Electron Microscopy of the Stratified Epithelium Lining the Excretory Canal of the Dogfish Rectal Gland

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ABSTRACT In spite of a renewed interest in the rectal (salt-secreting) gland of the spiny dogfish, *Squalus acanthias*, the morphology of the stratified epithelium lining the central lumen and large ducts of this gland has been mentioned only briefly. The fluid removed from the duct of the rectal gland has been shown by Burger and Hess ('60a,b) and Burger ('62) to be a concentrated sodium chloride solution. The function of the stratified epithelium in the elaboration of this fluid is unknown. It is of interest to know if the stratified epithelium has morphological specializations which might suggest its function.

The stratified epithelium of the central canal consists of surface cells, intermediate cells, and basal cells. Four types of surface cells can be distinguished: granular cells, mucous cells, flask-shaped cells, and cells with large mitochondria. The intermediate cells form a loose network. In the large extracellular spaces between the intermediate cells, free cells presumably of blood origin, can be seen. The basal cells lie on a basement membrane. There is a structural resemblance of the epithelium to that of the toad bladder.

Burger and Hess ('60a,b) and Burger ('62) catheterized the rectal gland of the spiny dogfish, *Squalus acanthias*, and obtained a fluid which was essentially a sodium chloride solution. It had a concentration about twice that of the dogfish blood plasma and greater than that of sea water. These physiological studies have led to a renewed interest in the morphology of elasmobranch rectal glands. Recent studies have been published on the histochemistry of elasmobranch rectal glands by Bernard and Hartman ('60), on the ultrastructure of rectal glands of *Squalus acanthias* by Bulger ('61, '63), and on the ultrastructure of these glands in *Urolophus* (round sting-ray) by Doyle ('61, '62a,b).

The rectal gland of *Squalus acanthias* is a finger-shaped organ. In a cross section of this gland, a central lumen can be seen surrounded by three concentric layers: an inner layer of stratified epithelium, a thick intermediate layer of radially oriented secretory tubules, and an outer fibromuscular capsule. All of the previous studies have been concerned with the layer of secretory tubules which are the presumptive site of salt secretion. A morphological study of the inner lining epithelium was undertaken for several reasons. (1) Since no more than a mere mention that this layer exists can be found in the literature, a study seems warranted on purely morphological grounds. (2) The stratified epithelium which lines the central canal may be specialized in such a way as to prevent the equilibration of the rectal gland fluid with the body fluids. (3) It is also possible that the stratified epithelium lining the central lumen of the rectal gland may actively modify the composition of the excreted fluid in some manner instead of assuming merely a passive role as a conduit. It would be of interest to see if structural features similar to those found in epithelia known to be active, such as toad bladder, might be found.

MATERIALS AND METHODS

The rectal glands were obtained from West Coast dogfish, *Squalus sucklii* (shown to be indistinguishable from *Squalus acanthias* by Bigelow and Schroeder, '48). (See Bulger, '63 for details.)

For light microscopy, rectal glands were fixed by a variety of methods. Tissues were dehydrated in 2-ethoxyethanol (Cellosolve) or ethanol and embedded in paraffin (with 3–6% piccolyte resin), methacrylate, or Epon. A variety of staining procedures were used. The periodic acid-Schiff reaction (PAS) was performed on normal sections and on sections after digestion with diastase, saliva, or α-amyl-

ase. No reaction was seen when the oxidation with periodic acid was omitted. The PAS reaction was also attempted after bromination in CCl_4 (control treated with CCl_4 alone) and after acetylation (controls: (a) not acetylated, (b) treated with 20% ammonia after acetylation) (Pearse, '61).

For electron microscopy, small pie-shaped pieces of tissue from the midsection of the rectal gland were routinely fixed in 2–4% osmium tetroxide buffered with s-collidine (Bennett and Luft, '59) at 0°C for one to one and one-half hours. After rapid dehydration in ethanol, the tissues were embedded in Epon epoxy resin by the method of Luft ('61). Sections were cut with a Porter-Blum microtome using glass knives and placed on copper grids covered with a thin carbon film. Sections were studied unstained or after staining with Millonig's ('62) alkaline lead tartrate for 10–20 minutes. The grids were examined with RCA 2A or 2C electron microscopes with external power supplies and Canalco stigmators. Pictures were taken on Kodak Fine Grain Positive film (Wood and Howard, '59).

Light microscopy

The epithelium lining the central lumen of the rectal gland is stratified, consisting of 2–5 layers of cells. In paraffin section the surface cells sometimes appear to be squamous and sometimes protrude into the lumen, so the epithelium has been classified as transitional (Crawford, 1899; Pixell, '08; Hoskins, '17; and Crofts, '25). This stratified epithelium can be seen to extend into the glandular tissue for varying distances forming excretory ducts or to be interrupted at other points where the secretory tubules empty directly into the central canal.

A variety of cell types makes up the stratified epithelium. These cells will be discussed with reference to their position in the epithelium (i.e., surface cells, intermediate cells, and basal cells).

A. Surface cells

In 1 μ sections of Epon-embedded material at least four types of surface cells have been identified. They are the granular cells (G), mucous cells (M), flask-shaped cells (F), and cells containing large mitochondria (L), (figs. 1, 2).

1. Granular cells. The majority of the surface cells generally appear cuboidal and contain granules near the luminal surface (G, figs. 1, 2). In paraffin sections the granules are PAS-positive. Under the same conditions the granules are resistant to bromination or digestion with α-amylase, malt diastase, or saliva when used in conjunction with the PAS procedure; however, acetylation blocks the PAS reaction. The nuclei are slightly irregular and deep indentations are sometimes seen. Granules of a larger size than the surface ones are often seen in the cytoplasm near and especially apical to the nucleus (figs. 1, 2).

2. Mucous cells. Round mucous cells (M, fig. 1) are noted in the surface layer. They are more abundant near the duct of the gland. The cells have basal nuclei and are filled with PAS-positive droplets presumed to be mucus.

3. Flask-shaped cells. A third surface cell type appears to be shaped like a flask (F, figs. 1, 2). It protrudes into the lumen only by a narrow apex which lacks the granules characteristic of the adjacent granular cells. The nuclei often appear indented.

