

THE ENDOPLASMIC RETICULUM OF GASTRIC PARIETAL CELLS

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ABSTRACT

An electron microscopic survey has been made of the gastric parietal or oxyntic cell of the human, cat, beaver, dog, hamster, rat, mouse, and bat, and of the corresponding cell type in two species of frog, two species of toad, and the horned lizard. A feature consistently found in the parietal cells of the mammals or their equivalent in the lower vertebrates is the agranular endoplasmic reticulum, which takes the form of branching and anastomosing small tubules approximately 200 to 500 A in diameter, sometimes expanded into flattened cisternae. In mammalian parietal cells this form of the endoplasmic reticulum is found only in limited amounts, but in the corresponding secretory cells of the amphibia and reptilia the tubular agranular reticulum is abundant. It is believed to comprise a more or less continuous system of channels, but owing to their tortuous course only short profiles are seen in thin sections. Immediately subjacent to the plasmalemma at the free surface, the cytoplasm is relatively free of organelles but is occasionally traversed by the agranular reticulum, which appears to be continuous at some points with the cell surface. The possible participation of the agranular endoplasmic reticulum in hydrochloric acid secretion is discussed.

INTRODUCTION

Among the several cell types in the gastric mucosa, the one that has attracted the greatest interest is the parietal cell or oxyntic cell, which is presumed to be responsible for hydrochloric acid secretion by the stomach. Since the first classical description by Heidenhain in 1870, there have been numerous cytological studies on this cell type, and the advent of electron microscopy has stimulated renewed interest in its mechanism of secretion. Several papers have been published recently describing the fine structure of the parietal cell in the dog, cat, rat, mouse, and human and of the corresponding cell in the frog and toad (5, 8, 11-17, 21-27). There has been general agreement on its principal cytological characteristics. The features which serve to distinguish the parietal cell from other cell types in the gastric mucosa are its large size, its conspicuous secretory canaliculus, and the

extraordinary abundance of its mitochondria. All the previous reports have also emphasized the presence of vesicular or vacuolar components of the cytoplasm, and some authors have attributed to these an important role in the secretory activity of the parietal cell.

The present paper reports the results of a survey of the fine structure of parietal cells of a variety of species, including the human, cat, rat, bat, mouse, hamster, dog, and beaver, and an examination of the corresponding gastric secretory cell in two species of frog, two species of toad, and the horned lizard. These observations are generally in accord with earlier descriptions, with the exception that relatively few vesicles are seen in the parietal cells of the species examined. Instead, slender tubular profiles of smooth surfaced endoplasmic reticulum are found.

Lawn (16) described cytoplasmic vacuoles as characteristic of rat parietal cells and observed traces of a small tubular system which was interpreted as connecting the vacuoles. More recently, Sedar (25) has published a beautifully illustrated and comprehensive description of the oxyntic cell in the bullfrog gastric mucosa. Our observations are in general agreement with Sedar's, differing only with respect to the 20 to 200 μ vesicular components, which we find to be less prevalent in our material than was reported by him. This appears to be due to differences in preparative techniques.

MATERIALS AND METHODS

The material consisted of specimens of gastric mucosa from the following mammals (numbers used in parenthesis): mice (9), rats (3), hamsters (2), cats (5) kittens (4), bats (28), dog (1), beaver (1), human (1). The amphibian species included *Rana pipiens* (2), *Rana clamitans* (3), *Bufo marinus* (3), *Bufo americanus* (1). The only species of reptile examined was *Phrynosoma* (3). The stomach tissues were obtained under ether anesthesia or after killing the animal by cervical dislocation. All the tissues were fixed immediately

after removal except for the human material, which was obtained some 60 minutes after gastrectomy. In the earlier part of this study the whole stomach or small strips were removed after injecting cold fixative into the lumen of the stomach, in a manner similar to that used by Palay and Karlin (19) with rat duodenum. This procedure was found to be unnecessarily wasteful for fixing small amounts of tissue from larger animals. Therefore, the procedure more frequently followed consisted of excising a small piece of the mucosa and cutting it into 1 mm cubes in a drop of fixative. The results obtained by the two methods were not significantly different.

The fixative consisted of 1 per cent or 1.33 per cent osmium tetroxide buffered between pH 7.1 and 7.5 with veronal acetate or with *s*-collidine (1), and contained 0.25 M sucrose (4). Fixation was carried out in about 1 ml of fixative for each sample of gastric mucosa. The vial containing the fixative was maintained at 0–4°C for 45 to 90 minutes, and the tissues were then dehydrated with a graded series of cold ethanol solutions (50, 80, 95, and 100 per cent) at such a rate that they reached absolute alcohol within 5 minutes. Dehydration was continued in several changes of absolute alcohol at room temperature for 2 to 3 hours. The tissues were then infiltrated with butyl methacrylate containing 10

