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The Ultrastructure of Chrysaora quinquecirrha Strobilae

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THE ULTRASTRUCTURE OF

CHRYSAORA QUINQUECIRRHA STROBILAE

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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ABSTRACT

Scyphistomae and early strobilae of the scyphozoan Chrysaora quinquecirrha were fixed and sectioned for light microscopy. Strobilating polyps chosen for examination possessed four or five constrictions, but the tissue segments between constrictions showed no externally visible signs of metamorphosis and feeding tentacles were still present.

Ultrastructural observations revealed that there appears to be an increased fibrogenesis in strobilating polyps in regions of the mesoglea bordering the constrictions. Bundles of fibers in parallel array are found at branch points of the mesoglea near constricting regions. These bundles may play a role in constriction stabilization or act as a substrate for cell migration in the strobilating polyp. Peculiar dense bodies are present in the mesoglea and epidermal nuclei of strobilating polyps but are absent in the mesoglea and nuclei of non-strobilating polyps. Microfilament bundles are found in the gastrodermis of non-strobilating polyps, running at right angles to the oral-aboral axis of the animal.

THE ULTRASTRUCTURE OF *CHRYSAORA QUINQUECIRRHA* STROBILAE

INTRODUCTION

One of the characteristics of the coelenterates is the alternation of polyp and medusa in the life cycle. The alternation represents a shift from a stage which can reproduce sexually, the medusa, to one which can reproduce asexually, the polyp. In the Class Scyphozoa the polyp, or scyphistoma, can reproduce asexually by budding, by the deposition, in some species, of chitinous podocysts which later germinate into polyps, and by the process of strobilation.

The two major studies on the morphology and histology of scyphozoan polyps and their development are those of Percival (1923) on Aurelia and Chuin (1930) on Chrysaora hysocella.

The scyphistoma of Chrysaora quinquecirrha is a chalice-shaped polyp about one to four millimeters long. The protruding cruciform mouth is bordered by eight to twenty-four tentacles and together form the oral disc. The body region consists of a cup-shaped hydranth and slender stalk which terminates aborally in the basal disc, the point of attachment to the substrate. The gastrovascular cavity is divided by four endodermal septa which extend from the tentacular ring to the junction of the hydranth and stalk. By definition, the position of the septa marks the two vertical interradial planes which delineate the four gastric pouches. Four peristomial pits are located

interradially on the oral disc. Four longitudinal muscle cords run from their points of attachment on the pits through the mesoglea of the septa and the stalk to the basal disc. Four ostia or holes pierce the septa lateral to the longitudinal muscle cords.

The cells of the scyphistomae of Chrysaora quinquecirrha are organized into two tissue layers: an outer epidermal layer and an inner gastrodermal layer. Between these two tissue layers is a layer of collagenous material (G. Chapman, 1966), the mesoglea, which contains small amoeboid cells.

The epidermis is primarily composed of epithelio-muscular cells interspersed with neurons, interstitial cells, and cnidoblasts. Epithelio-muscular cells are characterized by large intracellular vacuoles, a sparse cytoplasm, apical granules, and a layer of muscle filaments which run in an oral-aboral direction at the base of the cells (Hyman, 1940). The epithelio-muscular cells of the scyphistoma have, in addition, a branch perpendicular to the longitudinal main fiber forming a "T-" or "L-" shaped muscle fiber (Chapman, 1965). Contraction of the muscle fibers in the epithelio-muscular cells of the body results in a change of cell shape from roughly cuboidal to columnar (D. M. Chapman, 1966). Ganglia and neurosecretory cells are similar in structure and characterized by an irregular nucleus with several nucleoli, sparse endoplasmic reticulum, numerous free ribosomes, glycogen granules, and a well-developed Golgi apparatus (Dietz, 1971). In addition, neurosecretory cells contain electron-dense, membrane bound granules varying in size

from 100 to 160 nm. Neurosensory cells, defined by Lentz (1966) in respect to Hydra as ganglia or neurosecretory cells possessing cilia, lie between the epithelio-muscular cells at right angles to the other nerve cells (Dietz, 1971). All neurons contain microtubules (Dietz, 1971). The microtubule containing processes of nerve cells often occur in groups next to the mesoglea (Dietz, 1971). Small undifferentiated interstitial cells are interspersed between epithelio-muscular cells, as are cnidoblasts containing nematocysts in various stages of development (Hyman, 1940).

The gastrodermis consists primarily of two cell types. One, the gland cell, is characterized by a large number of inclusions, presumably of a mucoid nature (Hyman, 1940). The other, the digestive cell, is characterized by many vacuoles containing loosely arrayed amorphous material and a sparse cytoplasm. In contrast to Hydra, there are no circular muscle fibers at the base of these cells next to the mesoglea (D. M. Chapman, 1966). Neurons and interstitial cells are found in the gastrodermis also, but are less numerous than in the epidermis (Hyman, 1940).

The pharynx and free edges of the septa are lined with columnar, ciliated cells, histologically different from gastrodermis or epidermis and described by D. M. Chapman (1966) as the "scyphopharynx-filament complex."

The mesoglea of the scyphistoma consists of a gelatinous, fibrous layer containing amoeboid cells. The basal lamina-like outer layer, especially that near the epidermis, is strongly

PAS-positive, while the middle is less PAS reactive (Chapman, 1970). The medusan scyphozoan mesoglea is probably a simple polymeric gel. The fibrous component is identified as collagen by its characteristic x-ray diffraction pattern, its high content of hydroxyproline, hydroxylysine, proline and glycine, and its property of contracting when heated (G. Chapman, 1966). Its banding is variable and often it does not have a 660 Å pattern. A PAS-positive component of the mesoglea is associated with the fibers (Bouillon and Vandermeersche, 1956).

The fibrous nature of the scyphistomal mesoglea is apparent in electron micrographs of Aurelia (Chapman, 1970). In the tentacle of the scyphistoma, the mesogleal fibers are oriented longitudinally in extended tentacles and randomly in contracted ones. The fibers have a beaded appearance. Chapman (1970) indicates that this banding has a 660 Å periodicity, but a comparison between his micrographs and with electron micrographs in this thesis seems to indicate that he erred by an order of magnitude; that is, the periodicity is 66 Å. These fibers are sensitive to collagenase but not to trypsin. Sensitivity to collagenase must be coupled to other evidence in order to identify the nature of the fibers, since bacterial collagenase can contain other proteases. However, the existence of collagen in medusan mesoglea strongly suggests that scyphistomal mesoglea may contain collagen as a fibrous component.

In the morphogenetic process of strobilation, the hydranth of the polyp becomes ringed by one or more constrictions, beginning at the oral end, which eventually cut completely through

the animal. The tissue between constrictions undergoes a metamorphosis to develop into ephyrae which are eventually freed from the scyphistoma. The metamorphosis and release of ephyrae correspond to the order in which the constrictions appear. Thus, on a single scyphistoma, one can see pulsating ephyrae at the oral end and undifferentiated rings of tissue toward the base of the hydranth. After all ephyrae are released, the polyp regenerates a new mouth and tentacles and resumes its former mode of existence (Percival, 1923; Chuin, 1930).

Indications of approaching strobilation include elongation of the polyp (Percival, 1923; Chuin, 1930), color changes (Chuin, 1930), and a shift or resorption of tentacles (Chuin, 1930; Littleford, 1939). Loeb (1970) describes a process of "neck formation," characterized by a single constriction below the base of the tentacles, which follows elongation. This process does not always lead irreversibly to strobilation. Spangenberg (1968) failed to observe elongation in Aurelia preceding strobilation.

There have been few studies of the cytological events occurring during the initiation of strobilation. Chuin (1930) states that the regions of constriction are characterized by two or three rows of actively dividing cells in the epidermis and gastrodermis, resulting in diffuse cell boundaries between cells and the formation of a syncytium; the cells also contain granular inclusions. In contrast, the cells in the bulging regions are columnar, non-dividing and clearly defined, and contain no granulations. However, he states that this difference between the

two regions is absent when constrictions first appear.

Previous ultrastructural studies of Chrysaora quinquecirrha have dealt primarily with the tentacles (Burnett and Sutton, 1969; Perkins et al., 1971) and nematocysts (Sutton and Burnett, 1969) of the medusa. The only ultrastructural studies of scyphozoan polyps are those of Chapman on the tentacles of Aurelia (1970) and Dietz (1971) on Chrysaora. The only study of the ultrastructure of the strobilating polyp is that of Dietz (1971), who investigated the correlation between strobilation and neurosecretory granules found in the epidermal neurosecretory cells of the hypostomal region at the base of the tentacles.

The mechanisms by which the constrictions are formed and maintained are not understood and have received little attention from previous investigators. Dietz (1971) observed an apparent contraction or enlargement of muscle fibers along the inner edge of the epidermis of the hypostomal region at the base of the tentacles during segmentation. She conjectures that the change in diameter of the muscle bundles is correlated with the occurrence of constrictions during strobilation and may, in fact, be a causative factor.

Since the mesoglea of the scyphistoma is a major supporting structure in the polyp and is the layer which joins the two cell layers, it might be expected to play a major role in any morphogenetic event such as strobilation. This expectation is reinforced by a series of papers on the mesoglea of Hydra. Shostak, Patel and Burnett (1965) demonstrated that the mesoglea of Hydra acts as a substrate for cell migration. Hausman and Burnett (1970)

have recently implicated the fibrous mesoglea of Hydra in a morphogenetic role. In the process of budding, the oral-aboral fiber system breaks down in a localized region at which buds form. They postulate that the fiber system serves as a supporting ladder over which cells can move. When the migrating cells reach the point where the fiber system has broken down, their normal longitudinal path is interrupted and they move out to form a bud. A new fiber system is formed in the longitudinal axis of the bud over which migration continues. When the bud forms a complete animal and separates from the parent, the longitudinal system of the parent is reconstituted and body growth continues. The mesoglea may have similar roles in Chrysaora scyphistomae.

D. M. Chapman (1966) has observed in Aurelia that when a non-strobilating polyp contracts, the cells of the outer epidermal layer change shape from cuboidal to columnar, while the gastroderm is thrown into folds. In contrast, in the folding of the body wall in strobilation, the cell layers are closely apposed and the gastroderm does not bulge away from the epidermis (Chapman, 1966). This change in the associative tendencies of the cell layers may reflect a change in the composition of the mesoglea and an increased adhesiveness of the cells to this layer.

This study examines the fine structure of the mesoglea and adjacent portions of the cell layers of strobilating and non-strobilating polyps in order to investigate any differences which may accompany the formation and maintainance of the constrictions of strobilation. These constrictions do not occur in non-strobilating polyps. Some physical mechanisms must be

responsible for the constrictions and their maintainance. In the scyphistoma, the causative factors may lie either intracellularly in the two tissue layers or extracellularly in the mesoglea. The mesoglea of the scyphistoma contains a fibrous component and an amorphous component. In the process of constriction formation and maintainance, one may find a change in the proportions of these components or a spatial rearrangement of one component. Such a change in the components of the mesoglea may be accompanied by a visible change in adjacent cells. Contractile mechanisms within the cells such as microfilaments or muscle fibers may play a role in the process of constriction formation and maintainance.

MATERIALS AND METHODS

Polyps of the scyphozoan Chrysaora quinquecirrha were cultured in York River, Virginia water with salinities from 19-22 °/₀₀. The cultures were fed once weekly with Artemia nauplii. The polyps were divided into two groups:

A. Non-strobilating, cold-conditioned polyps cultured at 15° C;

B. Strobilating, cold-conditioned polyps. Cold-conditioned polyps that had been maintained at 15° C for at least six months were induced to strobilate by being placed at 25° C in artificial sea water (Spangenberg, 1965) diluted to 20 °/₀₀ and containing 0.2 µg/ml potassium iodide, which is a requirement for strobilation.

Strobilating polyps chosen for examination possessed four or five constrictions, but the tissue segments between constrictions showed no externally visible signs of metamorphosis and feeding tentacles were still present. Polyps reached this stage of strobilation in 48-72 hours after being placed in artificial sea water at 25° C.