4. Cells with large mitochondria. Occasionally a fourth type of surface cell can be identified which lacks the distinguishing characteristics of the above cell types. This cell contains granules which stain with Altman's acid aniline fuchsin and toluidine blue and appear to be mitochondria (L, fig. 1).

B. Intermediate cells

The intermediate cells (I, figs. 1, 2) located between the surface and basal cells represent a diverse group. The most numerous variety appears to form a loose network of cells and processes, and large intercellular spaces occur between the cells. These spaces accommodate another group of cells, most of which are presumed to be migrating leucocytes (W, figs. 1, 2).

C. Basal cells

The basal cells (B, figs. 1, 2) rest on an irregular PAS-positive basement membrane. They have indented nuclei

and scanty cytoplasm but the lateral borders of adjacent basal cells generally remain in close approximation.

Electron microscope

The electron microscope was used to further characterize these various cell types.

A. Surface cells

1. Granular cells. This most abundant cell type (figs. 3–8) contains a layer of granules in the apical cytoplasm just beneath the cell membrane. The granules appear round, oval, or disc-shaped but some irregular shapes may be seen. The electron density of the granule is extremely variable after staining with Millonig's lead tartrate solution. The substance of the granule appears granular or fibrillar (figs. 4, 7, 8).

Microvilli are seen on the free surface of the granular cells. The apical cell membrane displays unit membrane structure and is covered by an external layer of delicate filaments radiating outwards (fig. 4). These filaments appear to be similar to the *antennulae microvillares* seen by Yamada ('56) in gall bladder epithelial cells. In the cytoplasm of the apical region and in the microvilli a filamentous material is found. Lying among these filaments are seen the granules mentioned above and many vesicles of varying size and density (fig. 4).

The cytoplasm contains the usual organelles. The Golgi apparatus (figs. 5, 6) is large and consists of several flattened cisternae which form an arc around part of the nucleus. The arc generally covers the apical or apical-lateral part of the nucleus. Occasionally several stacks of shorter cisternae are seen external to the long ones (fig. 6). Numerous vesicles of varying density and size are seen in the vicinity of the membrane stacks. In close spatial association with the Golgi apparatus, a group of spherical bodies may be seen. They are filled with circular membrane profiles (figs. 5, 6, 7).

The mitochondria are unusually small and their profiles are round or elongate. They are more abundant in the cytoplasm around the nucleus and are excluded from the apical region. The mitochondrial matrix contains a few cristae and dense granules (figs. 3, 5, 6).

The nuclei often have deep cytoplasmic indentations (figs. 3, 5). Nucleoli are seen frequently.

The cytoplasm also contains some rough-surfaced and smooth-surfaced endoplasmic reticulum, presumptive RNP (ribonucleoprotein) particles, vacuoles, apical multivesicular bodies, presumptive lipid bodies, intracytoplasmic filaments, occasional centrioles, composite bodies (Bulger, '63), and other unidentified bodies (figs. 3–8).

At the apical junction between granular cells, the cell membranes lie in particularly close approximation (figs. 3, 4, 7, 8). Although the unit membranes were not resolved or traced into the region in question, it is likely that this close approximation is a specialization similar to a tight junction (Choi, '60; Farquhar and Palade, '61, '63). Beneath this area of close approximation, two types of specialized attachment areas can be identified. Desmosomes similar to those described by Odland ('58) are seen (fig. 8). In addition, structures which appear to be miniature desmosomes are found (arrow, fig. 8).

2. Mucous cells. The mucous cells appear round rather than of the usual goblet configuration (fig. 3). The nucleus lies basally and the upper part of the cytoplasm is filled with mucous granules. The granules vary in size, and the membrane surrounding them shows discontinuities, either real or artifactual. Their contents are fibrillar but the concentration of fibrils varies.

Thin wisps of cytoplasm are sometimes seen between the granules which contain vesicles and presumed RNP particles. A thin rim of cytoplasm can also be identified around the edge of the cells. This cytoplasm contains elongate mitochondria, cisternae of rough-surfaced endoplasmic reticulum, several layers of smooth-surfaced membranes, and vesicles, although not all of these features are illustrated in figure 3.

3. Flask-shaped cells. A small neck piece of the flask-shaped cell borders the lumen (fig. 9). This cell type can, therefore, be classified as a surface cell. The predominant feature of this cell type is the

myriad of smooth-surfaced elements that fill the cytoplasm. Vesicles varying in size and electron density are the most prevalent feature especially in the apical region of the cell. The smooth-surfaced elements become larger and more irregularly shaped near the basal part of the cell. Cisternae of rough-surfaced endoplasmic reticulum can occasionally be seen in the basal region of this cell type.

The mitochondria are elongate and contain a pale staining matrix. They are considerably larger than the mitochondria of the granular cell but resemble the mitochondria of the mucous cell.

Other cytoplasmic organelles include: a well-developed Golgi apparatus (fig. 9, inset), intracytoplasmic filaments, multivesicular bodies, vacuoles, and frequent profiles of centrioles.

4. Cells with large mitochondria. This fourth cell type is distinguished by the absence of apical granules and the presence of large mitochondria (fig. 10). The apical surface has microvilli covered by *antennulae microvillares*. Vesicles of varying size and density are located beneath the microvilli embedded in a layer of fine filaments. Beneath this filament is a layer of larger filaments which can be seen running into the cell attachment areas on the lateral cell membrane in a manner similar to the equivalent structure in the granular cells.

The large mitochondria have closely packed cristae, dense matrix, and many intramitochondrial granules. They bear a remarkable resemblance to the mitochondria of the secretory tubules of this gland.

Irregularly shaped units of smooth-surfaced and rough-surfaced endoplasmic reticulum appear in the cytoplasm of this cell. The Golgi apparatus may appear as single or multiple units. Also seen in the cytoplasmic matrix are: apically located multivesicular bodies, presumptive lipid droplets, free RNP particles, composite bodies, and unidentified bodies.

Cells with similar morphology can sometimes be found in the other layers of the epithelium.

B. Intermediate cells

These cells form a loose network between the apical and basal layers. Large intercellular spaces are present between these cells. The cytoplasm of this cell type resembles that of the basal cell described below.