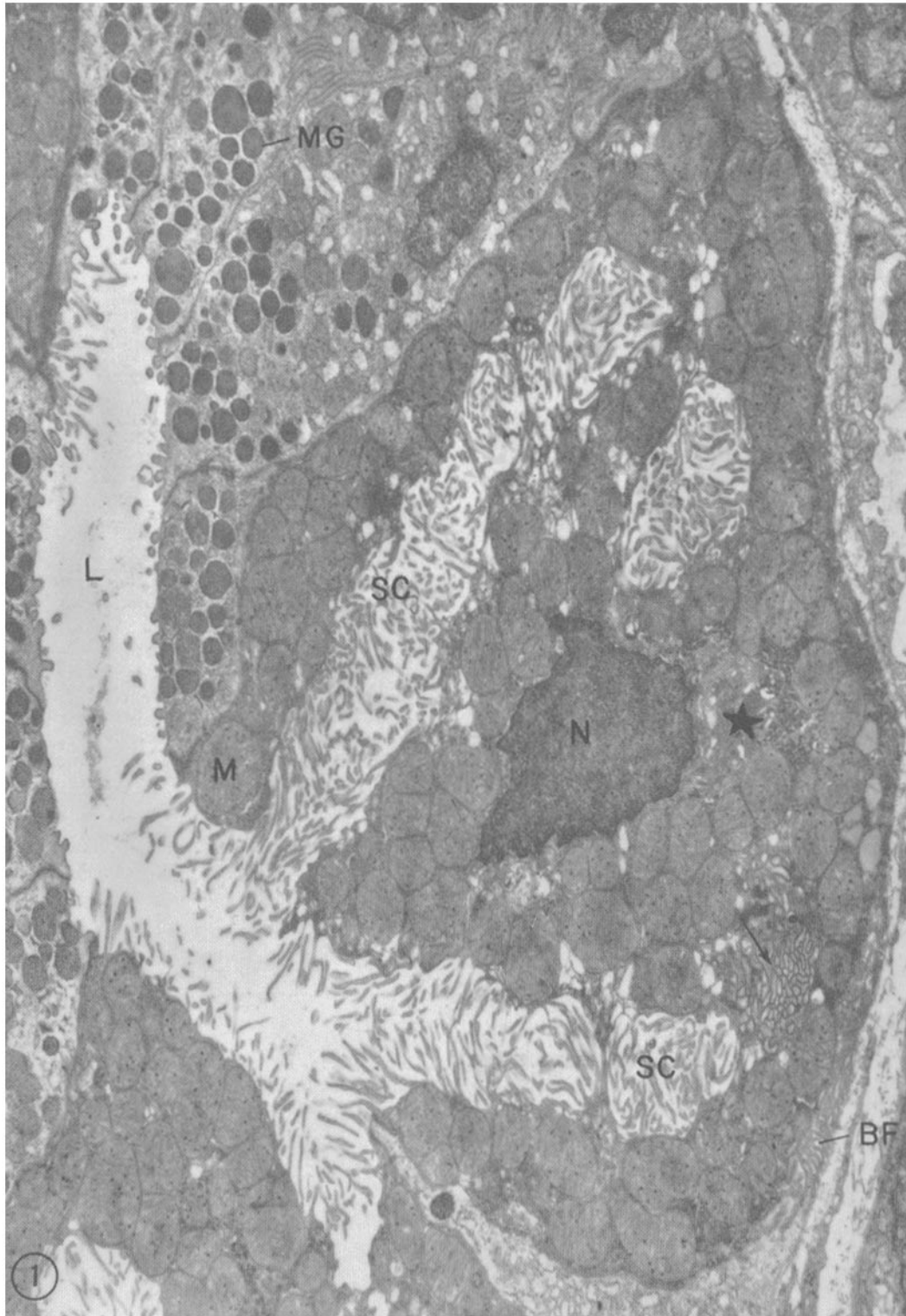
Key to Labeling

<i>AER</i> , agranular endoplasmic reticulum	<i>MG</i> , mucous granule
<i>BF</i> , basal folds	<i>N</i> , nucleus
<i>BM</i> , basement membrane	<i>P</i> , pseudopodia
<i>D</i> , desmosome	<i>SC</i> , secretory canaliculus
<i>GER</i> , granular endoplasmic reticulum	<i>TB</i> , terminal bar
<i>L</i> , lumen	<i>Z</i> , zymogen granule
<i>M</i> , mitochondria	

FIGURE 1

An electron micrograph of a gastric gland from the stomach of a hibernating bat (*Myotis lucifugus*). A parietal cell and parts of several mucous cells are shown. The section through the parietal cell includes a dense nucleus (*N*) and a Golgi complex (star) located between the nucleus and the base of the cell. The remaining cytoplasm is densely packed with large mitochondria which have numerous intramitochondrial granules. An extensive view of the secretory canaliculus (*SC*) is shown with numerous long microvilli lining the open lumen. A small terminal portion of the canalicular lumen at the lower right (arrow) is occluded by numerous interdigitating microvilli. The basal surface of the cell has unusual folds (*BF*) that resemble microvilli in section. A capillary is in close apposition to the base of the parietal cell. The upper left region of the illustration shows parts of several mucous cells containing dense mucous granule (*MG*) in the apical cytoplasm. In contrast to the long microvilli of the parietal cell projecting into the glandular lumen (*L*) those of the mucous cell are stubby. Apical parts of the two other parietal cells appear in the upper and lower left corners.

× 9500.



to 30 per cent methyl methacrylate and catalyzed with 2 per cent Luperco. Final blocks were made by placing the tissues in gelatin capsules filled with a similar mixture which had been prepolymerized to a syrupy consistency. Polymerization was completed in an oven at 45°C or at room temperature with ultraviolet light. Uranyl nitrate as recommended by Ward (28) was found to be essential for the preservation of the tubular form of the reticulum in the non-mammalian forms and was sometimes beneficial in the mammalian tissue. Other embeddings were made in Epoxy resin, using Epon 812 as described by Luft (18), but this embedding medium did not show any marked or consistent advantage over methacrylate for this tissue.

All micrographs illustrating this paper are of methacrylate-embedded tissue. Rough estimations of acidity of the gastric juice were made by means of indicator paper, but the small size of some stomachs and the presence of food in the lumen made readings difficult and of questionable significance.

Blocks were sectioned on a Porter-Blum microtome with glass knives, and sections showing interference colors of yellow to golden hue were picked up on carbon- and celloidin-coated grids. The sections were then stained with lead hydroxide, according to Watson (29), and "sandwiched" with celloidin or methacrylate (20). Micrographs were taken at magnifications of 2000 to 10,000 on an RCA model EMU-3E electron microscope and enlarged photographically to the desired size.

OBSERVATIONS

The most distinctive feature of the mammalian parietal cell is the so-called *intracellular canaliculus*. Although this tortuous channel lies within the general limits of the cell, electron micrographs clearly show that it is lined by a membrane continuous with the plasmalemma on the free surface

of the cell (Fig. 1). Thus the lumen of the canaliculus is actually extracellular at all points. Therefore, the term *secretory canaliculus* will be used in the present communication, since it seems more appropriate than intracellular canaliculus.

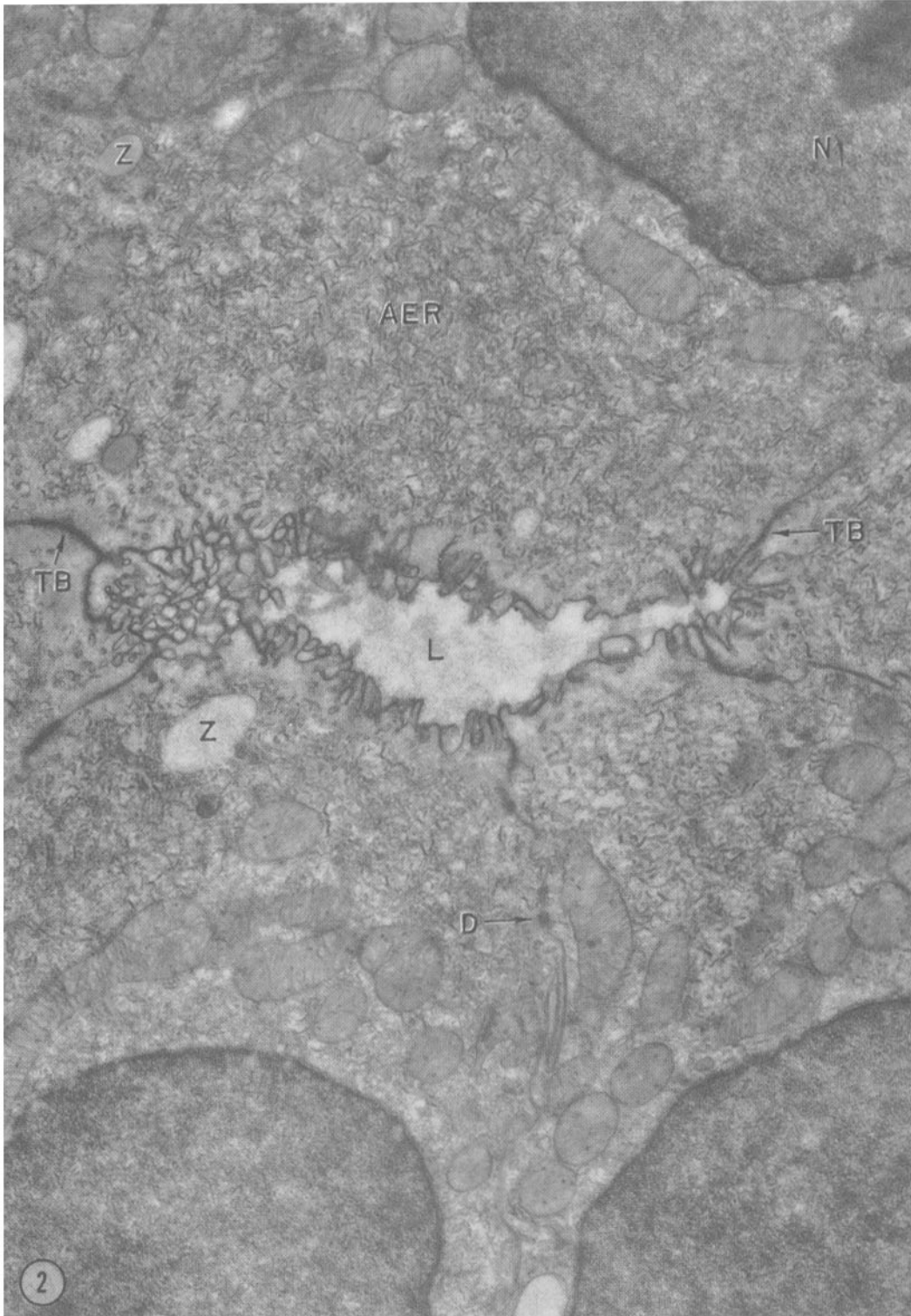
The canaliculus is lined with numerous microvilli that are limited by a smooth surfaced membrane contrasting with that bounding the microvilli of the adjacent mucous cells, which is often covered by exceedingly fine filamentous projections that give it a furry appearance (Fig. 6). The cytoplasm in the interior of the microvilli shows no special structural differentiation and is continuous with the finely granular ectoplasmic layer of the cell body. The parietal cell microvilli vary in length in secretory canaliculi of different degrees of patency. In closed canaliculi the microvilli appear shorter and thicker and those on opposite sides interdigitate (Figs. 1, 5, and 6). In canaliculi in which the lumen is open the microvilli are usually long and slender. The microvilli are usually simple, digitiform processes, but those bordering the patent secretory canaliculi of rodent parietal cells are occasionally branched. This does not seem to be a common finding in cat, beaver, or human parietal cells, which usually have microvilli shorter than those of the other species that were studied.

