FINE STRUCTURE OF THE MYOEPITHELIUM OF THE ECCRINE SWEAT GLANDS OF MAN

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ABSTRACT

The secretory coils of glutaraldehyde-osmium tetroxide–fixed and Epon-Araldite–embedded eccrine sweat glands from the palms of young men were studied with the electron microscope. The myoepithelial cells lie on the epithelial side of the basement membrane and abut other epithelial elements directly. The irregularly serrated base of the cell has dense thickenings along the plasma membrane which alternate with zones bearing pits; the smooth apical surface lacks dense thickenings, is studded with pits, and conjoined to secretory cells by cccasional desmosomes. Masses of myofilaments, 50 A in diameter, fill most of the cell and are associated with irregular dense zones. In cross-section the arrangement of the myofilaments seems identical with that of the I band of striated muscle, and the dense zone has typical Z band structure. A few microtubules and cytoplasmic cores bearing profiles of the endoplasmic reticulum, filamentous mitochondria, and glycogen granules penetrate the fibrillar masses and run parallel to the oriented myofilaments. In the perinuclear zone, Golgi membranes, rough- and smooth-surfaced elements of the endoplasmic reticulum, mitochondria, glycogen, microtubules, lipid, pigment, and dense granules are variable components in the cytoplasm. The interrelationships of the myoepithelial cells with the secretory cells suggest that the former may act as regulators, controlling the flow of metabolites to the secretory epithelium.

INTRODUCTION

Myoepithelial cells are common components of many vertebrate glands that take their origin from the embryonic ectoderm. They have been studied by cytochemical and the electron microscopic techniques in salivary glands (24, 40–42, 44–46); in lacrimal glands (25, 26, 40); in mammary glands (5, 11, 15, 22, 42, 44); in the prostate (38); in the Harderian gland (4, 25); and in apocrine) (14, 16, 19, 48) and eccrine (8, 13, 18, 30, 32, 33 sweat glands. All of these investigators agree that the myoepithelial cells lie on the epithelial side of the basement membrane, and most authors note the similarity between filaments in the cytoplasm of smooth muscle and myoepithelium. The literature shows that although the myoepithelial cells of various glands may differ in size and shape, they are essentially similar in their fine structure. In some glands the contractile function of the myoepithelial elements has been clearly demonstrated (16, 27, 46) and the similarities in fine structure between the myoepithelial elements of the different glands suggest that they all are contractile cells.

In studies seeking the elements basic to all intracellular contractile systems, the organization of every type of contractile cell should be considered. In this respect, striated muscle has been investigated intensively and some progress is now being made in elucidating the structure and function of smooth muscle (21, 34), but for lack of information or from oversight the myoepithelial cell has often

been neglected (12). Superficially, myoepithelial cells resemble smooth muscle cells, but close examination reveals that they are not alike in their fine structure. It is important that these differences between smooth muscle and myoepithelium be clearly delineated and that comparisons also be made with striated muscle. Such an exposition is presented in this paper.

Myoepithelial cells are especially well developed in the secretory segments of eccrine sweat glands; developmental and cytochemical studies appear in the literature, and pertinent physiological data are available on sweat secretion. These glands thus afford an appropriate site for the study of the myoepithelial elements and their possible relationship to the secretory process.

MATERIALS AND METHODS

Biopsy punches were taken under nerve block from the palms of healthy male volunteers 23 to 35 years old. The specimens were placed immediately in cold fixative at pH 7.2, and individual secretory coils of eccrine sweat glands were dissected from the dermis under a dissecting microscope. The fixative was adjusted to 320 osmolarity and contained 5.6 ml biological grade glutaraldehye (36.4 per cent), 50 ml 0.1 M sodium cacodylate, 1.5 gm sucrose and 44.4 ml distilled water (35). The tissue was fixed for 2 hours, rinsed briefly in 0.1 M sodium cacodylate containing 5 gm sucrose per 100 ml, and postfixed in a 1 per cent aqueous solution of osmium tetroxide for 10 minutes. Dehydration was carried out in ascending concentrations of acetone, and the tissue was infiltrated and embedded in an Epon-Araldite mixture (47).

