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The fine structure of resting and active cells in the submucosal glands of the fowl proventriculus

BY PETER G. TONER
Department of Anatomy, University of Glasgow

INTRODUCTION

The domestic fowl has two stomachs, the proventriculus, or glandular stomach, which secretes the gastric juices, and the gizzard, or muscular stomach, which has a mechanical function. The proventriculus has an elaborate system of submucosal glands which make up most of the thickness of its wall. The glands contain only one principal exocrine cell type, the submucosal gland cell, which is generally assumed to secrete both the acid and the zymogenic component of the gastric juice. Aitken (1958), however, has pointed out that there is no conclusive evidence from light microscopy to support this view and, indeed, that some histochemical results indicate that it may not be so. The present study was undertaken in an attempt to interpret the functions of this cell type from observations on resting and activated cells.

MATERIAL AND METHODS

Seven adult white Leghorn hens were starved for 24 hr. to ensure that the gland cells were in the resting state (Chodnik, 1947). The birds were anaesthetized by intramuscular or intraperitoneal 'Sagatal' and ether. At operation, the proventriculus was laid open by a longitudinal incision and the pH of the contents was taken, using Universal Indicator paper. Chilled fixative was then injected into the submucosa, and a small piece of tissue was removed from the injected area, placed in fresh fixative, and trimmed into smaller pieces for processing. Fixation was continued for 1 hr. The fixative used was Zetterqvist's (1956) isotonic 1% osmium tetroxide solution, buffered at pH 7·4. Seven birds were allowed to reach the resting stage by starving for 24 hr., and were then injected subcutaneously with 5 mg. of histamine phosphate in 1 ml. of water. 20–30 min. after injection these birds were operated on, and tissues were obtained as before.

The tissues were washed, dehydrated in an ethanol series, and embedded in Araldite by the short method of Luft (1961). Some of the tissues were dehydrated according to Ito's schedule (Ito, 1961), reaching absolute ethanol within 5 min., while others were treated according to a conventional schedule, reaching absolute ethanol in 1 hr.

Thin sections were cut on the Huxley ultramicrotome and mounted on copper grids without supporting films. The sections were stained for 30 min. in a 1% methanol solution of lead acetate. Sections were examined in the Philips E.M. 75b electron microscope, at magnifications of up to 10,800.

OBSERVATIONS

The resting cell

The pH of the contents of the proventriculus in starved animals was usually between 5 and 7. This low level of acidity was regarded as an indication that active secretion was not proceeding.

General appearance

The epithelium is of the cuboidal or low columnar type. The cell apices are rounded and bulge into the lumen of the gland (Pl. 1, fig. 1). Although the lateral cell membranes are not always closely apposed, gross clefts between adjacent cells are rare. The dentate appearance of the epithelium recorded from light microscopic observations (Calhoun, 1954; Chodnik, 1947) is thus not apparent.

The cell boundaries

The free surface of the resting cell is smooth and without microvilli. There is no apical terminal bar, typically found between epithelial cells in most situations. There is, however, a terminal bar situated near the base of the cell (Pl. 3, fig. 3). Distal to this (on the luminal side) the lateral cell membranes are apposed, or separated by a variable interval, but there are no desmosomes. Between the terminal bar and the base of the cell, adjacent lateral membranes cover loosely interlocking protrusions of cytoplasm.

Infoldings of the basal cell membrane occur at intervals along the base of the cell. These membrane infoldings isolate cytoplasmic shelves, which appear in section as membrane-bound tongues of cytoplasm at the base of the cell (Pl. 5, fig. 5). A well-defined basement membrane underlies the epithelium but does not follow the invagination of the basal cell membrane.

The cytoplasm

The apex of the cell is packed with many round, clear cytoplasmic vacuoles with smooth bounding membranes, which also occupy most of the supranuclear cytoplasm and cause the cell apex to bulge into the lumen of the submucosal gland (Pl. 1, fig. 1; Pl. 3, fig. 3). Similar vacuoles are found close to the lateral cell membrane as far as the level of the terminal bar. The vacuoles have a diameter of about 0·1 μ. There are no apparent connexions between vacuoles, and no evidence that they form a continuous system. No true tubular profiles were seen in any cell, although elongated vacuoles were occasionally observed. The morphology of this system of vacuoles was not affected by variations in the rate of dehydration of the tissues during processing. A similar system of vacuoles described in the mammalian parietal cell (Sedar, 1955) was classified by Palade (1956) as the smooth-surfaced endoplasmic reticulum.

Typical cisternae of the granular endoplasmic reticulum are a feature of the perinuclear and basal cytoplasm (Pl. 3, fig. 3; Pl. 5, fig. 5), but, altho ugh wel organized, the endoplasmic reticulum is not as complex as that of the mammalian gastric chief cell (Helander, 1962). Granular cisternae are infrequently seen between the vacuoles of the smooth endoplasmic reticulum. R.N.P. particles are attached

to the membranes of the granular reticulum and to the cytoplasmic surface of the outer nuclear membrane. Spiral patterns of particles are often seen when the cisternal membranes are sectioned tangentially. Free R.N.P. particles are found lying singly or in small groups throughout the cytoplasm.

In the basal cytoplasm of some cells there are occasional elongated bodies within the cisternae of the granular endoplasmic reticulum. They measure about 700 Å. in thickness and up to 1·5 μ in length, and they often display a fine regular transverse striation with a period of about 130 Å (Pl. 8, fig. 14). Such intracisternal structures could represent sheets of material corresponding to the form of the flattened cisternae of the granular reticulum. The insert to Pl. 8, fig. 14, shows a cisterna containing one of these bodies sectioned obliquely.

Mitochondria are most numerous in the supranuclear cytoplasm and are oval or cylindrical in shape (Pl. 6, fig. 8). They are 1–2 μ long by about 0·8 μ in diameter. Mitochondria cut in their long axis have an average of 25 cristae per micron, compared with the 30 per micron observed by Hally (1959) in the mammalian gastric parietal cell. This indicates a high rate of oxidative cell metabolism. The mitochondrial matrix is of moderate density and contains many small dense particles of irregular shape, around 400 Å. in diameter (Pl. 6, fig. 8). Apical mitochondria lie amongst the vacuoles of the smooth endoplasmic reticulum, while basal mitochondria are often closely related to the cisternae of the granular endoplasmic reticulum (Pl. 6, fig. 8).

The Golgi apparatus as seen by the light microscope is a reticular structure lying around the nucleus. Because of this reticular arrangement, thin sections often show the Golgi apparatus in one cell in several parts, each part having the typical arrangement of dilated sacs or vacuoles, with smooth bounding membranes, and a few Golgi vesicles.

In Pl. 7, fig. 9, three parts of the Golgi apparatus are seen near the base of a cell and nearby, beside the Golgi sacs, a few unusual isolated membrane pairs can be made out. There are several similar fragments lying close together, and these could represent separate parts of one complicated structure. The same arrangement is seen in Pl. 7, fig. 10, where two membrane pairs appear to be closely connected with the Golgi apparatus. Such structures are denser and more evenly spaced than the typical membranes of the Golgi lamellae, from which they are quite distinct. Moreover, they are never associated with Golgi vacuoles.

Membrane pairs corresponding to this description and found in close association with the Golgi apparatus can be distinguished in a substantial proportion of cells examined and may constitute a fourth component of the Golgi apparatus in these cells. Pale granules are occasionally found in association with the 'fourth component' (Pl. 7, fig. 11).