In the large intercellular spaces, a diverse group of free cells is seen. These are presumed to be wandering cells, mainly macrophages, granulocytes, and lymphocytes. The cell membranes of these cells often appear broken and the contents dispersed. Such an appearance could result from a particular susceptibility of these cells to preparation damage.

C. Basal cells

The basal cells rest on a thick (~ 800 Å) basement membrane which is separated from the basal cell membrane by a layer of intermediate density (fig. 11). A row of caveolae and vesicles are seen just inside the basal cell membrane. The lateral cell membranes interdigitate somewhat with the adjacent basal cells. Near the basement membrane this interdigitation occasionally appears to be reinforced by a single desmosome.

The cytoplasmic features resemble those of the granular cell but lack the apical modifications and associated granules. The cytoplasm contains small mitochondria with few cristae and dense intramitochondrial granules; intracytoplasmic filaments; some smooth-surfaced endoplasmic reticulum, mainly in the form of small irregular cisternae; some rough-surfaced endoplasmic reticulum, mainly in the same form; irregularly shaped nuclei with cytoplasmic indentations; large Golgi apparatus similar to that seen in the granular cell and associated with spherical bodies; presumptive lipid droplets; and some large vacuoles.

DISCUSSION

Burger and Hess ('60a,b) studied the composition of the fluid obtained by catheterization of the duct of the rectal gland. Due to the gross structure of the gland, the fluid collected in those studies has been exposed to the stratified epithelium lining the large ducts and central region of the gland. It is, therefore, of interest to know if the stratified epithelium serves entirely as a passive conduit or has the ability to alter the composition of the secreted fluid.

The variety of cells located in the surface layer of the stratified epithelium may indicate some special physiological role for this tissue.

The cytoplasm of the cell with large mitochondria closely resembles that of the cell found in the secretory tubule of this gland (Bulger, '63). It may be a similar cell which demonstrates less membrane interdigitation due to its position in the stratified epithelium.

A marked resemblance was noted between the cells of this stratified epithelium and the cells of toad bladder transitional epithelium although the epithelium of the rectal gland is composed of more cell layers. The predominant surface cell type in each tissue is a cell with an apical layer of granules. Both epithelia contain mucous cells and flask-shaped cells (the mitochondria-rich cell of toad bladder) lacking the apical granules. The transitional epithelium of toad bladder does not appear to have a cell corresponding to the cell with large mitochondria found in the rectal gland. The similarities in morphology of these two tissues may reflect similar functional capacities. It is likely that both tissues would have specialized permeabilities which would tend to prevent equilibration of the secreted fluid with body fluids. It should also be noted that toad bladder is capable of active sodium transport (Leaf, '60; Leaf, Anderson and Page, '58).

The stratified epithelium lining the rectal gland lumen has been classified as transitional by the earlier investigators. Such a classification is not unreasonable due to the probable endodermal derivation of the rectal gland (Blanchard, 1878; Hoskins, '17), to the close morphological similarities between the stratified epithelium and transitional epithelium of toad bladder and to its role in containing and conducting to the surface a fluid with some similarities to urine. It is not known whether the thickness of the stratified epithelium changes with physiological state. A marked change in the thickness of the stratified epithelium similar to that in the urinary bladder seems unlikely due to the presence of the thick layer of secretory tubules surrounding the lumen. A distinct layer of smooth muscle is seen in the external capsule, however, which might be of some value in moving the fluid secretion from the tubules and central canal of the gland.

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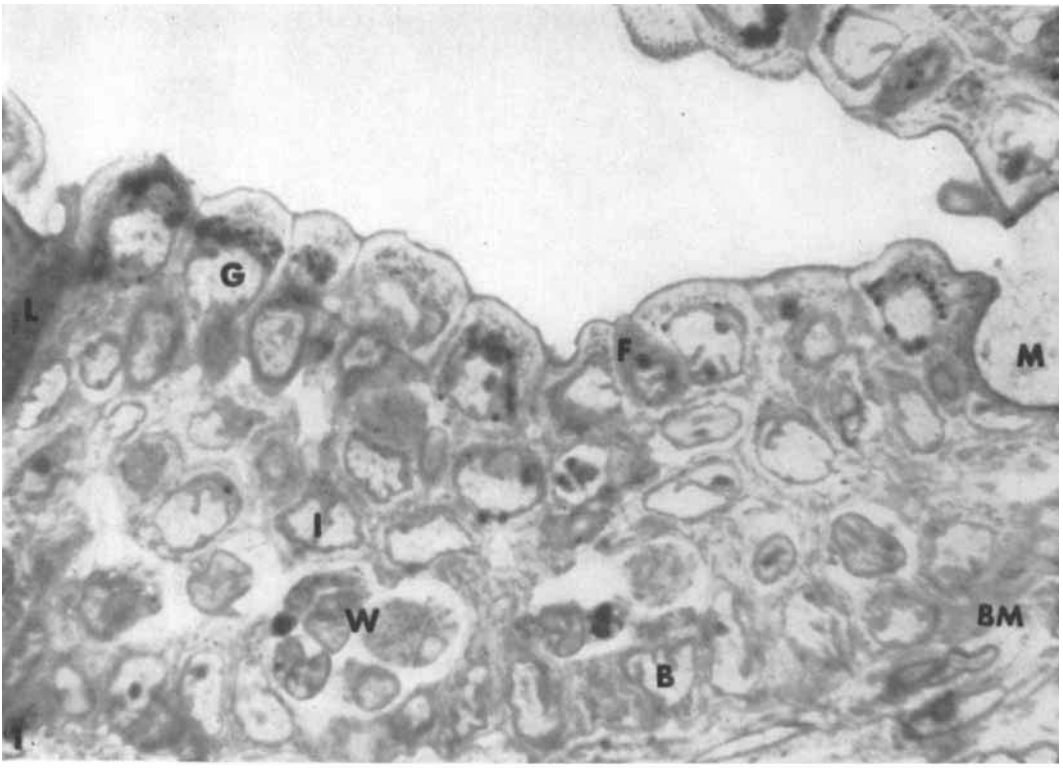
PLATE 1

EXPLANATION OF FIGURES

1 A light micrograph of a 1 μ Epon section showing the various cell types that comprise the stratified epithelium lining the central canal of the rectal gland. The majority of the cells lining the lumen are granular cells (G). Part of a mucous cell (M), flask-shaped cell (F), and cell with large mitochondria (L) are also seen in the photograph. The intermediate region of the epithelium consists of intermediate cells (I) and free cells (W), probably of blood origin. The basal cells (B) rest on the basement membrane (BM). $\times$ 1,120.

