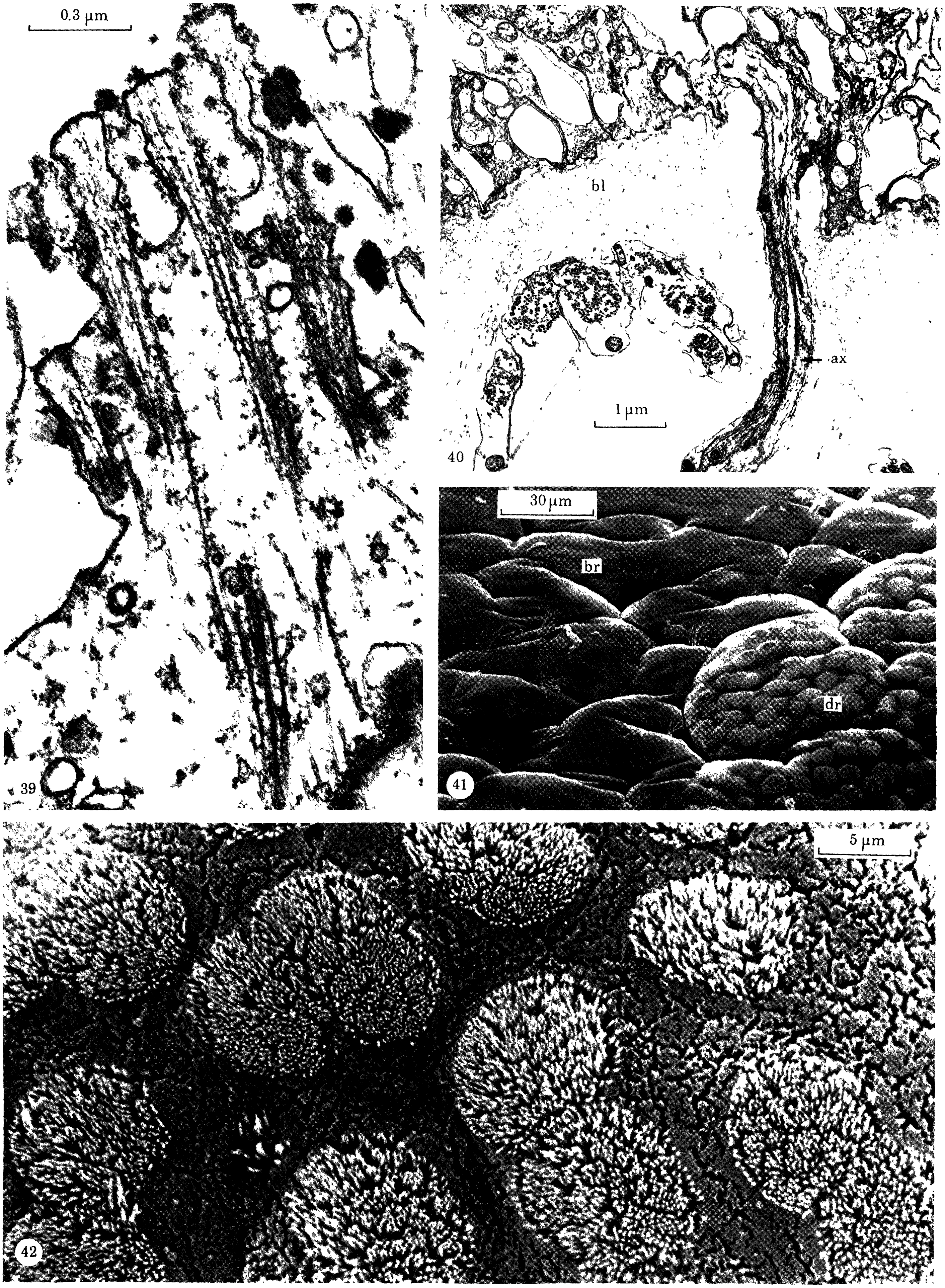
FIGURES 31–36. A series of transverse sections through the basal region of a kinocilium (k) and associated stereocilia (sc). Magnification for all figures shown in figure 36; fixative: osmium tetroxide.



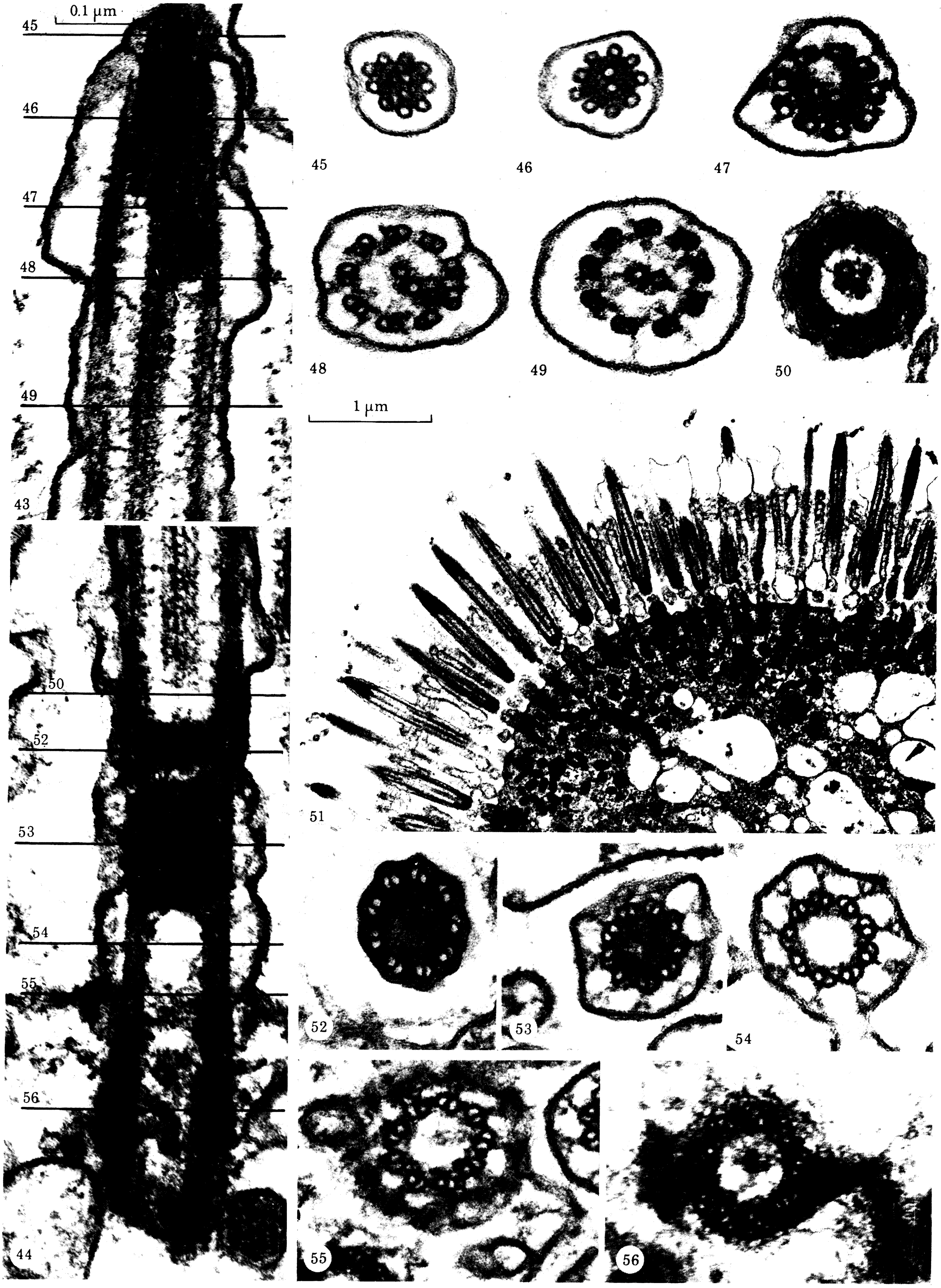
FIGURES 29 AND 30. For description see opposite.



FIGURES 31–36. For description see p. 54.



FIGURES 39–42. For description see p. 55.



FIGURES 43–56. For description see opposite.

and each branch, made up of fine filaments, extends to the basal region of alternate stereocilia where they appear to link with the microtubules extending into the stereocilia from the underlying cytoplasm (figure 39, plate 9). In other words, the tubules in each stereocilium are linked both to the cylinder of fibrous material and to alternate spokes radiating from the basal body. Distal to this region the triplets of the basal body are transformed to doublets (figure 34, plate 8) and these extend through the basal plate (figure 35) where the paired central tubules make their appearance to give the kinocilium the characteristic $9+2$ appearance (figure 36). Each wedge-shaped stereocilium projects some 0.5 μm from the surface of the cell to form a corolla round the base of the kinocilium. The stereocilia are linked to one another by a well developed fibrous glycocalyx.

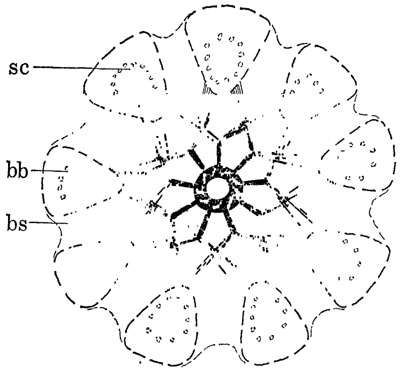


FIGURE 37

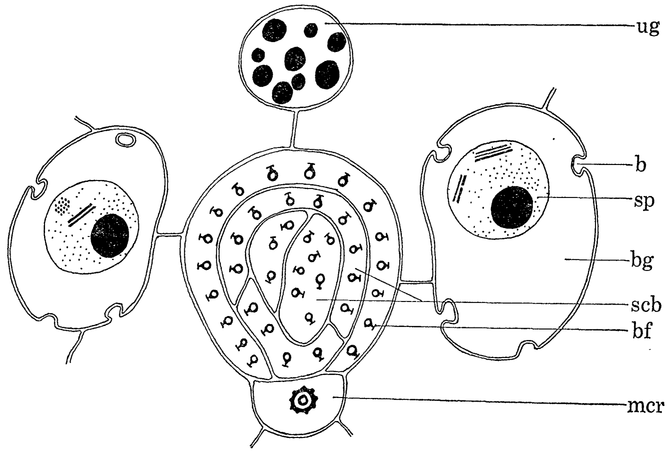


FIGURE 38

FIGURE 37. Diagrammatic plan view of the basal apparatus underlying a kinocilium. The limits of the sensory cell and of the nine stereocilia (sc) are indicated by broken lines.

FIGURE 38. Diagrammatic plan view of the elements which may comprise a type B complex. The cluster of ciliated sensory cells (scb) and paired gland cells (bg) are invariably present; note the orientation of the basal feet (bf) projecting from the basal bodies which underlie the cilia. The unpaired gland cell (ug) and monociliary sensory cell are not always present.

DESCRIPTION OF PLATE 9

FIGURE 39. A longitudinal section through three of the stereocilia which encircle the base of a kinocilium showing microtubules extending into them from the cytoplasm of the sensory cell; fixative: osmium tetroxide.

FIGURE 40. A transverse section through the basal region of the epithelium of a pallial tentacle showing a cluster of axons (ax) traversing the basal lamina (bl); fixative: osmium tetroxide.

FIGURE 41. Stereoscan electron micrograph of the outer face of the pallial curtain showing the basal (i.e. nearer the shell margin) region (br) largely devoid of cilia and the distal region (dr) with dense patches of short cilia.

FIGURE 42. The region (dr) in figure 41 at a higher magnification.

DESCRIPTION OF PLATE 10

FIGURES 43 AND 44. Longitudinal sections of the distal and basal region respectively of one of the short cilia present in the distal regions of the pallial curtain. The lines indicate the positions of the transverse sections shown in figures 45–50 and 52–56; fixative: osmium tetroxide.

FIGURES 45–50 AND 52–56. Transverse sections through the short cilia of the pallial curtain in the planes indicated in figures 43 and 44; fixative: osmium tetroxide. Magnification for all figures as in figure 43.

FIGURE 51. A section through one of the patches of cilia shown in figure 42 (plate 9); fixative: glutaraldehyde followed by osmium tetroxide.

The pallial curtains

The mechanism of swimming and other movements in *L. hians* has been described by von Studnitz (1931) and more recently by Gilmour (1967). As in all swimming bivalves the inner marginal folds of the mantle are greatly enlarged to form pallial curtains which serve to control the inhalant and exhalant currents and also play an essential role in the swimming mechanism (Yonge 1936). By opening the pallial curtains in one region and opposing them in other regions the animal controls the expulsion of jets of water from the mantle cavity and thus the resultant swimming movements. Lateral movements can result when one pallial curtain overlaps the other but typically in *L. hians* the control of both feeding and swimming currents is achieved by the outer faces of the pallial curtains being opposed as shown in figure 58. Electron microscopic examination of these outer faces reveals that while the basal half is covered by a largely nonciliated cuboidal epithelium (figure 41, plate 9; br) that over the distal half (dr), i.e. the surfaces which may be opposed, bears patches of short, rod-like structures suggestive of numerous colonies of bacteria. At higher magnifications (figure 42, plate 9), it is clear that the short, stumpy rod-like structures project from between the microvilli indicating that they are an integral part of the underlying epithelium and this is confirmed when sections through the epithelium covering the distal regions of the outer face of the pallial curtains are examined in the transmission electron microscope. The epithelium consists of nonciliated and ciliated cuboidal cells. The free surfaces of the former bear a dense array of microvilli while the latter in addition to microvilli also give rise to numerous short cilia only 2 µm in length, i.e. they project but a short distance beyond the tips of the microvilli (figure 51, plate 10).

The details of the structure of each cilium are shown in the series of electron micrographs on plate 10. Unlike the majority of cilia in the Bivalvia, whether they be motile transporting cilia or non-motile sensory cilia, these short cilia do not possess basal rootlets extending into the cytoplasm from the basal capsules (figure 44). The proximal end of the basal capsule exhibits the usual cartwheel structure and nine sets of triplets each set at an angle to the tangent to the cylinder they form (figure 56). A tapered basal foot projects laterally from one side of the cylinder with, on the opposite side, a dense plaque of fibrous material. In the distal region of the basal cylinder where the cilium begins to project from the cell (figure 55) the outermost tubule (tubule C) forming the triplets terminates and the remaining doublets are linked to one another and also, by way of radiating branched spokes, to the plasma membrane which now encloses the cilium (figure 54). Immediately proximal to the basal plate the region enclosed by the doublets is filled with an electron dense material the detailed arrangement of which it was not possible to determine (figure 53). The doublets extend through the electron dense basal plate (figure 52) and immediately distal to the plate the paired central tubules arise to complete the characteristic $9+2$ appearance of the axoneme (figure 50). The peripherally arranged doublets possess projecting dynein arms and radiating spokes appear to connect the doublets to the sheath round the central tubules (figure 49).

Turning to the tips of the cilia where they project beyond the microvilli it is clear even at low magnifications (figure 51) that this region of each cilium is modified by the presence of electron dense material lying largely within the peripheral tubules. This electron dense material appears as the peripheral doublets are transformed to singlets by the termination of sub-fibril B (figure 47) and normally it is in this region that the dynein arms, inter-doublet links and radial spokes also terminate. Transverse sections through this region (figure 46) indicate that the dynein arms are indeed absent but, although the details are difficult to make out, there is a suggestion that the electron dense material may represent 'thickened' or 'strengthened' interdoublet links and radial spokes in the tip region of the cilium. In any case the effect is to 'embed' the central and peripheral tubules in electron dense material and, in sections of material fixed in glutaraldehyde and osmium tetroxide, as opposed to osmium tetroxide only, it would appear that this electron dense material is also linked to the surrounding plasma membrane.

Observations on living animals

Gilmour (1963, 1967) suggested that the ability of *L. hians* to autotomize its tentacles plus the secretion of a viscous, acrid smelling mucus from the epidermal glands of the tentacles serves as a defence mechanism. Some of the feeding experiments described by Gilmour were repeated during the course of this work with essentially similar results. In particular, specimens of *L. hians* were introduced into tanks containing the common shore crab, *Carcinus maenas*. As in the experiments described by Gilmour, initial attempts by the crab to attack the bivalve resulted in the severance of a number of pallial tentacles which stuck to the chelae and mouth parts of the crab; the crab retreated and cleansed the mouth parts. Following three or four similar experiences the crab no longer attempted to attack the bivalve and indeed retreated whenever the bivalve approached.

From these experiments, as with those described by Gilmour, it is not clear whether the severance of the tentacles is a true autotomy or a result of the 'stickiness' and/or the tearing action of the crab's chelae. Gilmour noted that after autotomy all the epidermal gland cells of the autotomized region discharge mucus but that mucus could also be secreted by non-autotomized tentacles, particularly the posterior tentacles. This latter observation could not be confirmed during the present work.

When the pallial tentacles are stroked with a probe or spatula they perform gentle muscular movements and the animal may also react by swimming; the tentacles are not sticky nor do they autotomize. In a second experiment, portions of the tentacles were detached from the animal by snipping them cleanly with a sharp pair of scissors and allowing the detached portion to fall unimpeded to the bottom of the tank. Such tentacles lay passively on the tank bottom until touched gently with a probe. They immediately stuck to the probe and underwent violent muscular contortions which usually resulted in their becoming coiled round the probe. Finally, while the mechanical stimulation of individual tentacles or groups of tentacles still attached to the animal did not usually result in autotomy, mechanical stimulation of the mantle margin near the bases of the tentacles produced extensive autotomy of tentacles and, simultaneously, swimming movements of the animal. The autotomized tentacles stuck to the probe by way of a viscous thread-like material presumably ejected from the paired gland cells.