Round homogeneous bodies, about 0·8 μ in diameter, and bounded by a single smooth close-fitting membrane, lie below and around the nucleus, and are often found in groups around the Golgi apparatus; they are believed to be zymogen granules (Pl. 3, fig. 3; Pl. 5, fig. 5). There are pale and dark granules, the pale ones resembling in texture and density those sometimes associated with the 'fourth component' of the Golgi apparatus.

Pl. 8, figs. 12 and 13, illustrate pleomorphic dense bodies characteristically

present in the infranuclear cytoplasm. They are bounded by a single membrane, and have a composite dense interior containing granular areas and aggregations of dense irregular membranes. Myelin figures are sometimes found, and round pale areas, sharply demarcated from the dense material. Similar pale areas, resembling pale zymogen granules, may bulge from the side of the dense body, as if in the process of extrusion.

One or two typical vacuole-containing bodies, about 0·5μ in diameter, are present, usually in the apical cytoplasm (Pl. 3, fig. 3), and occasional smaller ones lie close to the Golgi apparatus. It is possible that they are formed here and subsequently pass to other regions of the cell, where they attain their full size. They contain only a few small vacuoles. In a few cells, a discrete bundle of fine parallel fibrils, with a suggestion of pairing, was observed in the basal cytoplasm (Pl. 5, fig. 5; Pl. 8, fig. 15).

The nucleus

The nucleus of the submucosal gland cell is large, round, regular, and situated basally. The texture of the nuclear material is uniformly granular and of relatively low density. There is little clumping of the chromatin. The nuclear envelope has the usual bilamellar structure interrupted at intervals by pores which appear to be closed by a single membrane (Pl. 8, fig. 13).

When the nucleus is sectioned tangentially, annuli may be seen around the exterior of the pores (Dawson, Hossack & Wyburn, 1955). Irregular granules of nuclear material are attached to the inner surface of the nuclear membrane, and may be closely packed. R.N.P. particles are attached to the outer surface of the outer lamella of the nuclear envelope. On rare occasions, the perinuclear cisterna appears to be continuous with the cavity of a cisterna of the granular endoplasmic reticulum. A prominent nucleolus may be seen.

The stimulated cell

The pH of the contents of the proventriculus in stimulated birds was under 2. This high level of acidity was taken to indicate that active secretion of gastric acid was occurring.

General appearance

The cell apices no longer bulge into the lumen of the gland, and their free surfaces are straight rather than rounded (Pl. 2, fig. 2; Pl. 4, fig. 4). Intercellular clefts are rarely found. After histamine stimulation there are marked changes in all parts of the cell membrane and in the vacuoles of the smooth endoplasmic reticulum.

The cell membrane

The apex and the entire free surface of the stimulated cell as far as the basally placed terminal bar have long bulbous microvilli lying at all angles to the cell surface and covering the potential distal intercellular space of the resting cell (Pl. 2, fig. 2; Pl. 4, fig. 4; Pl. 6, fig. 7). Occasionally, a diffuse layer similar to that described by Hally (1959) in the mammalian parietal cell microvilli may be seen

immediately below the cell membrane covering the microvilli. The cells are held in contact by the terminal bar close to their base (Pl. 7, fig. 9). Below this level, the interdigitations between cells are more complex, and the apposed membranes are in closer contact than in the resting cell.

The basal infolding of the cell membrane is more elaborate in the stimulated cell, and the expansion of the cytoplasmic shelves obliterates the spaces which were present between them in the resting cell. These shelves now lie in close apposition, parallel to the base of the cell (Pl. 5, fig. 6). A central region of increased density can occasionally be made out within these processes. Occasional vesicles appear to be forming in the basal cytoplasm by pinching off from the ends of the infoldings.

The smooth endoplasmic reticulum

The vacuoles of the smooth endoplasmic reticulum which filled the apex of the resting cell are now greatly reduced in number (Pl. 4, fig. 4; Pl. 6, fig. 7). There are some close to the cell membrane in the apical and lateral cytoplasm and a few lie within the bulbous microvilli on the free surface of the cell (Pl. 6, fig. 7). Of the remaining vacuoles, elongated forms are rather more common than in the resting cell. Because there is no bulging apex, the nucleus now lies nearer the luminal surface than in the resting cell, and the granular endoplasmic reticulum extends into the apical cytoplasm (Pl. 6, fig. 7). The Golgi apparatus is commonly infranuclear rather than paranuclear, and Chodnik (1947) attributed this change in their relative positions to the movement of the nucleus following the release of supranuclear zymogen granules. An alternative explanation is the loss of the apical mass of the smooth endoplasmic reticulum.

Apart from its relative situation there is no obvious change in the structure of the Golgi apparatus following histamine stimulation. The 'fourth component', as described above, is again present. There are no marked alterations in the appearance of the mitochondria, dense bodies, or vacuole-containing bodies following stimulation.

DISCUSSION

Form of the epithelium

The epithelium of the submucosal gland as observed with the light microscope has a characteristic dentate appearance due to wide and deep intercellular clefts extending from the apex of the cells almost to their base (Chodnik, 1947; Calhoun, 1954). In material fixed with isotonic osmium tetroxide these clefts were rarely present. They probably represent an artefact due to the shrinkage factor inherent in the routine histological fixatives, and made possible by the basal location of the terminal bars plus the absence of desmosomes. Elsewhere in the gastro-intestinal tract the epithelial cells are joined firmly to one another by apical terminal bars and by lateral desmosomes, and thus resist shrinkage separation at their distal poles.

Cell structure and function

The submucosal gland cells of the fowl proventriculus have the typical fine structure of both a zymogenic and an acid-secreting cell. They have the well-developed granular endoplasmic reticulum, the elaborate Golgi apparatus, and the

many zymogen-like granules characteristic of the mammalian gastric chief cell. They also have the extensive smooth endoplasmic reticulum, the large active mitochondria, and the basal infoldings of the cell membrane typical of the mammalian gastric parietal cell. Moreover, they show changes following histamine treatment, a recognized stimulant of gastric acid secretion. The present observations are consistent with the view that the submucosal gland cells of the proventriculus secrete both the acid and the proteolytic enzymes of the gastric juice. In this respect the fowl resembles the amphibian, where the cells of the gastric glands are not differentiated into acid- and enzyme-secreting types (Vial & Orrego, 1960; Sedar, 1961*a*, *b*).

The Golgi apparatus of the submucosal gland cell possesses the lamellae, vacuoles, and vesicles which are characteristic of this organelle in other sites (Dalton & Felix, 1954; Helander, 1962). In addition, a membrane pair, which may represent a fourth component, is commonly seen. Most workers believe that the zymogen granules of the mammalian gastric chief cell are formed in the Golgi apparatus (Helander, 1962; Kurosumi, 1961). As Chodnik (1947) describes, the granules in the submucosal gland cells are often grouped around the Golgi apparatus, and the 'fourth component' may be involved in their elaboration. It is possible, though less likely, that the granules are formed by the extrusion of pale areas from the interior of the dense cytoplasmic bodies (Pl. 8, figs. 12, 13), although these bodies more probably represent the structures described as lysosomes in other cell types. The striated intracisternal bodies of the granular endoplasmic reticulum do not seem to have any connexion with the zymogen granules; their periodicity suggests a crystalline structure.

The unusual position of the terminal bars in the submucosal gland epithelium allows the use of most of the lateral cell surface as well as the apical surface for secretory extrusion, and as such is analogous to the intracellular canaliculus of the mammalian parietal cell, which provides an estimated threefold increase in the secretory surface of the cell (Hally, 1959). The basal shift of the terminal bar increases the available secretory surface by a factor of six.