Both open and closed canaliculi may be found in neighboring cells of the gastric mucosa of hibernating bats and in fasting animals of other species, as well as in animals recently fed and actively digesting food. Thus the patency of the secretory canaliculus cannot be correlated with the physiological state of the animal. The significance of this variation is not known.

FIGURE 2

An electron micrograph of a section including the lumen of a gastric gland from *Rana clamitans*. This frog, collected locally during the summer months, was stimulated with histamine chloride (500 µg/100 g body weight) 45 minutes before fixation. With indicator paper the pH of the gastric juice was between 1 and 1.5.

The apical parts of five cells border the glandular lumen (*L*), which is patent in the central region but partially occluded at one edge. The lumen is lined by microvilli. Arising in the clefts between microvilli are occasional membrane-bounded tubular elements that appear to be in continuity with a concentration of tubular elements of agranular reticulum (*AER*) in the subjacent cytoplasm. This region of the apical cytoplasm has been described by previous investigators as being occupied by numerous vesicles and vacuoles. Some zymogen granules (*Z*) seem to have lost part of their dense contents during tissue preparation and appear as light granules. Well developed terminal bars (*TB*) and desmosomes (*D*) are found between adjacent cells. × 15,000.



The mitochondria of the parietal cells are larger and very much more numerous than those of adjacent cell types, and often occupy nearly all of the cytoplasm except for a narrow zone immediately surrounding the secretory canaliculus. Their internal structure is much the same in all the species examined. The matrix is rather dense and the cristae are numerous and regular in their

they do not exist in appreciable numbers in the living cell.

Their probable source is most clearly brought out by a study of the gastric glandular tissue of the frogs, toads, and horned lizard. The gastric mucosa in these forms, unlike that in the mammal, has a single cell type which presumably secretes both acid and digestive enzymes. Cells of this type bor-

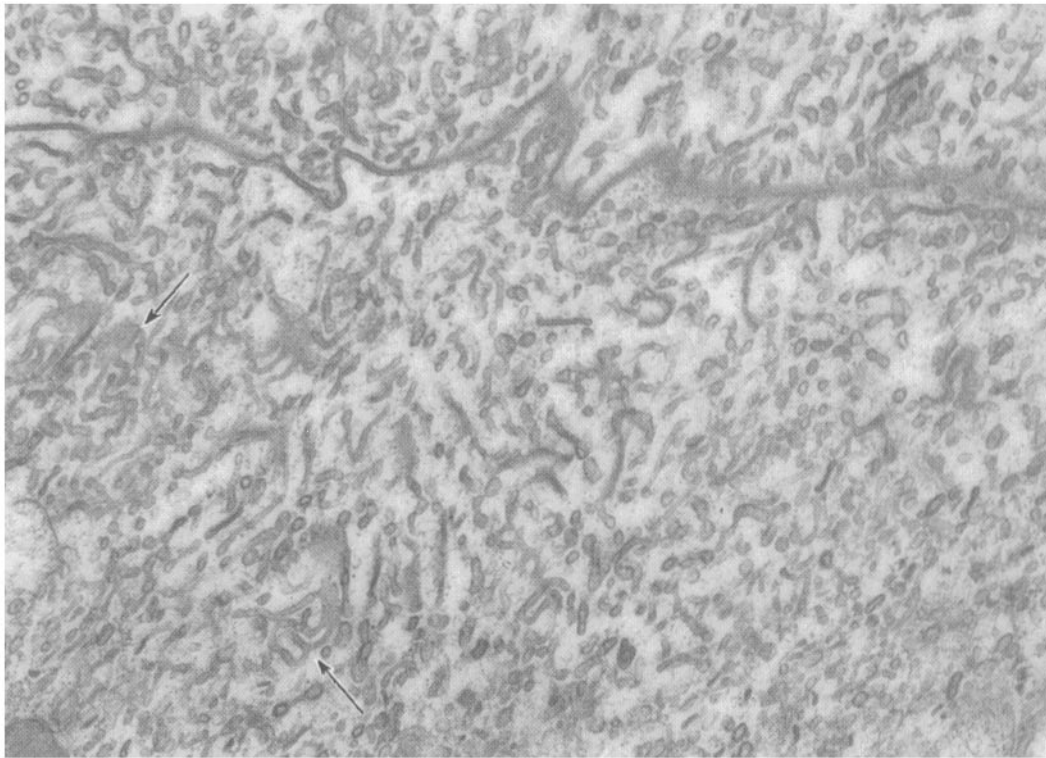


FIGURE 3

Parts of two secretory cells from a fasted *Rana pipiens*. The lumen of the secretory duct is virtually obliterated by the close apposition of the cells. The branching, tortuous pattern of the agranular endoplasmic reticulum is particularly apparent in certain areas (arrows). At several points the tubular elements appear to be continuous with the plasmalemma. $\times 26,000$.

orientation. Intramitochondrial granules are present in varying numbers (Figs. 1, 2, and 9).