Discussion

(*a*) *Sensory cell/gland cell complexes*

With the exception of studies on certain specialised sensory receptors such as eyes, statocysts, etc., and a recent paper by Moir (1977) on ciliated receptors in *Placopecten*, there has been little ultrastructural work done on peripheral ciliated receptors in bivalves, although ciliary tufts suspected of having a sensory function have been frequently reported. The tentacles of *L. hians* are of particular interest in this context since, on morphological grounds at least, they appear to possess at least three types of ciliated receptor, two having the form of multiciliated tufts and the third a monociliary receptor with the base of the axoneme or kinocilium surrounded by a corolla of stereocilia.

The most commonly occurring type of receptor (type B) consists of a dense tuft of 35–40 relatively short, stiff non-motile cilia borne by a cluster of 4–6 cells which, as is usual in many invertebrates, are primary sensory neurons. Of particular significance is the relationship between the characteristic pattern presented by these ciliated sensory cells at the surface of the tentacle and the orientation of the basal foot and paired central tubules of the individual cilia forming each tuft. In motile cilia the latter features are related to the plane of ciliary beat (Gibbons 1961); this lies in the same plane as the basal foot and at right angles to the plane joining the two central tubules. The basal foot of each cilium comprising a type B ciliary tuft tends to lie in a plane which radiates from the centre of the tuft suggesting, were these motile cilia, that the effective beat of each cilium would be either towards or away from the centre of the tuft. The cilia are, however, non-motile and it has been suggested that such non-motile sensory cilia may possess a polarity of passive bending similarly related to the internal tubule arrangement and the orientation of the basal foot, and that passive movement of such cilia in the plane of the basal foot is excitatory (Barber 1974). If this is so, then passive displacement of a type B ciliated tuft in any direction will excite at least some of the cilia comprising the tuft and hence the associated sensory neurons. The basal feet underlying the 17–20 cilia comprising a type A ciliated tuft similarly radiate from a common centre although in this case the cilia are arranged in a simple circle and arise from a single cell which distally envelopes a gland cell.

Both chemo- and mechanoreceptors are commonly ciliated and no reliable morphological criterion has yet been found to distinguish receptors of the two modalities. Nevertheless, it is difficult to avoid the conclusion that the type B ciliated tufts and their associated neurons function primarily as multidirectionally sensitive mechanoreceptors. The same may also be true of the type A receptors although in this case their close association with a gland cell suggests the alternative or additional possibility that they are sensitive to chemical stimuli.

Monociliary receptors have been reported from a wide range of invertebrates (Ehlers & Ehlers 1977) but of particular interest in the case of *L. hians* is the complex basal apparatus associated with the single, long, stiff kinocilium and the surrounding corolla of stereocilia. When present the receptor is invariably associated with a type B complex but this association is probably a consequence of morphological rather than physiological factors. In plan view (figure 37) the symmetry and arrangement of the fibres and filaments round the basal body of the kinocilium are suggestive of a series of stays or guy ropes round a central pole and indeed their function may be entirely mechanical serving to stabilize this basal region when the more distal regions are moved. Alternatively, the complex but symmetrical system of fibres and filaments could play a role in the transduction process assuming this occurs at the base of the kinocilium. Certainly, the form of the basal complex with its interconnections between the basal body and the stereocilia is well adapted to respond to any shift or vibration of the ciliary shaft and that the animals, and particularly the tentacles, are sensitive to vibration can be readily demonstrated.

The nature of the response by the animal to stimulation of the various receptors borne by the pallial tentacles is difficult to evaluate. Vibration results in gentle muscular movements of the tentacles and occasionally swimming movements by the animal as does also light mechanical stimulation of the tentacles. On the other hand, the slightest mechanical stimulation of a tentacle detached from the animal evokes violent muscular contortions of the tentacle and the discharge of the paired type B gland cells. This suggests that some inhibitory factor is removed when the tentacles are detached from the animal. It is by no means certain, however, that discharge of the paired type B gland cells is directly linked with stimulation of the type B ciliary receptors, notwithstanding the close morphological relationship that exists between them. Unlike the type A gland cell and the unpaired typed B gland cell, the paired type B gland cells do not open to the exterior; discharge of their contents is presumably a once only event brought about by the 'bursting' of the apical plasma membrane. The force which effects this 'bursting' and subsequent discharge is not clear but two features associated with the paired type B gland cells may be significant. Each gland cell, in common with the adjoining sensory cells, is invested by sheath cells possessing well developed tonofibrils. Secondly, the 'wall' of the gland cell possesses a well developed system of microtubules. While it would appear that the sheath cells serve primarily to anchor the gland cells to the basement lamina, the microtubules, in addition to reinforcing the gland cell 'wall', could if contractile also serve to extrude the cell contents when appropriately stimulated. There is, however, no evidence for this latter supposition nor is there any indication of a connection between the gland cells and the adjoining sensory cells or any other nerve cells. Extrusion of the contents of the paired type B gland cells may result simply from the violent muscular contortions and consequent pressures generated when a detached tentacle is mechanically stimulated. In this context the button-like invaginations of the plasma membrane which occur near the apex of the gland cells (figure 30, plate 7; b) may be significant in serving to anchor the body of the cell to the adjoining epithelial cells.

(*b*) *The epithelial cell*

The epithelial cells covering the tentacles are remarkable in that most of their volume consists of a single, large, membrane-bound vacuole: the cytoplasm is effectively restricted to a narrow zone underlying the plasma membrane. That this vacuolated appearance of the epithelial cells in sections of fixed material is not an artefact is clear from the examination of living tentacles under the light microscope. The vacuoles appear in the plane of focus as fluid filled 'circles' which undergo slight deformations and changes in diameter as the tentacle moves. As described by Gilmour (1967), the tentacles are capable of performing complex movements due largely to the occurrence at intervals along the length of each tentacle of muscular transverse septa each pierced by a pore guarded by a sphincter muscle. When all the pores are open blood is interchanged freely with the pallial haemocoele as the tentacle contracts and extends. Alternatively, if the pore in the basal septum is closed the entire tentacle acts as a constant volume system while if all the septal pores are closed the tentacle is divided into a series of autonomous constant volume units thus enabling localized movements to take place.

It would appear that the presence of the large fluid filled vacuoles within the epithelial cells enables these cells to accommodate readily to the various changes in shape and volume which the tentacles may undergo during movement. In effect, the fluid filled vacuoles, i.e. the epithelial cells, serve as readily deformable constant volume units surrounding the central cavity of the tentacle which may or may not undergo marked changes in volume as the tentacle performs various movements. Figure 57 represents diagrammatically one example of how such accommodation is achieved, in this case during an extension and contraction of the tentacle involving an interchange of blood with the pallial haemocoele. That is, the central cavity of the tentacle undergoes a marked change in volume.

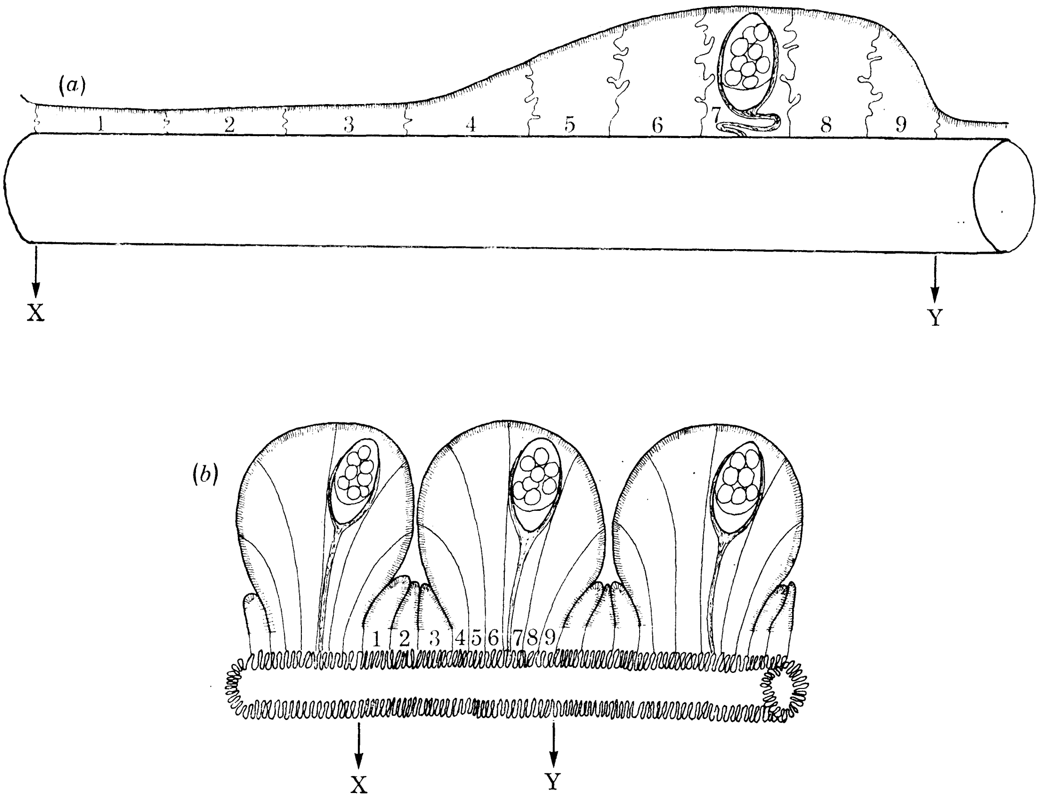


FIGURE 57. Diagrammatic drawings to show how the vacuolated epithelial cells accommodate to (*a*) extension, and (*b*) contraction of the pallial tentacles.

In figure 57*a* the internal cavity of the tentacle is at maximum volume with the epithelial cells more or less cuboidal and varying in height depending on whether they occur in the glandular or interglandular regions. In figure 57*b* the tentacle is shown in a contracted state with the volume of the internal cavity much reduced and the basal lamina thrown into a series of tight pleats. The epithelial cells have accommodated to these changes in two ways. The free surface of those cells in the glandular regions is relatively unchanged but the cells are now tall and more or less cone-shaped. In the interglandular regions the cells are similarly narrower and taller than in the extended tentacle but the free surface is thrown into a number of tight pleats, although as in the case of the epithelial cells of the glandular regions and due to the existence of desmosomes and microvilli, the apical surface area of the individual cells is unchanged. The differences between the two regions are correlated with the presence or absence of sensory cell/gland cell complexes and also explain why the gland cells do not extend to the basement lamina but are 'anchored' to the latter by way of sheath cells with their well developed tonofibrils.

In figure 57*a* the tentacle, or at least the internal cavity with its contained blood, is assumed to be at maximum volume. Such a condition would, in fact, not occur since localized movements of sections of the tentacle acting as constant volume units could not then take place. In practice the extension of the tentacle by the inflow of blood from the pallial haemocoele presumably stops short of this theoretical maximum. Even so, as noted by Gilmour (1963), the tentacles are capable of extending to some seven times their contracted length.

(*c*) *The pallial curtains*

The dense patches of cilia which occur over the distal half of the outer faces of the enlarged inner marginal folds are remarkable for their short length and the electron dense material which occurs at their tips. It was at first thought they represented some type of sensory receptor but although the pallial curtains are richly supplied with nerves these appear to be associated with the well developed musculature and occasional cells bearing tufts of longer non-motile cilia present over this surface; the latter are clearly sensory receptors. It is suggested that the patches of short stiff cilia serve as an 'anti-slip' device when the distal regions of the pallial curtains are opposed (figure 58) during normal pumping activities or swimming movements. If this is so, then the electron dense material at the tips of the cilia could represent a strengthening of the tips and the cilia could be regarded as analogous to the steel studs present in certain types of car tyres. Such an arrangement would have the advantage of resisting shearing forces while at the same time offering little resistance to the separation of the pallial curtains by muscular contraction.

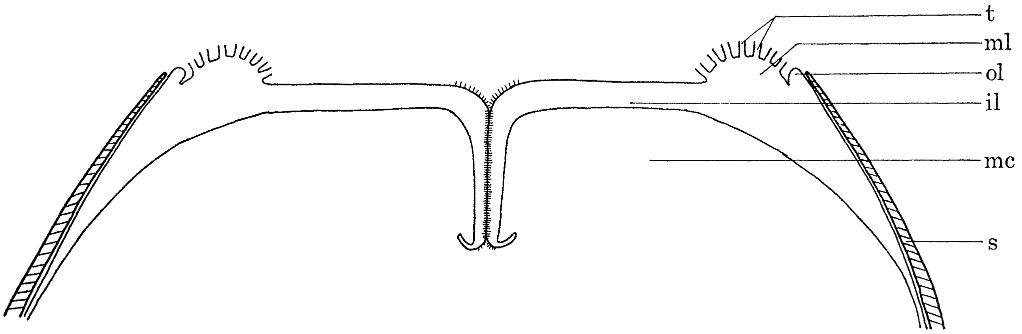


FIGURE 58. Diagrammatic representation of the mantle margins of *L. hians* showing the apposition of the distal regions of the greatly enlarged inner marginal folds (pallial curtains), i.e. the regions bearing the patches of short stiff cilia shown in figure 42 (plate 9).

The presence of strengthening or reinforcing material at the ciliary tips could have other consequences. The cilia may or may not possess all the apparatus necessary for motility but the 'cementing' together of the peripheral and central tubules at the tips would effectively inhibit intrinsic ciliary movement by preventing any sliding of the peripheral tubules relative to one another. On the other hand, and provided the cementing material possesses some degree of elasticity, limited passive bending of the cilia could occur but when the extrinsic force producing this was removed the individual cilia would return to the stiff, upright position. This concept could apply to the non-motile sensory cilia associated with the pallial tentacles and with this in mind transverse sections through the tips of the cilia forming the type B sensory tufts were re-examined. In the case of 'normal' motile cilia the matrix round the ciliary tubules tends to become less electron dense where the peripheral doublets are transformed to singlets. In these sensory cilia, however, the matrix between the singlets and paired central tubules shows a marked increase in electron density in this region (figure 29, plate 7; inset) similar to, although not as extensive as, that present in the short cilia of the pallial curtains. Thus, here also, the electron dense material binding together the ciliary tubules at their tips could serve to hold the cilia straight and more or less stiff while at the same time allowing temporary passive displacements associated with sensory reception to occur.

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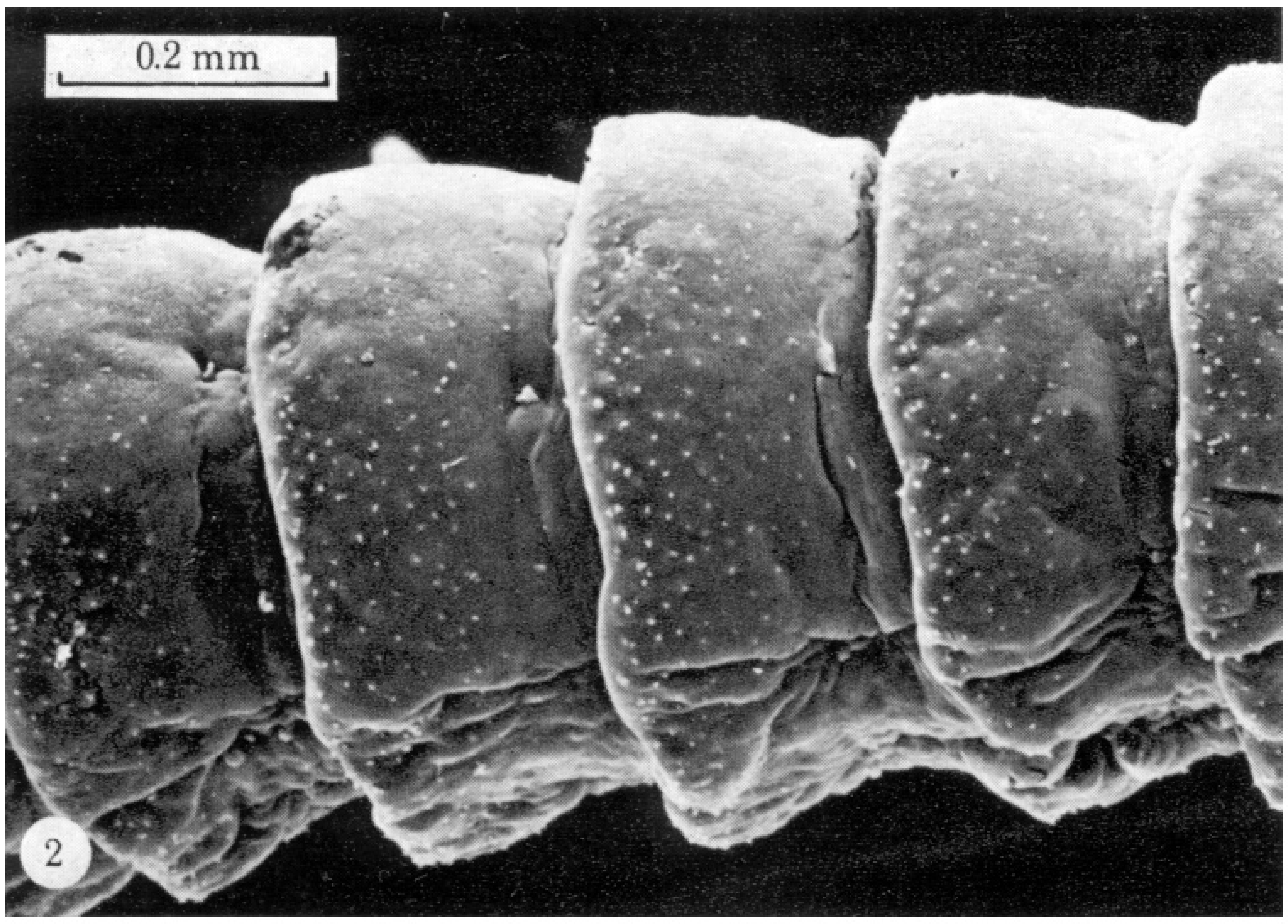
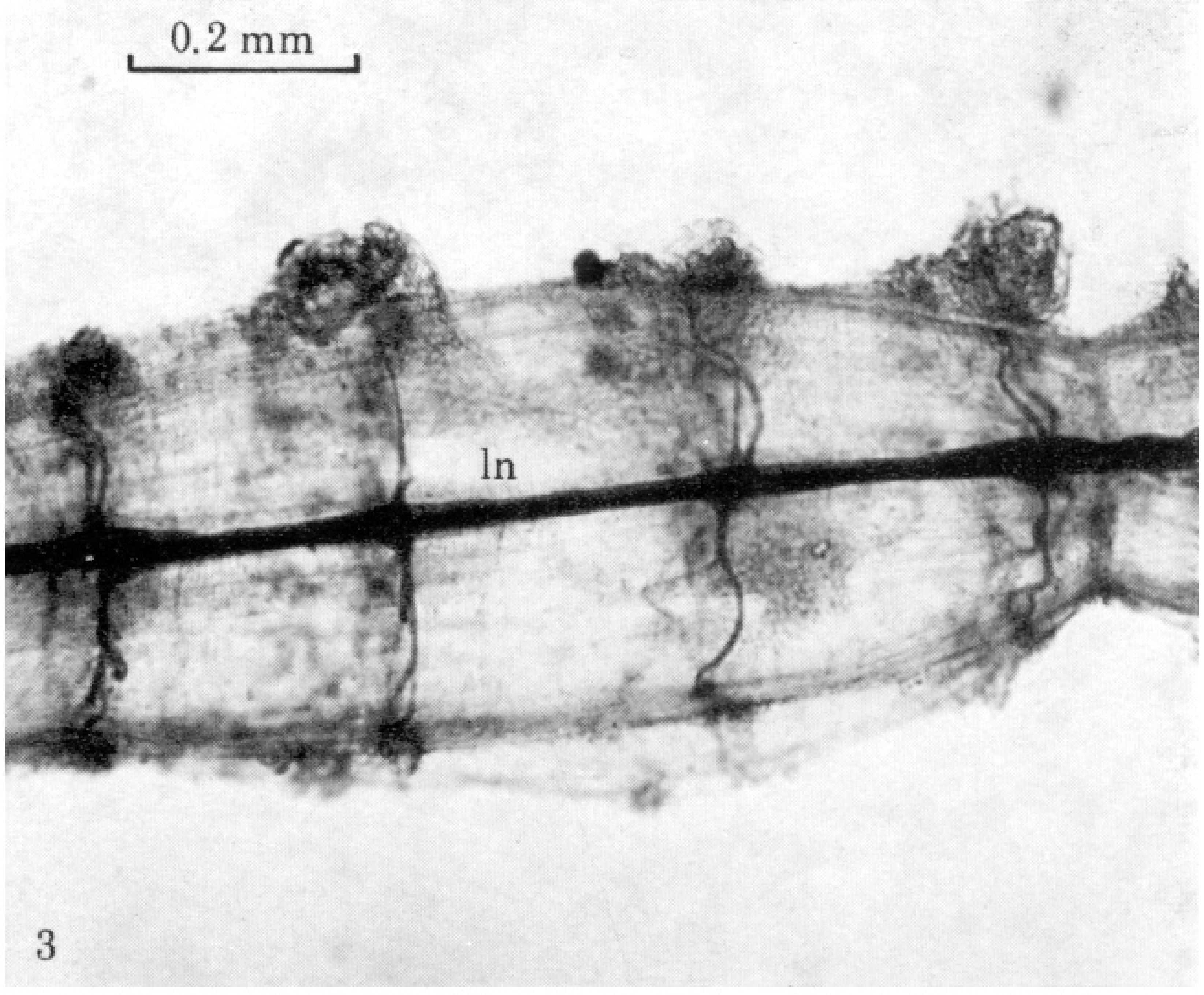
LIST OF ABBREVIATIONS USED IN THE FIGURES