The cytoplasmic vacuoles—numerous in the resting cell—are comparable to those present in the mammalian parietal cell (Kurosumi, Shibasaki, Uchida & Takana, 1958; Hally, 1959; Lawn, 1960; Sedar & Friedman, 1961) and in the acid-secreting cells of other species (Vial & Orrego, 1960; Sedar, 1961*a*). They are classified by Palade (1956) as smooth endoplasmic reticulum, but this is not universally accepted (Helander, 1962). Recent work suggests that the true form of the smooth reticulum is tubular and that the vacuoles are due to the distortion of such a system by faulty processing of the tissues (Ito, 1961; Sedar, 1962). Helander (1962), however, believes that the vacuoles are the true form. The present observations support Helander's views. The smooth reticulum in the submucosal gland cell remains predominantly vacuolar with conventional processing, and even after the rapid dehydration schedule of Ito (1961).

Results of stimulation experiments

Ito (1961) has failed to relate the structure of the acid-secreting cells of several species to their secretory state. The present investigation shows that the changes in the submucosal gland cells of the fowl are clearly correlated with the appearance

of a strongly acid secretion within the proventriculus, and similar changes, less pronounced than those in the fowl and excluding alterations in the basal infoldings, have been described in other species following various forms of stimulation (Lawn, 1960; Vial & Orrego, 1960; Hally, 1961; Sedar, 1961*b*; Sedar & Friedman, 1961; Helander, 1962).

Histamine treatment was followed by an increase in the surface area of the cell. The microvilli on the free surface augmented the already large secretory area, while below the terminal bar the extension of the basal infoldings increased the area available for the absorption of metabolites from the blood stream. The large-scale elaboration of acid secretion appears to require the participation of extensive cell surfaces. The diffuse layer under the membrane of some of the microvilli in these cells, and the central dense zone sometimes seen in the basal processes, might be connected with the transport of water or ions across the cell membrane.

The reduction in the numbers of vacuoles, and the peripheral distribution of those which remain following stimulation, confirm that this system is involved in acid secretion and suggest that stimulation causes the release of the contents of the vacuoles at the cell surface. The increased area of the free surface of the stimulated cell could be due to the incorporation of the membranes of the vacuoles into the apical cell membrane, and might thus be secondary to their release, rather than a primary manifestation of activity. This explanation, however, cannot account for the expansion of the basal infoldings below the terminal bar.

SUMMARY

1. The fine structure of the submucosal gland cells in the proventriculus of the fowl has been studied in the fasting and in the histamine-stimulated animal. Several unusual structural features are described.

2. The appearance of the cells is consistent with the view that they secrete the acid as well as the zymogenic component of the gastric juice.

3. Stimulation with histamine provokes acid secretion. Simultaneous changes are seen in the apical and basal cell membrane, and in the extent and distribution of the smooth endoplasmic reticulum.

4. The present findings are discussed with reference to recent studies on acid-secreting cells of other species.

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EXPLANATION OF PLATES

Abbreviations

B.M.	Basement membrane	*Cap.*	Capillary
D.B.	Dense body	*Fib.*	Fibrils
G.	Granule	*G.E.R.*	Granular endoplasmic reticulum
Go.	Golgi apparatus	*Inf.*	Infolding of cell membrane
M.	Mitochondrion	*MV.*	Microvillus
My.	Myelin figure	*N.*	Nucleus
N.P.	Nuclear pore	*Sch.*	Schwann cell
S.E.R.	Smooth endoplasmic reticulum	*V.C.B.*	Vacuola containing body
T.B.	Terminal bar	*Z.*	Zymogen granule

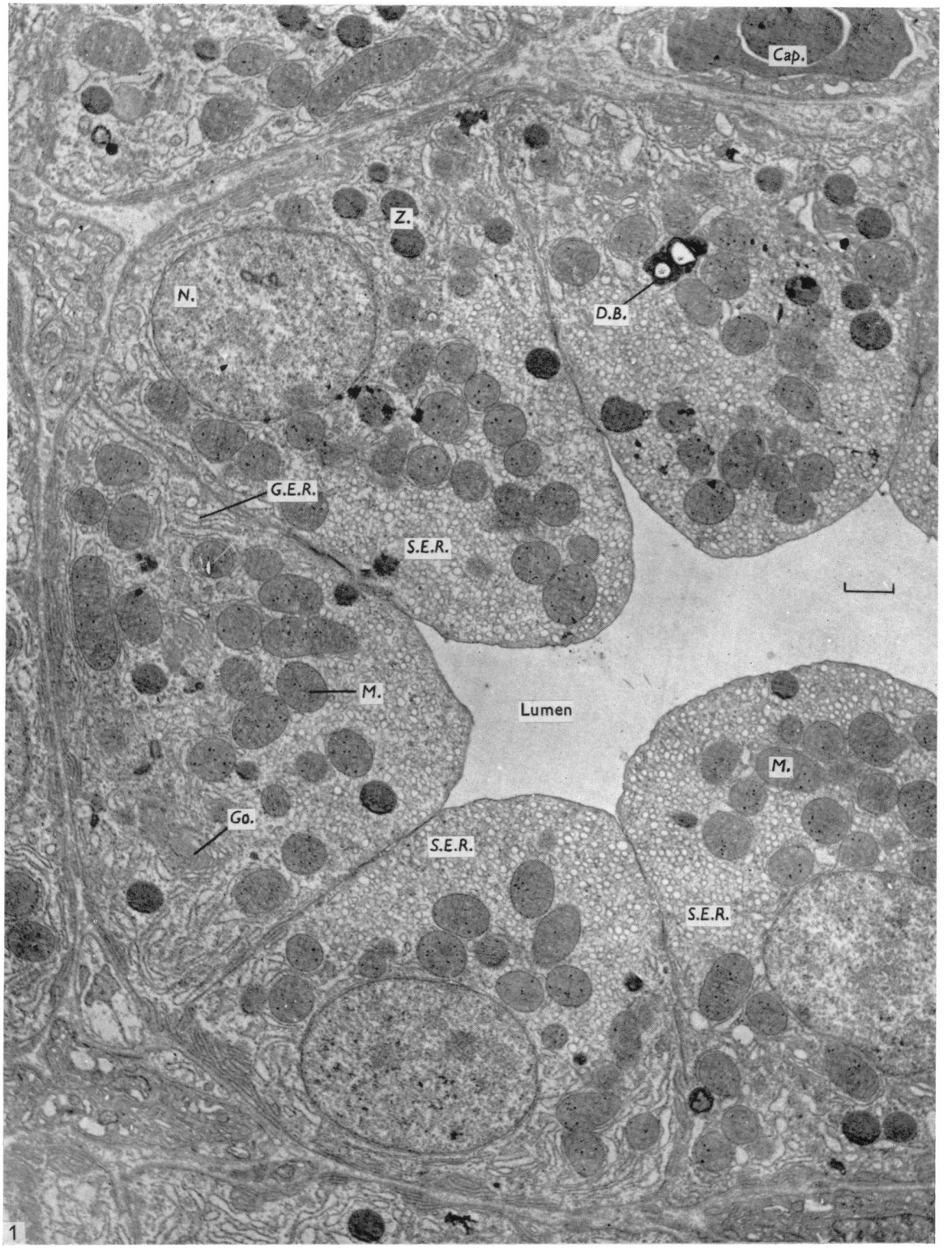
Scale line = 1 μ unless otherwise indicated.

PLATE 1

Fig. 1. The submucosal gland in the resting state. The apical parts of the cells are rounded and smooth. There are no gross clefts between cells.