2 A light micrograph of a 1 μ Epon section of the stratified epithelium. The surface is lined with granular cells (G) in which the granules appear at the luminal border of the cells (arrow). One flask-shaped cell (F) is seen with its apex protruding into the lumen. Intermediate cells (I), free cells (W), and basal cells (B) can be identified. Many of the free cells in this region contain granules in the cytoplasm. $\times$ 1,400.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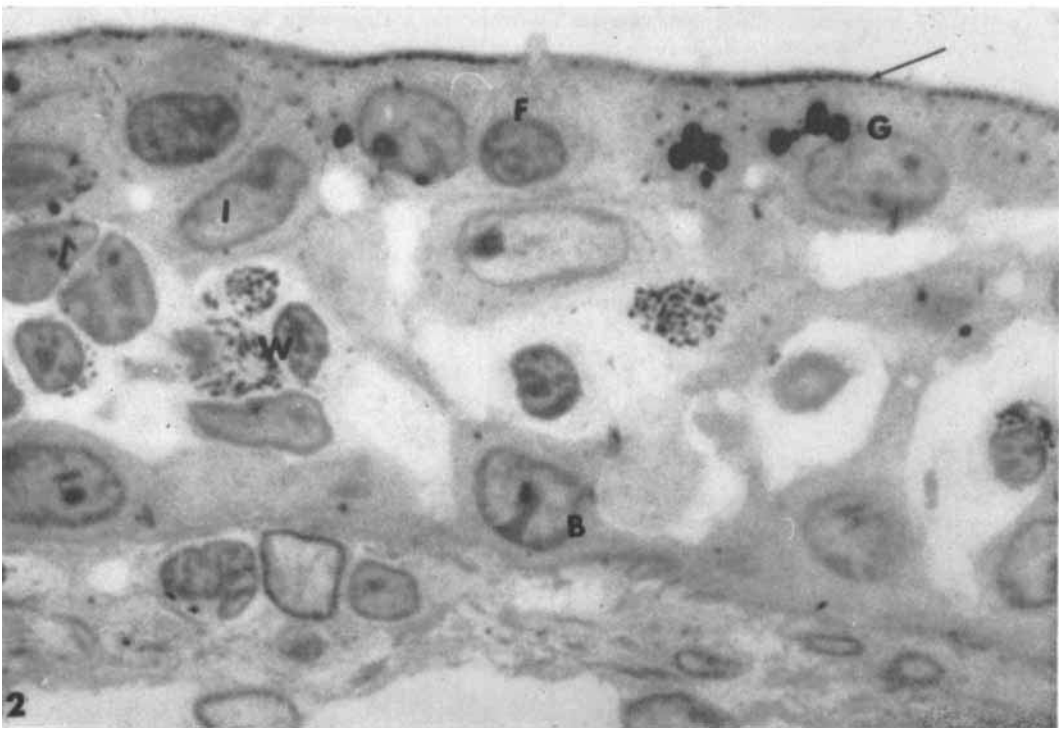
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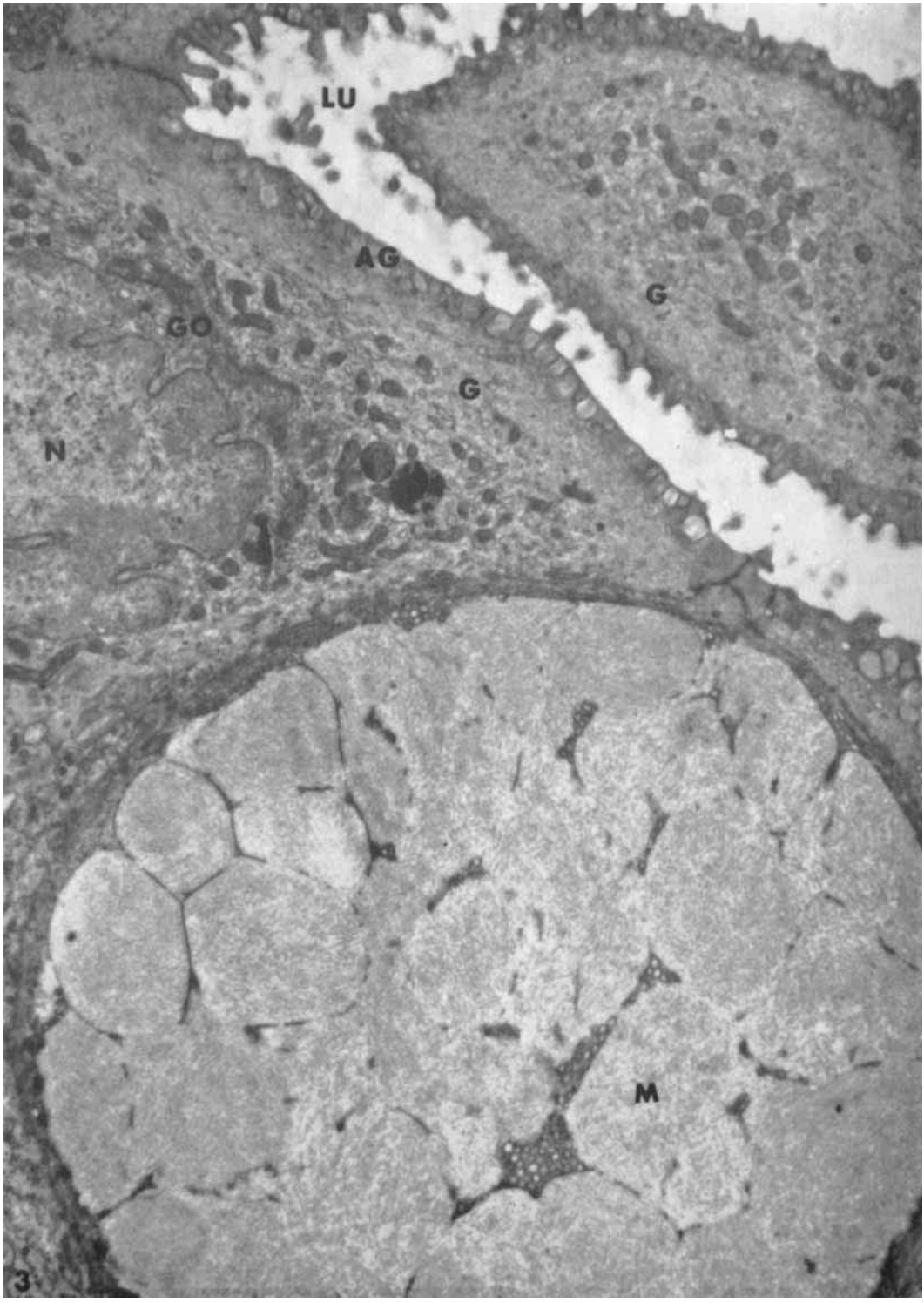
PLATE 2