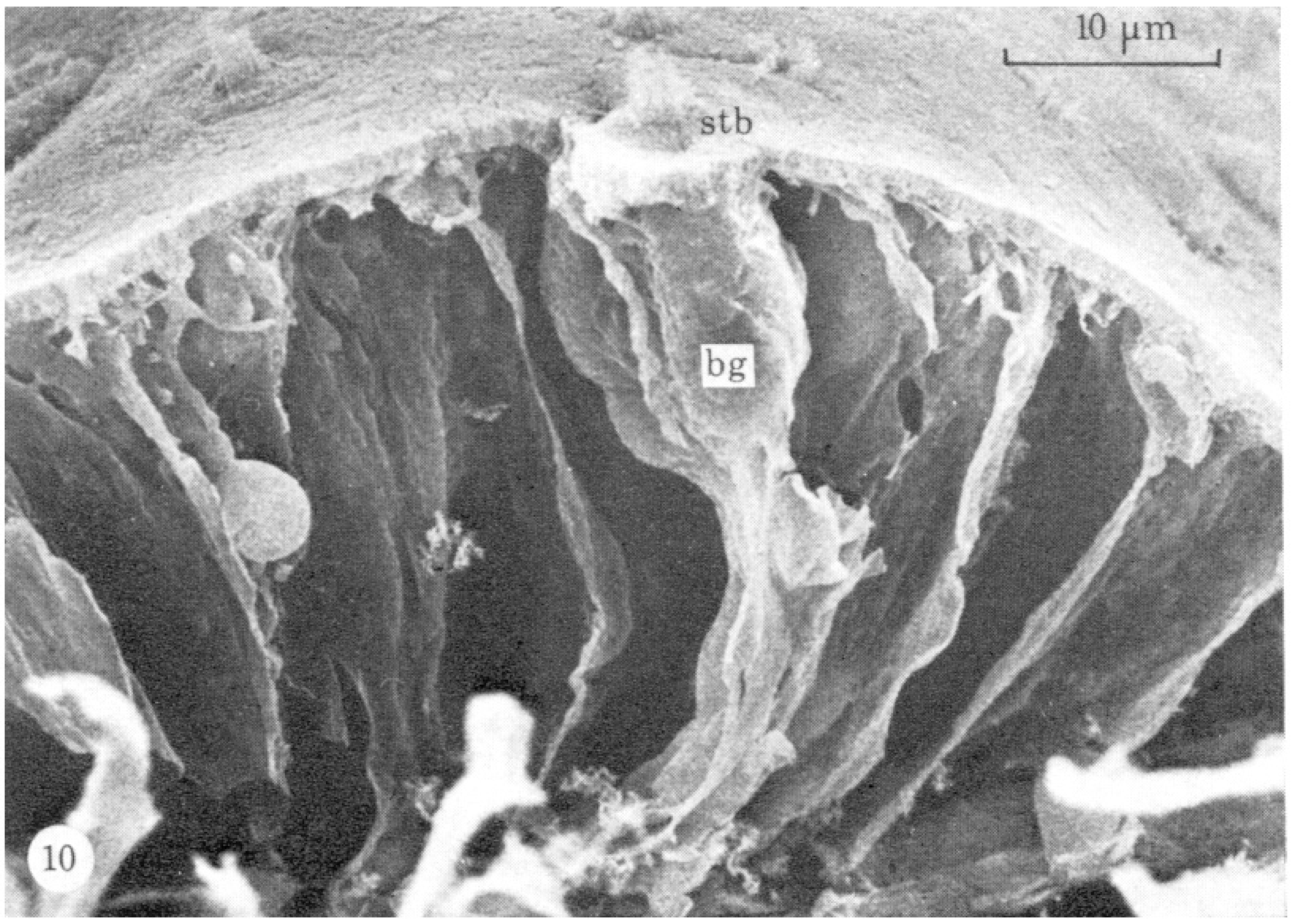
ag	type A gland cell
ax	axon
b	button-like invagination
bb	basal body
bf	basal foot
bg	paired type B gland cells
bl	basal lamina
br	basal region of middle lobe
bs	basal sheath
cts	connective tissue
dr	distal region of middle lobe
ec	epithelial cell
ga	Golgi apparatus
h	haemocoele
il	inner lobe
ilm	inner longitudinal muscle
k	kinocilium
ln	longitudinal nerve
mc	mantle cavity
mcr	monociliary sense cell
ml	middle lobe
mv	microvilli
n	nucleus
ol	outer lobe
olm	outer longitudinal muscle
pg	pigment granule
rm	radial muscle
rn	radial nerve
s	shell
sc	stereocilia
sca	type A sensory cell
scb	type B sensory cell
sd	septate desmosome
sp	secretory sphere
ss	sheath cell
sta	type A sensory tuft
stb	type B sensory tuft
t	pallial tentacle
ug	unpaired gland cell
v	vacuole

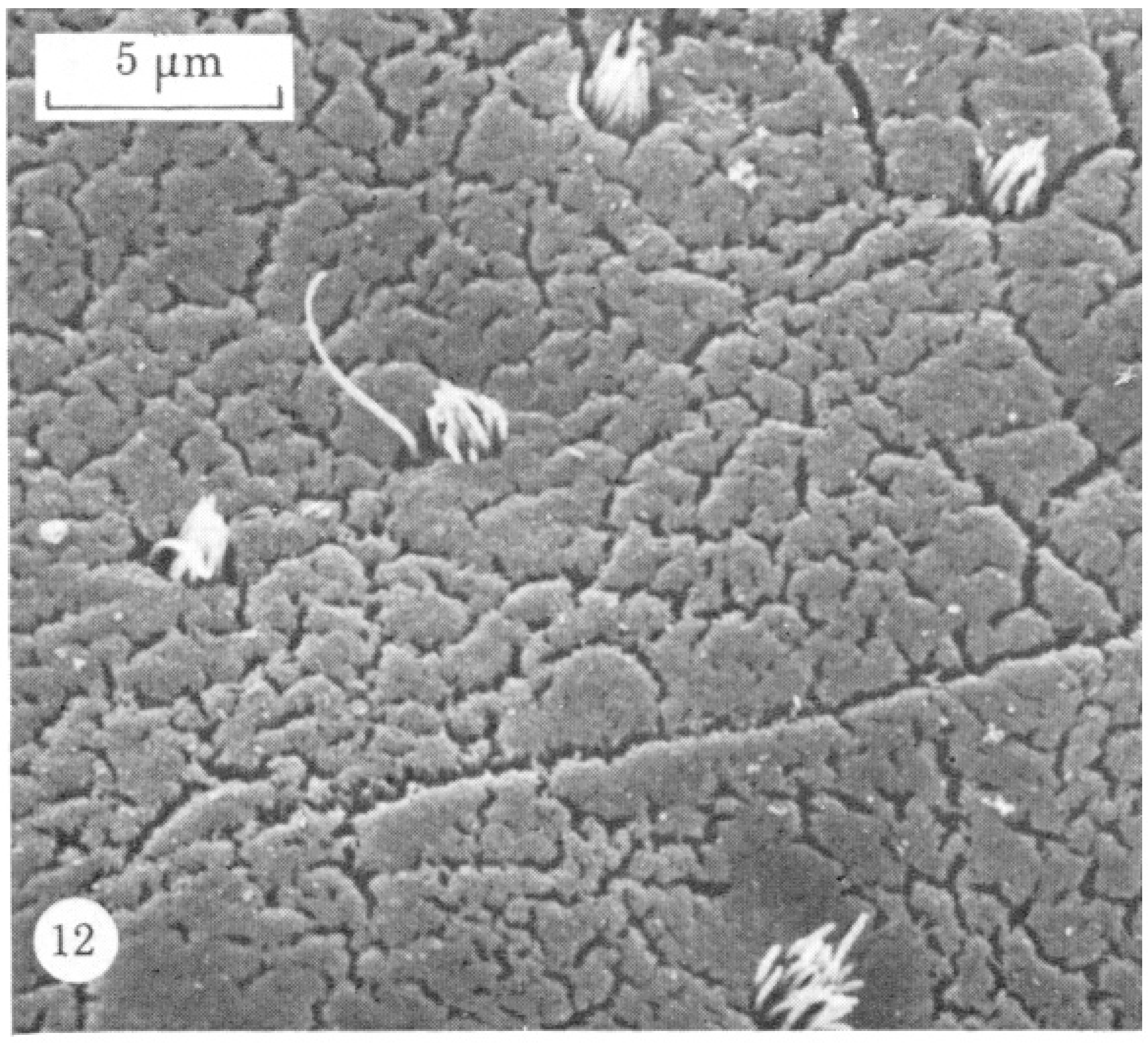


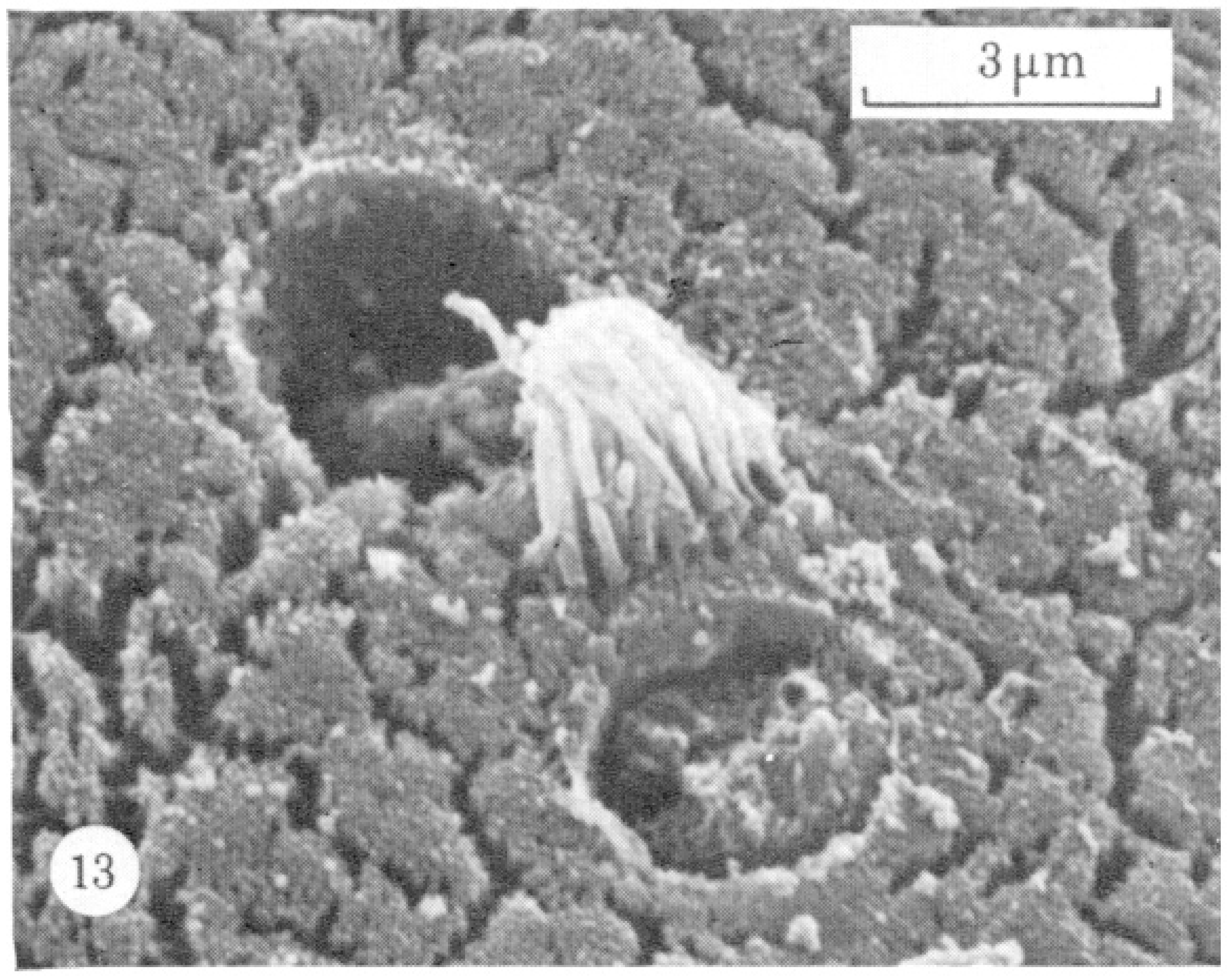


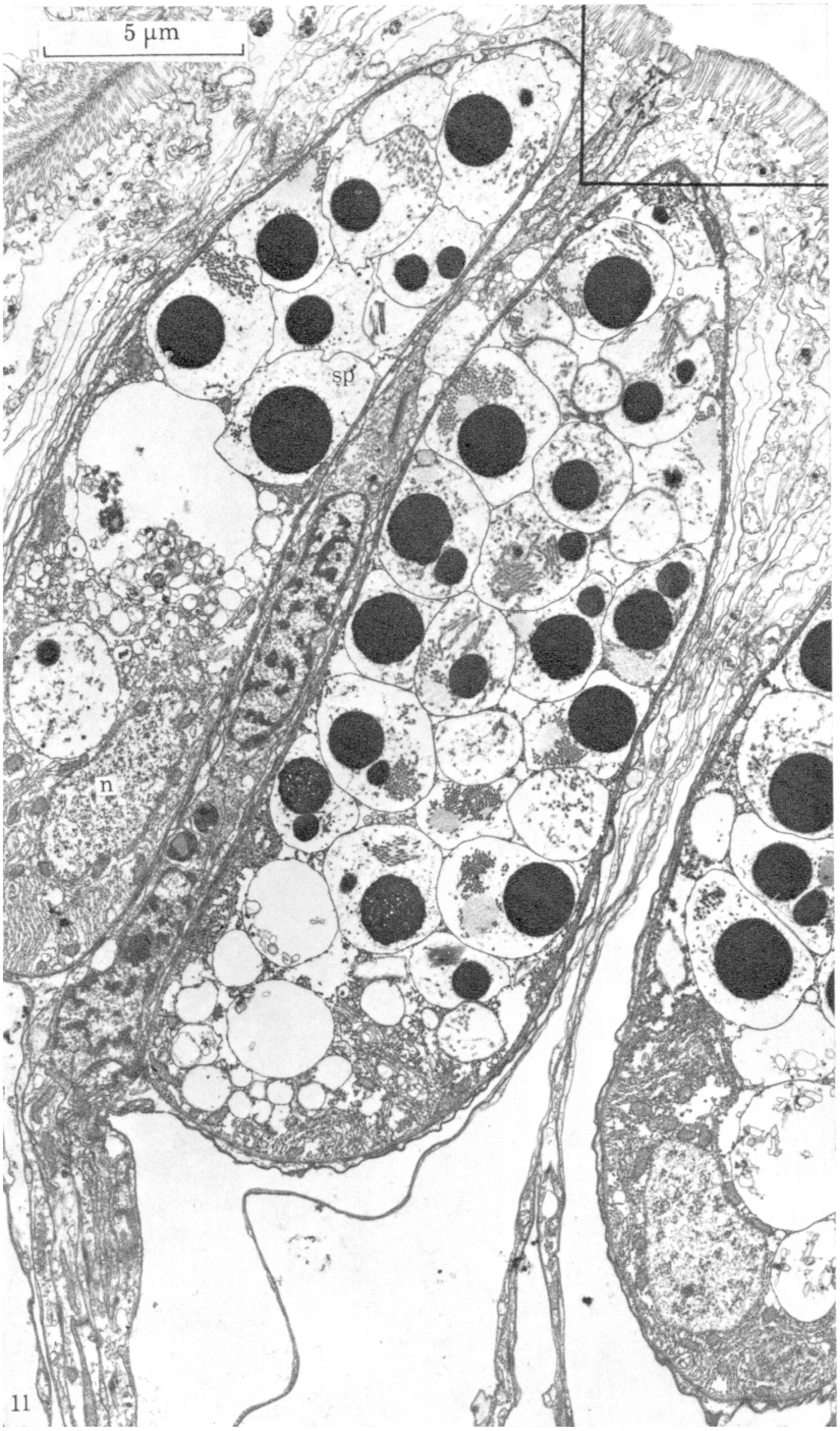
Figures 2–5. For description see opposite.

