THE ARCHITECTURE OF THE ACCESSORY REPRODUCTIVE GLANDS OF THE DESERT LOCUST
IV. FINE STRUCTURE OF THE GLANDULAR EPITHELIUM

By T. R. ODHIAMBO
Department of Zoology, University College, Nairobi, Kenya

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The male desert locust, *Schistocerca gregaria*, has two masses of thin glands, each mass containing 16 glands. The glands in each mass are arranged in a precise manner, which is a mirror image of the arrangement to be found in the other gland mass. They produce secretions which participate in the production of the spermatophore and most of its contents during mating. The fine structure of these glands is described in detail on the basis of an electron-microscope study of sectioned glands and their secretions.

It is revealed that the characteristics of the glandular epithelia and their corresponding secretions lead to the division of the accessory glands into nine distinct types. This finding strengthens the recent division of the glands into nine types based on histological, histochemical, and phase-contrast features.

One gland produces a proteinaceous, crystalline secretion (gland 1), three types of glands produce a minutely fibrous secretion (glands 2 and 4, and 'homogeneous' glands), three other gland types produce a globular secretion (glands 6, 11 and 12), and one gland type has a lipoid secretion (gland 3). Gland 16, the functional seminal vesicle, does not produce a recognizable secretion. The cytoplasmic organelles that are concerned in the secretory process, and the manner in which their development varies with each gland type, are discussed.

Introduction

The histology and histochemistry of the accessory reproductive glands (ARGs) of the desert locust has been reported in a previous paper in this series (Odhiambo 1969*a*). It appeared from this study that the accessory gland complex consisted of nine types of glands, segregated

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vertically by the characteristics of their secretions and the cytological features of the various glandular epithelia. It is the purpose of the present paper to provide a detailed account of the fine structure of these various gland types. Such an account can be justified on several grounds: first, present knowledge of the structure of the male ARGs is extremely limited, although the glands provide the structural materials for the formation of the spermatophore as well as supplying some active materials concerned in sperm transfer (Davey 1958); secondly, the glandular epithelium displays a number of fine-structural peculiarities that are intrinsically interesting and add to our growing knowledge of the secretory apparatus and processes in cells; thirdly, the study will further establish the characterization of the ARGs into nine distinct types of glands; and fourthly, it will establish a basis upon which experimental work on the development and differentiation of these glands can be assessed.

In two previous papers (Odhiambo 1969*b*, *c*), the fine structure of the muscular sheath that surrounds each ARG and the microtubules which are prevalent in the glandular cytoplasm have been described. In the present paper, fine-structural observations on the various glandular epithelia of the locust ARGs will be reported and discussed.

Materials and methods

The accessory gland complex of the male desert locust, *Schistocerca gregaria* Forskål, consists of two masses each containing 16 ARGs held together by fat body and tracheae (Odhiambo 1969*a*). The individual glands are short, up to about 8.5 mm long; the glands take an irregular course in the gland mass, each gland nevertheless taking a characteristic course (figure 1). For ease of preparation for electron microscopy, the glands were processed as intact gland masses.

Gland masses were freshly dissected from sexually mature adult locusts and fixed and processed for electron microscopy as described in detail elsewhere (Odhiambo 1966). Briefly, the material was fixed in a buffered solution of osmium tetroxide, embedded in Araldite epoxy-resin, sectioned, and double-stained in uranyl acetate and lead citrate. Observations were made with a Zeiss EM 9 and a Philips EM 200 electron microscopes.

The lateral plasma membrane

The 'lateral' plasma membrane is generally highly convoluted, but of more functional interest are its specializations in regard to contact attachments with neighbouring cell membranes, i.e. septate desmosomes and terminal bars (figure 2).

The *terminal bars* of Farquhar & Palade (1963) occur at the apical end of the lateral plasmalemma (figure 49, plate 22). At this region, the opposing plasma membranes of adjoining cells are regularly parallel to each other, separated by an intercellular space of only approximately 150 Å. The intercellular space circumscribed by the terminal bar does not appear to contain any specific structure although it does seem to contain some fairly electron-dense, minutely divided material (figure 49, plate 22). Internal to each plasma membrane at this region is a thick layer (100 to 150 Å) of electron-opaque material, apparently composed of minutely fibrillar structures tangentially orientated along the plasmalemma (figure 78, plate 32). Thus, apart from the lack of organized structure in the intercellular space, the structure of the terminal bar described here is rather similar in general organization to that of vertebrate desmosomes (Tamarin & Screebny 1963).

In the course of examining the fine structure of the various locust ARGs in this paper it will become clear that the terminal bars demarcate an area of the cytoplasm subjacent to the gland lumen that is usually relatively free of many of the cytoplasmic organelles (see, for example, figure 33). This area is more obvious in certain gland cells than in others (compare figures 2 and 33). This so-called *terminal-web* region (Sjöstrand 1963), containing numerous thin filaments which seem to terminate within the microvilli and in the environs of the terminal bars, is thought to function as a stiffening and stabilizing element in the apical cytoplasmic region (Trier 1963); the terminal bar, on the other hand, is considered to offer a stable and mechanical contact between adjacent cells (Elbers 1964).

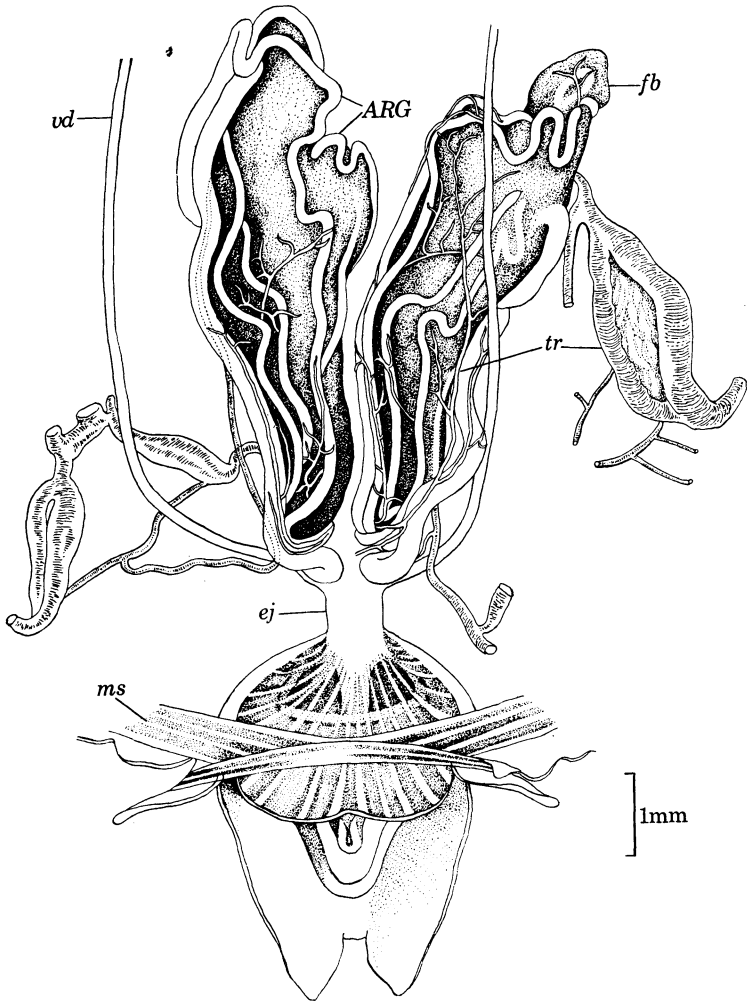


FIGURE 1. Drawing of the accessory reproductive gland system of the mature male desert locust to indicate the disposition of some of the glands as seen from a dorsal dissection. The system's interrelationships with the fat-body, tracheae, vas deferens, and the ejaculatory duct are also shown.

Apart from the terminal bar, opposing plasma membranes are attached by means of *septate desmosomes*. The latter are found along the lateral cell membranes, except at the terminal bar region. In transverse section, the septa of the desmosomes are about 90 to 120 Å thick and 120 to 150 Å wide, regularly spaced out at intervals of 100 Å, thus keeping the adjacent plasma membranes 200 Å apart (see figure 6 in Odhiambo 1969*b*). The septa do not in fact abut

directly on to the plasma membranes: there is a space of 25 to 40 Å between the ends of the septa and the plasma membranes themselves. In superficial sections of the lateral plasma membranes, these septa appear as continuous, circumferentially oriented helical fibrillar structures (figures 84 and 85, plate 33). Locke (1965) has described similar structures in insect epidermis, and has concluded that the desmosomal septa are not straight sheets joining the lateral plasma membranes together, but instead form a hexagonal network of septa arranged as the walls of symmetrical intercellular compartments.

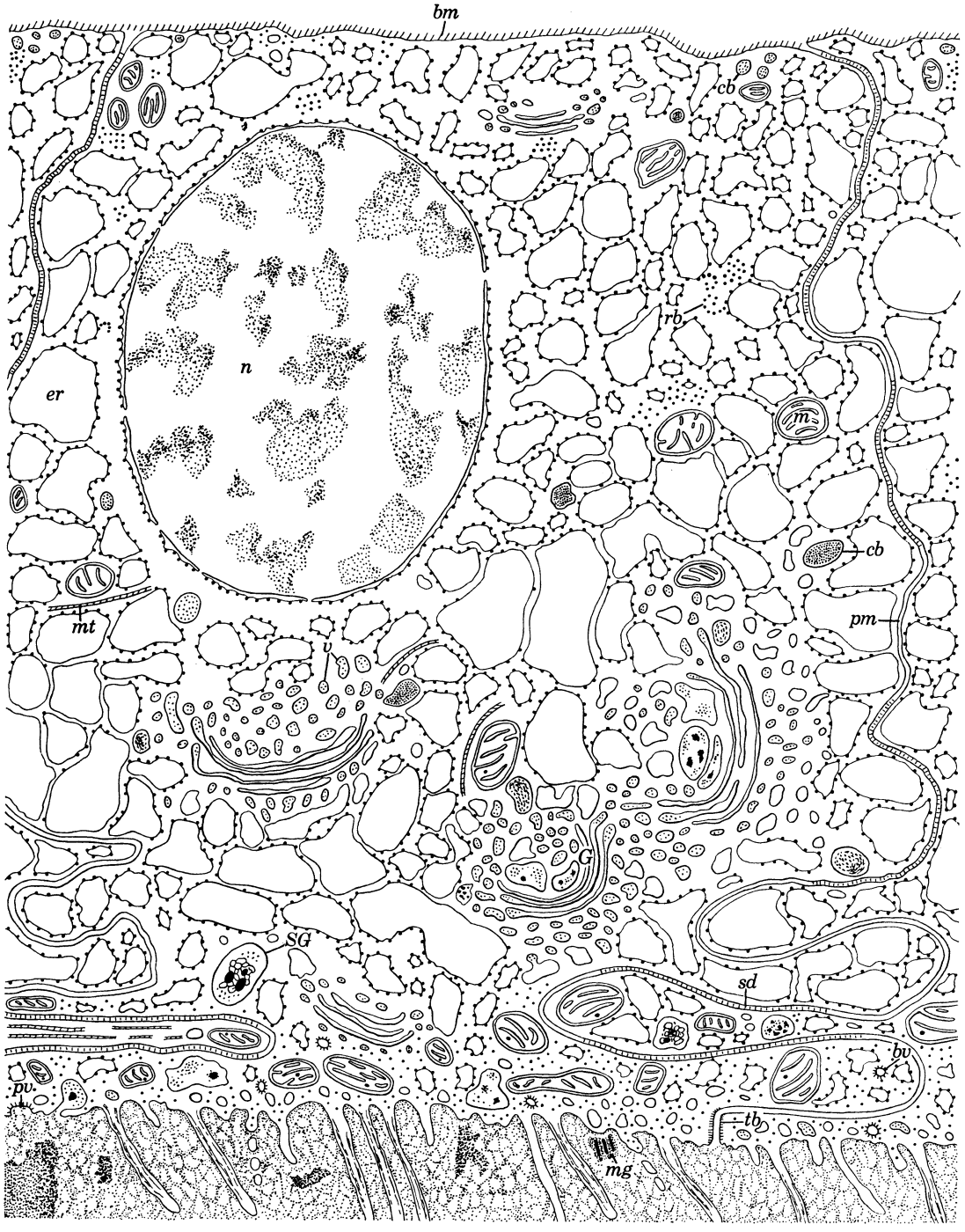


FIGURE 2. Drawing of a cell of gland 1 summarizing its cellular substructure.

Septate desmosomes between adjacent cells seem to be of great importance in ensuring simultaneity of secretory function in glands arranged in the form of a thin epithelium, this is apparently so by reason of their high permeability to ions and to fairly large molecules. This problem has been studied in an elegant series of experiments by Kanno & Loewenstein (1964, 1966) and Loewenstein & Kanno (1964) using the larval salivary glands of *Drosophila*. By driving a current of ions (K^+, Na^+, Cl^-) from the interior of one cell to the interior of the adjacent cell, and observing the amount of leakage of the current through different regions of the cell membranes, they found that the electrical resistance across the 'basal' plasmalemma and along the intercellular space is high, while the resistance across the lateral plasma membranes (which have septate desmosomes) is extremely low and is about equal to that of the cytoplasm alone (Loewenstein & Kanno 1964). This evidence indicated to them that there was no substantial diffusion barrier between adjoining cells in the salivary gland epithelium. The conclusion was confirmed by tracer studies using fluorescein sodium and other molecules (Kanno & Loewenstein 1964, 1966): injection of fluorescein sodium, for instance, into one cell led to the whole salivary gland becoming fluorescent within 3 to 20 min, while there was no leakage at all either into the bathing solution or into the glandular lumen. Loewenstein & Kanno (1964) implicated the septate junction as being especially involved in the low resistance to diffusion.

Histological and histochemical observations reported in a previous paper (Odhiambo 1969*a*) have shown that intense secretory production in the locust ARGs is largely confined to the distal half of the glands, while the proximal half seems to be concerned principally with storage. Thus, although the prevalence of septate desmosomes along the intercellular spaces of these glands may imply more or less free intercommunication between adjoining cells, there seems to be another factor or factors that impose a gradient in the secretory processes of the glandular epithelium.

Types of accessory glands and their fine structure

Certain common fine-structural features of the locust ARGs—the muscular sheath, microtubular structures, and junctional complexes in the lateral plasma membrane—have already been described (Odhiambo 1969*b*, *c*). In the following pages, the ultrastructure of the rest of the glandular epithelium will be described in some detail. The nomenclature of the nine gland types in the ARG complex is that recently established by Odhiambo (1969*a*).

Gland 1

The whole glandular cytoplasm is characterized by the enormous development of the rough-surfaced endoplasmic reticulum (figure 2). In this gland type, the endoplasmic reticulum (ER) appears in the form of swollen vesicles, 0.6 μm or more in diameter, practically crowding out all other cytoplasmic organelles (figure 3, plate 2; figure 7, plate 3). A number of more or less elongate mitochondria are found in the niches between adjacent ER vesicles (figure 3); microtubules (figure 4, plate 2; figure 6, plate 3) and lysosome-like bodies (figure 3) are also found in such situations. Much more prominent than these latter cell organelles are the Golgi elements. The latter occur as stacks of saccules, with peripherally distributed small smooth-surfaced vesicles (figure 3). Centrally located in the Golgi apparatus is the so-called *condensing vacuole* (figure 3) of Caro & Palade (1964). The significance of the condensing vacuoles in the secretory process has been suggested by the work of Caro & Palade (1964). In a combined autoradiographic and electron-microscopic investigation of protein synthesis and fate of secretory granules

in the guinea-pig pancreatic exocrine cell, they have concluded that: (*a*) exportable proteins are synthesized on the membrane-attached ribosomes; (*b*) these products are then transported in some way by the ER to the Golgi apparatus, perhaps by way of the small, smooth vesicles found at the periphery of the apparatus; (*c*) the secretory products are sequestered into membrane-bound smooth vesicles; (*d*) their secretory products become progressively concentrated, possibly by the withdrawal of water, within the large vacuoles (the so-called condensing vacuoles) centrally located in the Golgi complex; and thus (*e*) zymogen granules are eventually formed.

Evidence for the participation of the Golgi apparatus in the synthesis of mucopolysaccharides (or glycoproteins) has come from the work of Peterson & Leblond (1964), amongst others. After systemic injection into rats of tritiated glucose—which is known to be a precursor of polysaccharide synthesis—and sodium sulphate-^{35}S, they found that both tracers simultaneously labelled only mucus-producing cells (e.g. goblet cells of the colon, ileum, and duodenum submucosal mucous gland cells; and surface mucous cells of the stomach). The label was identified over the Golgi region within 5 to 15 min of the injection, and persisted there for about 1 h; later on the label appeared over the secretory granules, which contained mucus. Peterson & Leblond hypothesized that the protein moiety was first synthesized on the ribosomes attached to the ER, the protein products then migrated to the Golgi zone, where monosaccharide residues were actually linked to the protein moiety to produce the glycoprotein molecules. Thus the linking of protein to carbohydrate may be the essential step in the so-called sequestration or packaging of secretory products in the Golgi region. The uptake of the sulphate label at the Golgi zone was thought by these workers as an indication that sulphation occurred here, and that it probably took place after polysaccharide synthesis.

There is now a body of ideas as to the manner in which glycoproteins may be produced by the combined machinery of the rough ER and the Golgi complex. What is not so clear in this scheme is the part played by the small peripheral vesicles of the Golgi apparatus. This matter will be examined in more detail in connexion with our discussion of the ultrastructure of 'homogeneous' glands (see below). Suffice it to say here that the small vesicles are thought to

Description of plate 2 (gland 1)

Figure 3. General survey of the basal cytoplasmic region. Particular note should be taken of the two types of secretory vesicles, one containing a sparse, fibrous material (SG_1), the other containing a more compactly arranged fibrous substance with some electron-dense granules (SG_2). × 32500.

Figure 4. Golgi units (*G*) are quite common, even in the perinuclear region. In the environs of the Golgi complex are frequently found cytoplasmic bodies (*cb*) and two kinds of secretory vesicles (SG_1 and SG_2). × 24000.

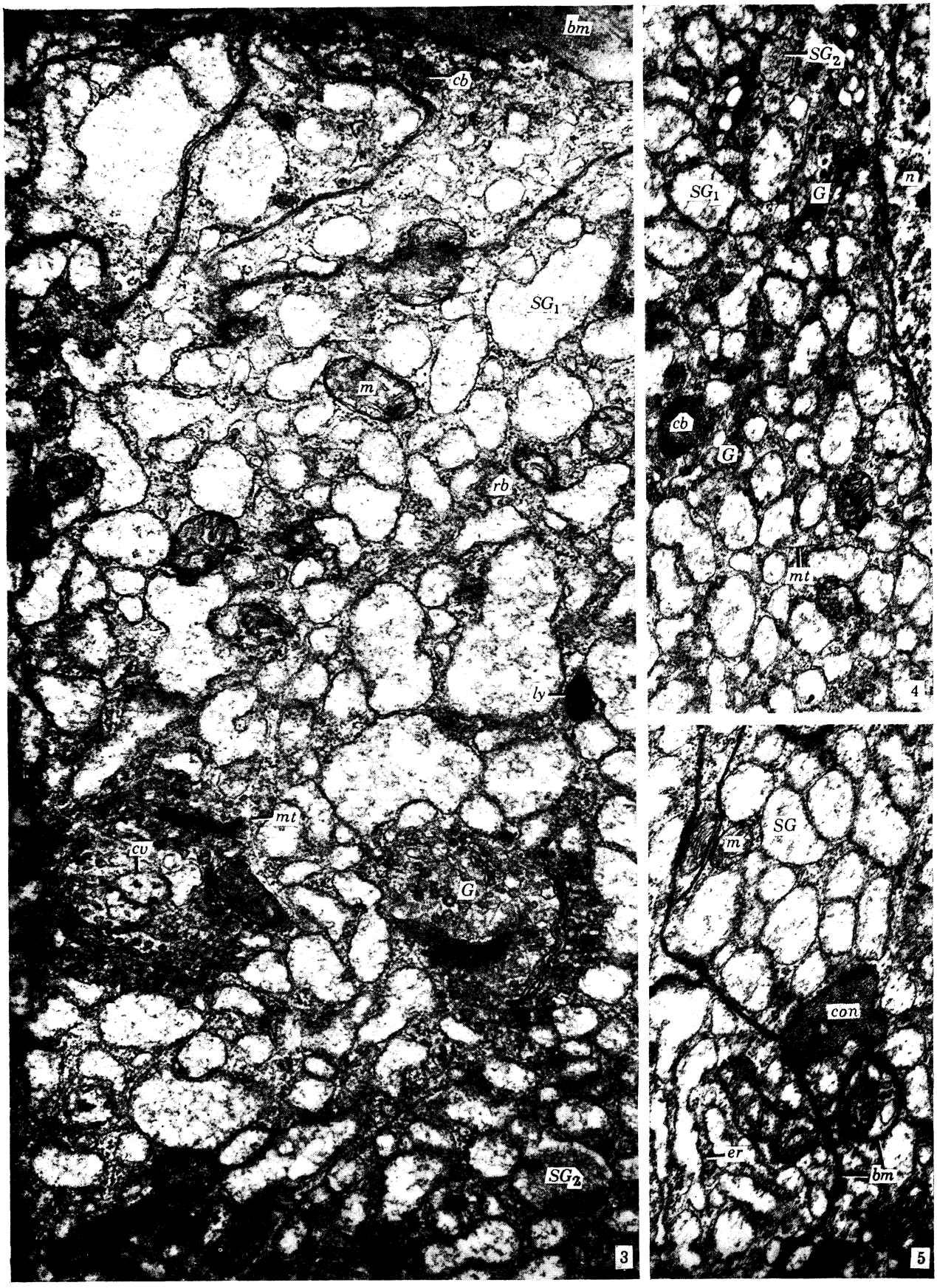
Figure 5. The plasmalemma in the lateral cell region may be quite convoluted and may sometimes also carry connective tissue material deep into the cell (*con*). × 32500.

Description of plate 3 (gland 1)

Figure 6. The apical cytoplasmic region showing the swollen secretory vesicles of two kinds (SG_1 and SG_2), pinocytotic vesicles being formed at the luminal plasmalemma (*pv*), and some coated vesicles (*bv*). The gland lumen contains an electron-dense secretion (*mg*) that resembles the material contained in one kind of secretory vesicle (SG_2). × 32500.

Figure 7. Recently extruded electron-dense secretion at various stages of polymerization and crystallization (mg_1, mg_2, mg_3). Also shown is a coated vesicle (*bv*) in the immediate neighbourhood of a Golgi apparatus (*G*) in the apical cytoplasmic region. × 52500.

Figure 8. The apical cytoplasmic region exhibiting two types of small vesicles in the terminal-web region: numerous small smooth vesicles (*v*) and a few coated vesicles (*bv*). The former vesicles, or vesicles resembling them closely, may sometimes be seen fusing with secretory vesicles (*arrow*). × 52000.



FIGURES 3 to 5. For description see facing page.

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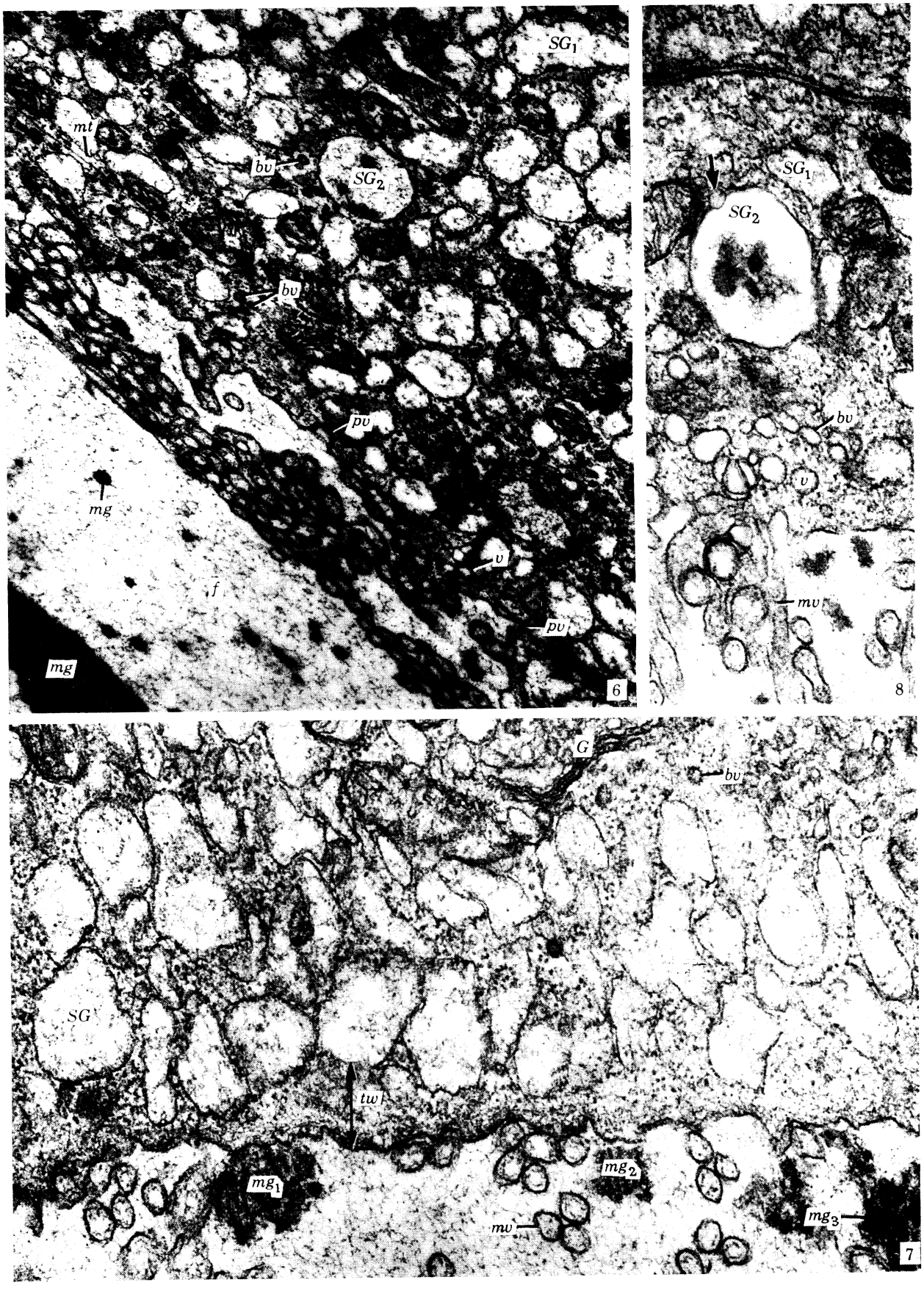


FIGURES 6 to 8. For description see p. 90.

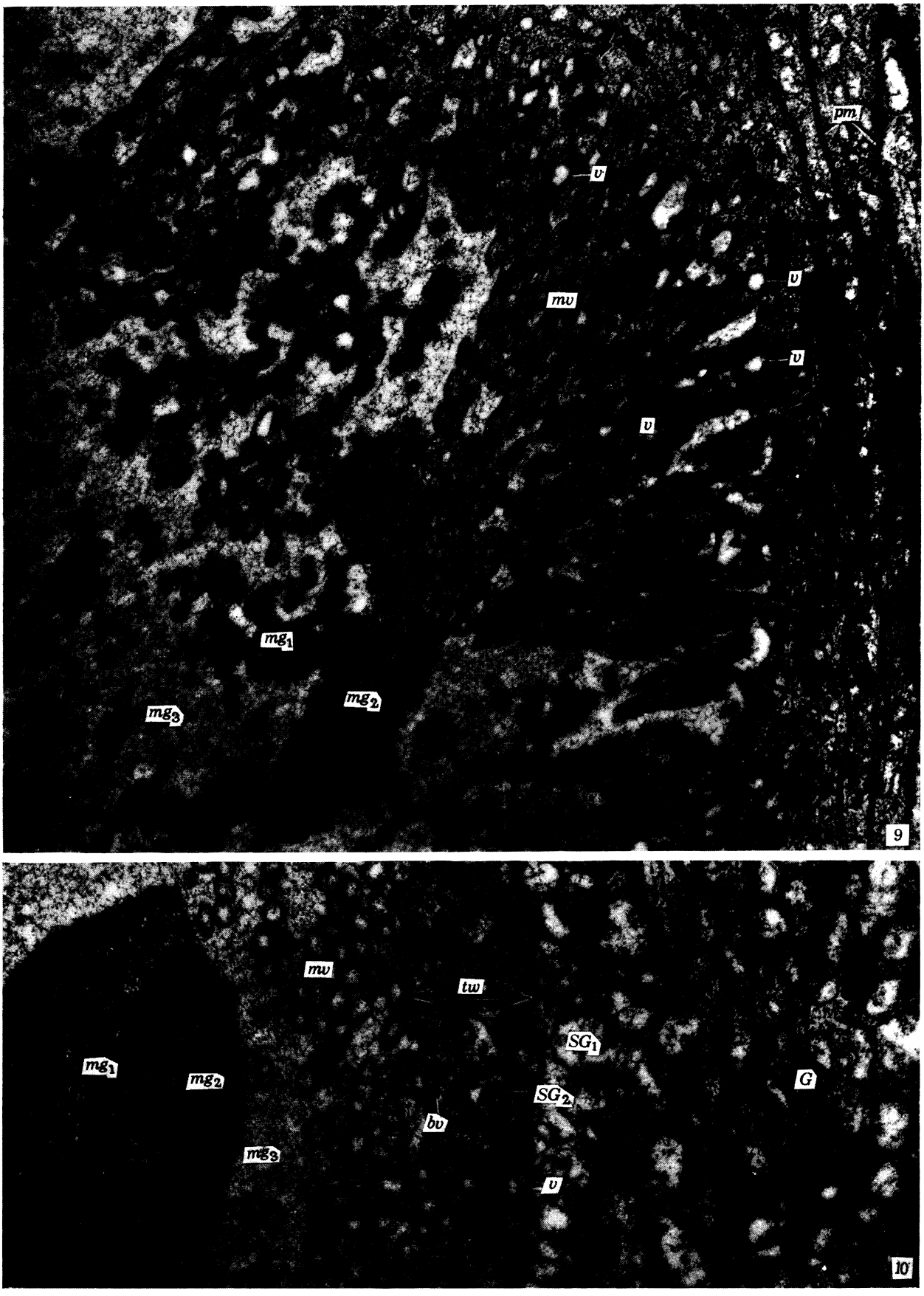
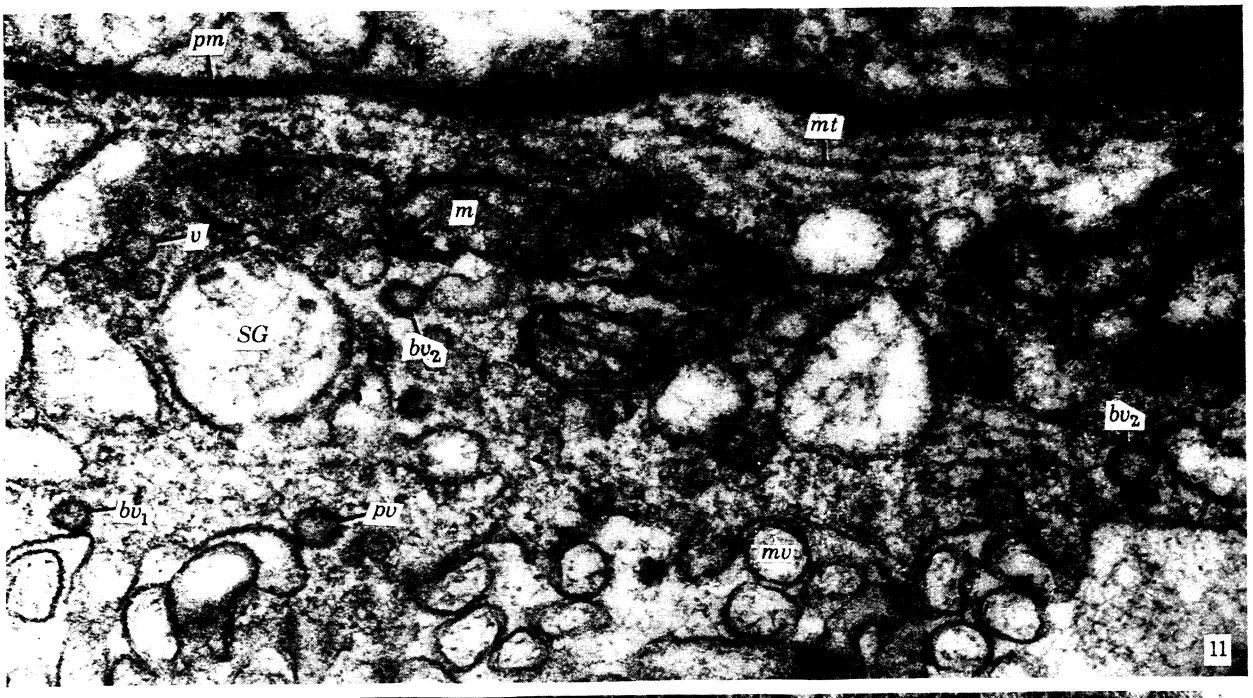


FIGURE 9. Luminal region of cytoplasm to show the microvilli (*mv*) between which secretion seems to be extruded into the lumen (*arrows*). The lateral plasmalemma (*pm*) is very convoluted here. Three types of secretory material can be recognized before its polymerization takes place (mg_1, mg_2 and mg_3). × 32500.

FIGURE 10. Newly polymerized secretion in the lumen, comprising a crystalline component (mg_1) and a coarsely fibrous base (mg_2). × 39000.



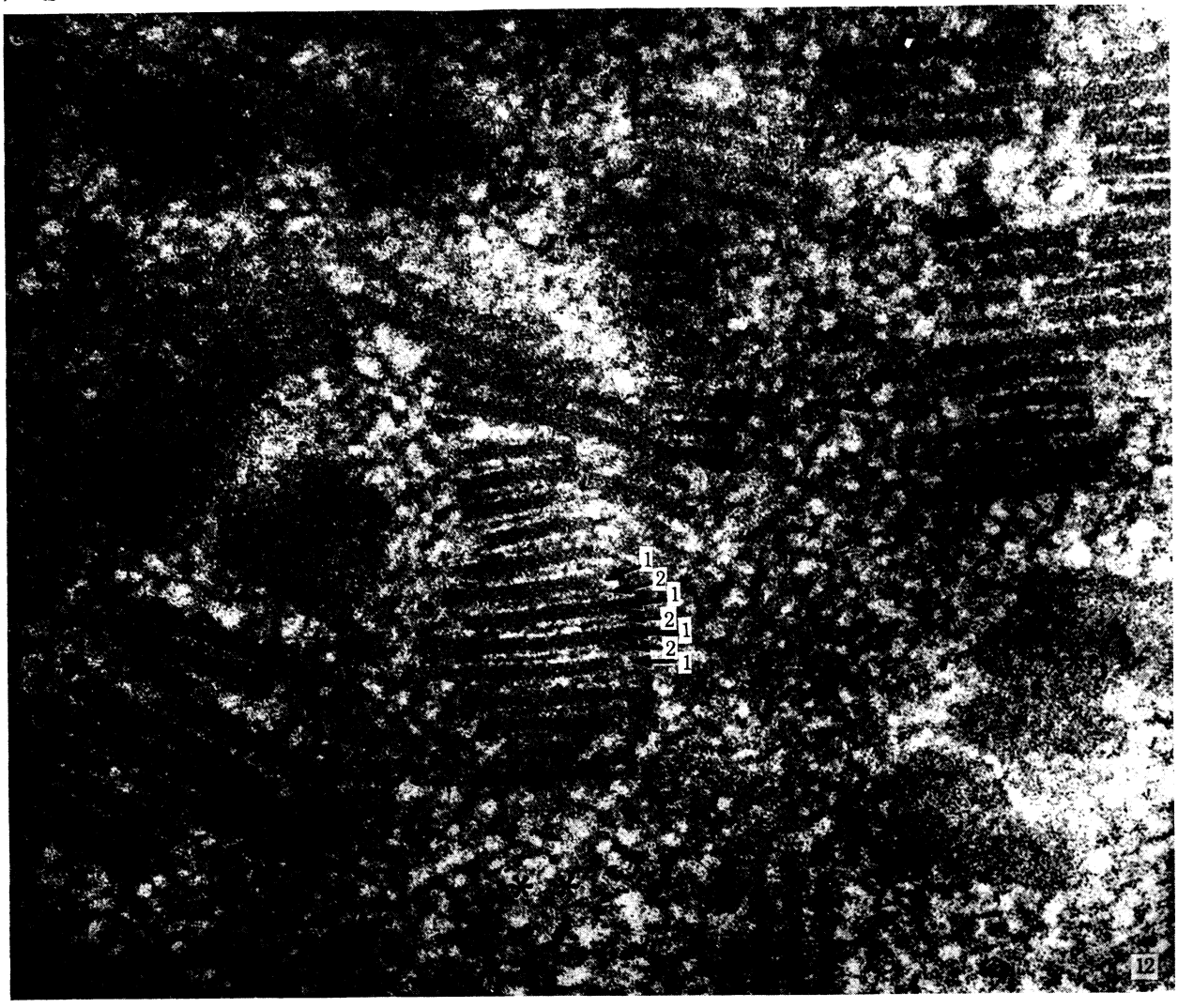


FIGURE 11. Caveolae (*pv*) formed at the luminal plasmalemma transform into coated vesicles (bv_1 and bv_2) found in the apical cytoplasmic region. Non-coated vesicles (*v*) of similar size also occur in this region. Also shown are microvilli (*mv*) in transverse section with filamentous structures inside them. × 77500.

FIGURE 12. Thick (*1*) and thin (*2*) fibrils of a crystalline granule embedded in a course fibrous material (*two stars*). Also shown are oblique end-views of crystalline structures (*one star*). × 137500.

function as 'shuttle carriers' between the rough ER, the smooth-surfaced portion of the ER adjoining the Golgi complex, and the condensing vacuoles. Associated with these vesicles are the so-called *coated vesicles*, which arise from the luminal plasmalemma and which seem to be used for sampling luminal contents in connexion with the progress of the secretory process (figures 3 and 6; figure 10, plate 4; figure 11, plate 5). More information about this will, also, be given later.

Enormous secretory vesicles are usually found in the mature gland (figure 5, plate 2; figure 7, plate 3). There are apparently two types of these secretory vacuoles: the first type contains a finely divided, loosely dispersed fibrous substance; while the second type contains dark electron-dense granules in addition to a more or less hexagonally organized, fine, closely knit fibrous material (figures 3 and 4, plate 2; figures 6 and 8, plate 3; figure 10, plate 4). In the lumen are also found masses of electron-dense granules apparently imbedded in a closely knit fibrous material (figure 6; figure 13, plate 6). The lumen does not, apparently, contain the rather amorphous loosely dispersed fibrous material located in the first type of secretory vesicles. It might well be that this material has still to undergo some further process of elaboration before attaining the more crystalline condition exemplified by the contents of the second type of secretory vesicles. If this is so then the further process of elaboration may take place in the condensing vacuoles of the Golgi complex (figure 3), from where secretory vesicles of the second type may move outward towards the glandular lumen (figures 6, 8 and 10). Certainly, condensing vacuoles have contents of a similar nature to that of the secretory vesicles of the second type (figure 3). These vesicles empty their contents through the luminal plasmalemma, in between the microvilli (figure 9, plate 4).

Gland 1 is particularized by its possession of highly crystalline, glycoprotein granules (figure 13). It appears that the highly organized structure of the granules is only achieved within the lumen. Recently extruded secretion does not immediately polymerize into the crystalline granules, but it aggregates into fairly large masses, each component apparently keeping its integrity (figure 9). Later, the two components seem to come together and produce the large crystalline masses: the electron-dense component largely forms the arrays of linear, fibrillar structures, while a more finely fibrous material forms the matrix holding the granules together (figure 10; figure 12, plate 5). The closely knit fibrous material found in secretory vesicles of the second type apparently forms the non-crystalline fraction of the luminal secretion (figures 9 and 10).

The crystalline granules exhibit a wide range of sizes, from granules as small as 0.3 μm in diameter to enormous bodies more than 6 μm in diameter. Growth of the granules seems to be accomplished by the addition of fibrous components to the edges of the mature granules and their polymerization soon thereafter. Under high magnification, the linear fibrillar bands that polymerize from the dense electron-dense component of the secretory vesicles comprise two kinds of fibrils: the large fibrils (approximately 150 Å in diameter) regularly alternating with thin fibrils (about 50 Å in diameter) with a macroperiod of 300 to 325 Å (figures 12 and 14; figure 15, plate 7; figure 17). The fibrils, especially the larger kind, appear beaded (figure 16, plate 7). In the case of the large fibrils, something like 18 to 20 longitudinal rows of beaded structures may be discerned; the latter appear to be helically arranged. In any one plane, only certain portions of the granule show these arrays of oriented fibrils; such bundles vary somewhat in width, but the latter is generally no more than 0.1 to 0.4 μm (figure 13).

A similar fibrillar structure has been reported by Rouiller & Fauré-Fremiet (1957) in the ciliate, *Frontonia*. The fusiform trichocysts exhibit proteinaceous fibrillar structure of thick transverse bands with a periodicity of 100 to 500 Å depending on the state of extension of the

trichocyst. Thinner bands in between the larger ones have also been seen. The periodic structure derives from a homogeneous matrix, which Rouiller & Fauré-Fremiet regard to be in a metastable state.

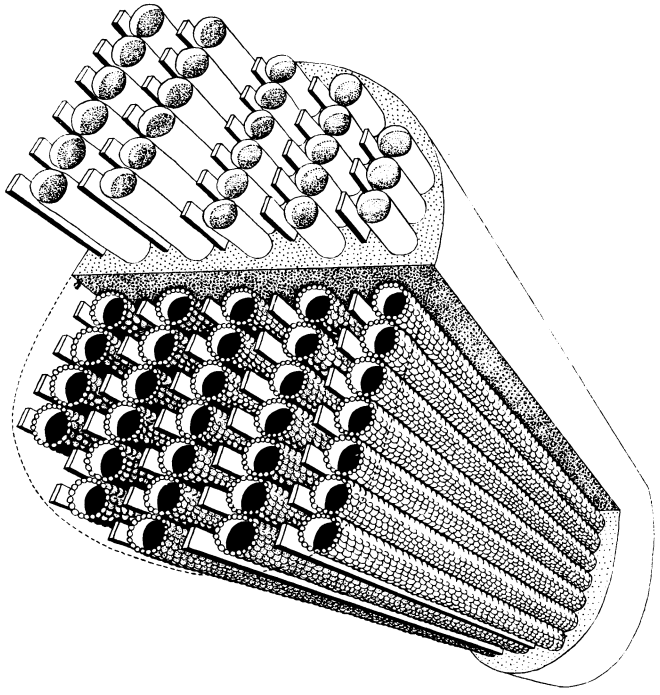


FIGURE 17. Schematic diagram of the three-dimensional arrangement of the fibrils of a crystalline granule in gland 1 secretion.

A previous histochemical study of gland 1 indicated that the large secretory granules in the lumen consisted largely of neutral mucopolysaccharide, while the secretion matrix stained for acid mucopolysaccharide (Odhiambo 1969*a*). There is neither histochemical evidence nor ultrastructural observations to suggest that the two fractions of the luminal secretion are partitioned as such within secretory vesicles in the glandular cytoplasm. The origin of these two fractions is, at the moment, not certain. However, it is thought that the ionic environment of the lumen may well set off the polymerization process within the gland lumen, resulting in the formation of proteinaceous crystals. In an analogous circumstance, collagen molecules are produced in a monomeric form but may be induced to polymerize into banded fibrillar structures by such diverse agents as salt solutions, adenosine triphosphate, and acid mucopolysaccharide (Gross, Lapière & Tanzer 1963).

Gland 2

The rough ER is extensively developed (figure 18; figure 19, plate 8). At the basal cytoplasmic region and near the Golgi apparatus, the ER tends to be in the form of more or less flattened cisternae, but in the rest of the cytoplasm the latter are enormously swollen (figure 19; figure 22, plate 10; figure 24, plate 11). These large vesicles contain a finely divided or fibrous material not unlike the finely fibrous substance found within the lumen of the gland itself (figure 24; figure 25, plate 12).

There is a large quantity of smooth ER in the form of small vesicles. The latter are concentrated in two major areas—in the apical cytoplasmic region, particularly in the terminal-web

FIGURE 13. Fibrils of a large crystalline granule seen in transverse section (*1*). Also shown are crystalline fibrils shown in longitudinal section (*2*), the amorphous material within the crystalline zone (*3*), and the coarsely fibrous matrix (*4*). The secretion in the lumen also consists of small, electron-dense granules (*mg*) and minutely fibrous bulk secretory material (*f*). × 32500.

FIGURE 14. High-power micrograph of crystalline fibrils in transverse section. The thick fibrils appear hollow. × 65000.

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FIGURE 15. Crystalline granule with thick (*1*) and thin (*2*) fibrils. The ends of the thick fibrils sometimes tend to fray (*arrow*), and show beading. × 107500.

FIGURE 16. Thick fibrils (*arrows*) of a crystalline granule at high magnification showing apparent beading. × 217500.

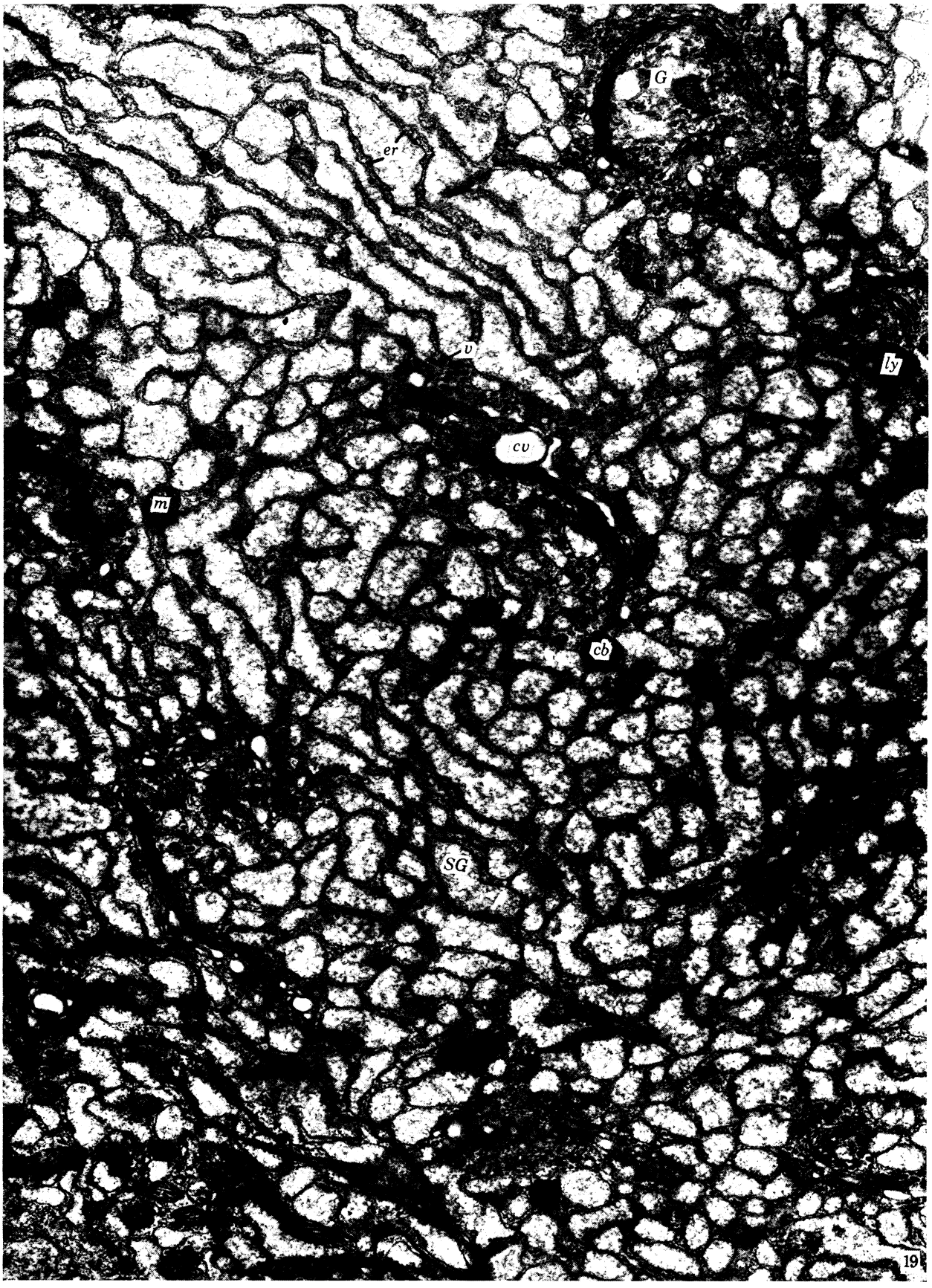

FIGURE 19. The cytoplasm is dominated by swollen cisternae of the rough ER (*er*), secretory vesicles (*SG*), and enormous Golgi complexes (*G*) having large condensing vacuoles (*cv*). These almost crowd out mitochondria (*m*). A number of cytoplasmic bodies (*cb*) are found near the Golgi elements. × 24000.

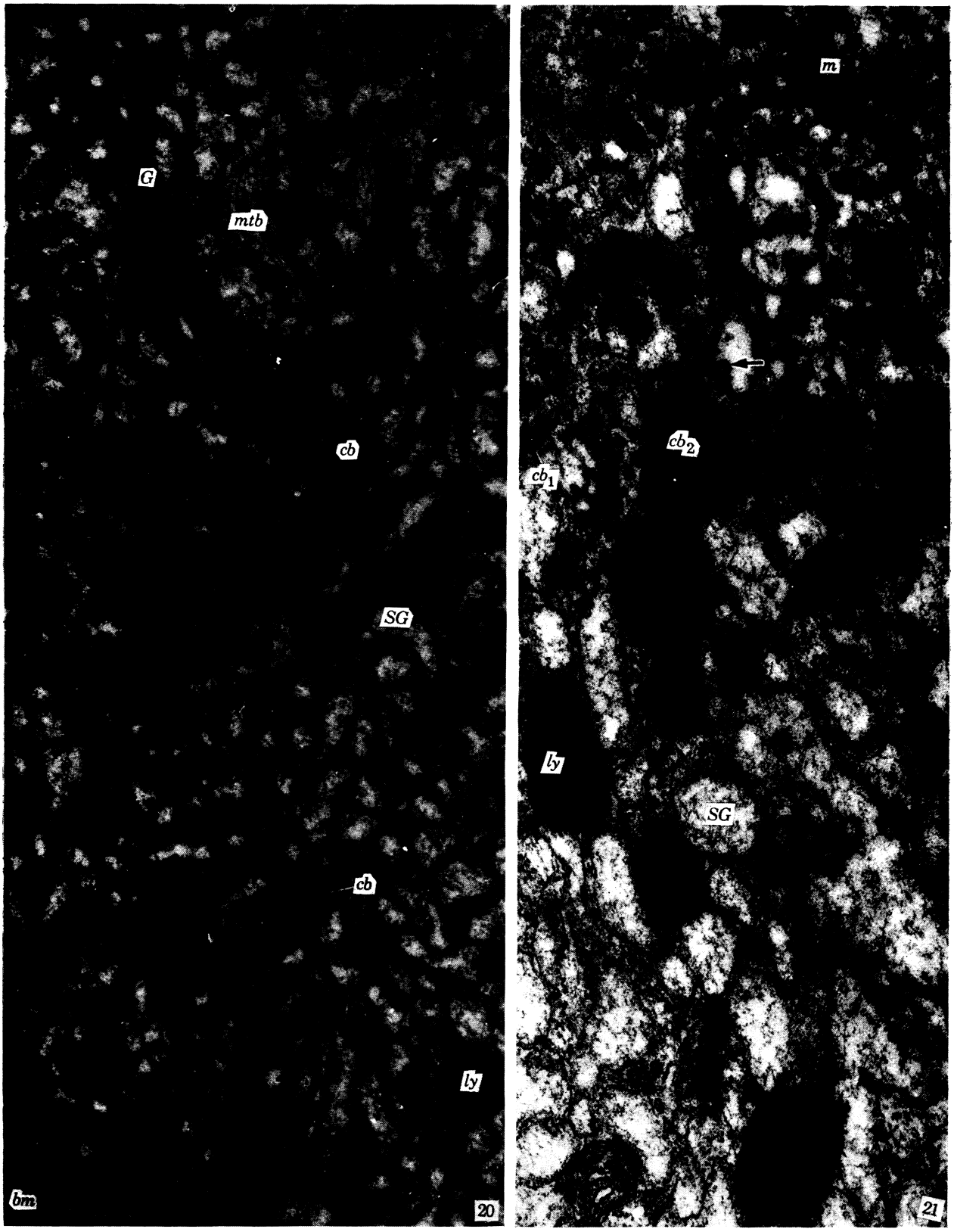

FIGURE 20. Basal cytoplasmic region contains numerous cytoplasmic bodies (*cb*) and some lysosome-like bodies (*ly*). Golgi units (*G*) are small. × 22500.

FIGURE 21. Cytoplasmic bodies (cb_2) seem to grow by fusing with smaller like bodies (cb_1). Some large vesicles of unknown nature also seem to engulf smaller vesicles (*arrow*). × 41000.

area (figure 23, plate 10; figures 24 and 25), and as a constellation of numerous small vesicles in the environs of the Golgi apparatus (figures 19 and 22). In the latter case, the small vesicles are bristly—the 'coated vesicles' of Bonnett & Newcomb (1966), Dumont & Anderson (1967) and others—and they seem to be closely associated with the smooth saccules of the Golgi apparatus. Indeed, there is some evidence that the coated vesicles may be pinched off from the smooth

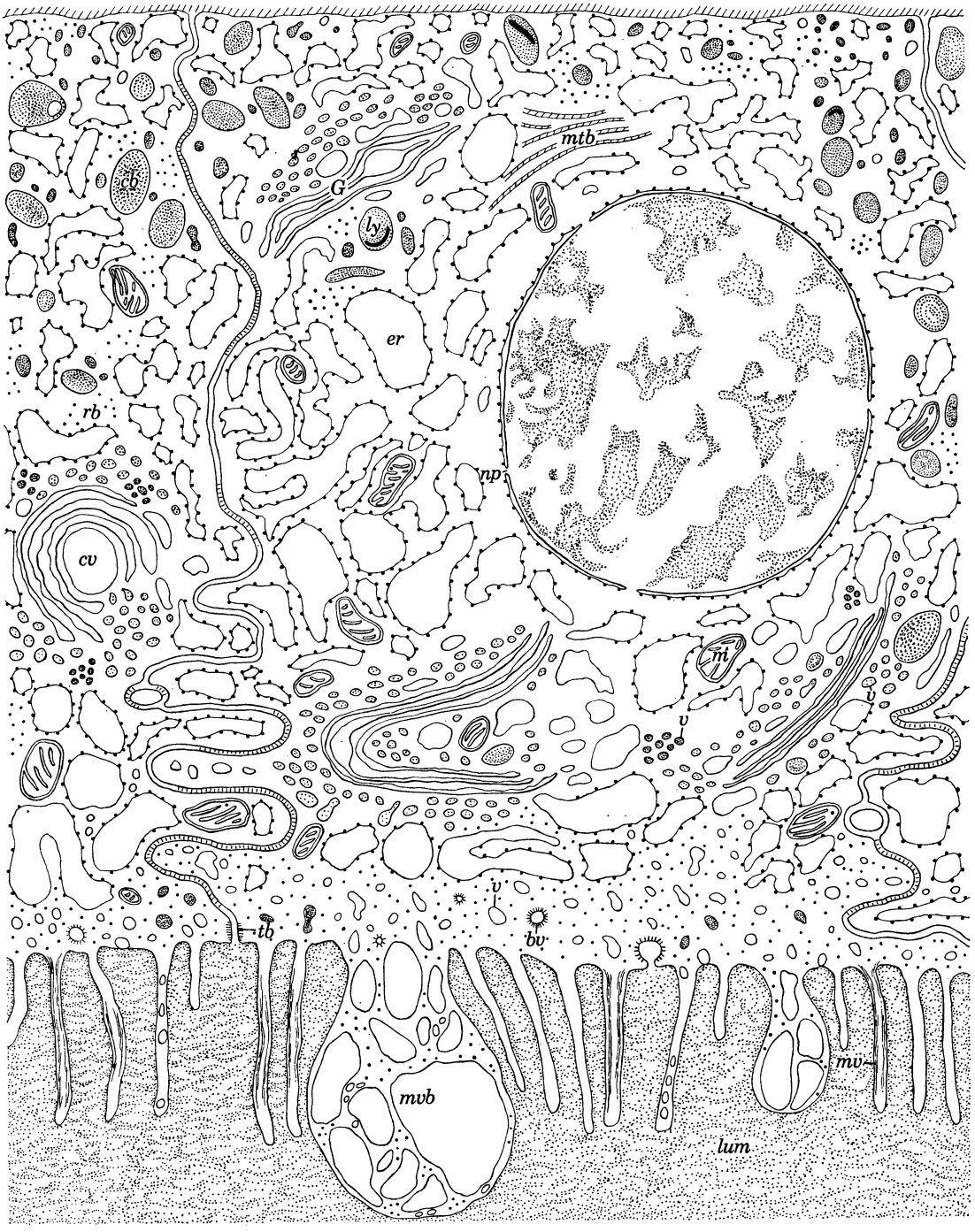

FIGURE 18. Diagram to summarize the substructure of a gland 2 cell. Note particularly the multivesicular body (*mvb*) among ordinary microvilli (*mv*).

saccules (figure 22). It is possible that these vesicles are used as vehicles for the interchange of materials between the Golgi apparatus and the rough ER.

The terminal-web region is much more distinctly delimited in this gland type than in many other ARGs (figure 24). The region, which is morphologically defined by the terminal bar, extends for a depth of approximately 1.5 μm. Apart from free ribosomes, pinosomes, and occasional microtubules, the most conspicuous organelles in this region are the small, smooth vesicles already referred to. Some of these smooth vesicles seem to have an electron-lucent content, while others contain a somewhat electron-dense non-granular substance; still others are not smooth, but are of the coated-vesicle type (figures 23 to 25). In regard to the latter, it is apparent that the coated vesicles in the apical cytoplasmic region are formed from the luminal plasmalemma (figure 24). What role these various types of small, smooth vesicles found in the terminal-web region play cannot be stated with certainty. The coated vesicles are also found in the apical cytoplasmic region outside the terminal-web area (figures 24 and 25). It is suggested that these vesicles may be used by the glandular epithelium to sample the luminal content of the gland, as was proposed when discussing gland 1.

The other two types of small, smooth vesicles are seemingly intimately associated with the macro-apocrine type of extrusion process—a secretion process peculiar to gland 2 among the ARGs (figure 25). Elaborated secretion is extruded into the gland lumen by a curious development of 'multivesicular bodies' at the luminal plasmalemma, in between the microvilli (figure 25). These bodies may reach enormous proportions; each contains several large secretory vesicles and a number of the small smooth vesicles also found in the terminal-web region (figures 23 and 25). The multivesicular bodies often rupture, leading to the release into the lumen of the secretory vesicles; perhaps these vesicles then lyse and thus release their finely fibrous contents. The physiological mechanisms determining the formation of the multivesicular bodies and their subsequent lysis are not known. Analogous structures have occasionally been noted in certain vertebrate cell-types, e.g. thyroid, apocrine sweat gland, and mammary gland. Kurosumi (1961) suggests that the formation of such apical swellings of the plasma membrane may be the result of a local solation of the membrane, although he does not indicate what sort of agent would cause such solation. One possibility is that these small vesicles contain the enzymes that bring about solation, consequently the vesicles may be important in the regulation of transport and extrusion of secretory products at luminal region. In some support for this view are the observations: (1) that the small vesicles are also located within the unswollen microvilli (figures 23 to 25); (2) that they are always found in multivesicular bodies but not within all microvilli; and (3) that the small, smooth vesicles are relatively much smaller in the terminal ends of the multivesicular bodies as though the vesicles have gradually been depleted of their contents as they moved through the multivesicular body (figure 25).

The possible role suggested for the small, smooth vesicles (excluding the coated vesicles) does not exhaust other possibilities. They may be concerned in the transport of water from the lumen into the cytoplasm (Kurosumi 1961); or they may be involved in the bulk movement of secretory product from the apical cytoplasmic region into the lumen (Satir & Stuart 1965). One other problem still to be solved is the origin of these small vesicles. At present there is no structural evidence to suggest the mode and locale of their origin, except the fact of their preponderance in the terminal-web region.

The basal cytoplasmic region contains many so-called 'cytoplasmic bodies' in various size ranges (figure 20, plate 9). These organelles apparently move from this region and are

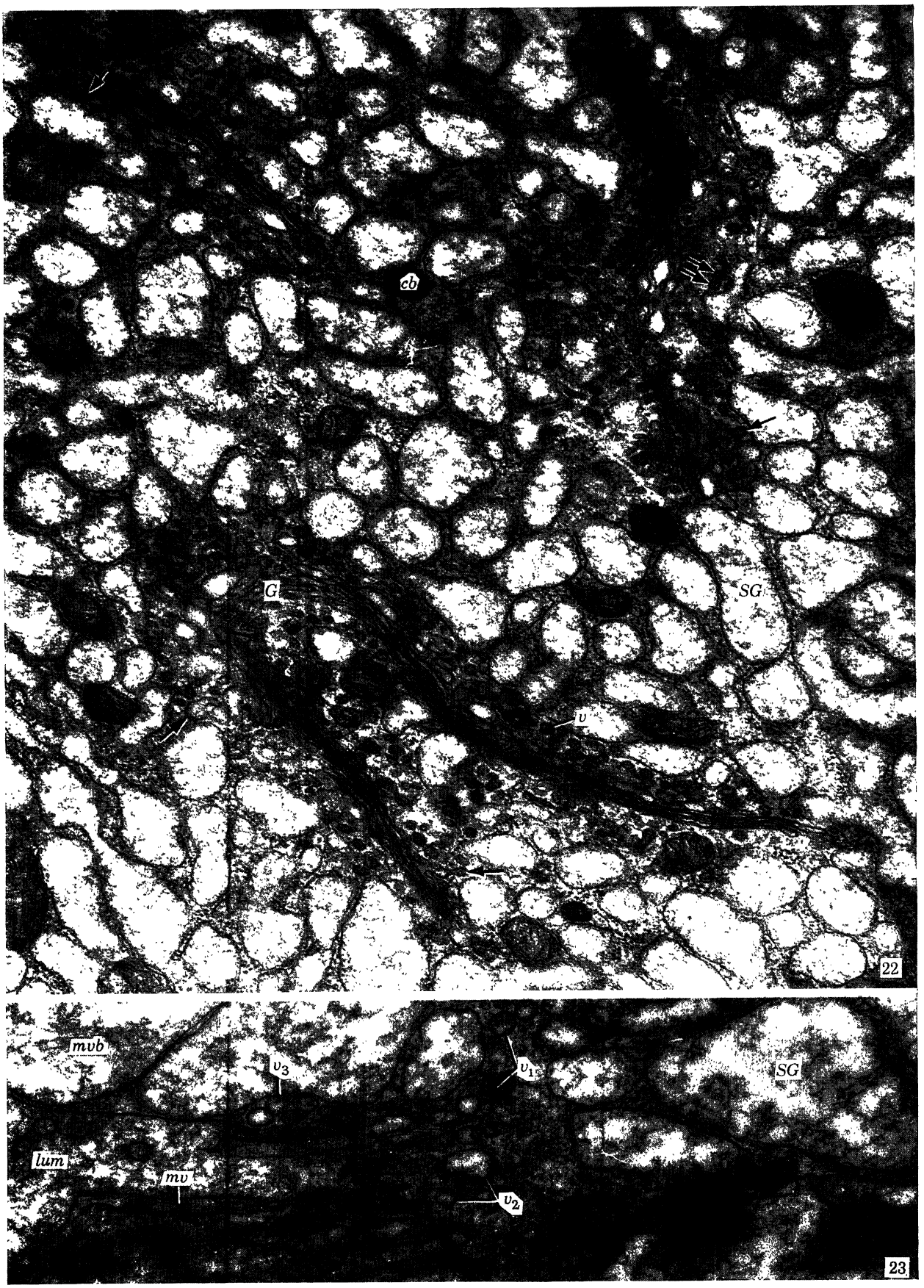

FIGURE 22. Golgi complex (*G*) has numerous peripheral vesicles with an electron-dense content (*v*), which seem to arise or fuse with either the Golgi saccules or cisternae of the ER (*arrows*). × 44000.