Material for electron microscopy was fixed 30 minutes at 25° C in 4 % glutaraldehyde in 0.1 M phosphate buffer (Lillie, 1965) at pH 7.3 and post-fixed 30 minutes at 25° C in 1 % osmium tetroxide in 0.1 M phosphate buffer at pH 7.3 with 0.2 M sodium

chloride. Dehydration in acetone was followed by embedding in Epon 812 (Luft, 1961). Polyps were sectioned parallel to the oral-aboral axis in the region of presumptive strobilation in the hydranth. In addition, strobilating polyps were sectioned in regions of constrictions. Sections were cut with a Porter-Blum MT-2B or an LKB Ultratome III ultramicrotome. The sections were stained with aqueous uranyl acetate and lead citrate (Venable and Coggleshall, 1965) and were examined with a Zeiss EM 9S-2 electron microscope.

Material for light microscopy was fixed 30 minutes in 4 % glutaraldehyde in 0.1 M phosphate buffer, dehydrated in a graded alcohol series and embedded in Paraplast (Fisher Scientific Co.). Serial sections were cut at 5 μ and 10 μ and stained with iron hematoxylin-eosin Y, Mallory's Triple Connective Tissue Stain, modified Masson's Stain for connective tissue and Picro-Ponceau (Humason, 1967). A Zeiss Photomicroscope II was used for light microscopy.

RESULTS

Cells of the hydranth

No differences were observed in cell fine structure between strobilating and non-strobilating polyps with the exception of cell boundaries next to the mesoglea, the previously reported (Dietz, 1971) depletion of presumptive glycogen granules in the strobilating polyp, and the presence of electron-lucent granules in some epidermal nuclei of strobilating polyps. The following general descriptions, with these exceptions, therefore apply to cells of both strobilating and control polyps.

The epithelio-muscular cells of the hydranth are columnar cells approximately 10-20 μ thick and 5 μ in diameter arranged in a single layer with their bases abutting the mesoglea and their apices forming the outer surface of the polyp (Hyman, 1940; Fig. 1). Adjacent cells are connected at their apical borders by septate desmosomes (Fig. 2). The cytoplasm is pressed against the outer boundaries of the cells by large intracellular vacuoles (Fig. 3). The cytoplasm at the apices of the cells contains granular, membrane-bound bodies 0.5-1.0 μ in diameter as well as free ribosomes (Fig. 3). The granules are probably similar to those described by Chapman (1968) in *Aurelia* scyphistomae which show a positive argentaffin reaction. Nuclei are located in the basal half of the cytoplasm (Fig. 1). In strobilating polyps,

the nuclei of some cells contain electron-lucent granules 200-300 Å in diameter (Fig. 4). These granules were not observed in the nuclei of non-strobilating polyps. Muscle fibers consisting of thick (170 Å) and thin (50 Å) filaments are found in the basal portion of the cells (Fig. 5). Osmiophilic droplets 1-2 μ in diameter are scattered throughout the cells (Fig. 6).

Cnidoblasts are small, round cells 6-8 μ in diameter located between the basal ends of epithelio-muscular cells (Hyman, 1940). They are characterized by well-developed rough endoplasmic reticulum and Golgi bodies and contain maturing nematocysts (Fig. 6).

The gland and digestive cells of the gastrodermis are club-shaped cells 20-50 μ thick and approximately 5-10 μ in diameter at their apical ends (Fig. 7). The larger osmiophilic inclusions, probably lipid droplets, are 1-2 μ in diameter and are non-membrane bound. Gland cells also contain apical flagella, as well as highly developed rough endoplasmic reticulum, Golgi bodies and numerous mitochondria. Digestive cells contain apical intracellular vacuoles enclosing amorphous material (Fig. 7). The free edges of the digestive cells possess microvilli like those found at the free edges of phagocytic and pinocytotic cells, and the total cytoplasm is sparse. In addition, membrane-bound bodies with granular inclusions, possibly lysosomes, are found associated with the vacuoles.

The gastrodermis of non-strobilating polyps contains bundles of microfilaments bordering the mesoglea (Fig. 8 and 9). The microfilaments are approximately 40-50 Å in diameter. The

bundles appear to insert at the junction between two digestive cells (Fig. 10). At these junctions, the apposing unit membranes lose their separate identities, although they are distinct at a distance away from the mesogleal cell surface. There are no microtubules associated with the microfilament bundles.

The neurons and interstitial cells of the gastrodermis resemble those of the epidermis.

Mesoglea of non-strobilating and strobilating polyps

A. Mesoglea of non-strobilating polyps.

The mesoglea of non-strobilating polyps in the presumptive strobilating region of the hydranth is generally amorphous in appearance (Fig. 11 and 12). It is characterized by a dense felt-work of material near the borders of the cells, by the presence of fibrous strands approximately 80-90 Å in diameter, and by a less densely stained region between the dense material bordering the cells. The material bordering the cells forms a band 100-500 nm in thickness and contains a few fibers parallel to the cell surface. The bands become wider in crevices formed by cell processes (Fig. 12). In addition, in these regions, the plasma membrane becomes diffuse and at scattered points short fibers may be seen at right angles to the cell surface. The cytoplasm of these digestive cells also contains similar fibers (Fig. 11).

The fibers found in the mesoglea have punctate striations about 60 Å apart. Bundles of these fibers are found throughout the mesoglea, generally paralleling the cell surface, and at

scattered points show cross links (Fig. 11). The shorter fibers found at right angles to the cell surface and the fibers in the cytoplasm at these points have a similar beaded appearance (Fig. 12). In all instances observed, these fibers radiate from gastrodermal cells.

B. Mesoglea of strobilating polyps.

In the strobilating polyp, the mesoglea in the bulging regions is tightly compressed between cell layers and is very thin, 0.3-0.5 μ. In the region toward the center of the body, the region where constriction has occurred, the mesoglea is thickened to about 5 μ and is branched (Fig. 13).

The mesoglea of the thin compressed region resembles the dense felt-work of the non-strobilating animal. In addition, it contains numerous non-membrane-bound particles 200-300 Å in diameter whose appearance differs from glycogen granules in that they have an electron-lucent center (Fig. 14). Small membrane-bound bodies are also present, which may be cell processes extending into the mesoglea or portions of amoeboid cells (Fig. 13).

The mesoglea toward the center of the body in branched regions bordering the actual region of constriction differs in several ways from that of the compressed regions. Large numbers of short fibers are found at right angles to the gastrodermis and are associated with gastrodermal cells having diffuse cell boundaries (Fig. 15). They are much more numerous than in the non-strobilating polyp, although they are the same size and have the same beaded appearance. Large clusters of fibers in parallel

array which are cross-linked at various points are also found in this region (Fig. 16-18). These long fibers are associated with the diffuse boundaries of membrane-bound bodies in the mesoglea which may be cell processes extending into the mesoglea or cells free in the mesoglea (Fig. 16-18). In addition, these fibrous bundles are found where one layer of gastrodermis is separated from another layer of gastrodermis by the branching of the mesoglea.

The mesoglea at the base of the hydranth where constrictions do not occur in strobilating polyps resembles that of non-strobilating polyps in its amorphous nature and relative lack of highly oriented fibrous material. However, in contrast to the non-strobilating polyp, the electron-dense, non-membrane-bound bodies 200-300 Å in diameter found in strobilating regions are present (Fig. 19).

DISCUSSION

It may be concluded from the study that increased production of mesogleal fibers by gastrodermal cells is associated with the formation of constrictions in the early strobila. Although no attempt has been made to determine the chemical nature of these fibers, it may be noted that they resemble in size and punctate appearance the collagenase sensitive fibers of Aurelia tentacles (Chapman, 1970) as well as the mesogleal fibers of Hydra (Haynes, Burnett and Davis, 1968). The mesogleal fibers of Hydra incorporate H^3-proline at a high rate, as do digestive and epitheliomuscular cells (Hausman and Burnett, 1971). On the basis of this evidence, Hausman and Burnett (1971) suggest that the mesogleal fibers of Hydra are collagenous in nature. The absence of a 660 Å banding pattern is often found in embryonic collagen as well as in the collagen of other invertebrates (see Dische, 1970 for a review).

The fibers in Chrysaora seem to radiate primarily from the gastrodermis. The apparent restriction of fiber production to cells of the gastrodermal layer is in contrast to the probable situation in Hydra, in which both cellular layers incorporate H^3-proline. Bouillon and Vandermeersche (1956) describe a concentration of PAS-positive material at the base of the gastrodermis and fibers arising from it in Limnocnida medusae. In

Chrysaora the orientation of fibers normal to the cell surface (Fig. 15) is noteworthy. A similar orientation exists in the mesogleal fibers of Hydra (Hausman and Burnett, 1971) and in fibroblasts involved in the synthesis of basal lamina (Sandborn, 1970). The diffuse appearance of the cell surfaces (Fig. 15-18) resembles that noted previously in fibroblasts involved in fibrogenesis (Bloom and Fawcett, 1968) and in differentiating cartilage cells in regenerating limbs of Amblystoma larvae (Hay, 1958).

The association of bundles of fibers with membrane-bound structures in the mesoglea (Fig. 16-18) is of considerable interest, and it would be worthwhile to determine if these are cell processes, and if so, to what cells they belong.

The fibers in the mesoglea of strobilating Chrysaora scyphistomae may play a morphogenetic role similar to that of the fibrous mesoglea in Hydra. In Hydra, cells produced by division along the trunk migrate vertically into the tentacles (Campbell, 1967). The presence of fibrous bundles toward the center of a constriction and the absence of these bundles in the bulging region may indicate a system over which cells arising from the active cell division observed in the epidermis and gastrodermis of the strobilating polyp can migrate out to form incipient ephyral tissue. The fibers may act as a barrier to the normal vertical migration of the cells,as may the branching of the mesoglea at points of constriction.

The process of constriction in the strobila may be compared with the formation of clefts and lobes in some developing vertebrate

structures, in which both intracellular and extracellular fibers have been implicated by ultrastructural studies. Bernfield and Wessells (1970) postulate that lobe formation in salivary gland is triggered by mucopolysaccharide-protein complexes associated with the cell surface which stimulate microfilament activity. Actual cleft formation is due to the contraction of intracellular bundles of 50 Å microfilaments. They note the presence of collagen at morphogenetically quiescent regions such as older clefts and postulate that the role of collagen is the stabilization of the clefts formed by microfilament contraction, citing evidence that these clefts become insensitive to concentrations of Cytochalasin B which previously would disrupt the microfilaments and cause a rounding up of the tissue. The increase in fibers adjacent to the constricting region in a strobilating polyp may serve a similar stabilizing function.

In this context, it is interesting to note the existence of bundles of 50 Å microfilaments in the gastrodermis next to the mesoglea of non-strobilating animals (Fig. 8-10). In the sections observed, these bundles run roughly at right angles to the oral-aboral axis. Chapman (1970) has observed such bundles in the gastrodermis of the scyphistomal tentacle. D. M. Chapman (1966) has stated that the elongation of Aurelia scyphistomae preceding strobilation is due to the elongation of the cells rather than to increased cell number. A contractile microfilament system in the gastrodermis running at right angles to the longitudinal axis of the polyp could function to cause this change in cell shape. Such a contractile microfilament system could also constrict the polyp.

Peculiar dense bodies with an electron-lucent center are present in the mesoglea and some epidermal nuclei of strobilating polyps (Fig. 4 and 14) but were not observed in non-strobilating polyps. Bodies of similar size and appearance whose composition or origin is unknown have been noted in the extracellular materials in vertebrate embryonic tissue such as developing salivary gland, lung, pancreas, skin, feathers and hair in which epithelio-mesenchymal interactions are thought to be occurring (see Bern-field and Wessells, 1970). Similar dense granules also occur in mitochondria from many tissues, where they are thought to be calcium salts (Fawcett, 1966).

SUMMARY

There appears to be an increased fibrogenesis in strobilating polyps in regions of the mesoglea bordering the constrictions. Bundles of fibers in parallel array are found at branch points of the mesoglea near constricting polyps. These bundles may play a role in constriction stabilization or act as a substrate for cell migration in the strobilating polyp. Peculiar dense bodies are present in the mesoglea and epidermal nuclei of strobilating polyps but are absent in the mesoglea and nuclei of non-strobilating polyps. Microfilament bundles are found in the gastrodermis of non-strobilating polyps, running at right angles to the oral-aboral axis of the animal.