PLATE 2

Fig. 2. The submucosal gland following histamine stimulation. The smooth cell apices have been replaced by irregular microvilli which reach down between cells as far as the terminal bars.



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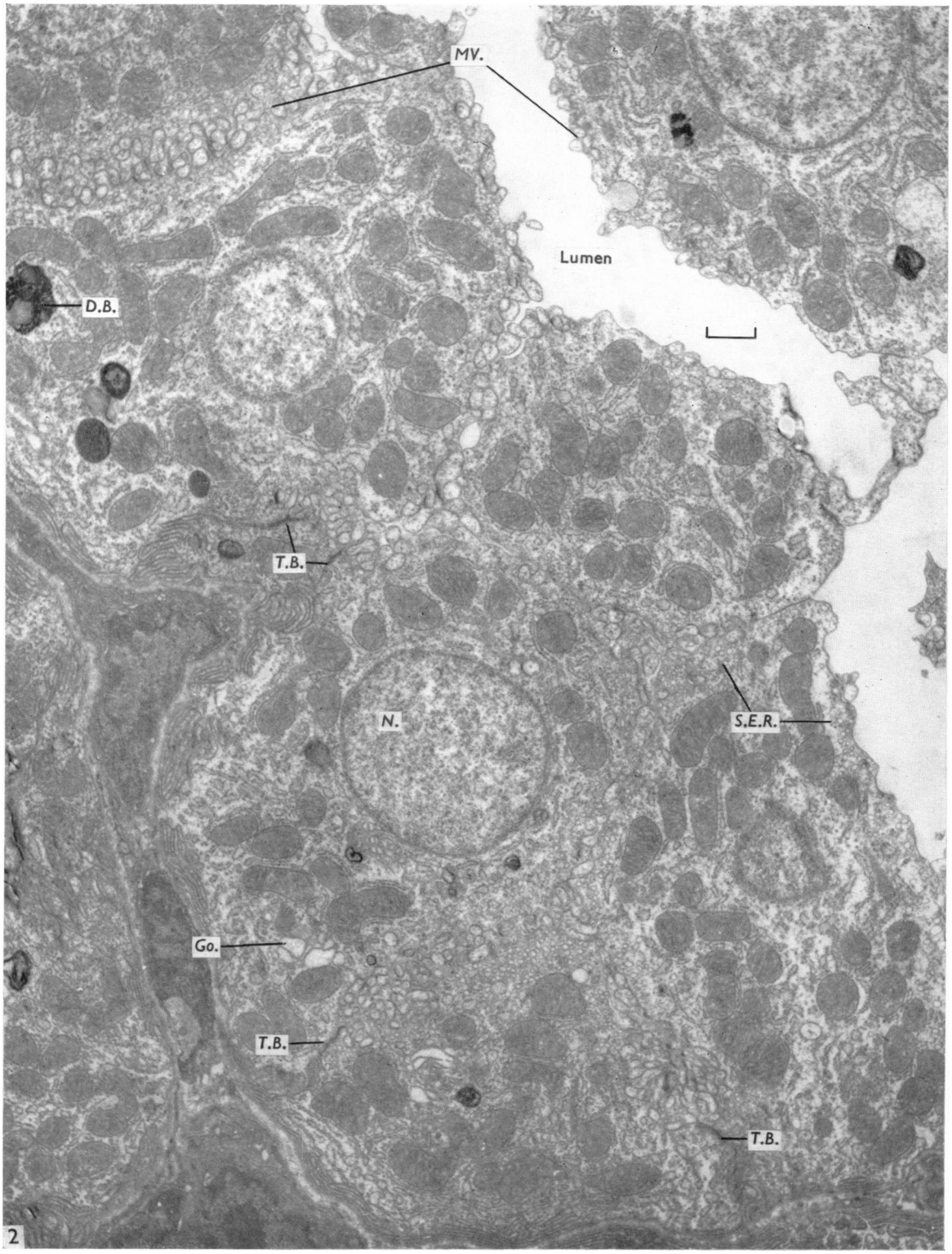