EXPLANATION OF FIGURE

3 An electron micrograph showing parts of several granular cells (G). The granular cell on the left contains apical granules (AG), a few microvilli, an irregular nucleus (N), a large Golgi unit (GO), and many small mitochondria. Part of a mucous cell (M) can be seen on the lower right filled with mucous granules which are separated from each other only by wisps of cytoplasm and incomplete membranes. Fixed with osmium tetroxide and stained with lead tartrate solution. × 8,500.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AG
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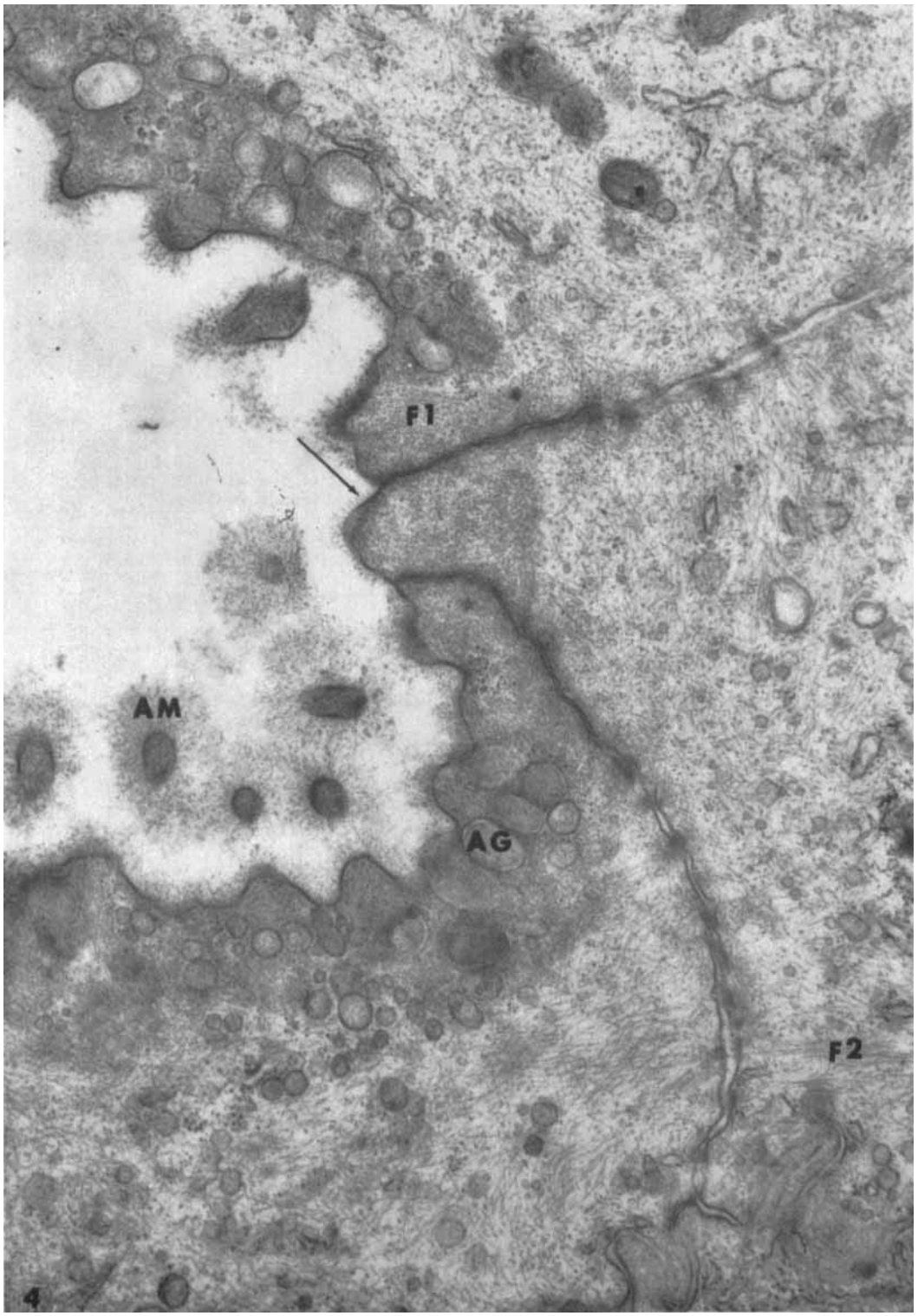
N
M
3

PLATE 3

EXPLANATION OF FIGURE

4 An electron micrograph showing the apical region of three granular cells. Fine filaments (AM) radiate out from the surface membrane and appear to be similar to the *antennulae microvillares* of Yamada. The apical plasma membrane shows the unit membrane structure (arrow). The apical granules (AG) vary in shape and density of the contents. They lie in a region which appears to be dense due to the presence of a feltwork of fine filaments (F1). The apical cytoplasm beneath the more densely appearing layer is also filled with filaments (F2) which can be seen to run into the desmosomes. Fixed with osmium tetroxide and stained with lead tartrate. × 30,100.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4