FIGURE 23. Luminal cytoplasmic region showing a secretory vesicle having a minutely divided secretion (*SG*), and in the terminal-web area small, smooth vesicles of two types: those having an electron-lucent content (v_1) and those having a fairly electron-dense content (v_2). Some of these vesicles are also found within microvilli and multivesicular bodies (v_3). × 41000.

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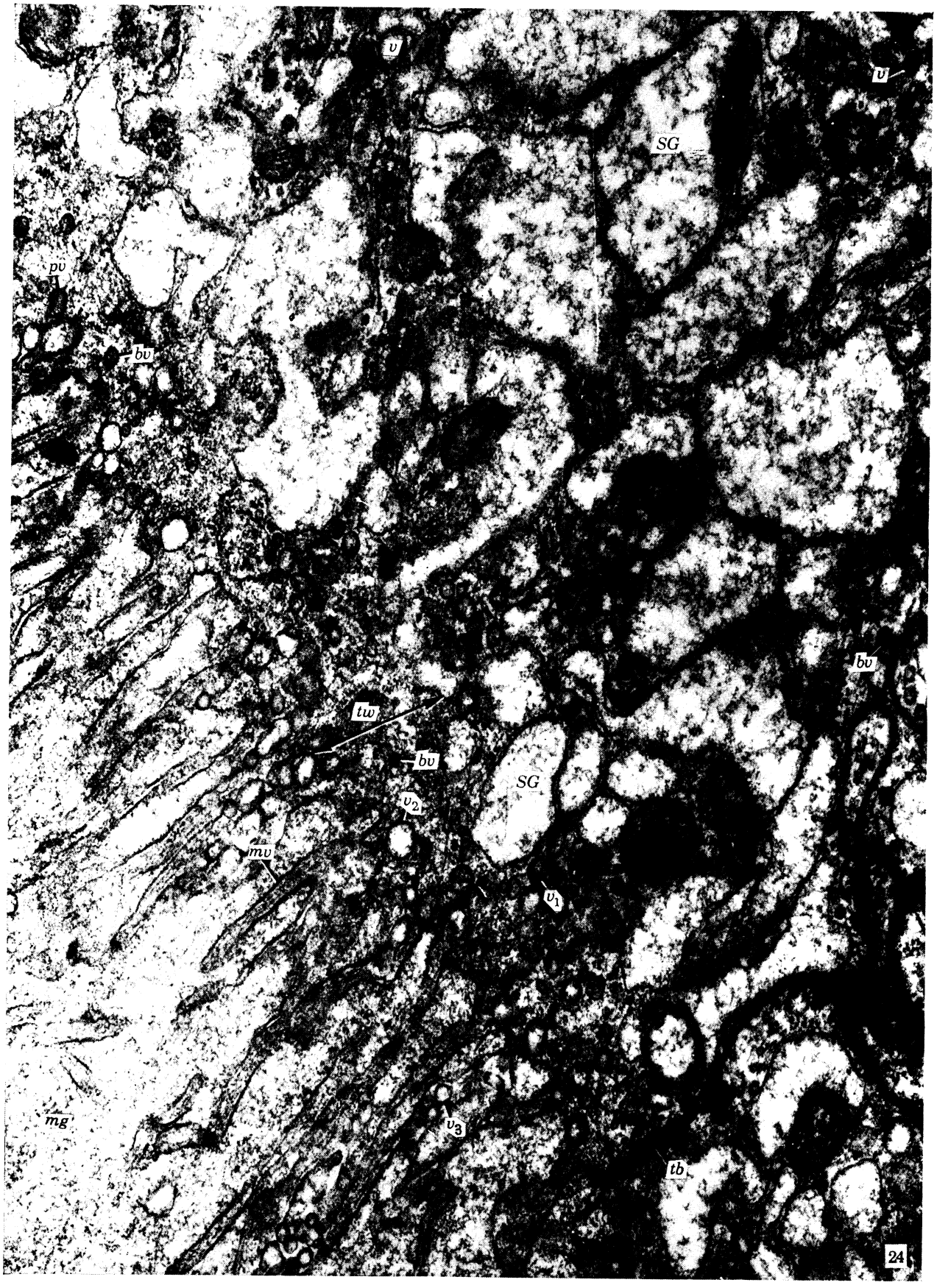


FIGURE 24. The microvilli have a fibrillar core (*mv*). The terminal-web region (*tw*) is well demarcated: it contains a minutely granular matrix in which are found small vesicles (v_1) with a somewhat dense content, and rather larger vesicles (v_2) that are more transparent. Some of the small vesicles (v_3) extend into the microvilli, and there are also a considerable number of small vesicles (*v*) in other parts of the apical cytoplasmic region. Pinosomes frequently form from the luminal plasmalemma (*pv*). × 41000.

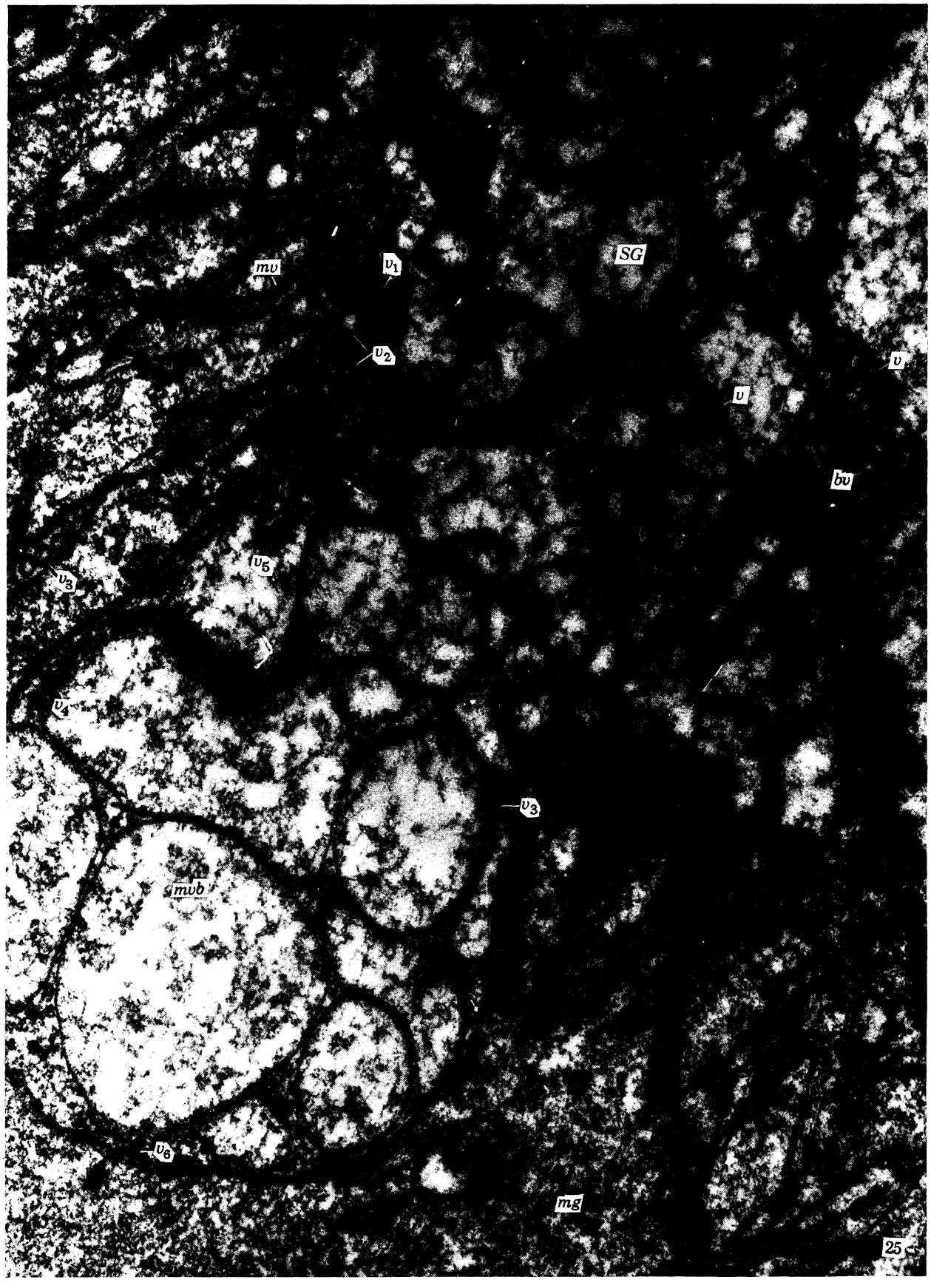
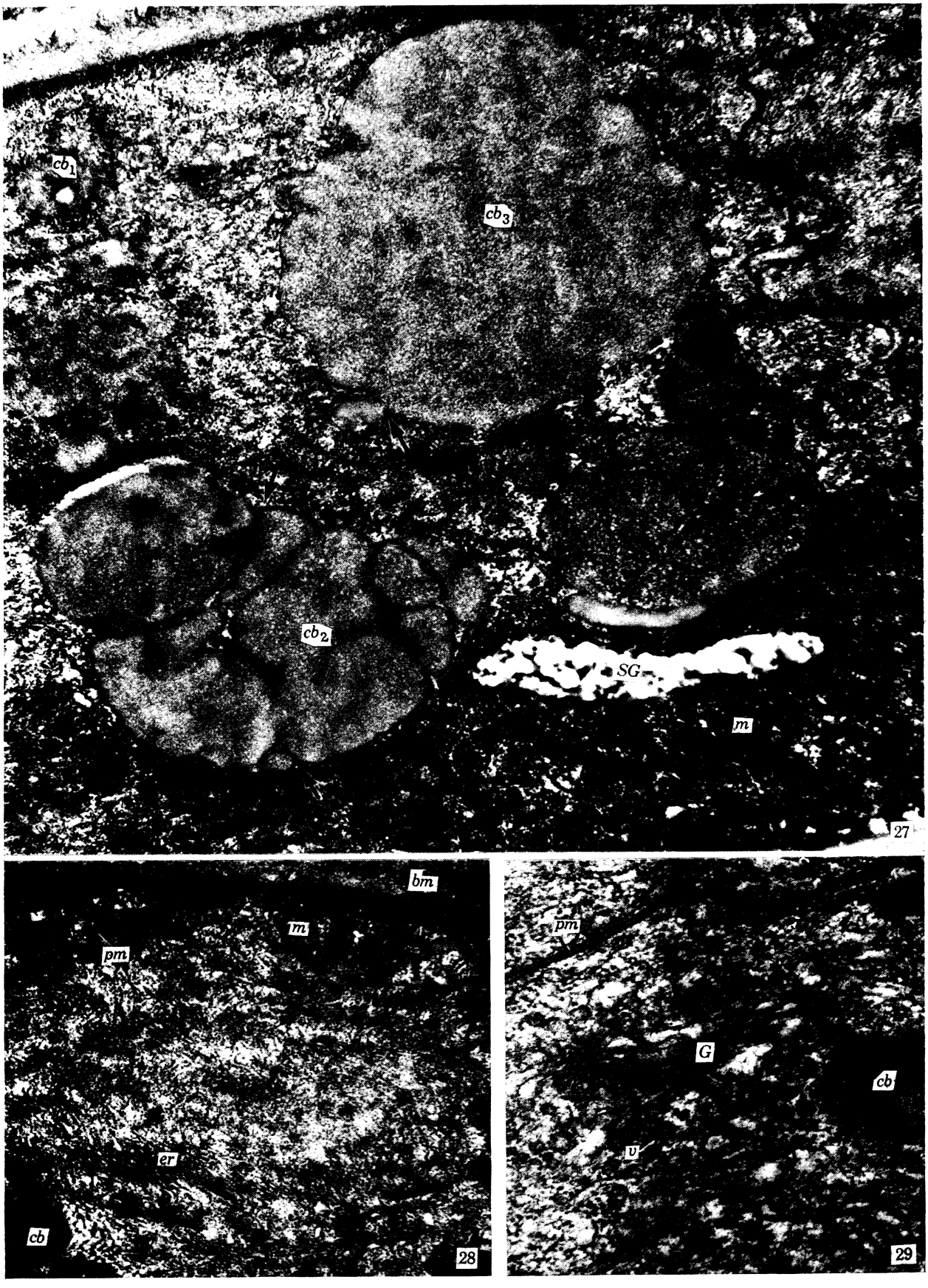


FIGURE 25. An enormous multivesicular body (*mvb*) may form in between other microvilli. Small vesicles (v_3) resembling those found in the terminal-web region (v_1 and v_2) may be located within the microvilli; some may also be found within the multivesicular body (v_4) and they seem to result from an inflow of such organelles from the terminal-web region (v_5). The mature secretion is a finely divided fibrous substance (*mg*). $\times$ 41000.



FIGURES 27 to 29. For description see facing page.

subsequently located in the immediate neighbourhood of the Golgi apparatus (figure 20). It is possible that these bodies are involved in the elaboration process in the Golgi region, as will be discussed in some detail when considering gland 11. Suffice it to state here that the cytoplasmic bodies may well contain precursor materials which may subsequently be processed into the final fibrous mucopolysaccharide secretion of gland 2 in the Golgi complex.

Somewhat resembling the cytoplasmic bodies are the lysosome-like bodies (figure 21, plate 9). These are distinguished by their possession of other cell organelles or other internal structure, whereas the cytoplasmic bodies contain a homogeneous substance. No detailed histochemical observations have been made of these two types of bodies in this study.

Gland 3 (*or gland* 5)

The ultrastructural study of this gland type has proved a most difficult problem because of the impossibility of effecting good fixation and embedding of the material. Indeed, even detailed histological observations of this gland type were hampered by this problem (Odhiambo 1969*a*). Histochemical tests showed that the glandular cytoplasm is acidic and the gland's secretion is an acidic lipoprotein complex (Odhiambo 1969*a*). It is well known that the usual fixatives (e.g. formalin, acrolein, controlled chromation, Bouin's fixative, glutaraldehyde, permanganate, and osmium tetroxide) and embedding materials (e.g. Epon, methacrylate, Araldite, Durcupan, Vestopal, ACM and Maraglas) do not preserve and retain most lipids (Casley-Smith 1967). In fact, currently, the only good procedure for recognizing lipids in an electron-micrograph is by their absence. In the case of gland 3 of the ARG complex, the glandular epithelium is very dense, obscuring most cytoplasmic detail, and the secretory material is only partly observed in the gland lumen (figure 30, plate 14).

In spite of these observational difficulties, it is apparent that the characteristic feature of the glandular cytoplasm of this gland type is one of extensively developed rough ER and rare Golgi elements (figure 26). The ER characteristically consists of parallel arrays of flattened cisternae (figure 28, plate 13; figure 30; figure 32, plate 15). In many micrographs (e.g. figure 27, plate 13), the distribution of this membrane system is obscured by the general density of the cytoplasmic matrix. In glands which have not reached their full secretory activity in the adult insect, the rough ER is more easily observed (e.g. figure 32). Consequently, it is reasonable to assume that the general electron-density of the ground substance of the cytoplasm may be due to secretory activity and the resulting product.

Since the final secretory product is a lipoprotein complex, the participation of the rough ER in the secretion process is expected. It is also possible that Golgi elements may be involved, but the latter are very rare in the mature gland (figure 26; figure 29, plate 13), although they are fairly widespread in the immature adult gland (unpublished observations). These observations are not surprising: in the mature locust fat body, Golgi units are both rare and small,

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Description of plate 13 (gland 3)

Figure 27. The basal cytoplasmic region contains a number of small cytoplasmic bodies (cb_1) and several large cytoplasmic bodies (cb_3) that might grow by the fusion of smaller bodies (cb_2 and arrows). The content of the secretory vesicle (*SG*) has been largely extracted during processing of the tissue. × 52000.

Figure 28. The flattened and closely parallel cisternae of the rough ER (*er*). × 39000.

Figure 29. Golgi elements (*G*) are rare and rather small in mature gland 3 cells. Cytoplasmic bodies (*cb*) are frequently located near the Golgi zone. × 57500.

although lipid globules in the fat body seem to arise initially in the Golgi apparatus during the earlier maturation stages of the tissue when Golgi elements are more obvious (Odhiambo 1967). If the progressive rarity of Golgi elements in gland 3 as it matures implies the progressive

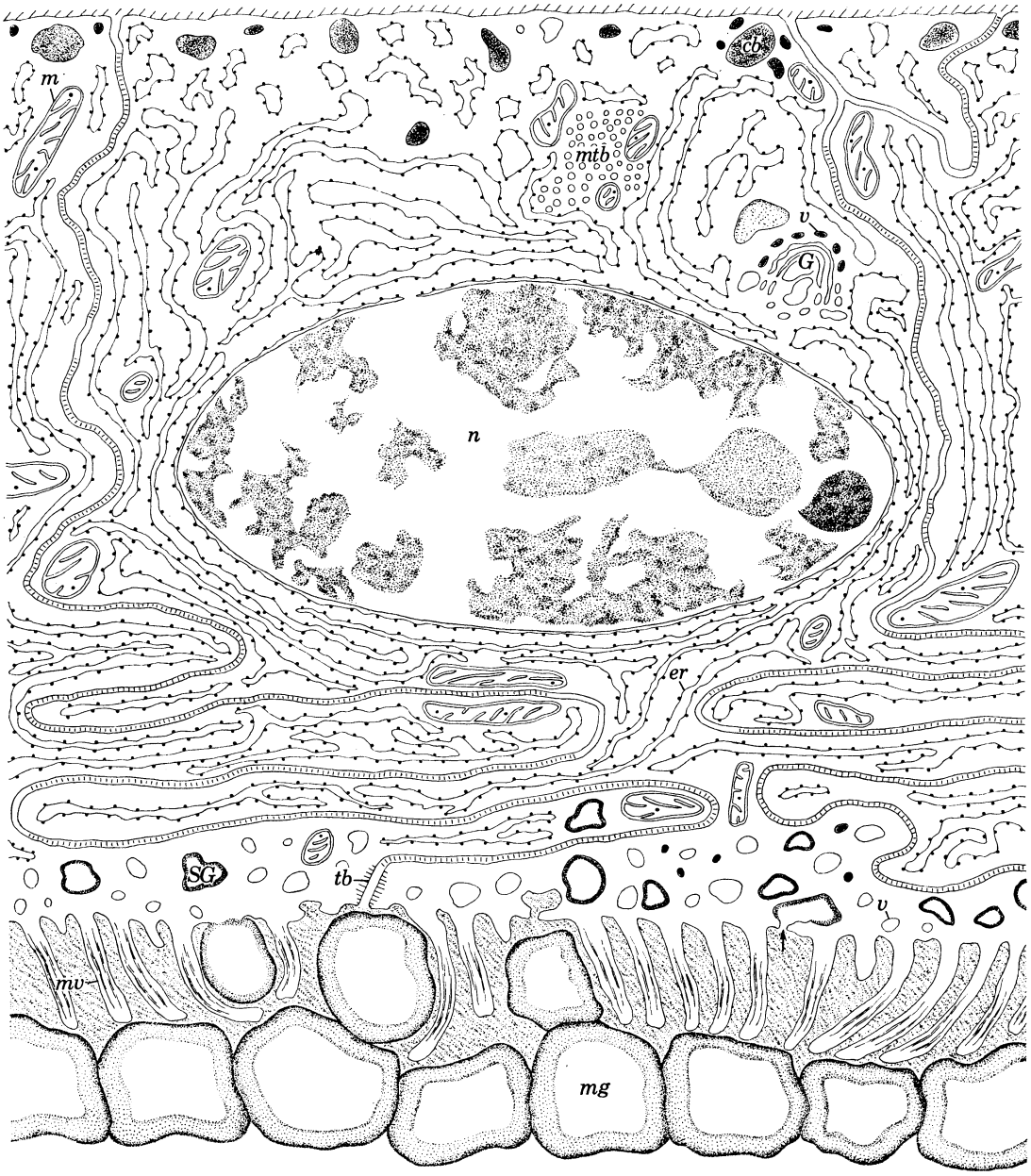


FIGURE 26. Diagram to summarize the general cell substructure of gland 3 (or gland 5). Note particularly the secretory granules (*mg*), the form the secretory vesicles (*SG*) take in the terminal-web region, and the manner in which the vesicles probably empty their contents into the lumen (*arrow*).

switching off of the secretory role of the Golgi apparatus, then it is possible that the lipid component of the final glandular product is formed first (in the Golgi apparatus) in the earlier stages of the maturation of the gland, and later this component is complexed with the protein component (produced in the rough ER) to form the characteristic secretion of the gland.

The final secretory product, as it is found within the lumen, is peculiar. It consists of globules

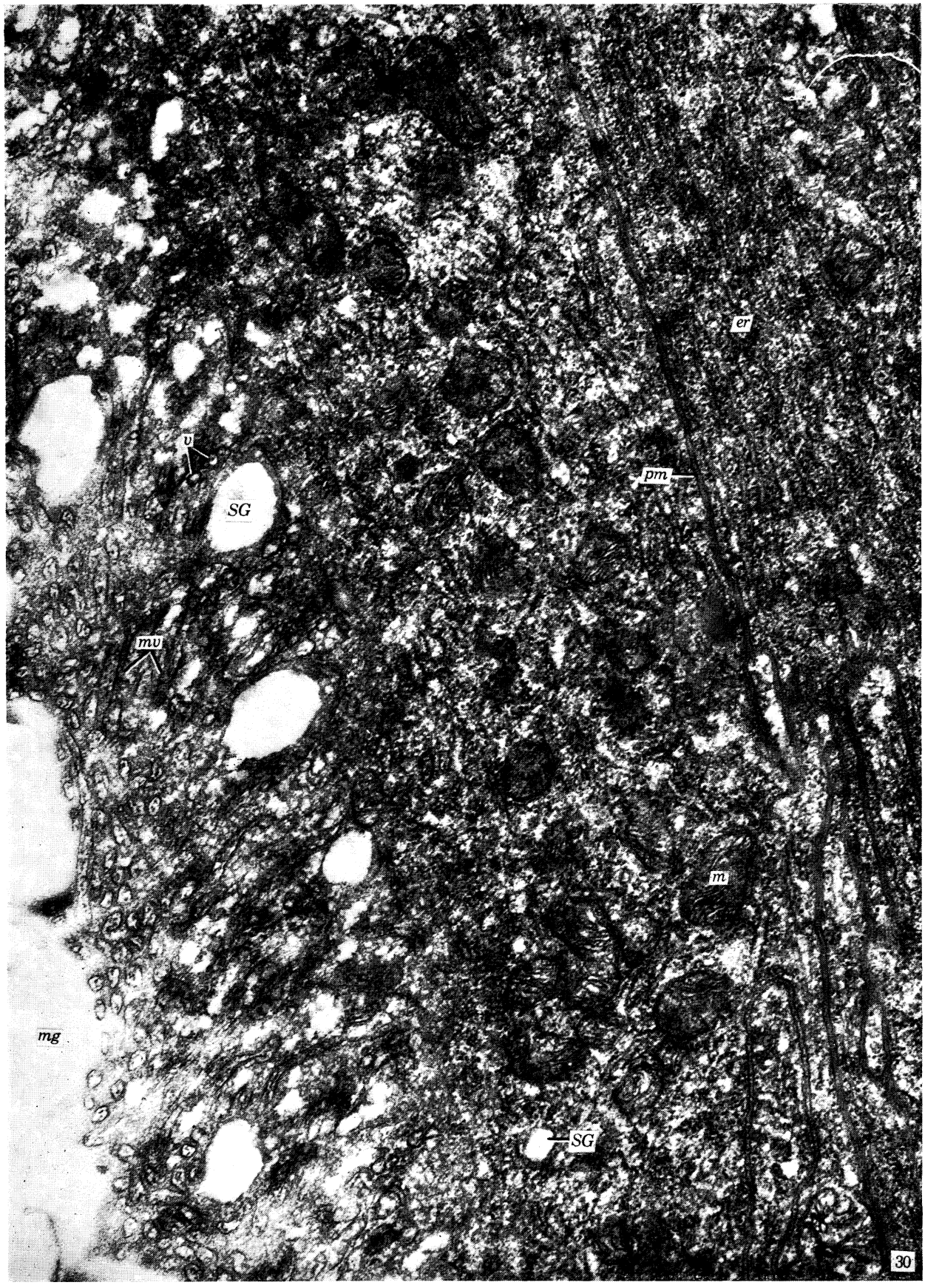


FIGURE 30. The apical cytoplasmic region showing secretory vesicles (*SG*) with an electron-dense rim and empty core, closely packed microvilli (*mv*) holding a dense substance in between, and a very convoluted lateral plasma membrane (*pm*). Note also the closely packed, parallel ER cisternae (*er*). × 44000.

(*Facing p.* 96)

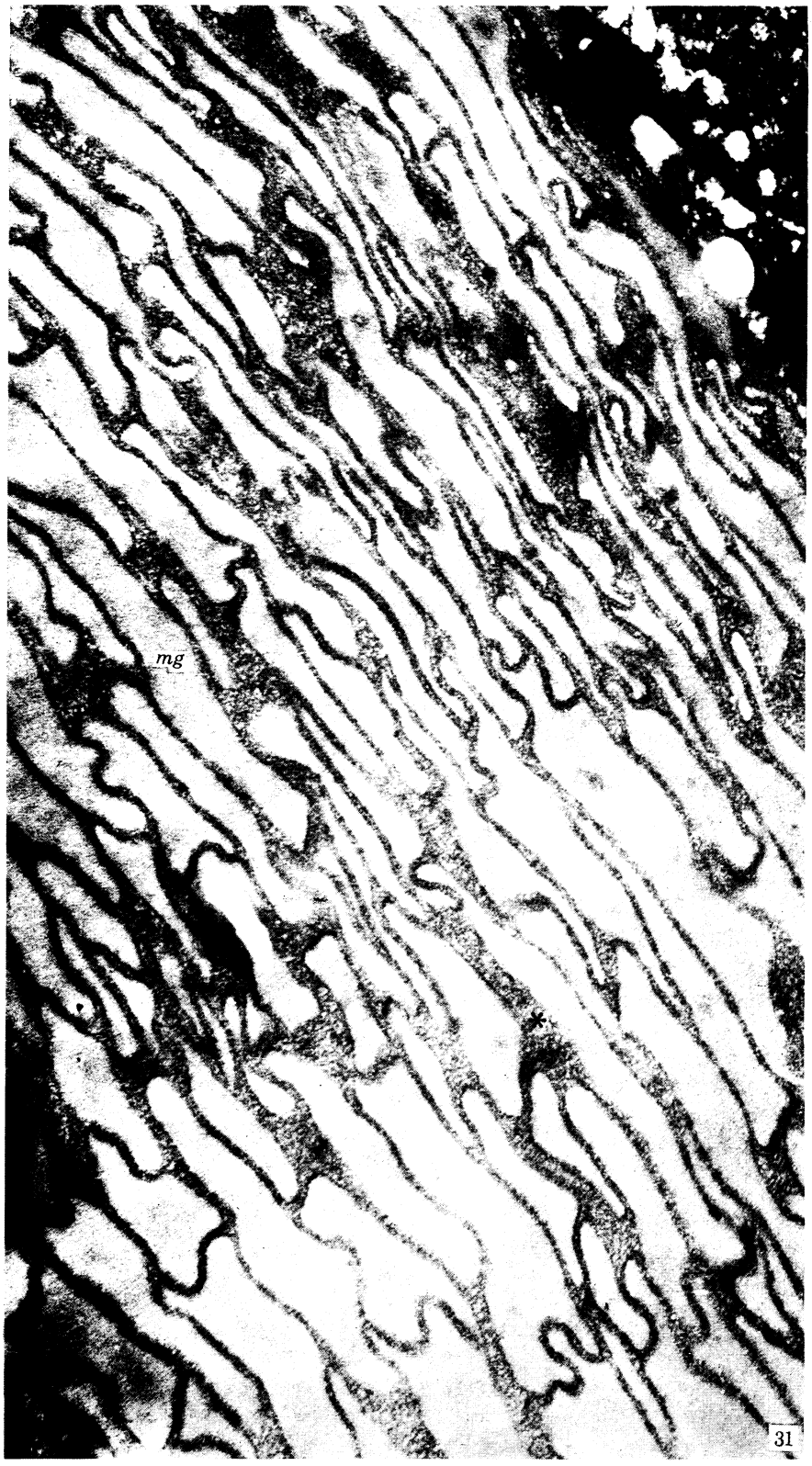
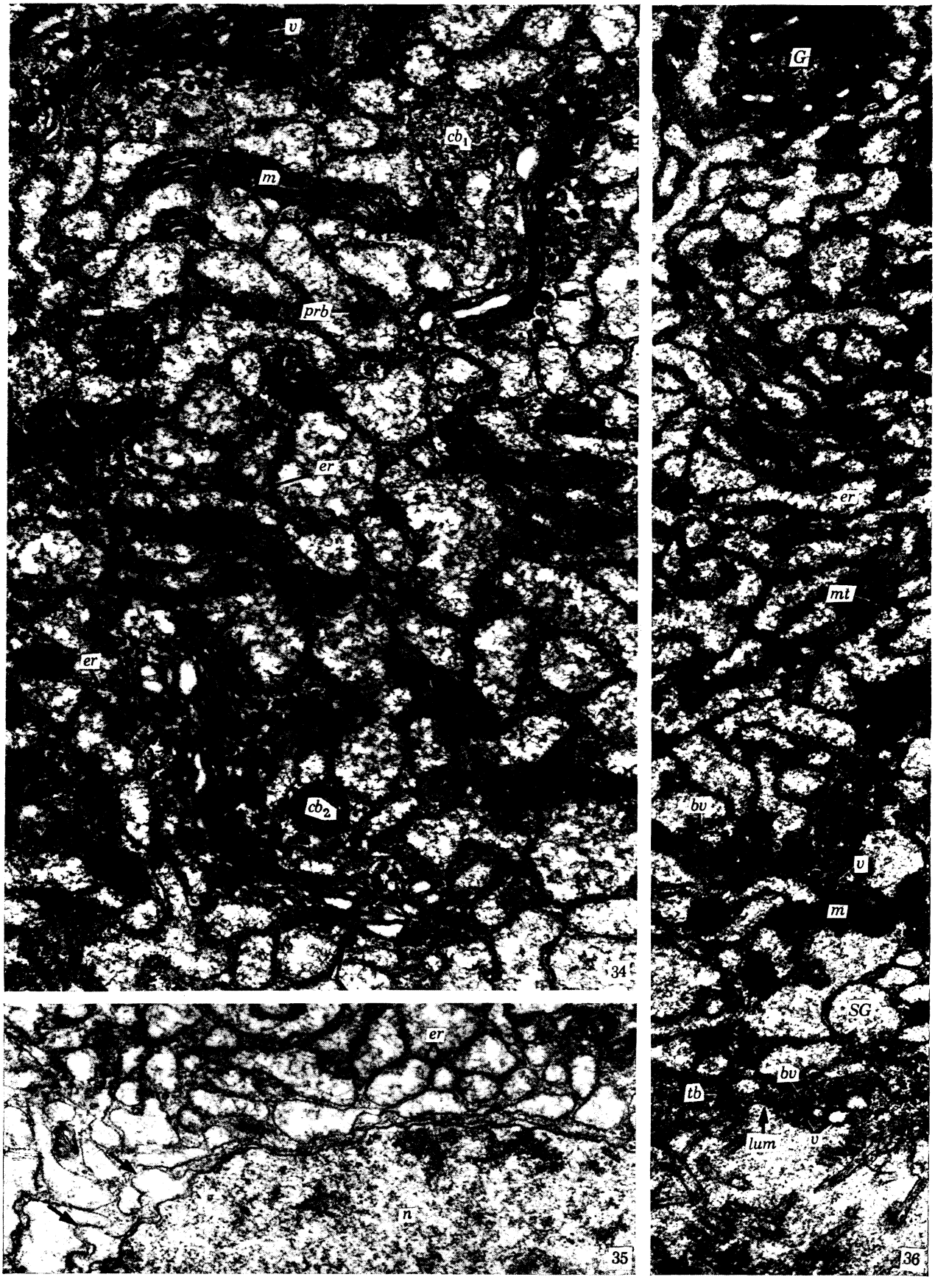


FIGURE 31. The luminal content consists of large globules (*mg*) of low electron-density surrounded by a granular cortical substance (*star*). × 52000.

FIGURE 32. Basal cytoplasmic region of a rather young (5-day-old adult) gland, with less general electron-density, allowing easier observation of cytoplasmic bodies (*cb*), mitochondria (*m*) and the rough ER (*er*). × 52000.



Figures 34 to 36. For description see p. 97.

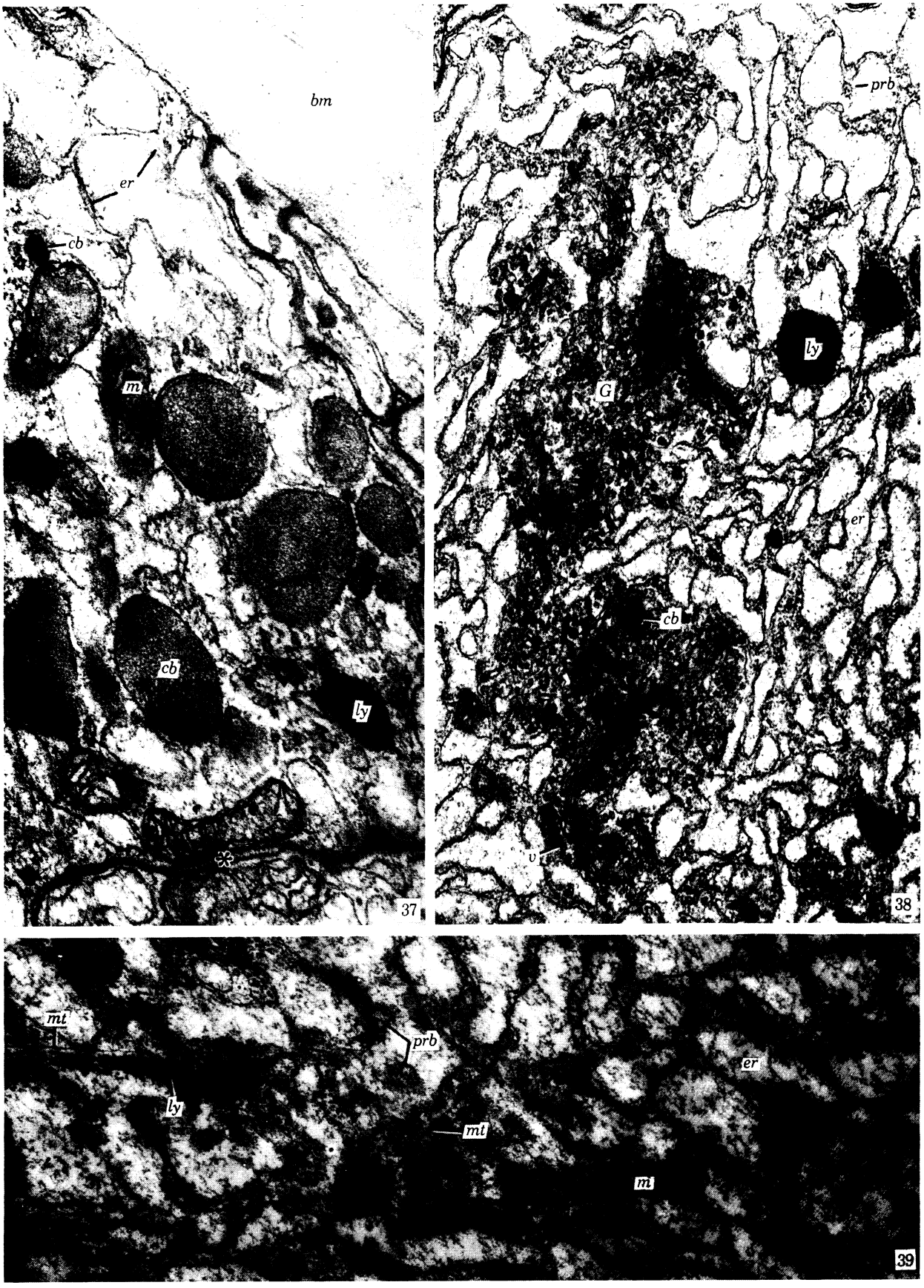


FIGURE 37. Cytoplasmic bodies (*cb*) are abundantly found in the basal cytoplasmic region, while lysosome-like bodies (*ly*) are few. Along the lateral plasma membranes may be found mitochondria in pairs closely apposed on either side (*star*). × 57500.

FIGURE 38. A number of Golgi units have combined to form one enormous complex (*G*). Within one unit may be seen a cytoplasmic body (*cb*). × 28500.

FIGURE 39. Many polyribosomes (*prb*) may be observed attached to the rough ER (*er*). × 38000.

of low electron-density—presumably the lipid component—surrounded by a thin layer of a dense granular substance, presumably largely representing the protein component (figure 31, plate 15). The regularity of this arrangement is striking, and may perhaps account for the appearance of a crystalline structure in the secretion mass under the light microscope (Odhiambo 1969*a*). In cases where the lipid component is leached out during the processing for electron-microscopy, the thin 'protein coat' of the secretion globules usually remains intact (figure 31). A similar observation obtains for mature secretory vesicles located in the apical cytoplasmic region (figure 30).

Cytoplasmic bodies are a constant feature of the basal cytoplasmic region of gland 3 (figure 26). Often these bodies assume enormous proportions, most likely by the fusion of cytoplasmic bodies (figure 27). The dense granular content of these bodies resemble very closely the protein coat of the secretion globules. It is possible, therefore, that these bodies contain the precursors for the elaboration of at least part of the secretion product of gland 3.

Gland 4

Although the physical features and behaviour of the secretions of glands 2 and 4 are quite distinct (Odhiambo 1969*a*), the cytoplasmic features of the two gland types are quite similar. The two principal differences arise in the ultrastructural nature of the secretory process, and in the relative extent of the Golgi elements.

The rough ER is moderately prominent in gland 4 (figure 33), and occurs mostly as enormously swollen vesicles (figure 33; figure 34, plate 16; figure 39, plate 17; figure 43, plate 19). Often, however, rather more flattened cisternae are encountered which may be continuous with swollen portions of the reticulum (figure 33; figure 41, plate 18). Such cisternae contain a minutely fibrous substance, which is also found in the lumen in between the two membranes comprising the nuclear envelope (figure 35, plate 16). Indeed, the nuclear envelope exhibits such clear blebbing that it encourages the idea that the latter may give rise to at least a portion of the rough ER in the general cytoplasm (figure 35).

A significant attribute of gland 4 cytoplasm is its widespread and extremely large Golgi units (figure 38, plate 17; figure 40, plate 18). Frequently, several Golgi units are confluent. The Golgi units have a swarm of small, smooth vesicles distributed peripherally over a large area (figure 38); some of these vesicles are observed apparently pinching off or fusing with the ER or with Golgi saccules (figure 34). A few small vesicles, resembling Golgi vesicles, are also observed some distance away from Golgi units (figure 42, plate 18; figure 43); it is possible that such vesicles are engaged in the shuttle function between the Golgi apparatus and the rough ER as has previously been suggested.

Description of plate 16 (gland 4)

Figure 34. The cytoplasm is dominated by swollen cisternae of the rough ER (*er*) and enormous Golgi complexes (*G*), near which may be found cytoplasmic bodies (cb_1). A cytoplasmic body (cb_2) containing a small vesicle similar to the peripheral vesicles (*v*) of the Golgi apparatus is shown close to the latter. Rather electron-dense Golgi vesicles can be seen in the process of pinching off from either the Golgi saccules or ER cisternae (*arrows*). × 39000.

Figure 35. The nuclear membrane shows frank blebbing (*arrows*). × 24000.

Figure 36. Mitochondria (*m*) occupy very small spaces in the cytoplasm in between the larger ER cisternae (*er*). There are large numbers of various sizes of small vesicles (*v*) and coated vesicles (*bv*) in the terminal-web area as well as in the rest of the apical cytoplasmic region. × 24000.

In view of the large quantity of Golgi elements in gland 4, it is of interest to note that this gland produces a comparatively larger proportion of polysaccharide than protein as compared

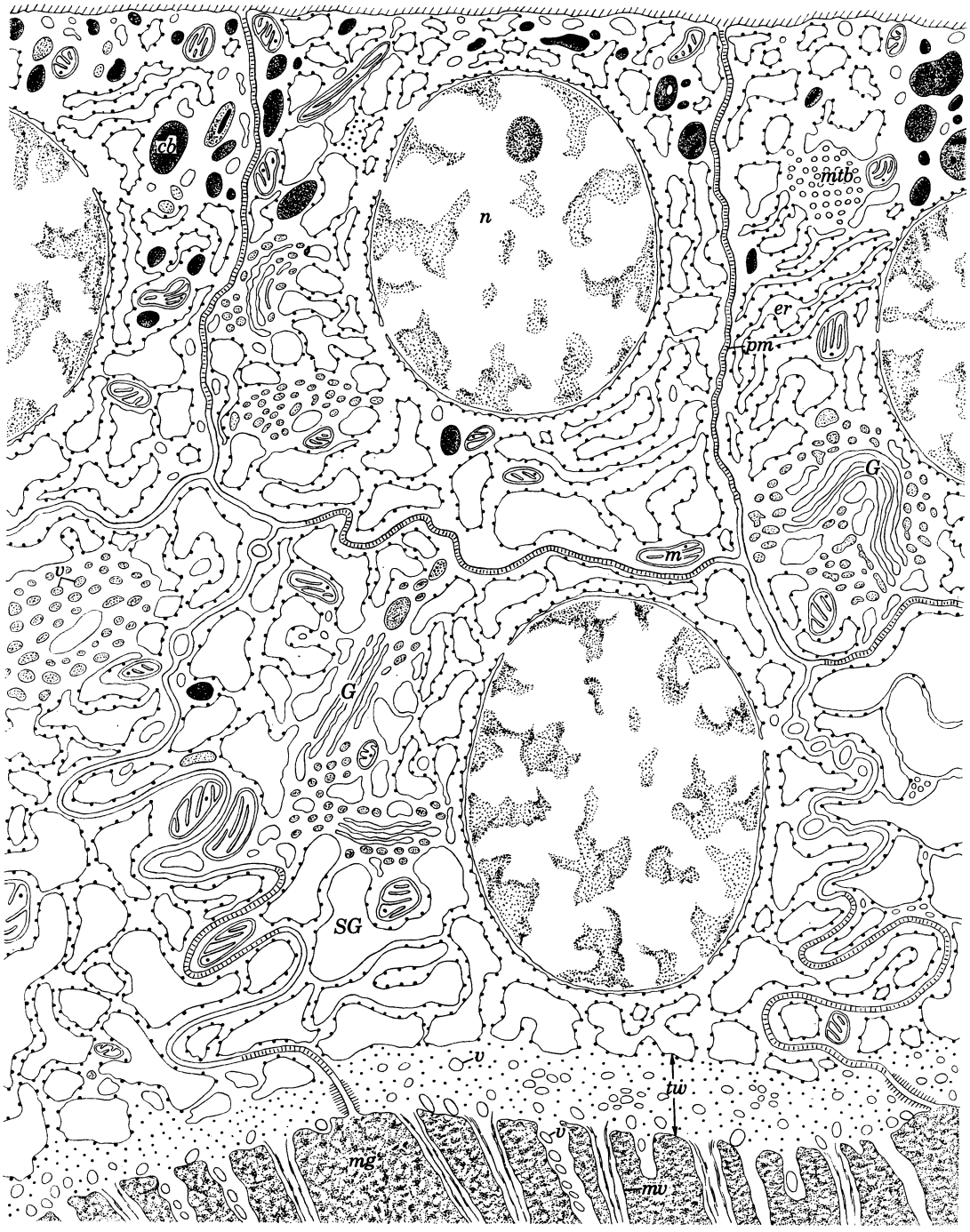


FIGURE 33. Diagram of a generalized cellular substructure of gland 4.

to the situation found in gland 2 (Odhiambo 1969*a*). Furthermore, Peterson & Leblond (1964) have shown that the polysaccharide moiety of glandular glycoprotein is synthesized by the Golgi complex.

The basal cytoplasmic region—just as we have seen in earlier gland types already discussed—is characterized by the presence of a large number of cytoplasmic bodies of various sizes, although a few lysosome-like bodies may also be found there (figure 37, plate 17). A feature possibly significant for the elucidation of the physiological functions of these cytoplasmic bodies is their frequent location within the immediate environs of the Golgi apparatus (figures 34 and 38).

The fine structure of the luminal area of gland 4 is quite different from that of gland 2. There are no multivesicular bodies, although infrequently there are a few clavate microvilli (figure 44, plate 20). Both clavate microvilli (figure 44) and the more common unswollen microvilli (figure 43) usually contain several small, smooth vesicles. Similar vesicles and coated vesicles may also be found in the terminal-web region (figure 36, plate 16) as well as in other parts of the apical cytoplasmic region (figures 36 and 43). Some suggestions have already been made as to their possible functions (see gland 2).

The mature secretion in the gland lumen is minutely granular but contains some finely fibrillar structures (figure 45, plate 20). This same secretion, or a similar substance, is observed in the secretory vesicles in the apical cytoplasmic region (figures 36, 43 and 44).

Gland 6

An outstanding feature of the cytoplasmic organization of this gland type is the occurrence and extent of greatly flattened parallel cisternae of the rough ER (figure 46; figure 47, plate 21). These occupy almost the entire cytoplasm: Golgi elements, on the other hand, are not especially conspicuous (figure 46; figure 48, plate 21), although when they do occur they exist as large units with numerous peripheral vesicles. It is noticeable that the cytoplasm exhibits many deposits of ribosomes, including polyribosomes (figures 47 and 48). The extensive development of the rough ER, and the associated polyribosomes, together with the scarcity of Golgi elements, are of interest since the secretory product of gland 6 consists of more protein than polysaccharide when compared to the situation in either gland 2 or gland 4 (Odhiambo 1969*a*).

Particularly prominent in the cytoplasm are the cytoplasmic bodies, which occur in large numbers in the basal region of the cell (figure 46), where they are found in various sizes—from very small to very large. Indeed, as it was indicated when discussing gland 3, the cytoplasmic bodies may grow by the smaller cytoplasmic bodies fusing with the larger ones. A common occurrence in the middle region of the cell is to find cytoplasmic bodies being closely associated with the Golgi apparatus (figure 47), although scattered cytoplasmic bodies may be found elsewhere in the cell (figure 47). These bodies, when in groups located near the Golgi apparatus, may also have a close association with microtubular bundles, which themselves are often distributed close to the Golgi units (figure 47). It has been suggested that the microtubular bundles in locust ARGs may be important for the mechanical maintenance of the cytoarchitecture of the glandular cells (Odhiambo 1969*b*).

Secretory vesicles, apparently produced in the Golgi region (figures 46 and 47), are translocated to the apical region (figure 49, plate 22), where they are somehow released into the lumen. While the secretory product within the vesicles appear to be finely fibrous (figure 49), that in the lumen—even only after just being extruded (figure 49)—occurs in the form of large globules of from 450 Å to 1.0 μm or more in diameter, and having a thin enveloping fringe of finely fibrous and electron-dense material (figure 51, plate 23). Clearly, there is a more or less instantaneous transformation of the secretory material at the time of its extrusion into the gland

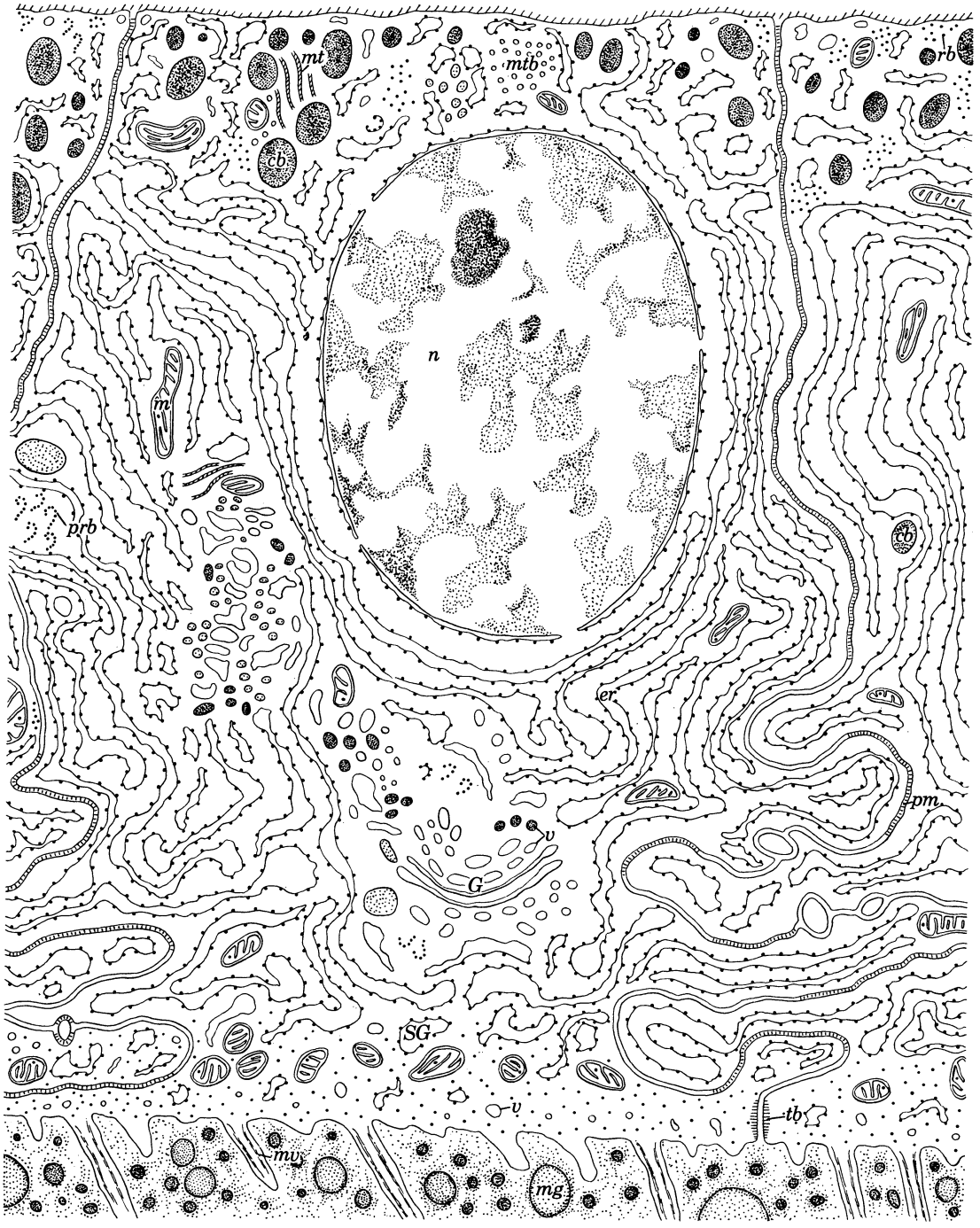


FIGURE 46. Generalized diagram of the subcellular structure of gland 6.

lumen. Whether this transformation is aided by the small, smooth vesicles found in the terminal-web region (figure 49; figure 50, plate 22), or whether instead it is due to some biochemical environmental factor in the lumen, is not known. Nevertheless, these globular secretion granules are peculiar to this gland type.

The electron-density of these secretion globules varies a great deal: from the electron-opacity of the very small granules, to the fairly electron-transparency of the large globules (figures 50

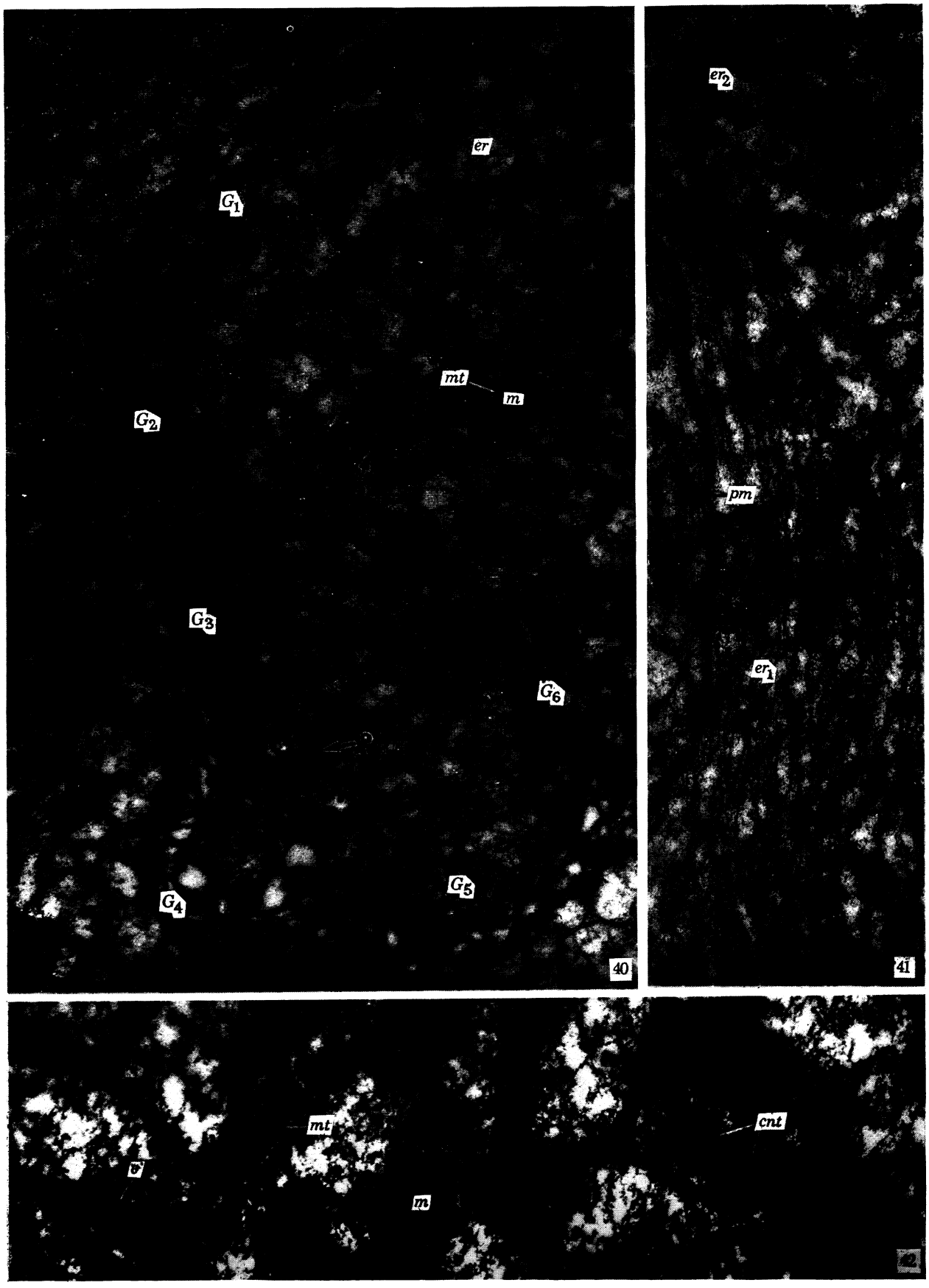


FIGURE 40. Six units combined into one enormous Golgi complex (G_1–G_6). There are some electron-dense granules near the Golgi units and mitochondria of unknown nature (?). × 32500.

FIGURE 41. Parallel arrays of rough ER cisternae (er_1) very often swell into vesicles (er_2), especially close to the Golgi apparatus. × 39000.

FIGURE 42. Apical cytoplasmic region having numerous small, smooth vesicles (*v*), some microtubules (*mt*), and a centriolar apparatus (*cnt*) in between swollen ER cisternae. × 52000.

(*Facing p.* 100)

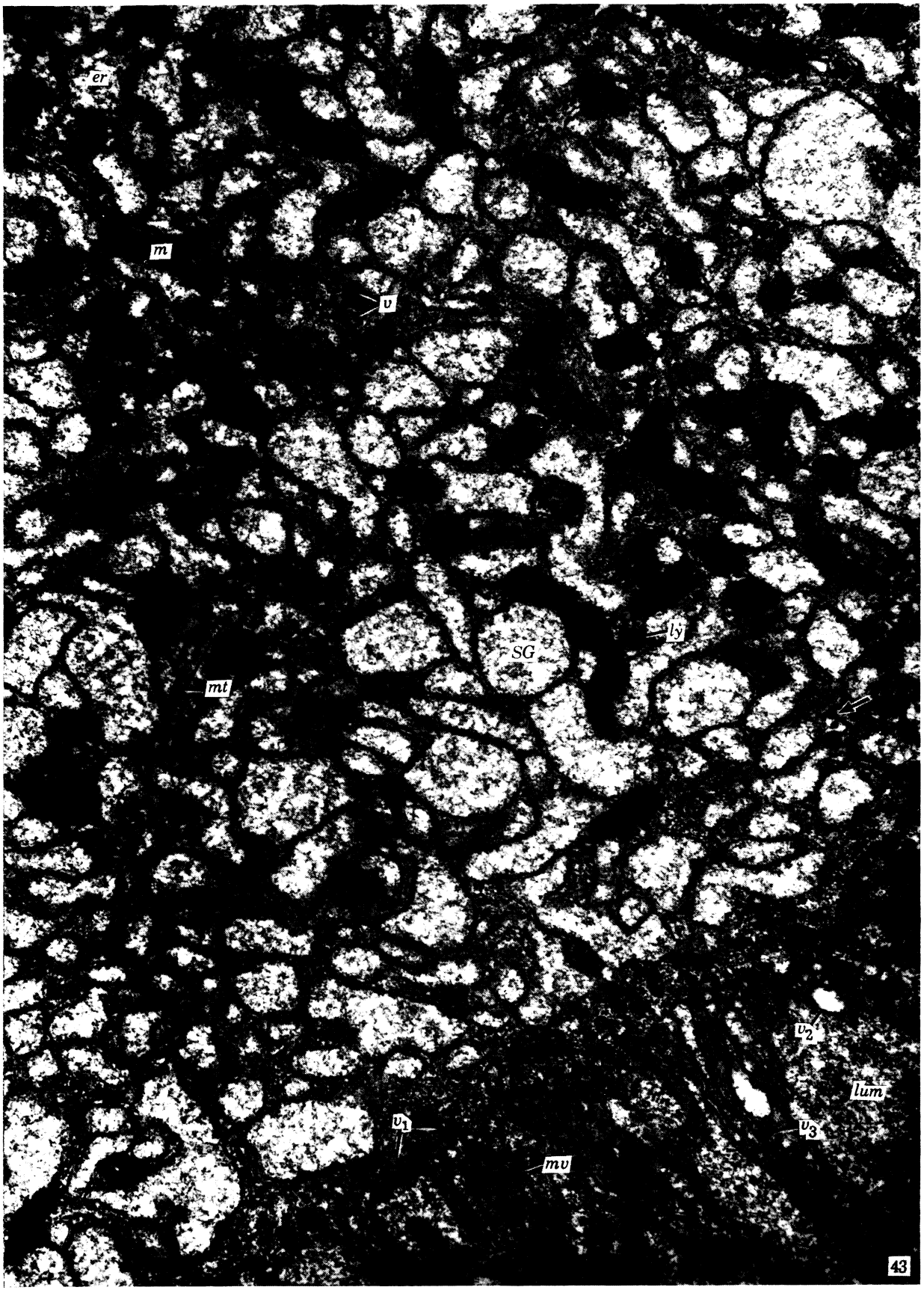


FIGURE 43. The contents of ER cisternae (*er*), what are considered as secretory vesicles (*SG*) and the lumen (*lum*) are very similar indeed. The terminal-web region is fairly well demarcated, with electron-dense content and small, smooth vesicles (v_1). Large vesicles (v_2) are sometimes observed at the base of microvilli; but more frequently, smaller vesicles (v_3) are seen within the microvilli (*mv*). × 32500.

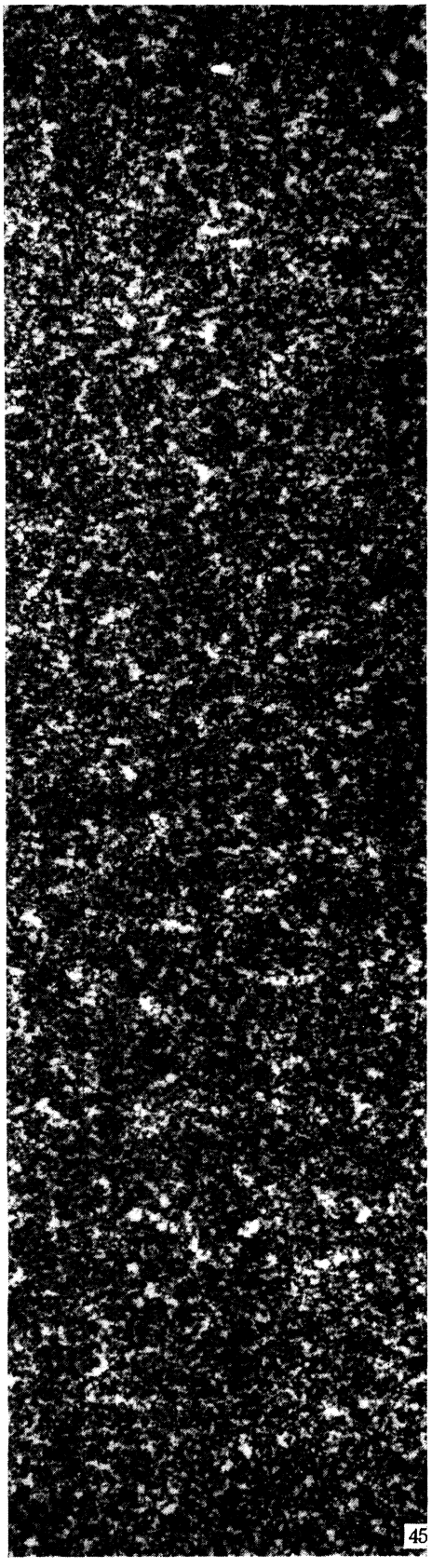


FIGURE 44. Microvilli are usually more or less straight cylindrical structures (mv_1), but in rare occasions in this gland the microvilli become clavate (mv_2). Note also the small, smooth vesicles (v) in the terminal-web region (tw). × 92000

FIGURE 45. The luminal content consists of minutely granular and fibrous components. × 39000.