FIGURE 1

Longitudinal section of an early strobila. Epidermis (E) and gastrodermis (G) are separated by the mesoglea (Me). Nuclei (N) of epithelio-muscular cells are located in the basal half of the cells. X 132.

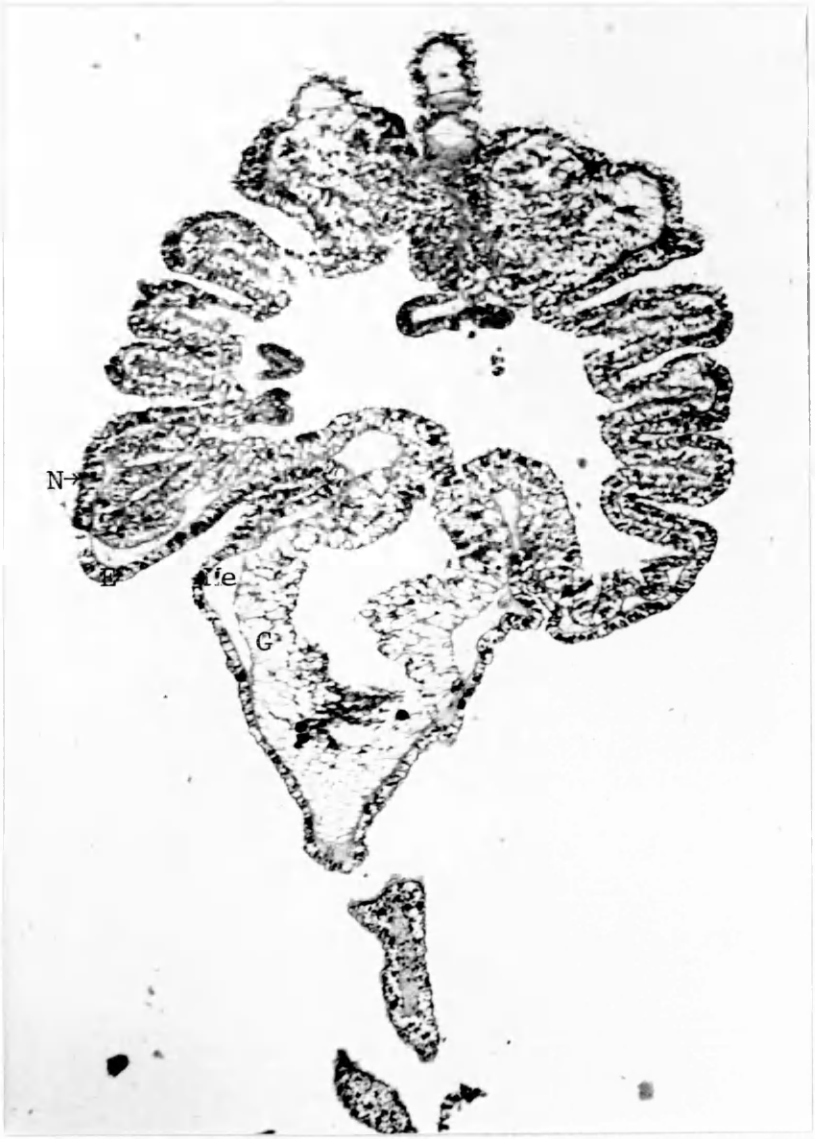

N
ie
G

FIGURE 2

Septate desmosomes (SD) connecting adjacent epithelio-muscular cells. X 59,000.

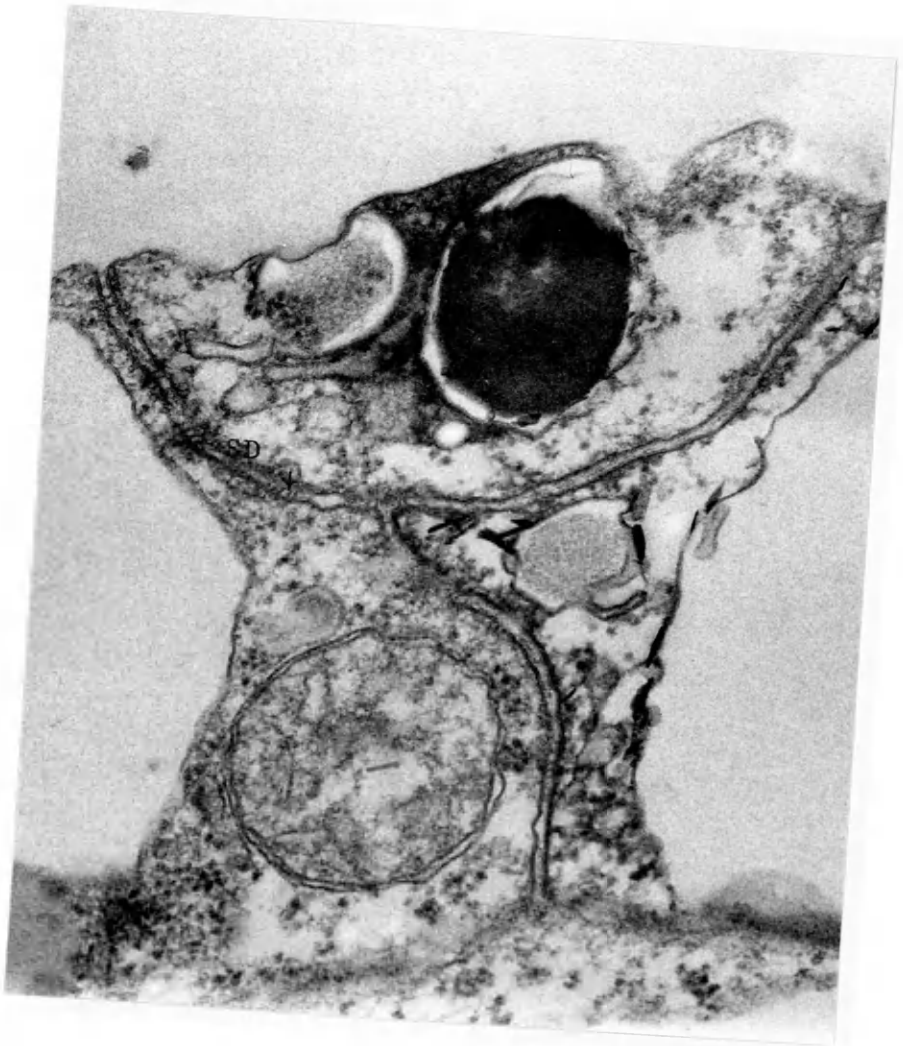


FIGURE 3

Argentaffin granules (A) found in apical third of epithelio-muscular cells which also contain large intracellular vacuoles (V). X 19,950.

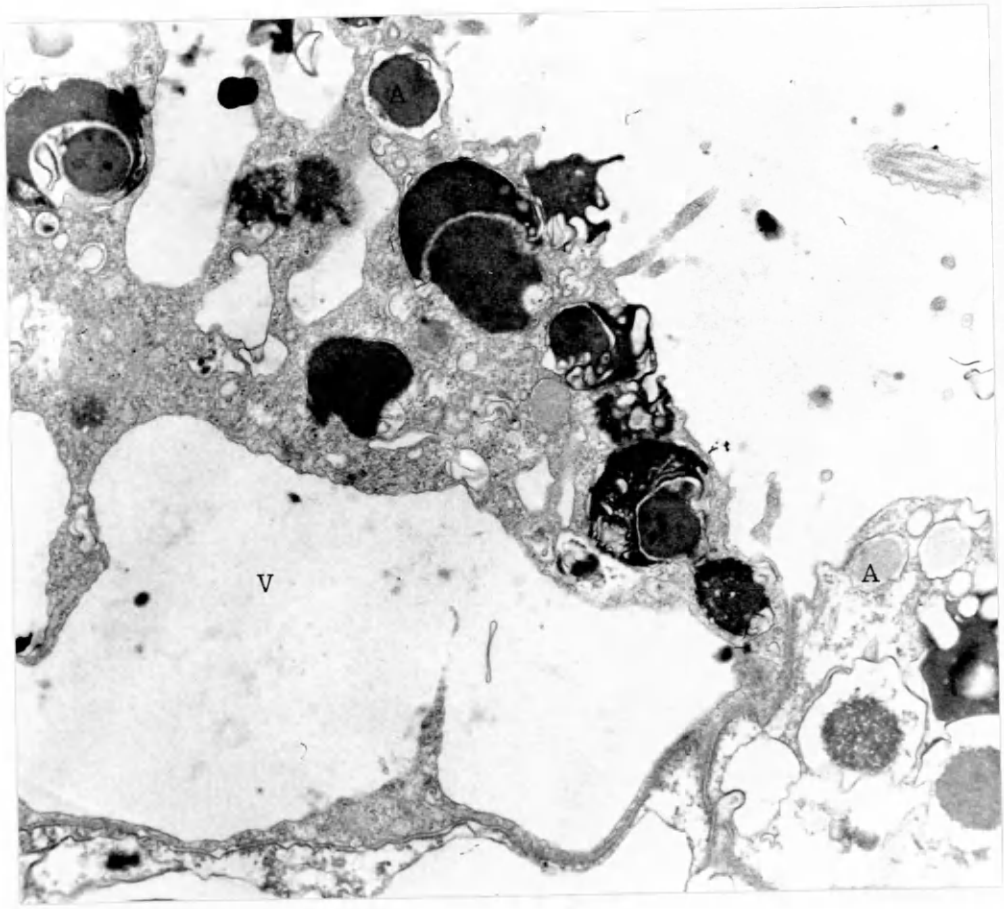

A
V
A

FIGURE 4

Epidermal nucleus (N) containing non-membrane-bound bodies (DB) 200-300 Å in diameter. X 28,500.

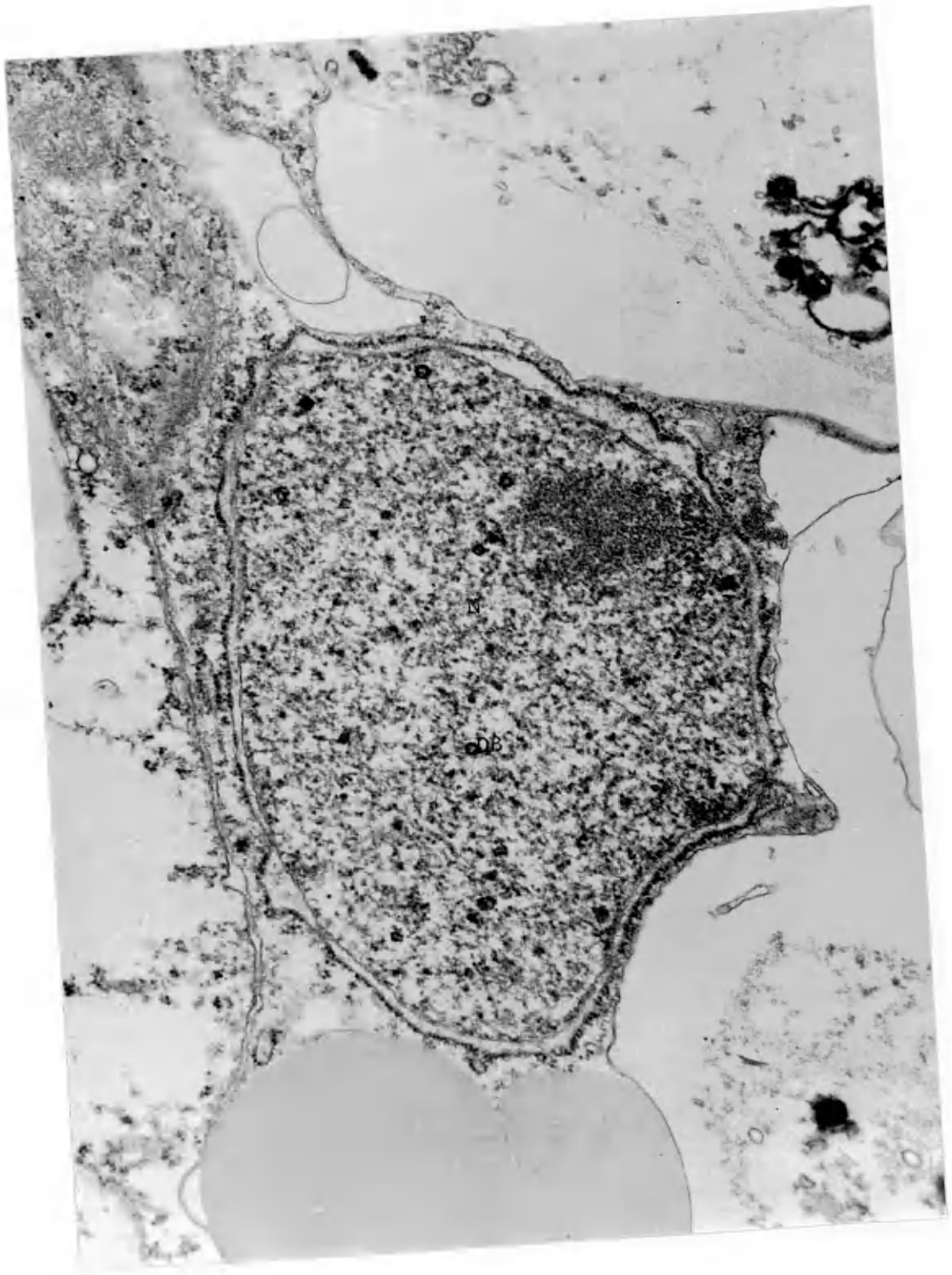

N
nb

FIGURE 5

Muscle fibers (M) of epithelio-muscular cells. X 19,950.