The structures that have hitherto been considered a characteristic feature of the parietal cells are vacuoles or vesicles variously estimated to be from 200 A to some 6000 A in diameter (12, 14-16, 25-27). With the methods of specimen preparation employed in the present study, such vesicular structures have not been a conspicuous feature of the parietal cells in any of the animal species examined, and it is considered likely that

der on the lumen of a gastric gland or on one or more intercellular canals or ducts but lack the secretory canaliculi typical of the mammalian parietal cells (Figs. 2 to 4). The surface does not bear typical slender microvilli, but instead has invaginations that demarcate broad, lobose cell processes. These often have an outer coating somewhat resembling the furry filamentous material investing the microvilli of the mucous cell (Fig. 4). In the depths of these infoldings of the cell surface, membrane-limited tubular elements of agranular

endoplasmic reticulum sometimes appear to be continuous with the plasmalemma (Figs. 2 and 3). The lumen of the reticulum may thus be in direct continuity with the extracellular space. Immediately beneath the cell surface there is often a layer of cytoplasm relatively poor in formed elements except for the occasional tubular connections of the endoplasmic reticulum with the surface (Fig.

where the tubular agranular reticulum is found in better preserved specimens.

In the mammalian parietal cell the abundant mitochondria tend to obscure the other organelles. This is particularly true when the secretory canaliculus is patent. The cytoplasm may then be so densely packed with mitochondria that little cytoplasmic matrix is visible. However, some

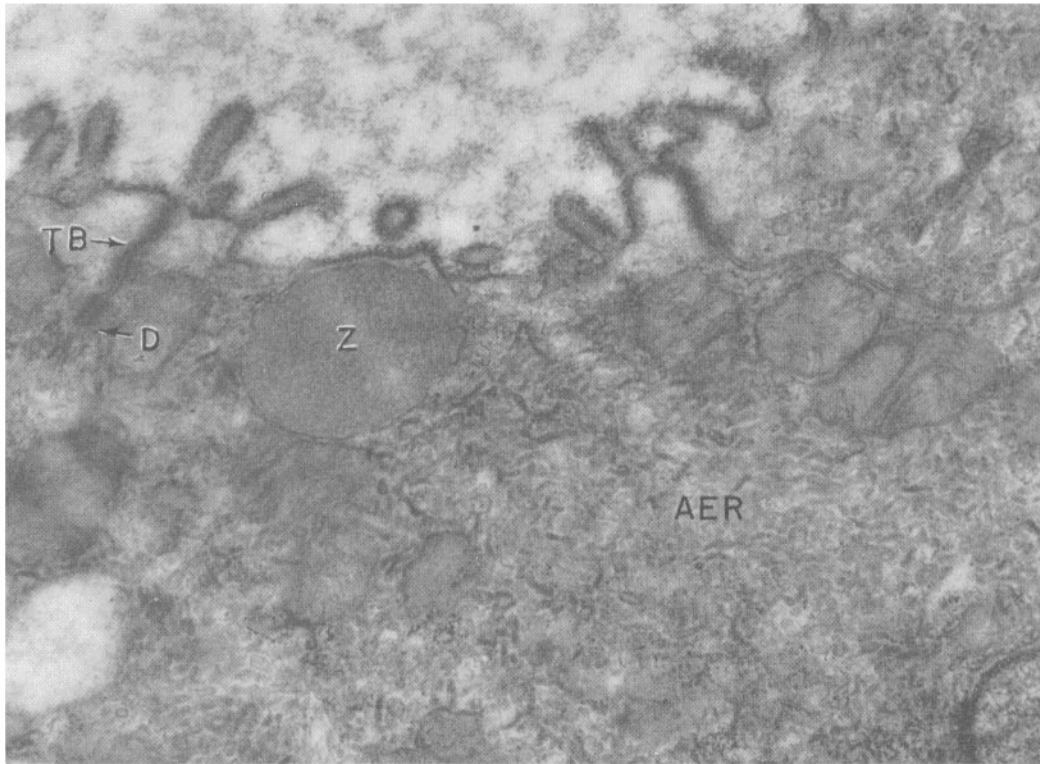


FIGURE 4

Parts of the luminal border of several secretory cells from a fasted toad, *Bufo marinus*. The plasmalemma in this area sometimes has a furry appearance not unlike that of mucous cells of mammalian species as shown in Figs. 1 and 6. In addition to the characteristic terminal bars (TB) between adjacent cells, a desmosome (D) may be seen at a lower level, between opposing cell membranes. Much of the cytoplasm is occupied by the smooth surfaced, tubular endoplasmic reticulum (AER). $\times 29,000$.

2). Deeper in the cytoplasm, the smooth surfaced tubules of the reticulum are exceedingly numerous and pursue a meandering course. In favorable sections, they can be seen to be interconnected to form a network or reticulum (Fig. 3). The tubules measure approximately 200 to 500 A in diameter, and in well preserved material vesicular profiles of larger dimensions are relatively uncommon. When preservation is less satisfactory, numerous vesicles of varying size and shape occupy those regions

agranular elements of the endoplasmic reticulum similar to those in the frog and lizard may be observed in the areas between mitochondria and in the relatively clear zone of cytoplasm near the secretory canaliculus (Figs. 5 to 12). Not all the elements of the reticulum are tubular in form. A few vesicular profiles that are not transverse sections of tubules are present in small numbers, but these may well be due to post mortem fragmentation of the tubular system. Some flattened agranu-