PLATE 4

EXPLANATION OF FIGURES

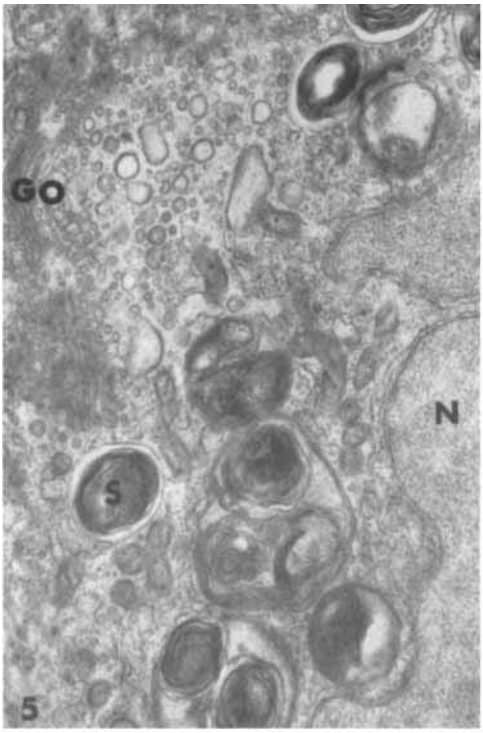
Figures 5–8 Electron micrographs of regions of the granular cell. Fixed with osmium tetroxide and stained with lead tartrate solution.

5 This electron micrograph illustrates the cytoplasm near the nucleus (N) of a granular cell. A Golgi unit (GO) is seen at the left. Spherical bodies (S) partially filled with membranous profiles can be seen in the cytoplasm. × 16,600.

6 A Golgi unit (GO) and spherical bodies (S) are seen in the cytoplasm of another granular cell. × 16,100.

7 The electron micrograph demonstrates what appears to be granule release. Granule *a* seems to be just beginning the process, granule *b* appears to be almost released, and granule *c* is free in the lumen. × 14,300.

8 A slightly oblique section of the border between granular cells is seen in this figure. A desmosome is seen at D and several smaller structures of similar morphology are seen beneath it (arrow). × 31,500.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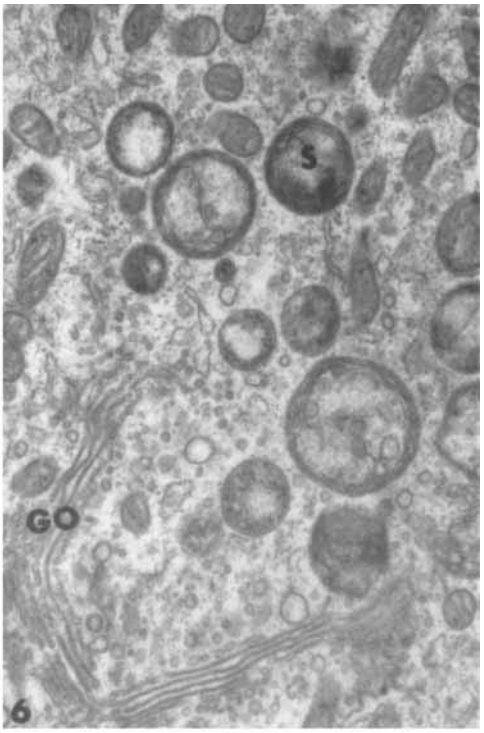
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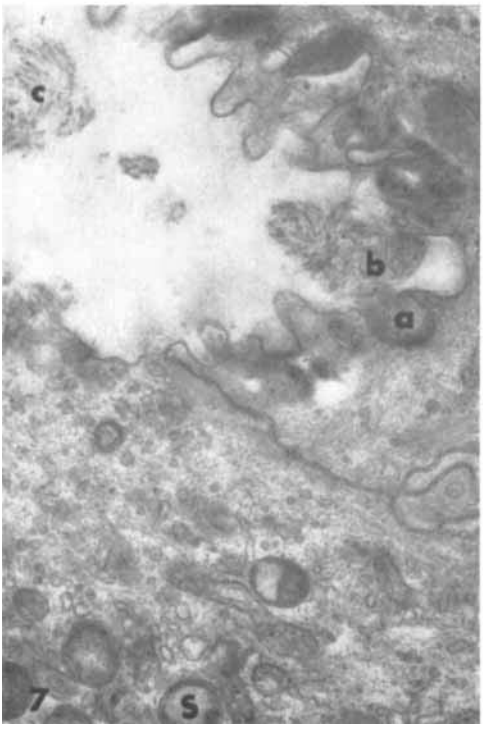
c
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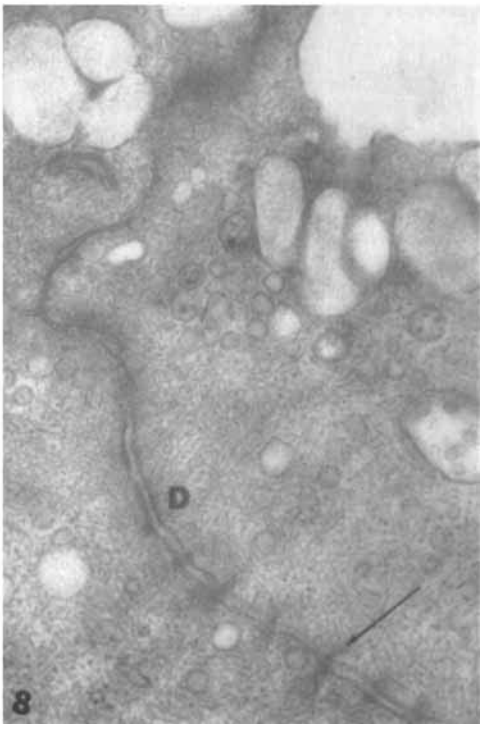
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PLATE 5

EXPLANATION OF FIGURE

9 An electron micrograph of a flask-shaped cell between two granular cells. The flask-shaped cell borders the lumen only in a small region. The cell is filled with a nucleus (N) and smooth-surfaced membranous profiles. The mitochondria (M) are larger than those of the granular cell. Fixed with osmium tetroxide and stained with lead tartrate solution. × 14,300.
Inset: A Golgi region from a flask-shaped cell. × 18,760.