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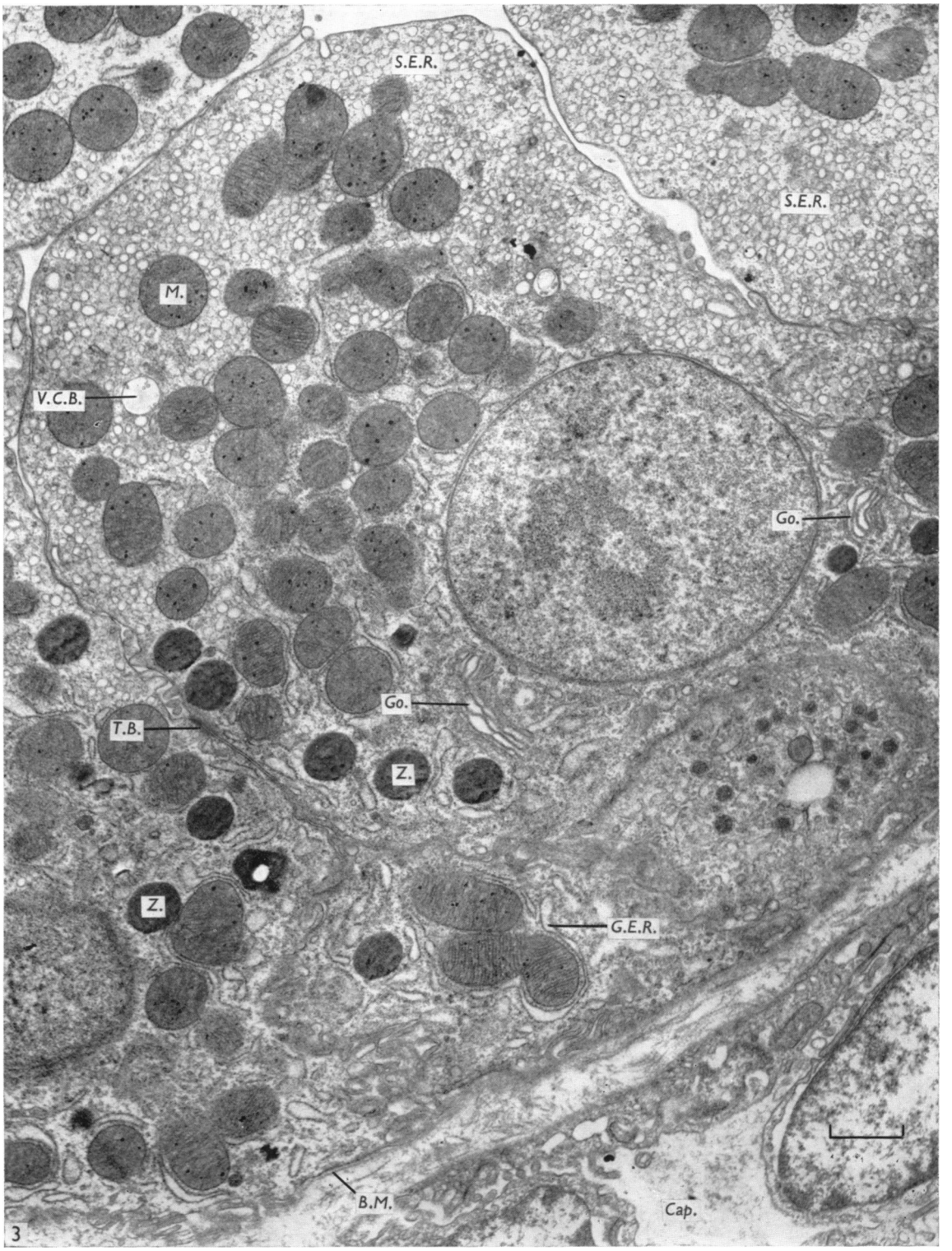
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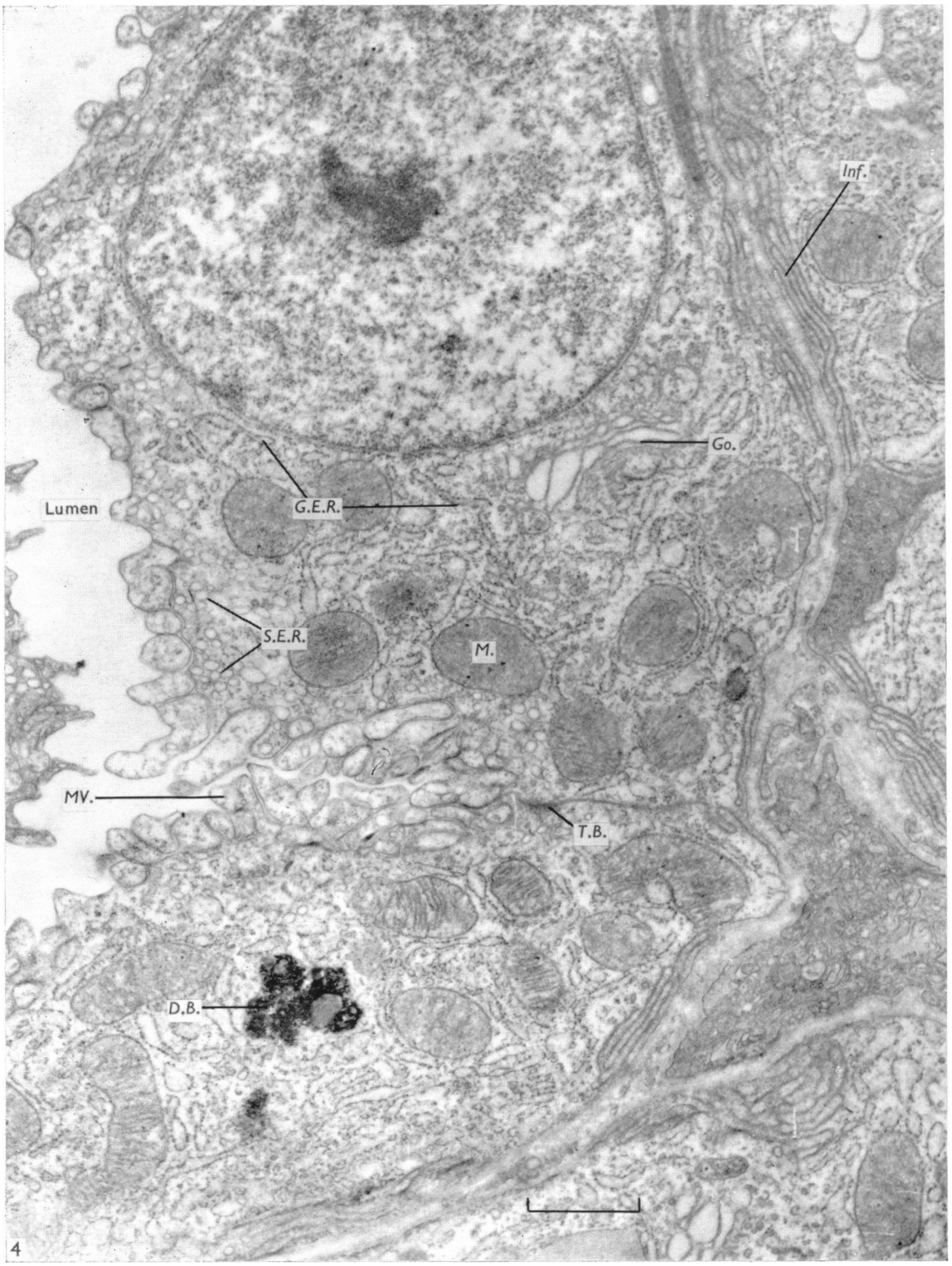
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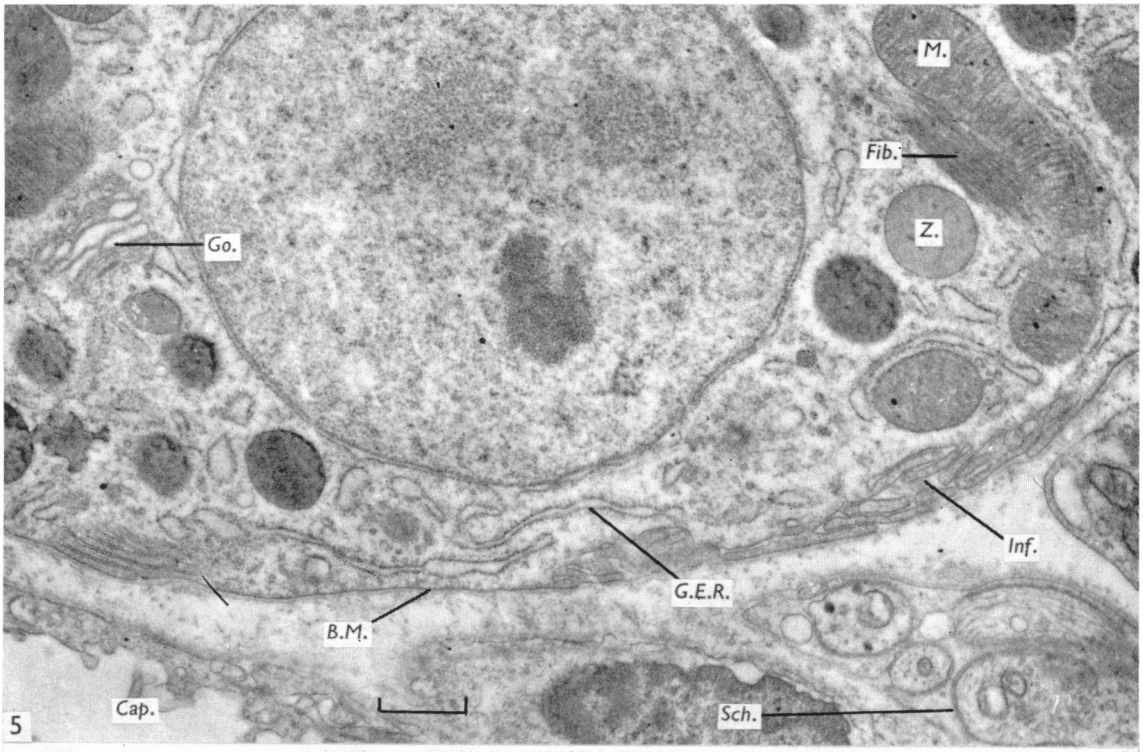
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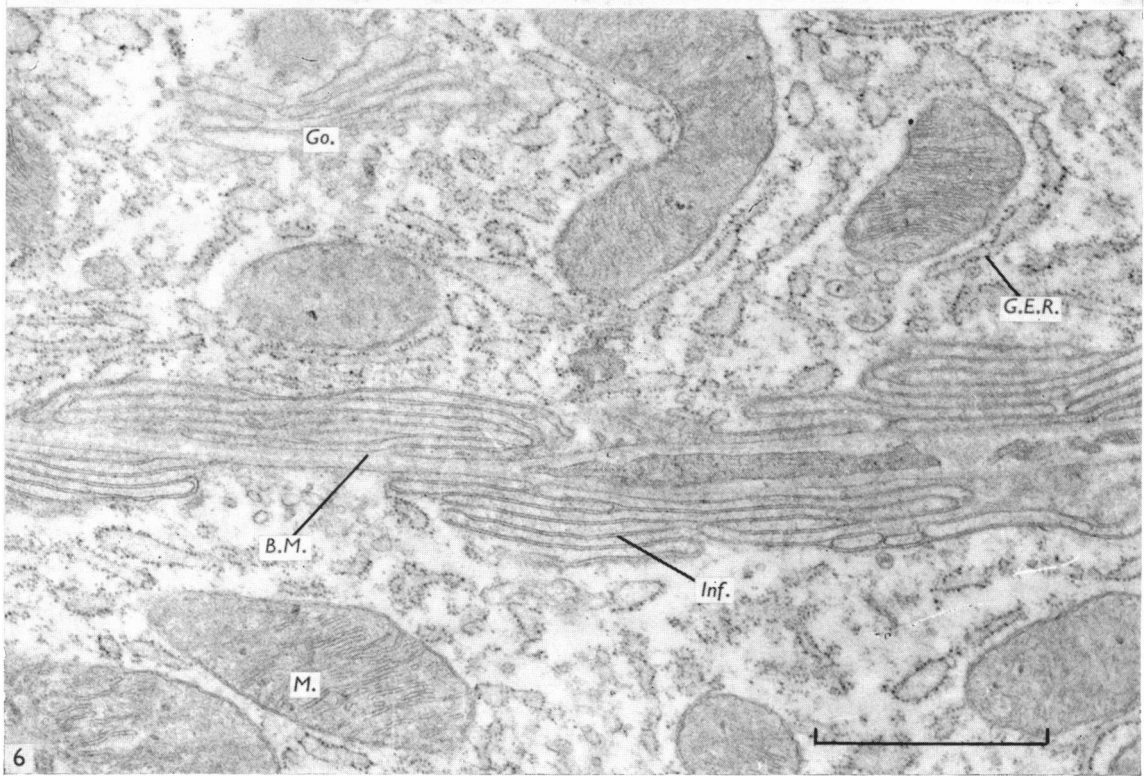
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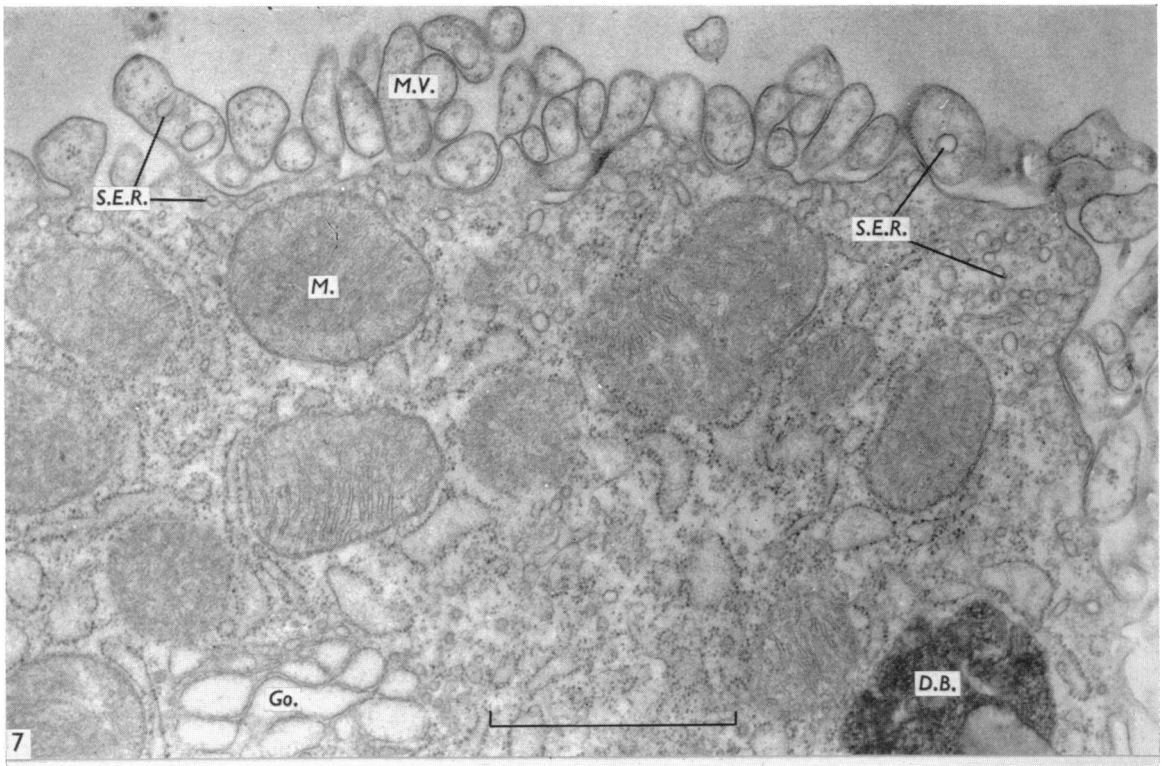
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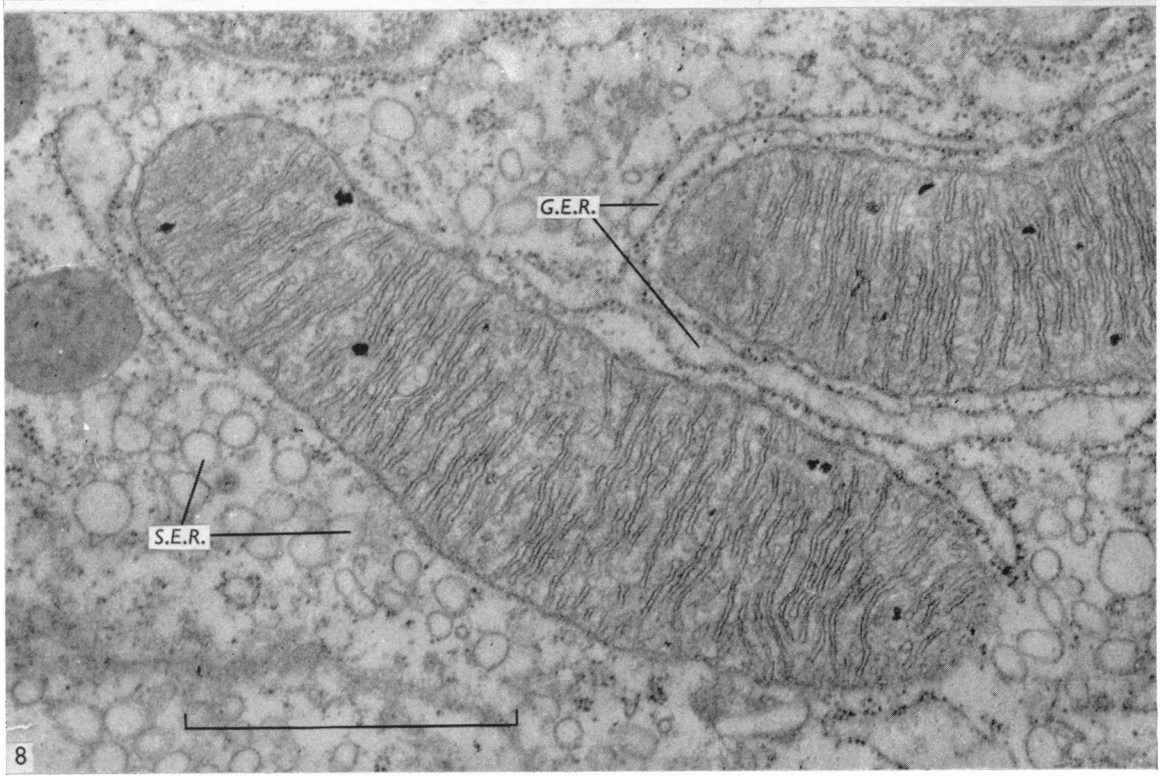
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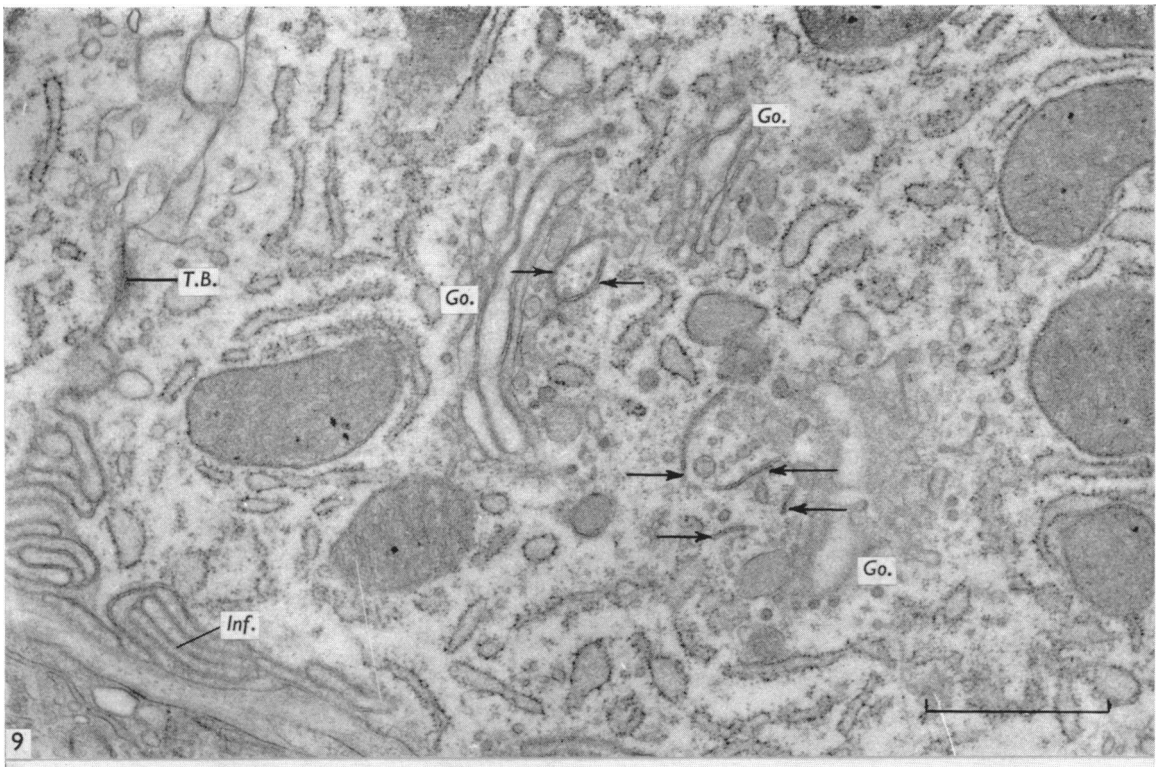
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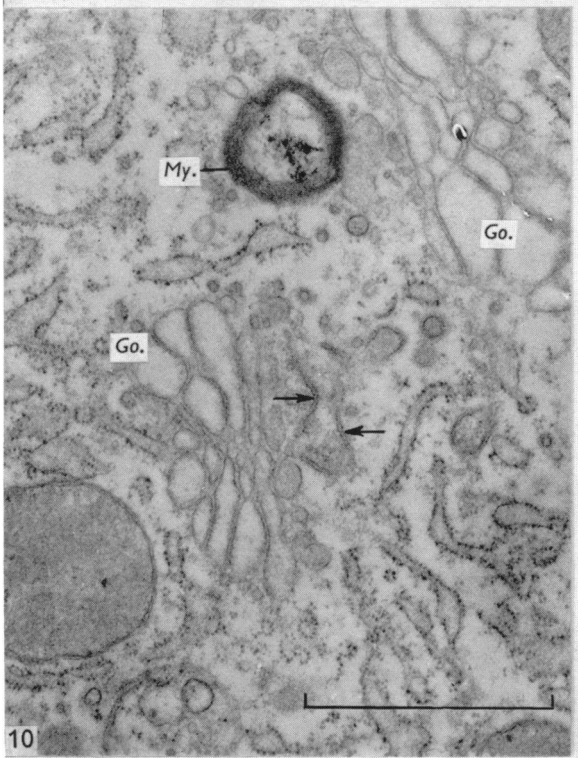
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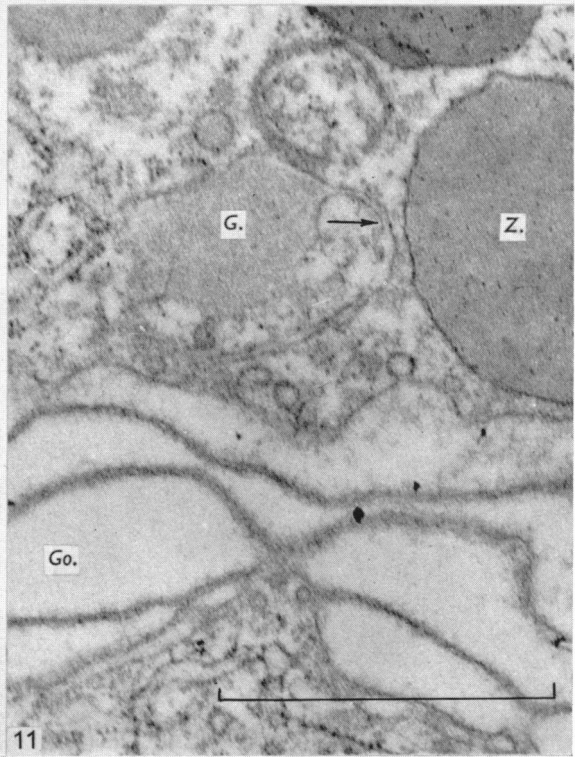
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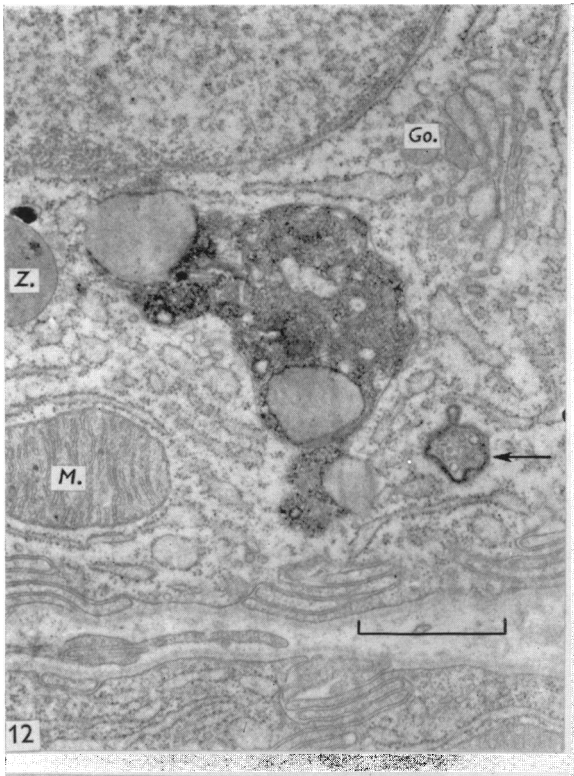