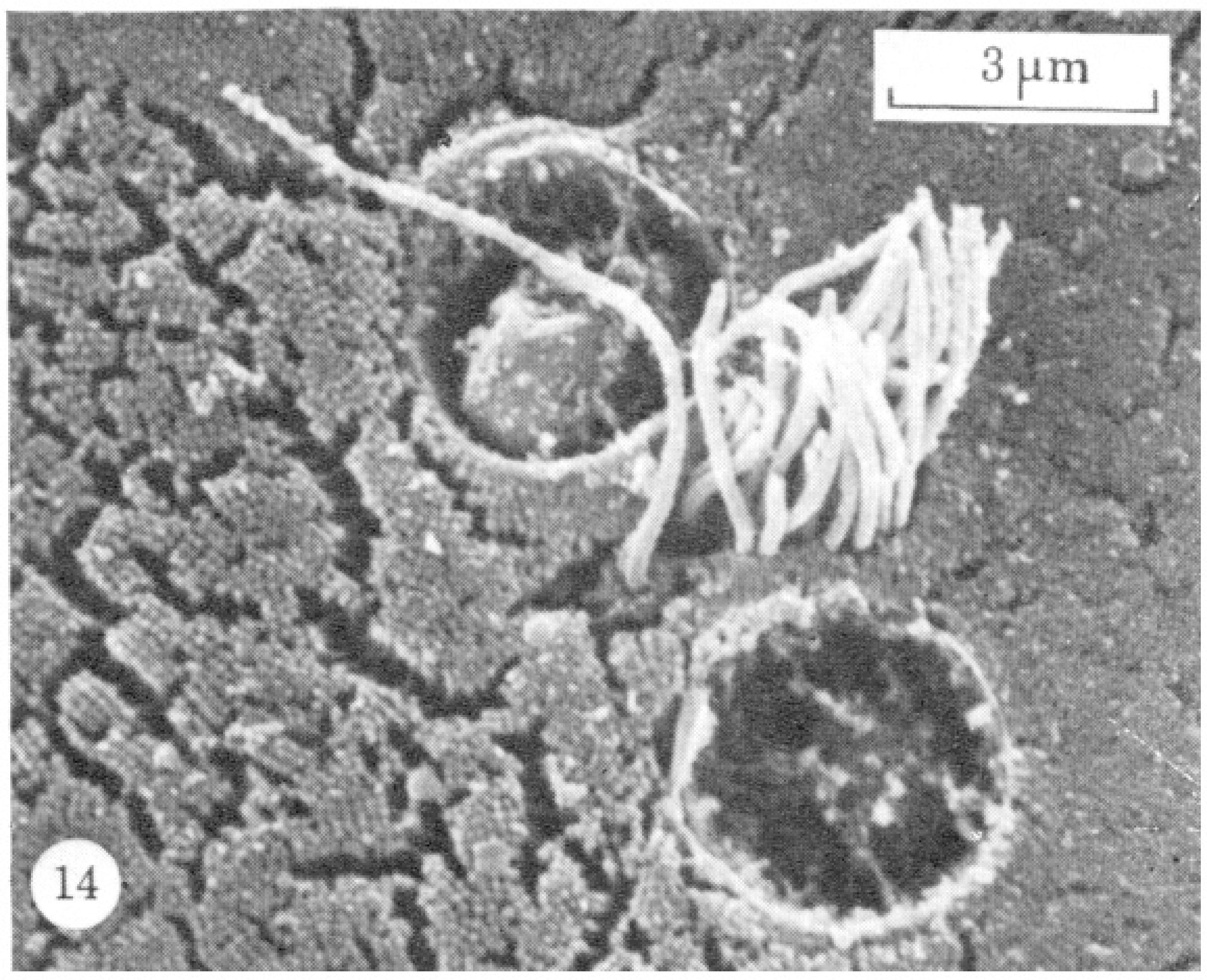
FIGURES 6–8. For description see opposite.