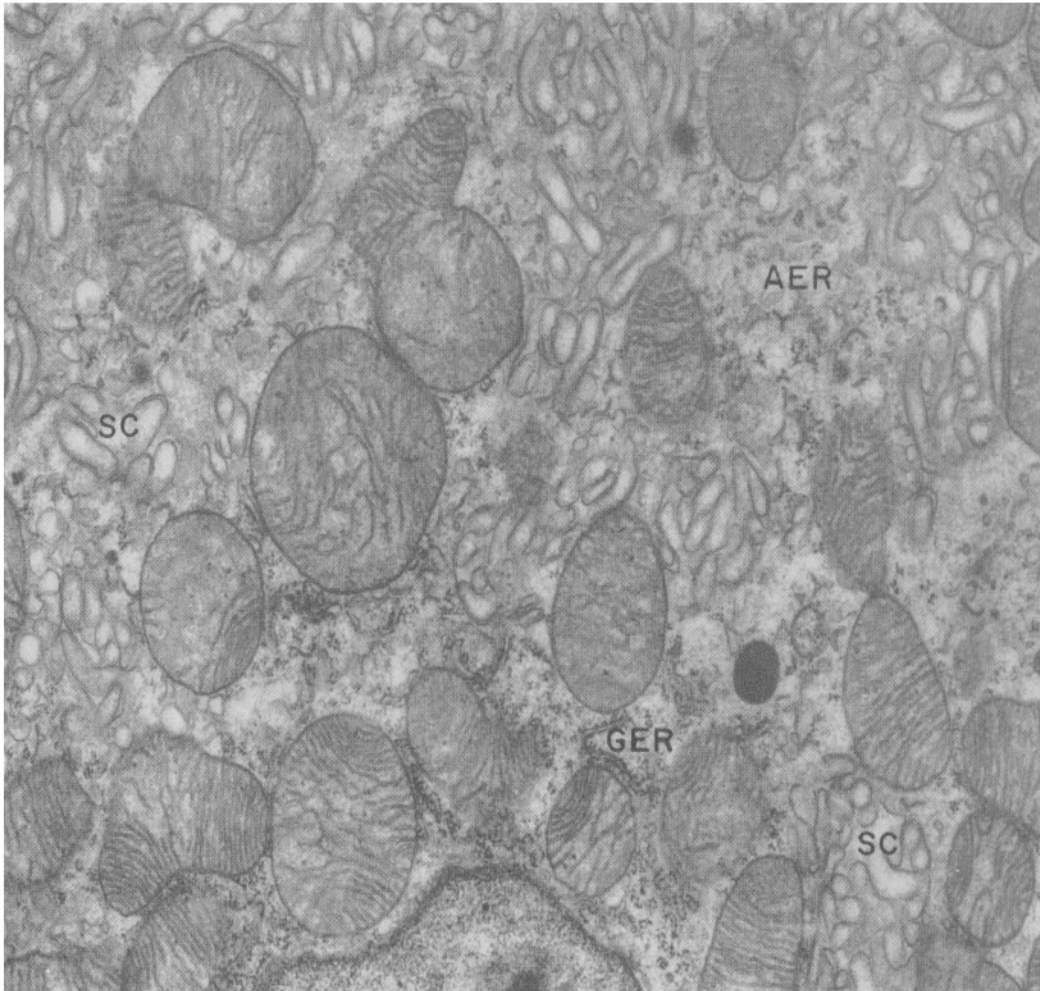


FIGURE 5

Part of a gastric parietal cell from an actively feeding adult mouse. The secretory canaliculus (*SC*) is almost entirely occluded and is recognizable only by the presence of its numerous closely interdigitated microvilli. The canaliculus appears to take an irregular course in the cytoplasm. Very slender elements of the agranular reticulum (*AER*) are found in the cytoplasmic matrix between the abundant mitochondria. In addition, some granular endoplasmic reticulum (*GER*) is present, as well as rosette-like clusters of free ribonucleoprotein particles. $\times 21,000$.

lar cisternae are intermixed with tubules. Cisternal profiles have been observed in all the mammalian parietal cells examined, but appear to be most obvious in the human gastric mucosa (Figs. 10 and 11). In addition to the smooth surfaced elements of the reticulum, the parietal cells of mammals and their counterparts in amphibia and reptiles also have variable amounts of the more common granular endoplasmic reticulum (Figs. 5 and 6). In addi-

tion, free ribonucleoprotein particles are often found in small rosette-like clusters in the cytoplasmic matrix. A typical Golgi complex is often observed in parietal cells, but it is usually small and situated between the nucleus and the base of the cell.

No consistent and characteristic changes have been noted in the fine structure of the parietal cells during increased functional activity of the gastric

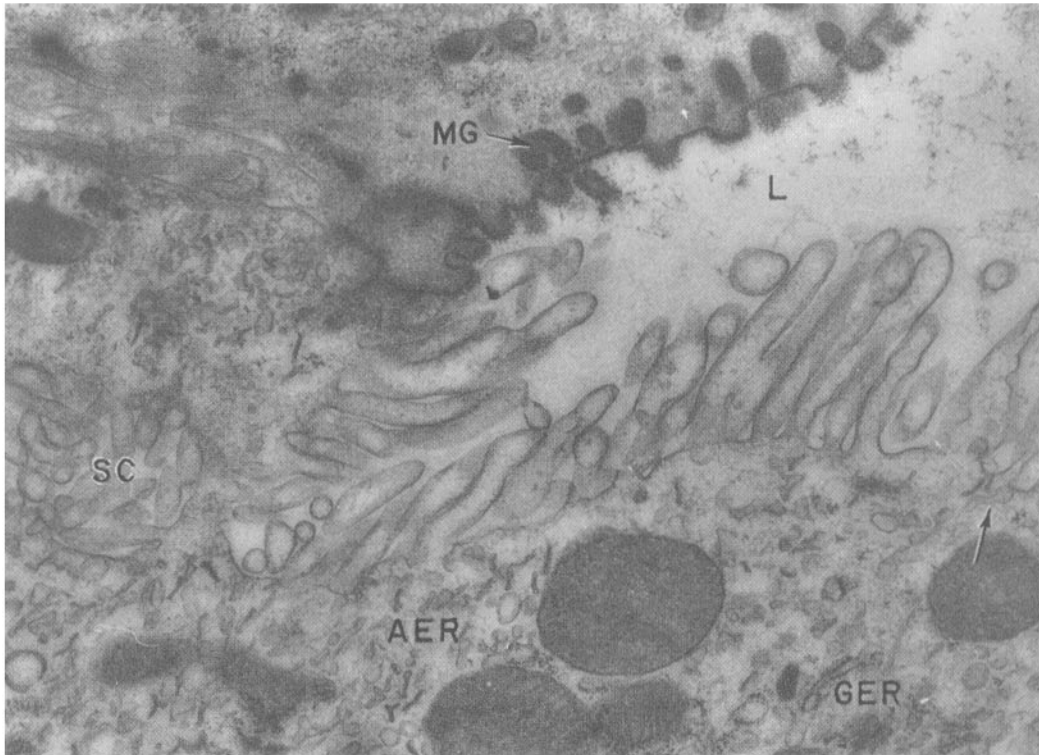


FIGURE 6

A section through the apical parts of a gastric parietal and mucous cell from an immature mouse. The lumen (*L*) of the gastric gland is lined by long, smooth surfaced parietal cell microvilli and the shorter mucous cell microvilli. The latter have a furry appearance owing to the presence of fine filamentous projections of their limiting membrane. Dense mucous granules (*MG*) are present in the cytoplasm immediately beneath the plasmalemma. An opening of a secretory canaliculus (*SC*) into the lumen of the gastric gland is included in the illustration. The parietal cell cytoplasm shows elements of the agranular endoplasmic reticulum (*AER*) in tubular or cisternal form. Some of the larger vesicular structures are interpreted as being due to distended elements of the endoplasmic reticulum, but others are probably frontal views of cisternae. Dense profiles of parallel membranes appear to be edge-on views of cisternae or flattened vesicles, while the less distinct, often broader elements (arrow) are interpreted as frontal views of similar structures. A small amount of granular endoplasmic reticulum (*GER*) is present at the lower right. $\times 23,000$.

mucosa. In mammalian stomachs shortly after feeding, the microvilli of the free surface are often replaced by blunt pseudopodia of irregular shape that project into the lumen of the gastric gland (Fig. 12). Their cytoplasm is usually homogeneous and devoid of organelles. Similar structures were observed by Kurosumi *et al.* (15) in the parietal cells of the rat. The significance of these tongue-like cytoplasmic projections is not clear, and their occurrence is not sufficiently consistent or general among the species studied here to warrant their being considered characteristic of all active parietal

cells. Sedar has reported a migration of smooth surfaced vesicles and their concentration near the free surface of the acid-secreting cell in the dog, cat, and frog gastric mucosa after stimulation (23, 24). So far we have been unable to demonstrate any clear-cut difference in the amount or in the form of the reticulum during different functional states, but admittedly our experience with this cell type has been more limited than that of Sedar and our experimental conditions have been somewhat different from his.