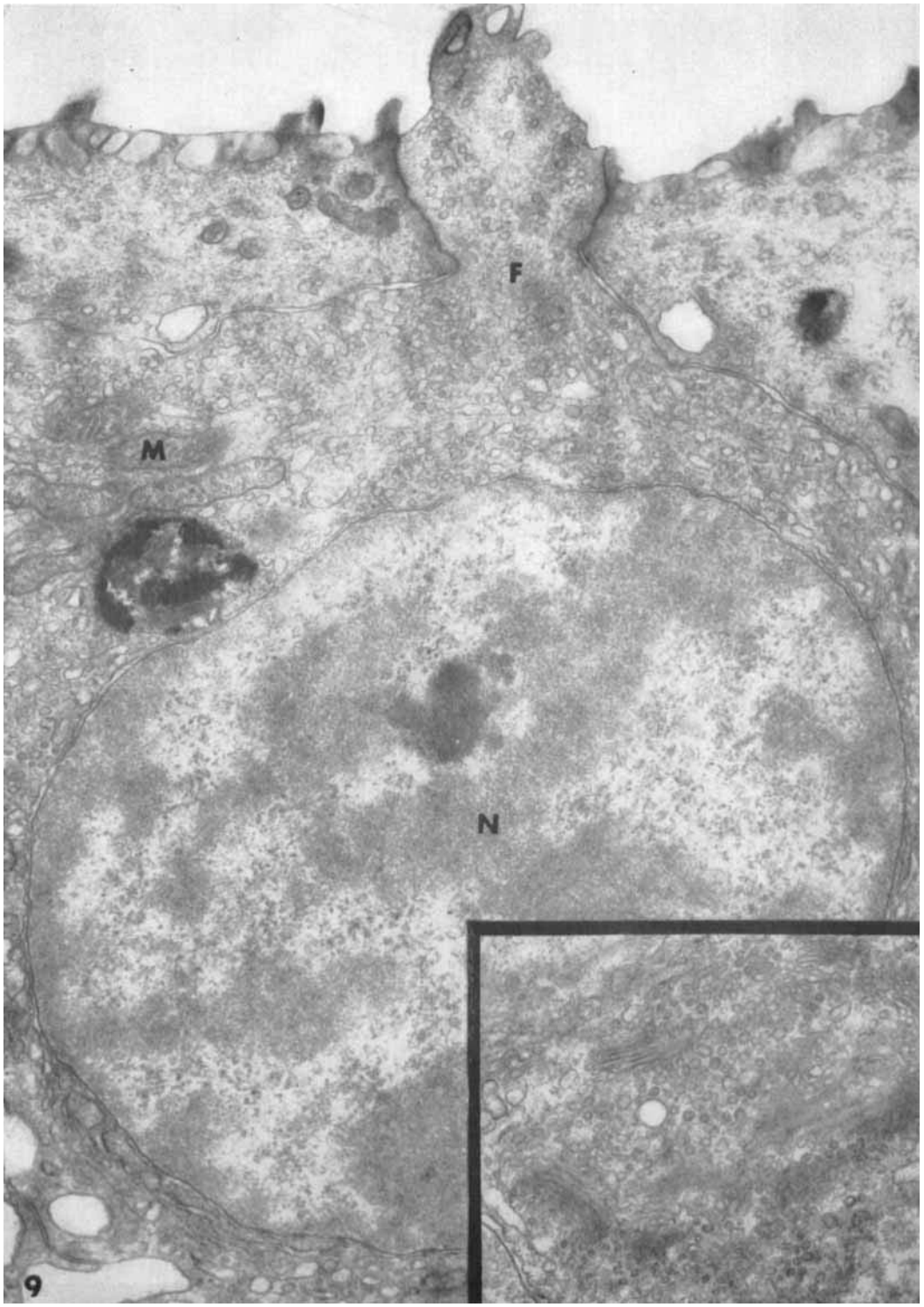
F
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PLATE 6

EXPLANATION OF FIGURE

10 Parts of three cells with large mitochondria (L) are seen in this partially tangential section of the surface cells. The larger size of the mitochondria (M) of this cell type is apparent when they are compared with the mitochondria of the granular cell (arrow). Clear vesicles (V) but not granules are located in the apical cytoplasm. Multiple Golgi profiles (GO) are seen in the central cell. Multivesicular bodies (MVB) are easily seen in the apical cytoplasm. Fixed with osmium tetroxide and stained with lead tartrate solution. × 13,400