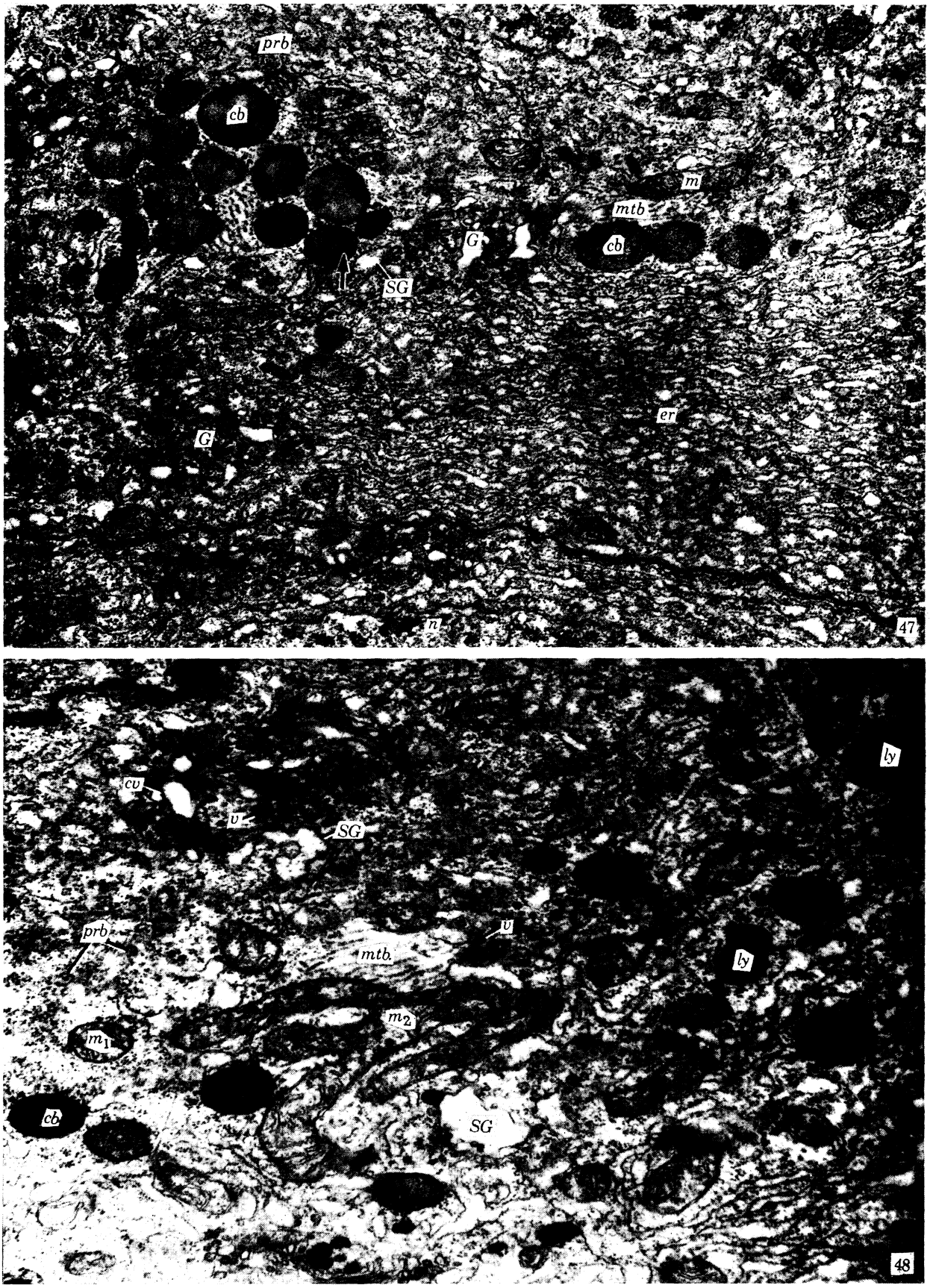


FIGURE 47. The rough ER (*er*) is extensively developed. There are many cytoplasmic bodies (*cb*) in this mid-cytoplasmic region, one of which shows another recently engulfed cytoplasmic body (*arrow*). × 24000.

FIGURE 48. Mitochondria (m_2) in this gland can assume complex forms, which frequently have closely associated microtubular arrays (*mtb*). The Golgi apparatus has rather large condensing vacuoles (*cv*) and very dense Golgi vesicles (*v*). There are abundant polyribosomes (*prb*) in the cytoplasm. It is possible that small vesicles add their contents to secretory vesicles (*SG*). × 32500.

and 51). This gradation in opacity, paralleling a corresponding gradation in size, suggests that there may be only one type of secretion granule; thus, the change in electron-opacity and size may simply be the result of fusion. Such a suggestion is supported by the apparent and frequent fusion of globules (figure 51). The latter occurs in a greater degree as the secretion mass moves down the glandular tube; consequently, near the posterior end of the tube, the secretion occurs as one more or less huge, irregular mass with a uniform electron-opacity (figure 52, plate 23).

The secretion globules seem to be bounded by a thin, somewhat discrete, electron-dense cortical layer (figures 49 and 51). In this, and other respects, the secretion globules of gland 6 closely resemble the mucus granules produced in the goblet cells of the vertebrate intestine (Hollmann 1963; Trier 1963).

An interesting ultrastructural observation of the microvilli of gland 4 is the occurrence of fine longitudinal filaments in the core of the microvilli and their extension into the terminal-web area (figure 49). These longitudinal filaments seem to have transverse bridges interconnecting them with similar filaments in the core. Further into the terminal-web region they extend into a veritable web of filaments, which are not in a longitudinal array as expected in the classical terminal web in vertebrate material (Bloom & Fawcett 1968). Such an arrangement is supposed to confer stability and rigidity to this region. Each microvillus also shows short filaments attached to the unit membrane and radiating outwards into the gland lumen, giving the microvilli a fuzzy appearance (figure 49). Similar filaments have previously been described in epithelial cells of vertebrate tissues, where they may form a distinct surface coat on the microvilli, and where the filaments are stated to consist of mucopolysaccharide (Fawcett 1965). A noticeable characteristic of all microvilli in locust ARGs is that they do not form a closely packed, parallel, highly ordered array such as is observed in the absorptive cells of vertebrates, e.g. intestinal mucosa and the proximal convoluted tubule of the nephron; instead, the ARG microvilli appear disorganized and perhaps labile structures.

'*Homogeneous*' *glands*

This gland type is the commonest in the male locust ARG complex, comprising glands 7 to 10 and 13 to 15 in each gland mass; they produce a neutral mucopolysaccharide secretion (Odhiambo 1969*a*). As might be expected of glands producing much exportable polysaccharide, the Golgi units are considerably widespread and frequent (figure 53; figures 56 and 57, plate 25). Each Golgi complex may have one or more very large condensing vacuoles and a constellation of small, smooth vesicles (figures 56 and 57). Some of these small vesicles, which apparently pinch off from the periphery of the Golgi saccules (figure 56), are occasionally found engulfed in cytoplasmic bodies adjacent to the Golgi apparatus or in recently released condensing vacuoles (figure 55, plate 24; figure 57; figure 58, plate 25). This relationship adds supporting evidence for the suggestion, previously advanced, that these small Golgi vesicles may act as shuttle carriers between elements of the secretory machinery.

The rough ER is extensively developed, although less so than in gland 6. But as in the latter, the ER is largely in the form of rather flattened cisternae, although a greater proportion of swollen cisternae is found here than in gland 6 (figure 54, plate 24). The cytoplasm contains relatively few free ribosomes, but there exist many deposits of polyribosomes (figure 54). The latter do not seem to have any preferred regional location: sometimes they are found very near the nuclear envelope; other times they are found in the neighbourhood of the Golgi apparatus; in any case they are generally attached to the ER membrane.

Many cytoplasmic bodies are found in the gland cell. Very frequently they lie near the Golgi apparatus (figure 57). Since the small Golgi vesicles contain a similar fibrous material to that seen in the bodies, one is tempted to suggest that the vesicles transport precursor material from the large cytoplasmic bodies to the Golgi complex, presumably for further elaboration.

Homogeneous glands show at great advantage 'pinocytotic' activity at the luminal surface (figures 59 and 60, plate 26). A large number of coated vesicles are found in the terminal-web area and beyond, and the formation of pinocytotic pits is often encountered at the luminal plasmalemma. The function of these coated vesicles is obscure. But there is no doubt that most of them are located in the terminal-web region. Furthermore, it is a general observation in the locust ARGs that the terminal-web region is almost free of any other cytoplasmic organelles including the mature secretory vesicles. Indeed, there exists a problem as to how secretory vesicles release their content into the gland lumen. It is perhaps reasonable to suggest that the secretion is parcelled out into minute packages at the border of the terminal-web region, these small units then traverse the latter region to empty their contents into the lumen by fusing with the luminal plasmalemma. If such a process were to go on indefinitely, the luminal plasmalemma would continue to expand at the expense of the ER. Perhaps the pinocytotic activity at the luminal surface is partly a counter-measure to keep pace with this membrane growth as well as being a means for sampling and calibrating the progress of secretion, as proposed earlier. This dual function of pinocytotic activity at the luminal surface seems plausible in view of the fact that it is evident in the purely glandular tubes of the ARG complex while it is almost non-existent in gland 16, the non-glandular seminal vesicle of the male locust.

The mature secretion in the lumen of homogeneous glands is finely divided, and contains numerous short fibrillar structures, approximately 400 to 600 Å long, embedded in it (figure 60). No such fibrillar elements are observed in the secretory vesicles in the cytoplasm (figures 54, 56 to 58, and 60). It is possible that a polymerization process takes place in the newly extruded secretion.

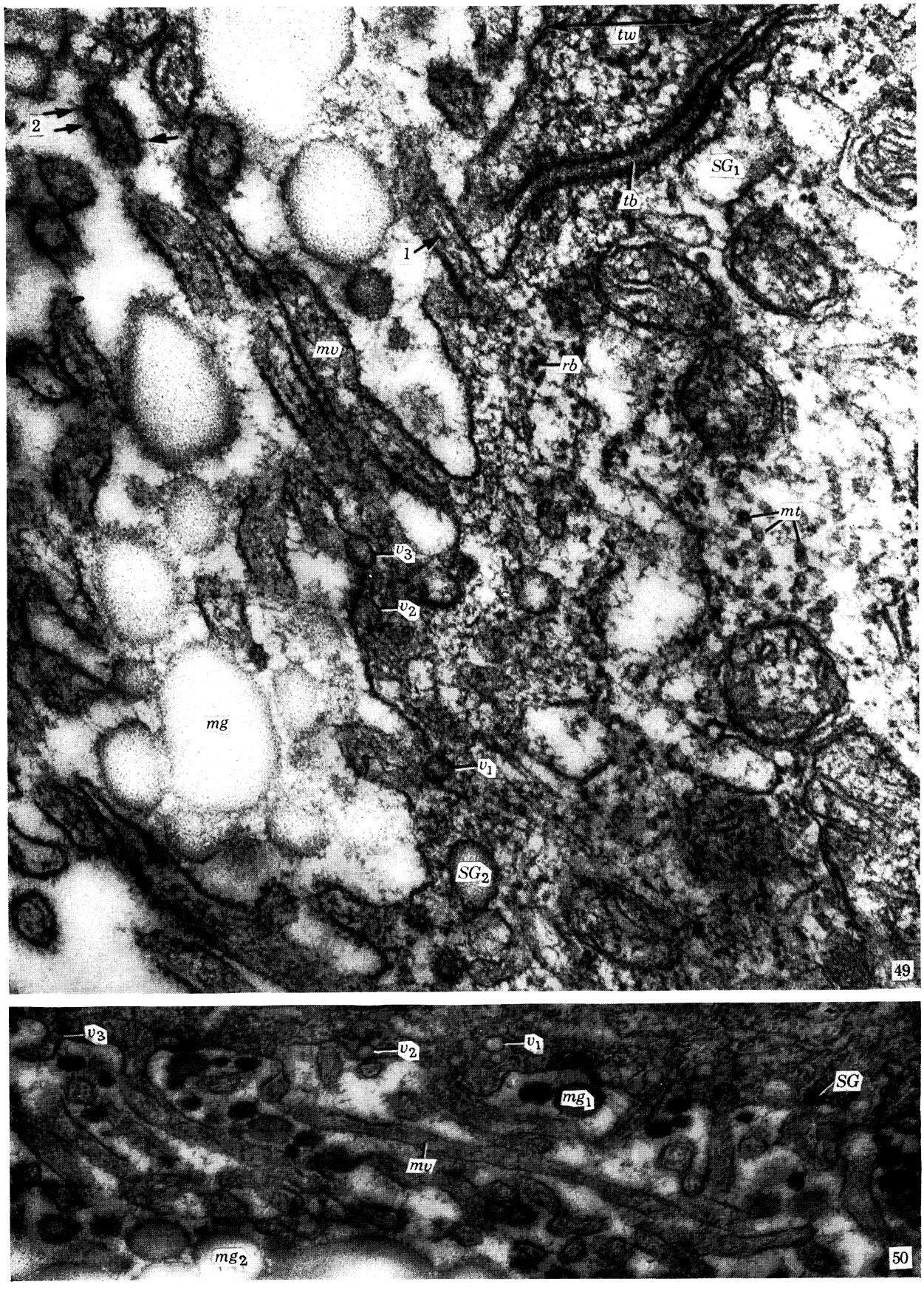
Gland 11

Gland 11 synthesizes a rather complex secretion comprising a neutral mucopolysaccharide mass in which are embedded large granules of various sizes which appear to consist of an acidic mucopolysaccharide; in addition, the granules also seem to contain some lipid (Odhiambo 1969*a*). The electron microscope reveals two major forms of secretion within the gland lumen: a disperse, coarsely fibrous substance; and large 'granules', consisting of more compactly arranged fibrous elements, embedded within the general secretion mass (figure 72, plate 30). Occasionally, the granules also exhibit 'empty' vacuities, which probably represent the former location of lipoid material leached out during processing of the tissue for electron microscopy;

Description of plate 22 (gland 6)

Figure 49. The terminal-web region as defined by the terminal bar (*tb*). Secretory vesicles (SG_2) are relatively small compared to those just outside this area (SG_1). There are a number of small, smooth vesicles (v_1), some of which seem to be fusing with the luminal plasmalemma (v_2) or entering the microvilli (v_3). The microvilli (*mv*) appear to have longitudinal fibrous filaments inside the core of the cylinder (*1*) and short filamentous material sticking on to the outside of the unit membrane (*2*). × 102500.

Figure 50. The small, smooth vesicles (v_1) found in the terminal-web region may also be observed apparently fusing with the luminal plasmalemma (v_2) or entering the microvilli (v_3). The secretory vesicles (*SG*) may be of about the same size but have a much more electron-dense content. The elaborated secretion may appear dense (mg_1) or translucent (mg_2) depending on size. × 52500.



FIGURES 49 and 50. For description see facing page.

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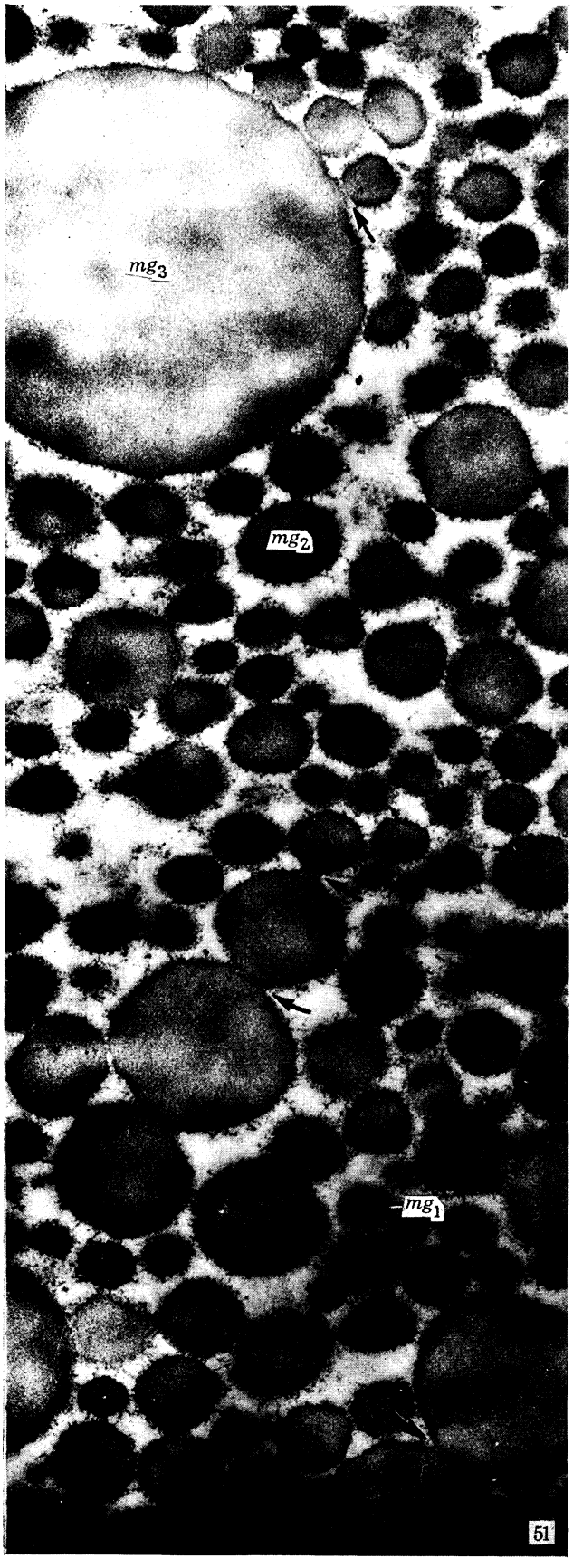


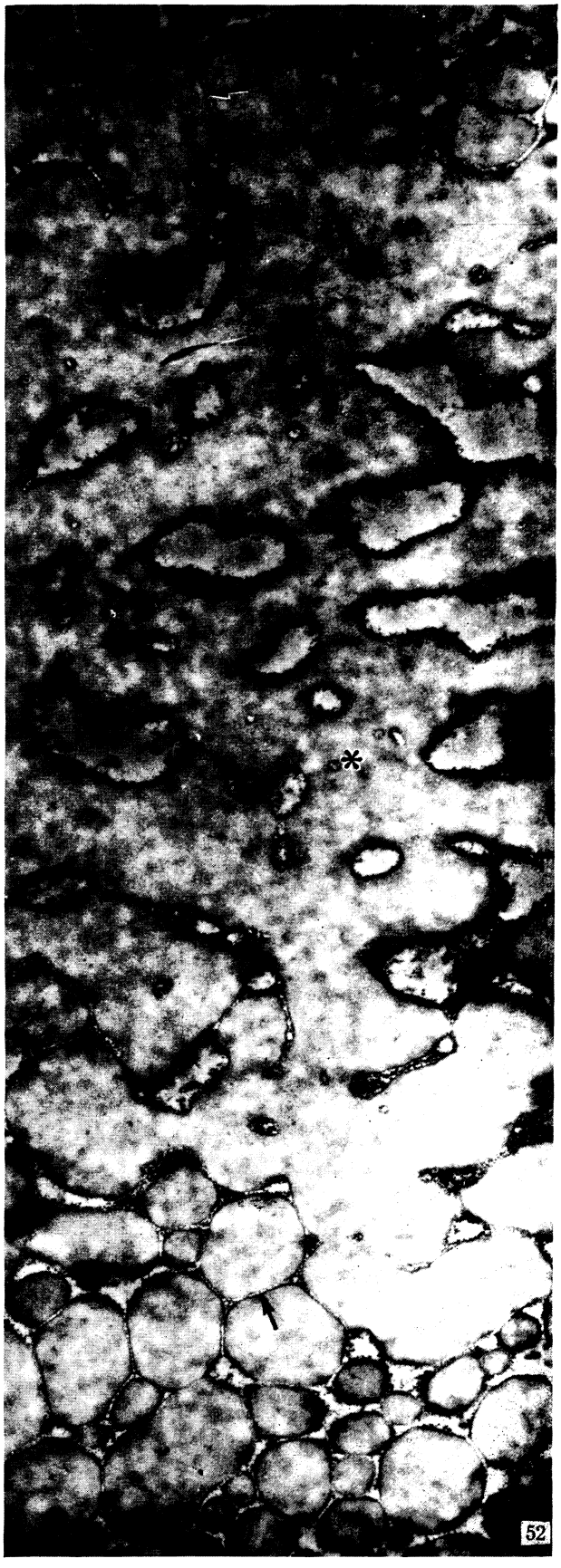


FIGURE 51. The luminal content consists of globules of various sizes, their electron-density becoming less with increasing size (mg_1–mg_3). Enlargement seems to be due to the fusion of globules (*arrows*). × 44000.

FIGURE 52. In the more proximal portion of the gland, the globules of secretion become more or less confluent (*star*). But some globules have still a persistent, dense, limiting cortex (*arrows*). × 137500.

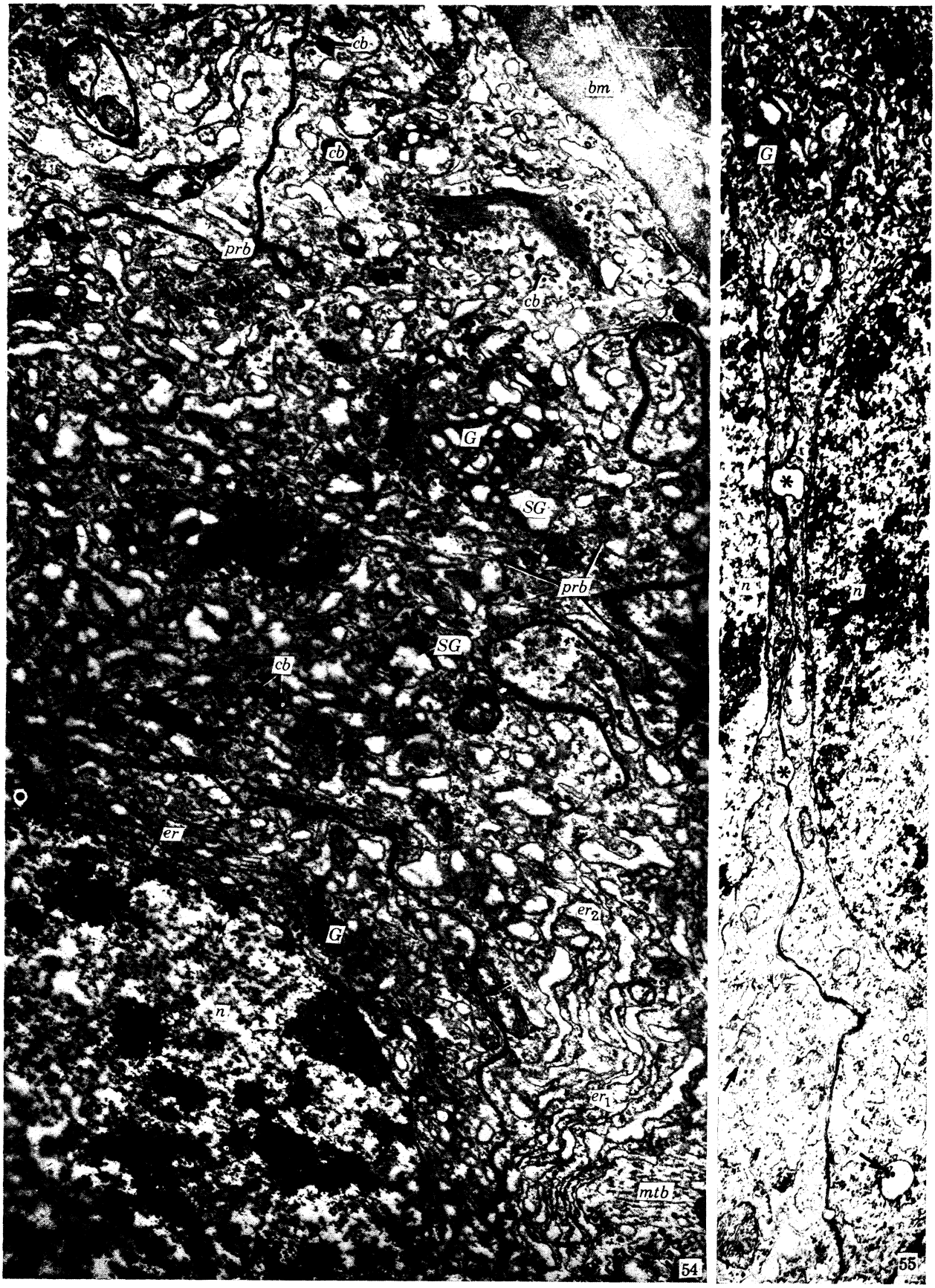
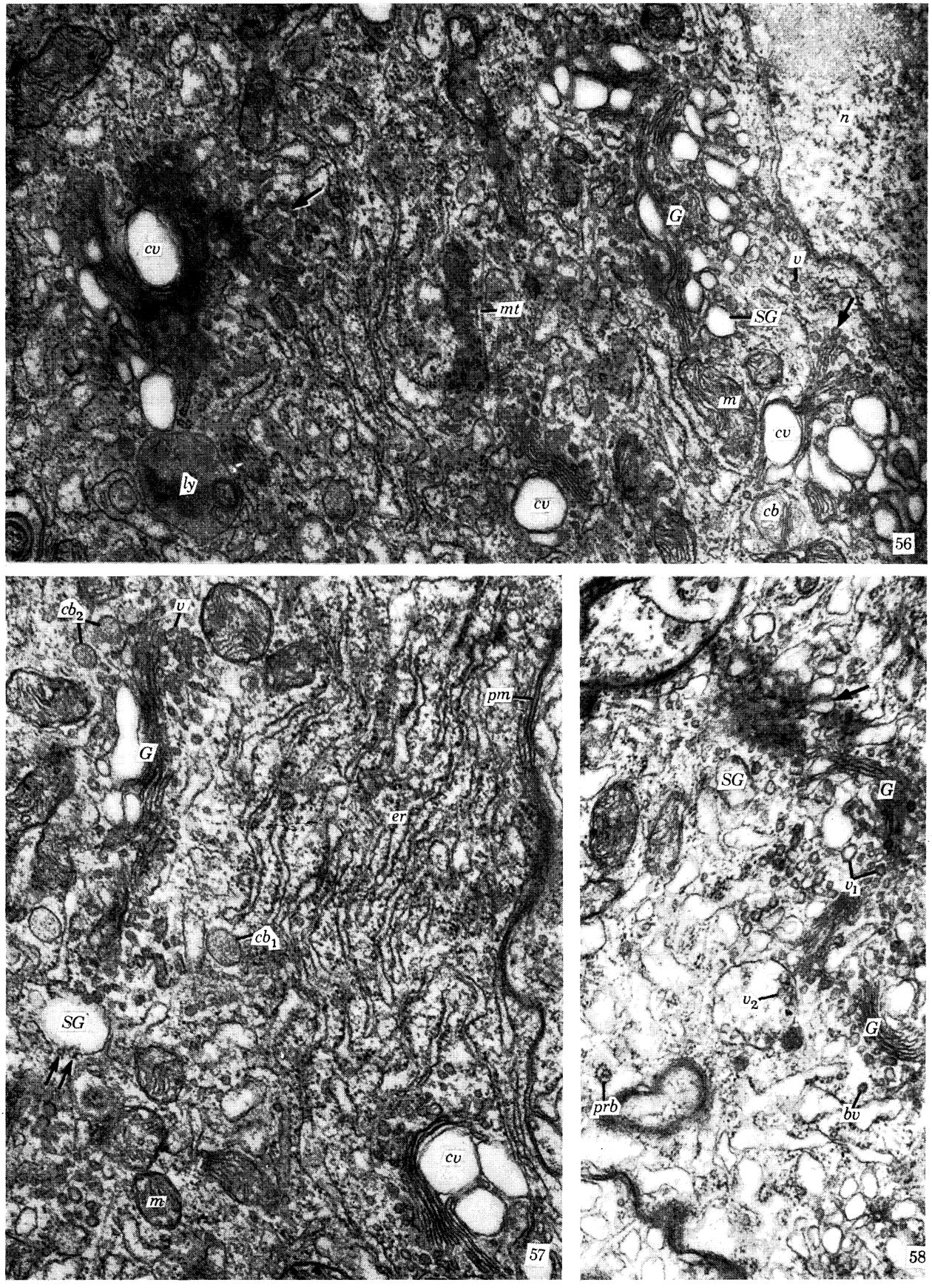


FIGURE 54. In some areas, the rough ER is found in the form of flattened cisternae (er_1); away from the perinuclear region, and especially in the neighbourhood of the Golgi apparatus (*G*), the ER is swollen into vesicles (er_2) which may later become secretory vesicles (*SG*). Note also a pair of mitochondria in close parallel apposition across the lateral plasma membrane (*arrow*). × 24000.

FIGURE 55. Internuclear region, showing several enlargements of the intercellular space (*stars*). Note also a number of moderately large vesicles (possibly secretory vesicles) with small, smooth vesicles in the course of fusing with them (*arrows*). × 22000.



FIGURES 56 to 58. For description see facing page.

the granules also bear tiny, highly electron-dense granules, 150 to 300 Å in diameter, which are found in the general secretion mass as well (figure 72). It is not clear how the substance of the secretory vesicles in the cytoplasm crystallizes into the large granules when it reaches the gland lumen. However, the secretory vesicles can easily be traced from the Golgi apparatus to the luminal surface by the nature of their contents.

Two forms of secretory vesicles may be distinguished in gland 11: those that contain a disperse fibrous substance, and those that possess a much more compactly packaged product (figure 66, plate 28; figures 70 and 71, plate 29). Both these forms may be recognized in the neighbourhood of Golgi units (figure 66) as well as at the luminal cytoplasmic region (figures 70 and 71). Indeed, in the case of the latter, the tiny electron-dense granules usually associated with the secretory product in the lumen are often seen in the secretory vesicles containing the compact fibrous fraction (figure 71). From the morphological evidence so far gathered, it may be speculated that the two major secretory components found in the gland lumen are largely packaged in to different forms of secretory vesicles.

The rough ER is moderately extensively developed in this gland type. It resembles somewhat the ER in gland 6 and in the homogeneous glands, where it consists largely of parallel arrays of flattened cisternae; but in gland 11, these cisternae frequently become inflated into vesicular structures (figure 61; figures 63 and 64, plate 27; figure 67, plate 28). These swollen vesicles usually contain a finely fibrous material rather similar to the secretory product in the gland lumen. The picture presented by the considerable development of the rough ER is thus one of a cell occupied in intense secretory activity of a proteinaceous product. This conclusion is further strengthened by the very frequent occurrence of polyribosomes in the cytoplasm, particularly in areas where the ER is still in the form of flattened cisternae, and therefore probably representing the initial stages in the biosynthetic process (figure 64; figure 68, plate 28).

Golgi elements are not usually widespread or abundant (figures 61 and 67). But they do possess two very distinct kinds of smooth, small vesicles: those with an electron-lucent interior, and those with a fairly electron-dense content (figures 61 and 66). The latter seem to be restricted to the immediate environs of the Golgi apparatus; there are also some observations indicating their merging with or forming from the ER in this area (figure 66). It is possible, therefore, that these electron-dense Golgi vesicles are engaged in a shuttle service between the Golgi complex and the ER.

The origin of the translucent Golgi vesicles is unknown. Zeigel & Dalton (1962) suggest that similar vesicles may arise from portions of the rough ER cisternae that have lost their ribosomes; and they regard such vesicles as the elements responsible for the removal of fluid from the Golgi zone. The fact that there are any such vesicles prompts one to speculate that there is no direct

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DESCRIPTION OF PLATE 25 (homogeneous gland)

FIGURE 56. Golgi apparatus (*G*) has very large condensing vacuoles (*cv*). *Arrows* indicate small, smooth vesicles (*v*) in the process of being budded off from the Golgi saccules. × 32500.

FIGURE 57. Quite frequently, cytoplasmic bodies (cb_2) are observed in the environs of the Golgi apparatus (*G*), although they are found elsewhere too (cb_1). Note also secretory vesicles (*SG*) with small, smooth vesicles fusing with the limiting membrane (*arrow*). × 39000.

FIGURE 58. Large vesicles, probably secretory vesicles, near the Golgi apparatus may sometimes contain small vesicles (v_2) resembling the small Golgi vesicles (v_1). Secretory vesicles (*SG*) have a fibrous content. *Arrow* points to small vesicles in the process of budding off from or fusing with the Golgi saccules. × 39000.

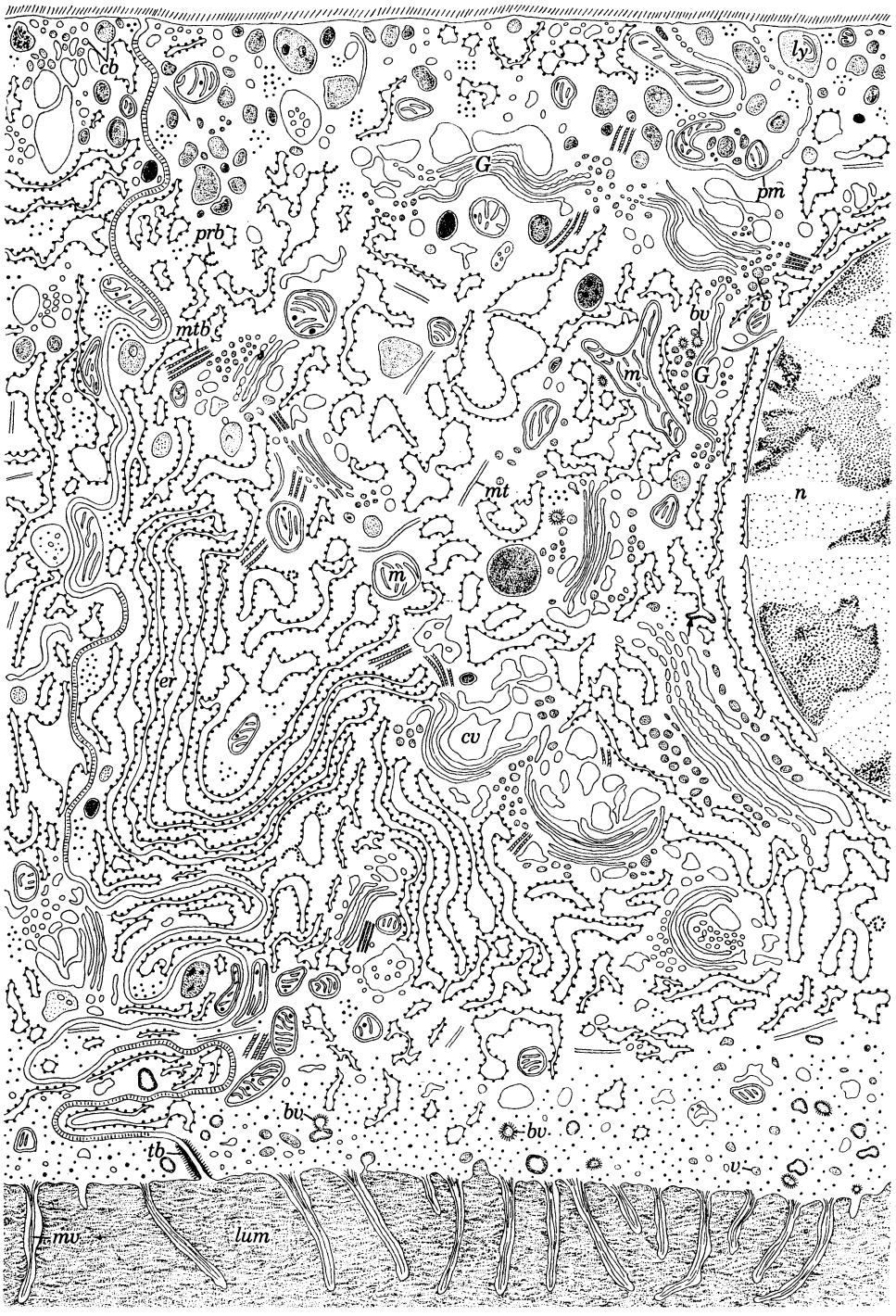


FIGURE 53. Diagram of a generalized cellular substructure of a 'homogeneous' gland.

and permanent continuity between the membrane-lined channel of the ER and that of the Golgi apparatus (Zeigel & Dalton 1962).

Cytoplasmic bodies occur widely in gland 11, but they are particularly abundant in the basal cytoplasmic region (figure 65, plate 27). In the latter region, the cytoplasmic bodies exist in a wide size range—from bodies having a diameter of 300 Å or less up to those with a diameter

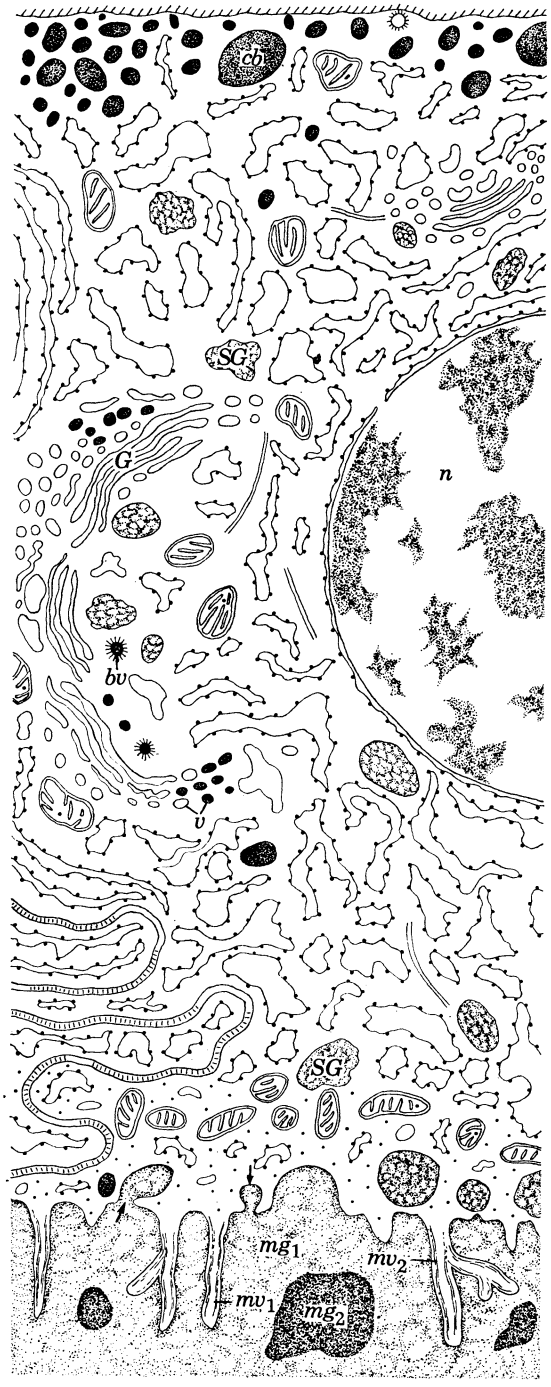


FIGURE 61

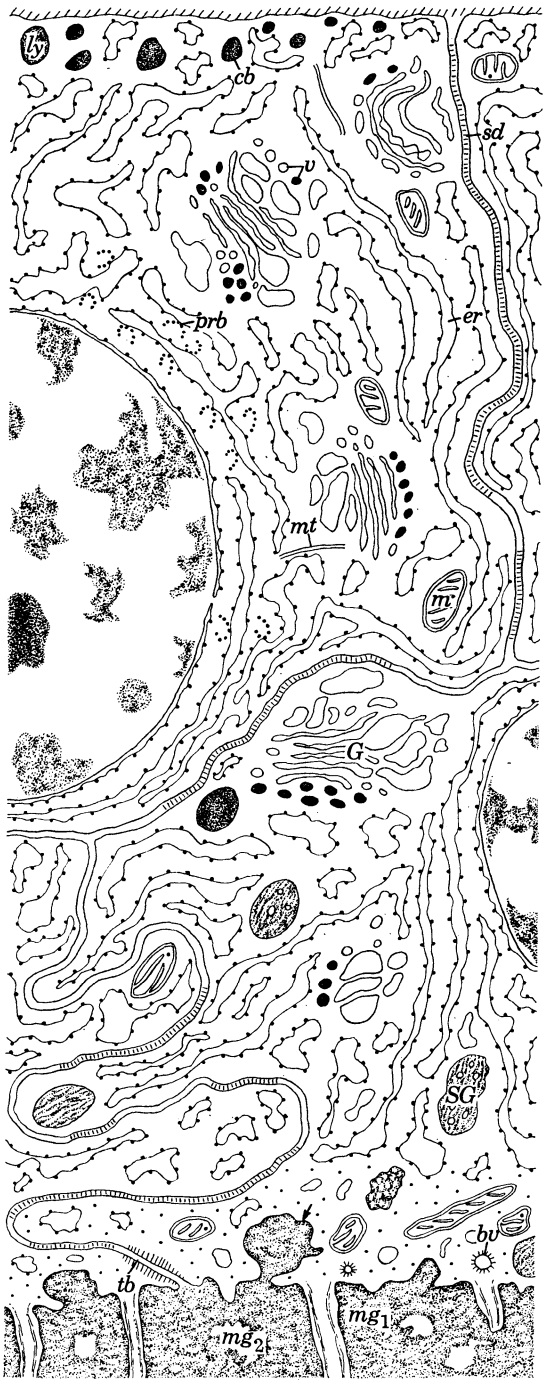


FIGURE 62

FIGURE 61. Generalized diagram of the subcellular structure of gland 11. Note the branched microvilli (mv_2) and the two components of the secretion (mg_1 and mg_2). The *arrows* point to the manner in which the elaborated secretion is extruded.

FIGURE 62. Generalized diagram of the subcellular structure of gland 12. Note the manner of extrusion of secretion (*arrow*), and the two components of the secretion (mg_1 and mg_2).

of 0.6 μm or more (figure 65)—and they seem to fuse to form larger bodies (figure 63). This is reminiscent of the situation in the locust fat-body cell, where there is intense pinocytotic activity and the resulting pinosomes seem to give rise to cytoplasmic bodies (Odhiambo 1967). In ARGs there is no obvious pinocytotic activity from the basal or lateral portions of the plasma membrane. Consequently, it is probable that precursor materials, if these are needed for biosynthetic activity, may enter the ARG cells in some other way, perhaps in molecular form and then be collected into the minute cytoplasmic bodies found at the basal cytoplasmic region.

By whatever mode cytoplasmic bodies arise, they seem to be equivalent to the so-called phagosomes (De Duve 1963; Novikoff 1961, 1963). Phagosomes are thought to be particularly involved in 'true' intracellular digestion or heterolysis, as opposed to autolysis carried out within 'derived' lysosomes, e.g. digestive vacuoles or residual bodies or autophagic vacuoles of De Duve (1963) and cytosegresomes of Ericsson & Glinsmann (1966). If this be so, and our identification of cytoplasmic bodies with phagosomes be confirmed by cytochemical and other techniques, then it is significant (*a*) that derived lysosomes are so rare in newly matured ARGs, and (*b*) that cytoplasmic bodies are often located within the Golgi zone (e.g. figure 66).

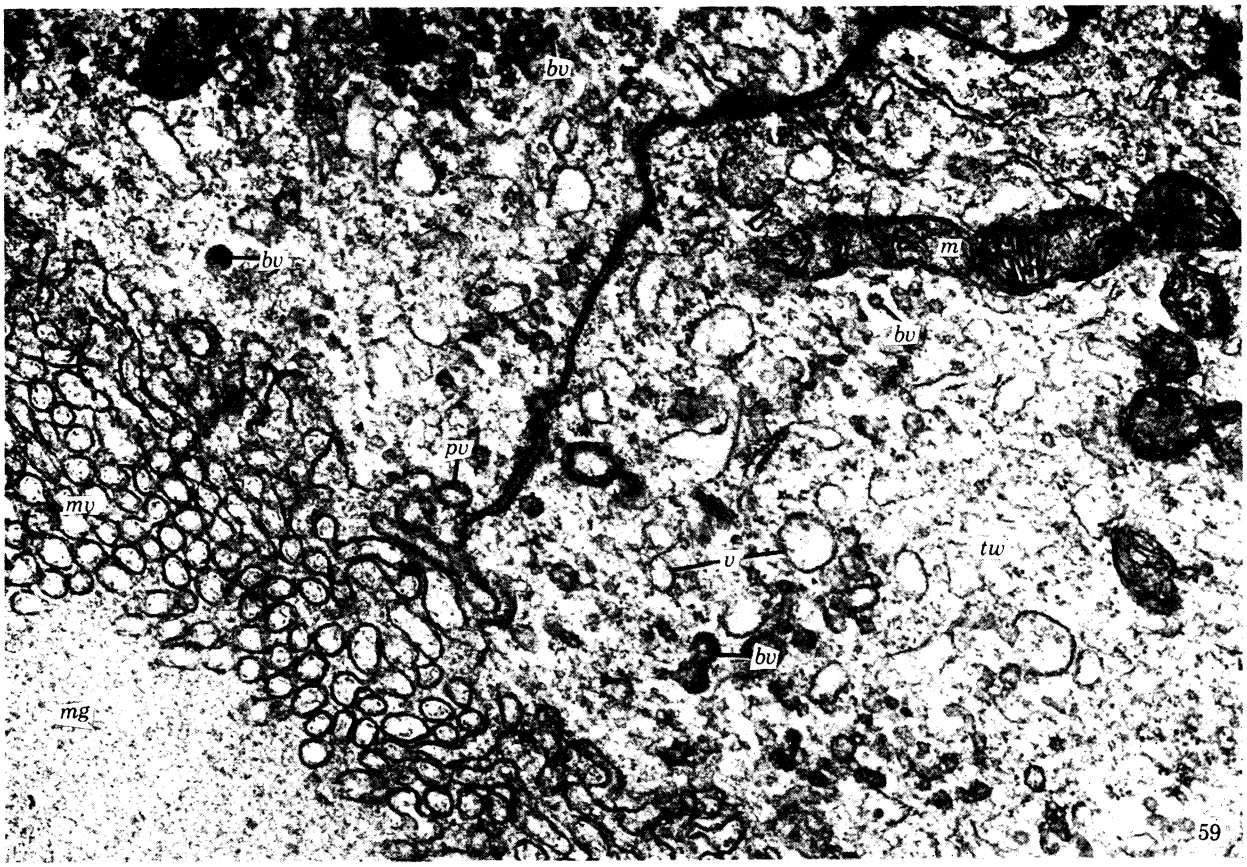
The luminal region of gland 11 is peculiar in at least two respects. First, there seems to be no well demarcated terminal-web region: in this gland, cytoplasmic organelles such as Golgi elements, the ER, and mitochondria are found almost right up to the luminal plasmalemma (figure 69, plate 29). Furthermore, large secretory vesicles occur at the very luminal surface, where their membranes presumably fuse with the plasma membrane, thus releasing the secretory product into the lumen (figures 70 and 71). This mode of extrusion of secretion is not apparently common in other locust ARGs: in the latter, small smooth vesicles are abundant in the terminal-web region and may possibly be involved in the release of the secretory products in small packages. Secondly, the luminal region in gland 11 is peculiar in that most of the microvilli are very variable in diameter and are branched; a few others are clavate, while some other microvilli are unbranched (figure 70). The functional significance of these morphological variants is not known.

Gland 12

The cytoplasmic organization of glands 11 and 12 is much alike (figures 61 and 62), although the physical and histochemical characteristics of the secretion of gland 12 is peculiar in several details: for instance, the globules that are embedded in the neutral mucopolysaccharide mass do not stain for polysaccharide or lipid, they seem to consist entirely or largely of protein (Odhiambo 1969*a*). Because of the cytoplasmic resemblances, only aspects of the structure of gland 12 that are distinctive will be discussed in the following paragraphs.

The cytoplasmic bodies, which are abundant in the cytoplasmic region (figure 73, plate 31), apparently eventually reach the Golgi zone (figure 73; figures 74 and 75, plate 31). In this area, one may observe what looks like the incorporation of cytoplasmic-body contents into the Golgi saccules: the same kind of finely divided material seen in cytoplasmic bodies is also recognized in the saccules (figure 73). Thus, the central importance of cytoplasmic bodies in the biosynthetic process is further vindicated.

The secretory granules are of two kinds: one type having a fine, sparsely distributed content (figure 75; figures 76 and 78, plate 32); the other kind containing a more densely packed fibrous secretion (figure 76). It is difficult to distinguish the first type of secretory vesicle from cytoplasmic bodies; and, similarly, it is a problem to know when a vesicle is a secretory vesicle and



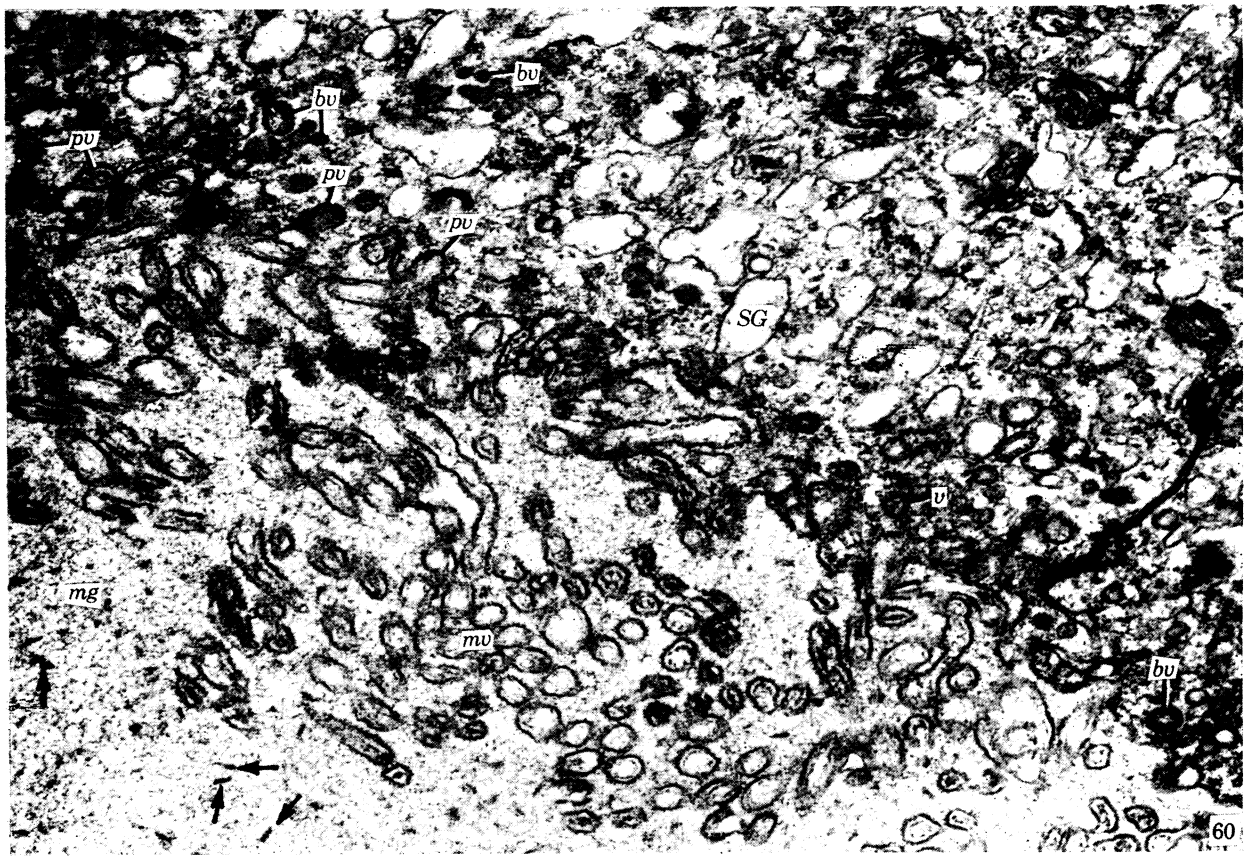
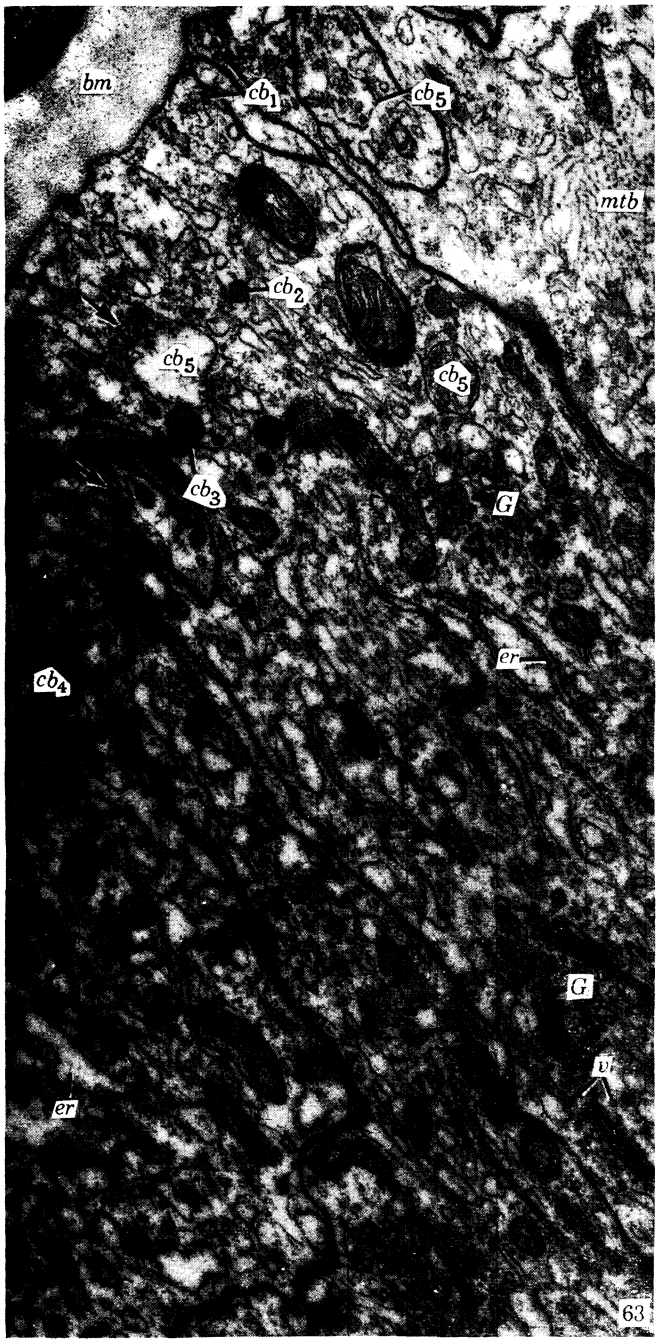


FIGURE 59. The apical cytoplasmic region. The terminal-web area (*tw*) contains small vesicles of various sizes (*v*) which seem to arise as a result of pinocytotic activity (*pv*). The luminal content (*mg*) consists of a minutely granular or fibrous substance. × 38000.

FIGURE 60. The luminal region, showing the secretion as consisting of short fibrillar structures (*arrows*) embedded in a minutely granular matrix. Note also the pinocytotic pits (*pv*) on the luminal plasmalemma, and the coated vesicles (*bv*). × 38000.

(*Facing p.* 106)



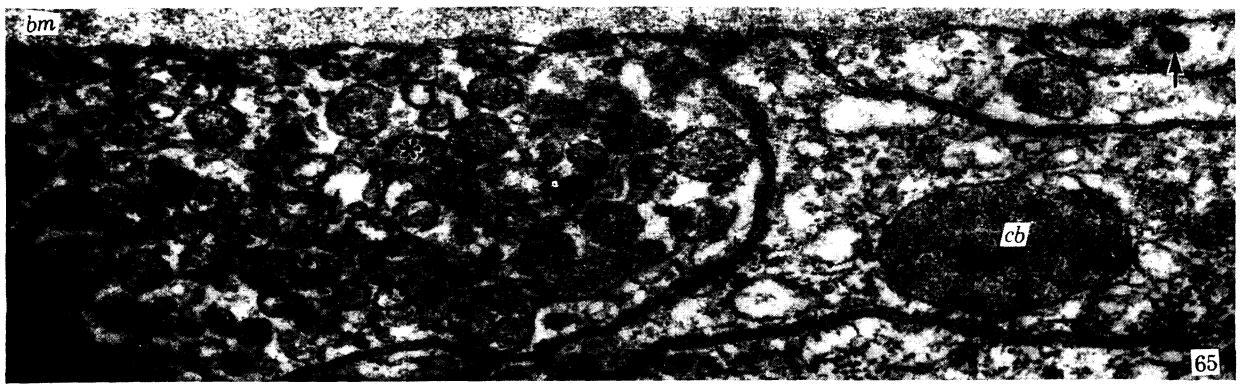


FIGURE 63. The basal cytoplasmic region showing cytoplasmic bodies of various sizes, from minute (cb_1) to large (cb_5). They seem to have grown to this large size by incorporating smaller bodies (*arrows*). But some of the vesicles being incorporated resemble Golgi vesicles (*v*). × 24000.

FIGURE 64. The Golgi units (*G*) are small, but they have a few small coated vesicles (*bv*) of unknown origin. Note also the large numbers of polysomes (*prb*). × 24000.

FIGURE 65. Numerous cytoplasmic bodies of various sizes are generally found in the basal cytoplasmic region (*star*). × 52000.

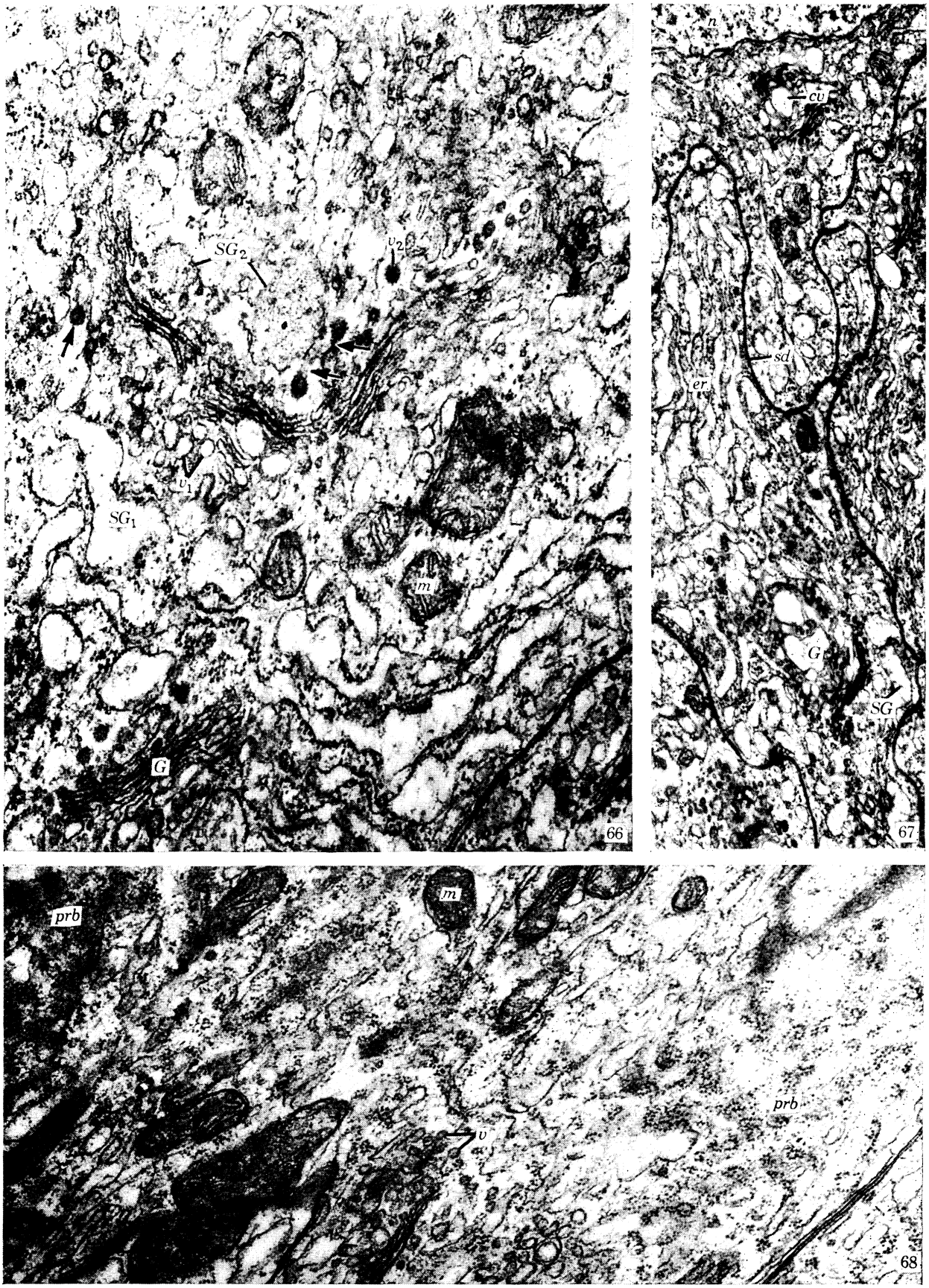
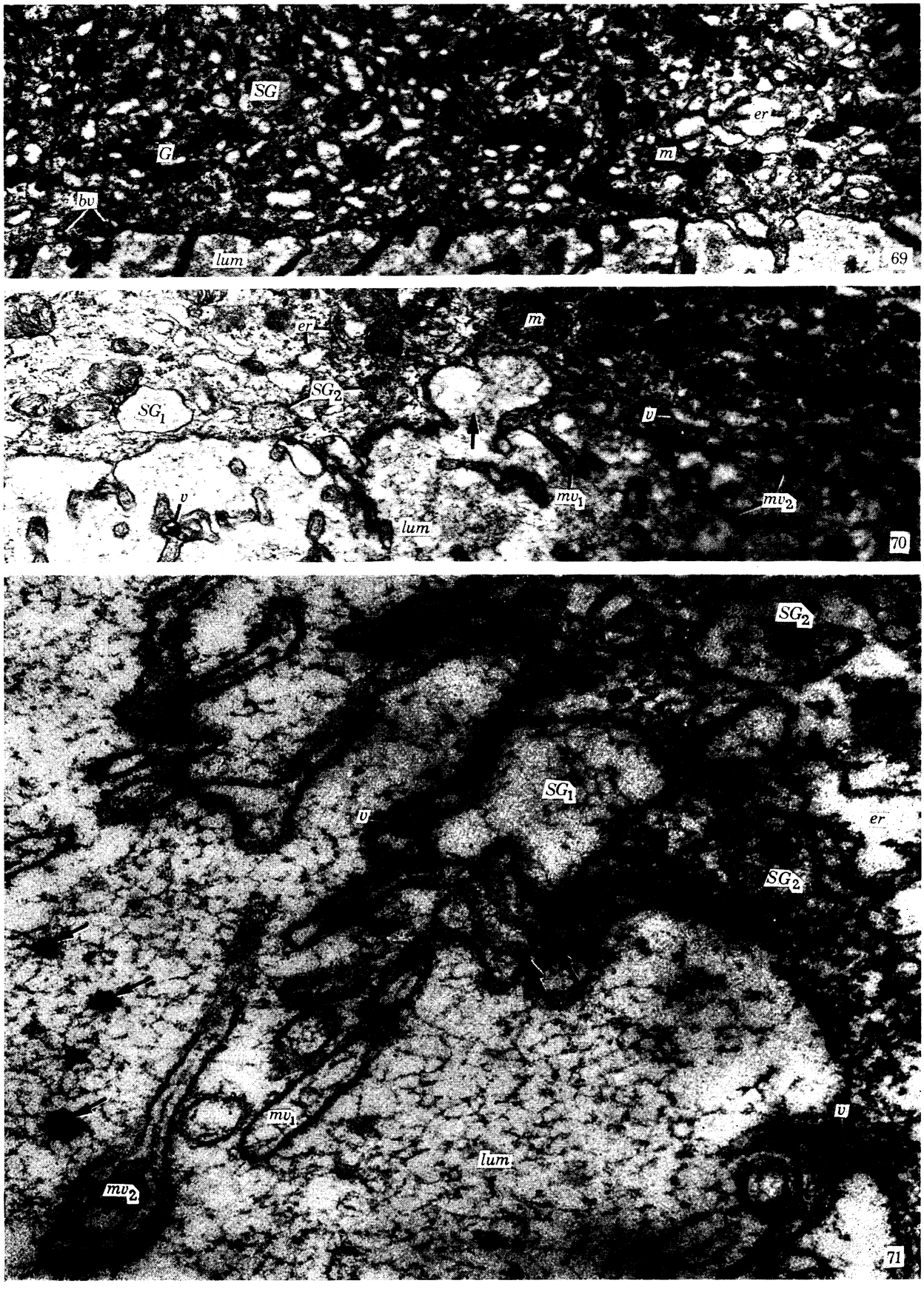


FIGURE 66. Secretory vesicles containing two kinds of secretion in the immediate neighbourhood of the Golgi apparatus (SG_1 and SG_2). Vesicles containing an electron-dense material (v_2) seem to be formed from the ER in the Golgi zone (*arrows*). Small vesicles with translucent content are also observed in the Golgi zone (v_1). × 52000.