Sections were cut at 600 to 900 A with a diamond knife on a Porter-Blum MT-2 microtome, mounted on both formvar-coated and uncoated grids, and stained with either uranyl acetate (43) or lead citrate (37). The tissue was examined and photographed in an RCA-EMU-3F microscope at initial magnifications of 4100 to 16,900 and enlarged photographically.

OBSERVATIONS

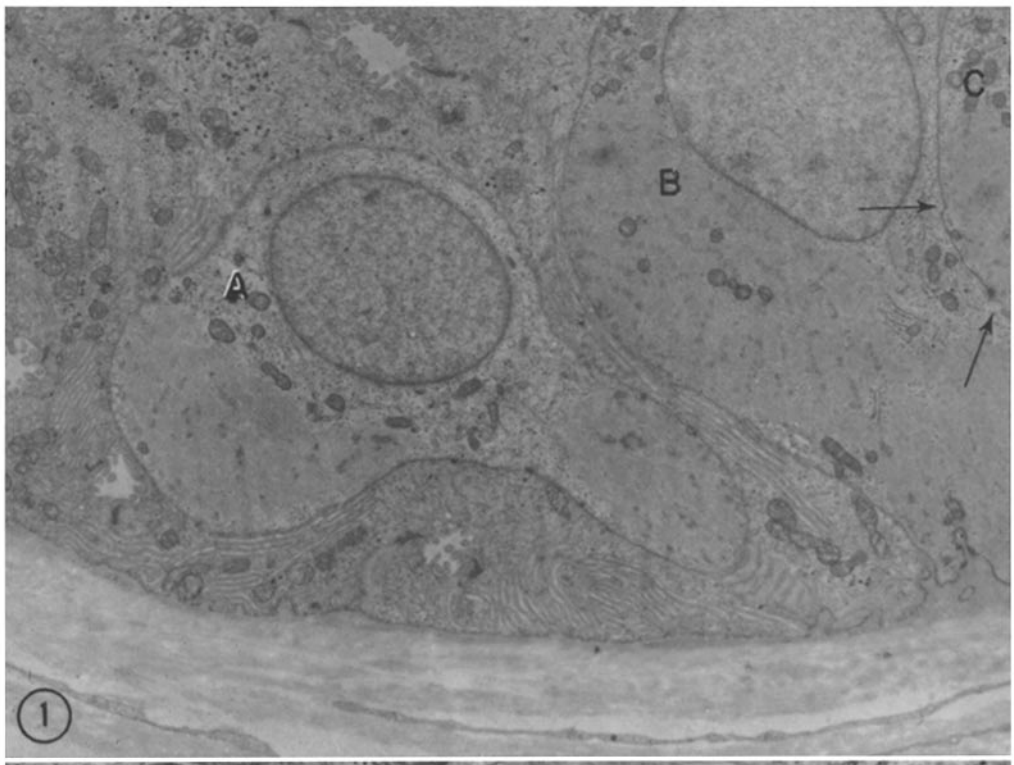
In the eccrine sweat glands of man the myoepithelial cells are restricted to the secretory segment of the gland; in the coiled duct, the straight duct, and the intraepidermal duct, there are none (31). Within the secretory segment the myoepithelium forms an incomplete pavement upon which the secretory cells rest. The myoepithelial cells are usually elongate and sometimes branched and they are aligned parallel to the long axis of the tubule (2, 31). Binucleate myoepithelial cells are observed occasionally but they are apparently an oddity.

Most of the cytoplasm of the myoepithelial cell is filled with dense masses of myofilaments (Figs. 1 and 2). The filamentous zones are positioned lateral and basal to the nucleus, restricting the other cytoplasmic organelles primarily to the region around the nucleus and to a thin rim of cytoplasm beneath the apical plasma membrane. Thin cores or columns of unmodified cytoplasm also penetrate intermittently among the filamentous masses. These cores of cytoplasm with accompanying profiles of the smooth-surfaced endoplasmic reticulum (SSER), glycogen granules, and dense, filamentous mitochondria vary in their dimensions (Fig. 3). The mitochondria within the columns are specifically oriented with their long axis parallel to the long axis of the myofilaments.