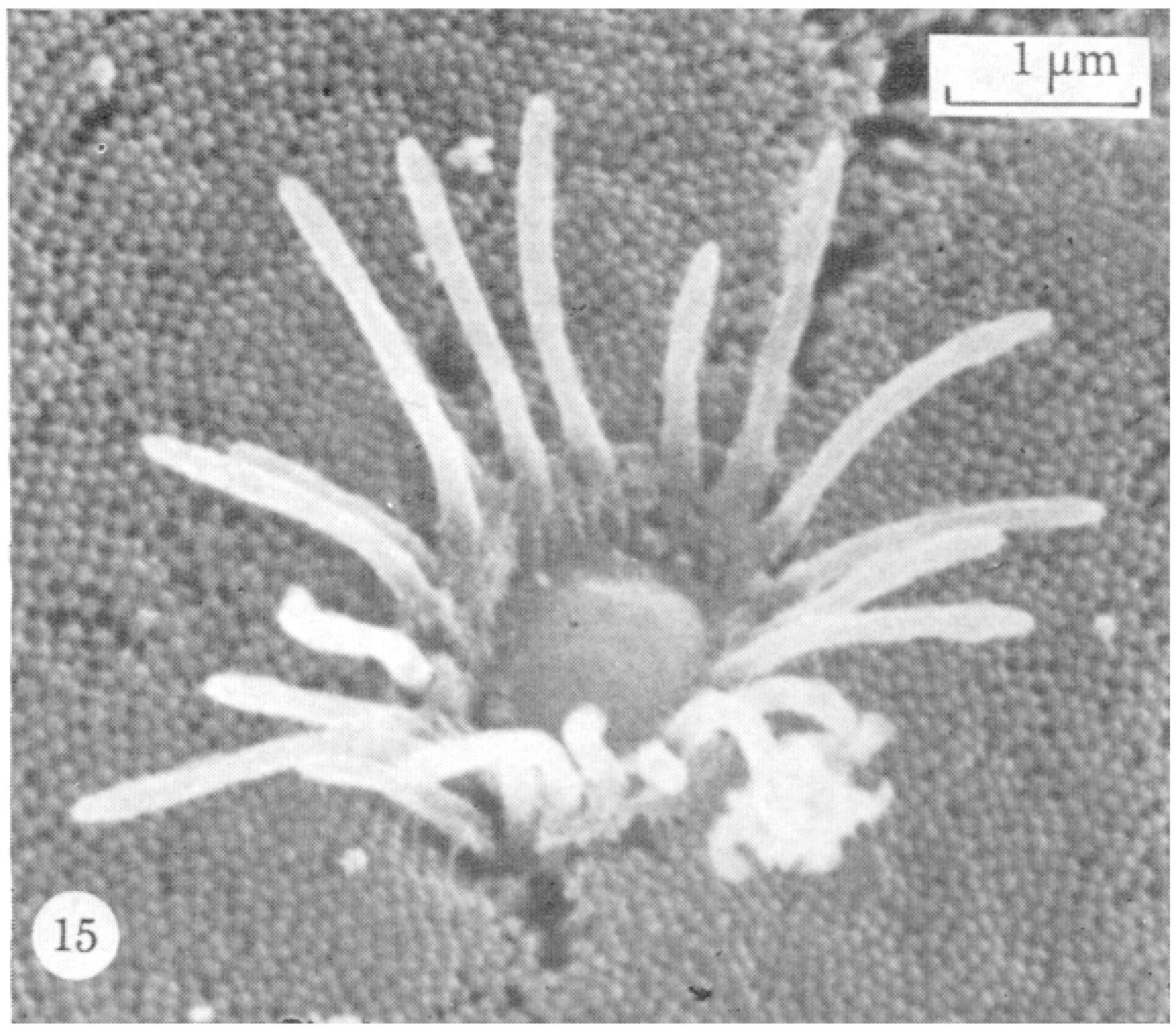




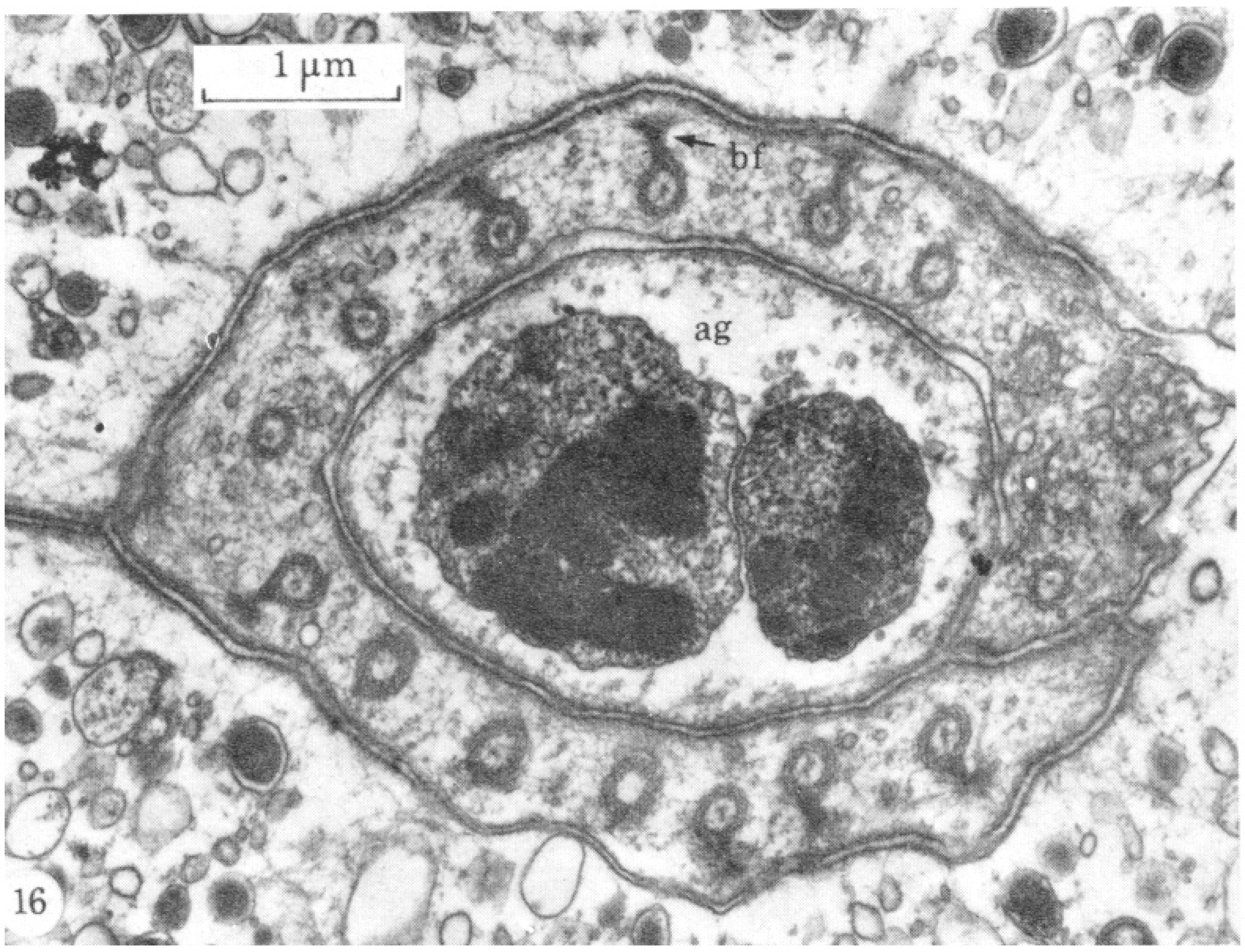


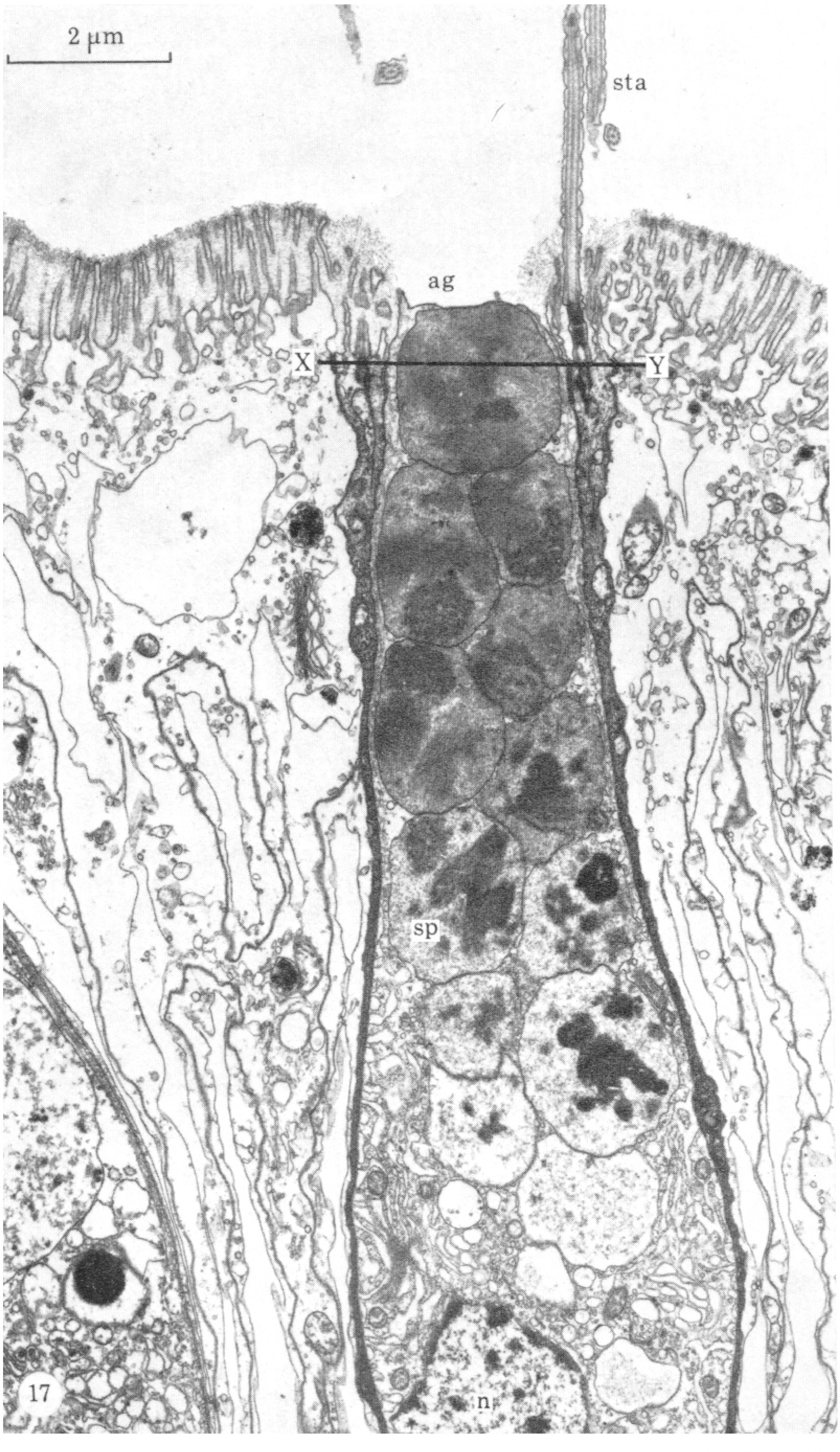




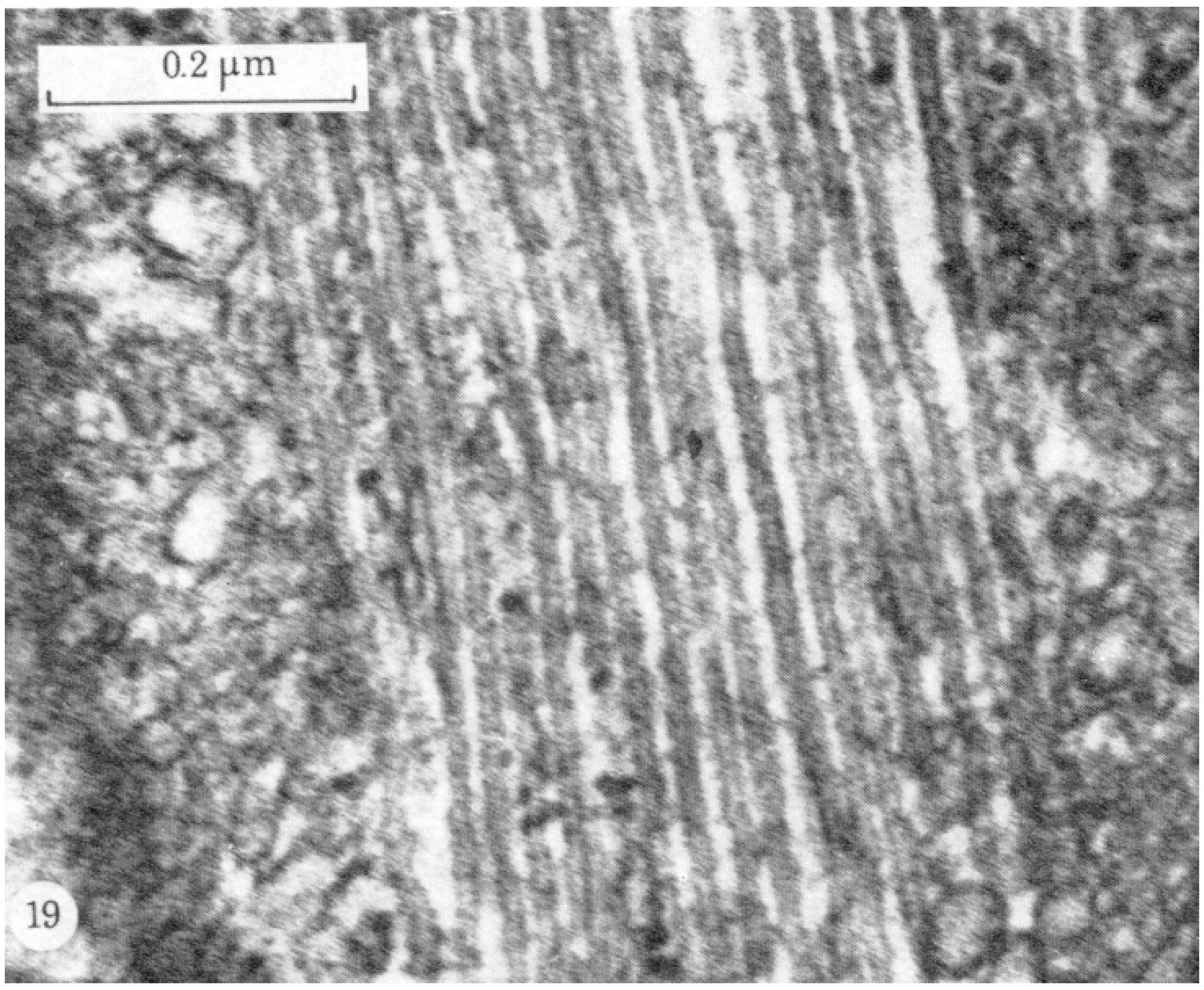


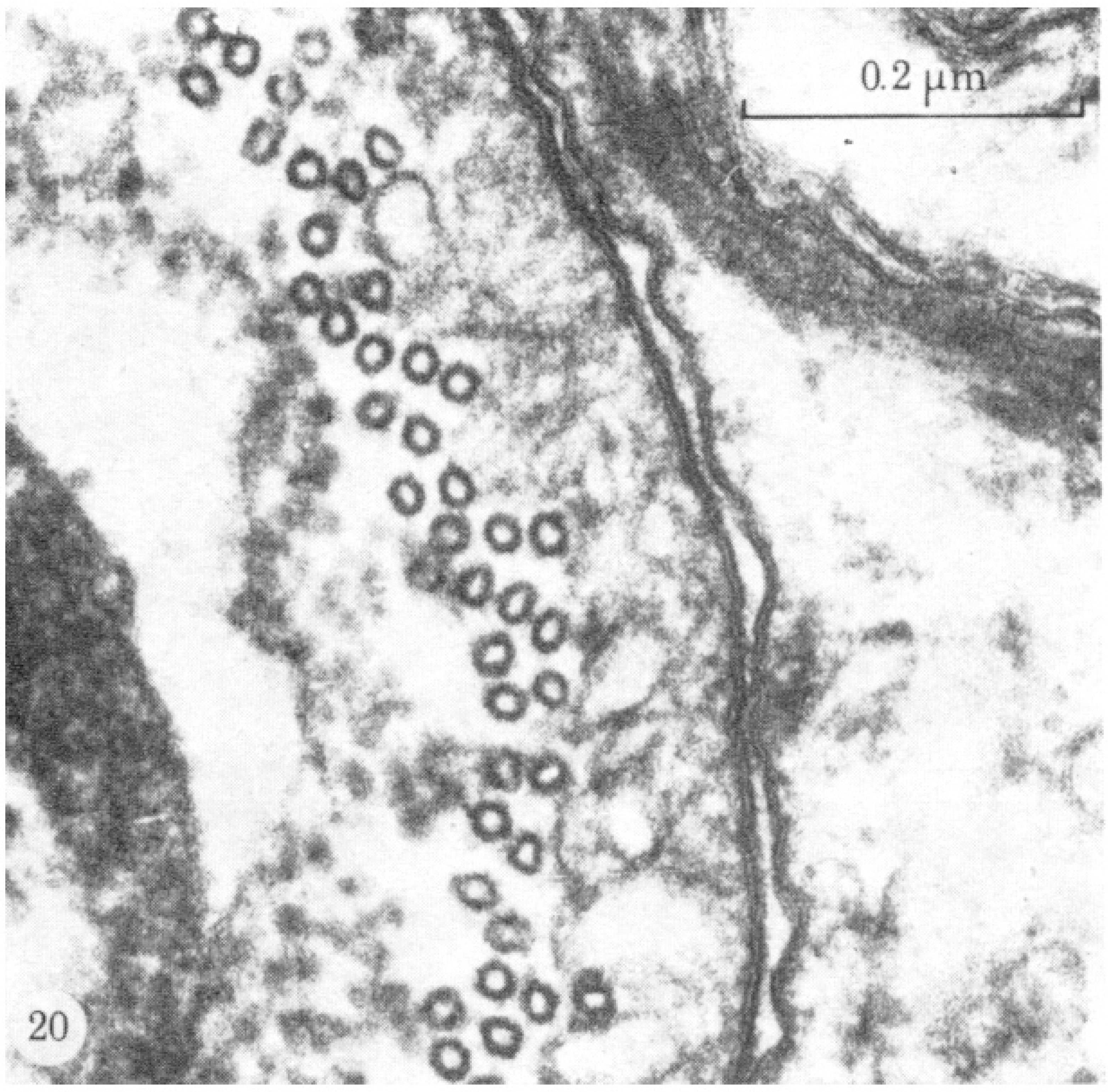
FIGURES 10–15. For description see opposite.

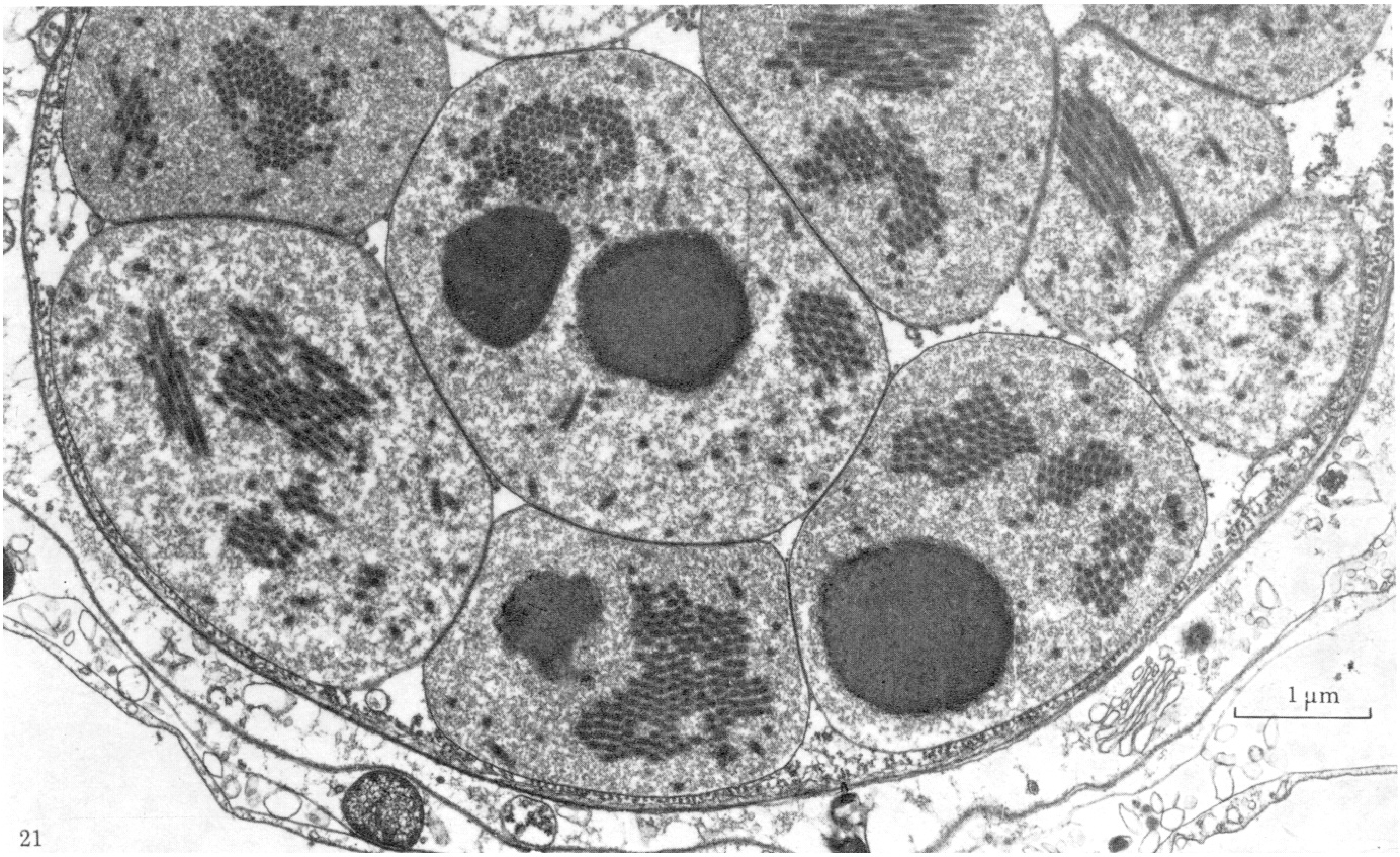


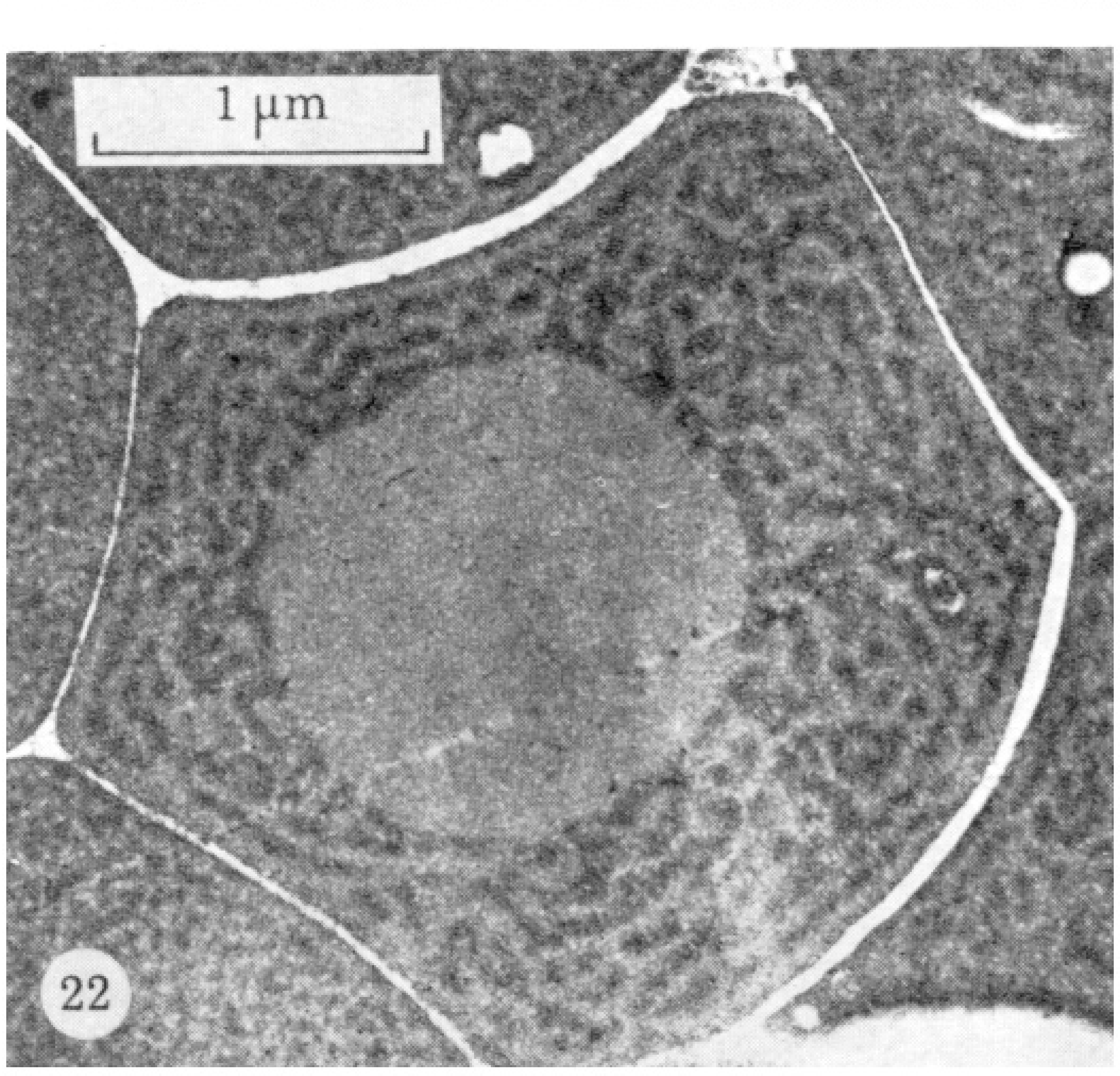


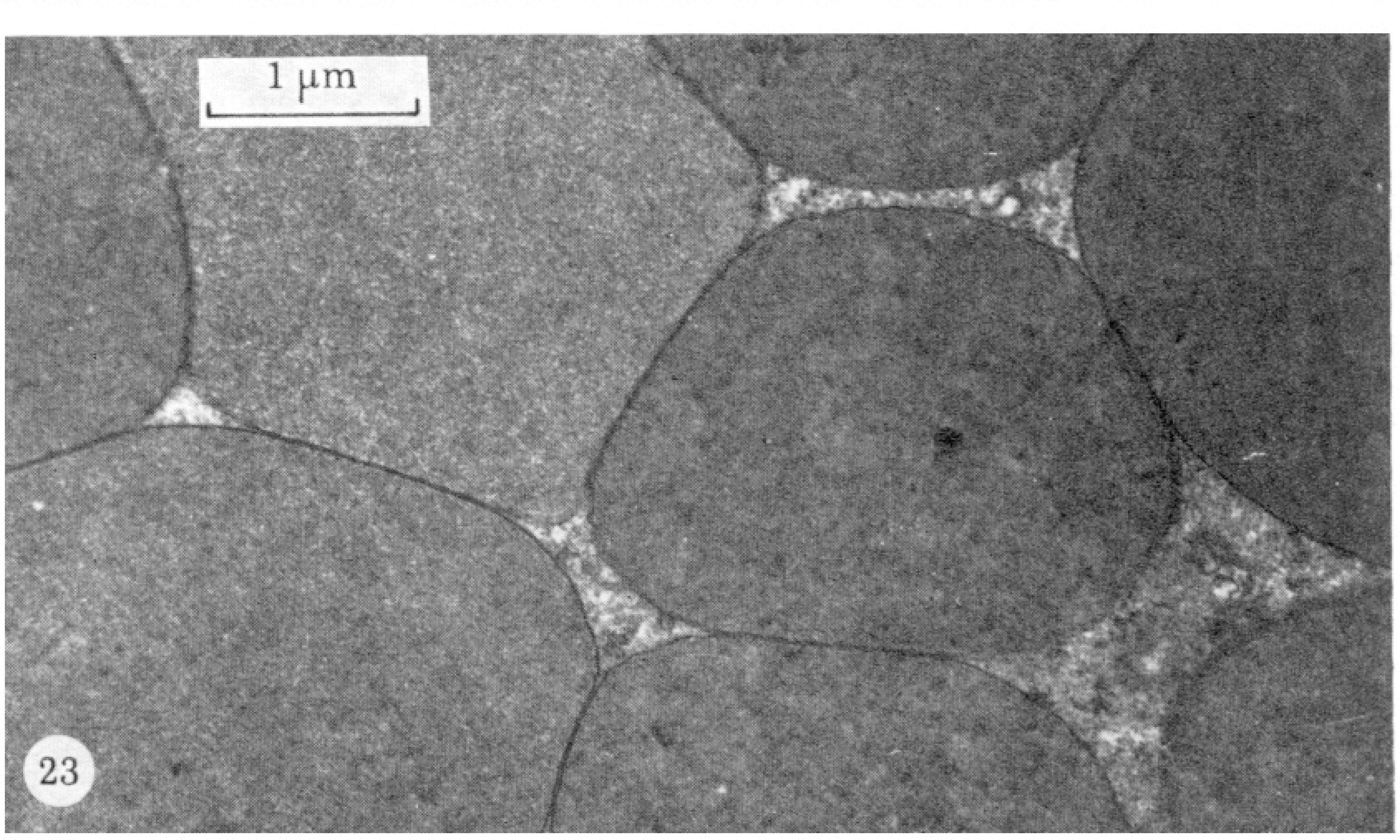
FIGURES 16–18. For description see p. 50.