FIGURE 67. Extensive and largely flattened rough ER (*er*). Golgi complexes (*G*) are rather small. × 24000.

FIGURE 68. Numerous polyribosomal deposits in the cytoplasm (*prb*). × 38000.



FIGURES 69 to 71 For description see facing page.

not just a swollen ER cisternae. In regard to the latter problem it is noted that the rough ER, which is normally rather flattened in gland 12, becomes swollen when it is adjacent to the Golgi apparatus (figure 75). Perhaps this is an area where material already processed by the greater proportion of the rough ER is stockpiled while waiting to be elaborated by the Golgi elements into the final mucopolysaccharide product.

The terminal-web region in gland 12 is much more distinct than in gland 11, and it has a few coated vesicles (figure 77, plate 32) and other small, smooth vesicles (figures 77 and 78). But the secretory vesicles still seem to traverse this region and empty their contents into the gland lumen in much the same way as in gland 11 (figure 78).

The final secretion product within the lumen consists largely of a minutely fibrous substance within which are embedded what are mainly electron-transparent 'globules' (figure 79, plate 32). What factors lead to this segregation of the secretion into two components is not clear. But it is possible that the two components are already segregated by the Golgi apparatus into two kinds of packages, as discussed earlier on.

Gland 16 (*the functional seminal vesicle*)

The cytoplasmic features of gland 16 are such that one is led to believe that the gland, if it is glandular at all, is not engaged in a particularly intense biosynthetic effort for export. For instance, the rough ER occurs as small, scattered elements (figure 80; figures 84 and 85, plate 34; figure 88, plate 35); again, Golgi units are very scarce and small (figure 80; figures 84 and 86, plate 34). Thus, the existence of these elements in gland 16, and of free ribosomes or their aggregates in the cytoplasm (figure 80; figure 83, plate 33; figures 84 and 88), may be principally concerned in tissue growth and maintenance. However, the cytoplasm contains a number of smooth-surfaced ER cisternae which may contain some secretory product of unknown nature (figure 88). A histochemical study of the epithelium of gland 16 does indicate it to be acidophilic (Odhiambo 1969*a*), which may well be imparted by the contents of these smooth ER cisternae.

Large membrane-bound vacuities, of various sizes, are often found within the cytoplasm (figure 80; figures 81 and 82, plate 33). They sometimes lie quite deep in the cell, and do not seem to have direct communication with the gland lumen (figure 81). Of peculiar interest is the varied content of these vacuities, comprising granular material, vesicles, rod-like substances, and bristly vesicles, all of which may possibly be remnants of a necrotic process (figure 82). Frequently, such vacuities are located in the apical cytoplasmic region (figure 88), from where they may presumably be extruded into the gland lumen. If so, then the varied bristly vesicles and other curious objects found in the gland lumen, particularly in the anterior half of the

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Description of plate 29 (gland 11)

Figure 69. There is no distinct terminal-web region, cytoplasmic organelles being found almost throughout the region. × 32500.

Figure 70. Some of the secretory vesicles in the apical region have a compact fibrous content (SG_2), others have a more sparsely fibrous substance (SG_1). These seem to extrude their secretion by their limiting membranes fusing with that of the luminal plasmalemma (*arrow*). The microvilli are rather scattered (mv_1) and may be branched (mv_2). × 24000.

Figure 71. Secretory vesicles have two types of contents (SG_1 and SG_2). The electron-dense granule found in one type (SG_2) may also be seen in the lumen (*arrow*). These secretions seem to be extruded by a reverse pinocytotic process (*two arrows*). × 92000.

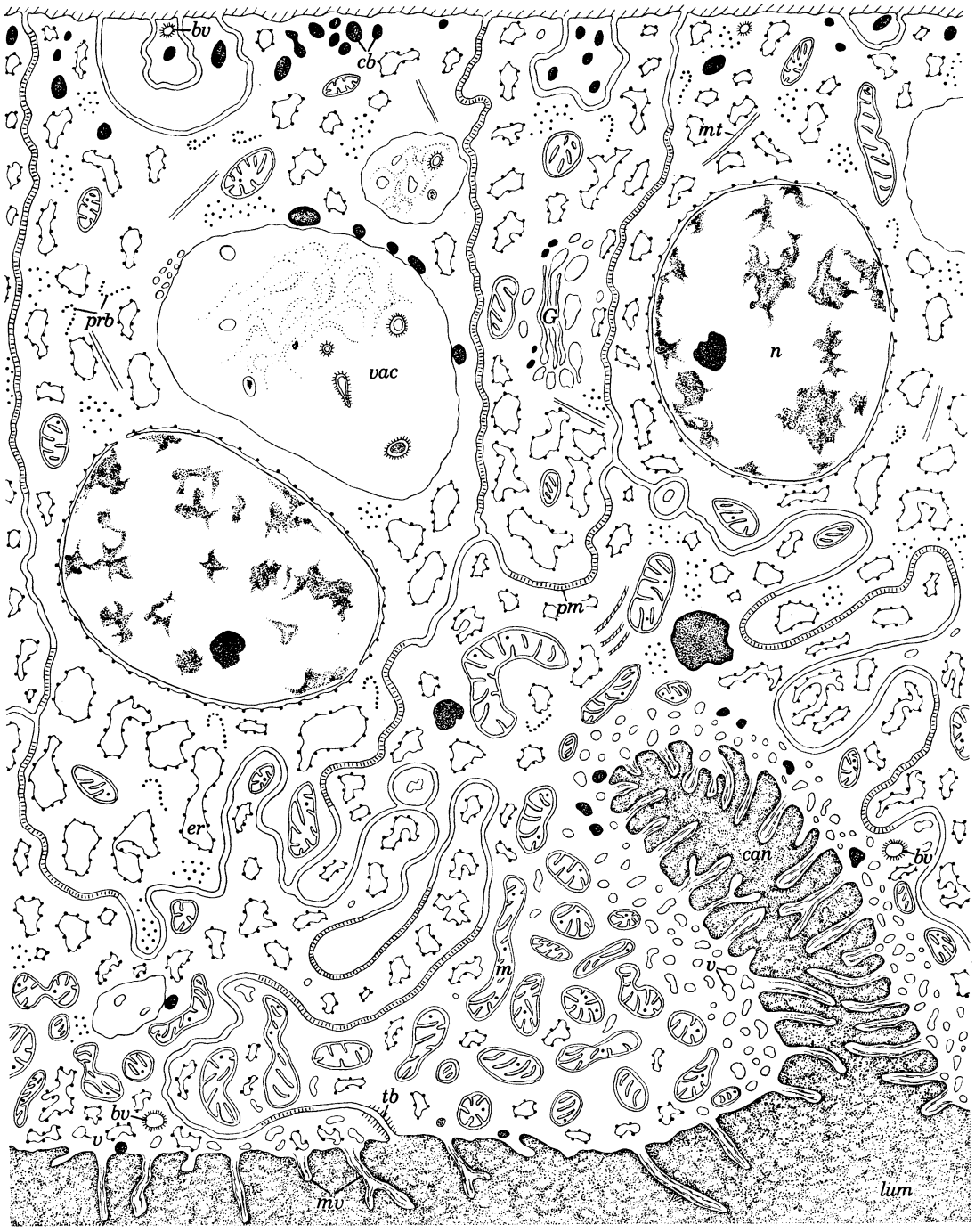


FIGURE 80. Diagram summarizing the cellular substructure of the apical or middle portion of gland 16 (or the functional seminal vesicle).

gland, may have their origin in the cytoplasmic vacuities (figure 90; figure 91, plate 36). But they may, in addition, be the result of the fragmentation and dissolution of the apical regions of the cytoplasm. In the anterior portion of gland 16, the apical portion of some of the cells lining the gland lumen in this multi-layered ARG (figure 80) may frequently be cut off and released into the lumen, where it is subsequently fragmented and lysed (figure 90; figures 91

and 92, plate 36). This finding further supports the light-microscope studies which reveal the release of so-called vesicular, slightly acidophilic material into the gland lumen (Odhiambo 1969*a*). Cell-death activity seems to accompany maturation processes in all ARGs in the early adult stage of the male locust; but in gland 16, this activity apparently continues throughout the adult life of the insect.

In the anteriormost portion of the gland, where this cell-death activity goes on most actively, there are few spermatozoa in the lumen (figure 92). But more posteriorly, the lumen is swollen with spermatozoa, where the latter are often arranged in an almost crystalline fashion (figure 95, plate 37). The very regular sperm arrangement is due to the insertion of heads of sperm bundles into a 'cap' of PAS-positive, densely fibrous material (figure 89, plate 35; figure 95). As it is to be expected, the anterior regions of the sperm bundles are more regularly oriented than the distal parts (figure 95).

The mature spermatozoon shows the normal general structure of the axial ciliary complex, comprising the two central fibres and the nine double outer fibres, with each of the nine subfibre A bearing two arms (Gibbons & Grimstone 1960). But the locust spermatozoon exhibits several unusual characters, some of which have already been recorded by Kaye (1964) in the cricket spermatid: the central fibres are dense and not hollow, and bear a central, more electron-opaque core; both the subfibres A and B possess an extra 'arm' which extends outwards; finally, there are nine 'accessory fibres' located just external to the doublets, these accessory fibres are also dense with a central opaque core (figure 93, plate 36). The whole spermatozoon is enclosed within a fibrous sheath of a unique structure: it seems to consist of rod-like elements, 40 to 60 Å in diameter, arranged in a hexagonal fashion (figures 93 and 94, plate 36).

There is a concentration of mitochondria in the apical cytoplasmic region adjoining the luminal surface (figures 80, 81 and 90). The functional significance of this distribution is not clear, except that at the luminal region are also found abundant smooth ER vesicles, which presumably contain an unknown secretion (figure 88). Another feature of outstanding interest is the formation of channels (canaliculi or crypts) which penetrate deep into the apical cytoplasm and are directly connected with the gland lumen (figures 80 and 88). The canaliculi are lined with short, branched microvilli (figure 88). Since the epithelium of gland 16 is multilayered, the frequent occurrence of the canaliculi may more intimately bring a considerable section of the epithelium into intercommunication with the luminal situation. These canaliculi are found most often in the anterior half of the gland.

The structural character of the microvilli changes according to the section of gland 16 examined. In the anterior half, some sections bear no microvilli at all (figure 92); but where the latter are present, they exist as short, branched structures (figures 80, 88 and 90). In the posterior portion of the gland, the microvilli are long, unbranched, and closely packed (figure 87, plate 34; figure 95). This regionalization presumably has some functional significance, as yet unknown.

Discussion

Characterization of the glands into types

An earlier study of the male locust ARG complex showed that the glands can be characterized into nine types by using histological, histochemical and phase-contrast techniques (Odhiambo 1969*a*). The same study also revealed that the glands are of a simple epithelial nature, only

three gland types consisting of more than one cell layer—glands 4, 12 and 16. An ultrastructural study has now established the fact that these nine gland types display a combination of characteristics that distinguish them one from another.

The simplest distinguishing characteristic has proved to be the fine-structural nature of the final secretory product. For example, the ultrastructural features of the secretions in glands 1, 3, 6, 11, 12 and 16 are so distinctive as to preclude any hesitation in identifying their origin at once. The identification of the other few remaining secretions—those of glands 2 and 4, and the 'homogeneous' glands—is more difficult on purely fine-structural grounds. But these glands can be typified on other characteristics, just as the rest of the ARGs can be further particularized by their cytoplasmic features. Only a few examples need be mentioned here: the so-called multivesicular bodies by means of which macro-apocrine secretion occurs in gland 2; the enormously swollen rough ER of gland 4; the branched or clavate microvilli of gland 11; and the canaliculi of gland 16.

Taking all these various features into account, it is clear that the cytoarchitecture of the locust ARG complex assumes a very simple form, in that the nine different kinds of secretions are produced by an epithelial tissue which has been compartmentalized 'vertically' into nine glands; it has not taken a more complex form, in which the glands would have been arranged serially in a 'horizontal' manner. The latter arrangement apparently obtains in some lepidopterous insects (Norris 1932; Musgrave 1937; Callahan & Cascio 1963). The simple, vertical

Description of plate 31 (gland 12)

Figure 73. The basal cytoplasmic region has numerous cytoplasmic bodies (cb_1) adjacent to the basement membrane (*bm*); further inward, the cytoplasmic bodies may attain enormous size (cb_2), sometimes adjacent to the Golgi apparatus (cb_3). The latter often contains similar fibrous material (*G*). Golgi apparatus has small vesicles (v_1) some of which contain a fibrous material (v_2). × 32500.

Figure 74. Cytoplasmic bodies (*cb*) and microtubular arrays (*mtb*) are often located near the Golgi complex (*G*). There are coated vesicles (*bv*) of unknown origin. × 38000.

Figure 75. Golgi units (*G*) are characteristically rather small, but they have in their neighbourhood cytoplasmic bodies (*cb*) and enormous ER cisternae (*er*). × 32500.

Description of plate 32 (gland 12)

Figure 76. Secretory vesicles have two types of contents (SG_1 and SG_2). Golgi saccules (*G*) appear to contain a fibrous material. × 39000.

Figure 77. The luminal region shown in an oblique section. The microvilli (*mv*) have a dense core. Coated vesicles (*bv*) are common. × 52000.

Figure 78. The terminal bar (*tb*), with dense filamentous material organized longitudinally along the bar. Some secretory vesicles (*SG*) contain an electron-lucent material, which can also be recognised in the lumen (*mg*). × 38000.

Figure 79. The luminal content comprises a minutely fibrous component (mg_1) and electron-transparent globules (mg_2). × 32500.

Description of plate 33 (gland 16)

Figure 84. Survey micrograph to show the sparseness of ER elements (*er*) and Golgi units (*G*). × 24000.

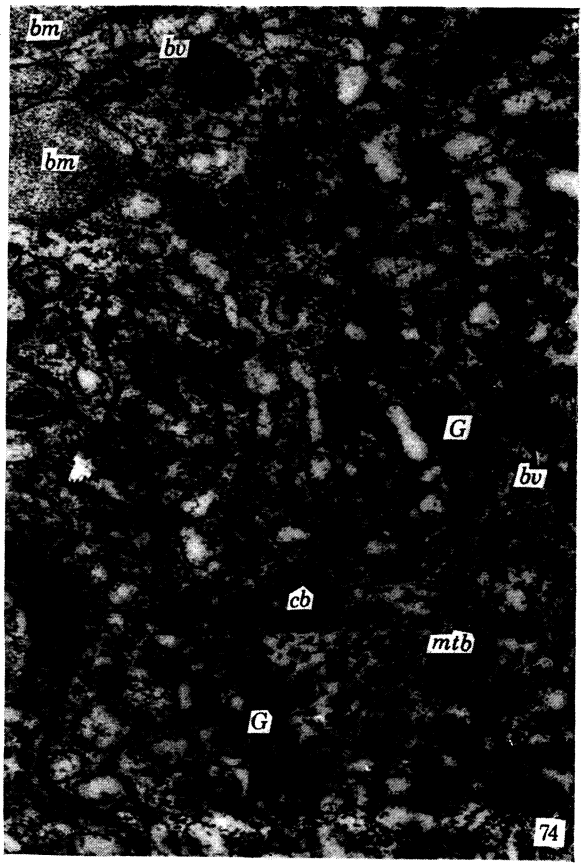
Figure 85. Septate desmosomes in tangential section. × 52000.

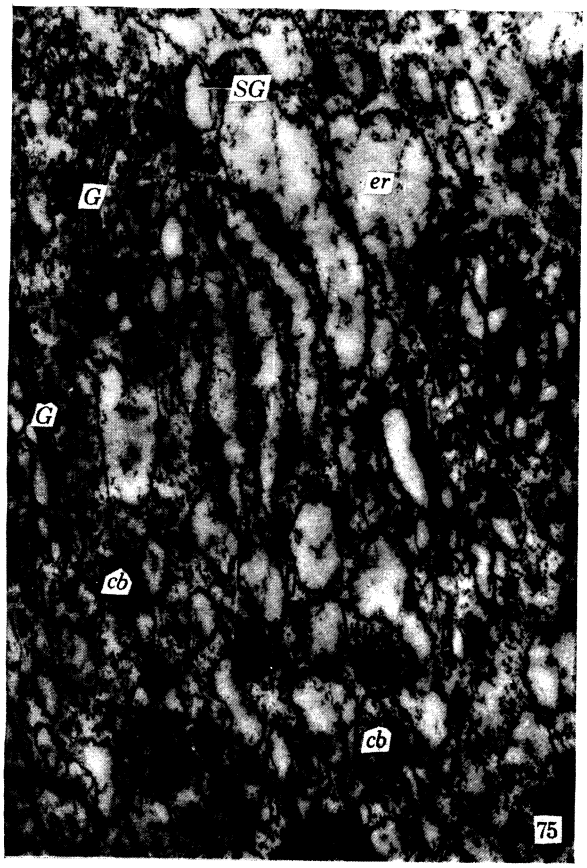
Figure 86. Some of the Golgi vesicles have a light content, some a dark substance (*v*). The Golgi units (*G*) are small in this gland. × 32500.

Figure 87. The long and closely packed microvilli (*mv*) in the proximal portion of the gland. They may have small, smooth vesicles (*v*) inside them. Note also coated vesicles (*bv*) and long fibrous filaments (*star*) in the luminal region. × 57500.

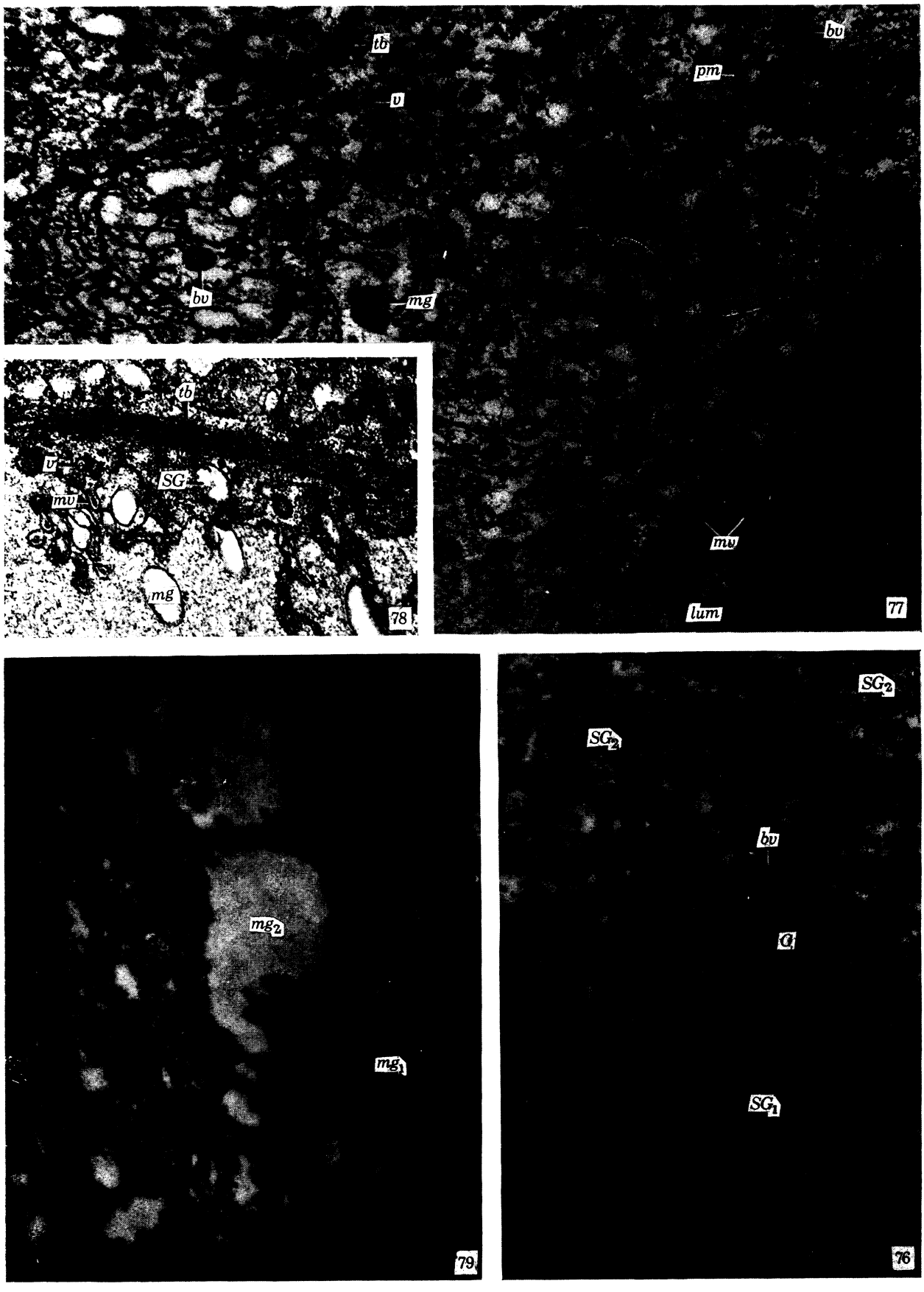
FIGURE 72. The secretion within the gland lumen consists of a matrix of finely fibrous material (mg_1) within which are imbedded minute electron-dense granules (*arrows*) and large fibrous granules (mg_2). The minute granules are also found in the latter (*arrows*). Note the empty 'vacuities' in the large granules (*star*). × 32500.

(*Facing p.* 110)

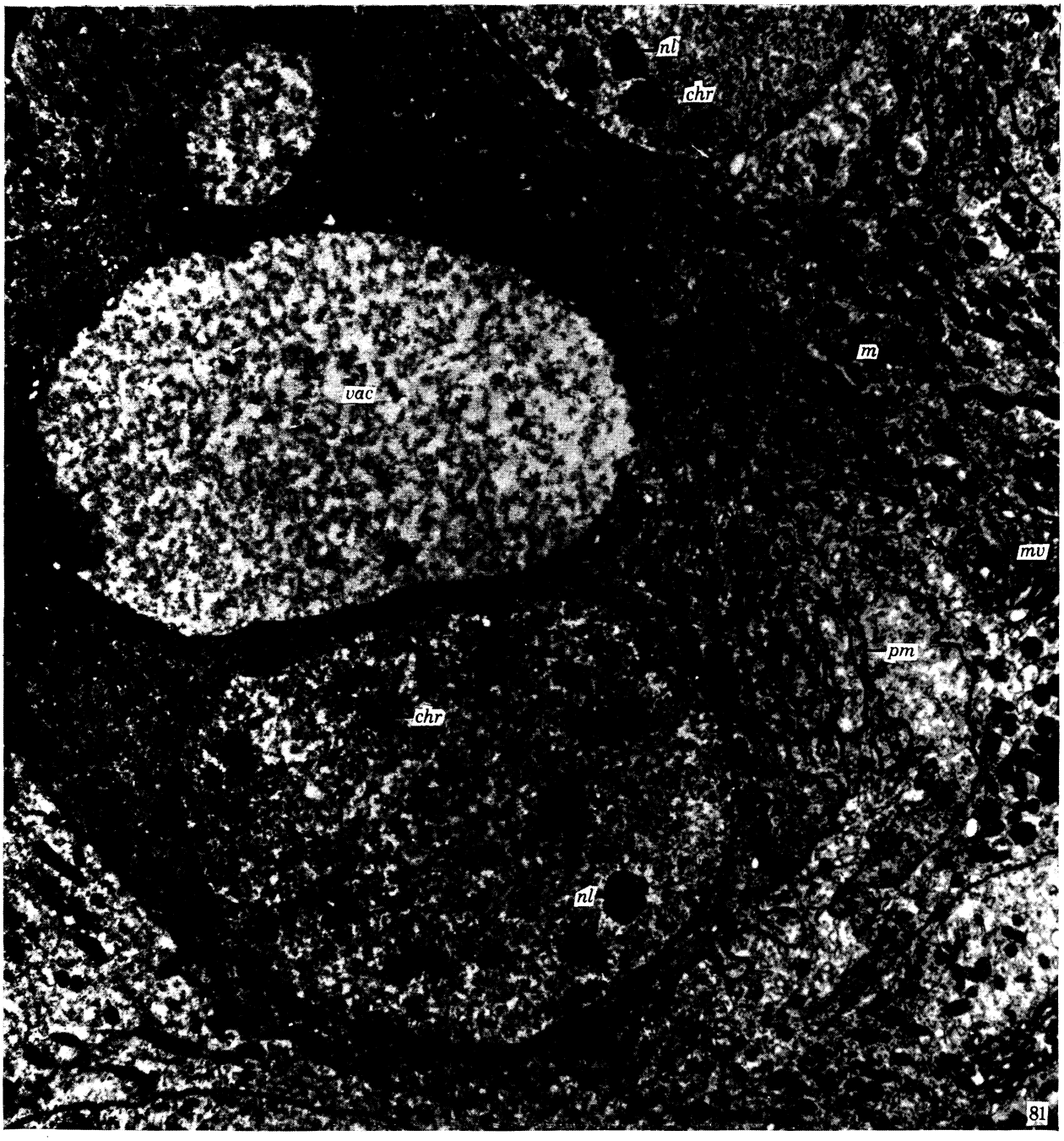


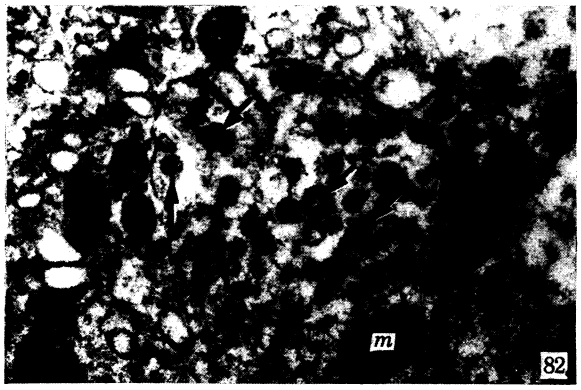


FIGURES 73 to 75. For description see p. 110.



FIGURES 76 to 79. For description see p. 110.





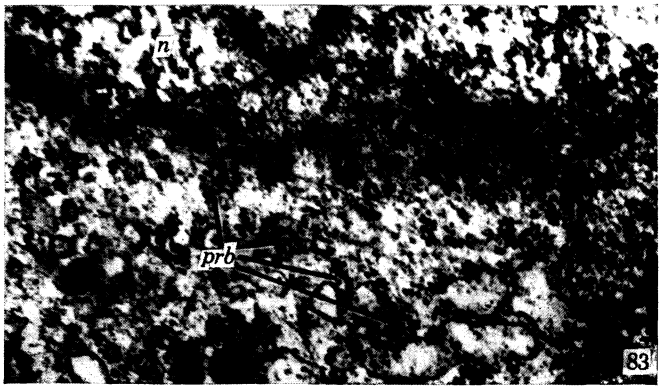
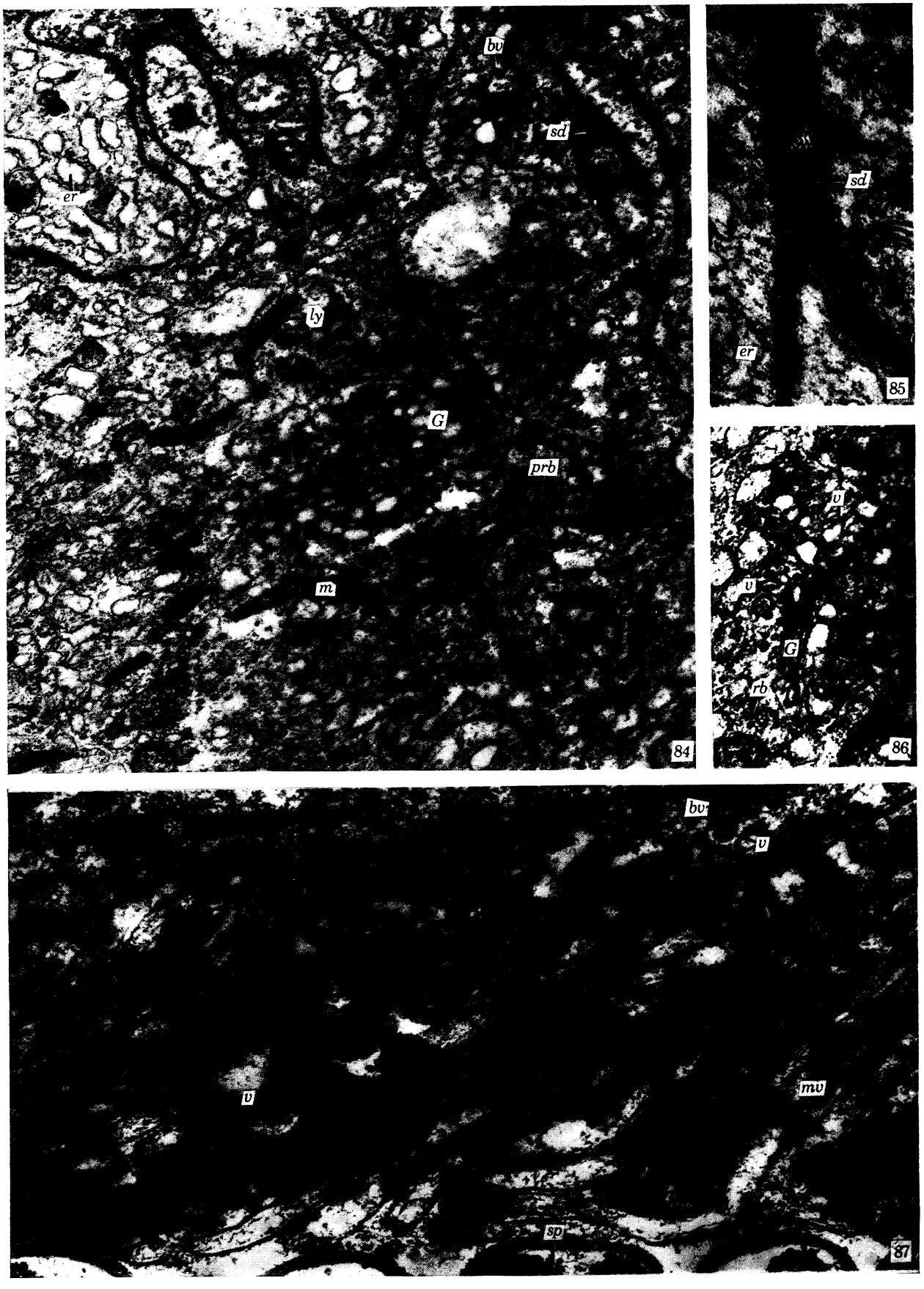


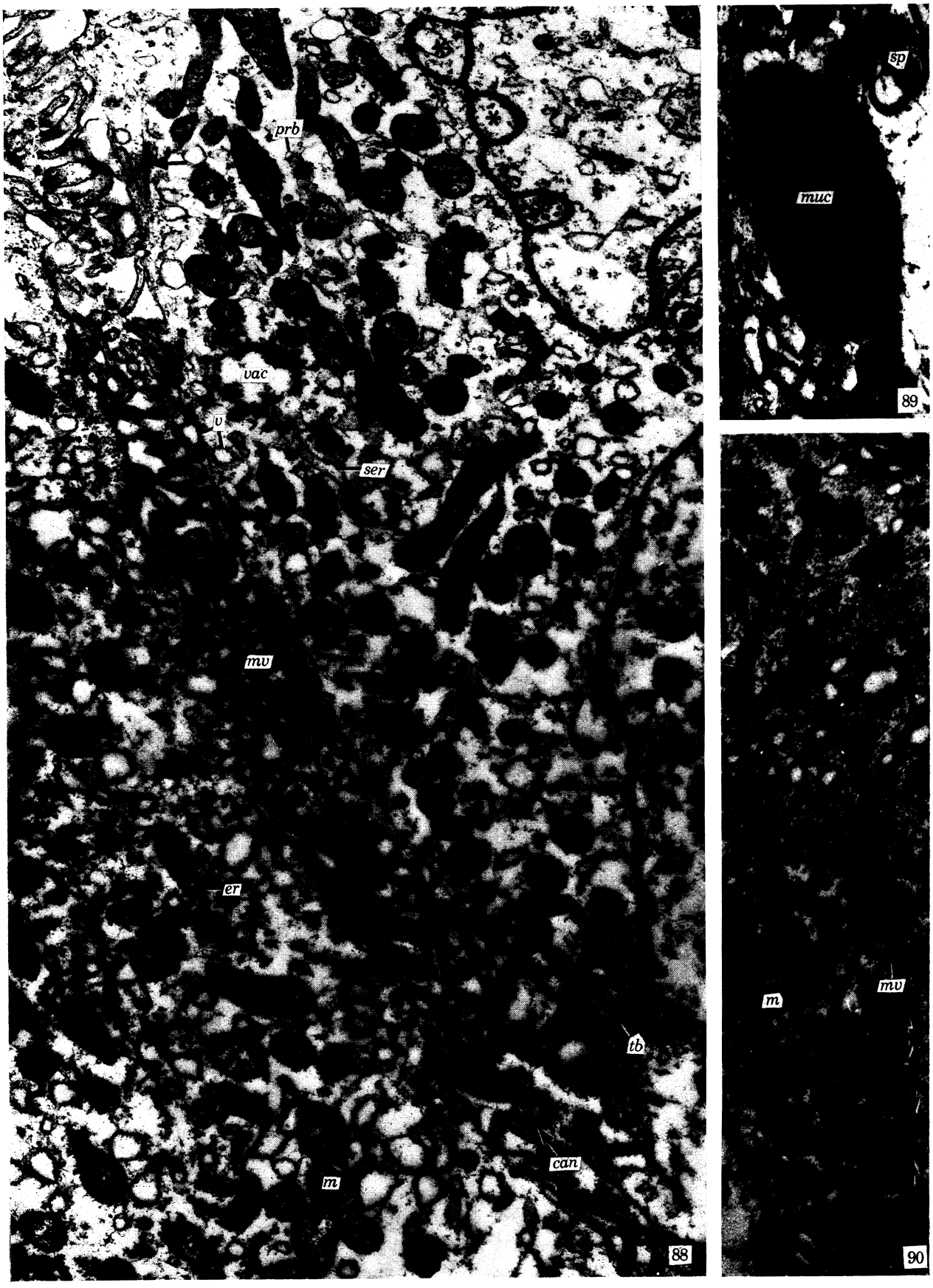
FIGURE 81. The cells may have vacuities of enormous size (*vac*). The epithelium is multicellular. × 7500.

FIGURE 82. The cytoplasmic vacuities contain all sorts of peculiar structures that appear to be breakdown products (*arrows*). × 23000.

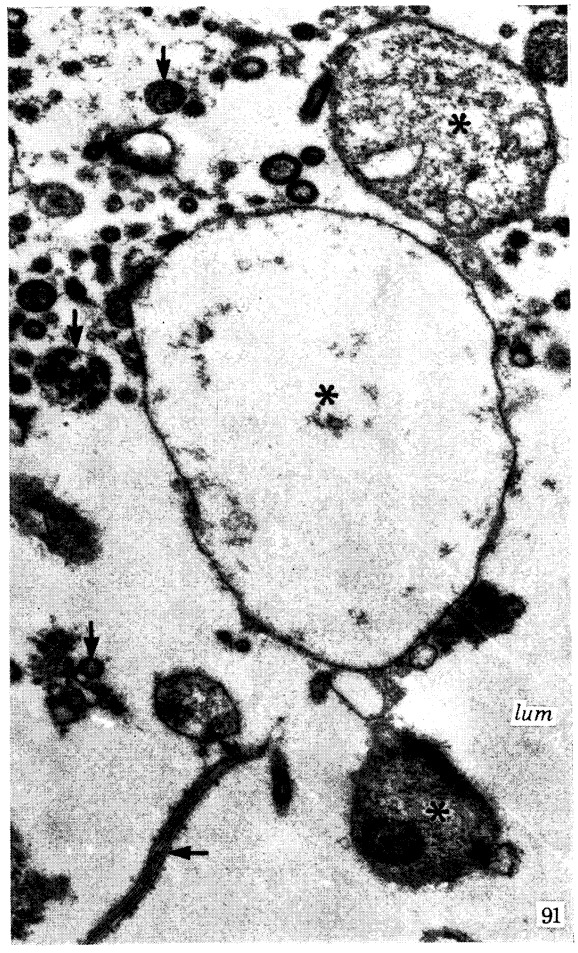
FIGURE 83. Perinuclear region, containing numerous polyribosomes (*prb*). × 52000.

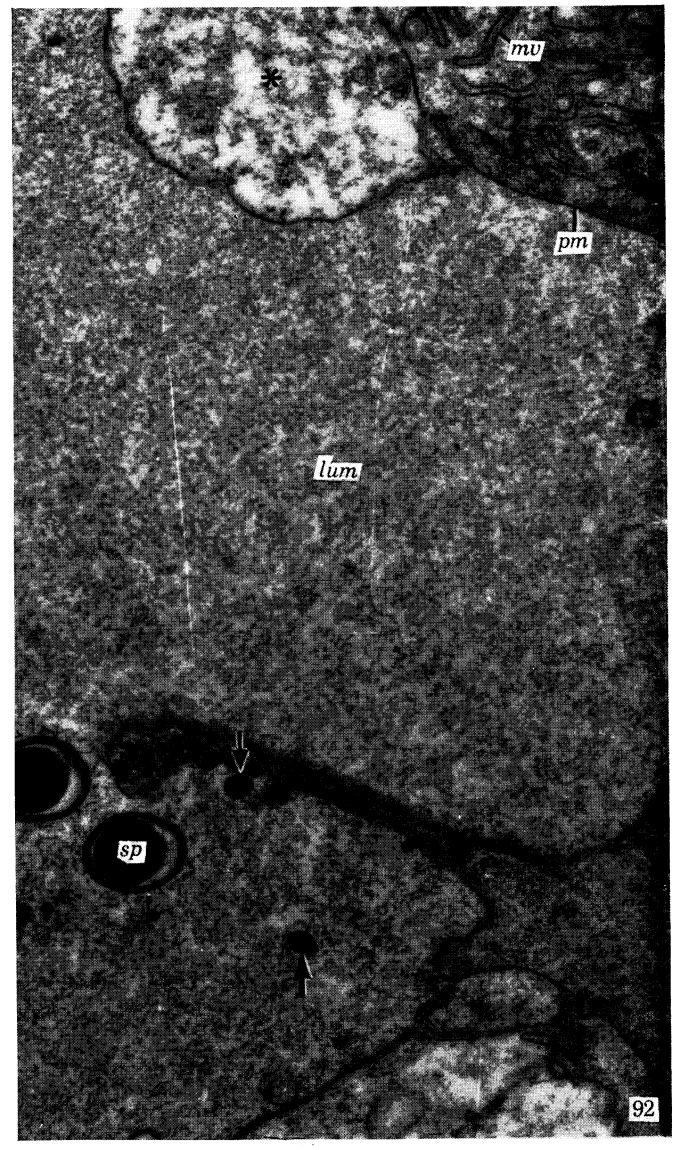


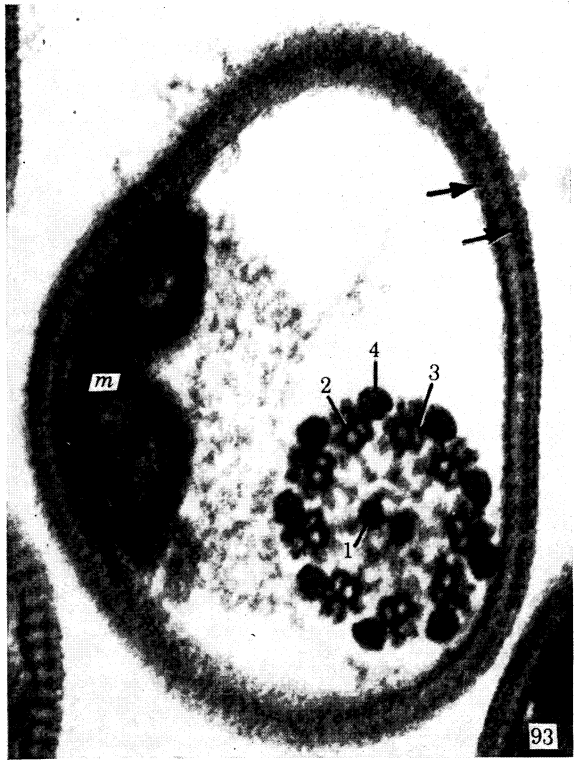
FIGURES 84 to 87. For description see p. 110.



FIGURES 88 to 90. For description see p. 111.







FIGURES 91 to 94. For description see p. 111.

FIGURE 95. Within the major portion of the gland, mature spermatozoa are arranged in almost crystalline fashion (*1–4*). This is due to the spermatozoa being embedded, by their heads, into a densely fibrous 'cap' (*muc*). Towards the tail-ends, the spermatozoa are less orderly oriented (*5*). Arrow indicates the spermatozoon's axial ciliary complex. × 9000.

arrangement of the locust ARG complex offers a relatively simple experimental material for investigating maturation processes, with the added advantage that one may, at the same time, observe the differential action of regulatory hormones (and other controlling factors) on the different cell types so conveniently isolated from each other.

Secretory apparatus and process

Gland 16 does not appear to produce a definite secretion of its own; rather it acts as a storage organ for the mature sperm released from the testis (Odhiambo 1969*a*). It is therefore not surprising to find that an electron-microscopic study of this gland reveals sparse rough ER and Golgi elements—the main cytoplasmic organelles concerned in the biosynthesis of products for export—although there is a quantity of smooth ER which may be engaged in secretion of as yet unknown identity. Thus, the glandular nature of gland 16 (or the functional seminal vesicle) is in doubt; that of the other gland types (glands 1, 2, 3, 4, 6, 11 and 12 and homogeneous glands) is not. These produce exportable substances, and they correspondingly possess a well-developed secretory apparatus.

An outstanding result of the present observations is the manner in which the secretory apparatus in the ARGs is modified according to the type of secretion it produces. For example, while in gland 3 (which produces an acidic lipoprotein complex) the Golgi apparatus is obscure, in gland 4 (which produces a neutral mucopolysaccharide) Golgi elements are a dominant feature of the cytoplasm. Again, while in gland 1 (producing a proteinaceous crystalline secretion) the rough ER takes the form of enormously swollen cisternae almost crowding out other cytoplasmic organelles such as mitochondria and microtubules, in 'homogeneous' glands (which produce a glycoprotein) the rough ER is largely arranged in the form of rather flattened, parallel arrays of cisternae. Obviously, specificity of a secretion calls for a corresponding specificity in the subcellular organization of the secretory machinery. No attempt has been made here to elucidate the manner in which this subcellular specificity has arisen, in the locust ARG, in an instance in which each of the ARG masses arises from a single ampulla of the diverticulum of the tenth embryonic abdominal segment (Else 1934; Roonwal 1937); but the question is an intriguing one.

DESCRIPTION OF PLATE 35 (gland 16)

FIGURE 88. Canaliculi (*arrow*) frequently penetrate the cytoplasm from the lumen. Such channels are lined with short microvilli (*mv*). In the cytoplasm are both smooth (*ser*) and rough ER (*er*). There are many interdigitations of adjacent cells (*stars*). × 24000.

FIGURE 89. Mucous sheath (*muc*) in which sperm heads are embedded. × 32500.

FIGURE 90. A large part of a cell being cut off and fragmented into the lumen (*star*). Note also the possible products of lysis in the lumen (*arrows*). The luminal region has a concentration of mitochondria (*m*) near the microvilli (*mv*). × 18000.

DESCRIPTION OF PLATE 36 (gland 16)

FIGURE 91. Cytoplasmic fragments (*stars*) and various breakdown products within the lumen (*arrows*). × 23000.

FIGURE 92. Anterior portion of the gland showing only a few isolated spermatozoa (*sp*). Note also a cytoplasmic fragment (*star*) and some lysis products (*arrow*) in the lumen (*lum*). × 22500.

FIGURE 93. A mature spermatozoon in transverse section. Note especially the various components (*1*, *2*, *3*, *4*) of the axial ciliary complex. The fibrous sheath enclosing the spermatozoon seems to consist, at least partly, of minute tubular elements (*arrows*). × 175000.

FIGURE 94. A mature spermatozoon (part) in oblique section. Note especially the structure of the sheath (*star*). × 102500.

It is not yet certain what function is carried out by the small, smooth-surfaced vesicles found in the periphery of the Golgi apparatus, which exist particularly abundantly in glands 1, 2 and 4. Caro & Palade (1964) think they may function as 'shuttle carriers' between the rough ER, the smooth-surfaced part of the ER adjoining the Golgi complex, and the condensing vacuoles of the Golgi apparatus. Employing the Gomori test for acid phosphatase activity, Novikoff (1963) and his associates have shown acid phosphatase activity in one saccule of the Golgi apparatus and in some of the small peripheral vesicles in renal cells and neurones of the rat; he also demonstrated this enzymic activity around the rim of the membrane limiting recently formed secretory granules of Paneth cells of the rat ileum. Cytochemical evidence of acid phosphatase activity has also been adduced by Osinchak (1964) in the hypothalamic neurosecretory cells of the rat. He labelled Golgi-derived membranes with thiamine pyrophosphate, and showed that some of the small vesicles recently pinched off from the Golgi saccules also stain for acid phosphatase. He proposed two alternative ideas as to the presence of acid-phosphatase activity in these structures: the activity may be involved in the synthesis or condensation of the secretion product, or, since it is absent in mature secretory vesicles, it may be entirely unrelated to the secretion process and simply be the result of carry-over from previous lysosomal activity. The cytochemical evidence for the suggested function of the peripheral Golgi vesicles acting as shuttle carriers is not as yet compelling, but at least nothing observed so far is against it. In any case, the idea is useful in interpreting electron micrographs, in which Golgi saccules are invariably surrounded by a constellation of small, smooth vesicles that are restricted to this region.

Also frequently found in the environs of the Golgi apparatus are the so-called cytoplasmic bodies. Similar bodies were first described in the locust fat-body cells where they are thought to contain precursors for lipid and carbohydrate biosynthesis (Odhiambo 1967), and may correspond to the organelles called 'protein granules' by Locke (1966) in the fat-body cells of the lepidopteran insect *Calpodes*. Locke (1966) has demonstrated, by injecting tritiated amino acids and a foreign recognizable protein (horse radish peroxidase) into the haemocoel, that the fat body sequesters blood proteins in the form of protein granules (or cytoplasmic bodies). In the case of the locust ARGs, any precursor materials must traverse the thin muscle fibre that encircles each of the glands (Odhiambo 1969*c*). It is consequently of interest to note that minute cytoplasmic bodies are generally found in the basal cytoplasmic region of the ARGs, especially near the basal plasmalemma. Presumably, the precursor materials traverse the muscle cells, by way of the connective tissue channels observed between adjoining muscle cells (Odhiambo 1969*c*), and then assemble at the basal plasmalemma to form small cytoplasmic bodies. Later on the latter combine to form larger bodies, which somehow migrate to the Golgi zone. This mode of entry of precursors is being advanced in view of the fact that pinocytotic activity at the basal plasma membrane is rare if not altogether absent.

I wish to thank Mrs D. McLachlan and Mr P. Lisamulla for technical assistance; the Department of Zoology, Cambridge, and the Makerere Medical School, Kampala, for electron-microscope facilities; Professor Sir Vincent Wigglesworth, F.R.S., for his interest in this study; and the British Ministry of Overseas Development and the University of East Africa's Teaching Materials Fund for research grants.

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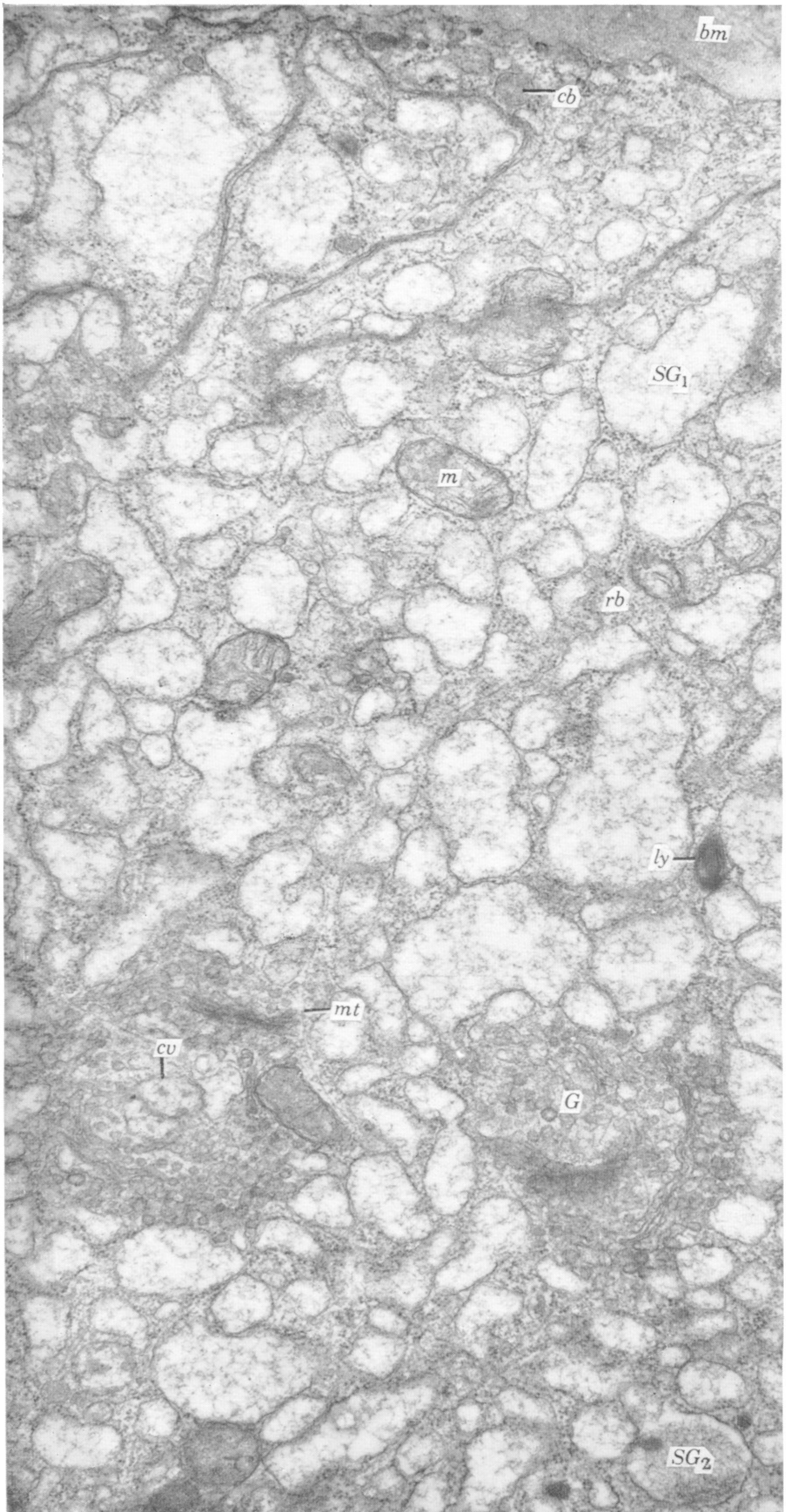
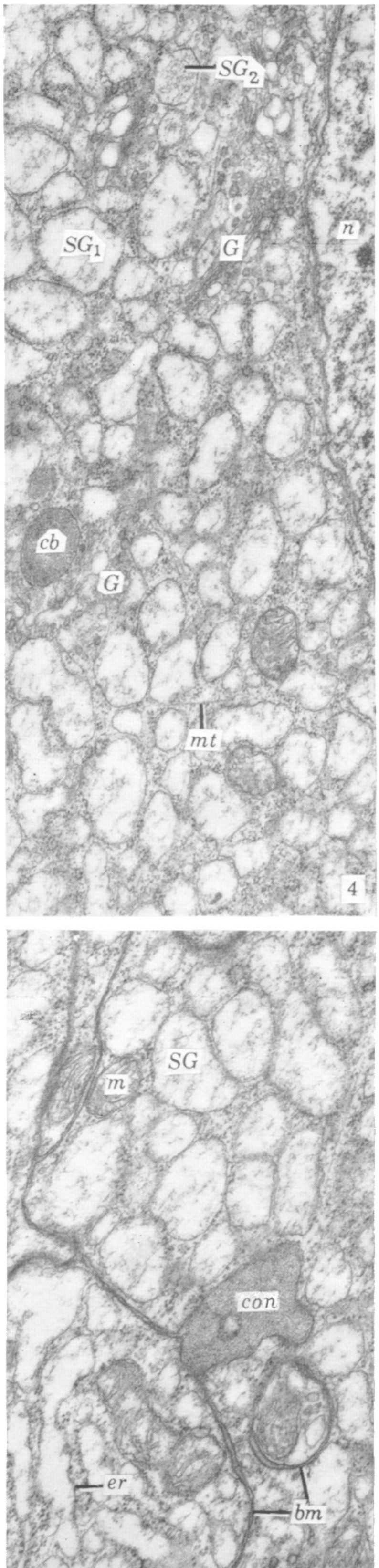
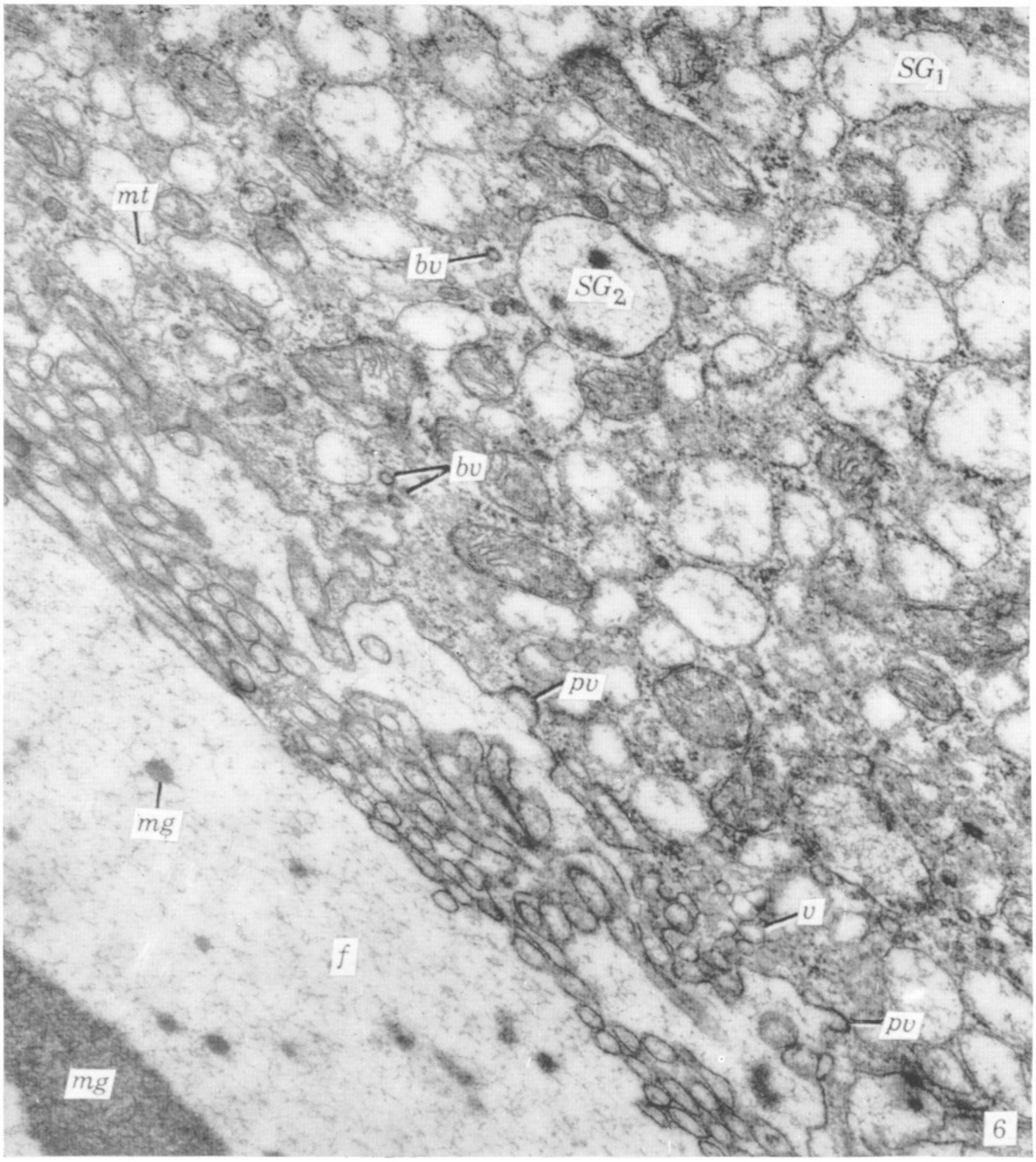
Abbreviations used on plates and figures

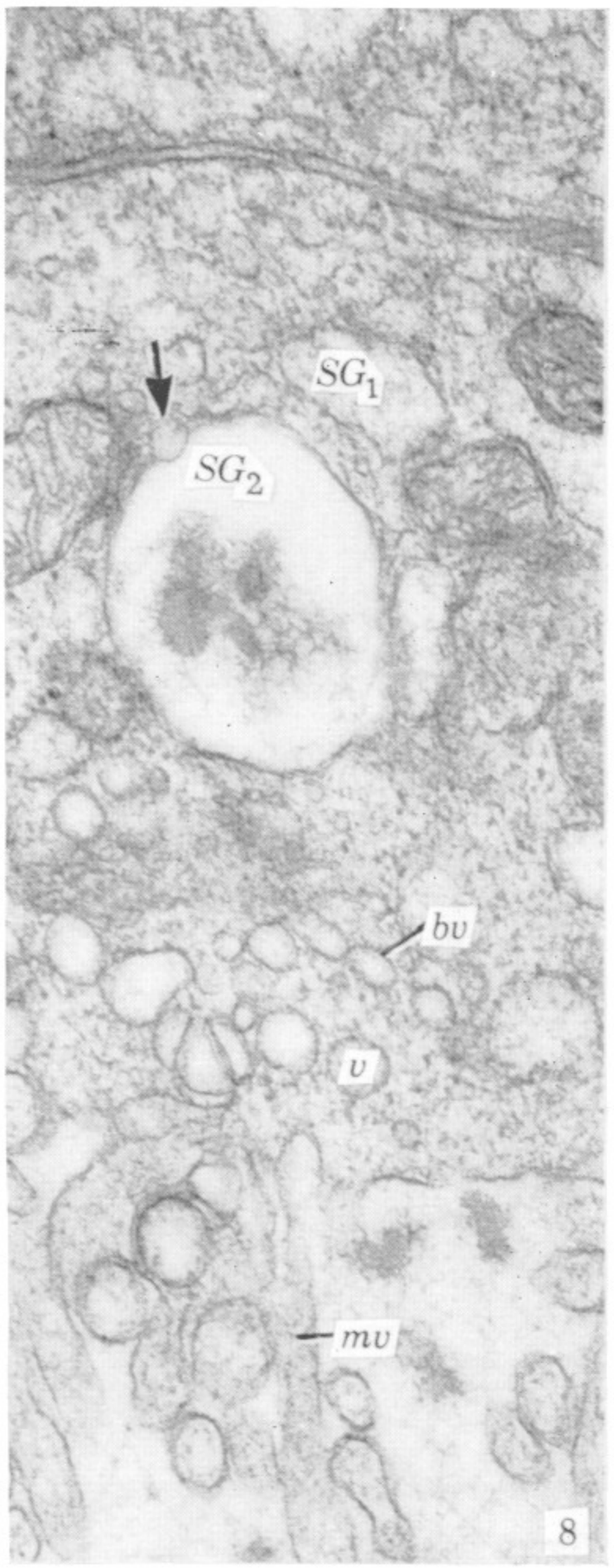
ARG	accessory reproductive gland
bm	basement membrane
bv	coated vesicle
can	canaliculus
cb	cytoplasmic body
chr	chromatin material
cnt	centriole
con	connective tissue material
cv	condensing vacuole of Golgi complex
ej	ejaculatory duct
er	endoplasmic reticulum
f	fibrillar structure
fb	fat body
G	Golgi apparatus
lum	gland lumen
ly	lysosome-like body
m	mitochondrion
mg	mature secretion mass
ms	musculature
mt	microtubule
mtb	bundle or array of microtubules
muc	mucilaginous cap holding sperm heads together
mv	microvillus
mvb	multivesicular body
n	nucleus
nl	nucleolus
np	nuclear pore
pm	plasma membrane
prb	polyribosome
pv	pinocytotic vesicle
rb	ribosome
sd	septate desmosome
ser	smooth-surfaced endoplasmic reticulum
SG	secretory vesicle
sp	sperm
tb	terminal bar
tr	trachea or air-sac
tw	terminal-web region
v	vesicle
vac	vacuity in the cytoplasm
vd	vas deferens

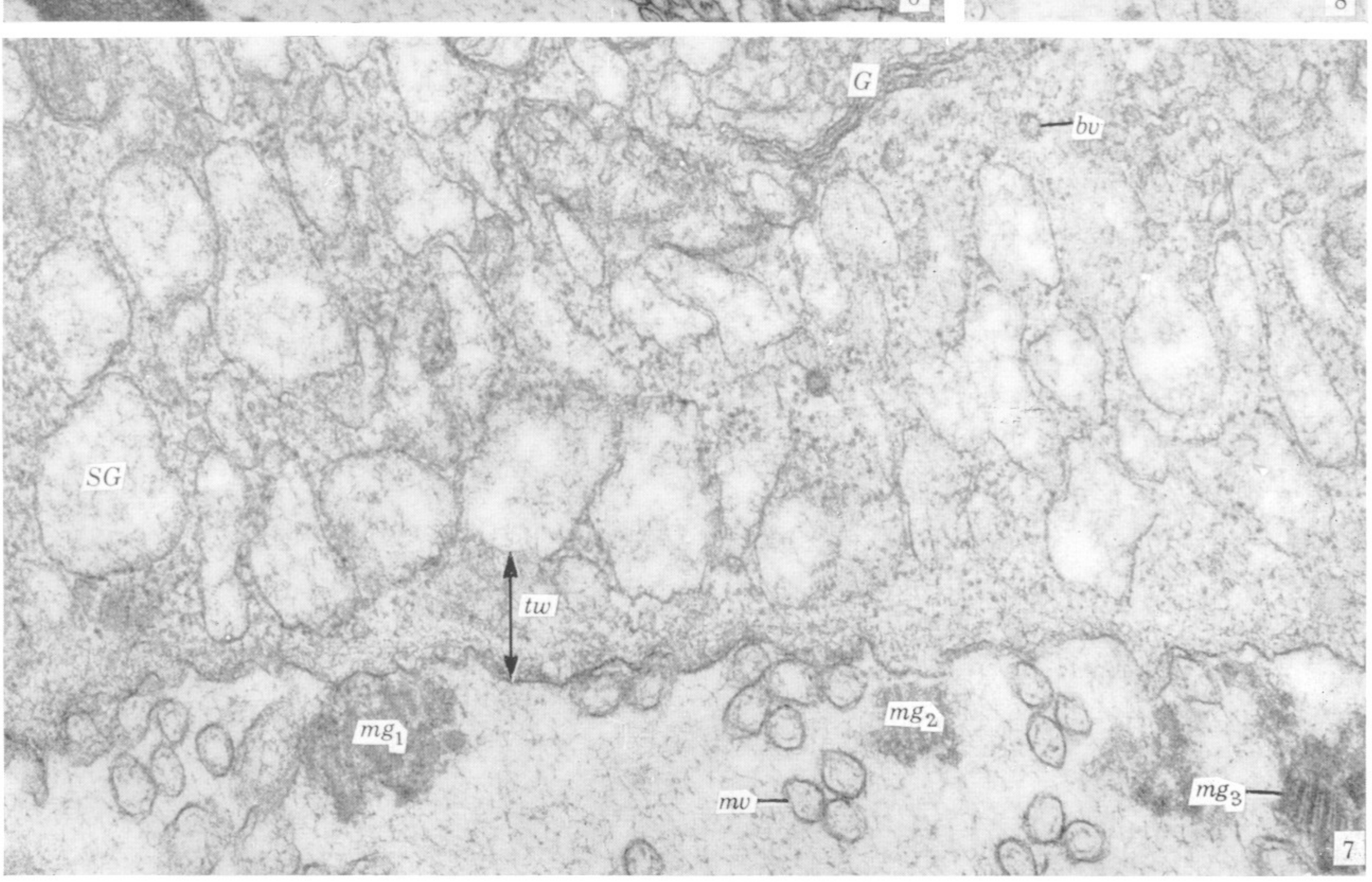




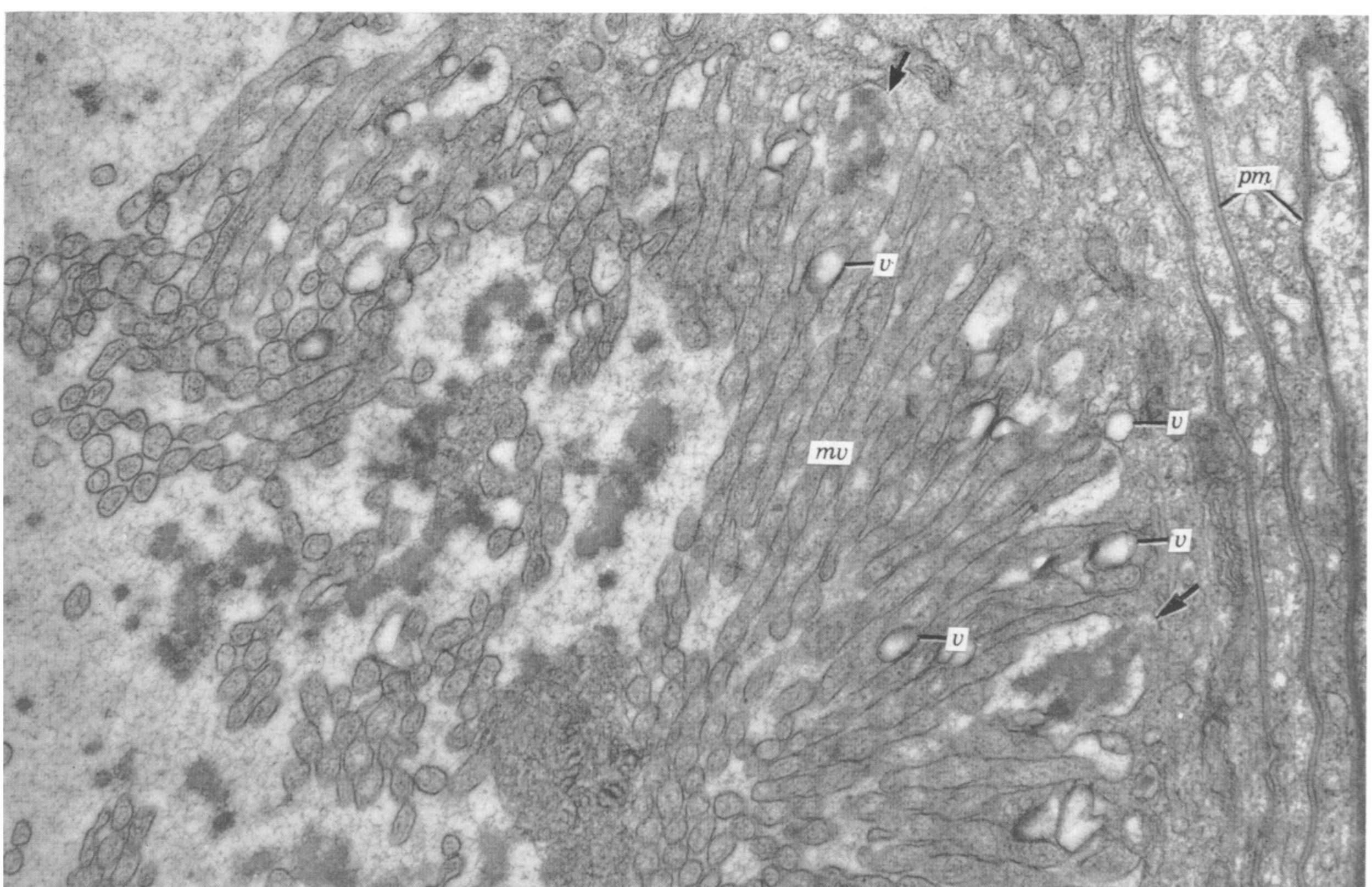
FIGURES 3 to 5. For description see facing page.