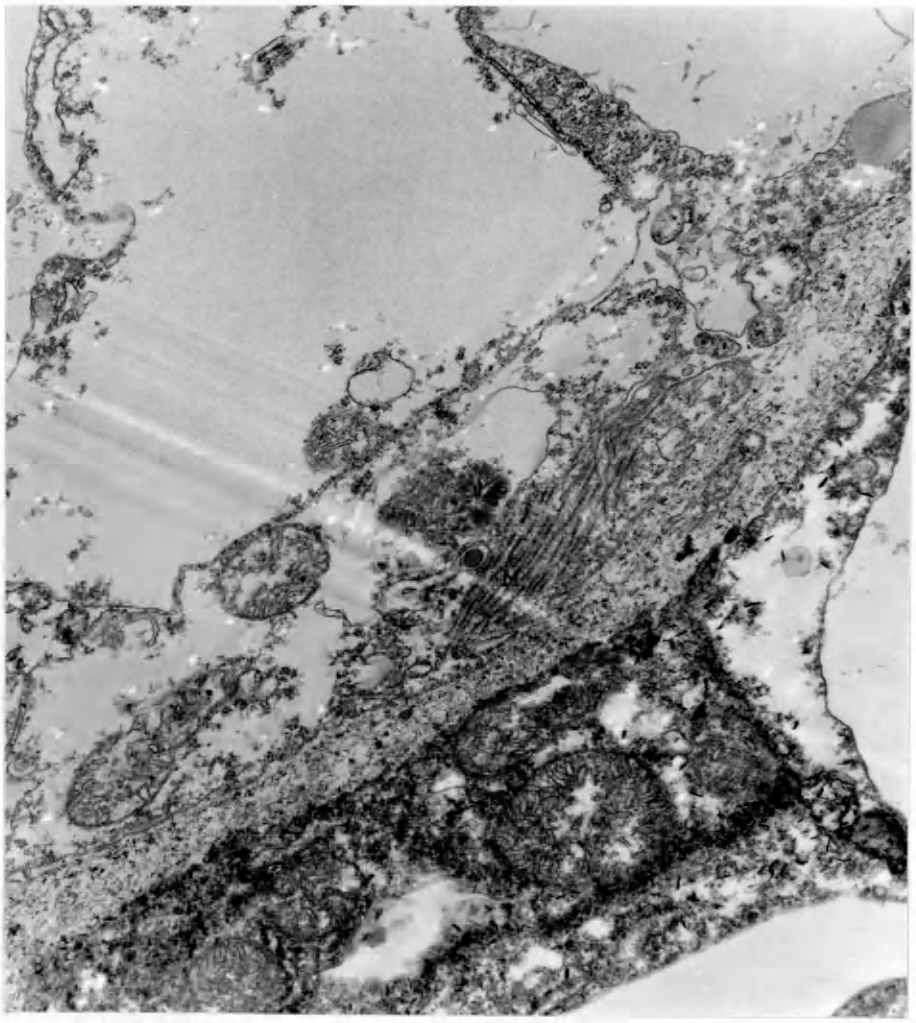


FIGURE 6

Cnidoblast (C) containing nematocyst (Ne). Osmiophilic droplets (OD) in epithelio-muscular cells. X 8,800.

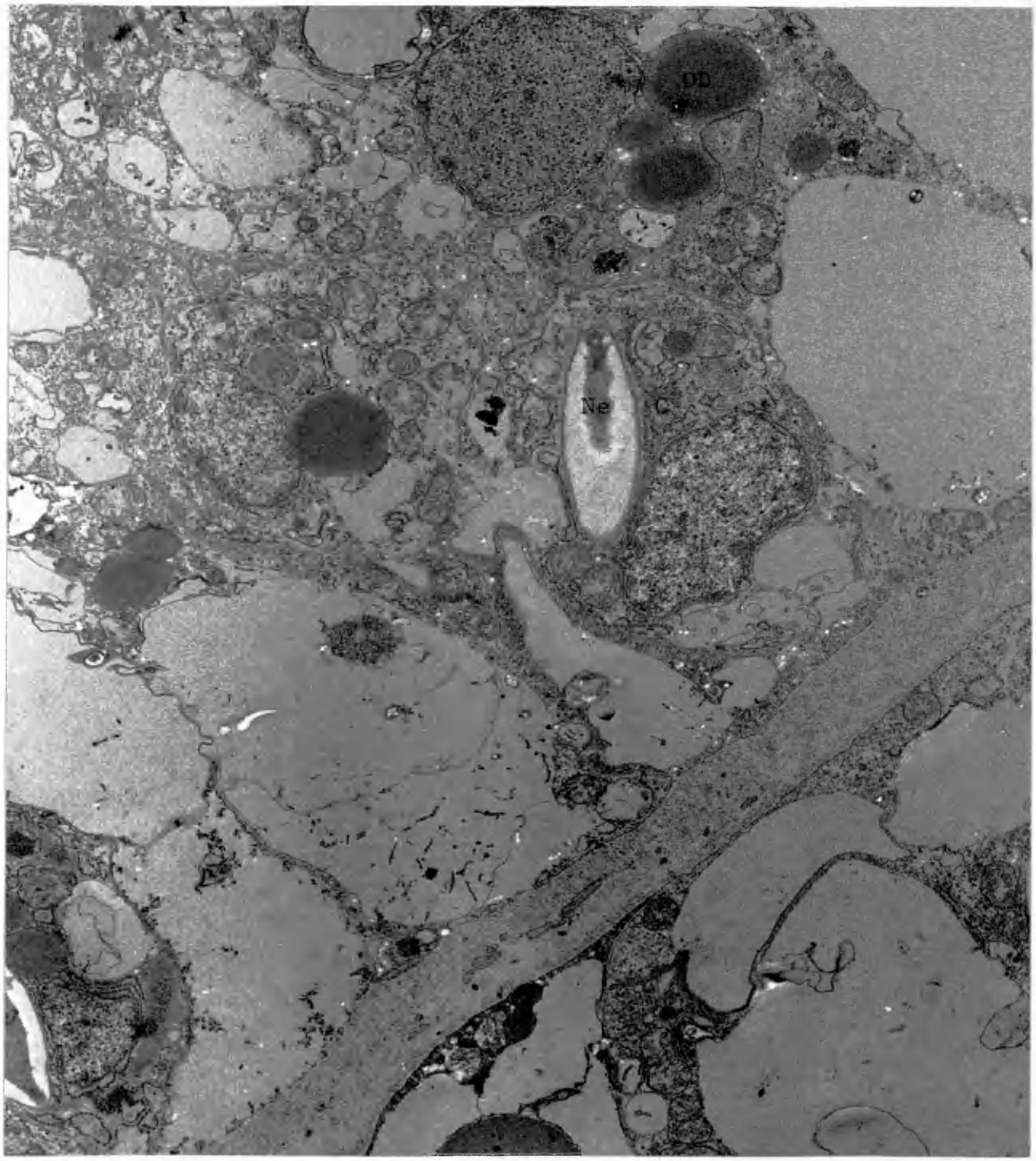

DD
Ne
C

FIGURE 7

Gland (G) and digestive (D) cells of the gastrodermis containing osmiophilic droplets (OD). Apical flagellum (AF) of gland cell. Intracellular vacuoles (V) of digestive cells with associated granular bodies, possibly lysosomes (Ly?). X 5,400.

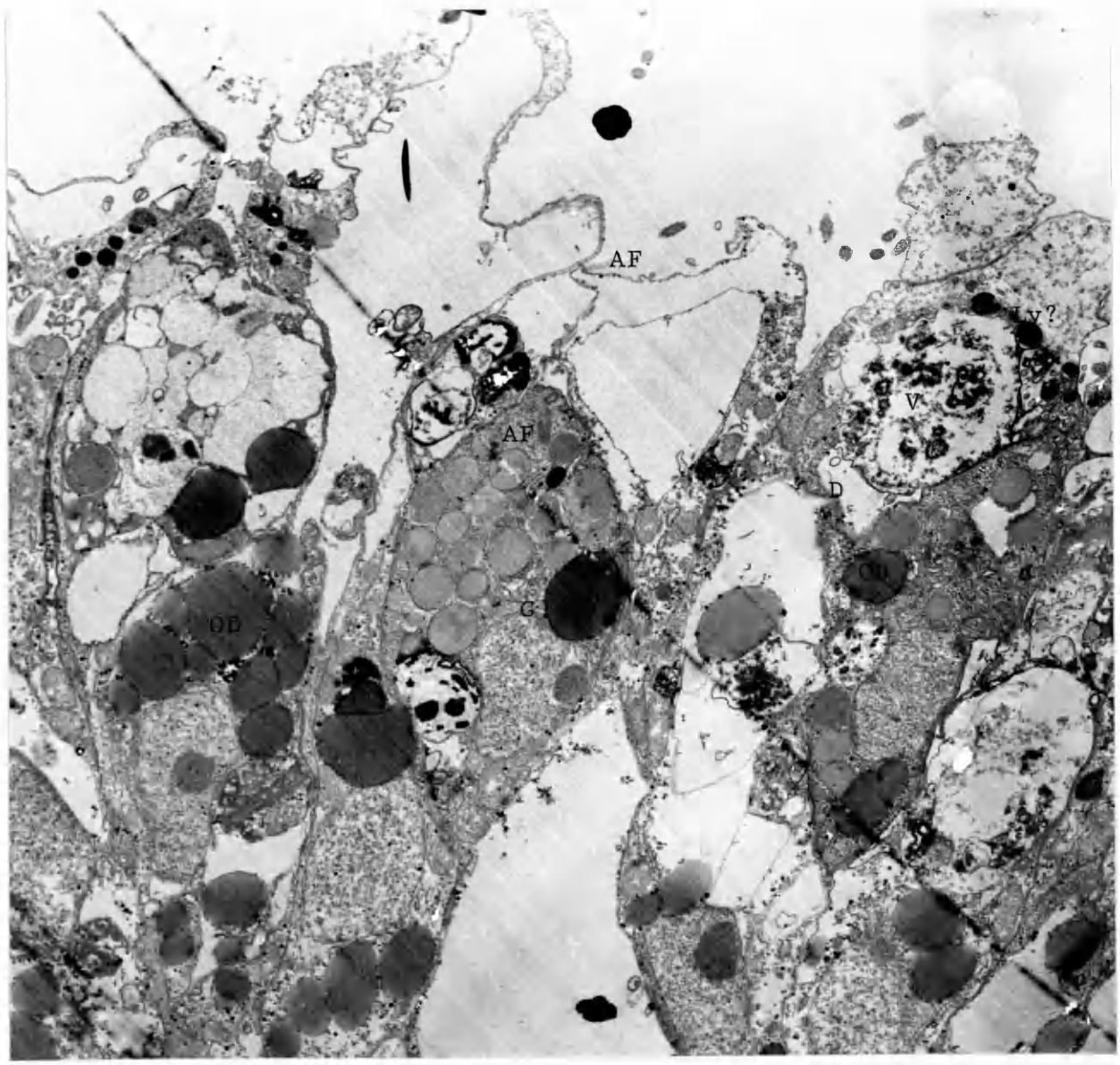

AF
AF
V?
V
D
OD
G

FIGURE 8

Microfilament bundle (Mf) in the gastrodermis, bordering the mesoglea (Me). X 46,550.