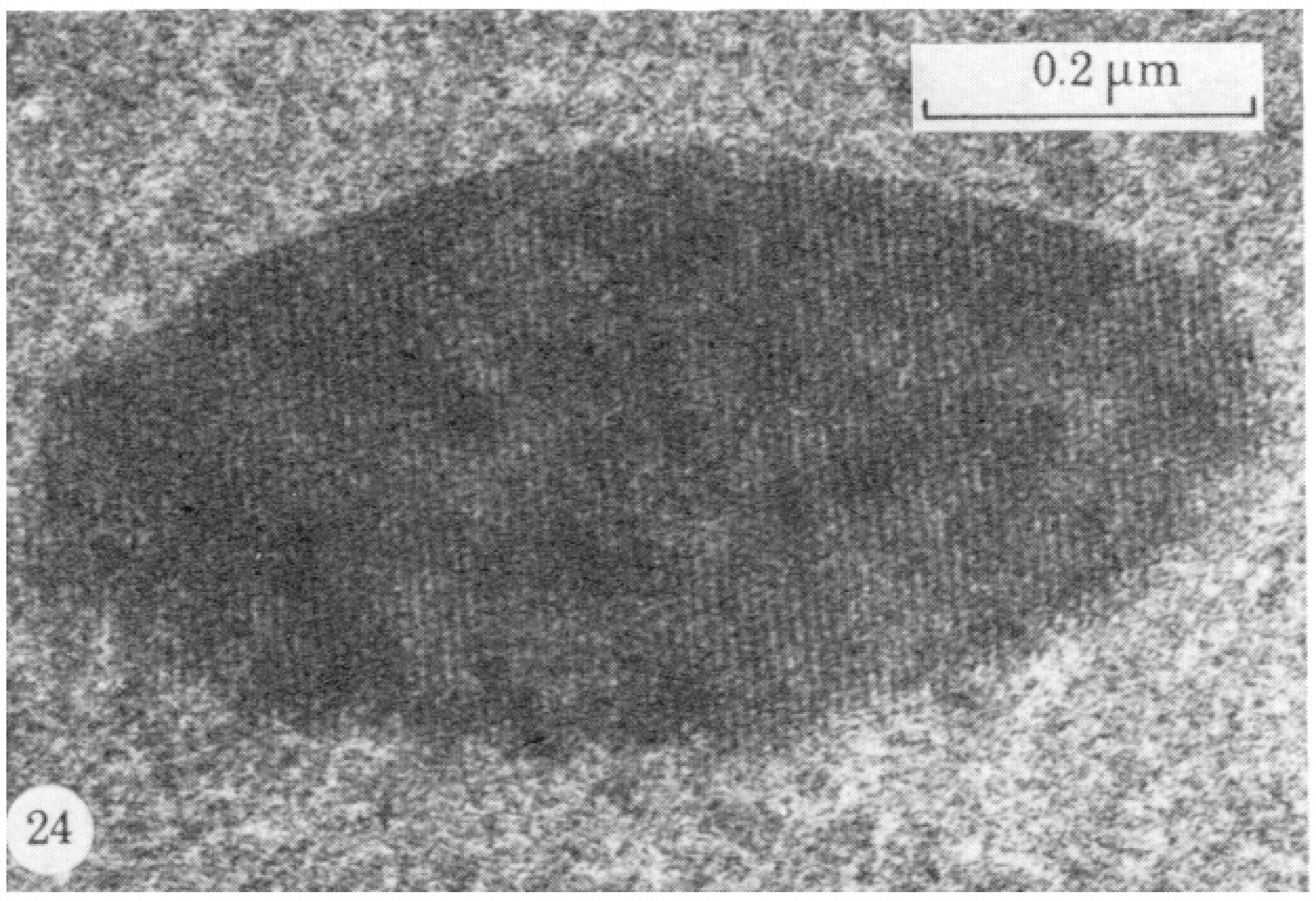








FIGURES 19–23. For description see p. 51.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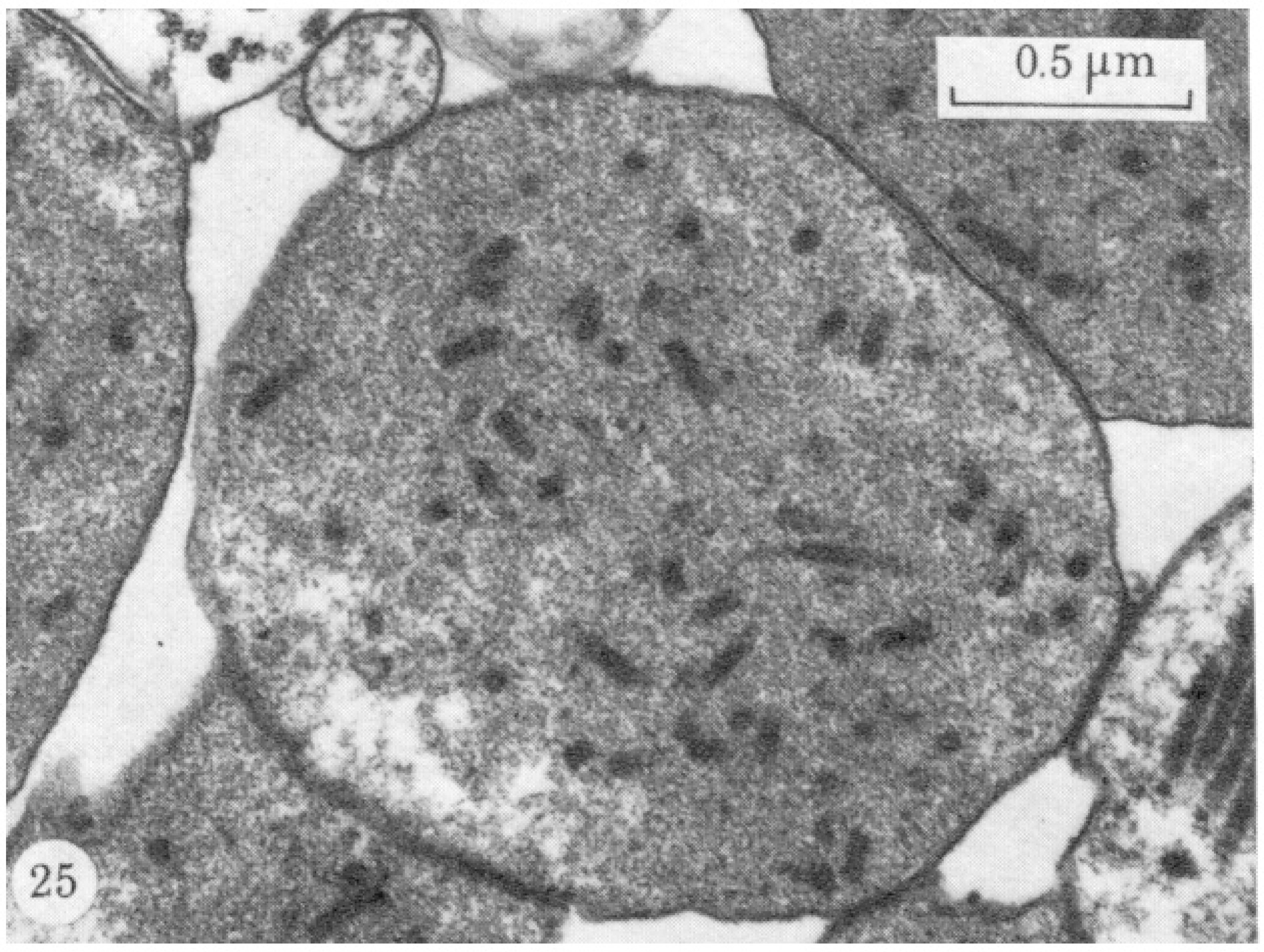
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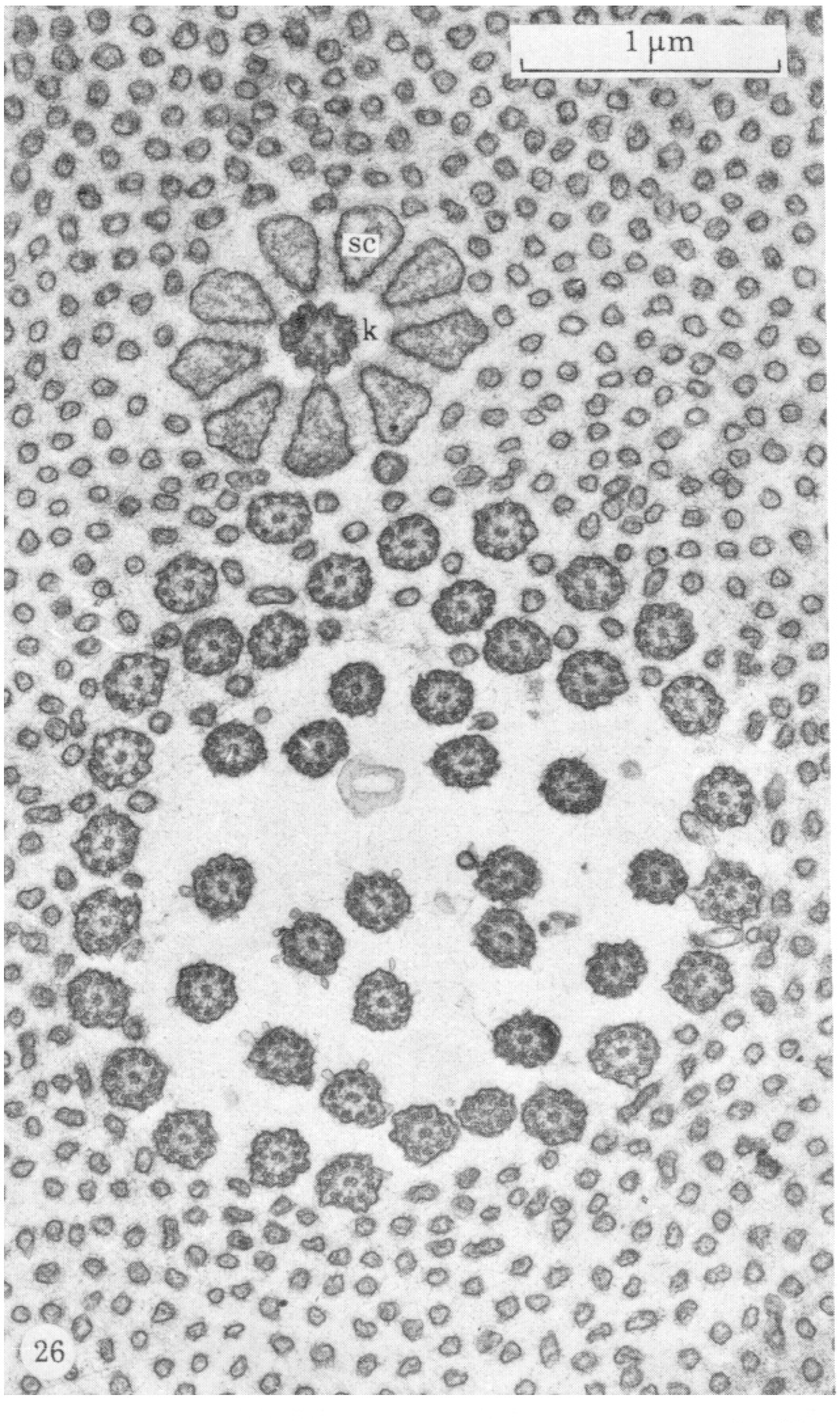
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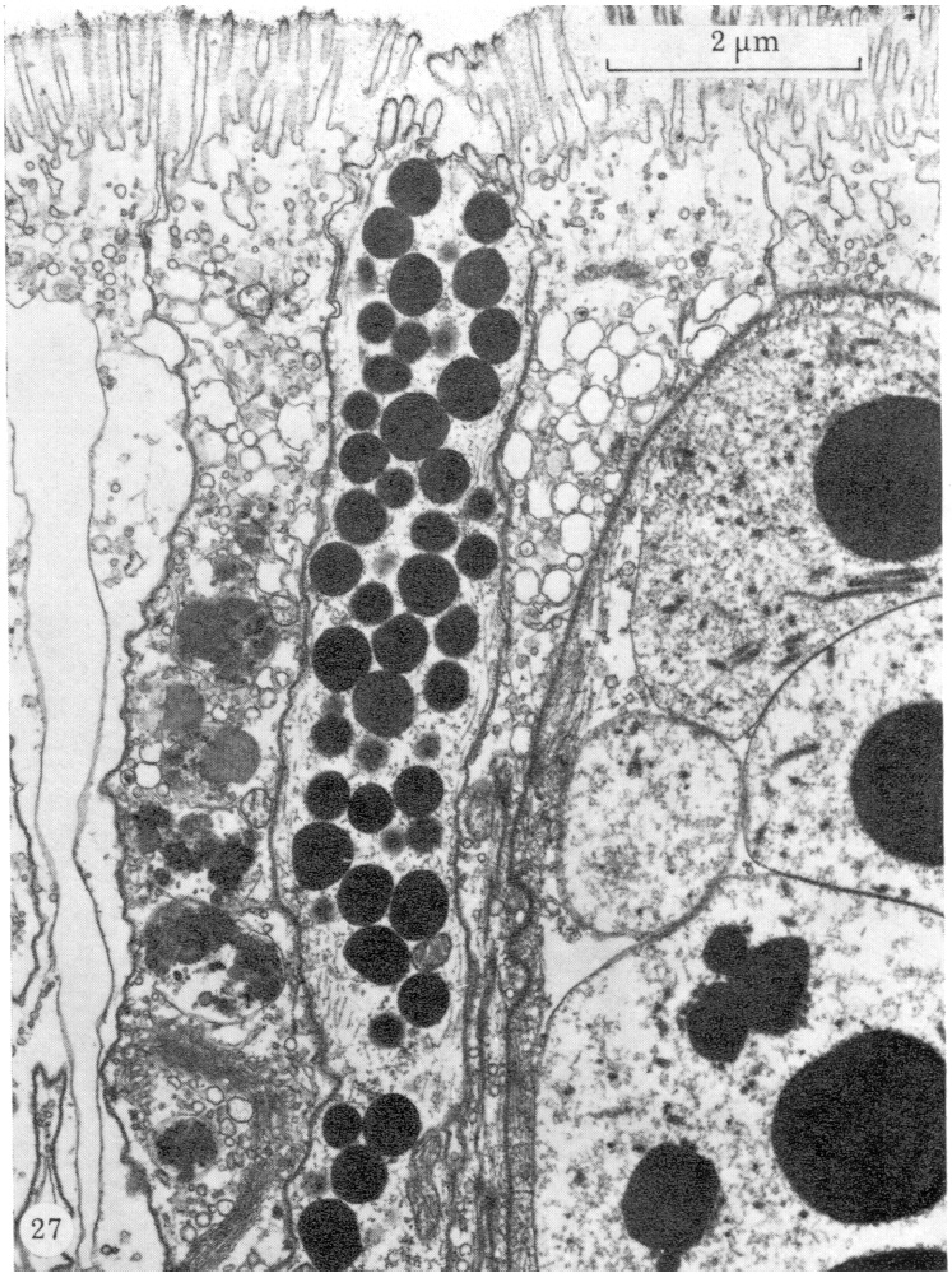
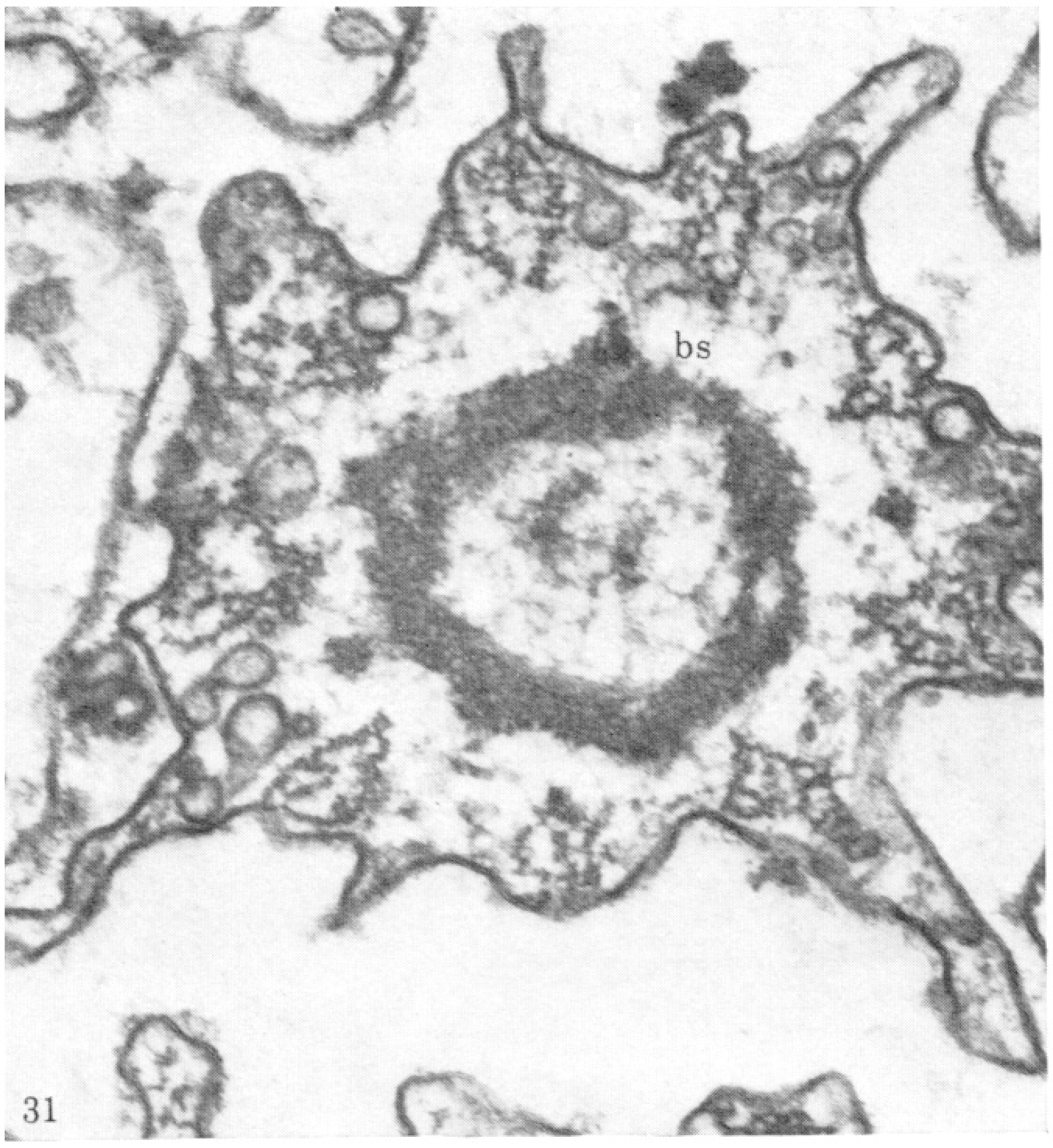
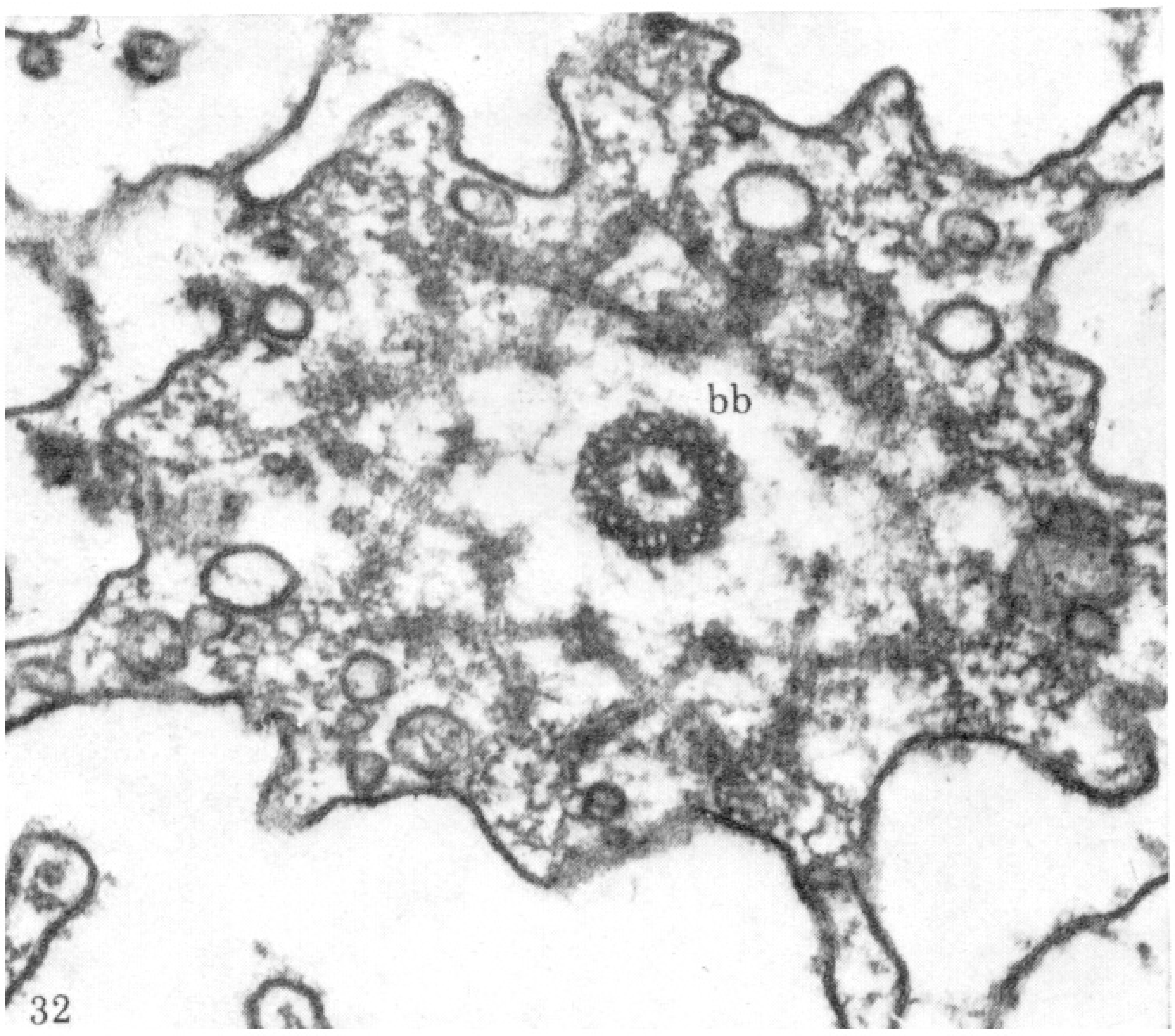