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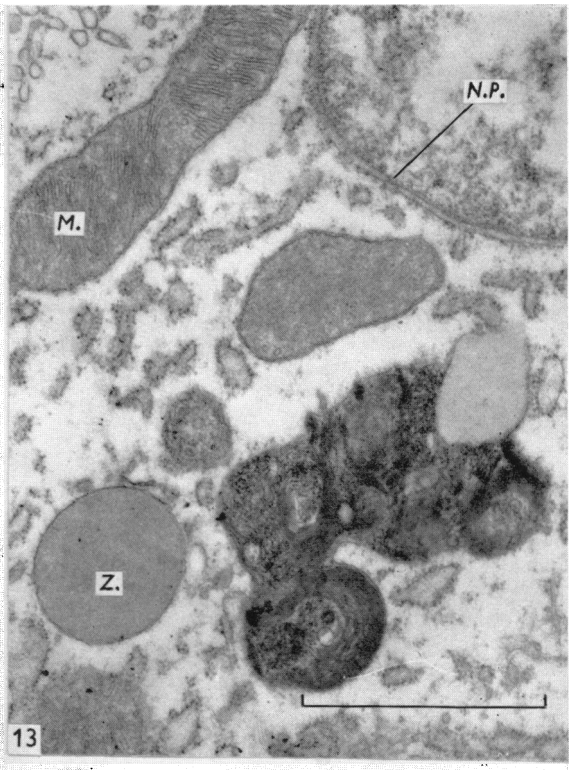