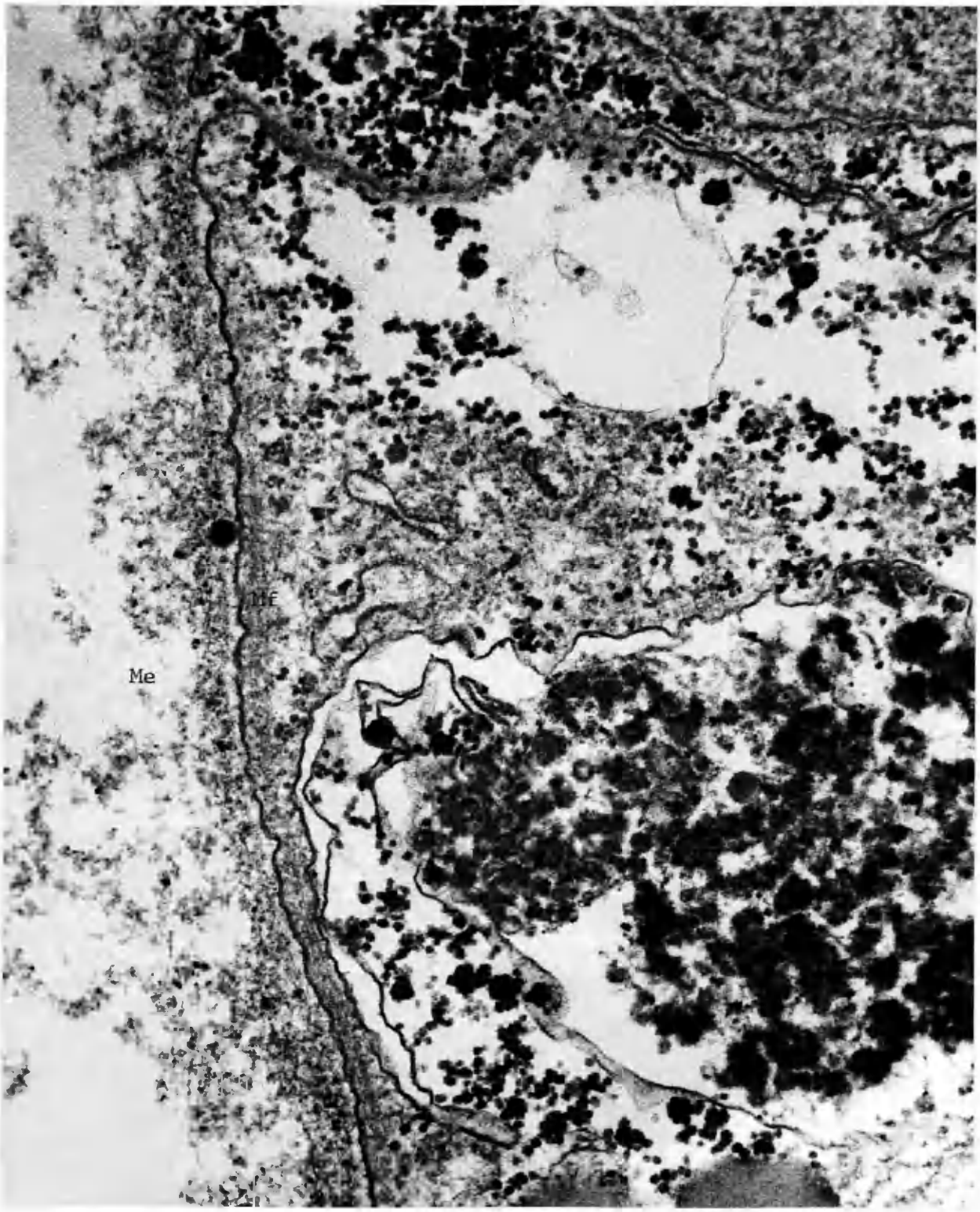

Mf
Me

FIGURE 9

Gastrodermal microfilament bundle (Mf) in the cell adjacent to that shown in Figure 8. X 70,000.

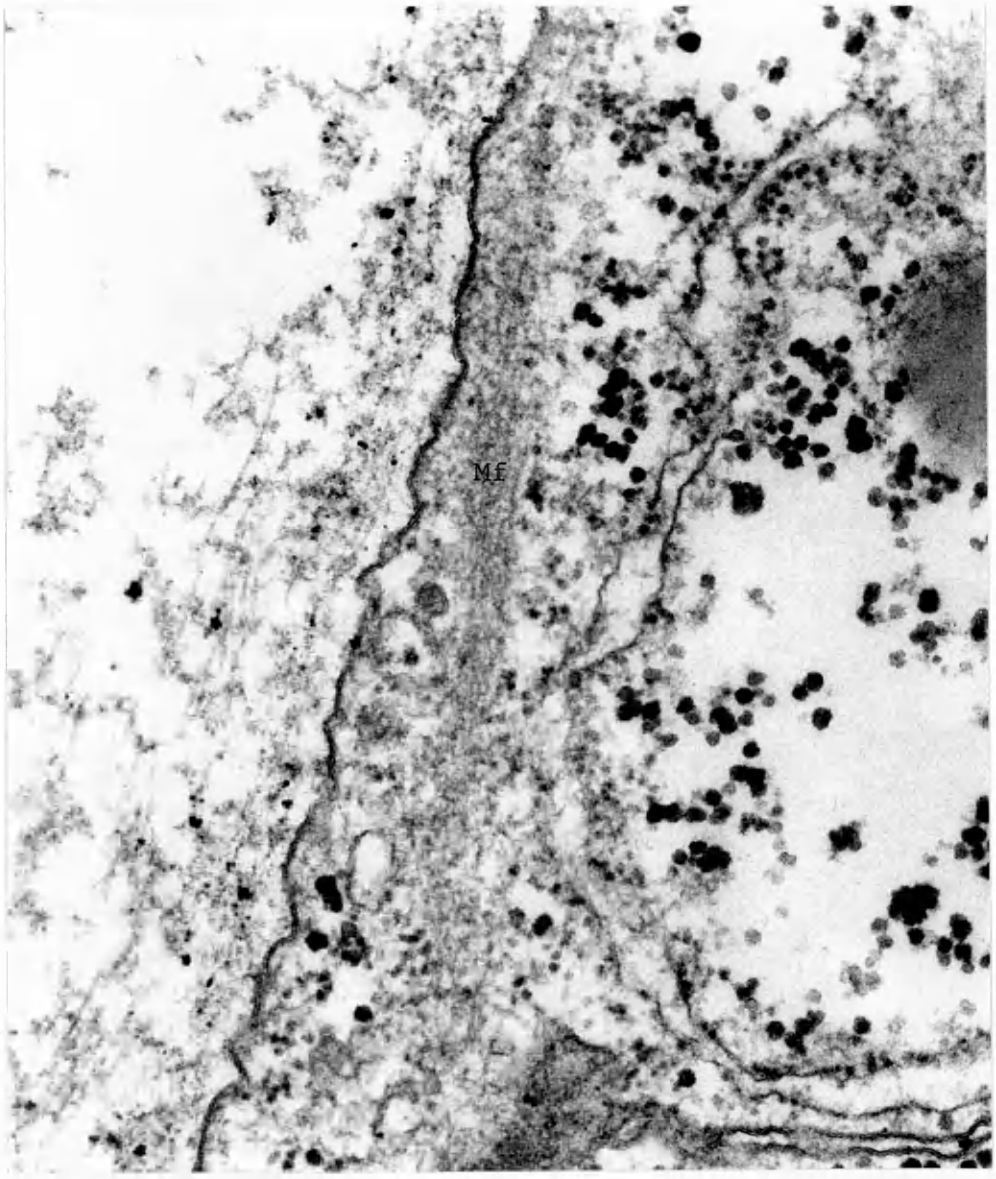

Mf

FIGURE 10

Gastrodermal microfilament bundle (Mf) inserting at cell junction. X 70,000.

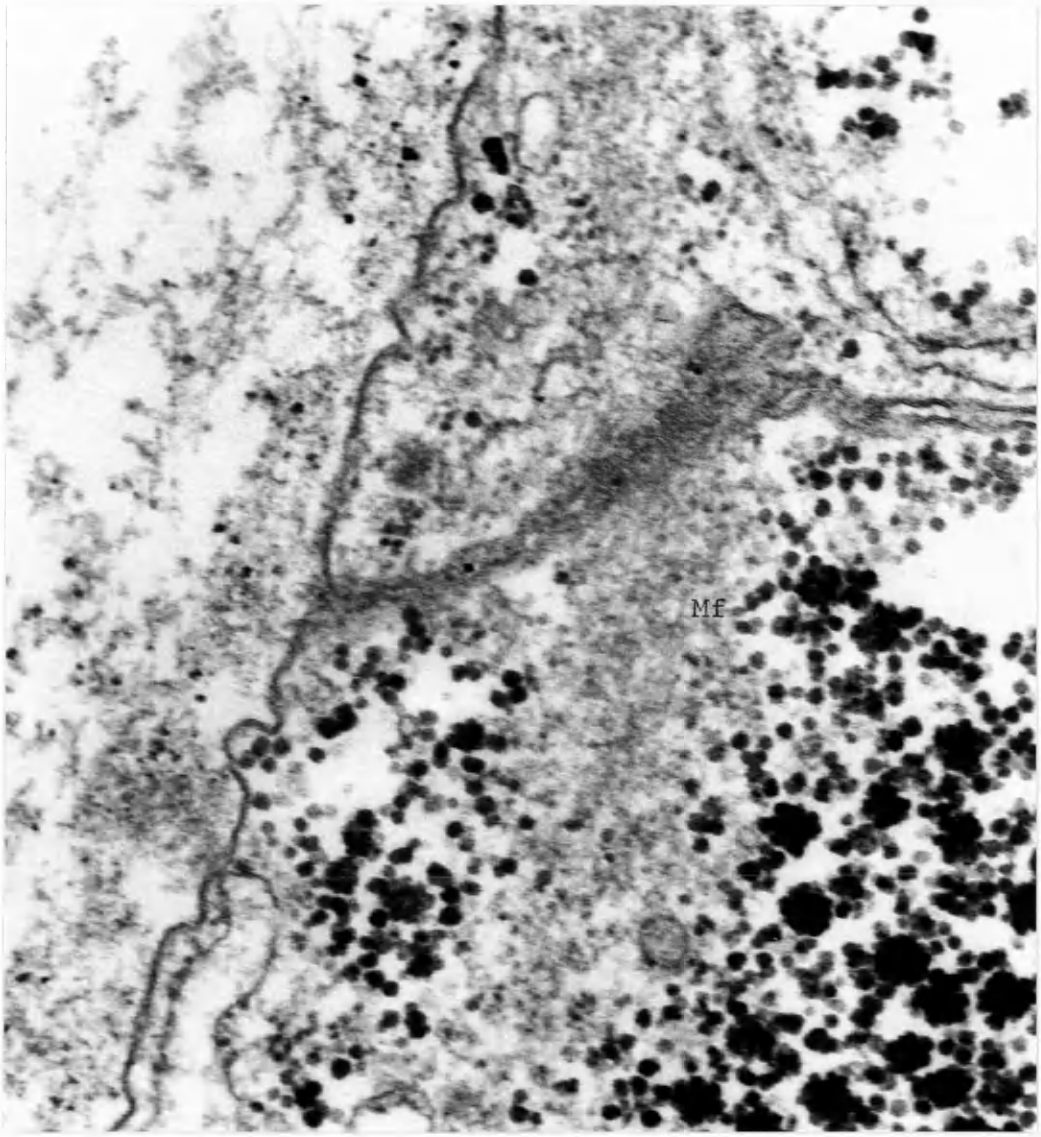

Mf

FIGURE 11

Mesoglea (Me) of a non-strobilating polyp. Note fibers (F) paralleling cell surface, feltwork bordering the cells (FB), and intracellular fibers (F). Some fibers are connected by cross-links (arrow). X 28,500.