27

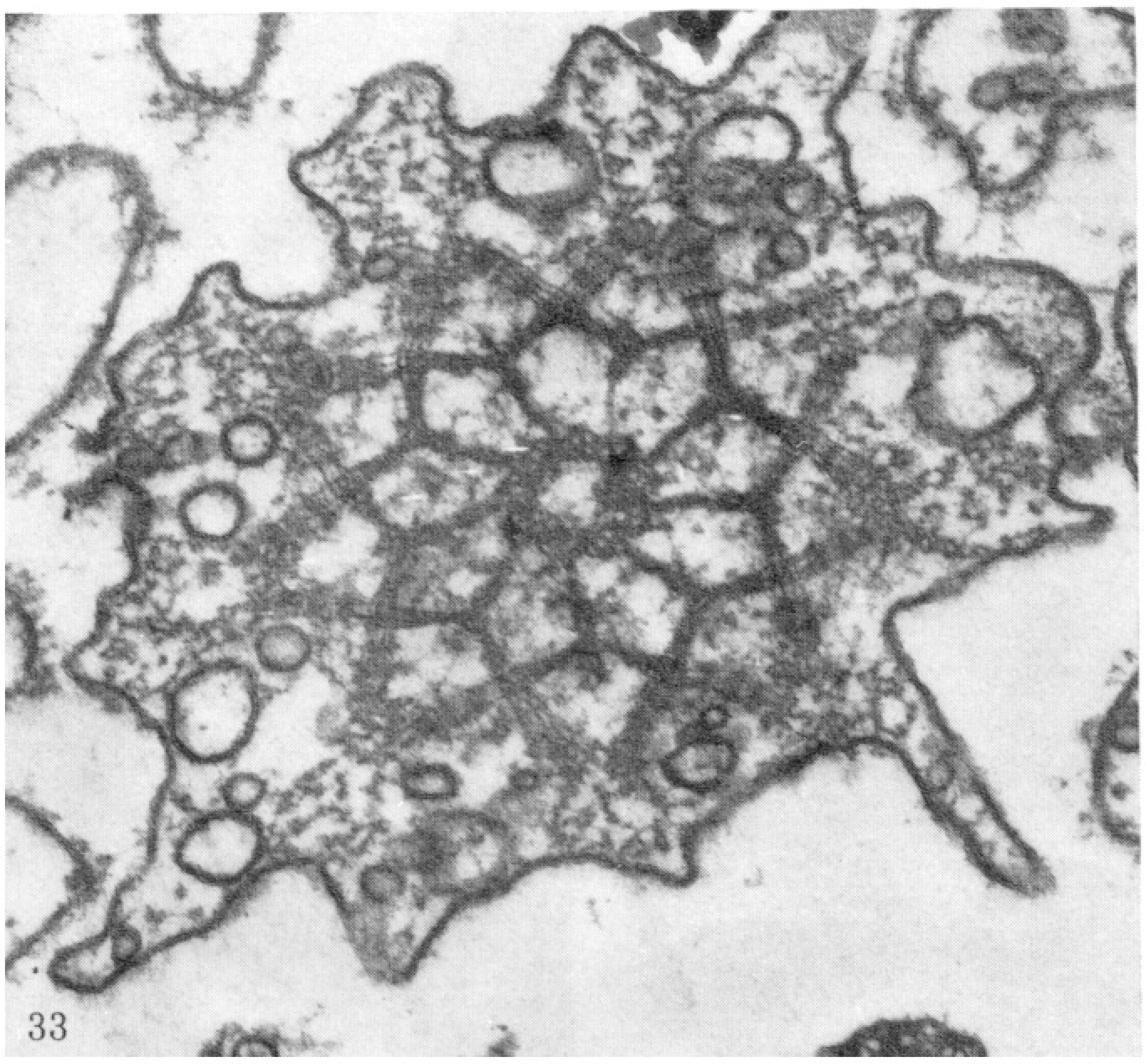

28

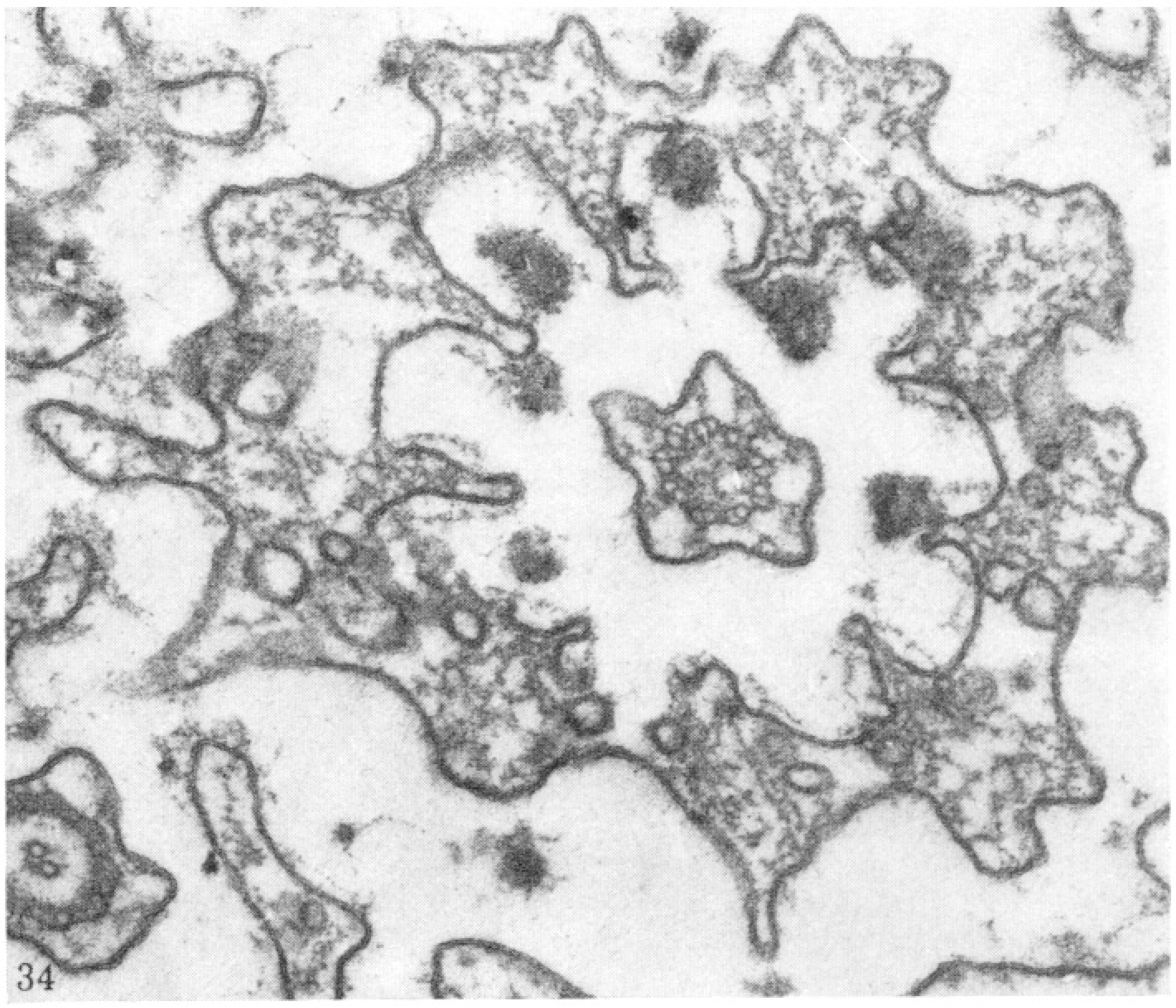
FIGURES 24–28. For description see opposite.

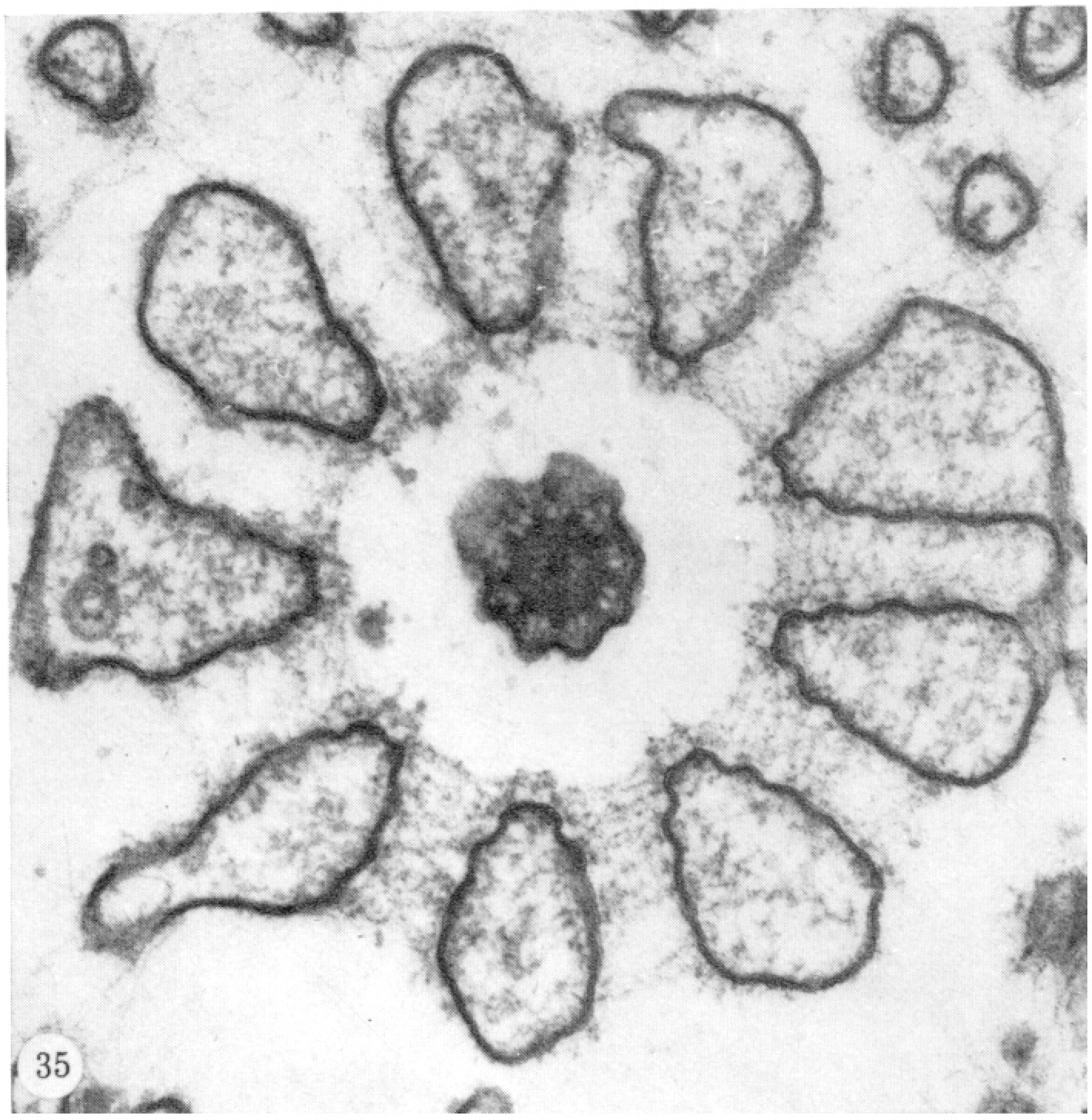
FIGURES 29 AND 30. For description see opposite.