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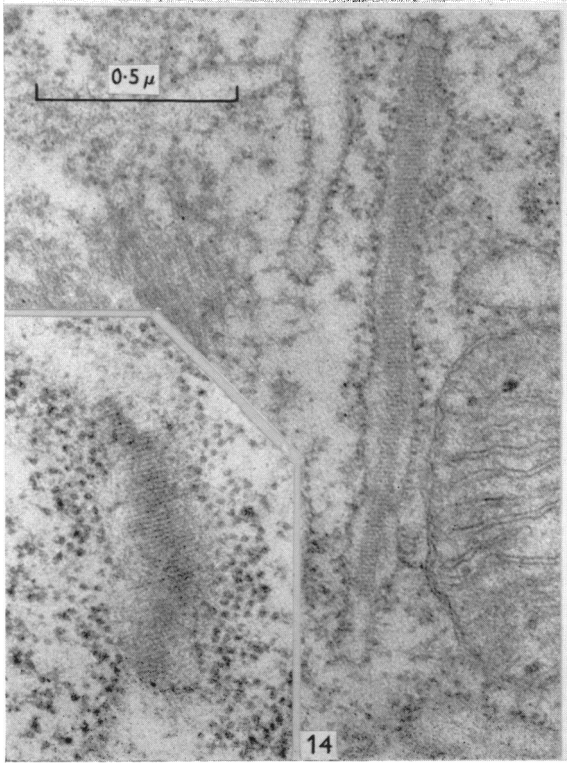