DISCUSSION

In our observations on thirteen or more species, we have found that parietal cells do not contain cytoplasmic vesicles and vacuoles in the large numbers reported by other investigators. Instead, there is an apparently continuous system of interconnecting tubular elements of the endoplasmic

reticulum devoid of associated ribonucleoprotein granules. The continuity of this agranular form of the endoplasmic reticulum appears to be particularly difficult to preserve. A similar tendency to break down into vesicles has been reported by Christensen and Fawcett (6) in the extensive agranular reticulum of the interstitial cells of the testis, and by Yamada and Ishikawa (30) in the corpus luteum of the mouse ovary. The apparent lability of this system of membranes serves to emphasize the importance of establishing depend-

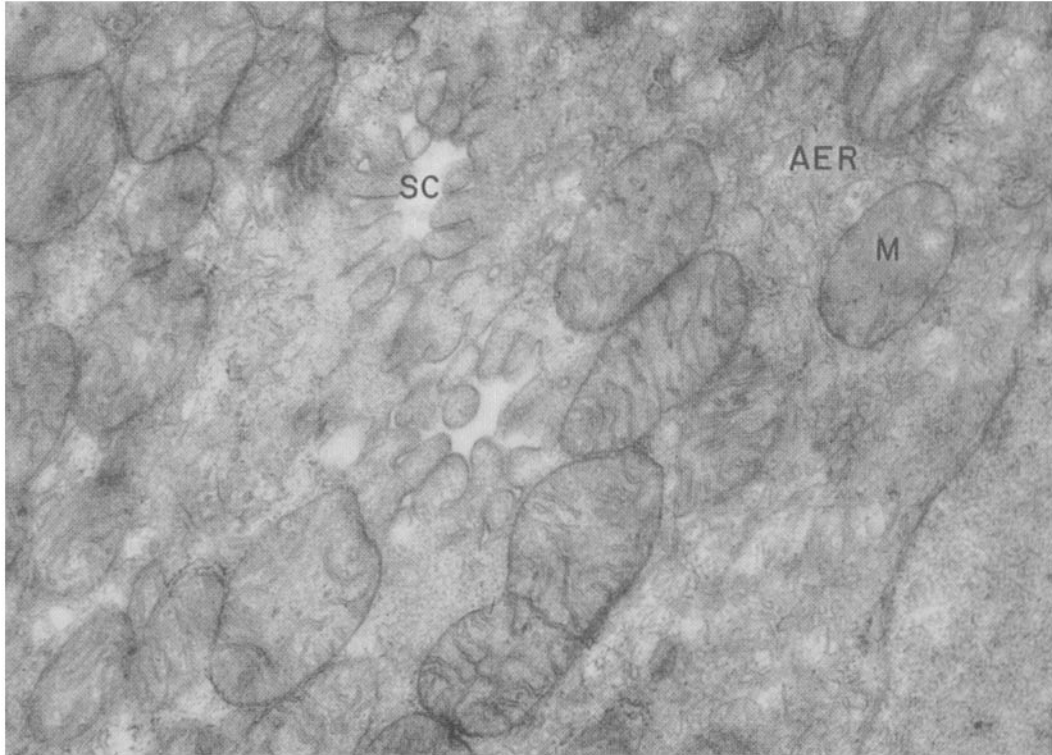


FIGURE 7

An area of a parietal cell from the stomach of a fasting mature cat, showing a secretory canaliculus (SC) with short, blunt microvilli typical of this species. The cytoplasm immediately beneath the microvilli is relatively free of membranous organelles. Among the numerous mitochondria (M) many randomly oriented elements of the agranular endoplasmic reticulum (AER) may be observed. $\times 29,000$.

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able criteria for the adequate preservation of particular tissues—a need recognized by many of the early cytologists at the light microscope level. The factors in the preparation procedure which seem to be most critical for the preservation of the tubular endoplasmic reticulum are dehydration and the final embedding medium. When methacrylate is used, uranyl nitrate (28) appears to favor the preservation of the tubular form. It is recognized, however, that we all depend upon procedures of killing, fixing, and embedding that are capricious, and the evaluation of the validity of our results is at best rather subjective. It might be argued that the vesicles and vacuoles described by others are a true representation of the structures of the living parietal cell and that our procedures have transformed the vesicles into tubules. It seems more likely, however, that a system of tubules has

fragmented and expanded into spherical units than that a series of membrane-limited spherical elements has been deformed into a network of tubules. Since more energy is required to maintain a tubular form than a spherical form, it would also seem more likely that vesicles may be a consequence of disruption of the tubules and enspherulation of the fragments. We do not wish to imply

Efforts to establish the structural correlates of functional activity in the parietal cells have been hampered in the past by the limited resolving power of the light microscope and by the lack of any direct demonstration that this cell actually secretes hydrochloric acid (9). The assumption that it does so is firmly ingrained in histological thinking but is based only upon indirect evidence.

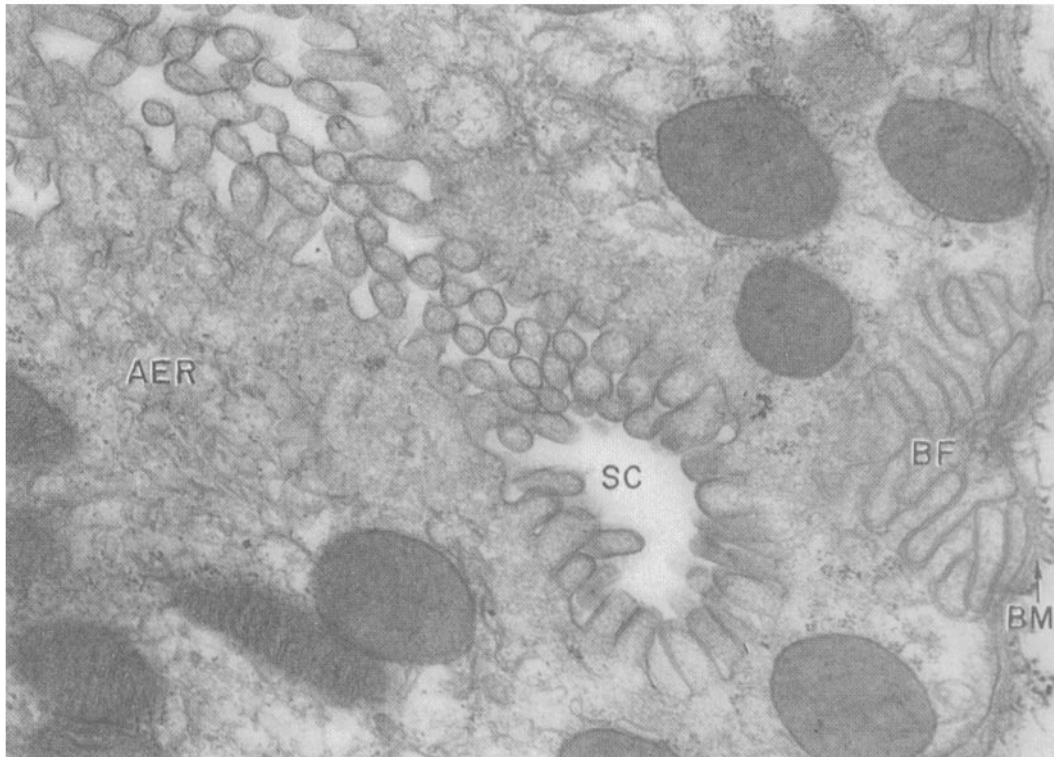


FIGURE 8

A basal part of a gastric parietal cell from an adult beaver stomach. The secretory canaliculus (*SC*) lined by numerous short microvilli is shown extending almost to the basal margin of the cell. The basal folds (*BF*) at the right of the figure bear a superficial resemblance to microvilli but are in fact broader folds of the surface and are located between the cell body and the basement membrane (*BM*). Agranular endoplasmic reticulum (*AER*) may be seen in the cytoplasmic matrix. $\times 35,000$.

that all vacuoles in electron micrographs of parietal or other cells are artifacts, for the presence of such structures in some living cells can be clearly established by phase contrast microscopy. In electron microscopic studies, however, empty appearing vesicular structures should be interpreted with caution, for they may have had a content of appreciable density that was extracted during preparation, and might have had an entirely different form if the tissue had been prepared by other methods.