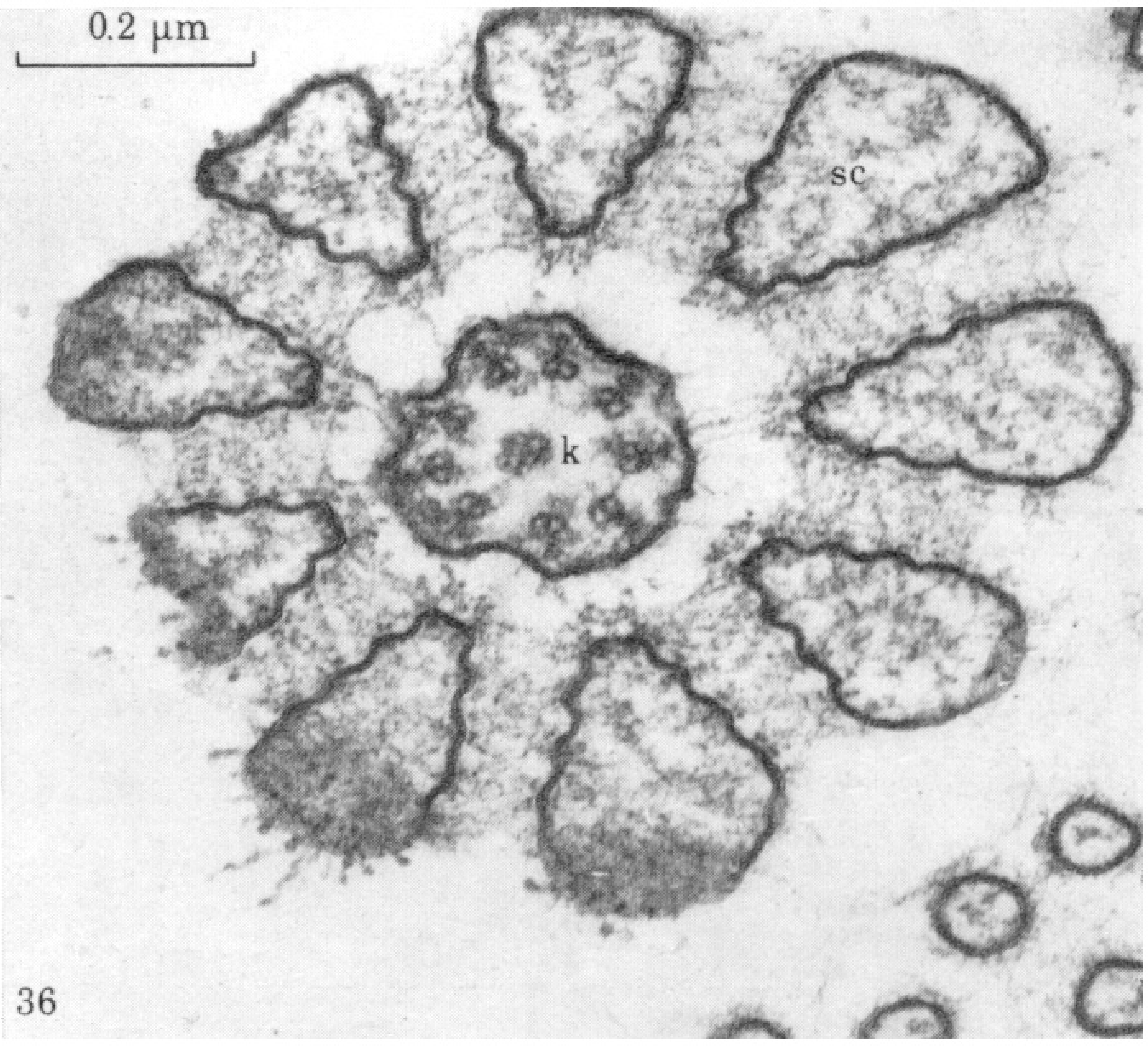




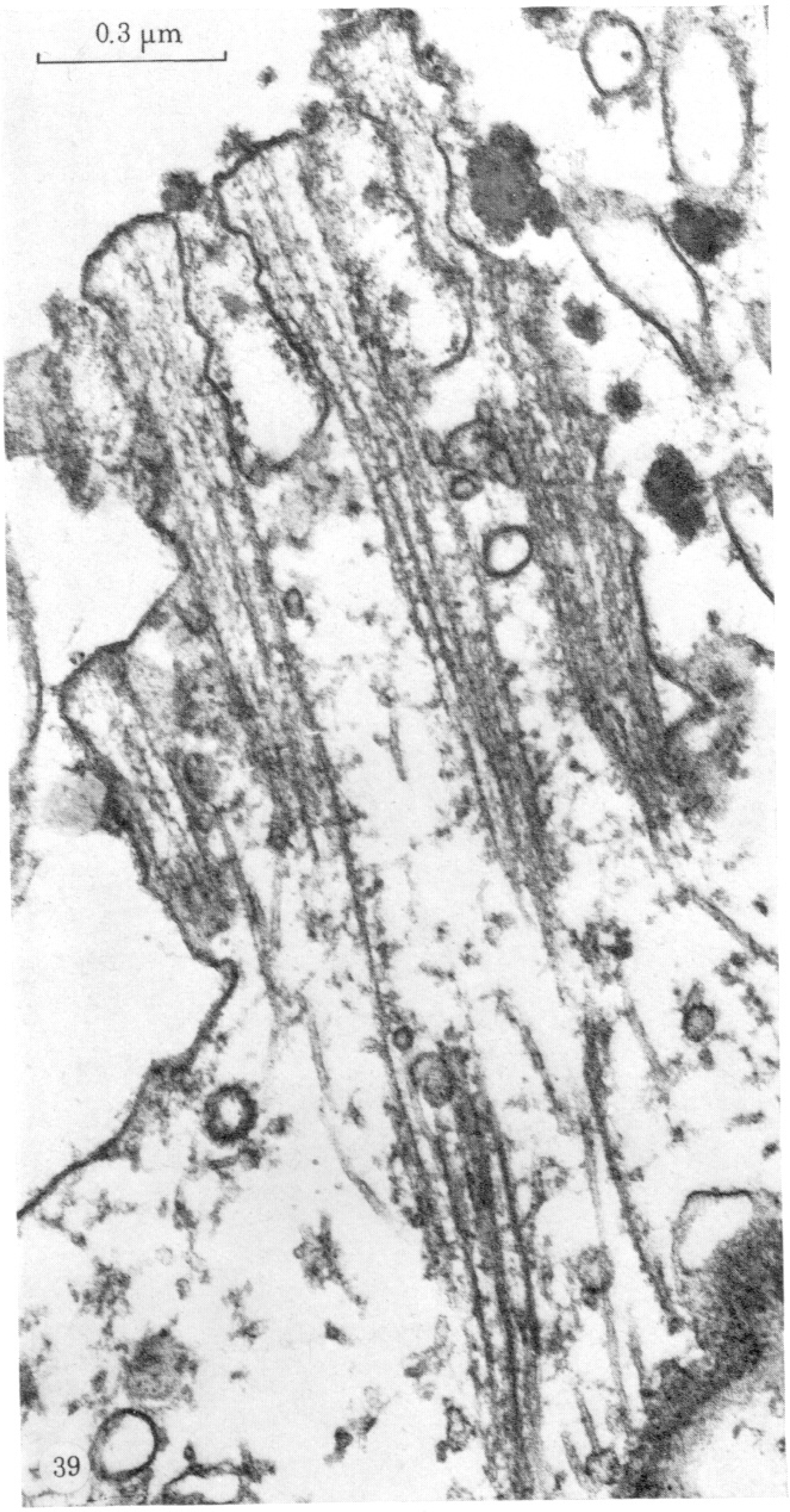


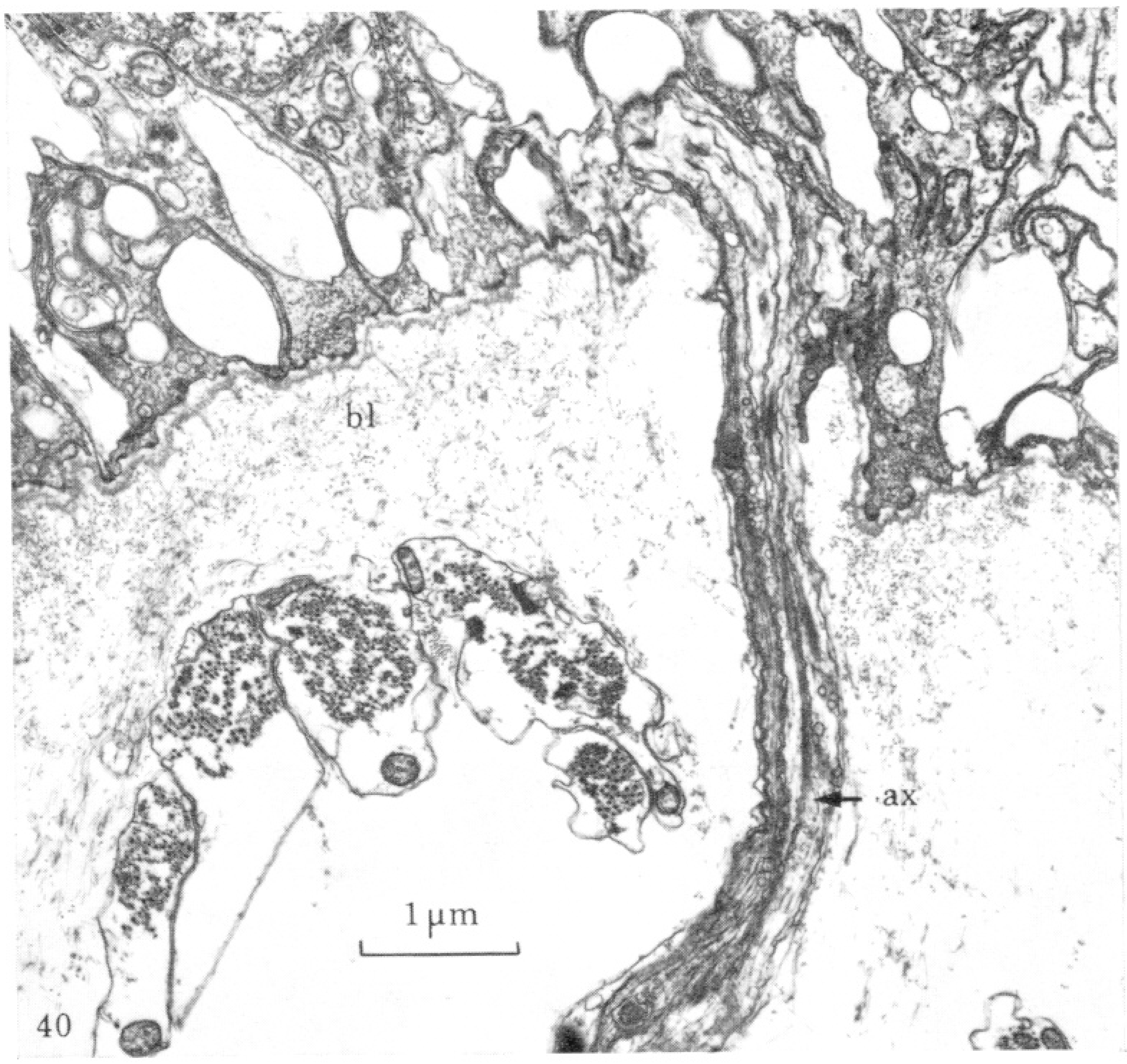


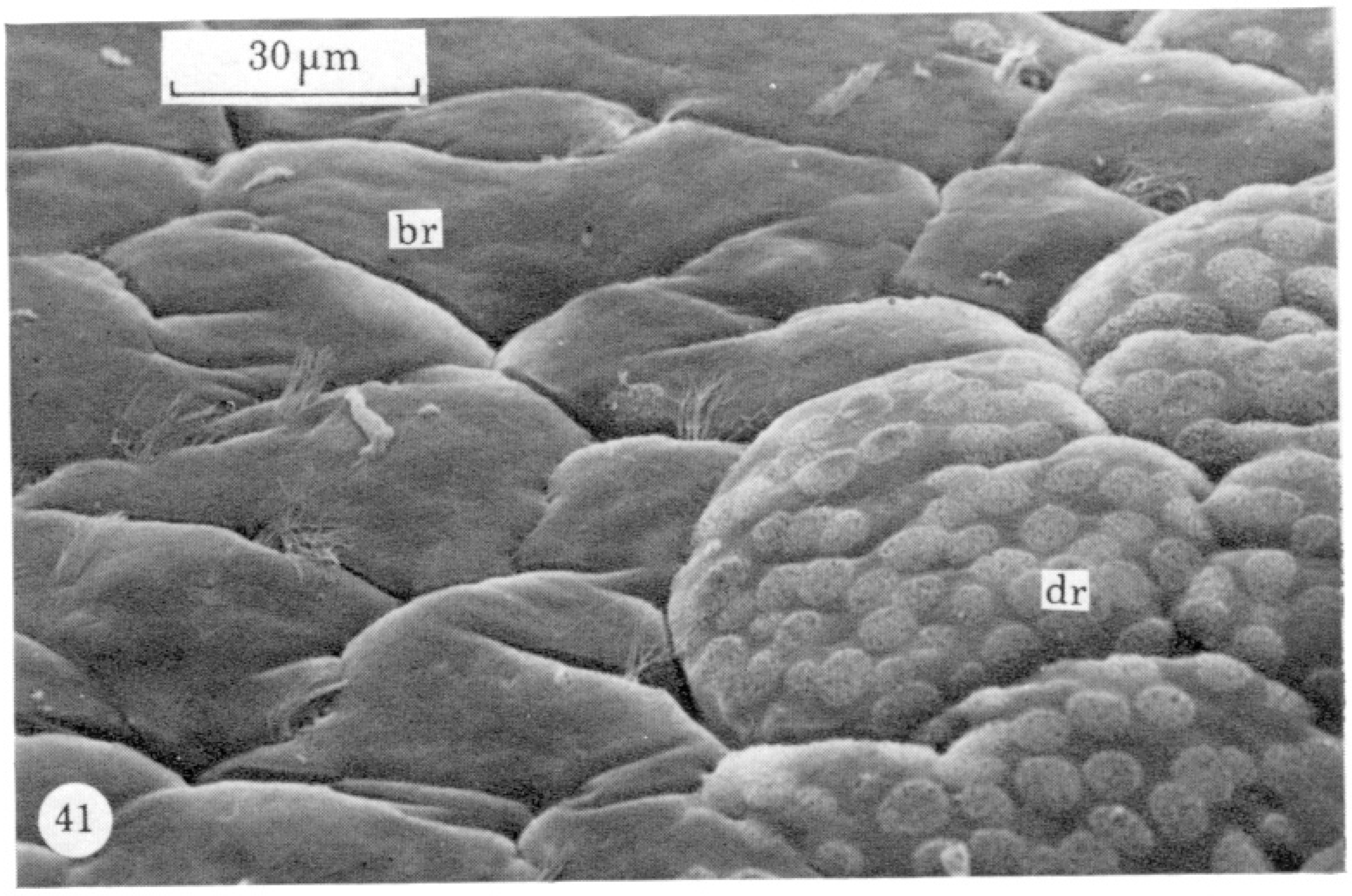


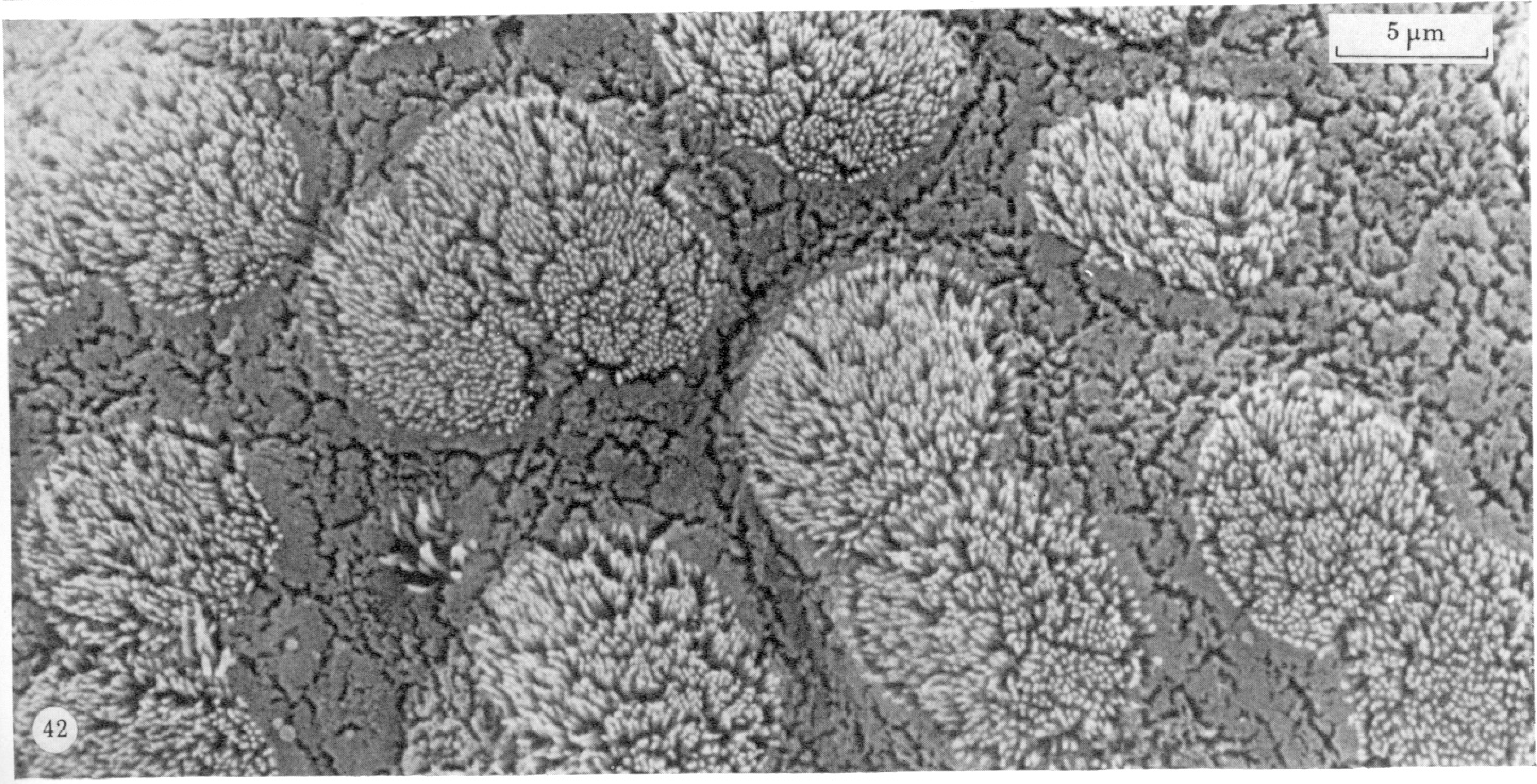


FIGURES 31–36. For description see p. 54.









FIGURES 39–42. For description see p. 55.

FIGURES 43–56. For description see opposite.