FIGURES 6 to 8. For description see p. 90.



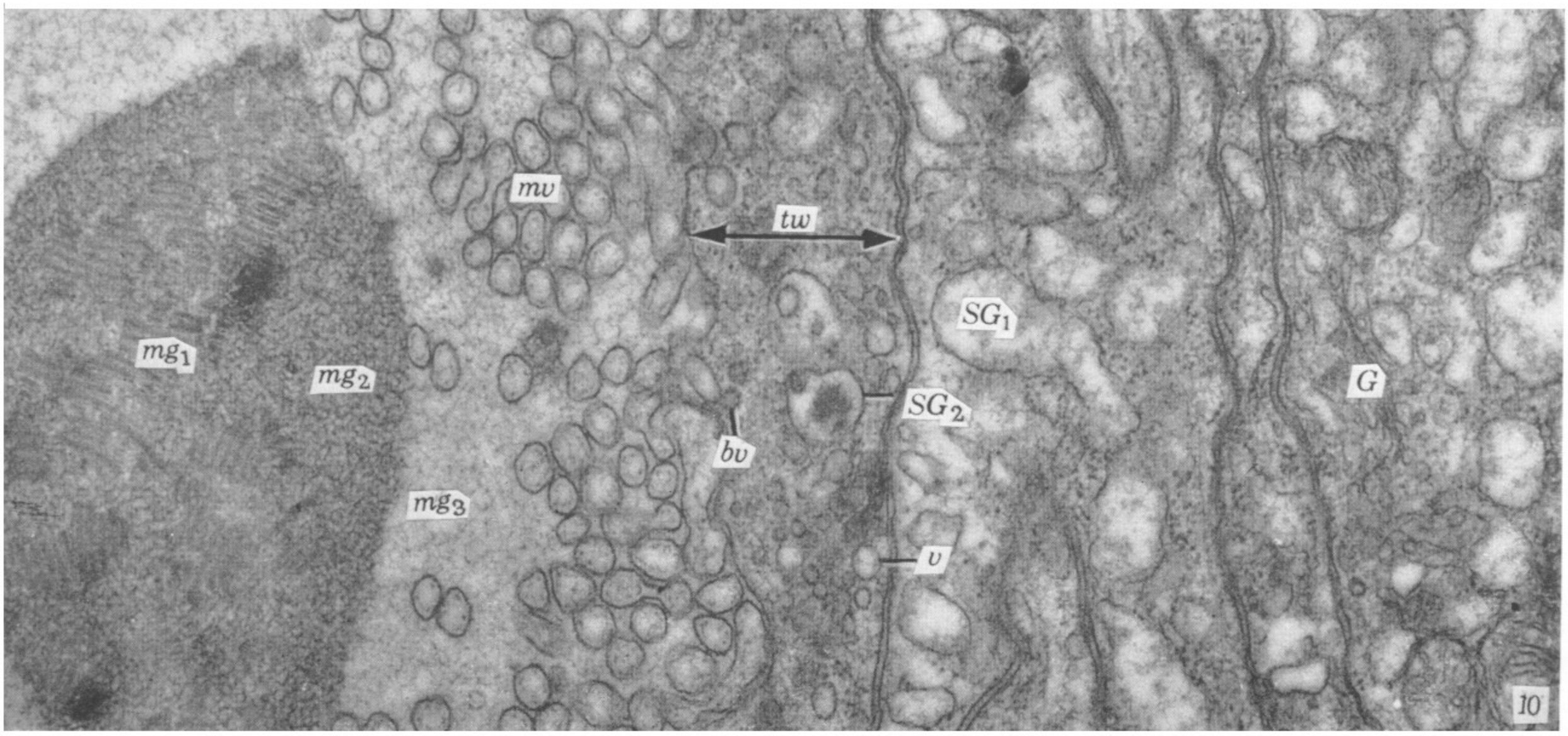
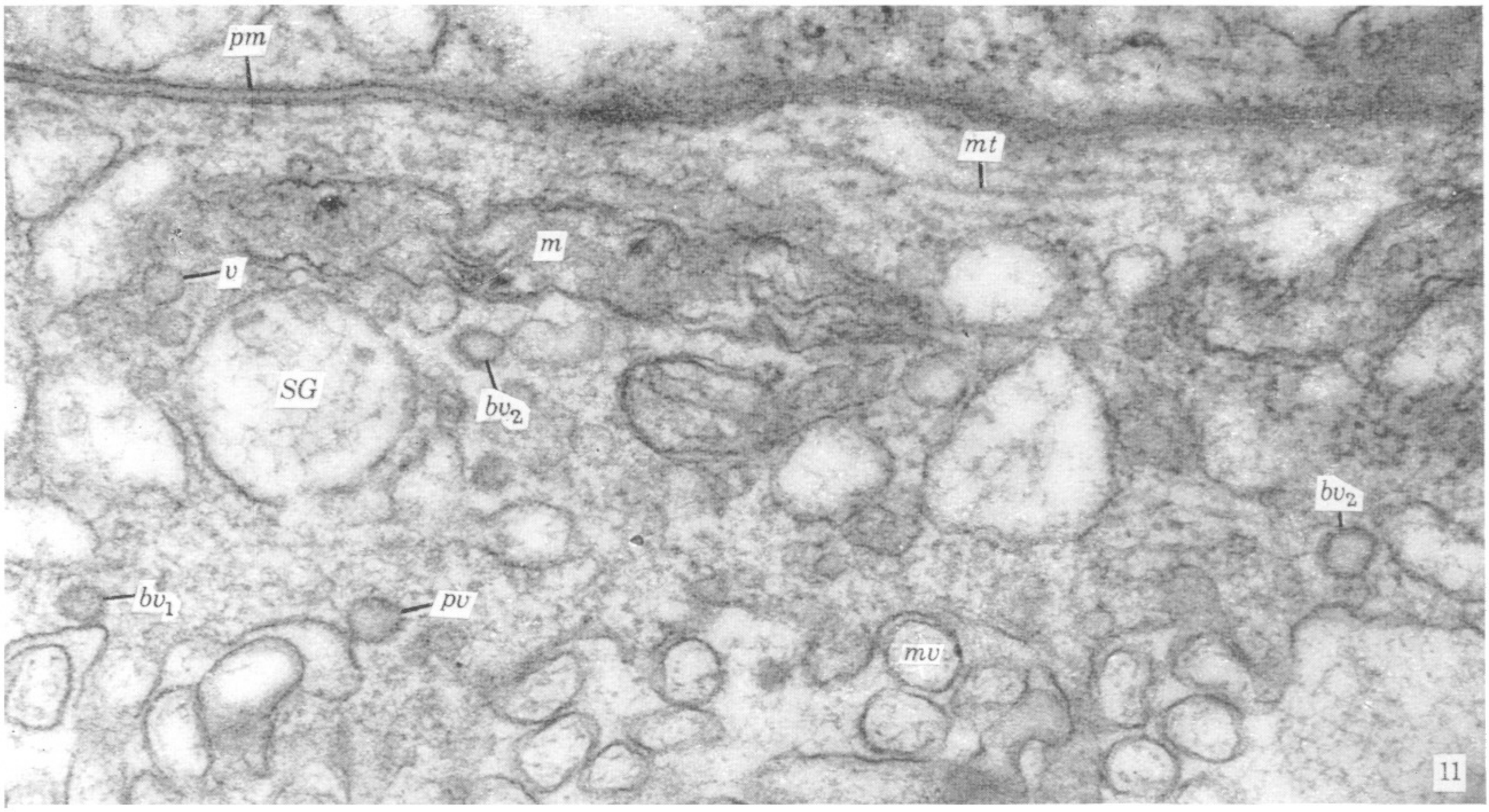


FIGURE 9. Luminal region of cytoplasm to show the microvilli (*mv*) between which secretion seems to be extruded into the lumen (*arrows*). The lateral plasmalemma (*pm*) is very convoluted here. Three types of secretory material can be recognized before its polymerization takes place (mg_1, mg_2 and mg_3). × 32500.

FIGURE 10. Newly polymerized secretion in the lumen, comprising a crystalline component (mg_1) and a coarsely fibrous base (mg_2). × 39000.



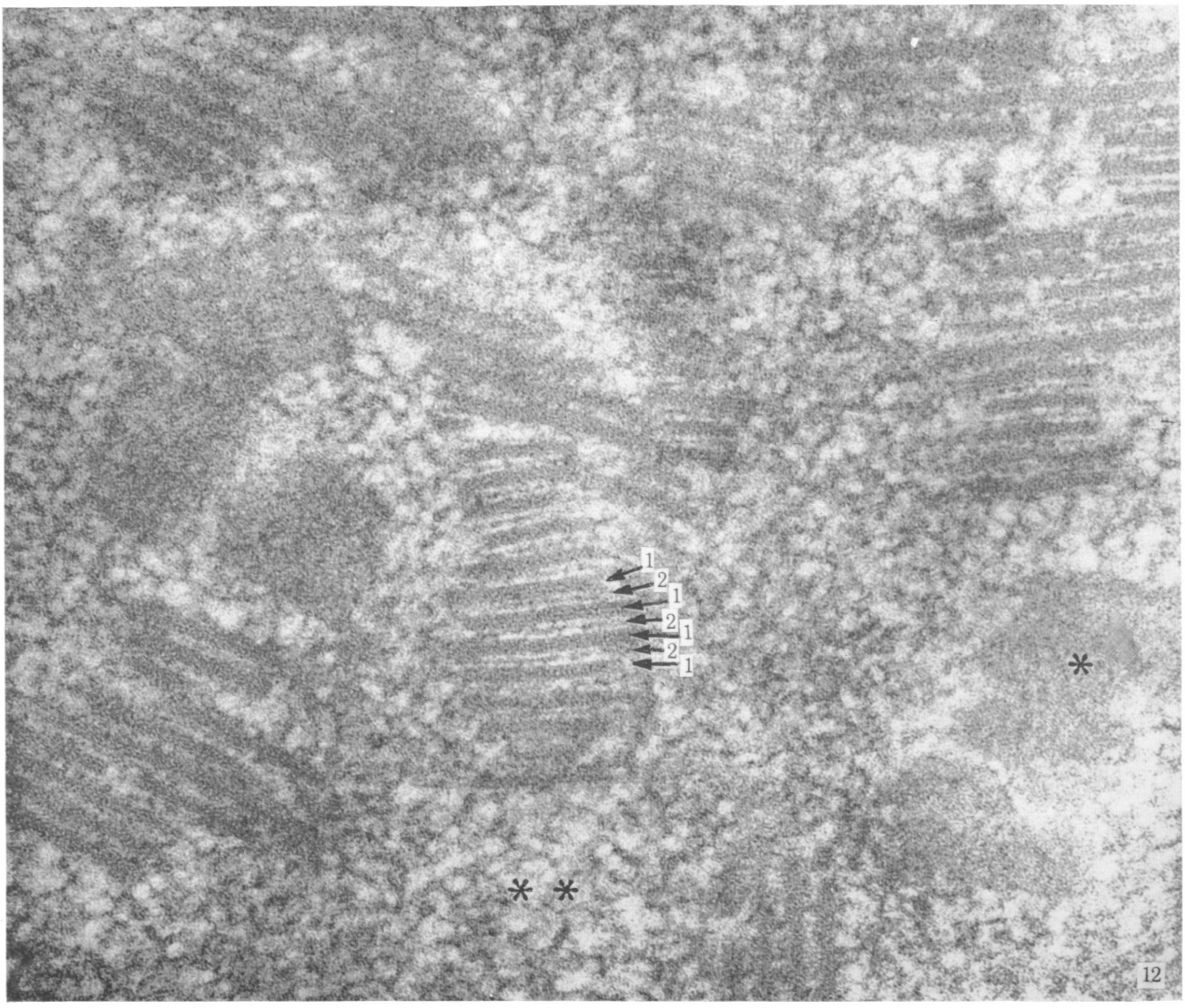


FIGURE 11. Caveolae (*pv*) formed at the luminal plasmalemma transform into coated vesicles (bv_1 and bv_2) found in the apical cytoplasmic region. Non-coated vesicles (*v*) of similar size also occur in this region. Also shown are microvilli (*mv*) in transverse section with filamentous structures inside them. × 77500.

FIGURE 12. Thick (*1*) and thin (*2*) fibrils of a crystalline granule embedded in a course fibrous material (*two stars*). Also shown are oblique end-views of crystalline structures (*one star*). × 137500.

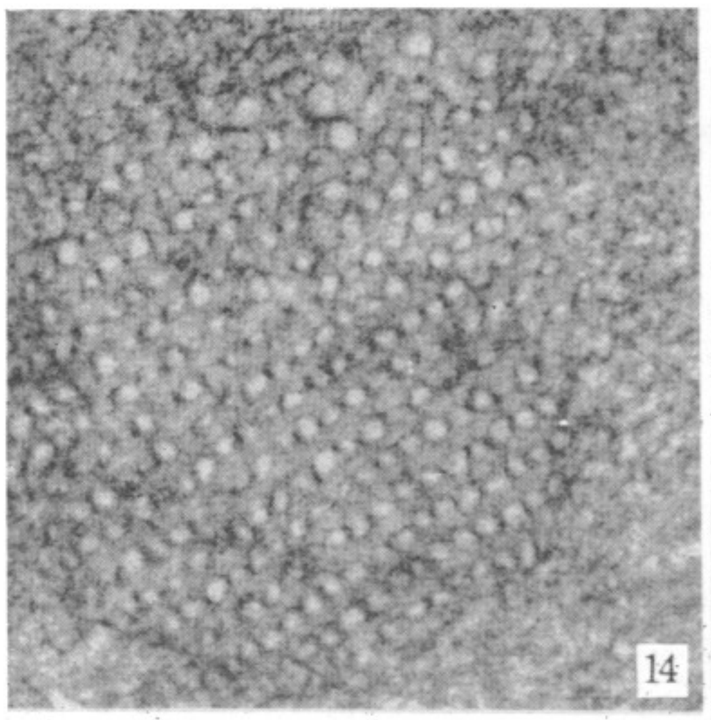


FIGURE 13. Fibrils of a large crystalline granule seen in transverse section (*1*). Also shown are crystalline fibrils shown in longitudinal section (*2*), the amorphous material within the crystalline zone (*3*), and the coarsely fibrous matrix (*4*). The secretion in the lumen also consists of small, electron-dense granules (*mg*) and minutely fibrous bulk secretory material (*f*). × 32500.

FIGURE 14. High-power micrograph of crystalline fibrils in transverse section. The thick fibrils appear hollow. × 65000.

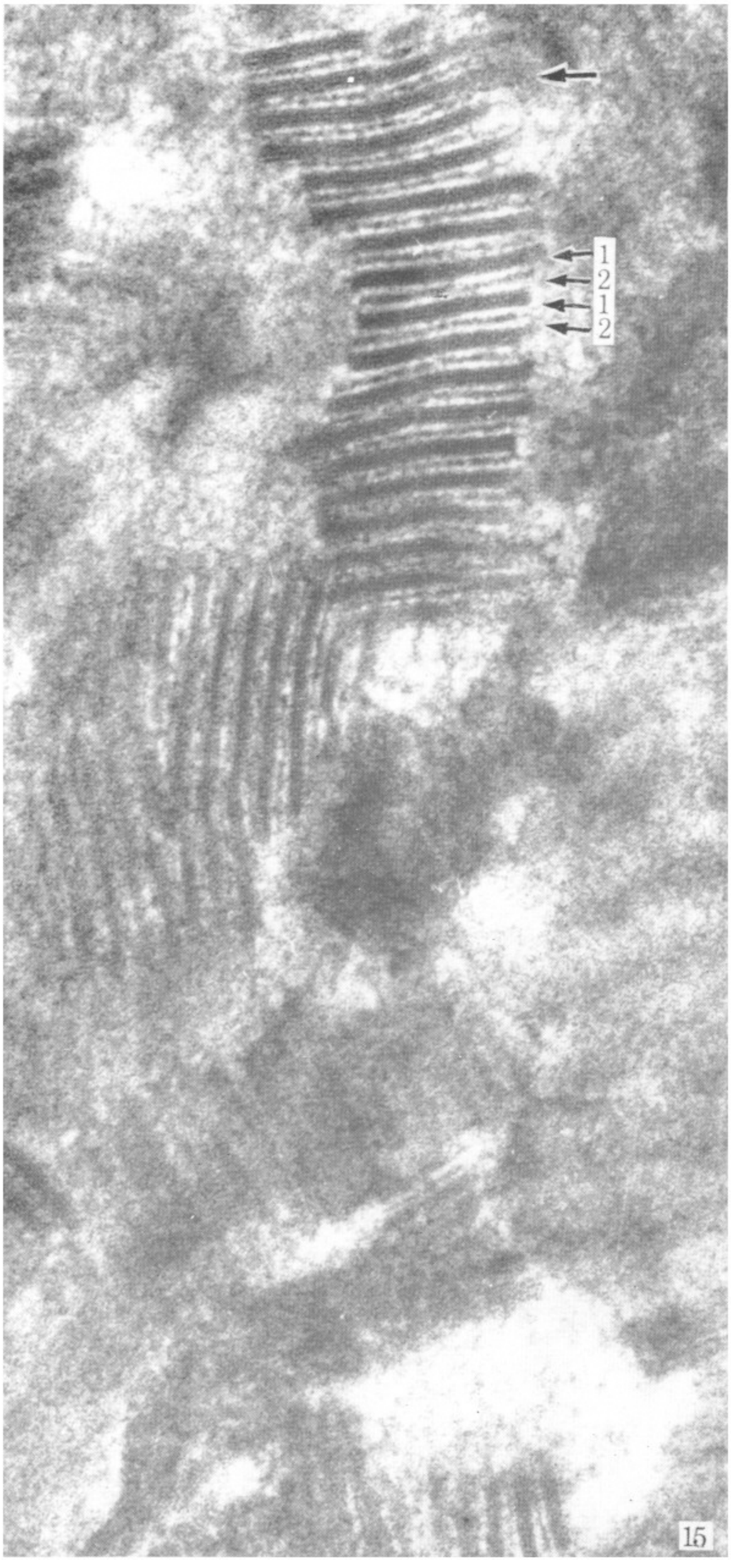


FIGURE 15. Crystalline granule with thick (*1*) and thin (*2*) fibrils. The ends of the thick fibrils sometimes tend to fray (*arrow*), and show beading. × 107500.

FIGURE 16. Thick fibrils (*arrows*) of a crystalline granule at high magnification showing apparent beading. × 217500.

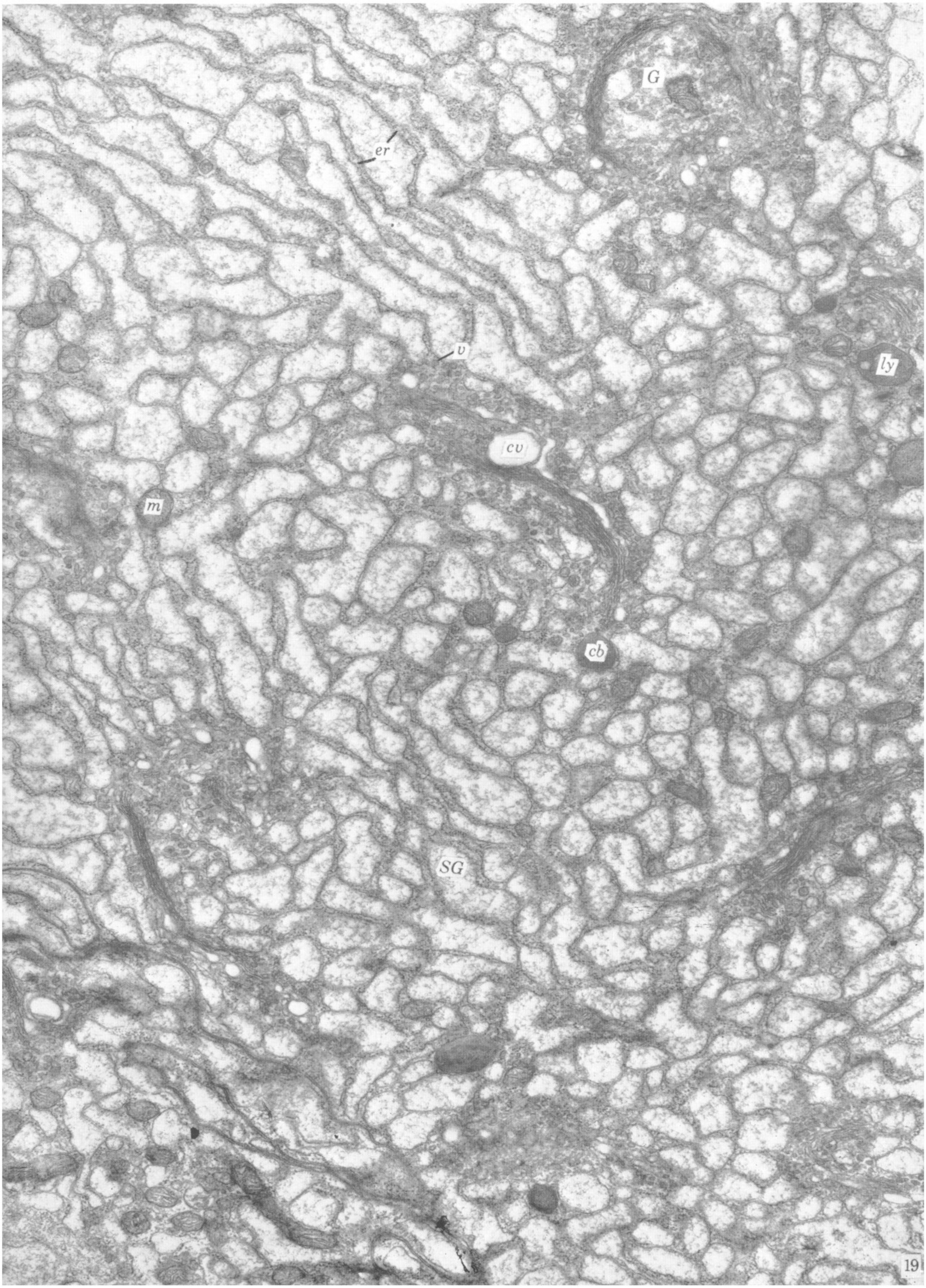
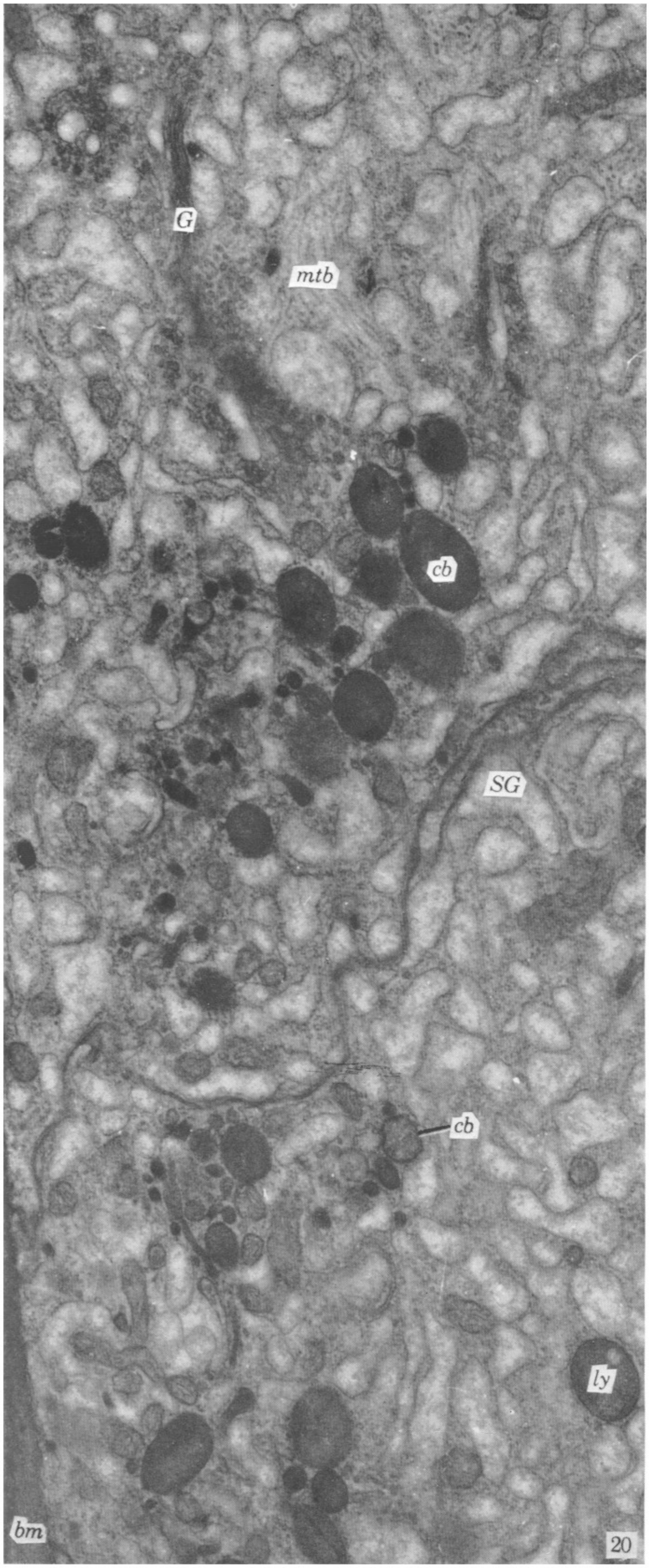


FIGURE 19. The cytoplasm is dominated by swollen cisternae of the rough ER (*er*), secretory vesicles (*SG*), and enormous Golgi complexes (*G*) having large condensing vacuoles (*cv*). These almost crowd out mitochondria (*m*). A number of cytoplasmic bodies (*cb*) are found near the Golgi elements. × 24000.



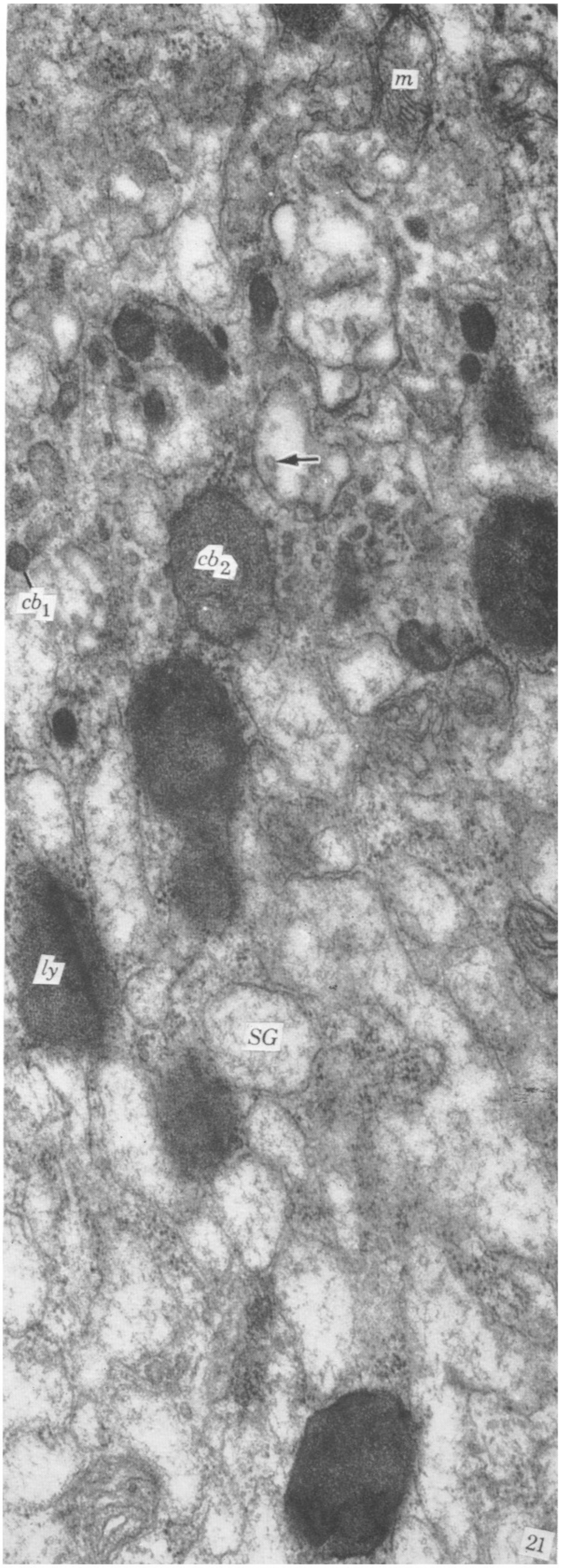
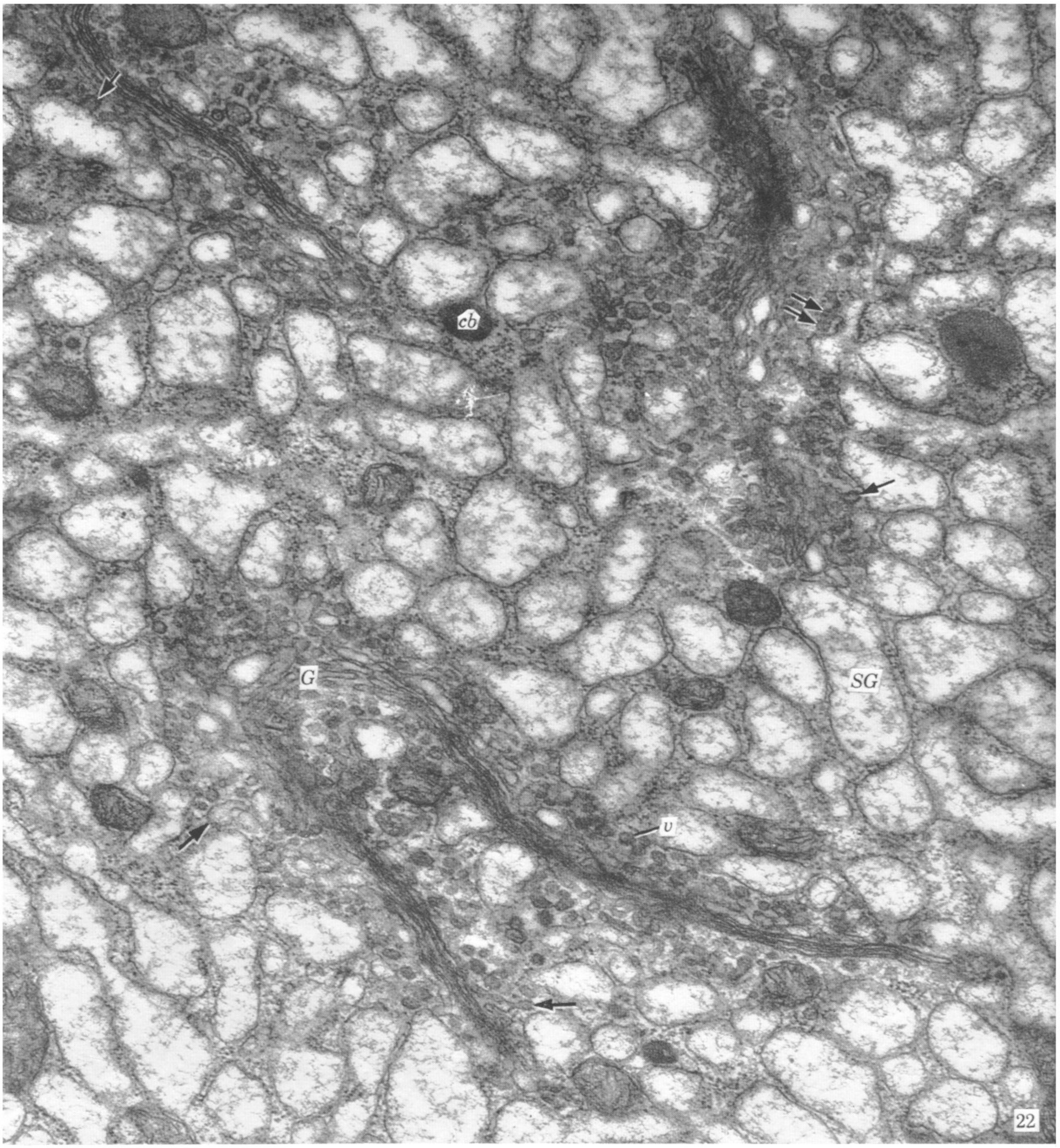


FIGURE 20. Basal cytoplasmic region contains numerous cytoplasmic bodies (*cb*) and some lysosome-like bodies (*ly*). Golgi units (*G*) are small. × 22500.

FIGURE 21. Cytoplasmic bodies (cb_2) seem to grow by fusing with smaller like bodies (cb_1). Some large vesicles of unknown nature also seem to engulf smaller vesicles (*arrow*). × 41000.



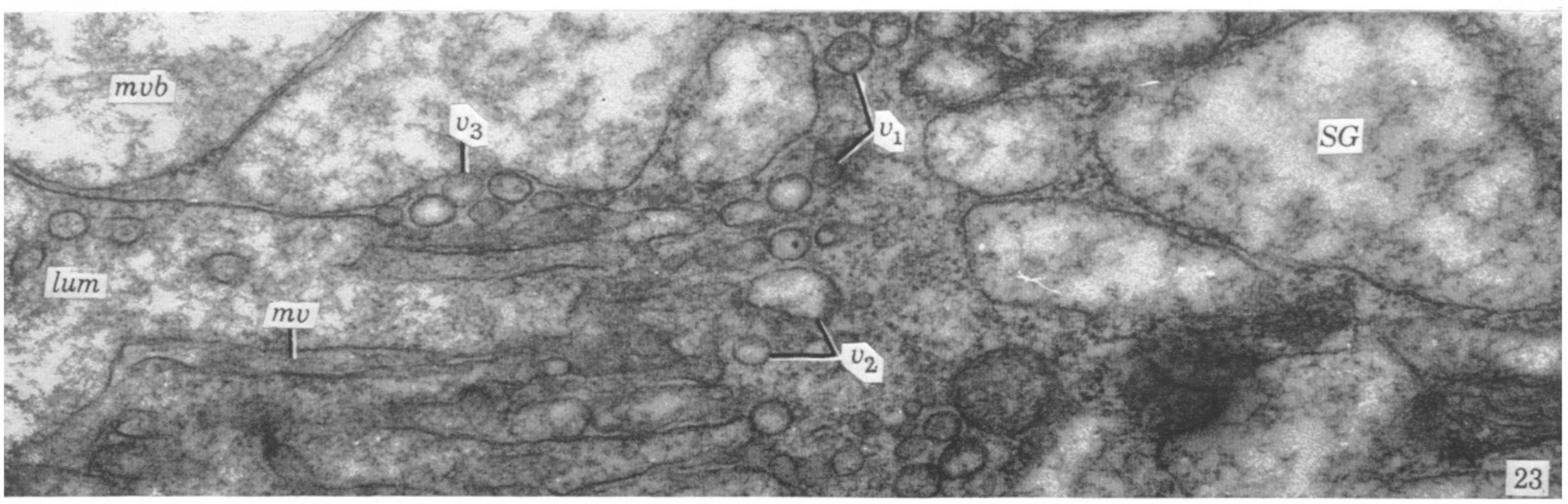


FIGURE 22. Golgi complex (*G*) has numerous peripheral vesicles with an electron-dense content (*v*), which seem to arise or fuse with either the Golgi saccules or cisternae of the ER (*arrows*). × 44000.

FIGURE 23. Luminal cytoplasmic region showing a secretory vesicle having a minutely divided secretion (*SG*), and in the terminal-web area small, smooth vesicles of two types: those having an electron-lucent content (v_1) and those having a fairly electron-dense content (v_2). Some of these vesicles are also found within microvilli and multivesicular bodies (v_3). × 41000.

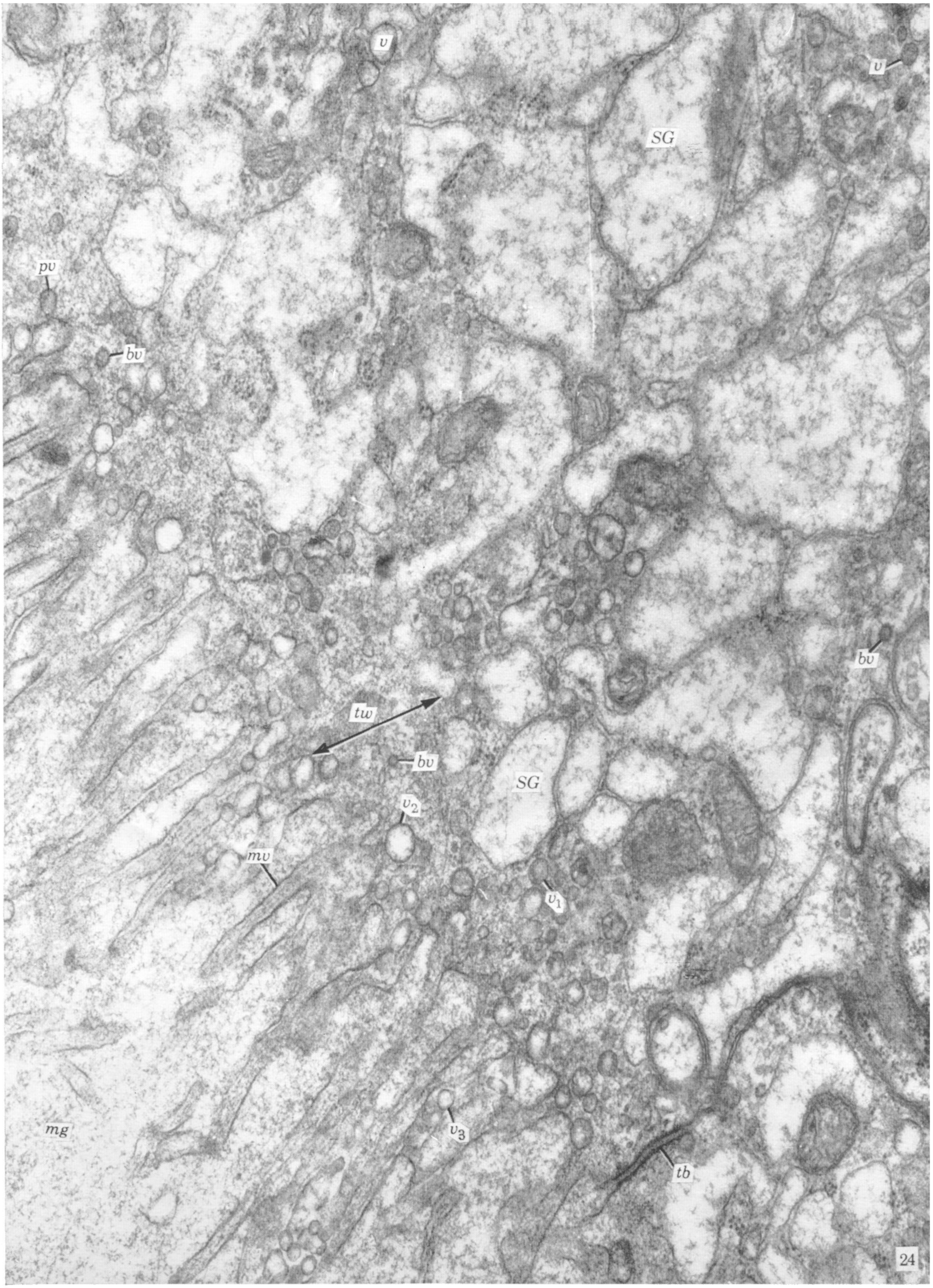


FIGURE 24. The microvilli have a fibrillar core (*mv*). The terminal-web region (*tw*) is well demarcated: it contains a minutely granular matrix in which are found small vesicles (v_1) with a somewhat dense content, and rather larger vesicles (v_2) that are more transparent. Some of the small vesicles (v_3) extend into the microvilli, and there are also a considerable number of small vesicles (*v*) in other parts of the apical cytoplasmic region. Pinosomes frequently form from the luminal plasmalemma (*pv*). ×41000.

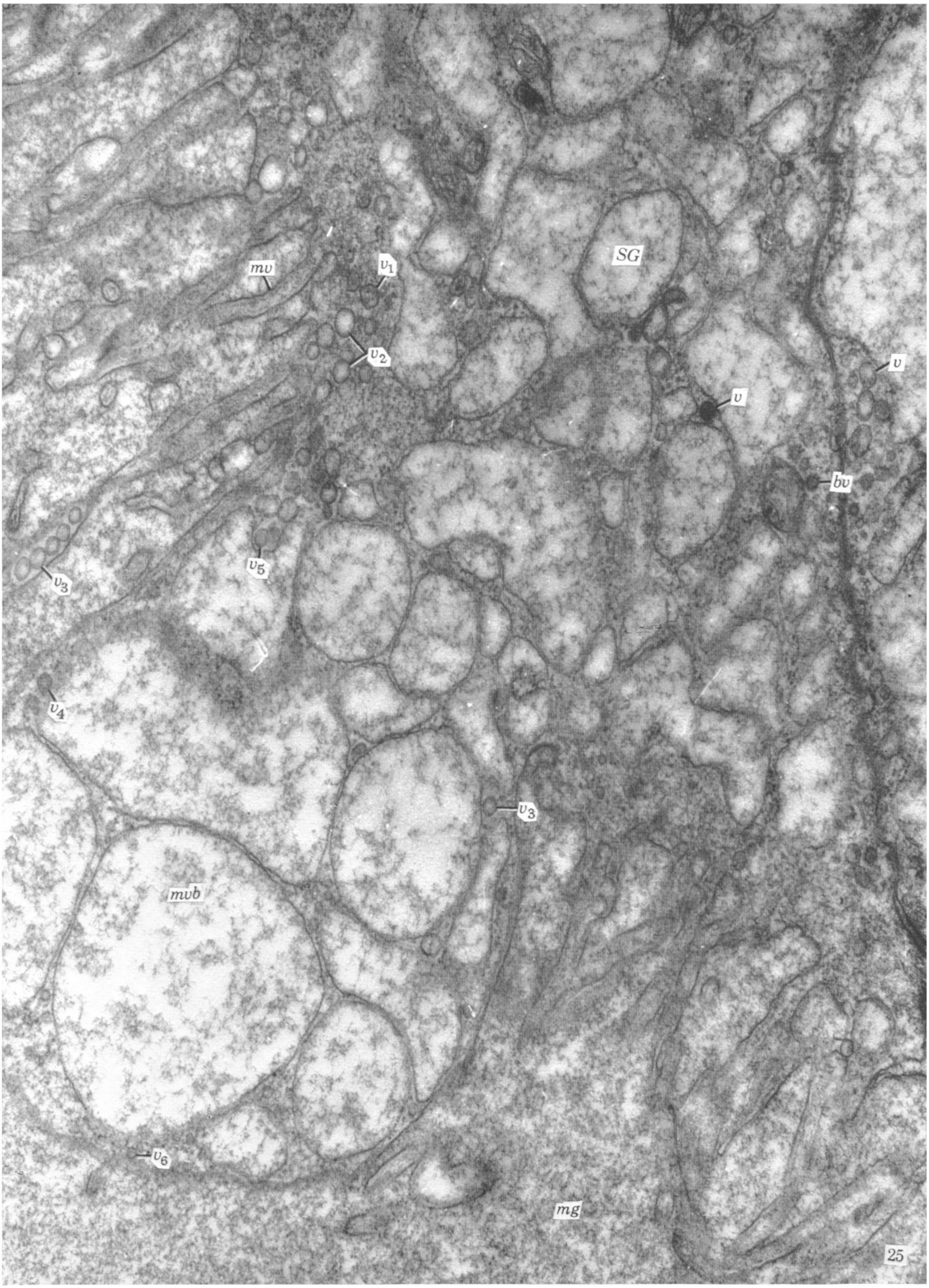
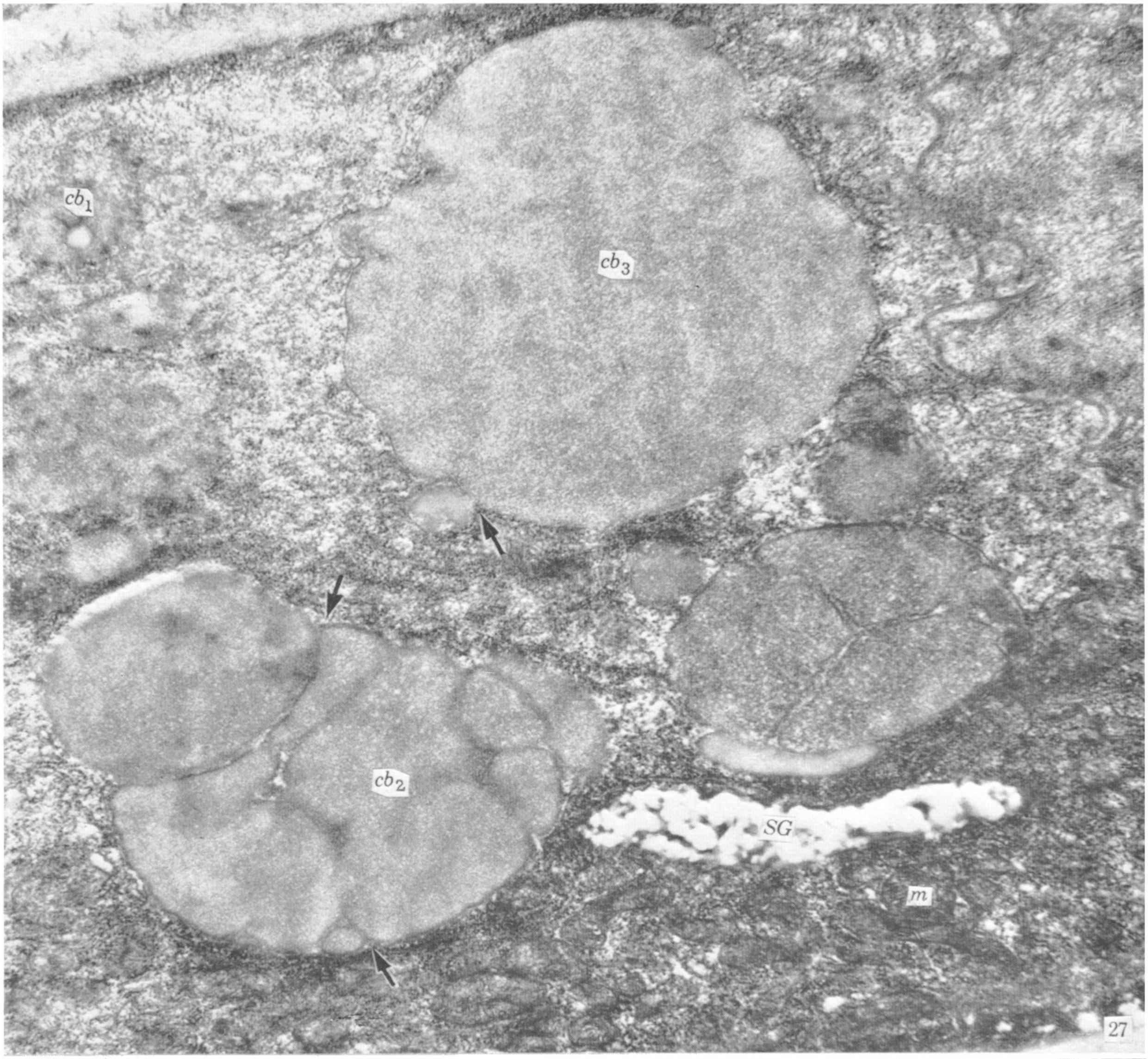
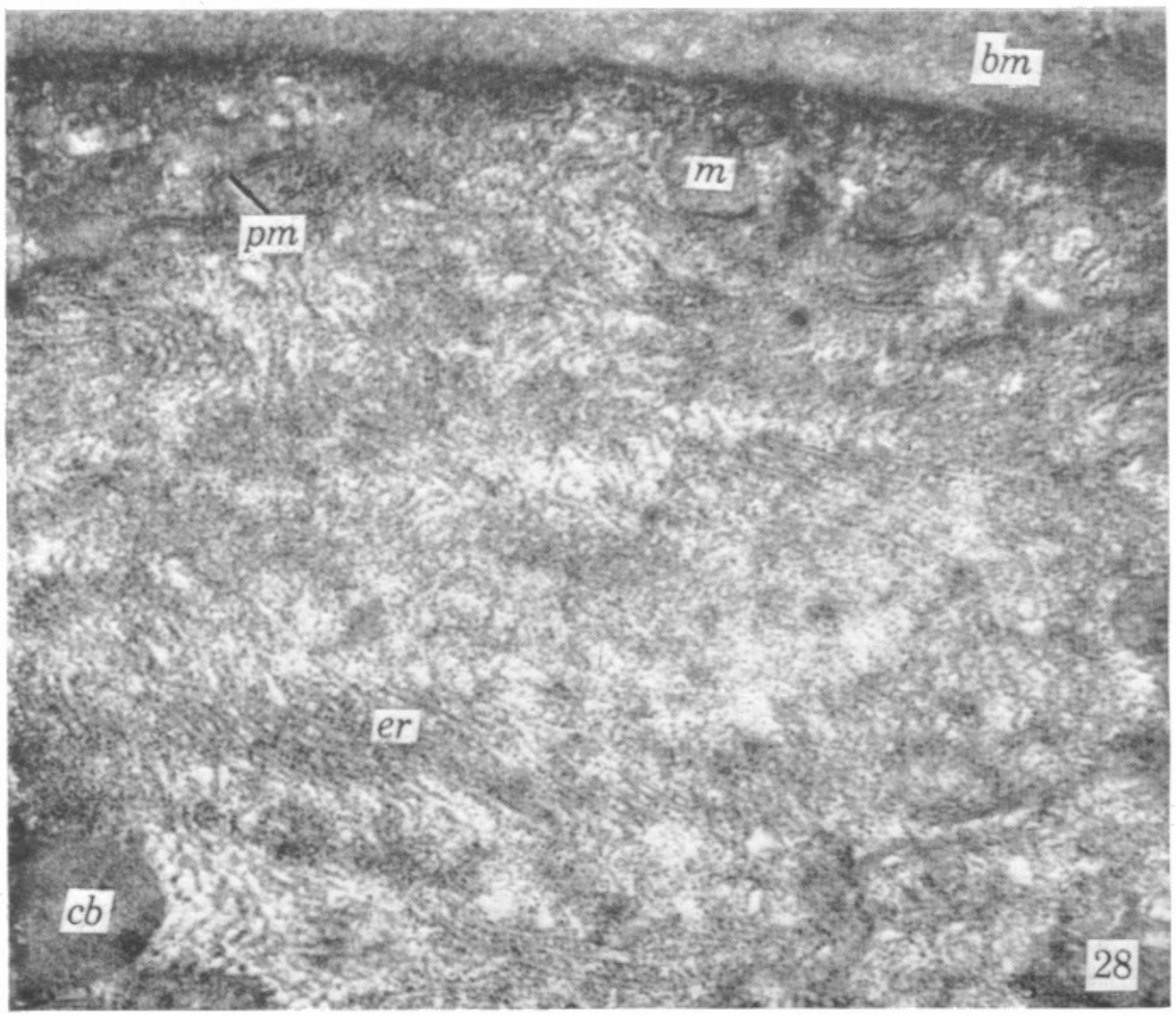
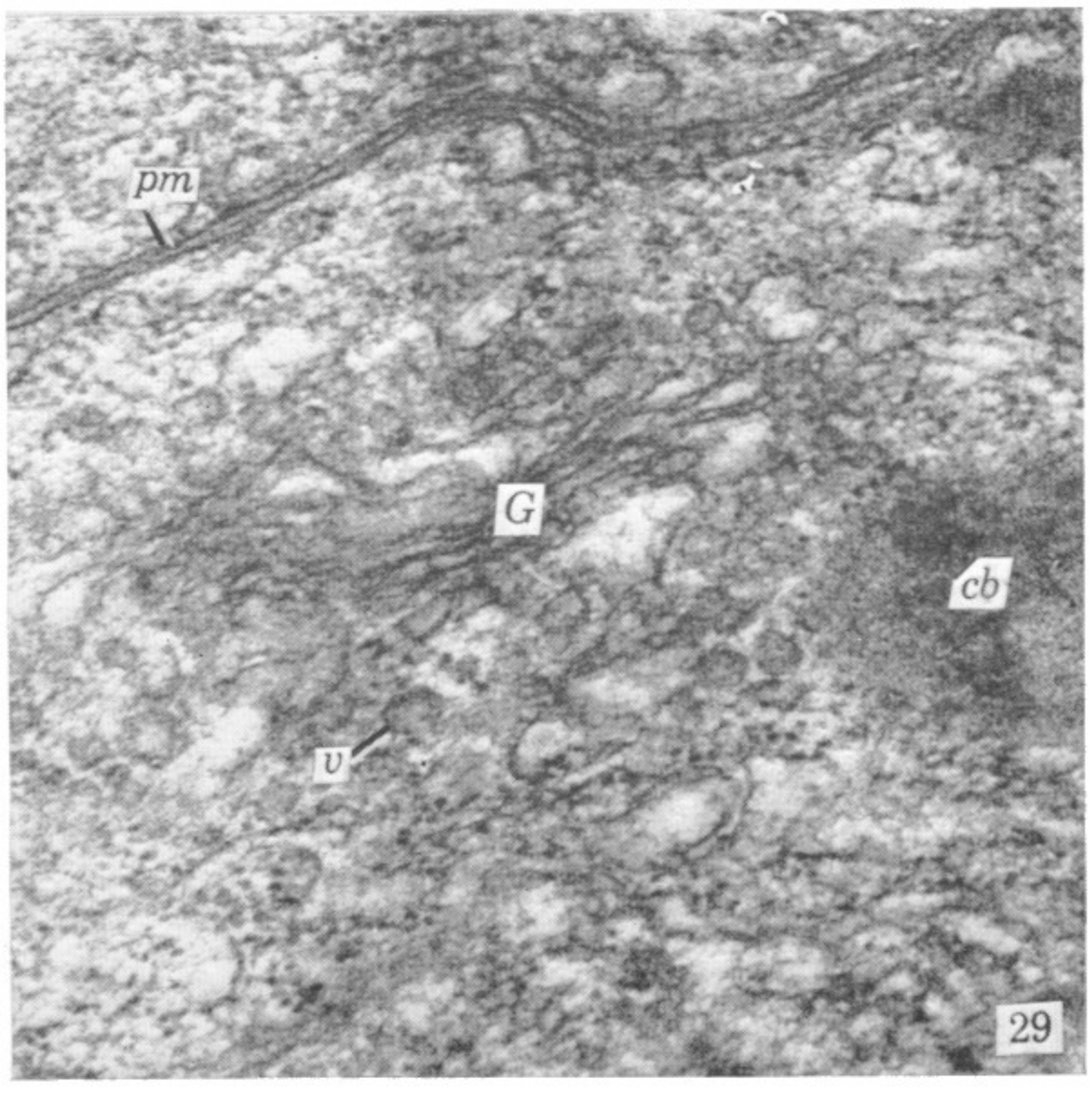


FIGURE 25. An enormous multivesicular body (*mvb*) may form in between other microvilli. Small vesicles (v_3) resembling those found in the terminal-web region (v_1 and v_2) may be located within the microvilli; some may also be found within the multivesicular body (v_4) and they seem to result from an inflow of such organelles from the terminal-web region (v_5). The mature secretion is a finely divided fibrous substance (*mg*). × 41000.







FIGURES 27 to 29. For description see facing page.