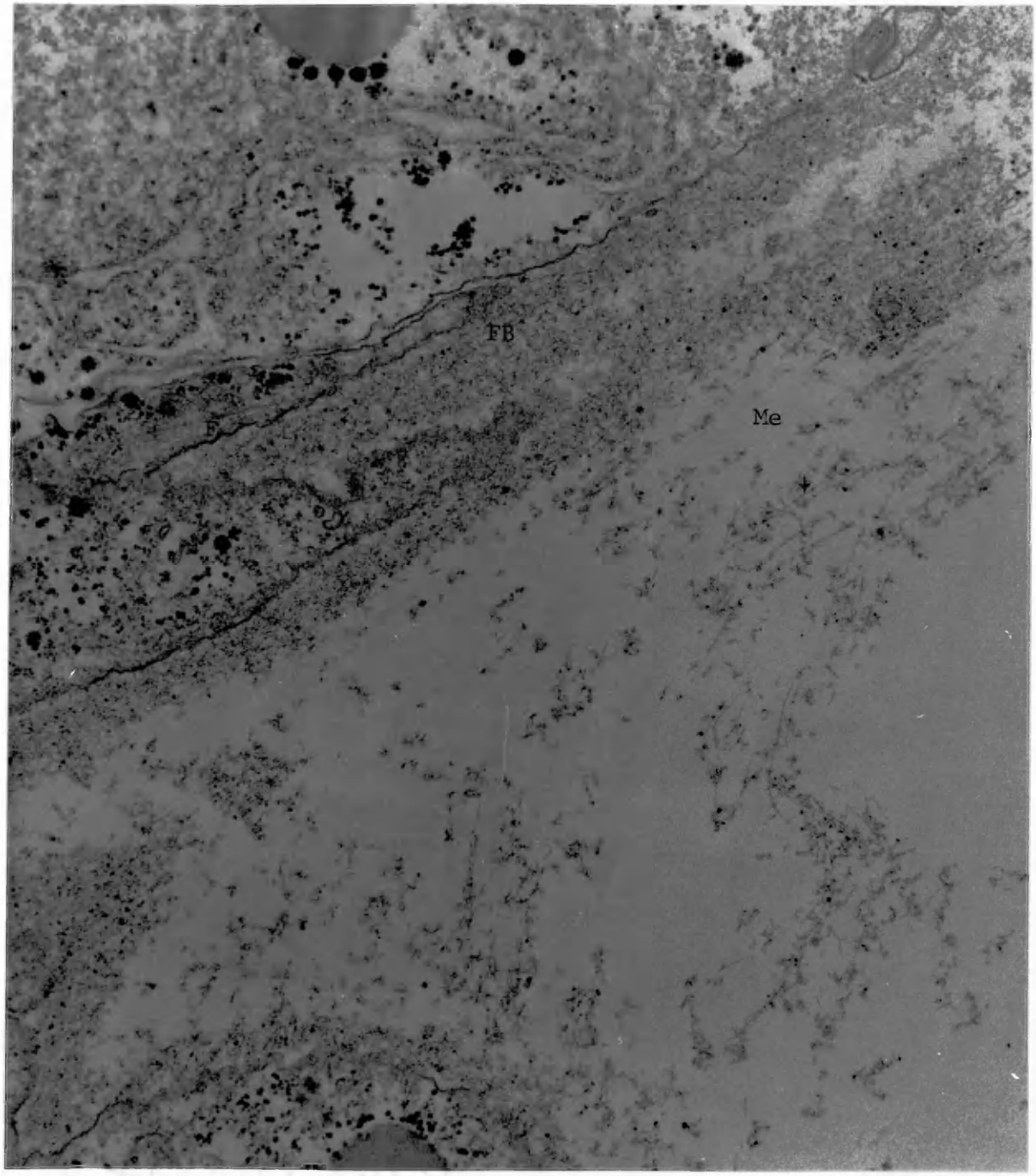

FB
Me

FIGURE 12

Mesoglea (Me) of a non-strobilating polyp. Note the thicker felt-work (FB) in crevices formed by cell processes, diffuse cell membrane (CM), and short fibers (F) at right angles to the cell surface of the gastrodermis (G). X 28,500.

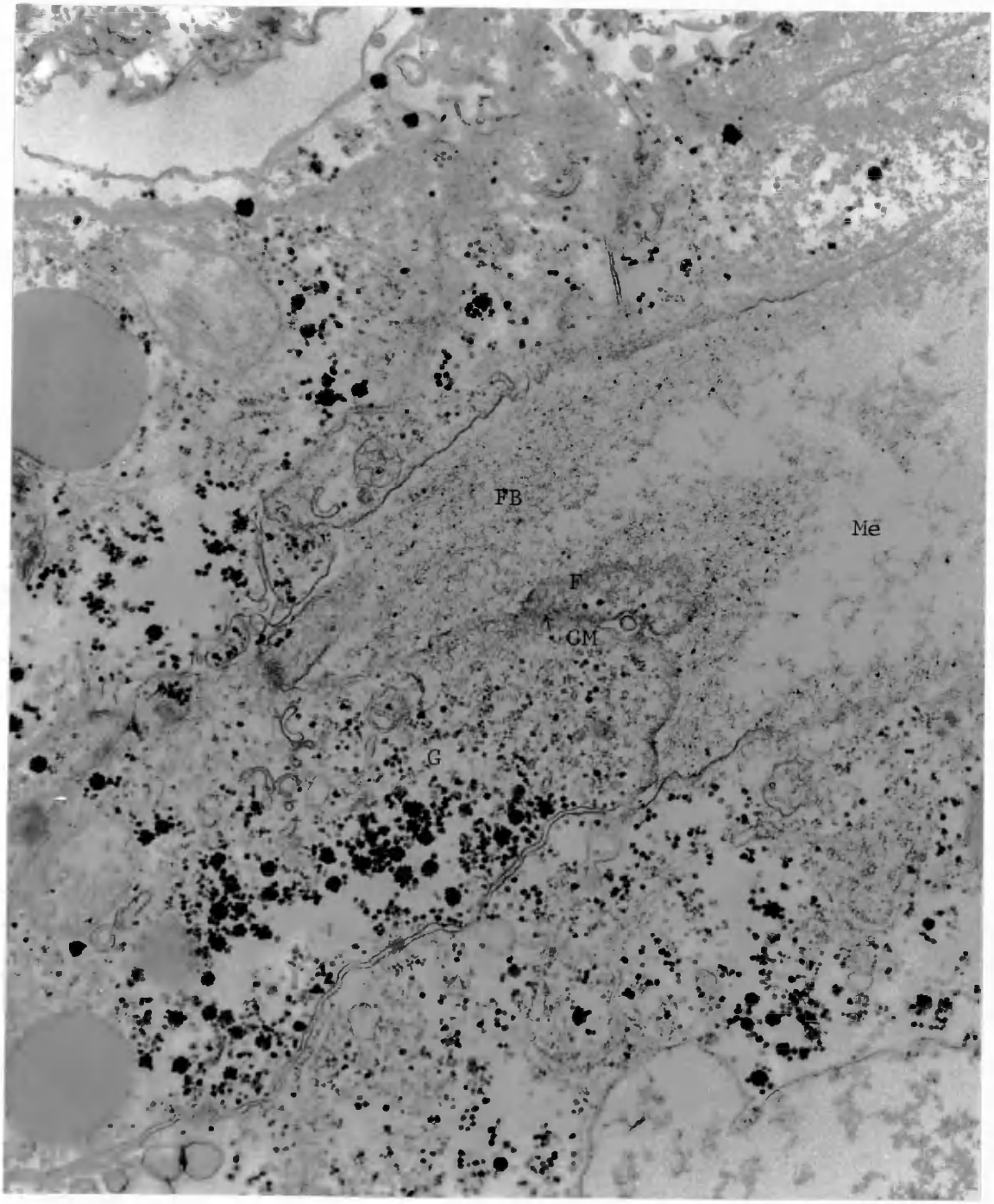

FB
Me
F
GM
G

FIGURE 13

Mesoglea (Me) of a strobilating polyp showing compression found in bulging regions (lower left) and branching found toward the constrictions (upper right). Membrane-bound bodies (MB) are found in the mesoglea. X 5,580.

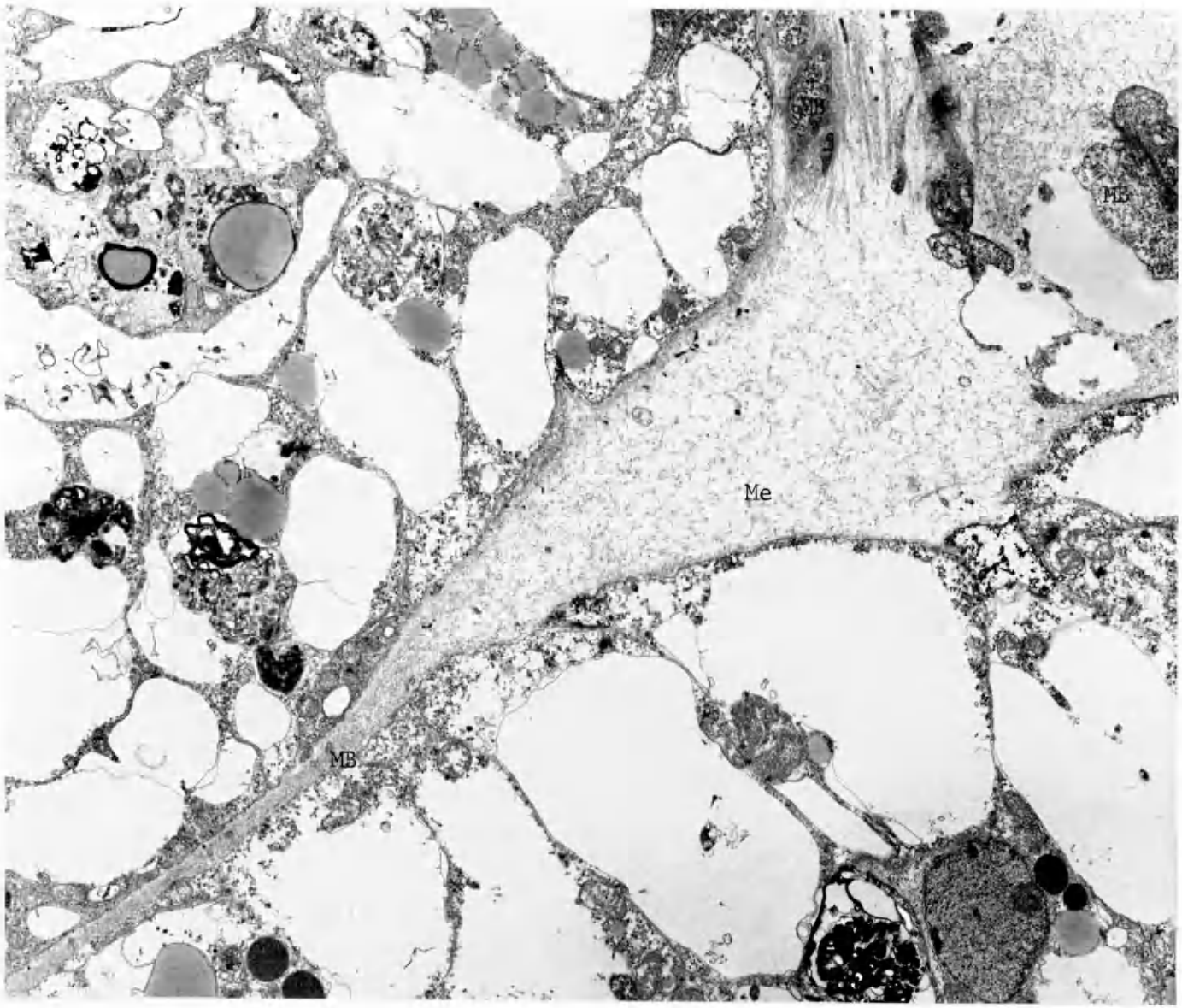

MB
MB
Me
MB

FIGURE 14

Mesoglea (Me) from the compressed region of a strobilating polyp containing dense bodies (DB) 200-300 Å in diameter. X 84,000.