The expectation that the electron microscope might reveal significant structural changes in the parietal cell after stimulation of hydrochloric acid secretion has not been borne out. It has not been possible, to date, to relate the observed variation in the patency of the secretory canaliculus to the level of acid secretion. The reported functional variations in degree of vacuolization or extent of the agranular reticulum are equivocal at best. In the common laboratory animals which feed more or less continuously there is a possibility that a

constant low level of acid is secreted by some of the cells (2), and that the population of parietal cells at any given moment may be in different phases of a secretory cycle (3). These circumstances would tend to minimize the structural differences between experimental stimulated and control animals and would becloud the functional interpretation of the

parietal cells, there is an increase in number and a mobilization of the smooth surfaced vesicles near the luminal surface (23, 24). He has suggested that the vesicles discharge their contents into the lumen by coalescing with the cell membrane in a process that is the reverse of pinocytosis. If the cytoplasmic membranes of these cells are involved

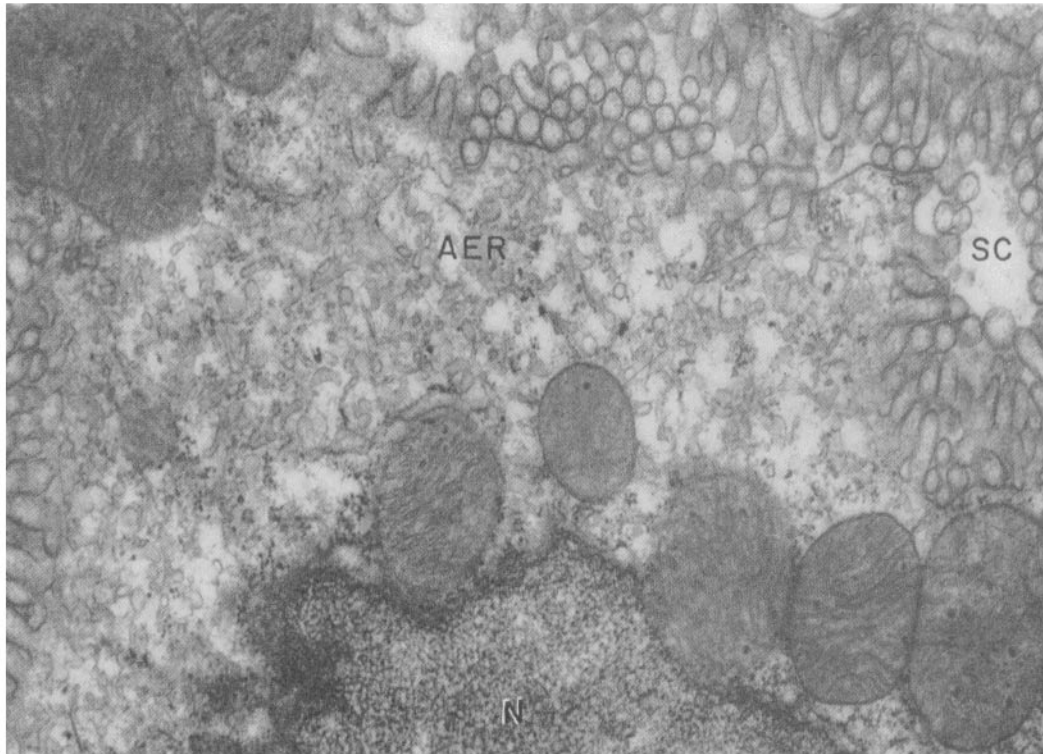


FIGURE 9

A part of a gastric parietal cell from an actively feeding adult hamster. The area of cytoplasm shown is bordered by microvilli which line the secretory canaliculus (SC). In the cytoplasmic matrix are numerous profiles of the tubular endoplasmic reticulum (AER). This area does not include as many mitochondria as some areas, but several are shown in close apposition to the nucleus (N). $\times 28,000$.

morphological findings. Our attempts to observe structural differences between parietal cells of fasting and recently refeed animals and pharmacologically stimulated animals have established no clear-cut morphological criteria of active secretion in the parietal cell.

It is tempting to speculate that the smooth surfaced endoplasmic reticulum within the parietal cell may in some way facilitate hydrochloric acid secretion, but to date we have no compelling evidence for this. Sedar has reported that after stimulation of frog secretory cells and of dog

in hydrochloric acid secretion, we would visualize this as occurring through the agency of a continuous system of tubules of the agranular endoplasmic reticulum which occasionally communicate with the surface, and not by the discharge of quanta of the cell product packaged in numerous separate vesicles.

Recently Curran (7) and Durbin (10) have independently proposed a theoretical mechanism whereby a secretion such as HCl might be transported into the gastric lumen. This hypothesis postulates two sets of "pores" arranged in series.

If the present observations on the parietal cells are interpreted in relation to this concept, the site of acid secretion would be either across the membrane limiting the tubular elements of the endoplasmic reticulum or the plasmalemma covering the microvilli of the secretory canaliculus. The membrane of the reticulum or of the microvilli

spaces between adjacent and opposing microvilli in the secretory canaliculi. When the dimensions of such a system are appropriate, the secretion of HCl across the first membrane could cause a flow of fluid through the second set of "pores" and the secreted fluid would then be transported to the lumen. Although highly speculative, at present,