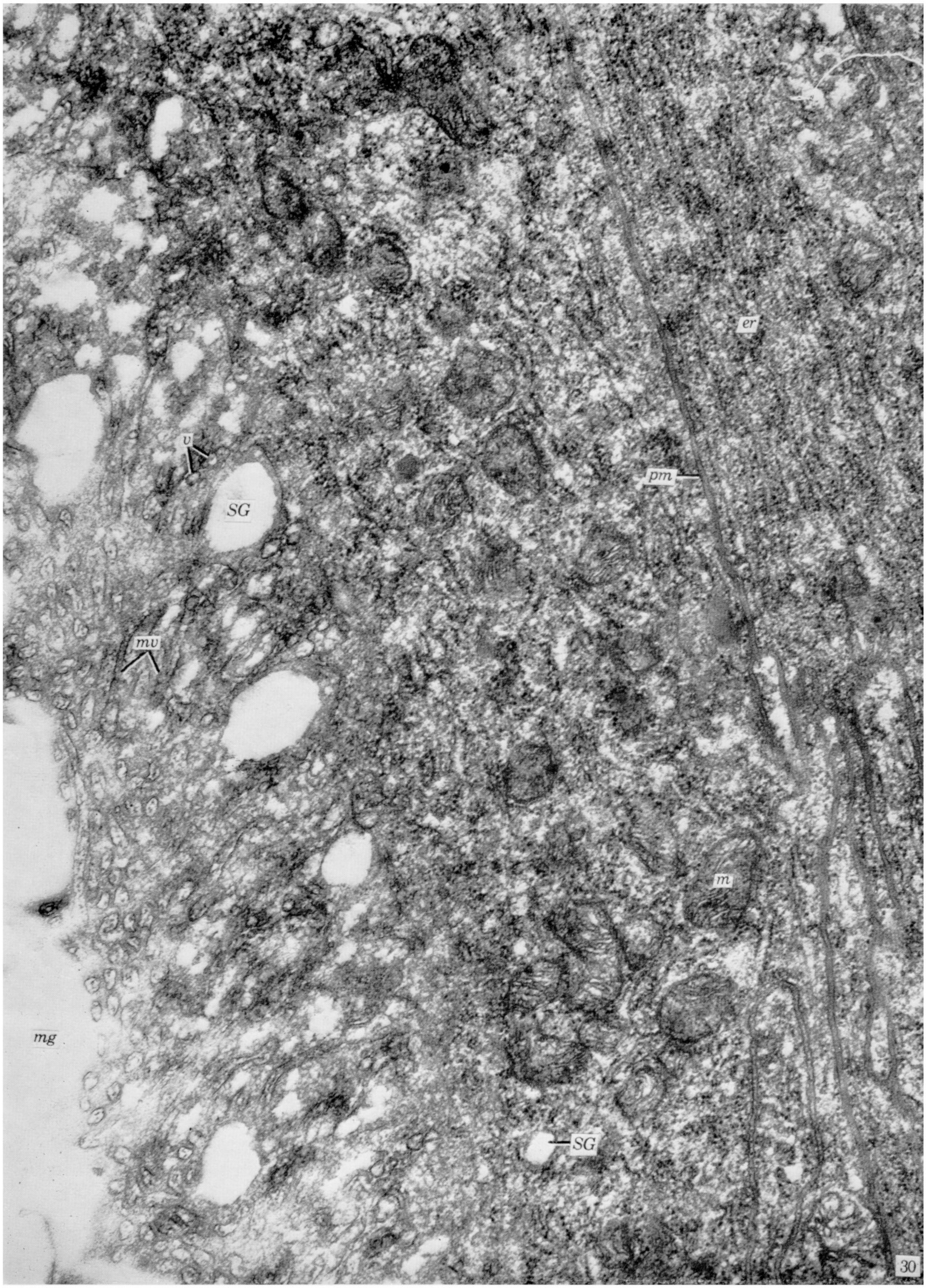
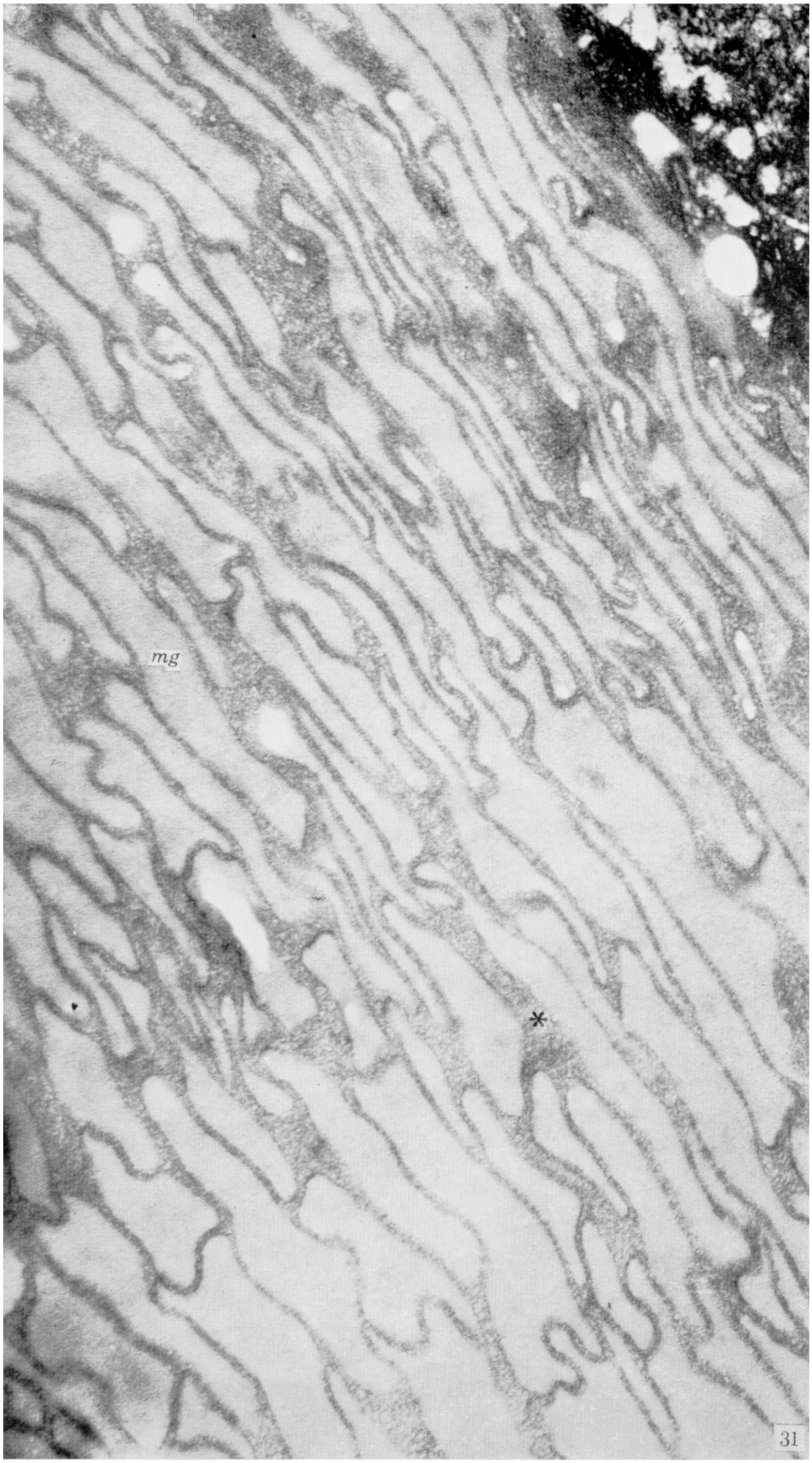


FIGURE 30. The apical cytoplasmic region showing secretory vesicles (*SG*) with an electron-dense rim and empty core, closely packed microvilli (*mv*) holding a dense substance in between, and a very convoluted lateral plasma membrane (*pm*). Note also the closely packed, parallel ER cisternae (*er*). × 44000.



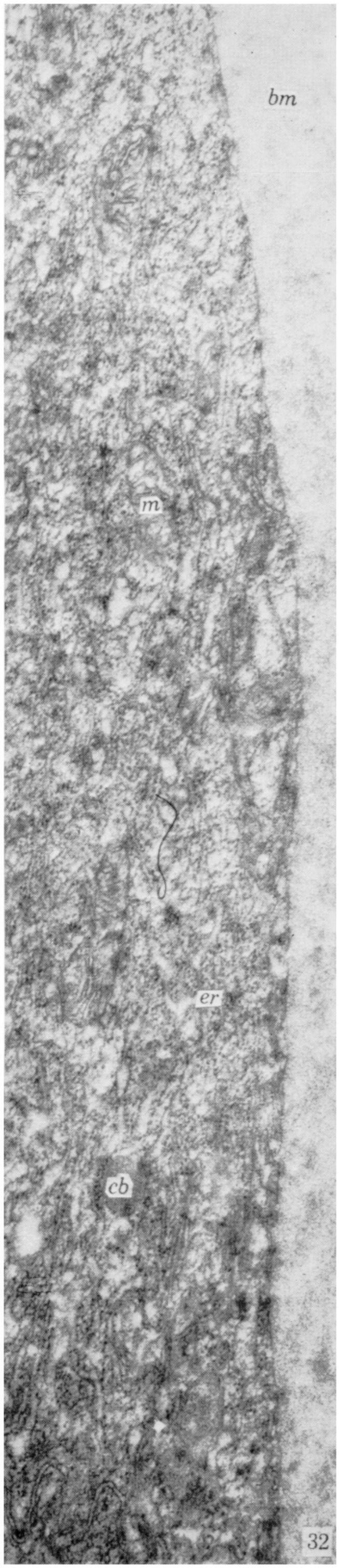
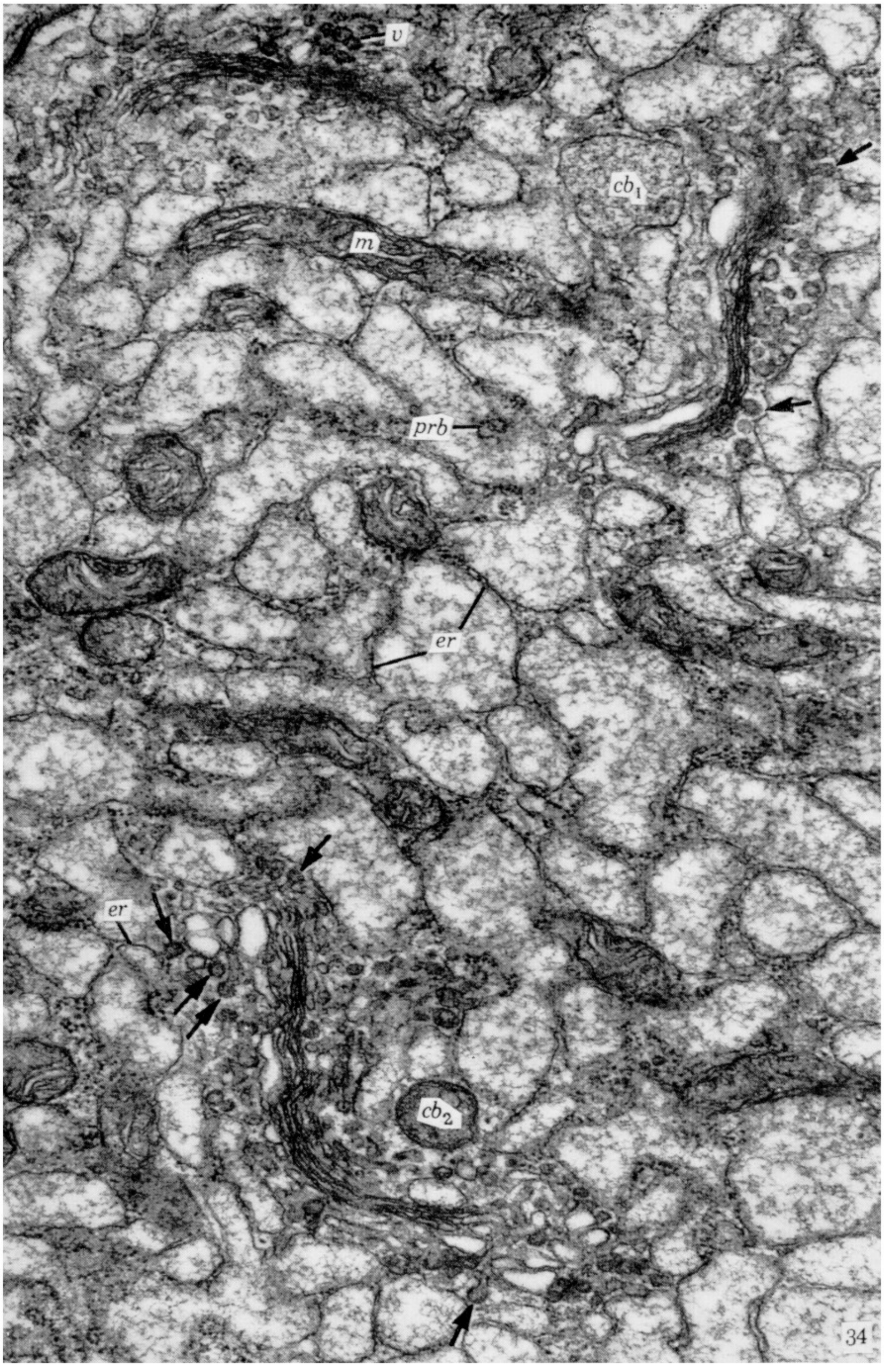
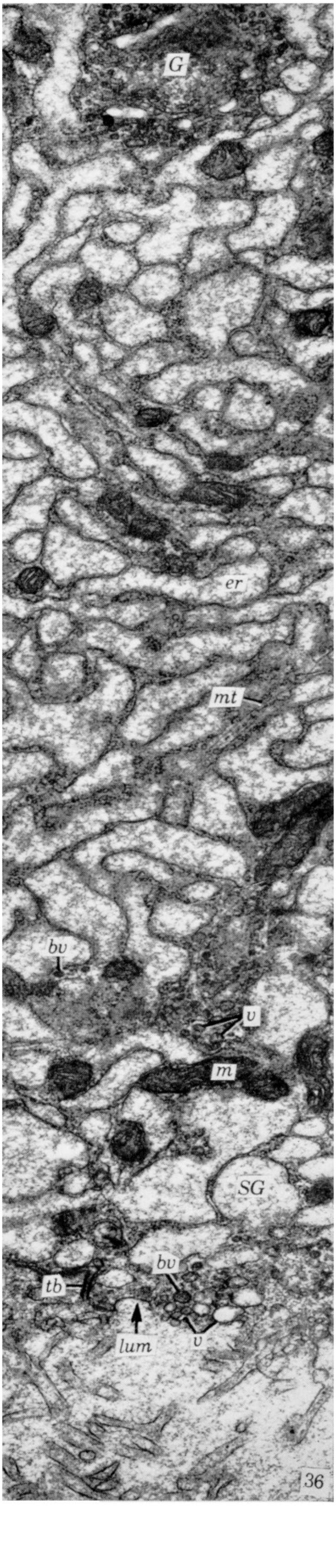
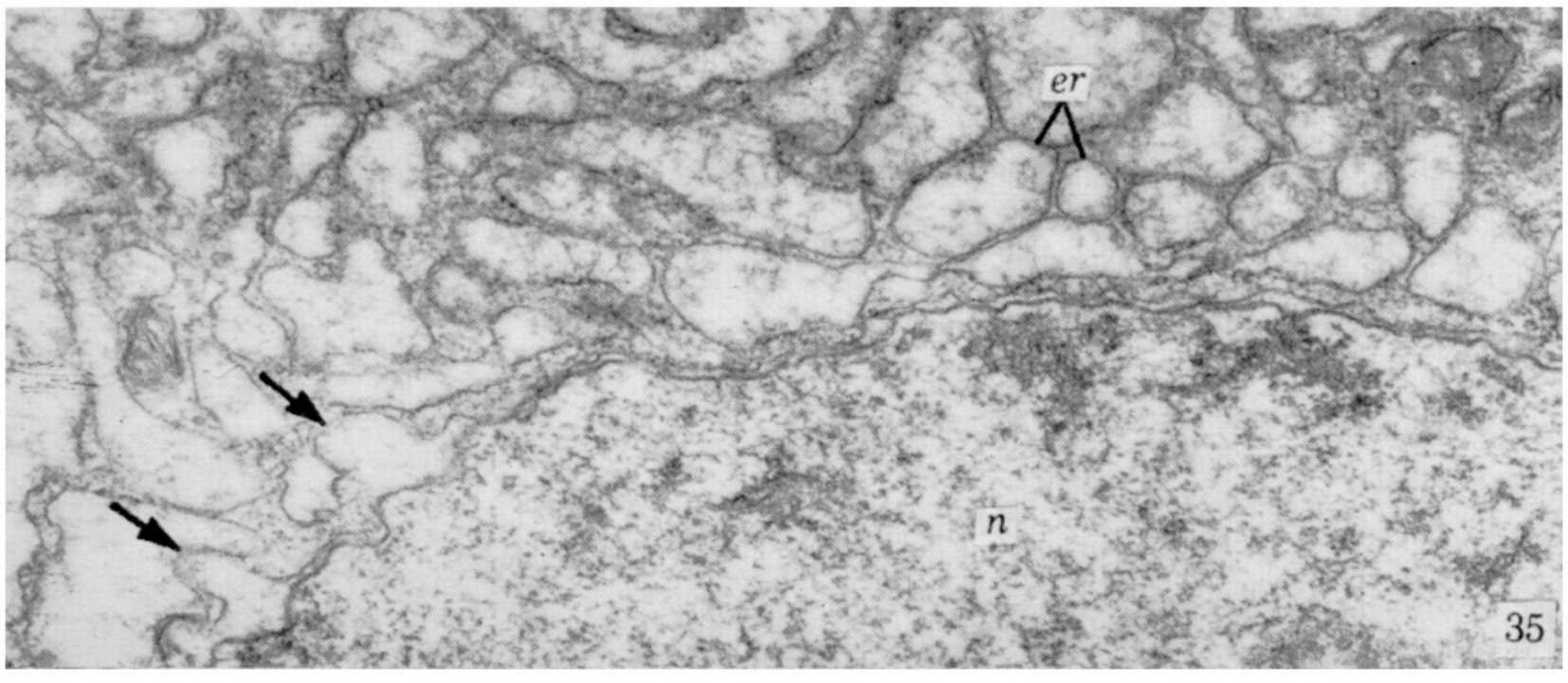


FIGURE 31. The luminal content consists of large globules (*mg*) of low electron-density surrounded by a granular cortical substance (*star*). × 52000.

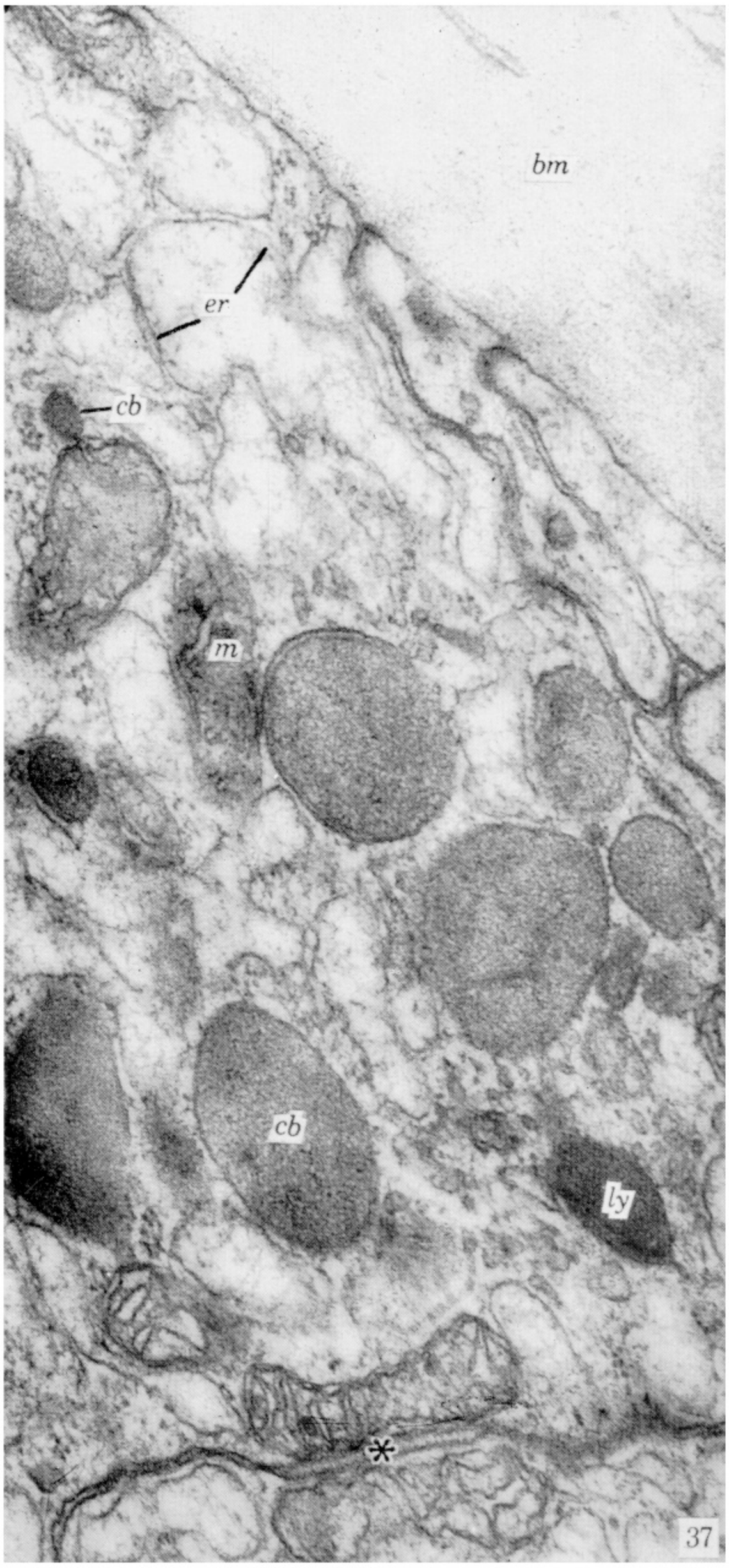
FIGURE 32. Basal cytoplasmic region of a rather young (5-day-old adult) gland, with less general electron-density, allowing easier observation of cytoplasmic bodies (*cb*), mitochondria (*m*) and the rough ER (*er*). × 52000.

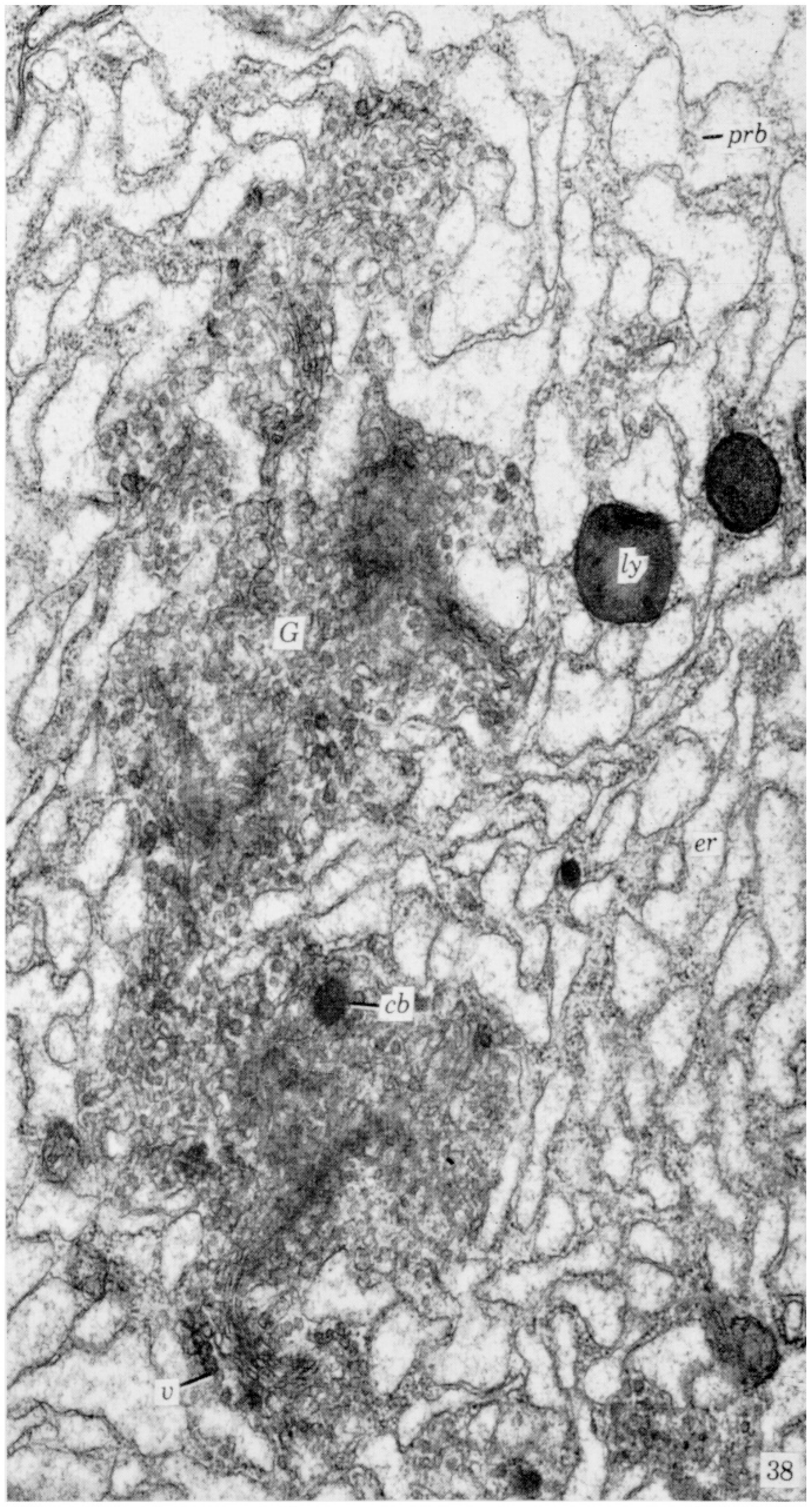






Figures 34 to 36. For description see p. 97.





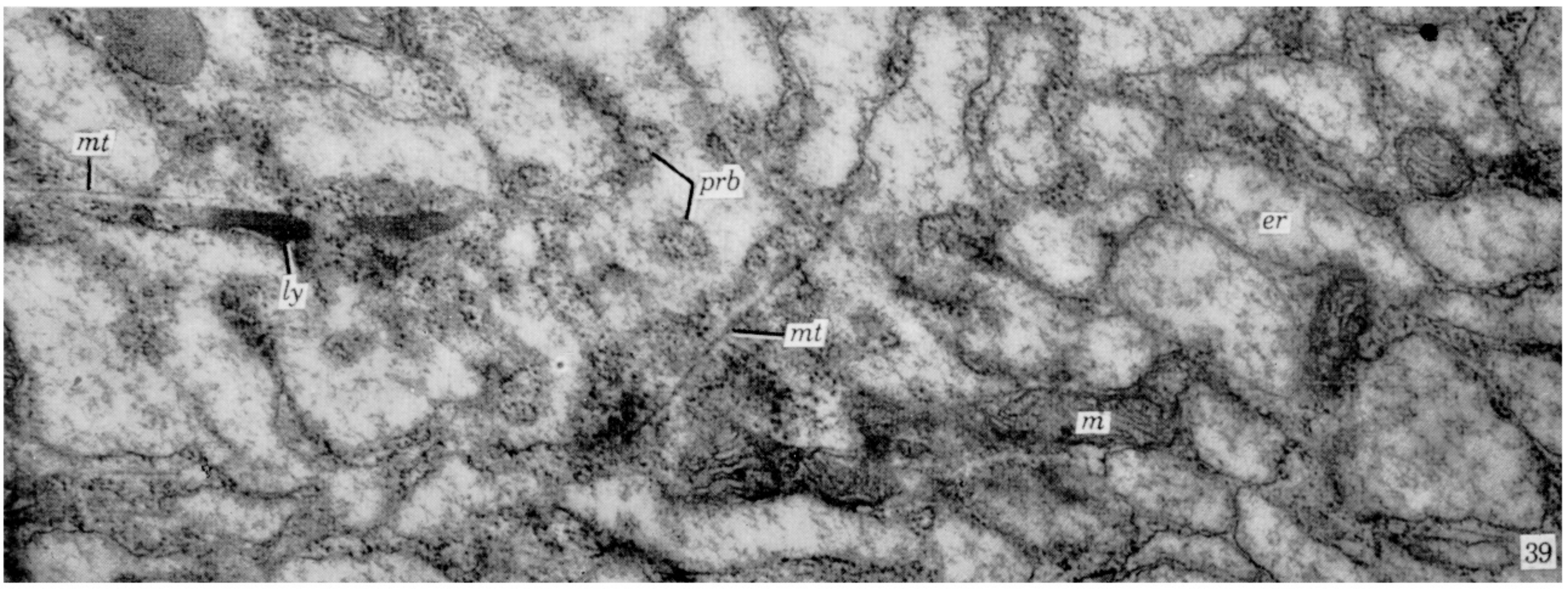
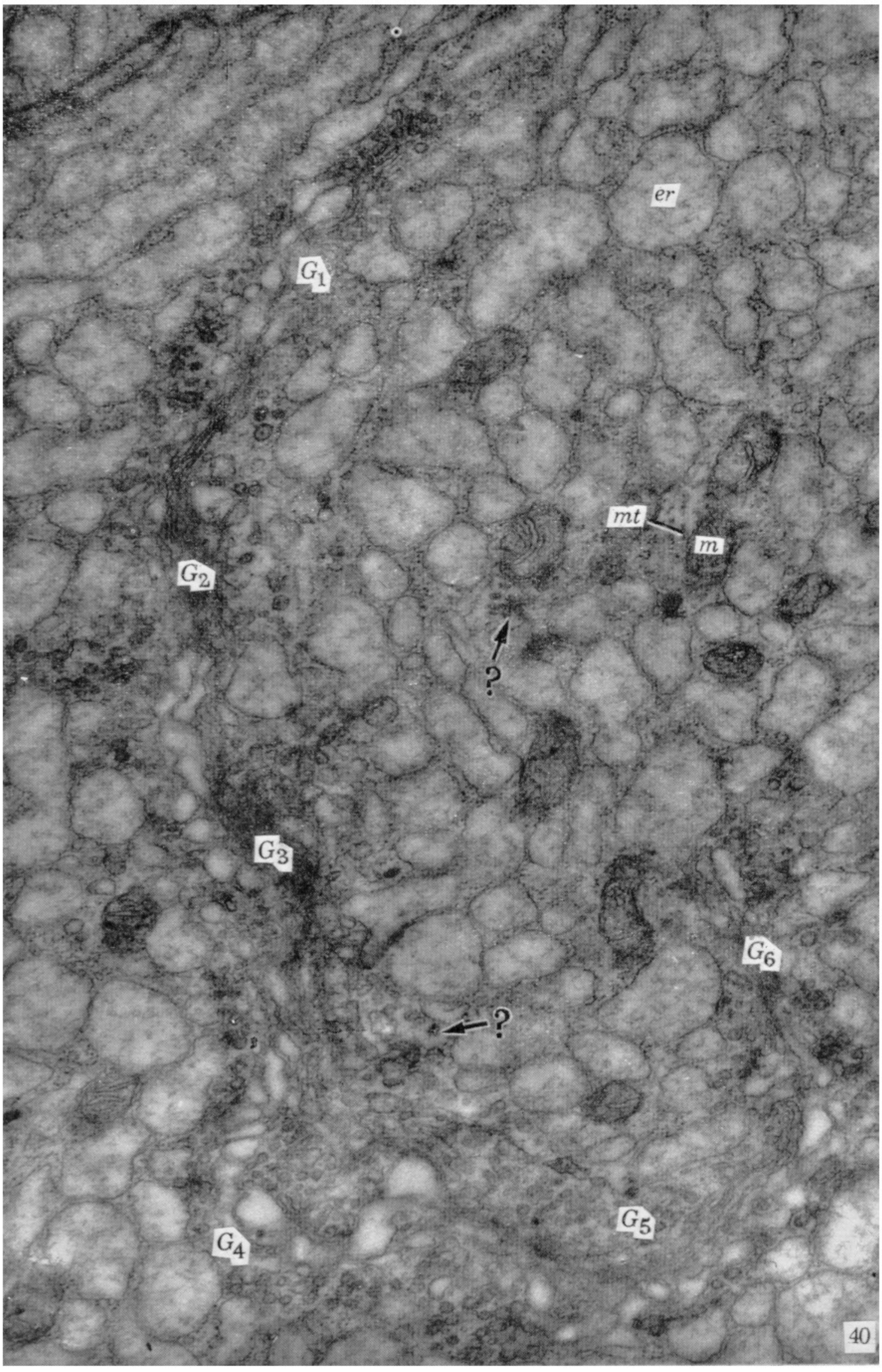
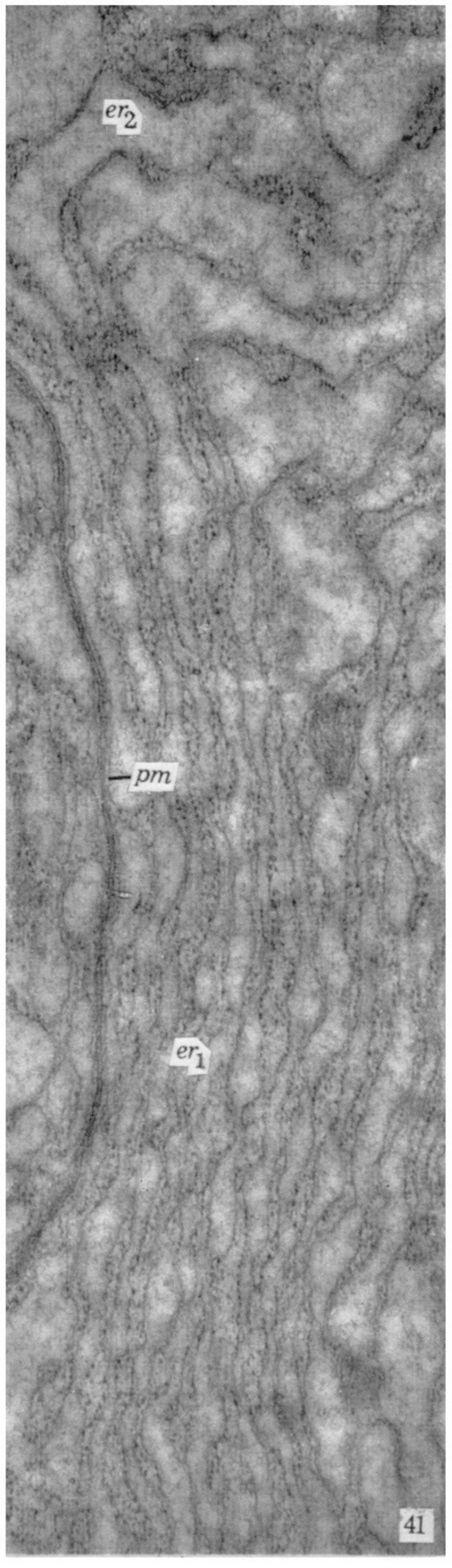


FIGURE 37. Cytoplasmic bodies (*cb*) are abundantly found in the basal cytoplasmic region, while lysosome-like bodies (*ly*) are few. Along the lateral plasma membranes may be found mitochondria in pairs closely apposed on either side (*star*). × 57500.

FIGURE 38. A number of Golgi units have combined to form one enormous complex (*G*). Within one unit may be seen a cytoplasmic body (*cb*). × 28500.

FIGURE 39. Many polyribosomes (*prb*) may be observed attached to the rough ER (*er*). × 38000.





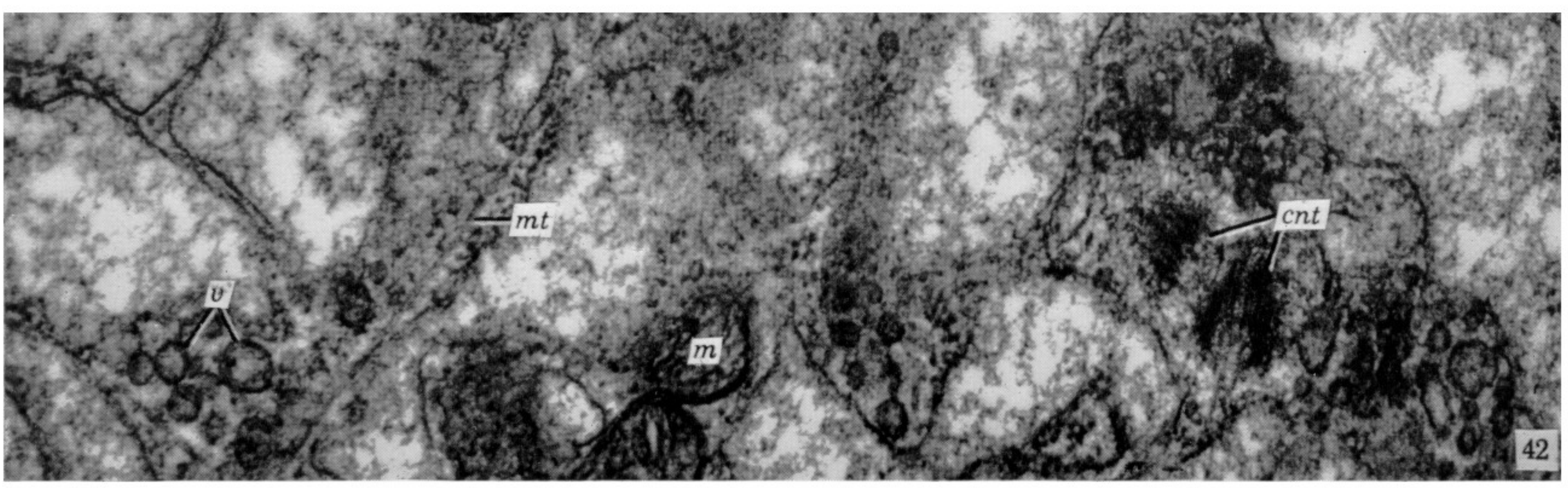


FIGURE 40. Six units combined into one enormous Golgi complex (G_1–G_6). There are some electron-dense granules near the Golgi units and mitochondria of unknown nature (?). × 32500.

FIGURE 41. Parallel arrays of rough ER cisternae (er_1) very often swell into vesicles (er_2), especially close to the Golgi apparatus. × 39000.

FIGURE 42. Apical cytoplasmic region having numerous small, smooth vesicles (*v*), some microtubules (*mt*), and a centriolar apparatus (*cnt*) in between swollen ER cisternae. × 52000.

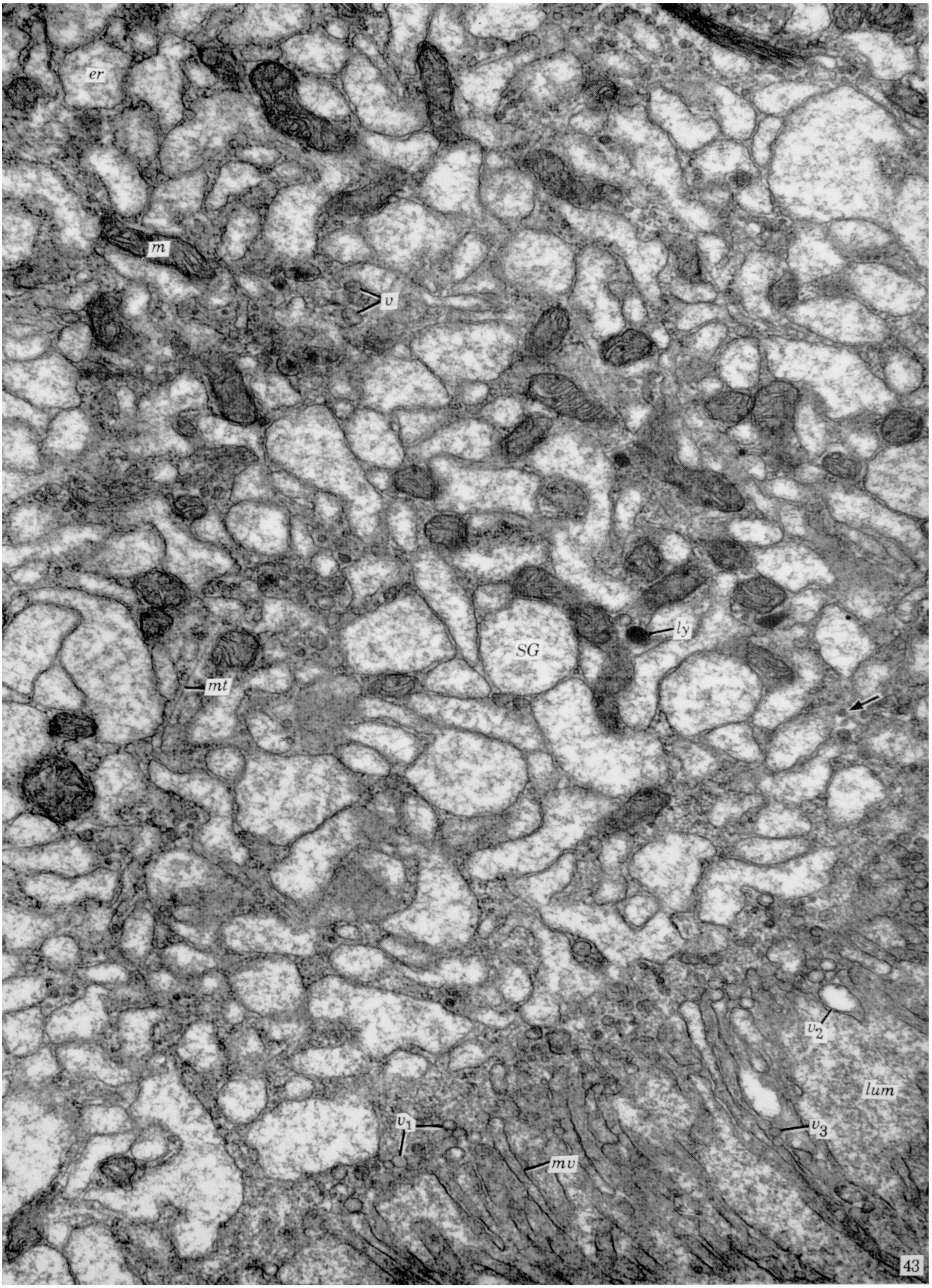
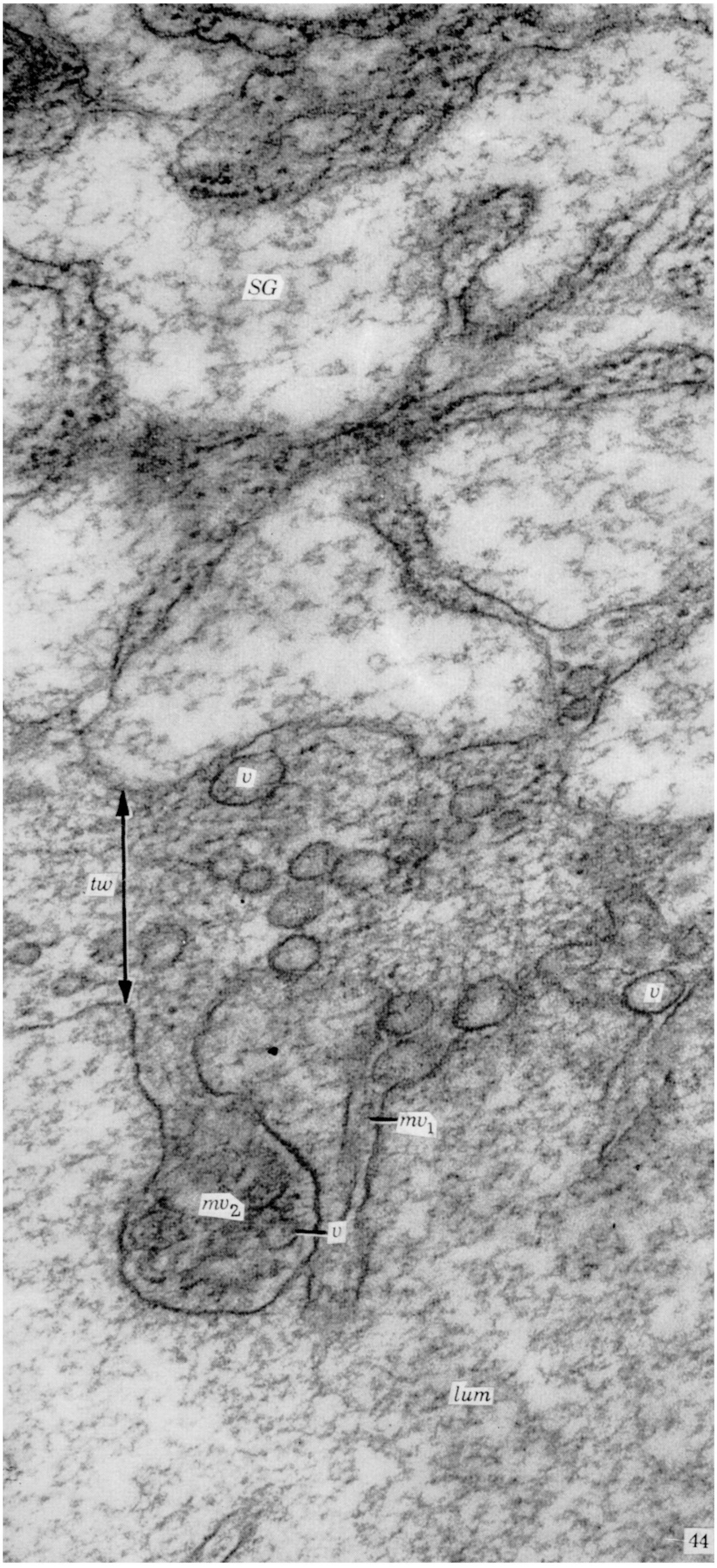


FIGURE 43. The contents of ER cisternae (*er*), what are considered as secretory vesicles (*SG*) and the lumen (*lum*) are very similar indeed. The terminal-web region is fairly well demarcated, with electron-dense content and small, smooth vesicles (v_1). Large vesicles (v_2) are sometimes observed at the base of microvilli; but more frequently, smaller vesicles (v_3) are seen within the microvilli (*mv*). × 32500.



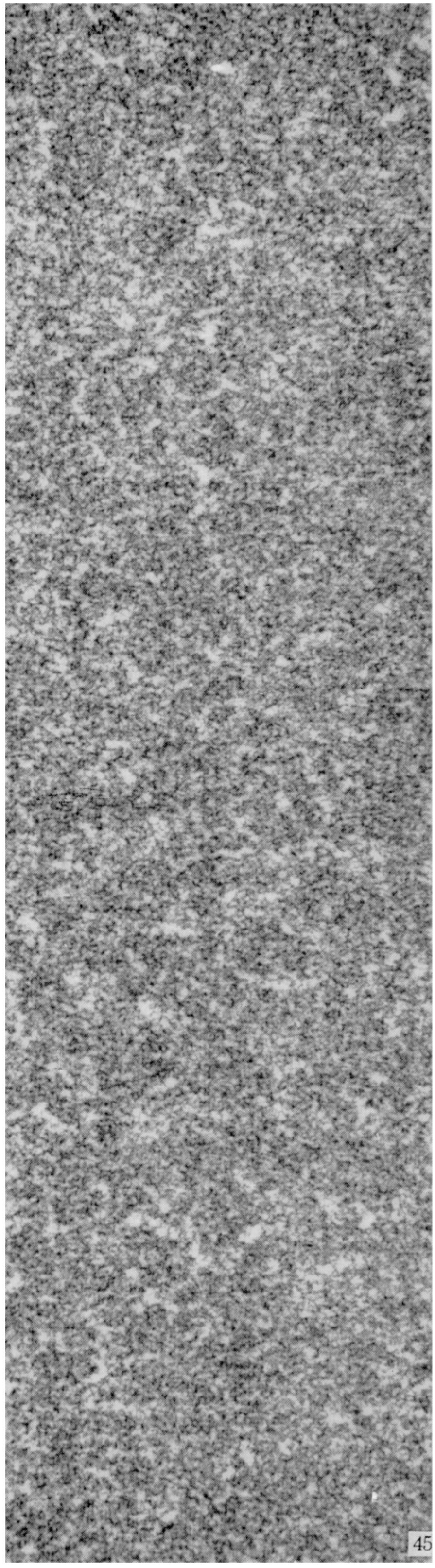
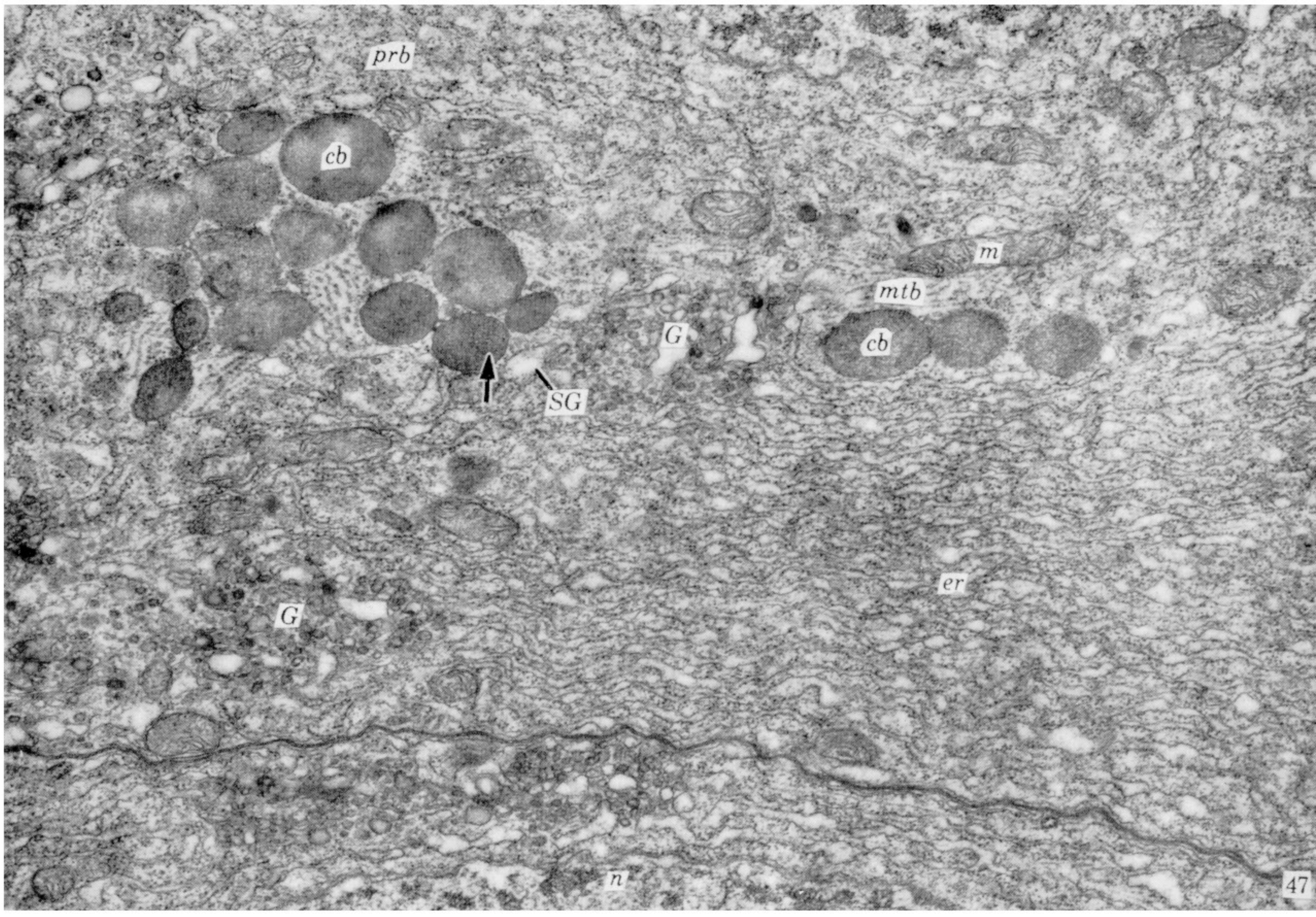


FIGURE 44. Microvilli are usually more or less straight cylindrical structures (mv_1), but in rare occasions in this gland the microvilli become clavate (mv_2). Note also the small, smooth vesicles (v) in the terminal-web region (tw). × 92000

FIGURE 45. The luminal content consists of minutely granular and fibrous components. × 39000.



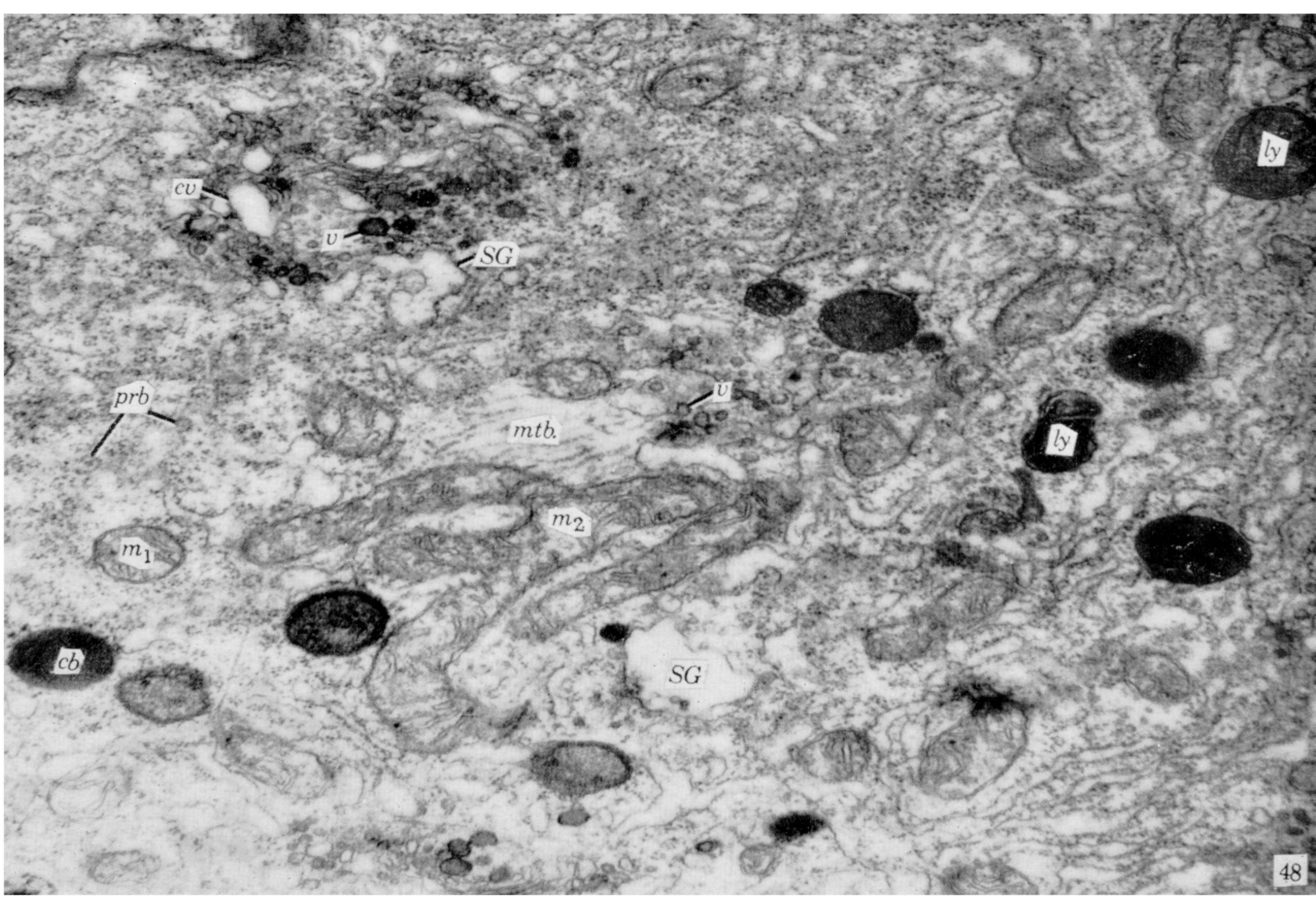
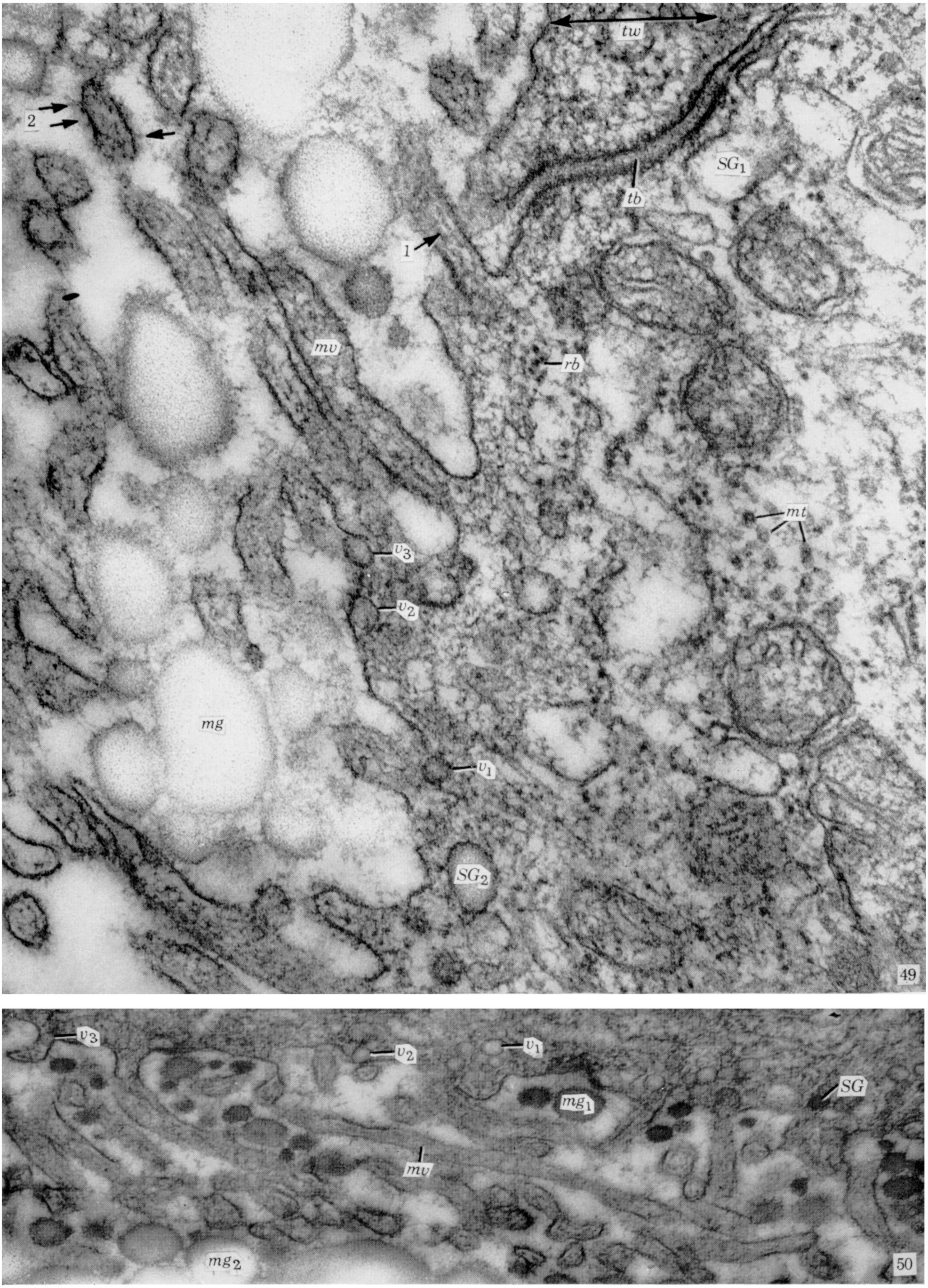
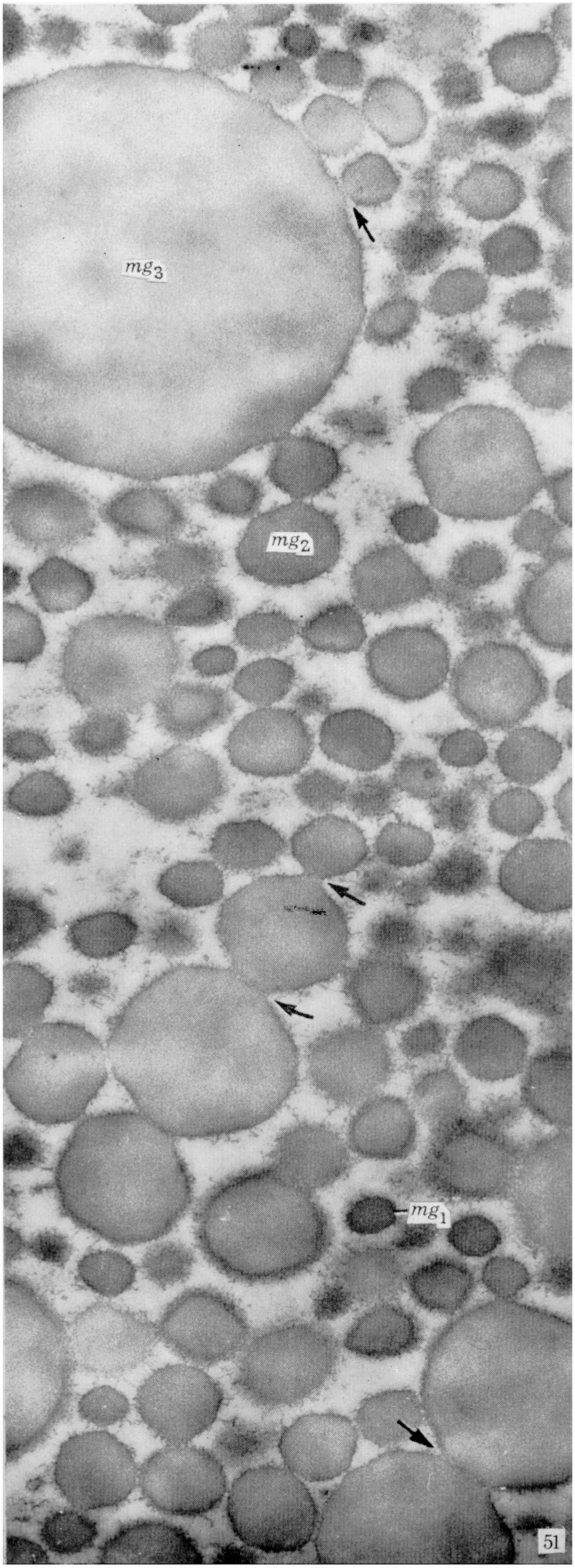


FIGURE 47. The rough ER (*er*) is extensively developed. There are many cytoplasmic bodies (*cb*) in this mid-cytoplasmic region, one of which shows another recently engulfed cytoplasmic body (*arrow*). × 24000.

FIGURE 48. Mitochondria (m_2) in this gland can assume complex forms, which frequently have closely associated microtubular arrays (*mtb*). The Golgi apparatus has rather large condensing vacuoles (*cv*) and very dense Golgi vesicles (*v*). There are abundant polyribosomes (*prb*) in the cytoplasm. It is possible that small vesicles add their contents to secretory vesicles (*SG*). × 32500.