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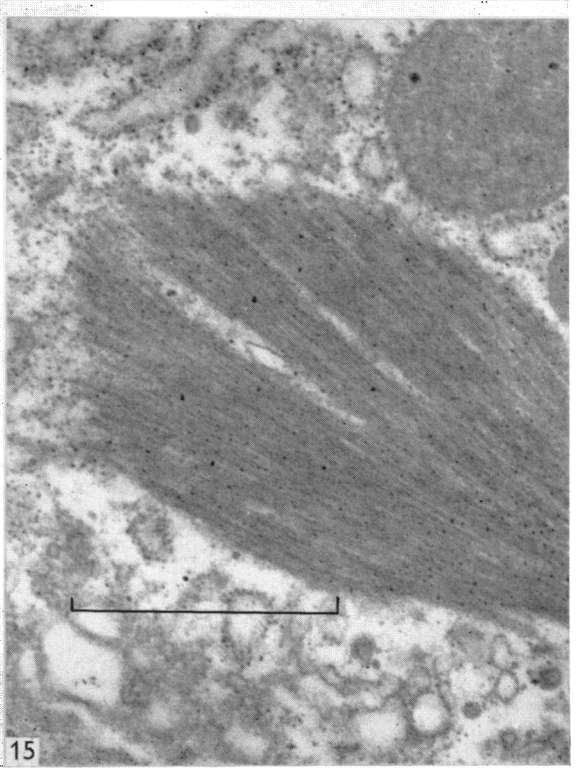

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PLATE 3

Fig. 3. A resting gland cell. The apical cytoplasm is filled with round, smooth-surfaced vacuoles. The nucleus is basally situated, and the Golgi apparatus lies on either side of it. Note the position of the terminal bar, and the distribution of the granular reticulum, smooth reticulum, and mitochondria. Part of an argyrophil cell is seen at the base of the submucosal gland cell.

PLATE 4

Fig. 4. A submucosal gland cell following histamine stimulation. The free surface as far as the terminal bar is covered by irregular microvilli. Few of the apical cytoplasmic vacuoles remain.

PLATE 5

Fig. 5. Base of a resting cell. The vacuoles of the smooth reticulum are not seen here, but cisternae of the granular reticulum are present. The basal infoldings of the cell membrane are poorly developed. The Golgi apparatus and zymogen granules can be seen. A bundle of dense fibrils lies beside a mitochondrion. A Schwann cell containing a few unmyelinated nerve fibres lies in the connective tissue beside a capillary.

Fig. 6. Base of a stimulated cell. The infoldings of the cell membrane have become much more elaborate. The basal surface of the cell is thus greatly increased in area.

PLATE 6

Fig. 7. Apical microvilli of a stimulated cell. Occasional smooth-surfaced vacuoles are seen within these microvilli, but most of them have disappeared from the apex and the other cytoplasmic constituents have taken their place.

Fig. 8. Mitochondria of the submucosal gland cell. The cristae are closely packed. A few cisternae of the granular endoplasmic reticulum lie in close relationship to the mitochondria. A number of vacuoles of the smooth reticulum are also seen.

PLATE 7

Fig. 9. Base of a stimulated cell. Note the basally placed terminal bar, with irregular microvilli above and interdigitations below. Several parts of the Golgi apparatus are present. In association with two of the sets of Golgi sacs, several fragments of a membrane pair can be made out (arrows).

Fig. 10. Golgi apparatus of a submucosal gland cell. Lamellae, vacuoles, and vesicles are all present. In addition, there can be distinguished the unusual membrane pairs (arrows) which may form a 'fourth component' of the Golgi apparatus.

Fig. 11. The 'fourth component' of this Golgi apparatus (arrow) appears to be giving rise to a pale granule of a texture similar to that of the adjacent zymogen granule.

PLATE 8

Fig. 12. A dense body in the base of a submucosal gland cell. Three pale areas are seen within it, two of them bulging from its side as if they were being extruded. An unusual inclusion lies near by (arrow).

Fig. 13. The interior of this dense body is made up mainly of irregular dense membranes and myelin figures. Compare the pale areas of this body with the near-by zymogen granule.

Fig. 14. This intercisternal body has a fine striation with a period of about 130 Å. Insert (same magnification) shows an oblique section of a cisterna with a similar inclusion.

Fig. 15. The fibrils composing this bundle run nearly parallel. There is a suggestion of pairing of fibrils.