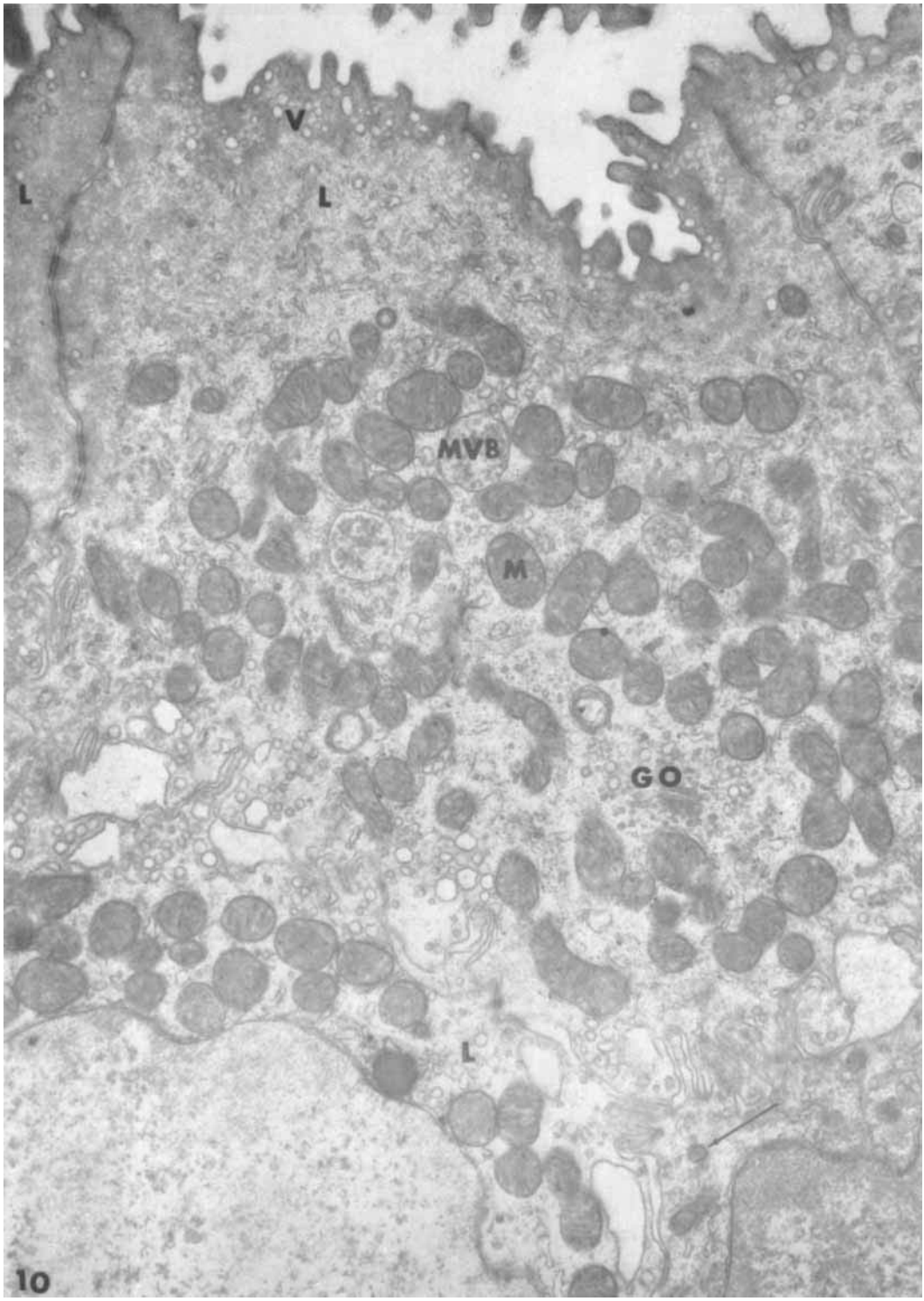
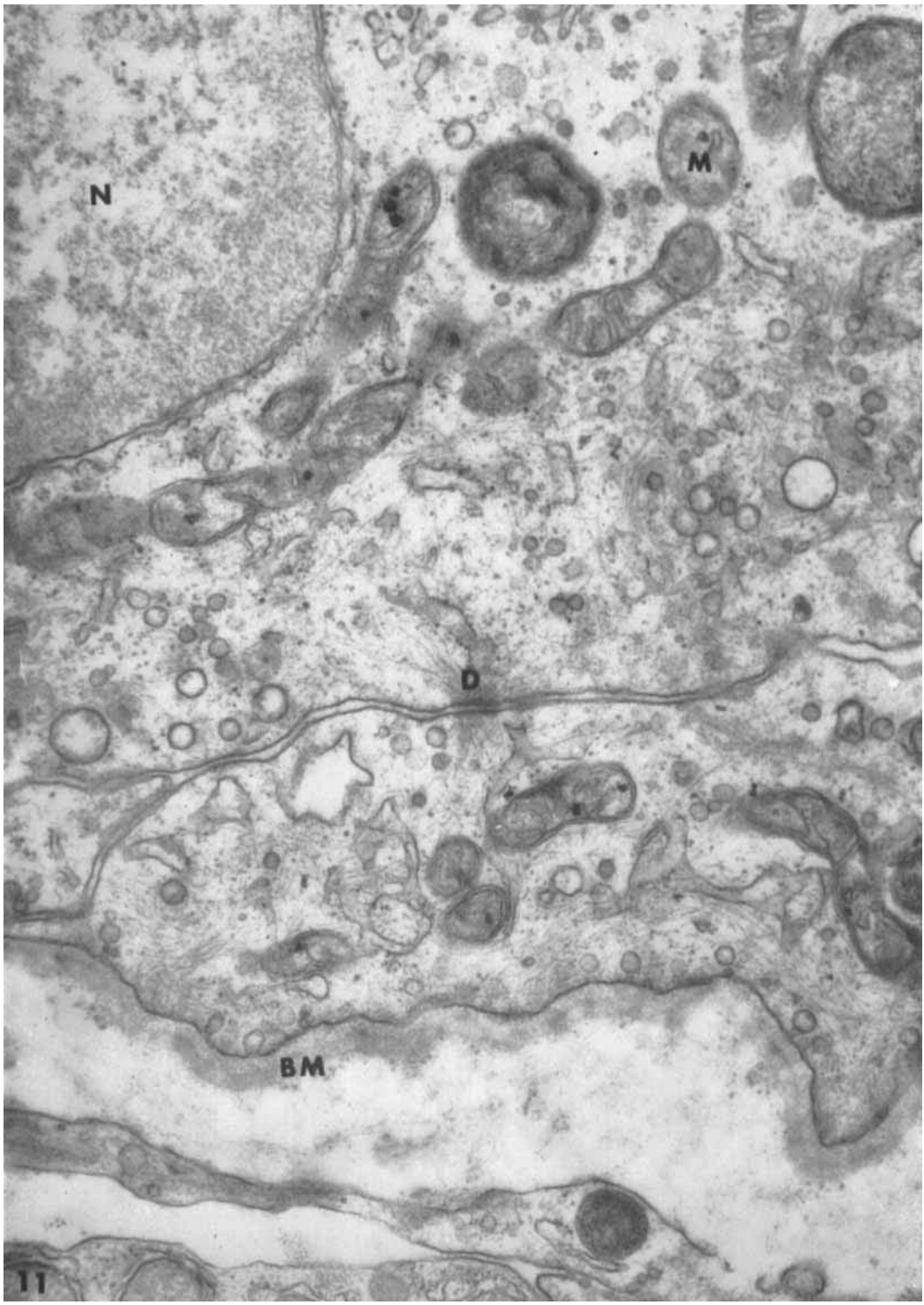

V
L
L
MVB
M
GO
L
10

PLATE 7

EXPLANATION OF FIGURE

11 An electron micrograph of the basal region of the stratified epithelium showing parts of two basal cells. A desmosome (D) can be seen. The basal cells lie on a basement membrane (BM). A layer of intermediate density is seen between the basement membrane and the basal cell membrane. At the bottom of the micrograph a capillary can be seen. The endothelial cell contains a dense granule which appears to be similar to those described by Odland ('61). Fixed with osmium tetroxide and stained with lead tartrate. × 30,400.


N
M
D
BM
11