FIGURES 49 and 50. For description see facing page.



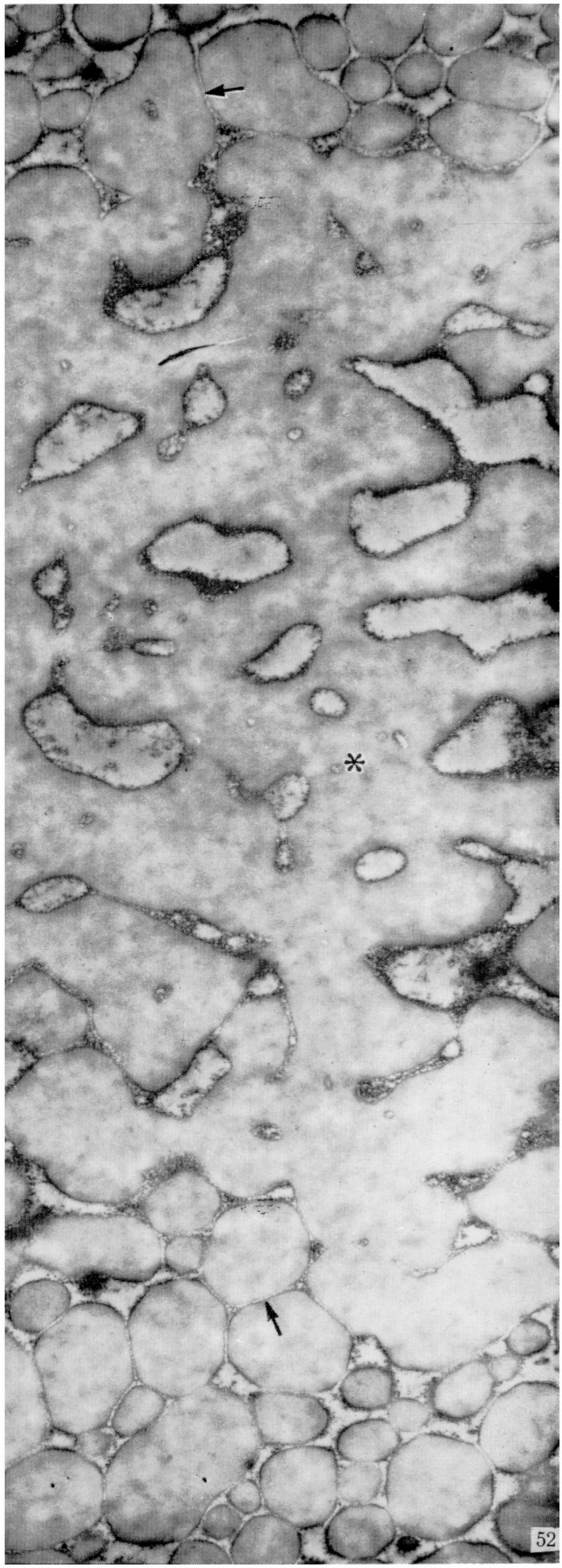


FIGURE 51. The luminal content consists of globules of various sizes, their electron-density becoming less with increasing size (mg_1–mg_3). Enlargement seems to be due to the fusion of globules (*arrows*). × 44000.

FIGURE 52. In the more proximal portion of the gland, the globules of secretion become more or less confluent (*star*). But some globules have still a persistent, dense, limiting cortex (*arrows*). × 137500.

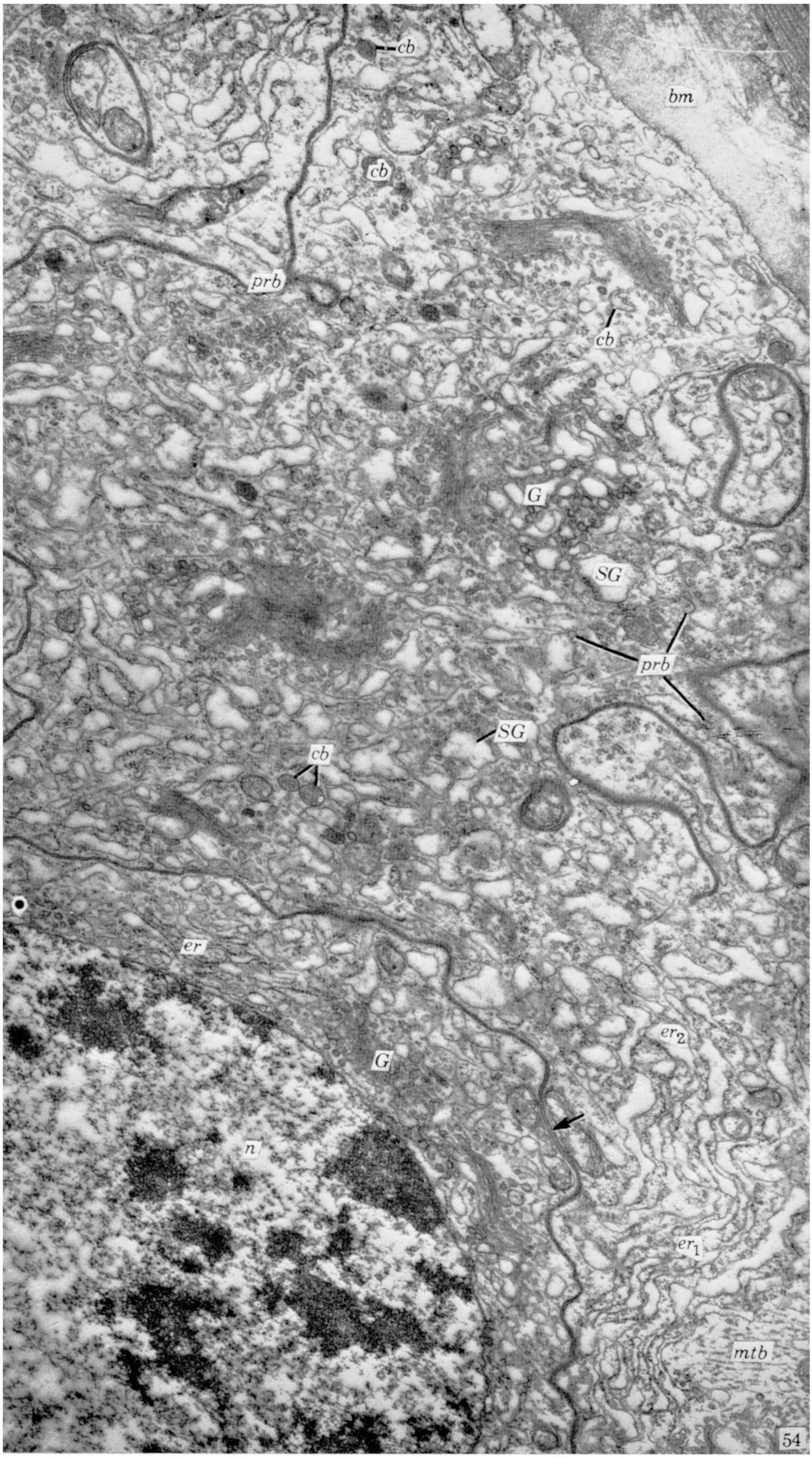
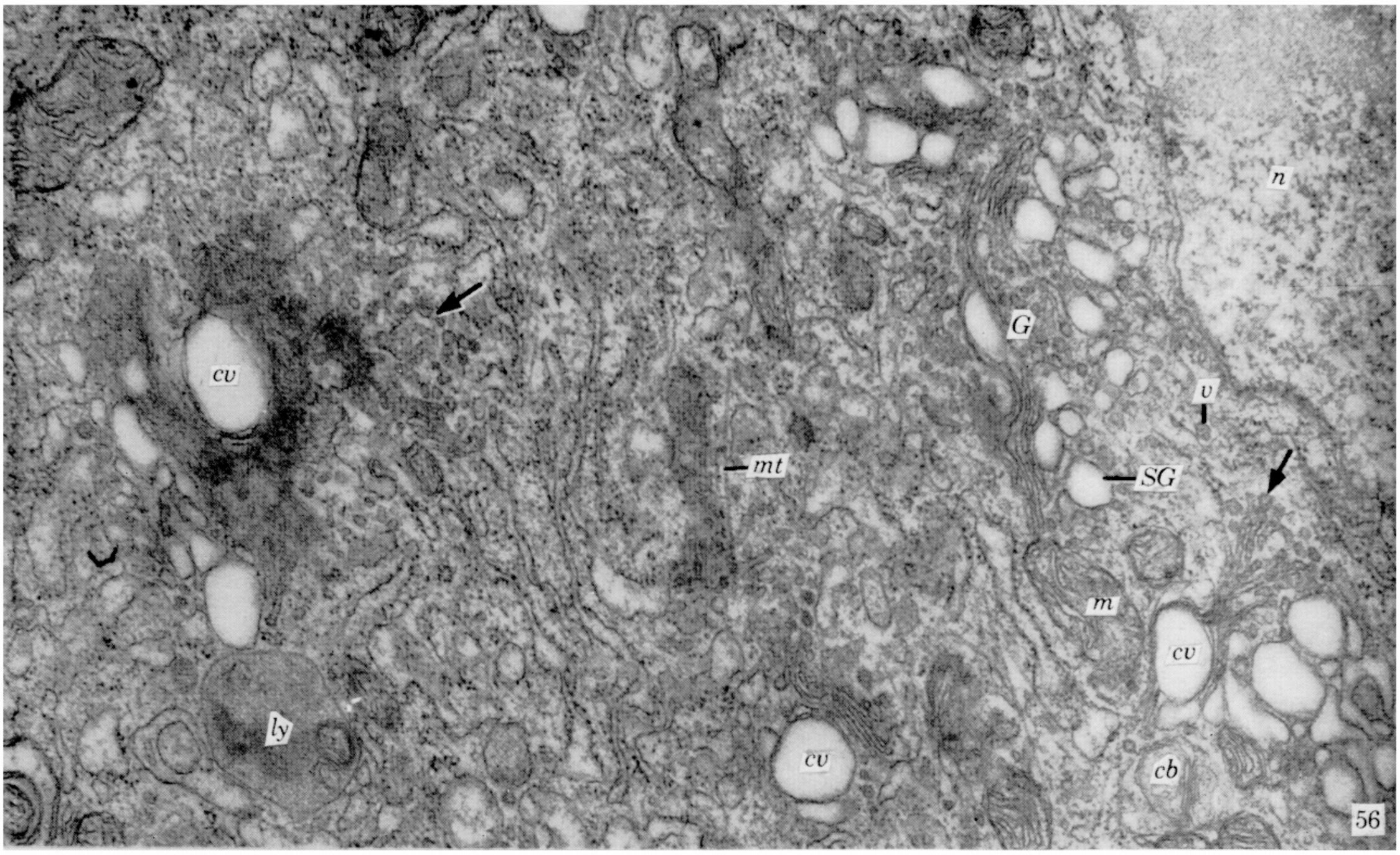
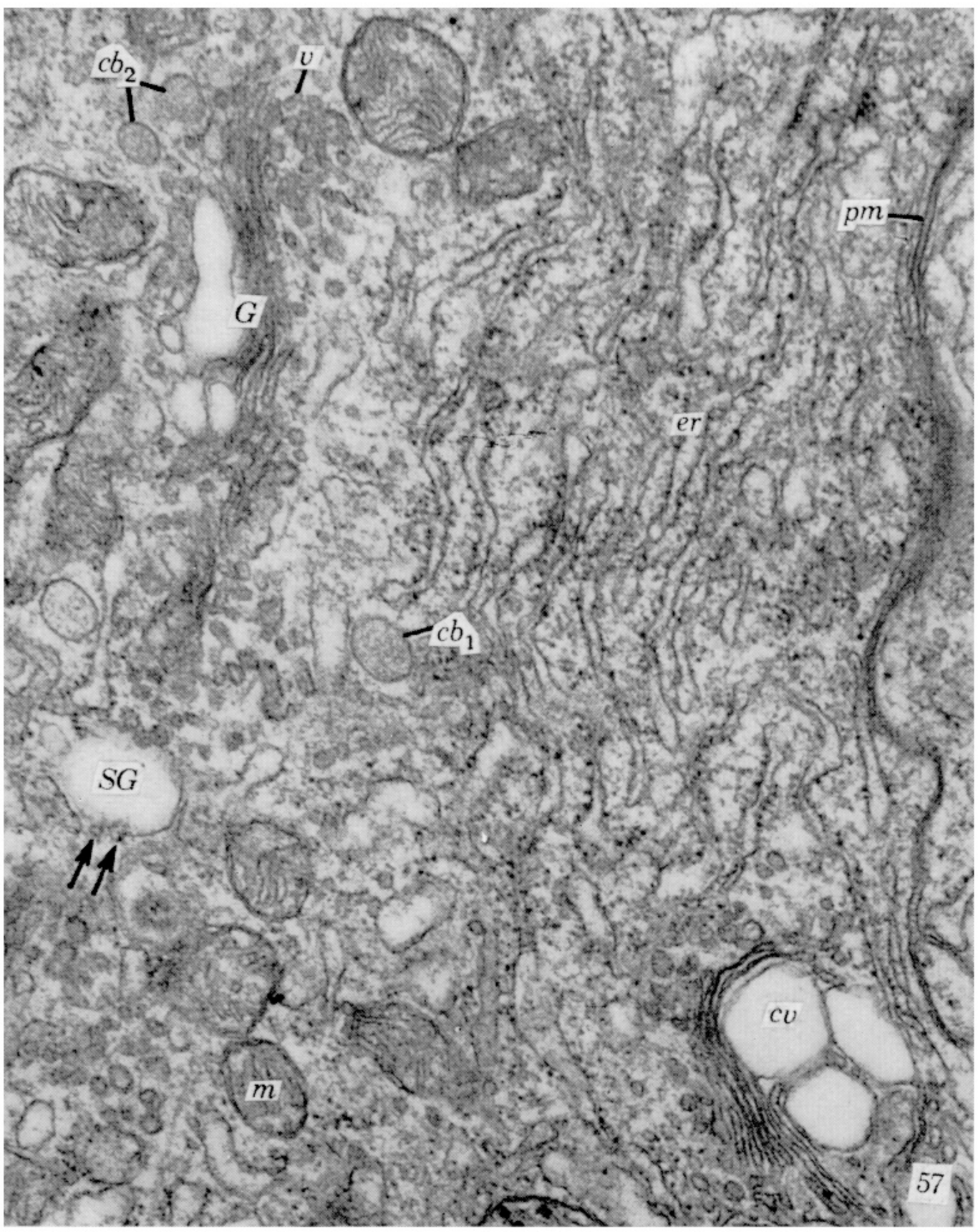
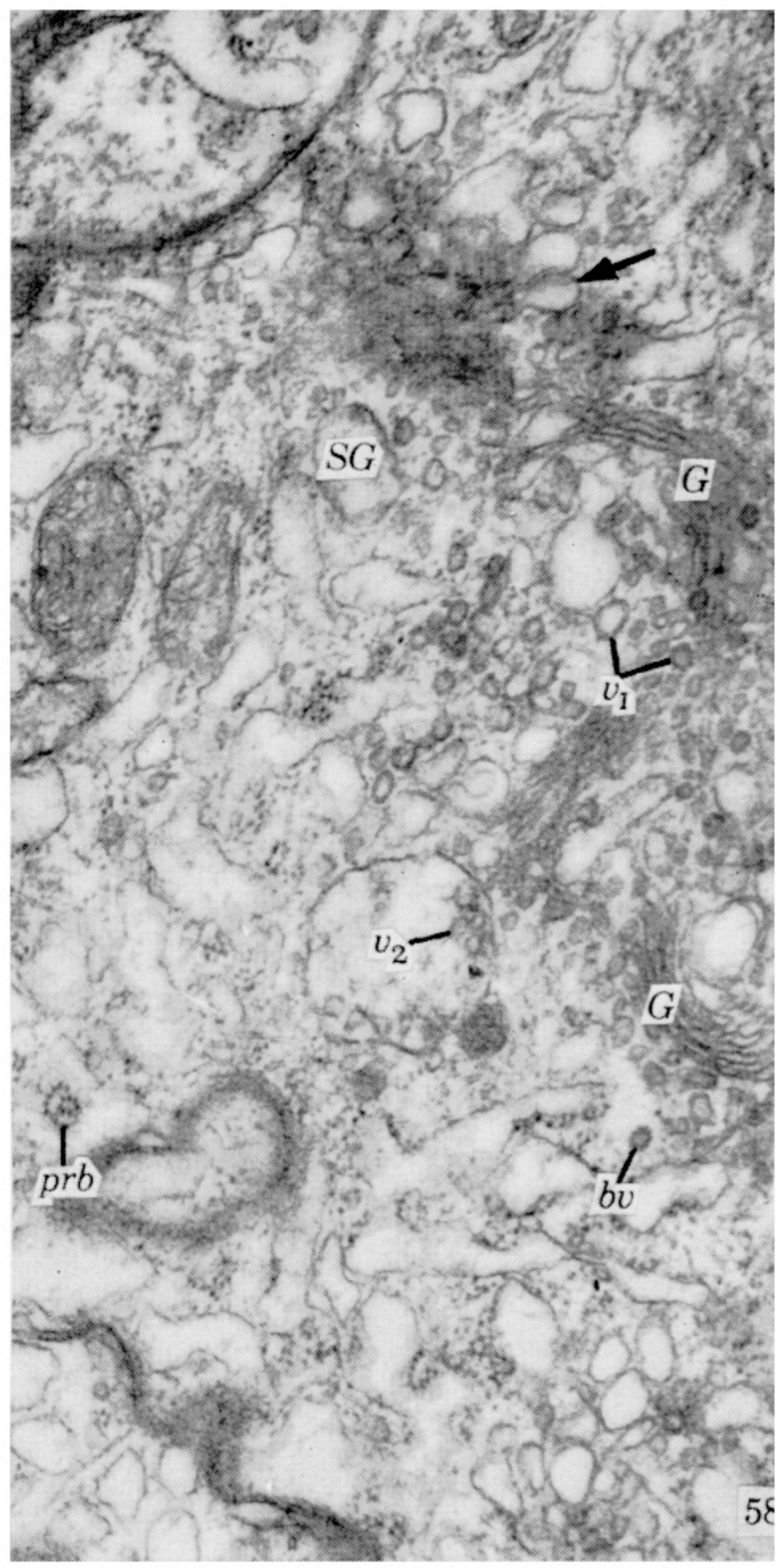


FIGURE 54. In some areas, the rough ER is found in the form of flattened cisternae (er_1); away from the perinuclear region, and especially in the neighbourhood of the Golgi apparatus (G), the ER is swollen into vesicles (er_2) which may later become secretory vesicles (SG). Note also a pair of mitochondria in close parallel apposition across the lateral plasma membrane (*arrow*). × 24000.

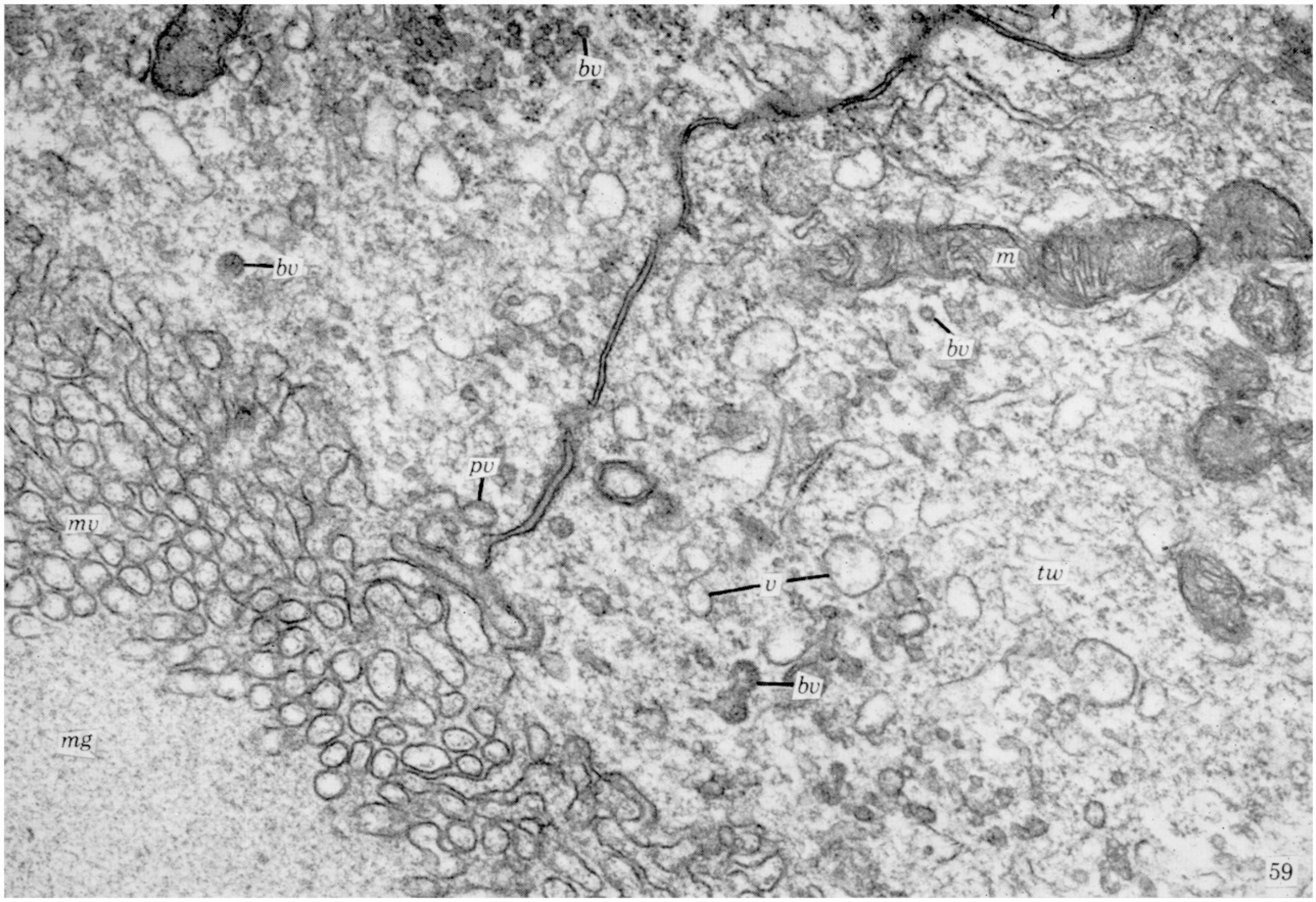
FIGURE 55. Internuclear region, showing several enlargements of the intercellular space (*stars*). Note also a number of moderately large vesicles (possibly secretory vesicles) with small, smooth vesicles in the course of fusing with them (*arrows*). × 22000.







FIGURES 56 to 58. For description see facing page.



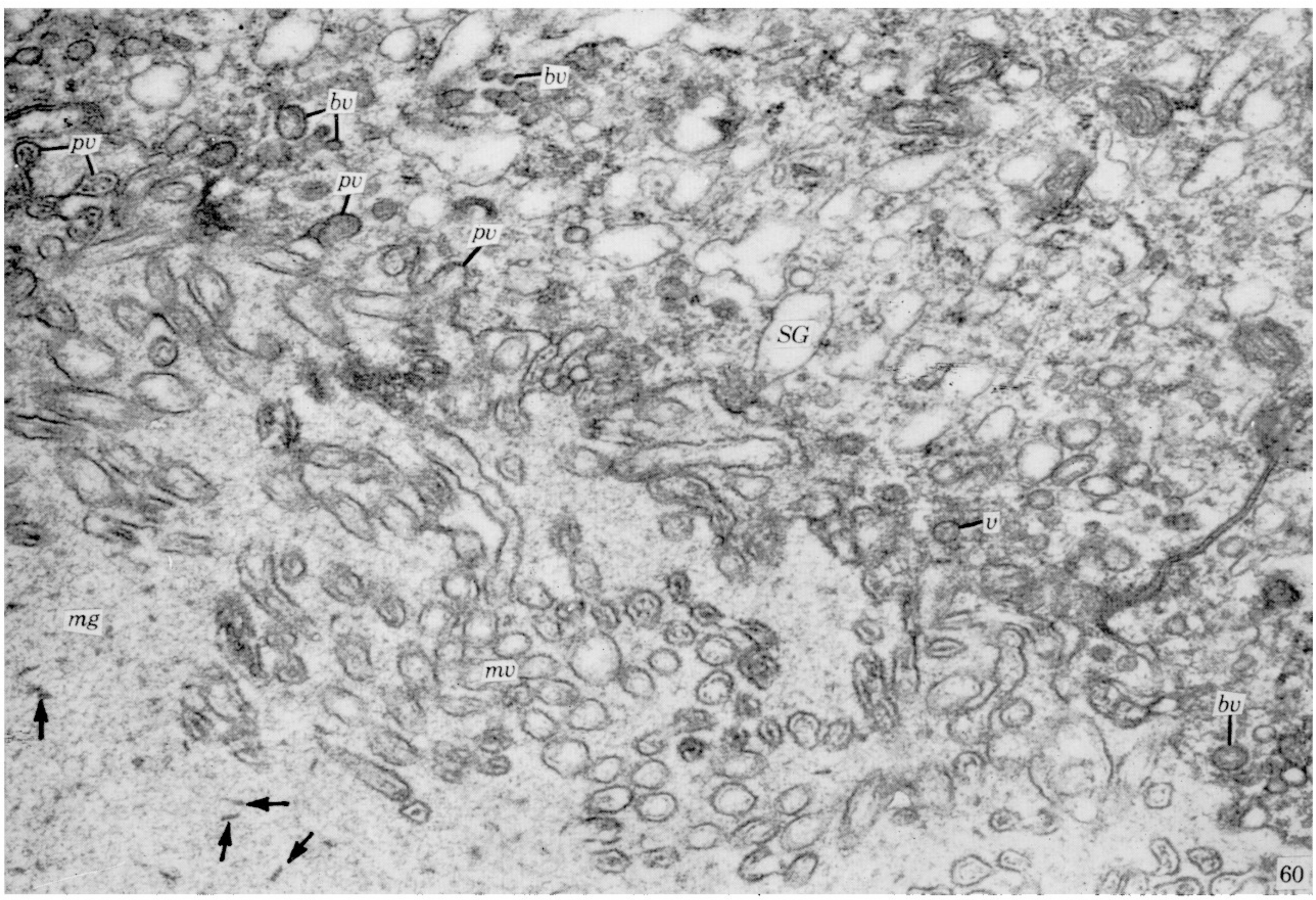
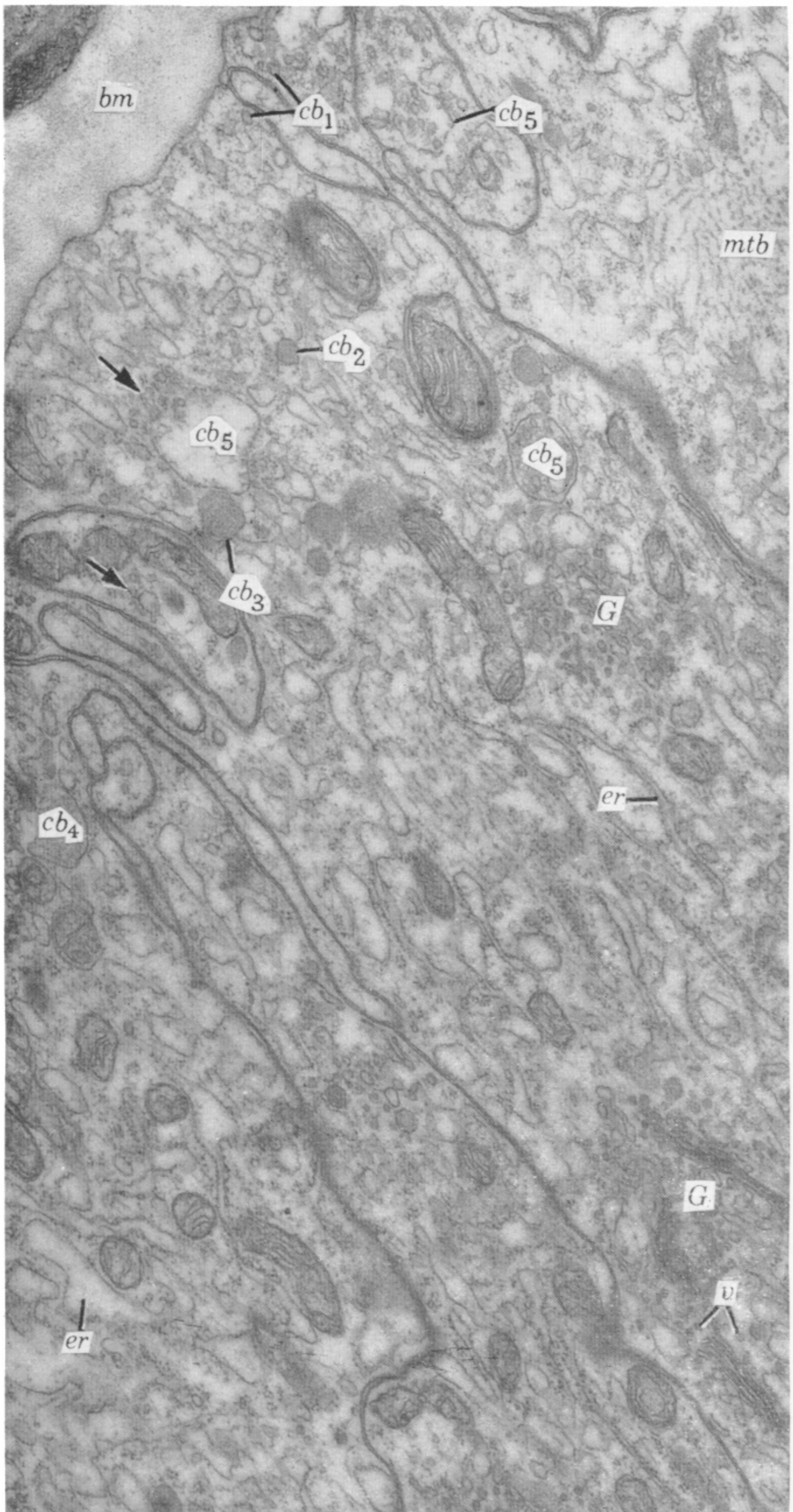
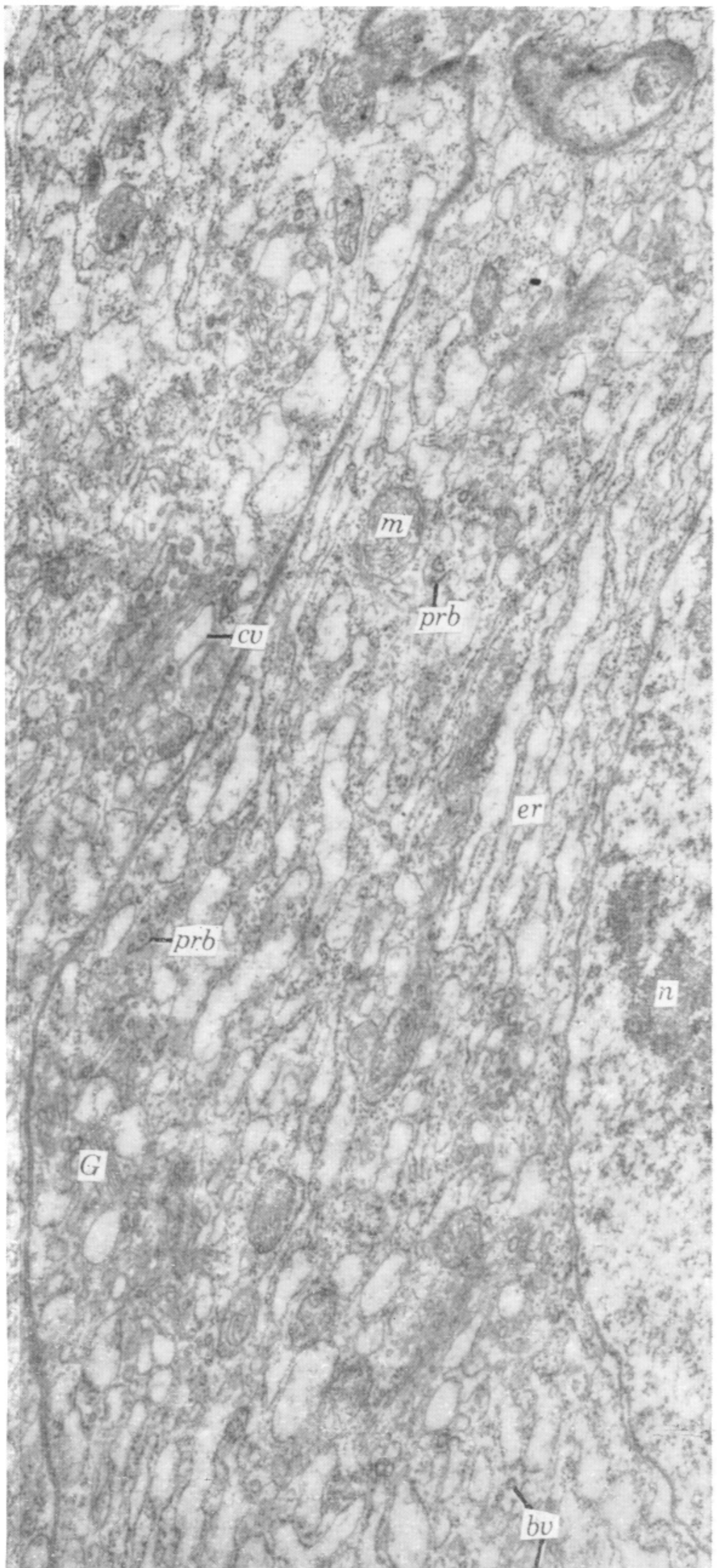


FIGURE 59. The apical cytoplasmic region. The terminal-web area (*tw*) contains small vesicles of various sizes (*v*) which seem to arise as a result of pinocytotic activity (*pv*). The luminal content (*mg*) consists of a minutely granular or fibrous substance. × 38000.

FIGURE 60. The luminal region, showing the secretion as consisting of short fibrillar structures (*arrows*) embedded in a minutely granular matrix. Note also the pinocytotic pits (*pv*) on the luminal plasmalemma, and the coated vesicles (*bv*). × 38000.





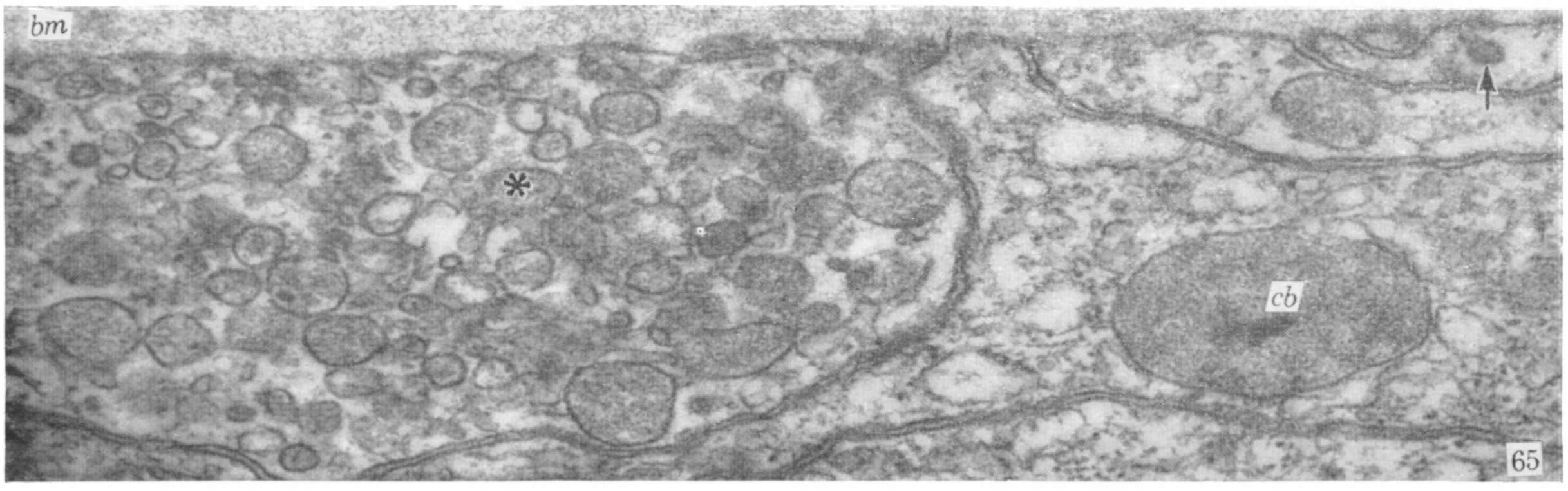
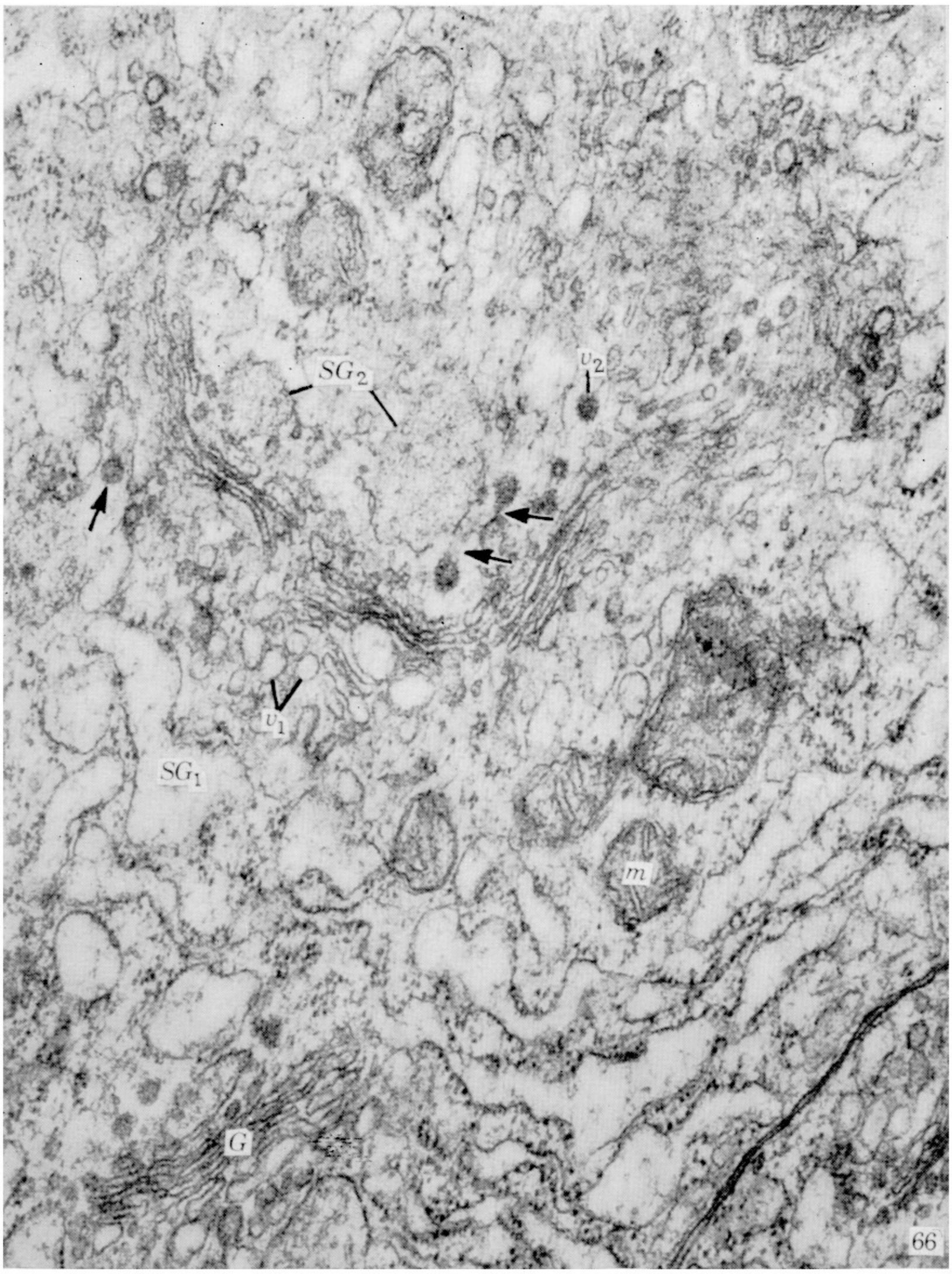
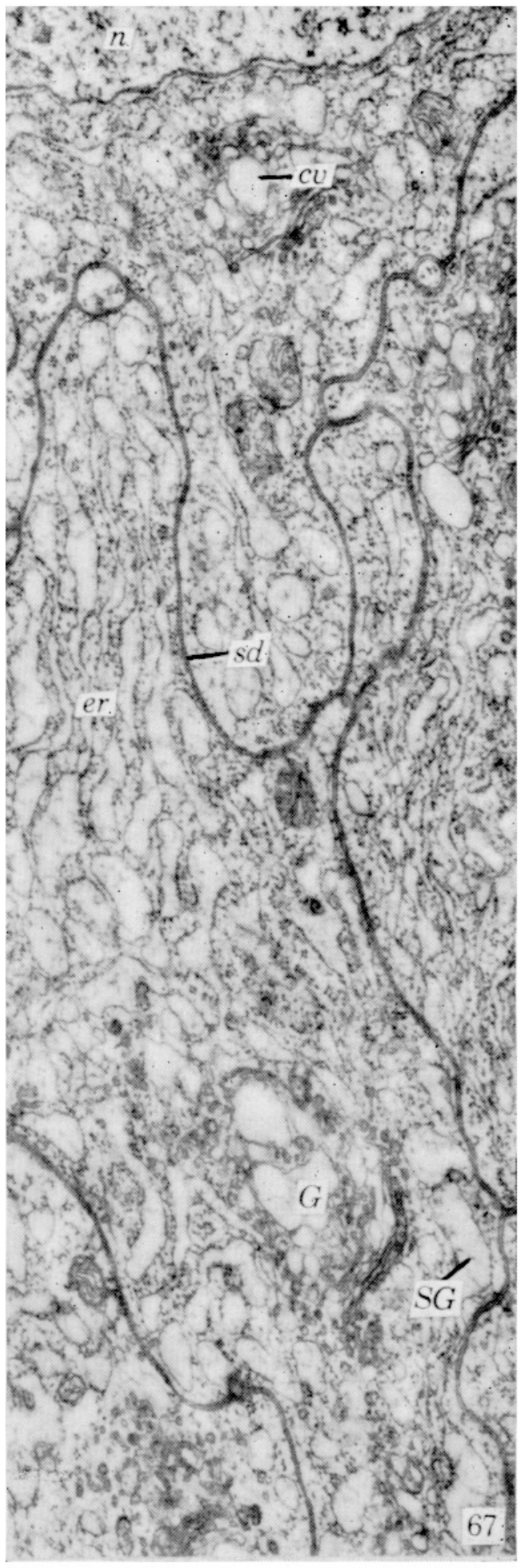


FIGURE 63. The basal cytoplasmic region showing cytoplasmic bodies of various sizes, from minute (cb_1) to large (cb_5). They seem to have grown to this large size by incorporating smaller bodies (*arrows*). But some of the vesicles being incorporated resemble Golgi vesicles (*v*). × 24000.

FIGURE 64. The Golgi units (*G*) are small, but they have a few small coated vesicles (*bv*) of unknown origin. Note also the large numbers of polysomes (*prb*). × 24000.

FIGURE 65. Numerous cytoplasmic bodies of various sizes are generally found in the basal cytoplasmic region (*star*). × 52000.





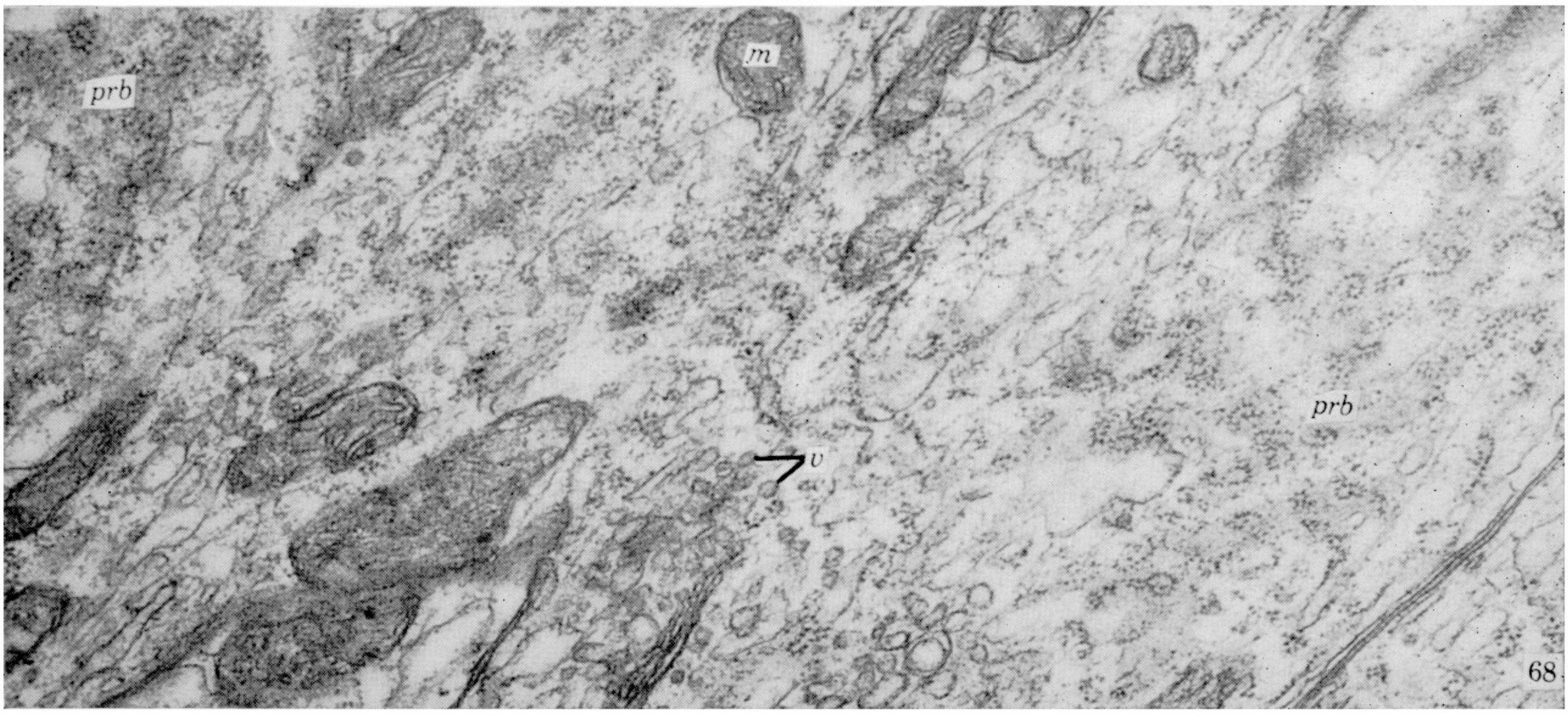
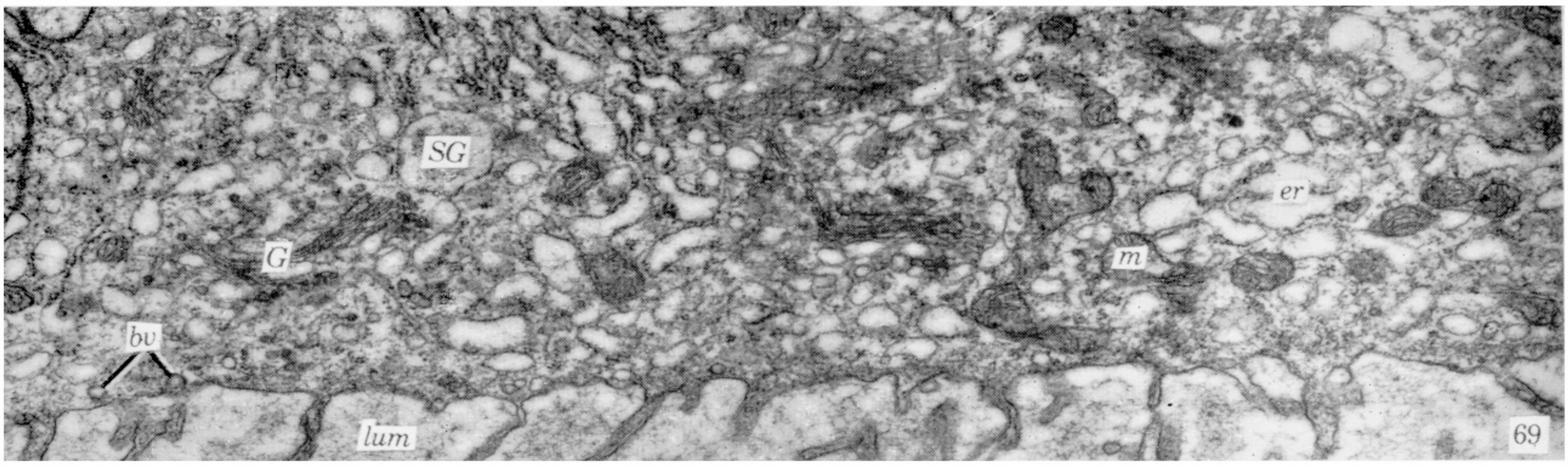
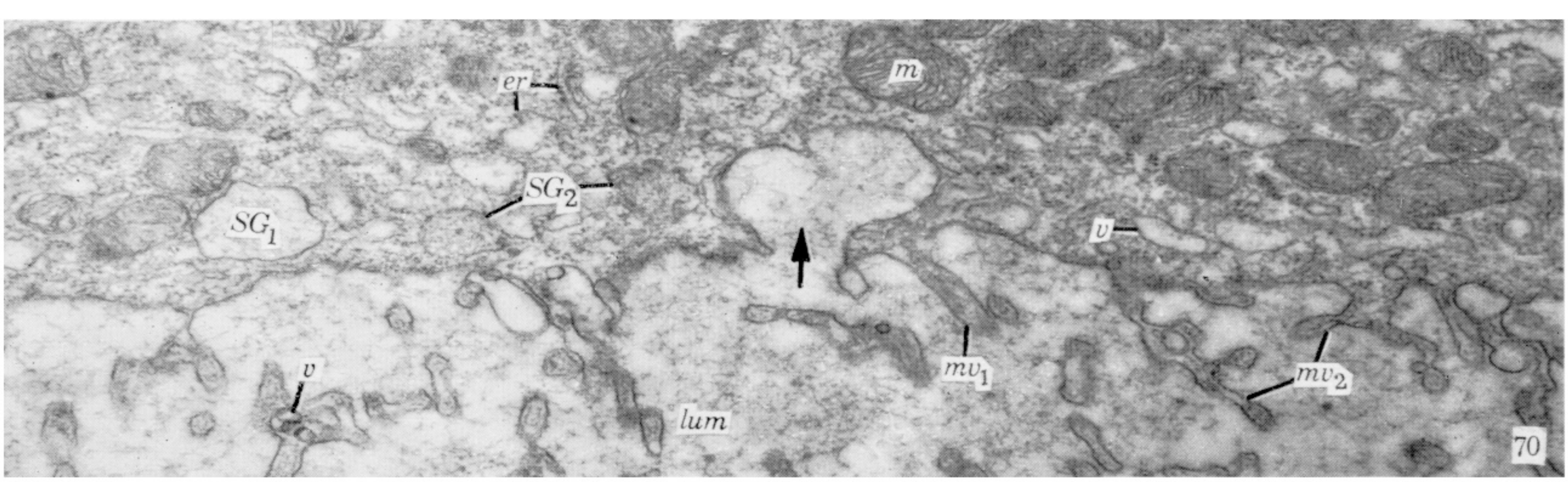


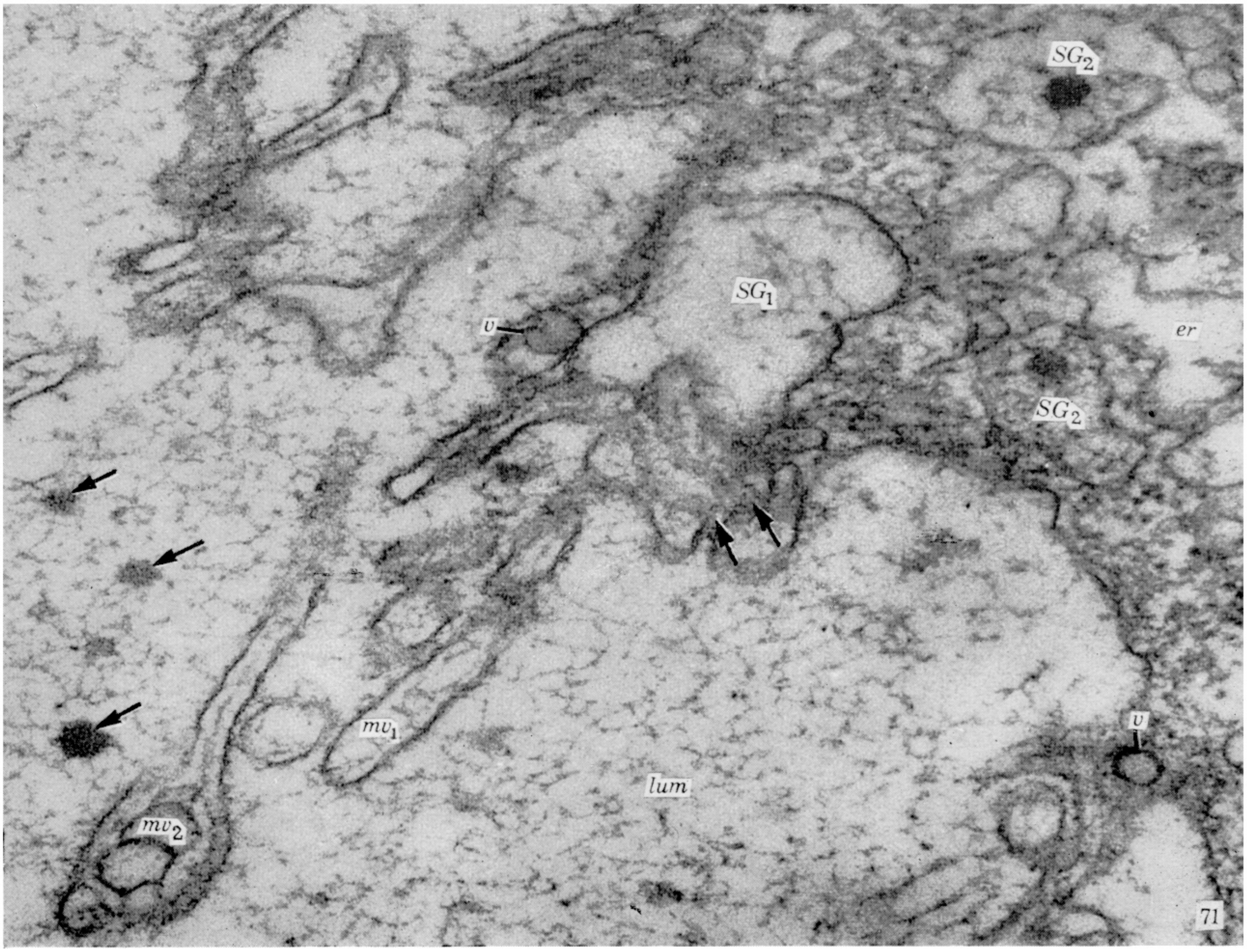
FIGURE 66. Secretory vesicles containing two kinds of secretion in the immediate neighbourhood of the Golgi apparatus (SG_1 and SG_2). Vesicles containing an electron-dense material (v_2) seem to be formed from the ER in the Golgi zone (*arrows*). Small vesicles with translucent content are also observed in the Golgi zone (v_1). × 52000.

FIGURE 67. Extensive and largely flattened rough ER (*er*). Golgi complexes (*G*) are rather small. × 24000.

FIGURE 68. Numerous polyribosomal deposits in the cytoplasm (*prb*). × 38000.







FIGURES 69 to 71 For description see facing page.