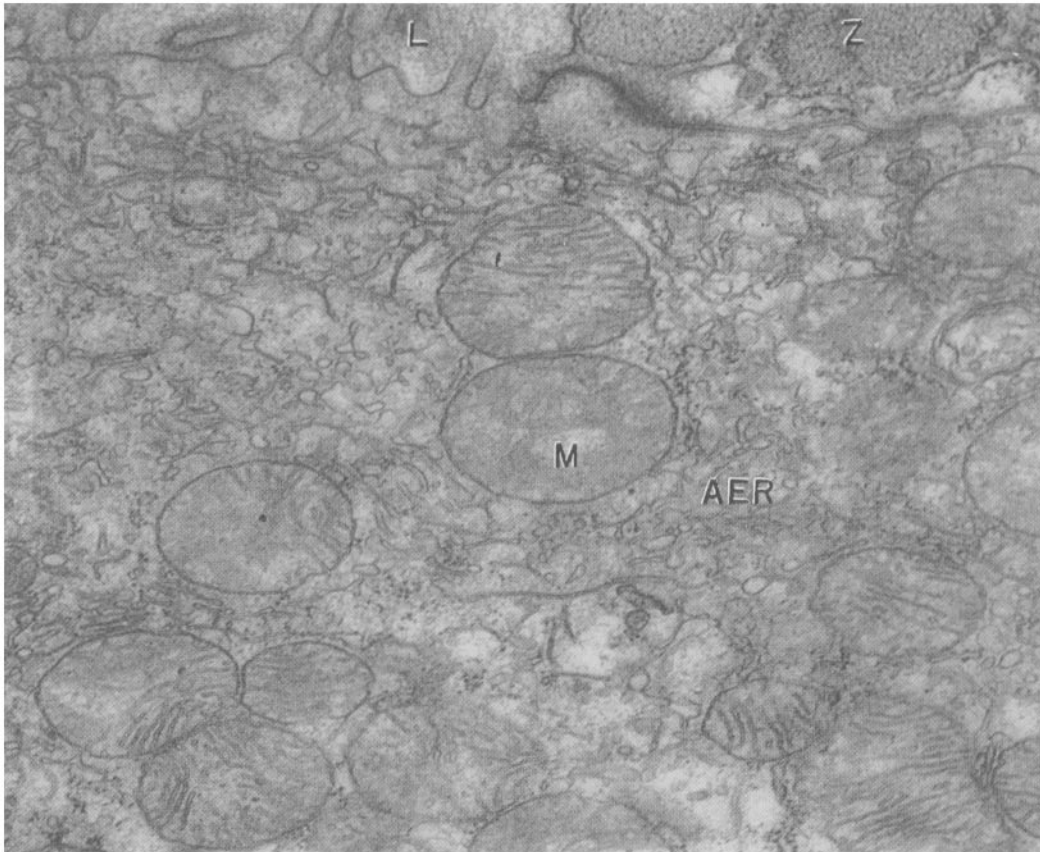


FIGURE 10

A part of the apical cytoplasm of a gastric parietal cell of the human. Among the mitochondria (*M*) are numerous elements of the agranular reticulum (*AER*). Some are tubular, but other long profiles are probably cisternae. Scattered elements of granular endoplasmic reticulum as well as free ribonucleoprotein particles are also present. A part of the glandular lumen (*L*) at the upper left and part of a chief cell with its zymogen granules (*Z*) at the upper right are shown. $\times 34,000$.

would be assumed to possess the first set of hypothetical pores, which should be very small. To date, there is no visual evidence for the existence of this set of pores, but they might well be of amicroscopic dimensions. The second set of pores, according to Curran and Durbin, should be much larger in diameter and thus might correspond either to the lumen of the agranular reticulum or to the

this mechanism is suggested as a possible method by which the secretion of the cell might be transferred to the gastric lumen.

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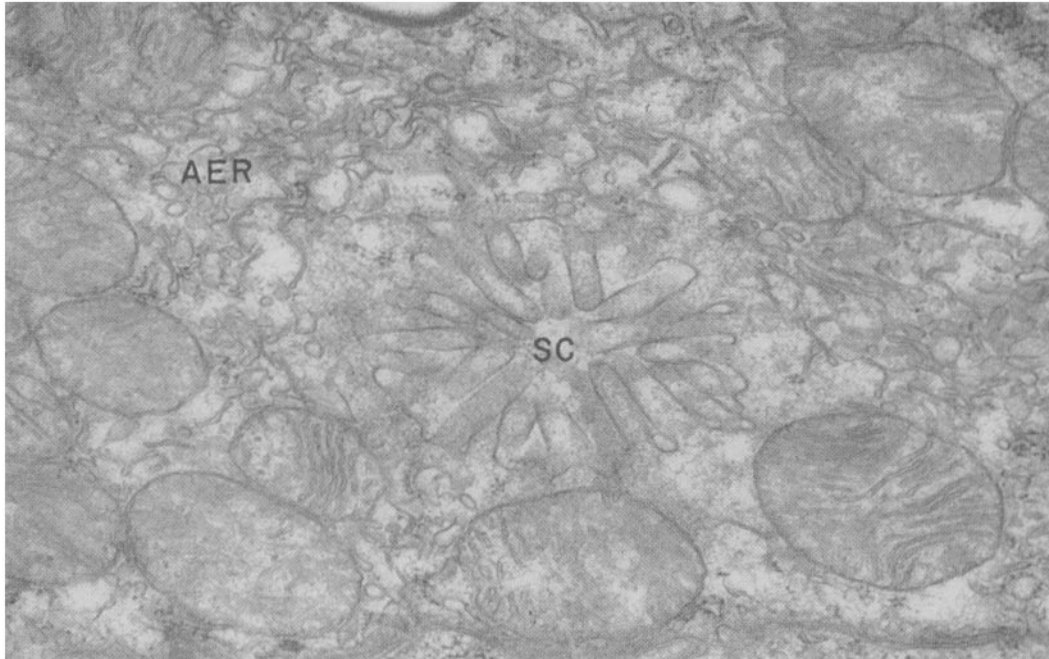


FIGURE 11

An area of a parietal cell from human gastric mucosa. This area shows a section through a secretory canaliculus (SC) almost occluded by the tightly packed microvilli. The cytoplasm immediately surrounding the canaliculus is relatively poor in membranous structures, but the large mitochondria are surrounded by numerous elements of the agranular reticulum (AER). $\times 33,000$.

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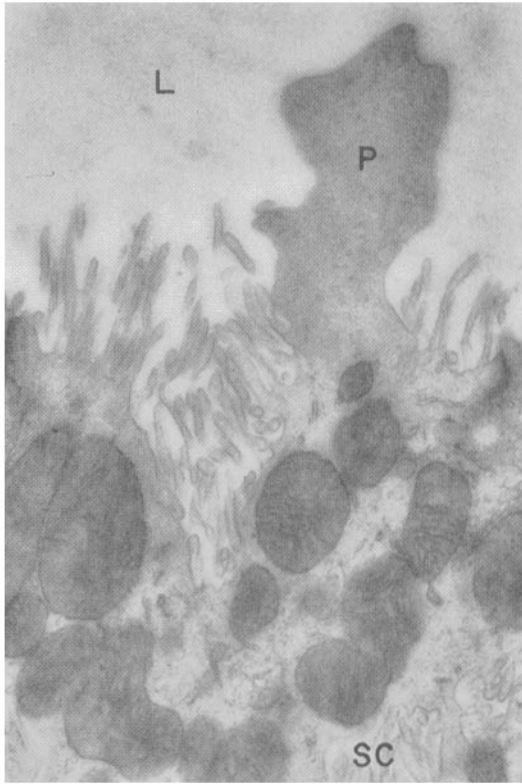


FIGURE 12

A part of the apical cytoplasm of a gastric parietal cell from a recently fed bat. The surface plasmalemma is usually in the form of microvilli, but occasionally blunt pseudopodia (*P*) of irregular shape project into the lumen (*L*). These processes are usually devoid of organelles and the cytoplasm appears similar to that in the microvilli. A small part of a secretory canaliculus (*SC*) is present at the lower margin, and elements of the endoplasmic reticulum may be seen among the mitochondria. $\times 19,000$.

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