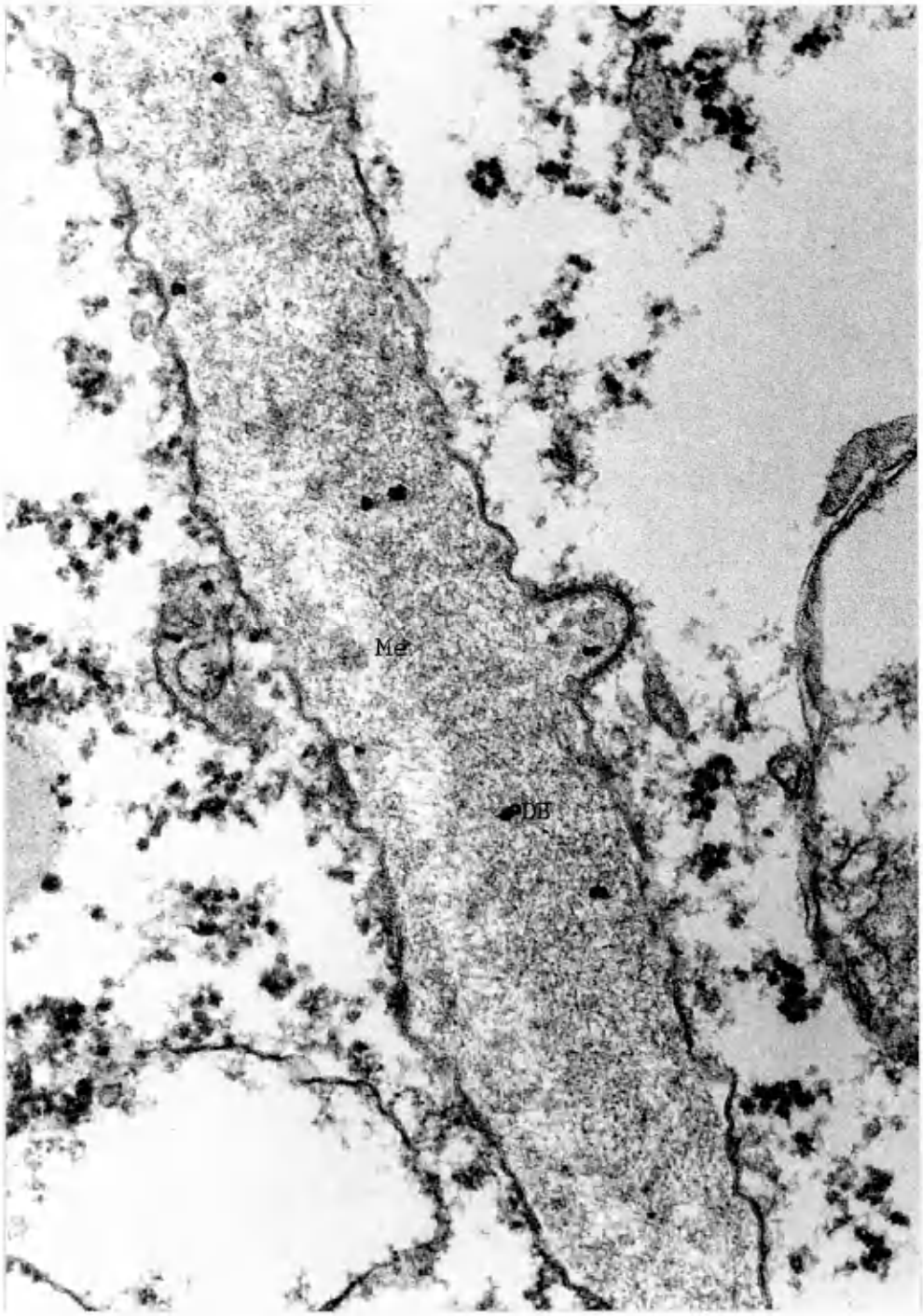

Me
DB

FIGURE 15

Fibrogenesis in the mesoglea (Me) near the constricted region of a strobilating polyp. Note the beaded fibers (F) normal to the gastrodermal cell surface (G) which has a diffuse appearance. X 29,500.

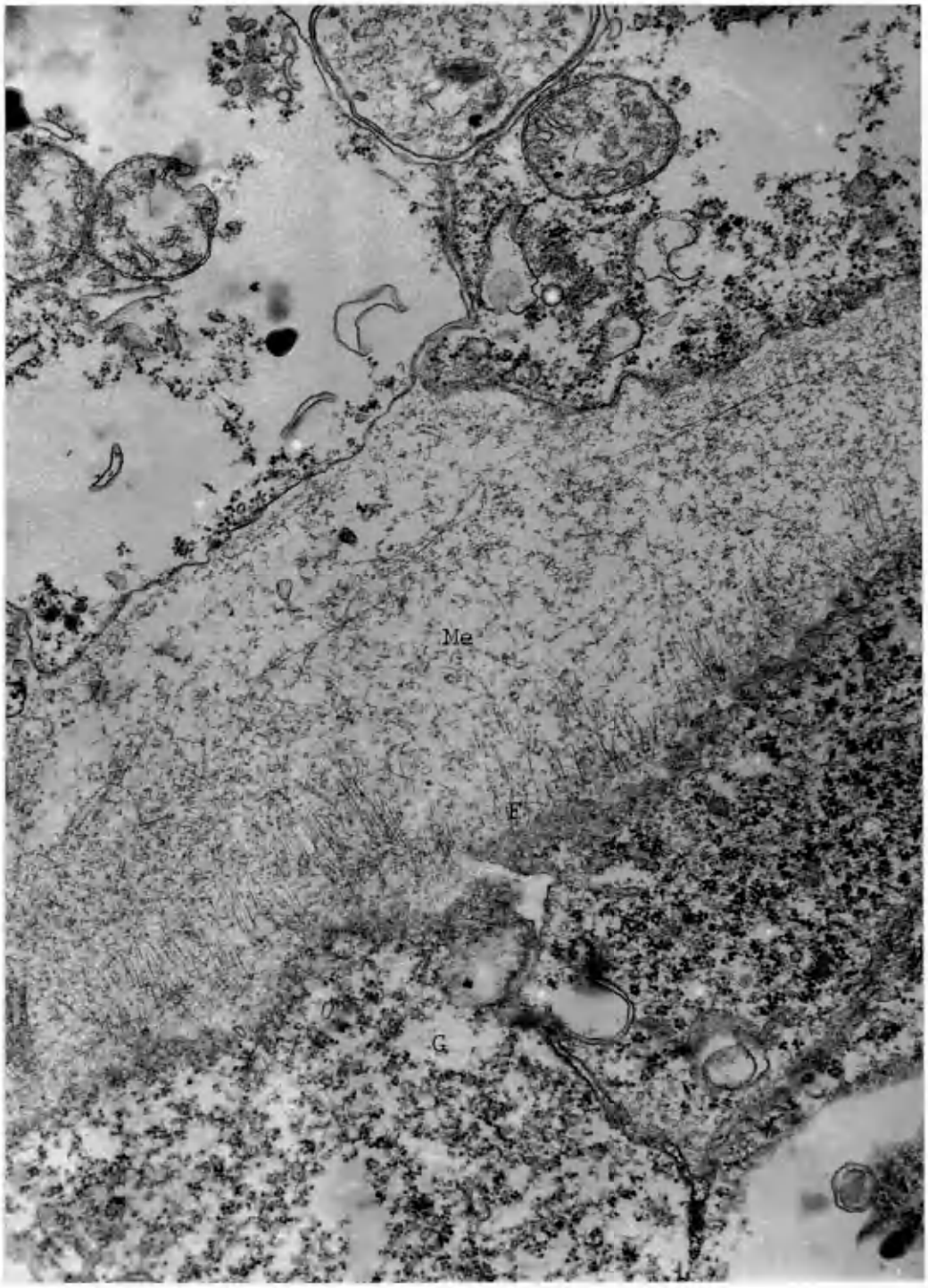

Me
E
G

FIGURE 16

Fiber bundles (F) in the mesoglea (Me) of a strobilating polyp. Fibers are cross-linked (arrow) and are associated with the diffuse boundaries of cellular elements (MB) in the mesoglea. X 28,500.

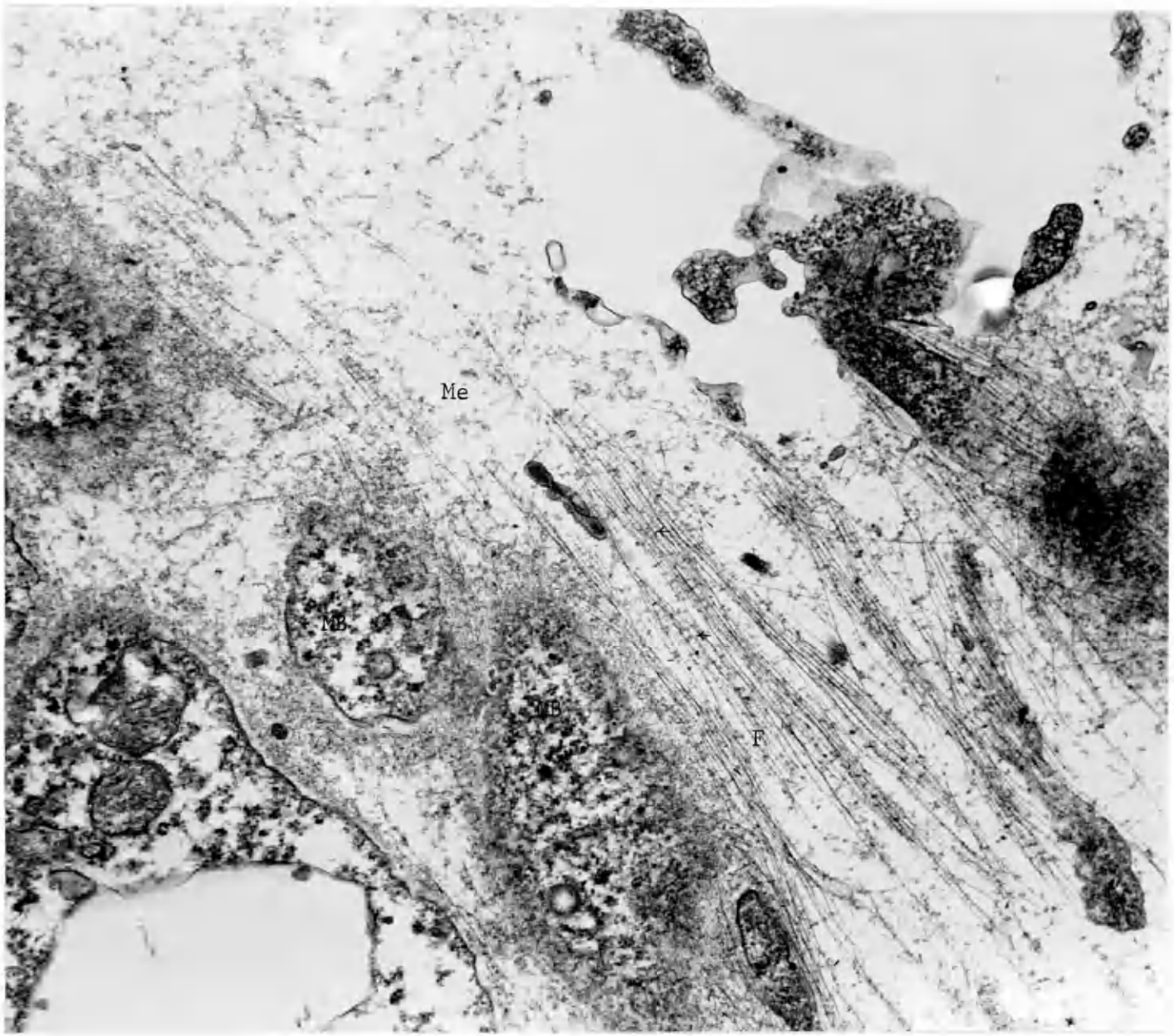

Me
MB
MB
F

FIGURE 17

Fiber bundles (F) in the mesoglea (Me) of a strobilating polyp. Fibers are cross-linked (arrow) and are associated with the diffuse boundaries of cellular elements (MB) in the mesoglea (Me). Similar intracellular fibers (IF) are also present. X 28,500.