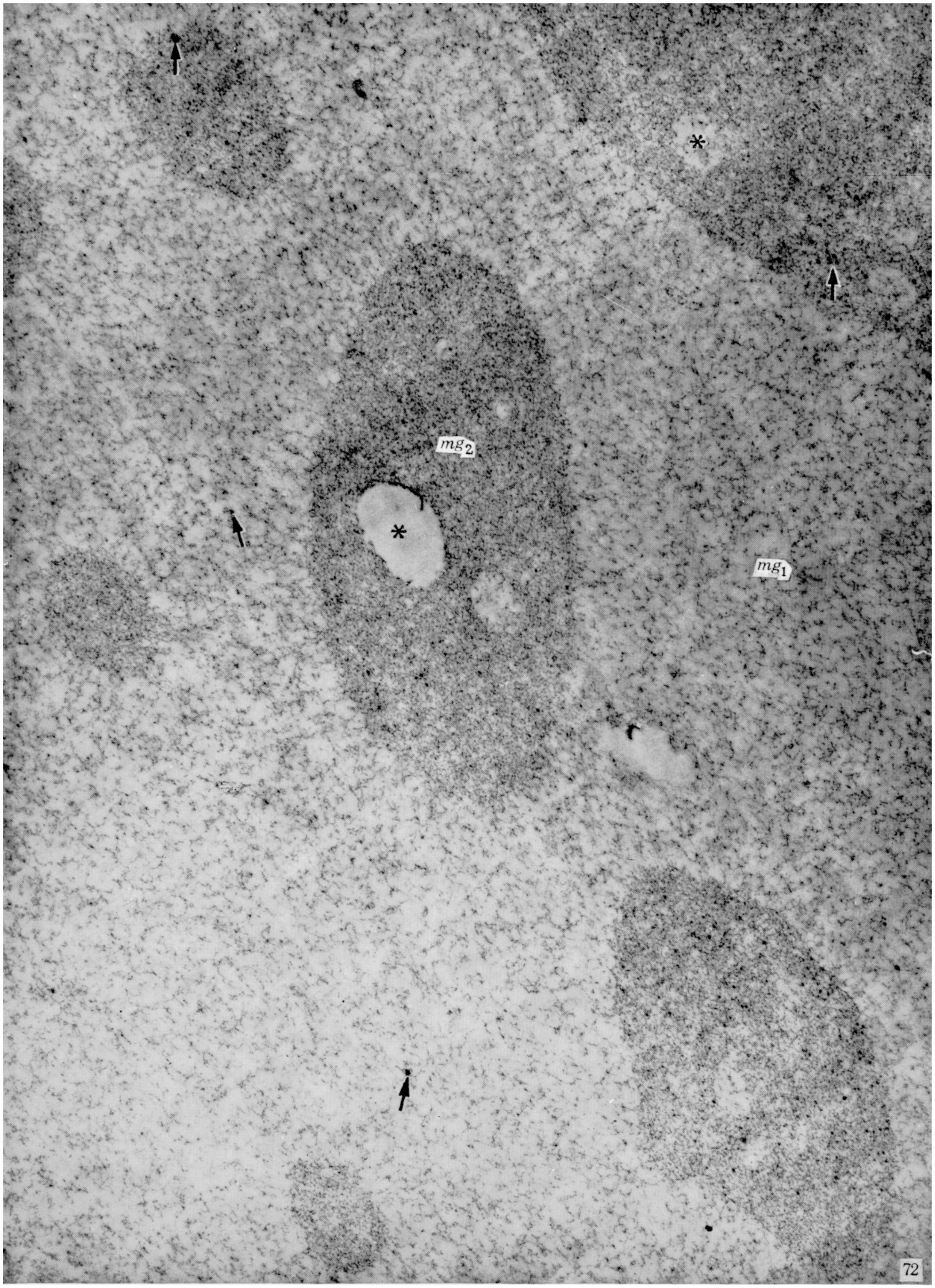
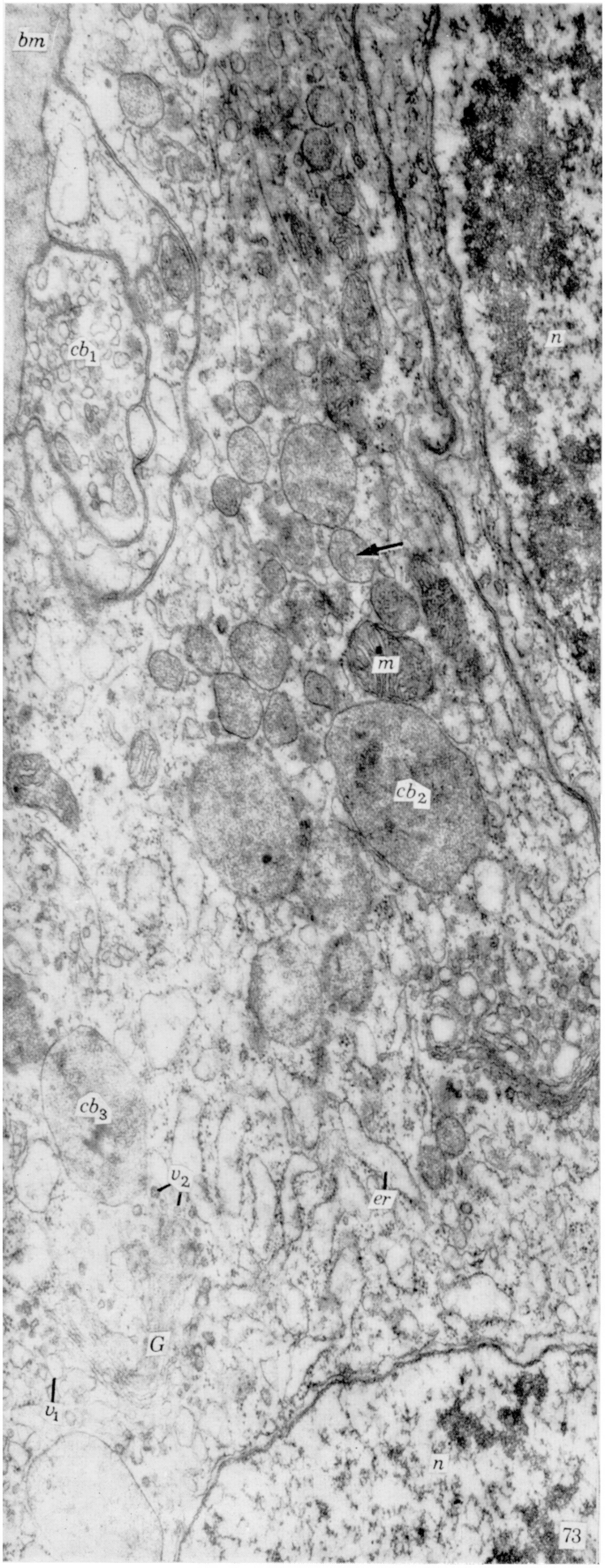
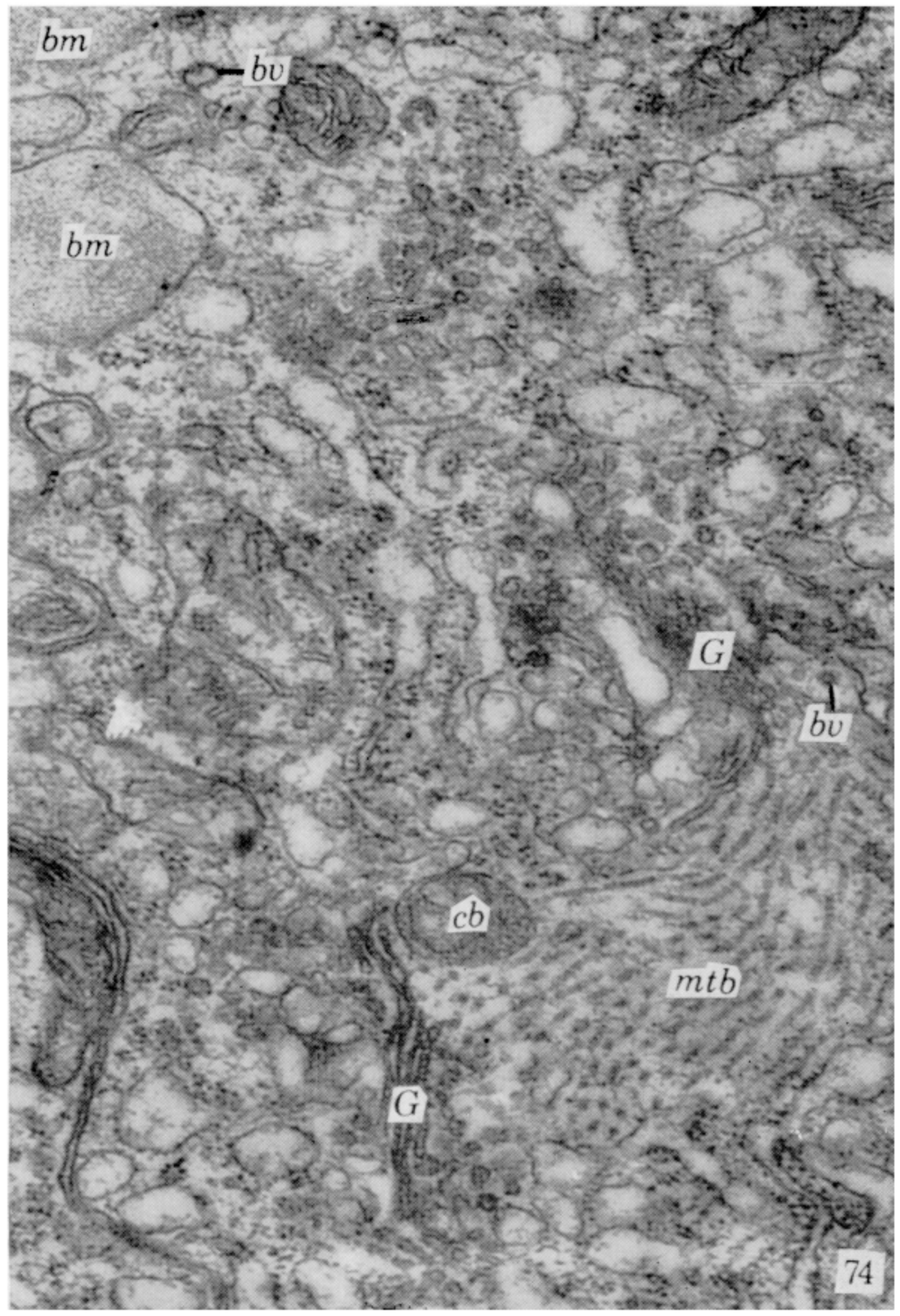
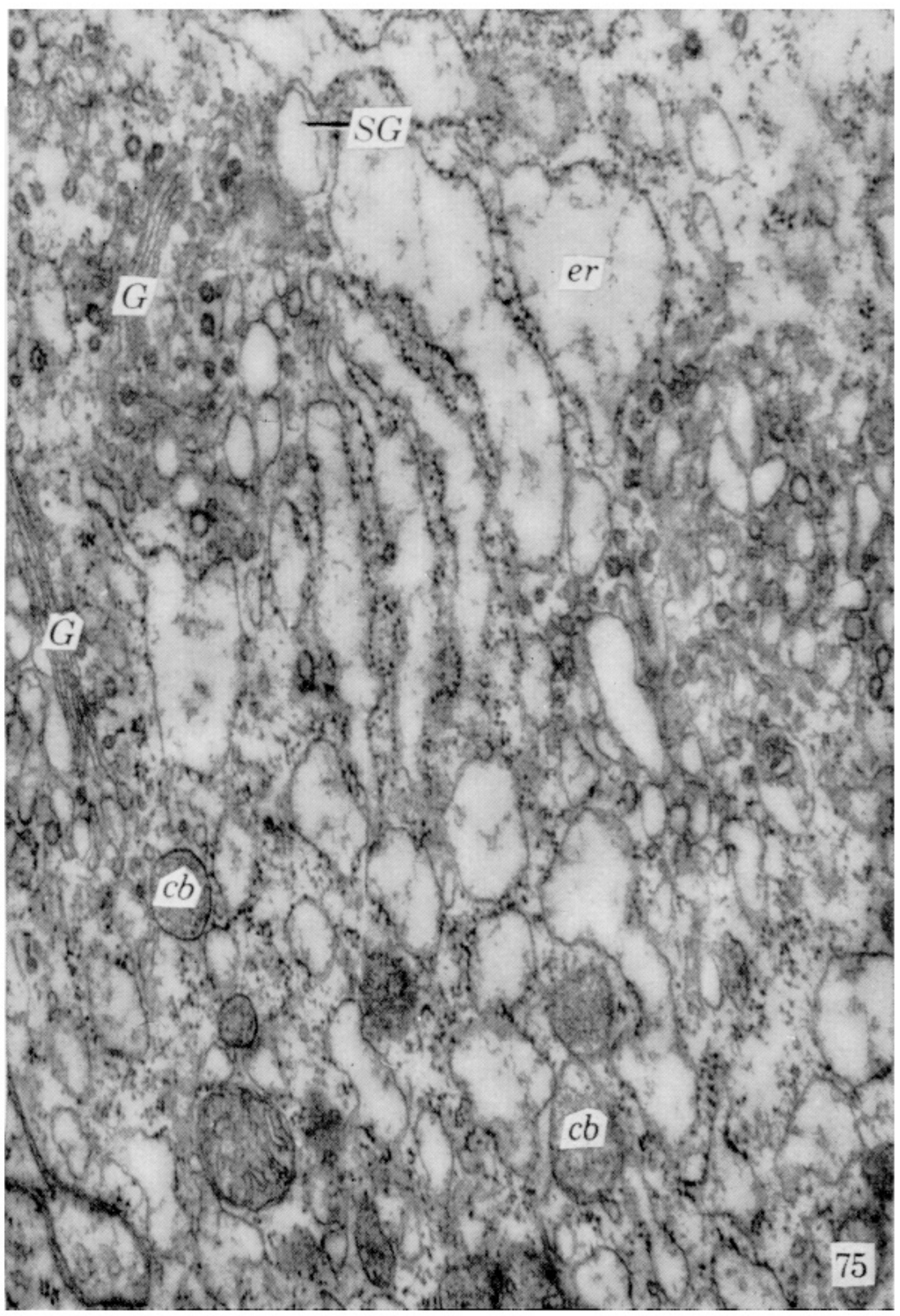


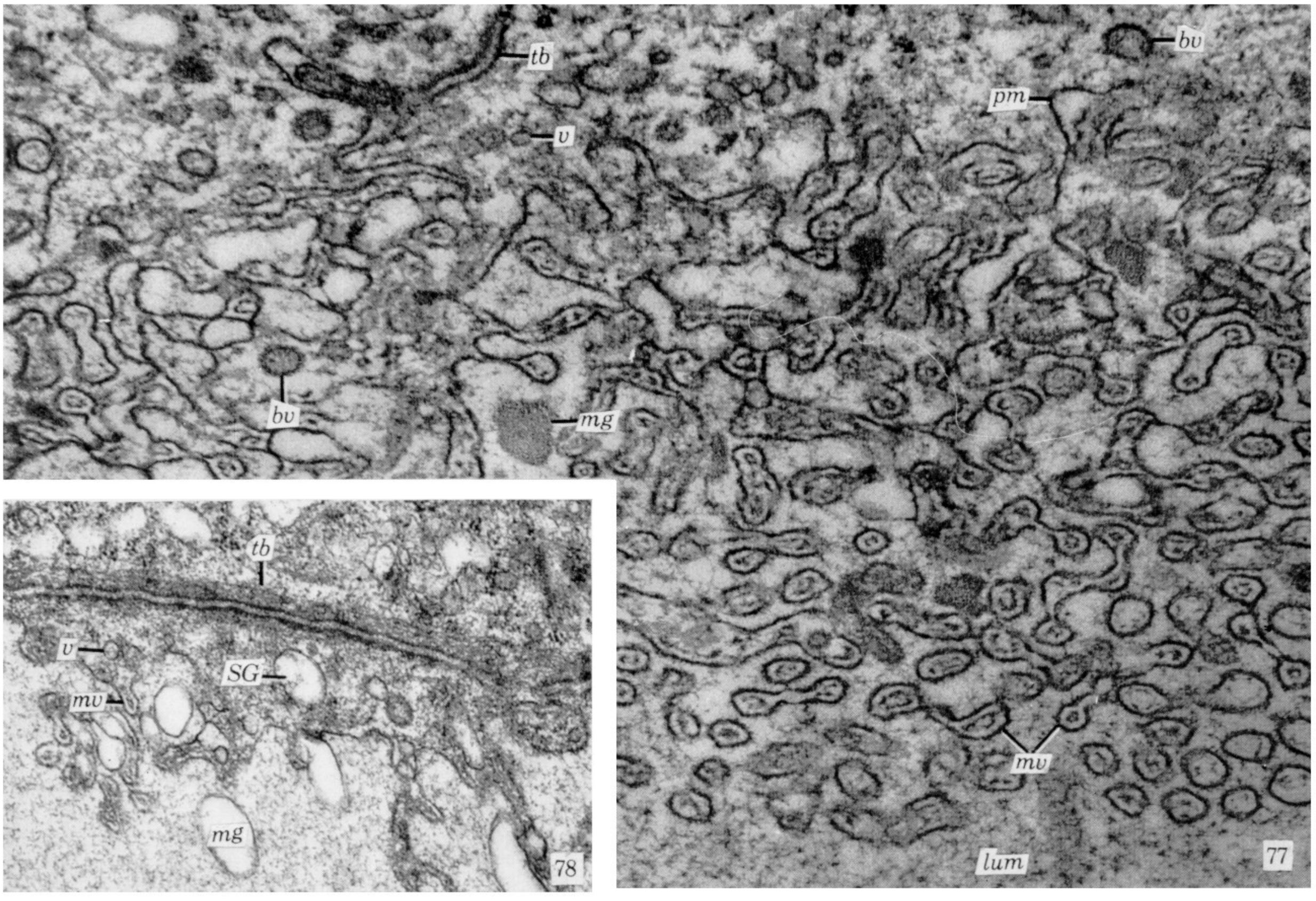
FIGURE 72. The secretion within the gland lumen consists of a matrix of finely fibrous material (mg_1) within which are imbedded minute electron-dense granules (*arrows*) and large fibrous granules (mg_2). The minute granules are also found in the latter (*arrows*). Note the empty 'vacuities' in the large granules (*star*). $\times 32500$.

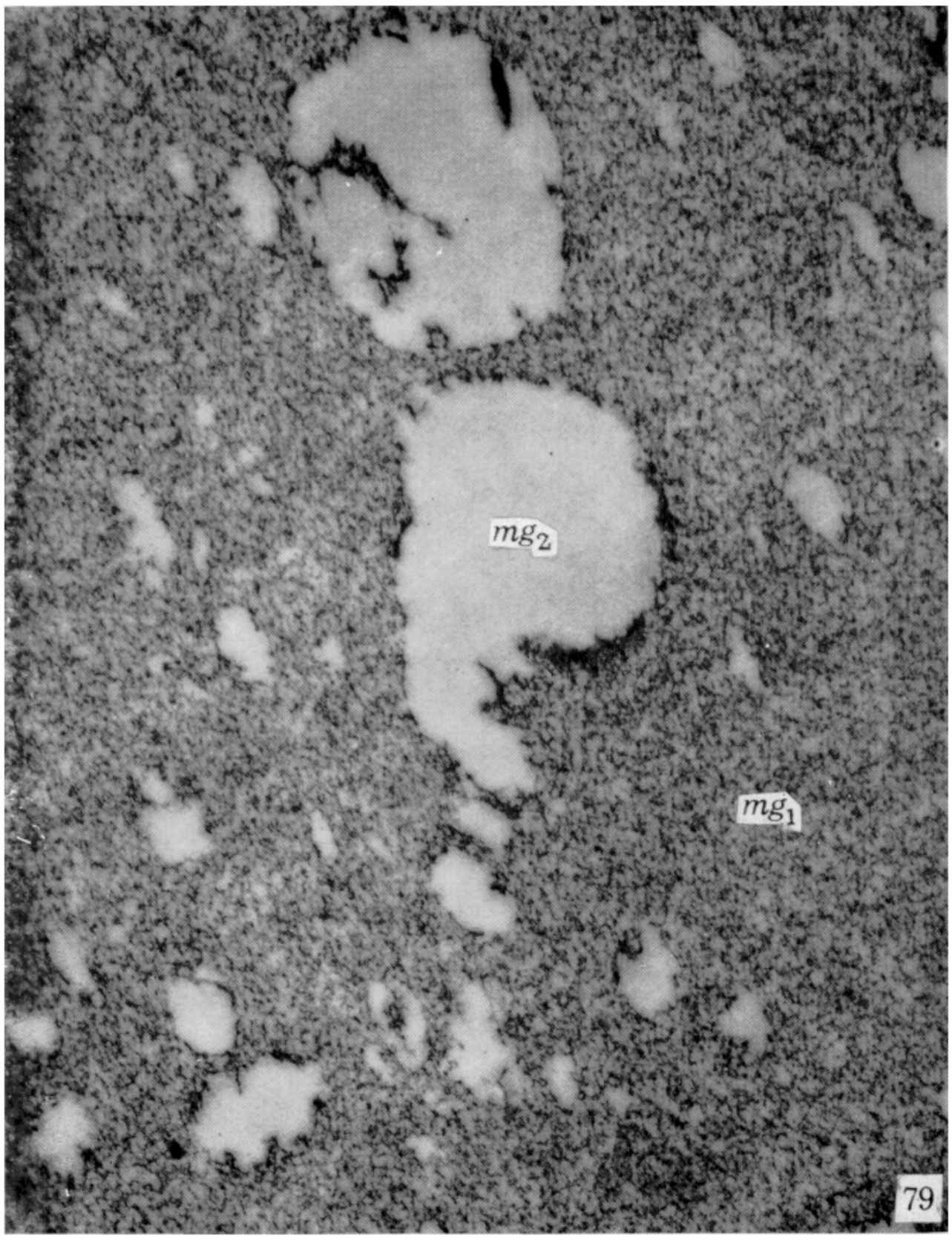


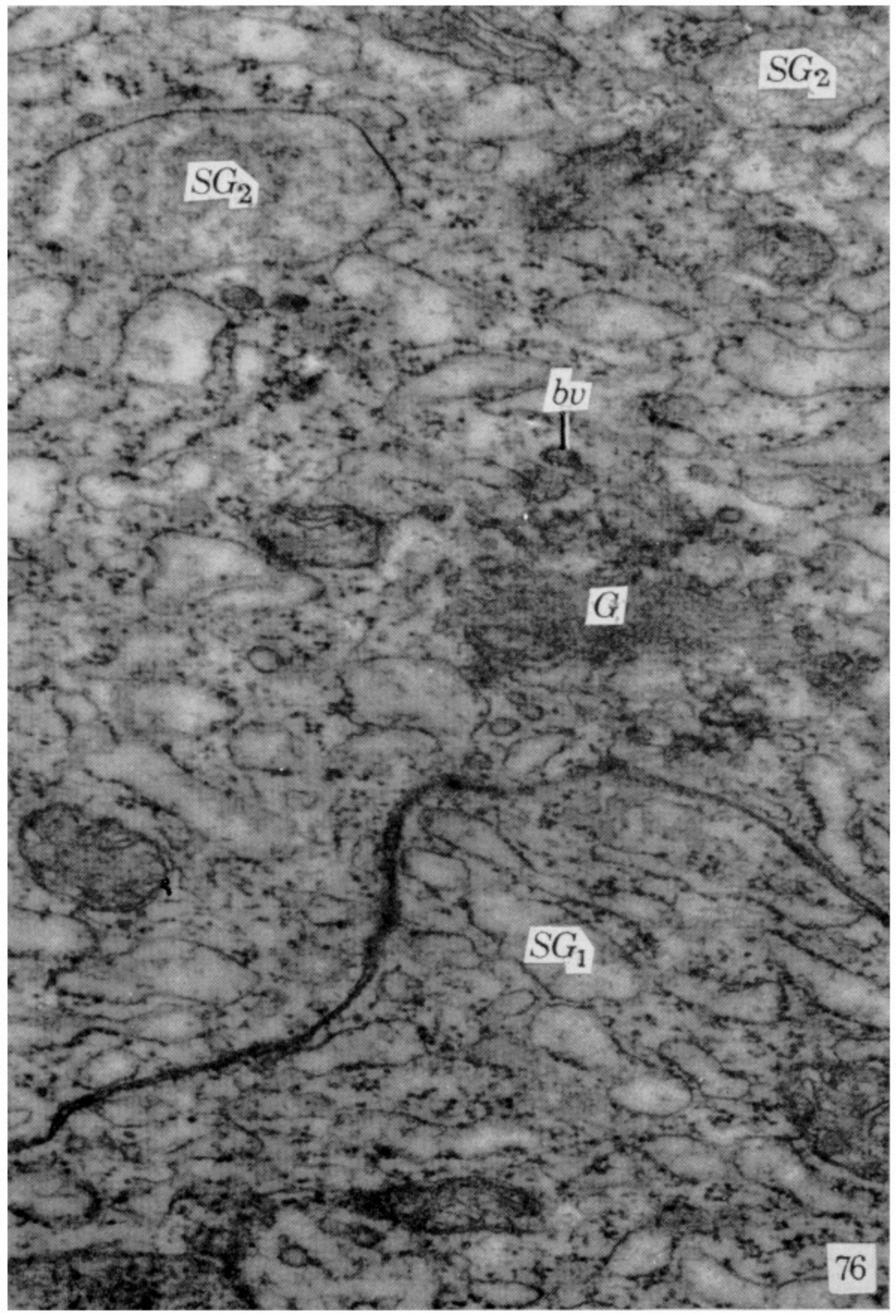




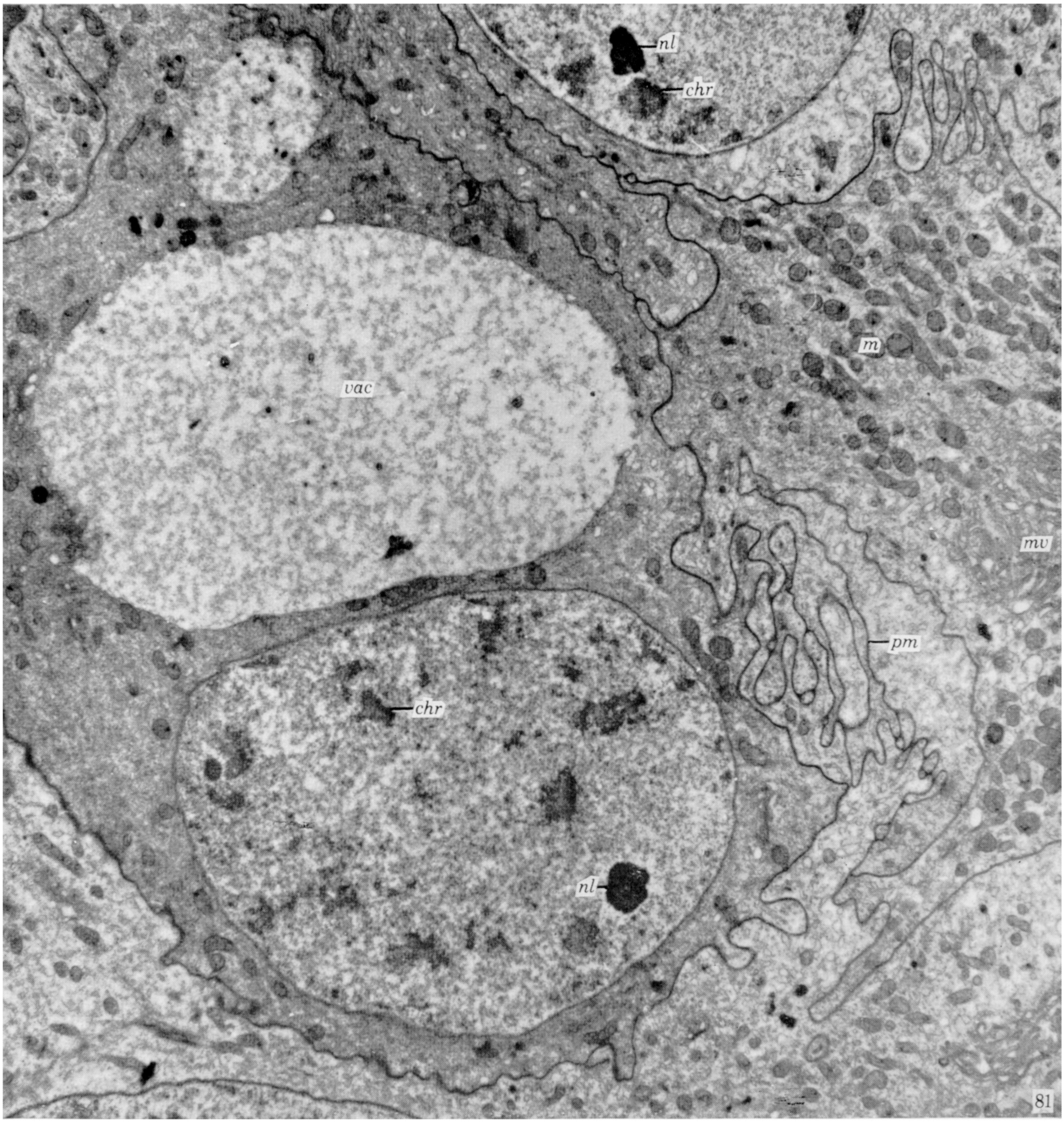
FIGURES 73 to 75. For description see p. 110.

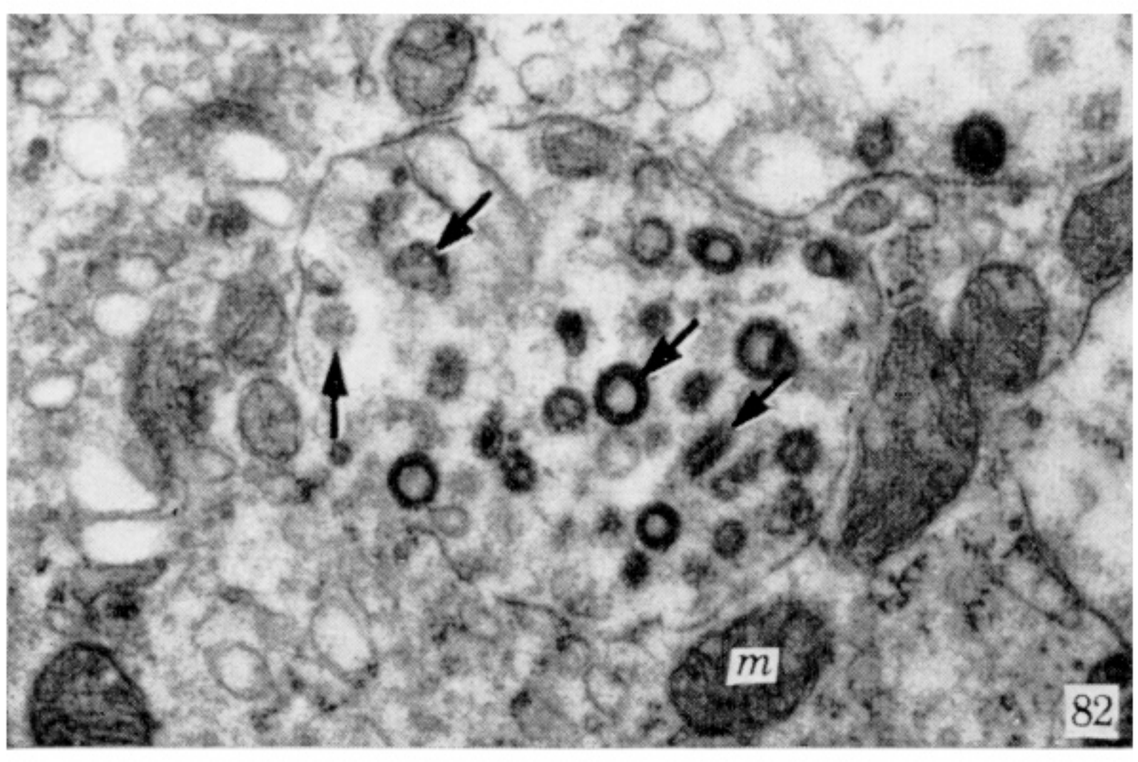






FIGURES 76 to 79. For description see p. 110.





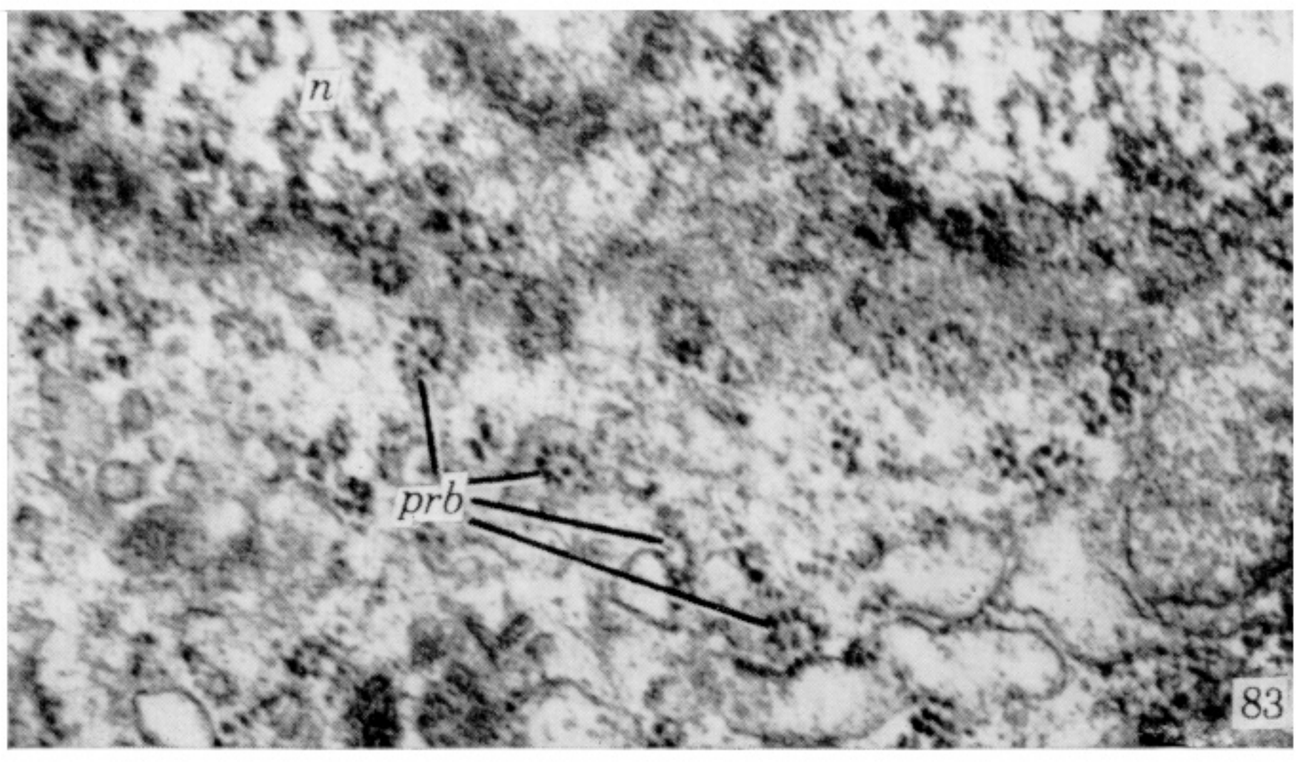
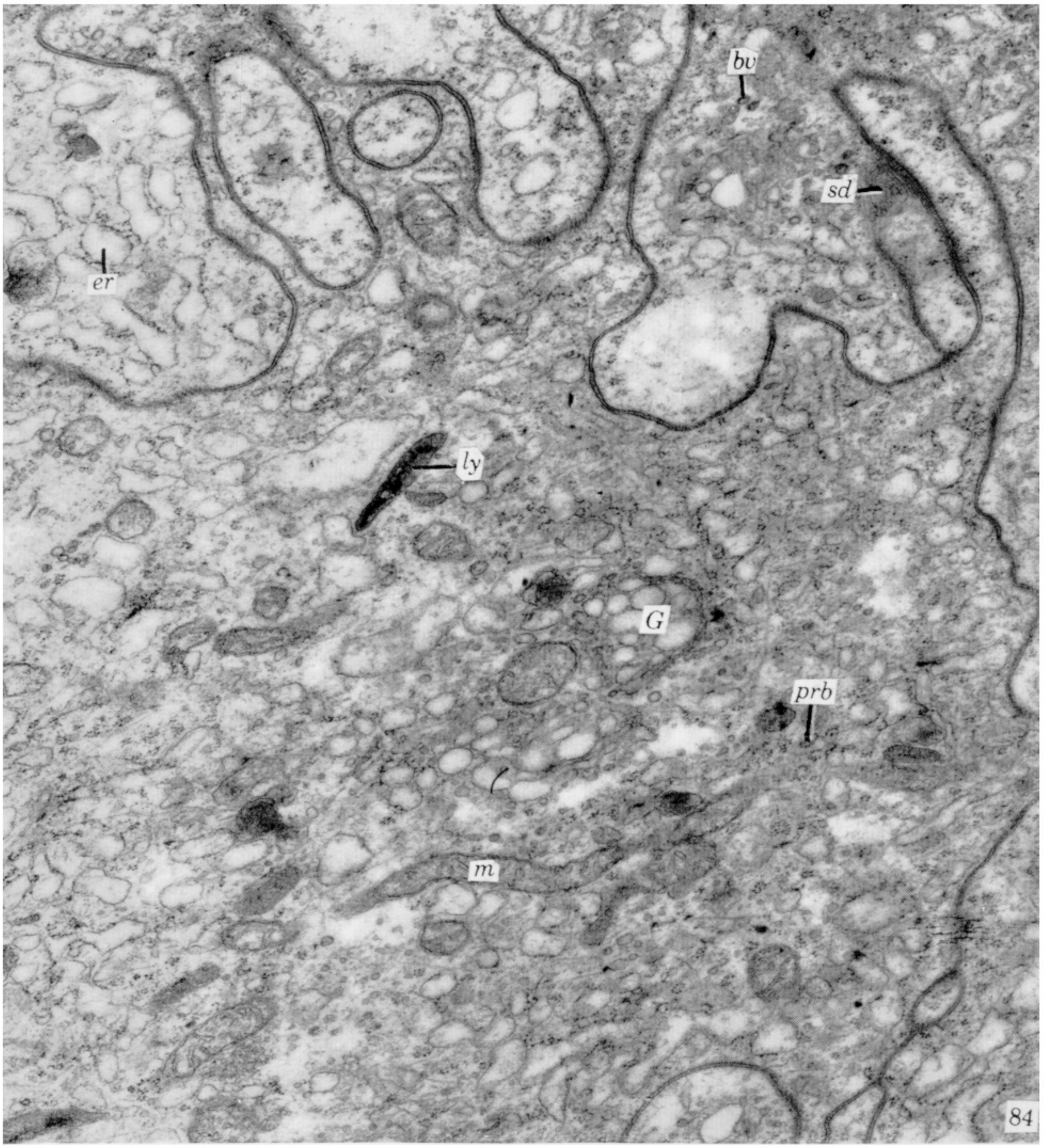
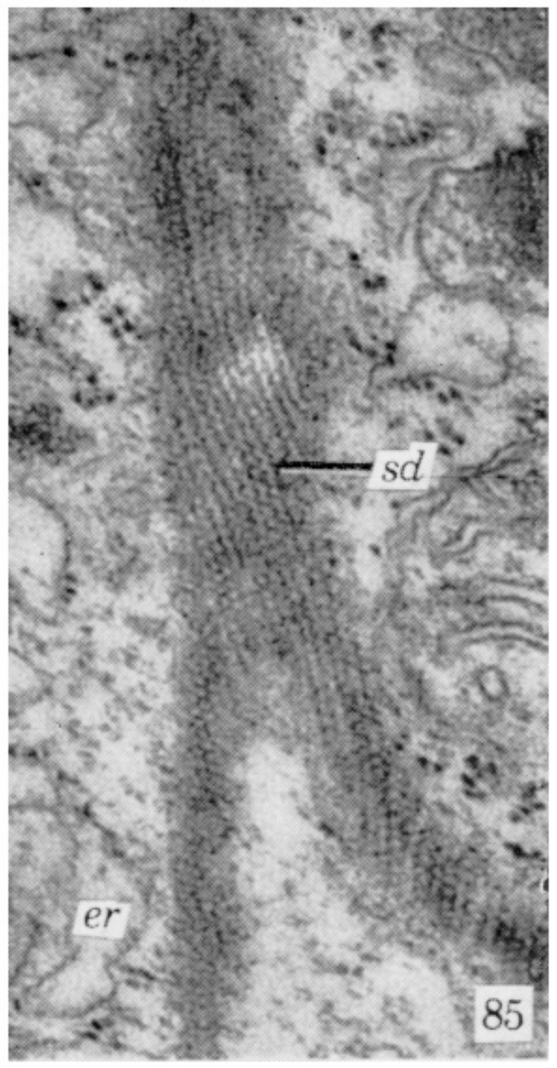


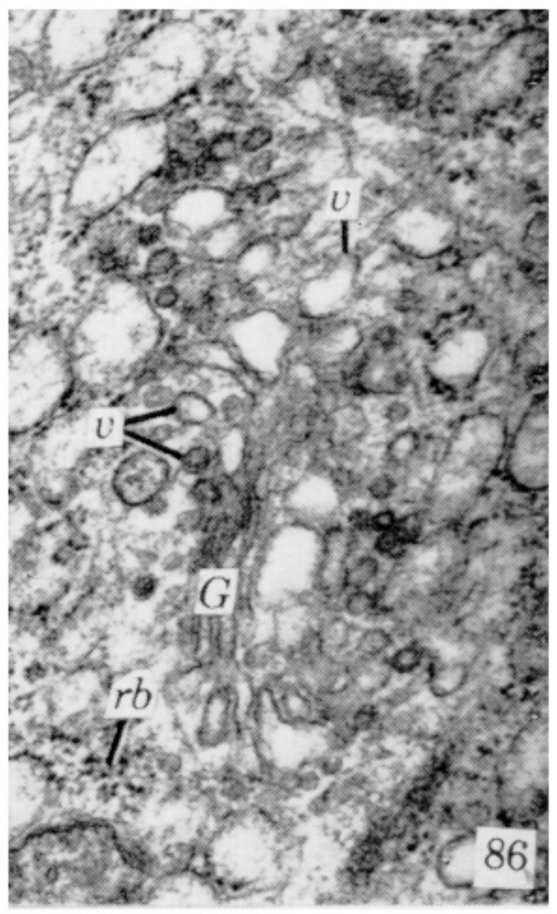
FIGURE 81. The cells may have vacuities of enormous size (*vac*). The epithelium is multicellular. × 7500.

FIGURE 82. The cytoplasmic vacuities contain all sorts of peculiar structures that appear to be breakdown products (*arrows*). × 23000.

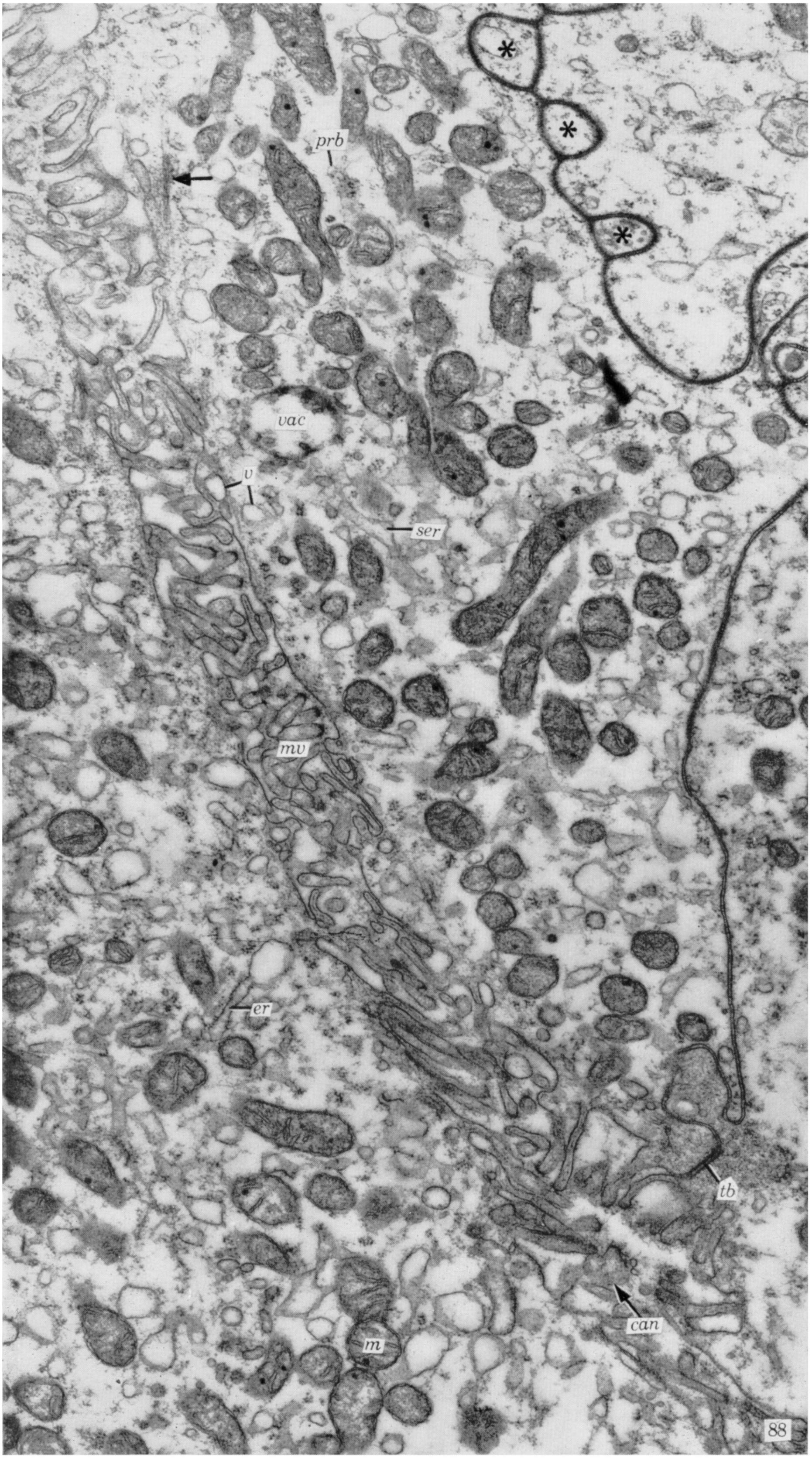
FIGURE 83. Perinuclear region, containing numerous polyribosomes (*prb*). × 52000.

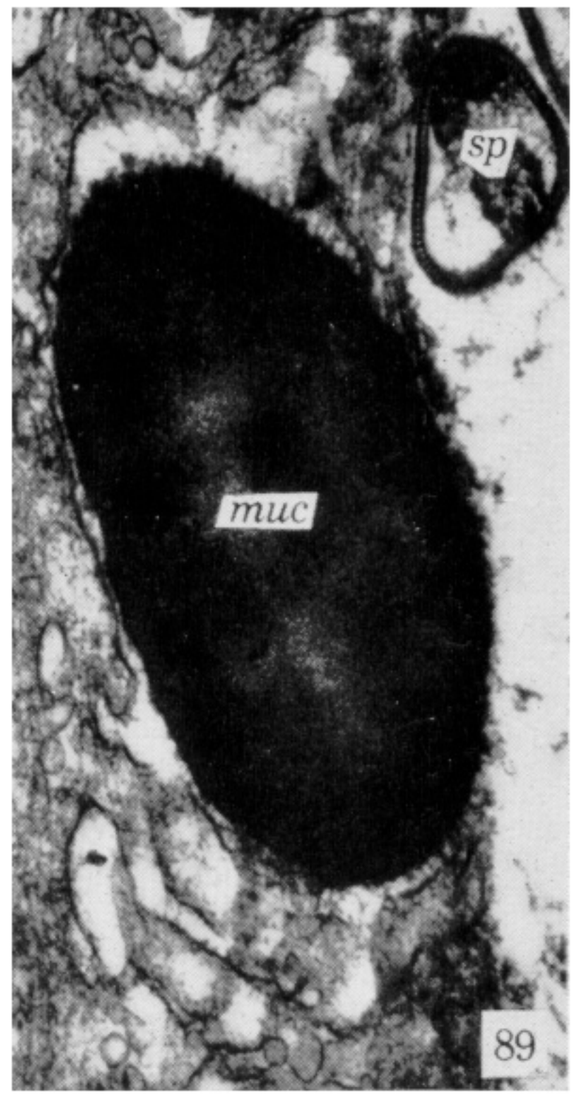


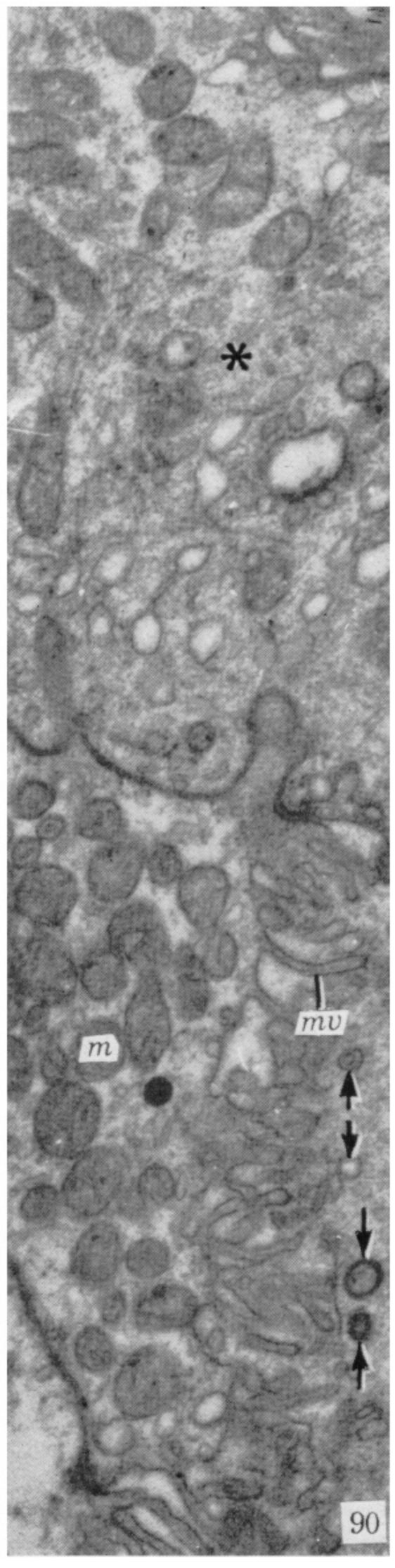




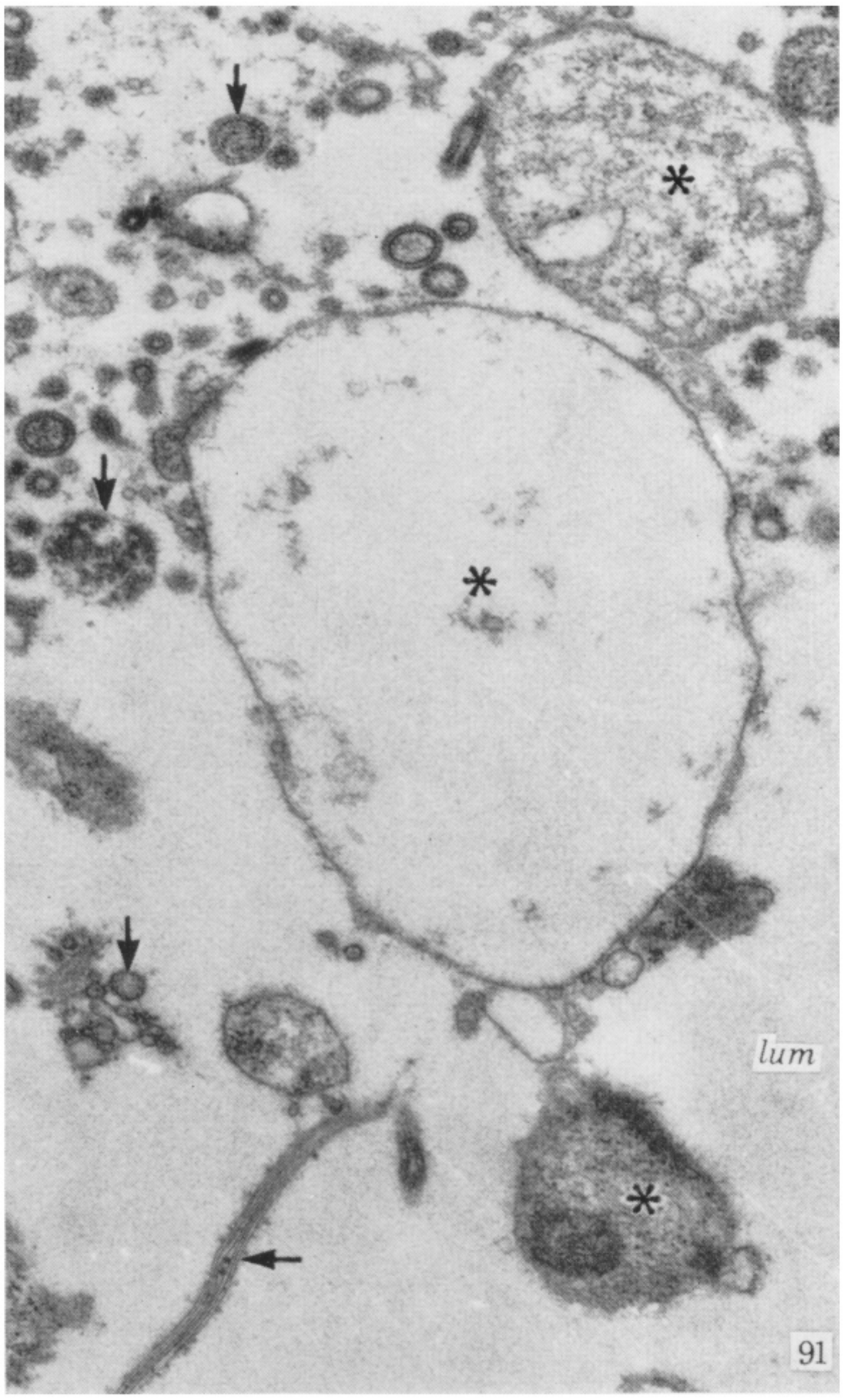
FIGURES 84 to 87. For description see p. 110.

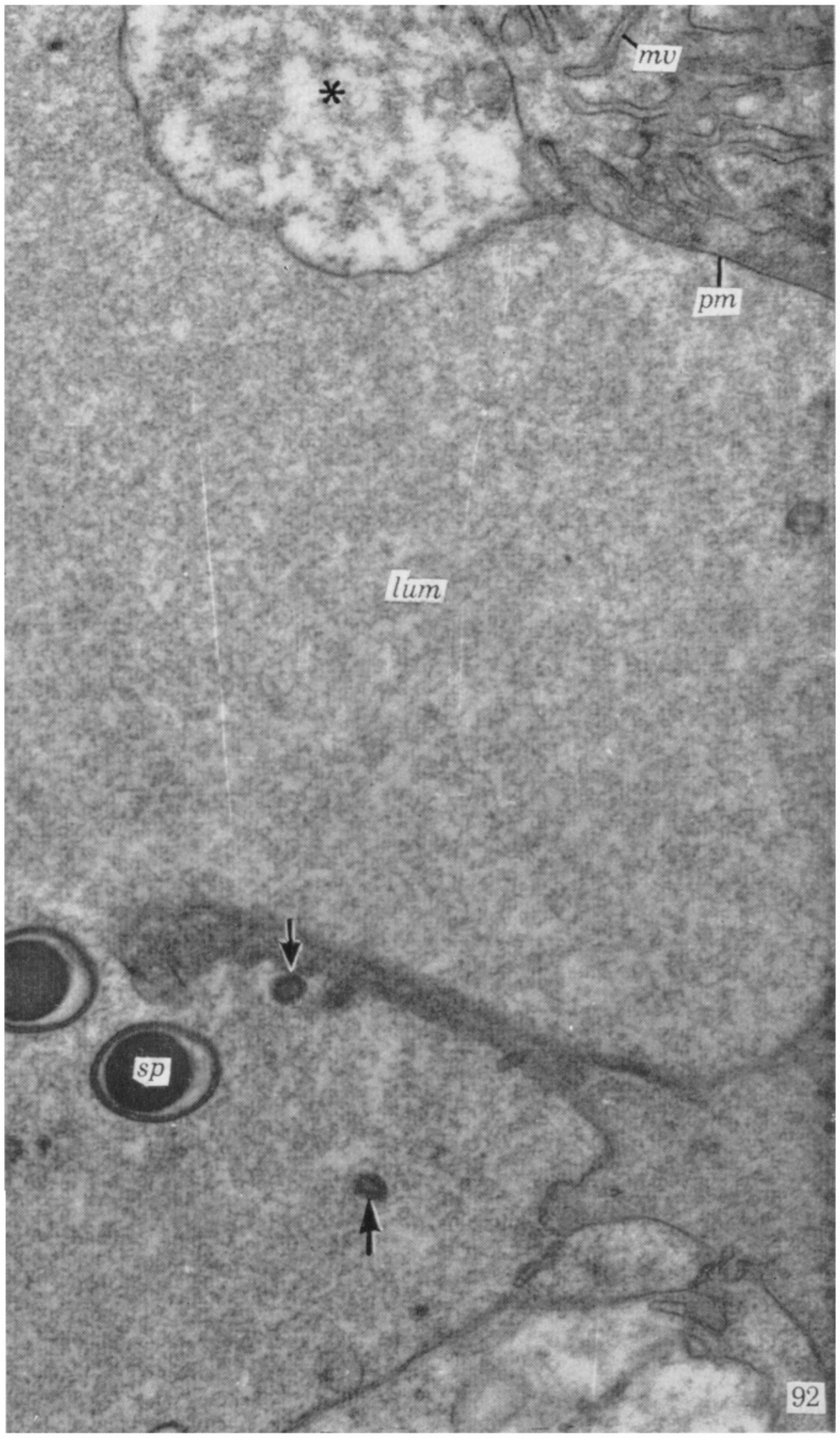


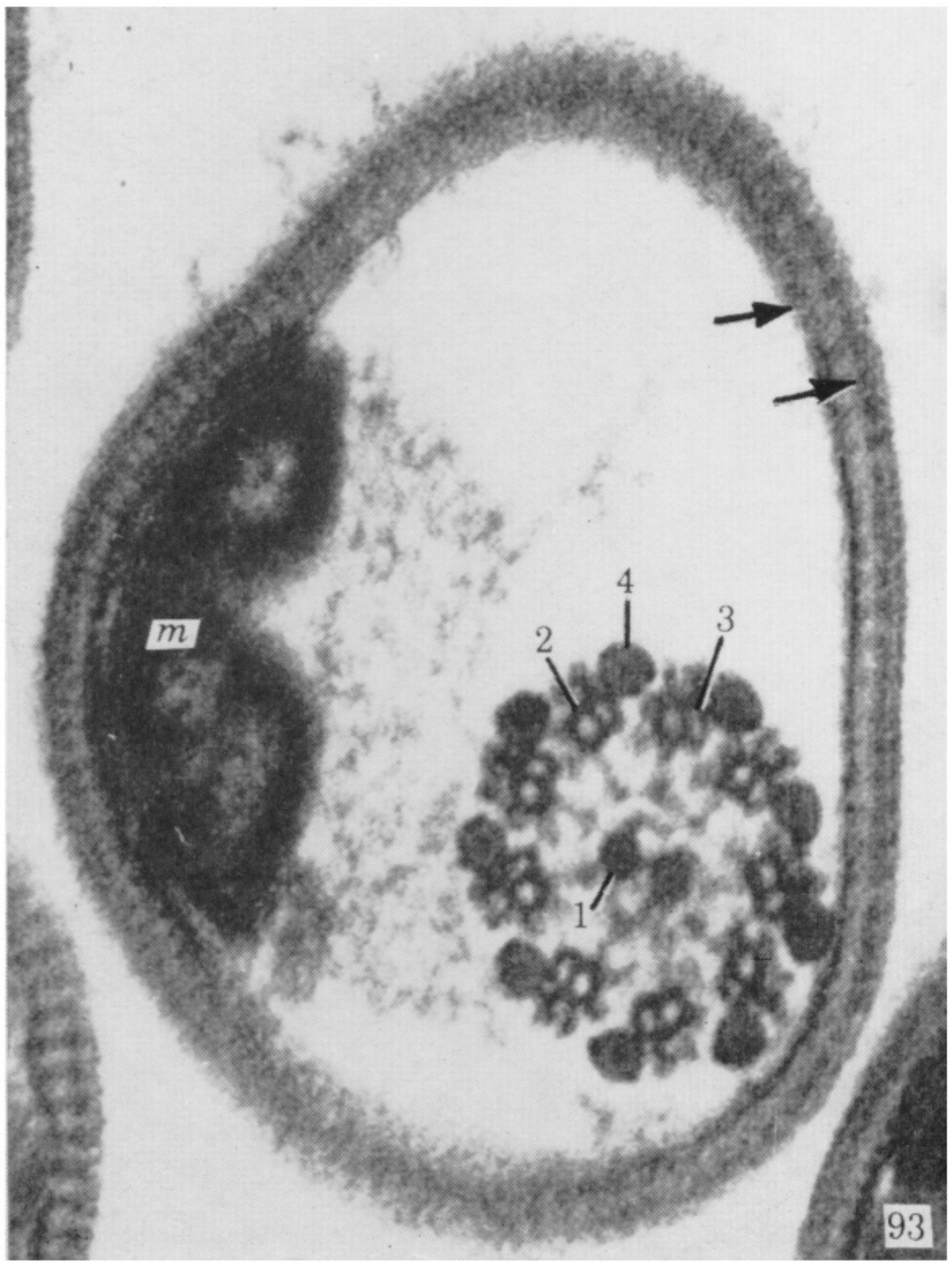


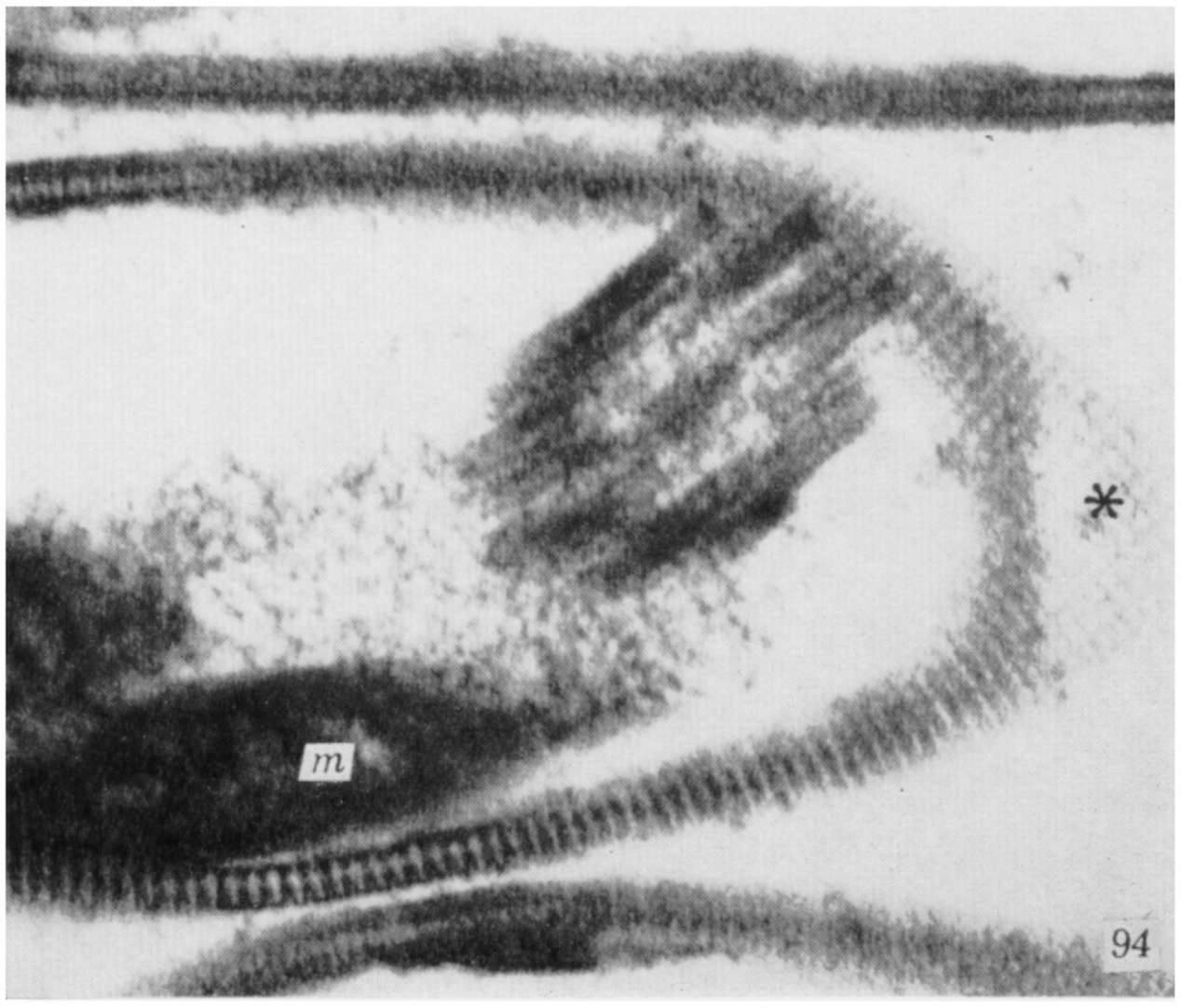


FIGURES 88 to 90. For description see p. 111.









FIGURES 91 to 94. For description see p. 111.

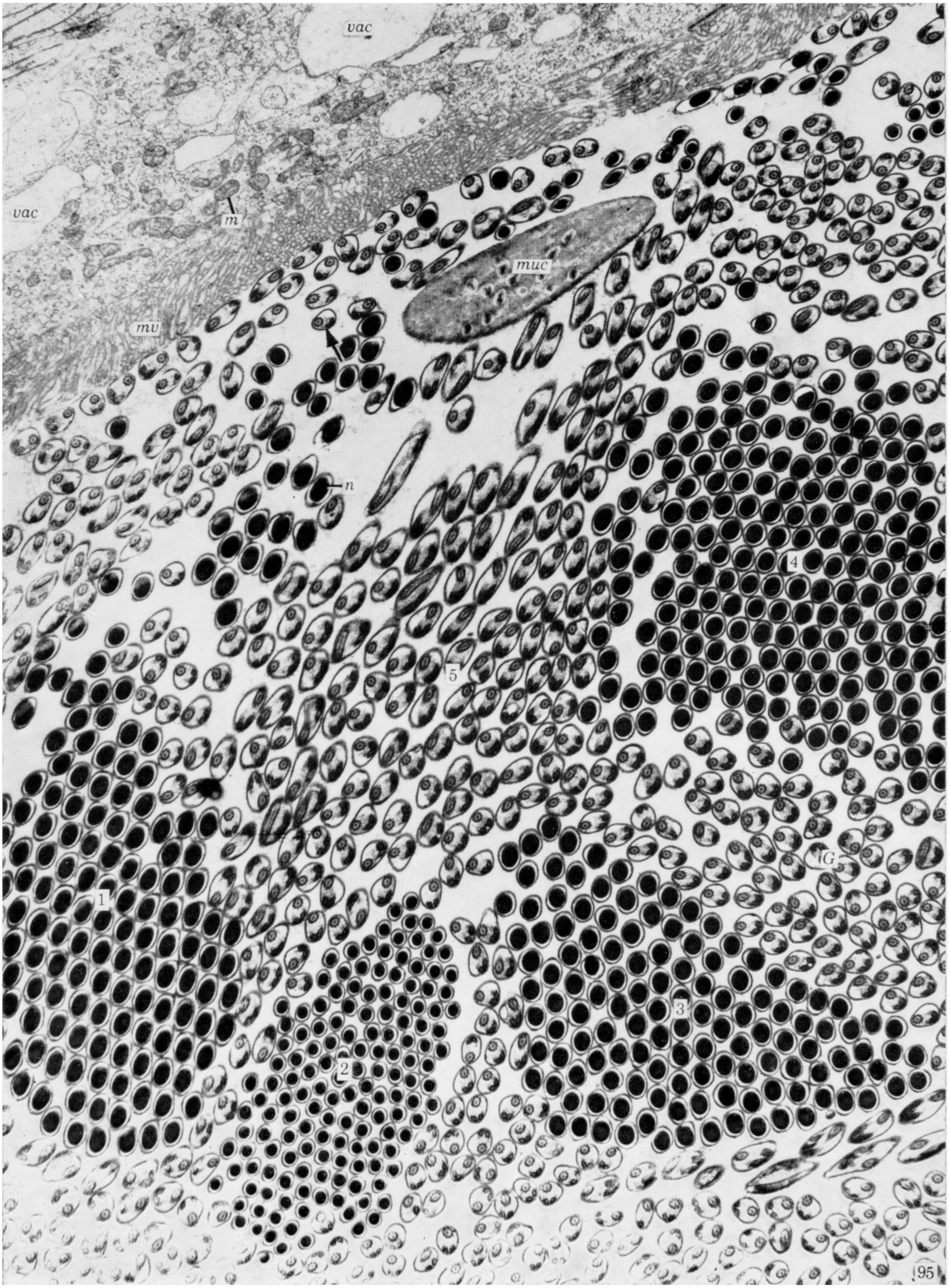


FIGURE 95. Within the major portion of the gland, mature spermatozoa are arranged in almost crystalline fashion (*1–4*). This is due to the spermatozoa being embedded, by their heads, into a densely fibrous 'cap' (*muc*). Towards the tail-ends, the spermatozoa are less orderly oriented (*5*). Arrow indicates the spermatozoon's axial ciliary complex. × 9000.