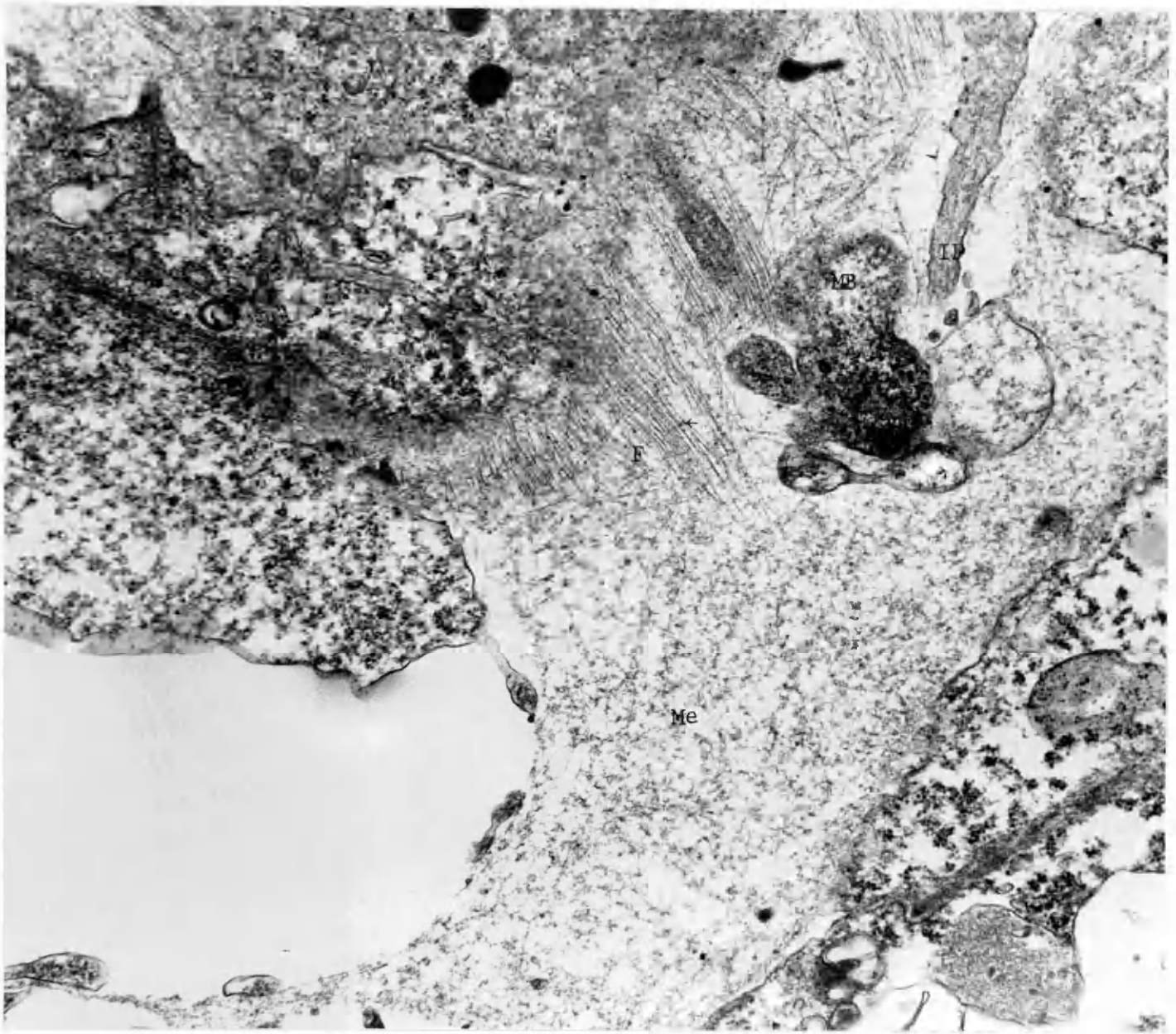

MB
IP
F
Me

FIGURE 18

Parallel arrays of fibers (F) in the mesoglea of a strobilating polyp which show cross-links (arrow) and are associated with cellular elements (MB) in the mesoglea (Me). X 47,500.

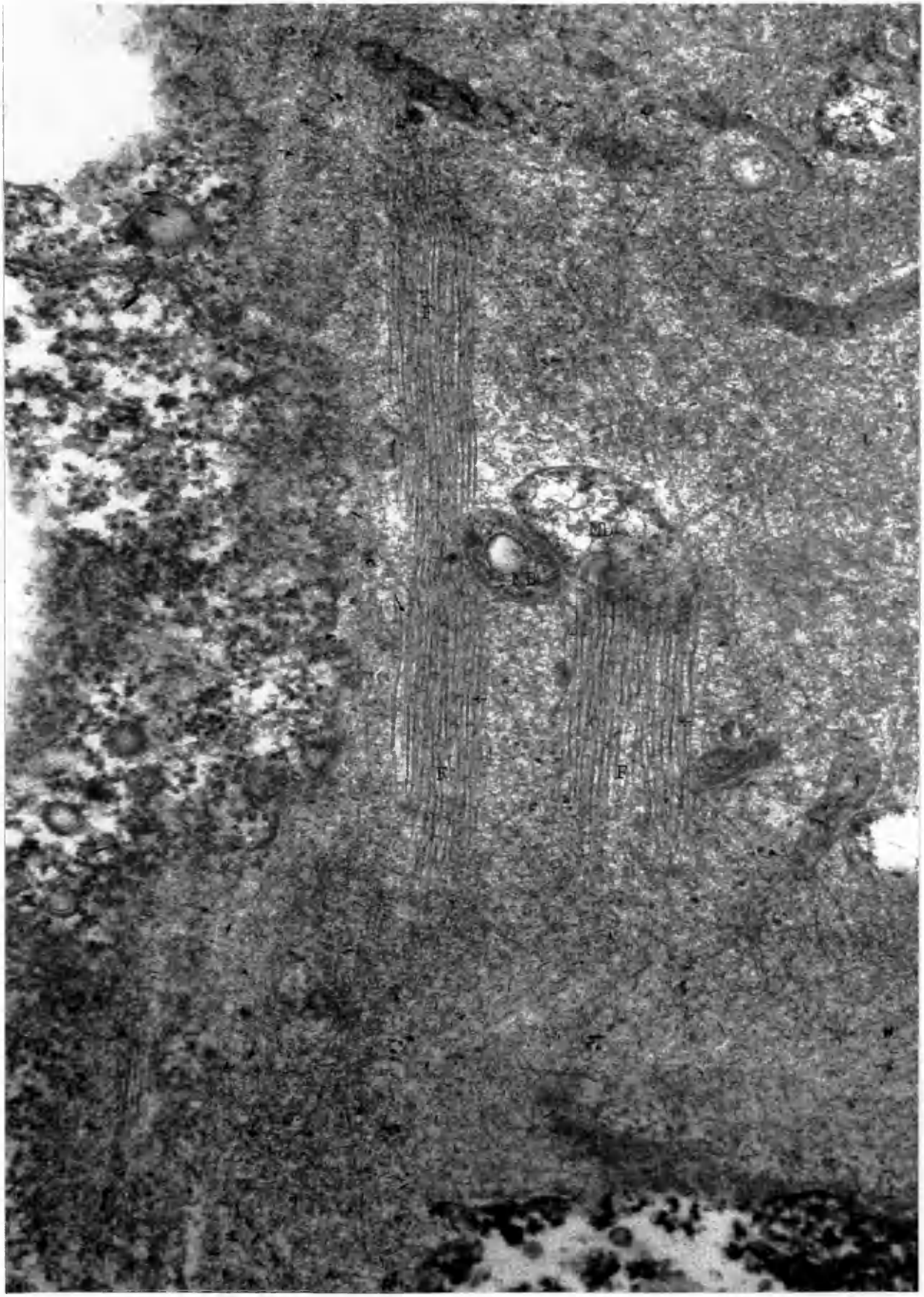
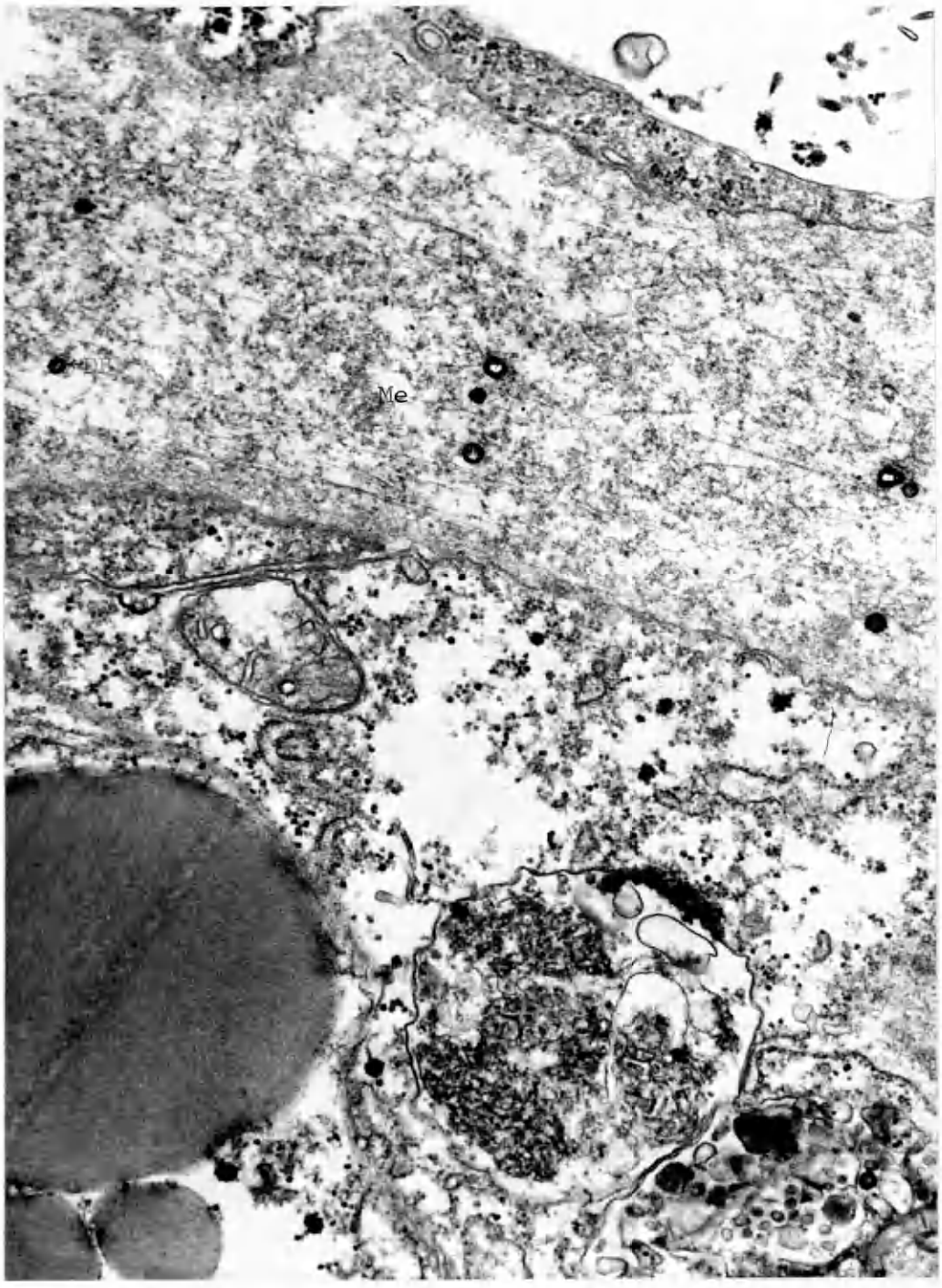

F
F
F
M
M

FIGURE 19

Mesoglea of the lower hydranth of a strobilating polyp (Me). Note the presence of dense bodies (DB). X 29,500.


Me

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