The base of each myoepithelial cell is sculptured

FIGURE 1 Parts of three (*A* to *C*) myoepithelial cells in the secretory coil of an eccrine sweat gland appear in this low power electron micrograph. The cell at the center has been cut at the level of the nucleus and does not appear to rest on the basement membrane. At the right, between the arrows, a desmosome and nexus join two adjacent myoepithelial cells. The interrelationships between the myoepithelial cells, the surrounding clear cells and the intercellular canaliculi are revealed clearly. Variation in the width of the amorphous adepithelial membrane, the fibrous basement membrane, and the processes of investing fibrocytes are also demonstrated. Lead citrate stain. × 7,500.

FIGURE 2 This micrograph illustrates some of the typical organization of a myoepithelial cell, including: masses of myofilaments, profiles of elements of the rough- and smooth-surfaced endoplasmic reticulum, small dense mitochondria, apical and basal specializations of the cell surface, and scattered glycogen granules. At the cell base, pits are limited to the invaginations of the plasma membrane; they are not present where dense zones border the cell membrane. Lead citrate stain. × 13,000.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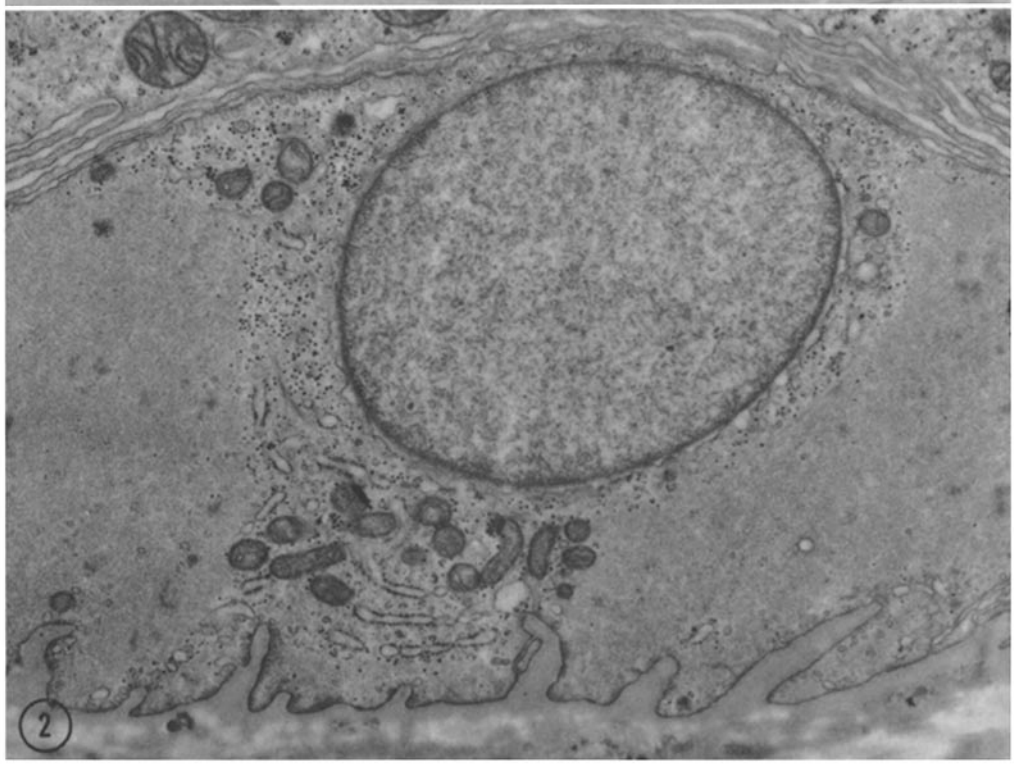
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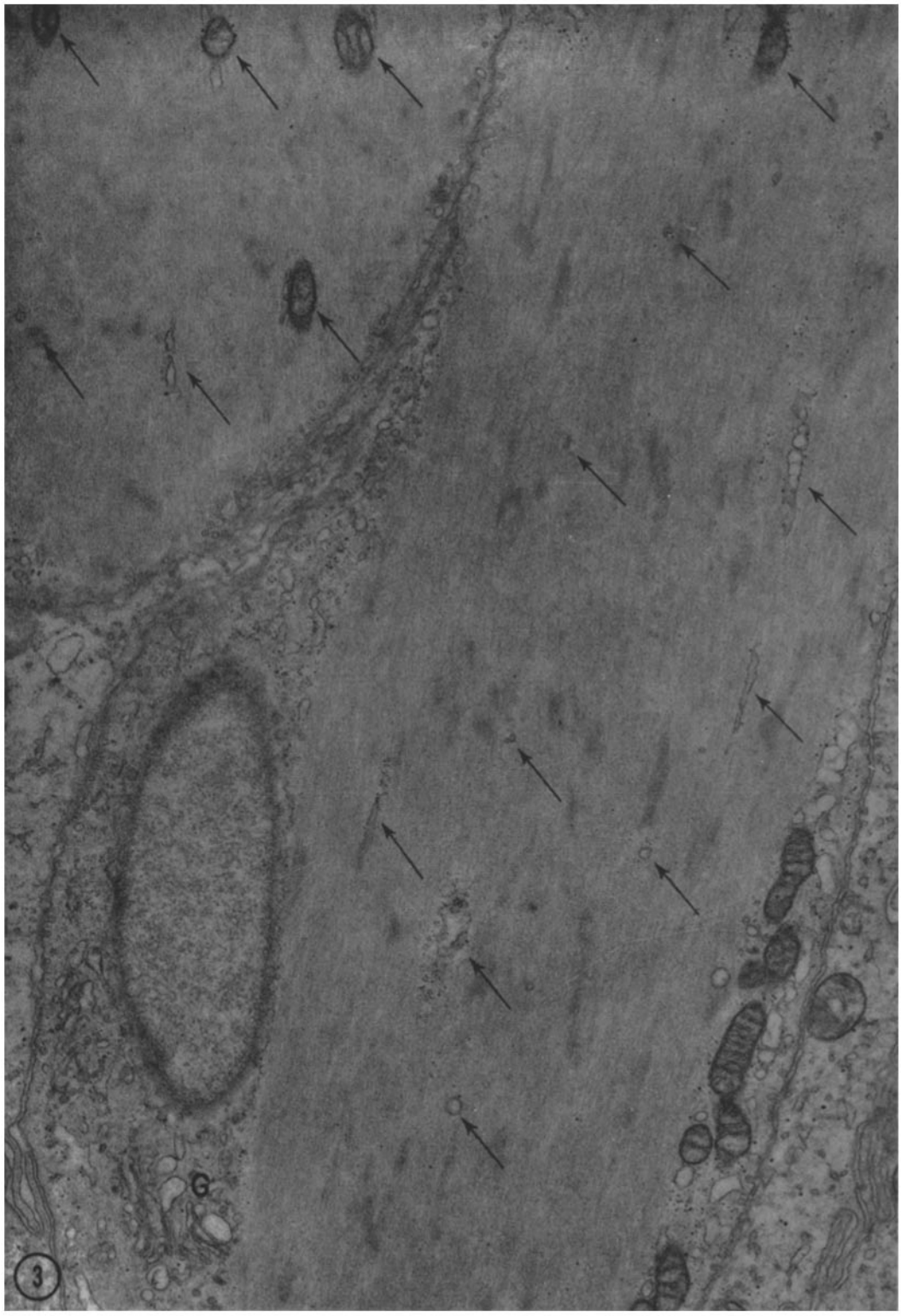


FIGURE 3 In these two myoepithelial cells the cytoplasmic cores (arrows) that penetrate the masses of myofilaments are well demonstrated. Some cores show only profiles of the SSER, others display profiles of mitochondria alone, and some have both. Dense zones are also scattered irregularly among the filamentous areas. Golgi membranes (*G*) appear in the perinuclear cytoplasm of one cell. Lead citrate stain. × 10,000.

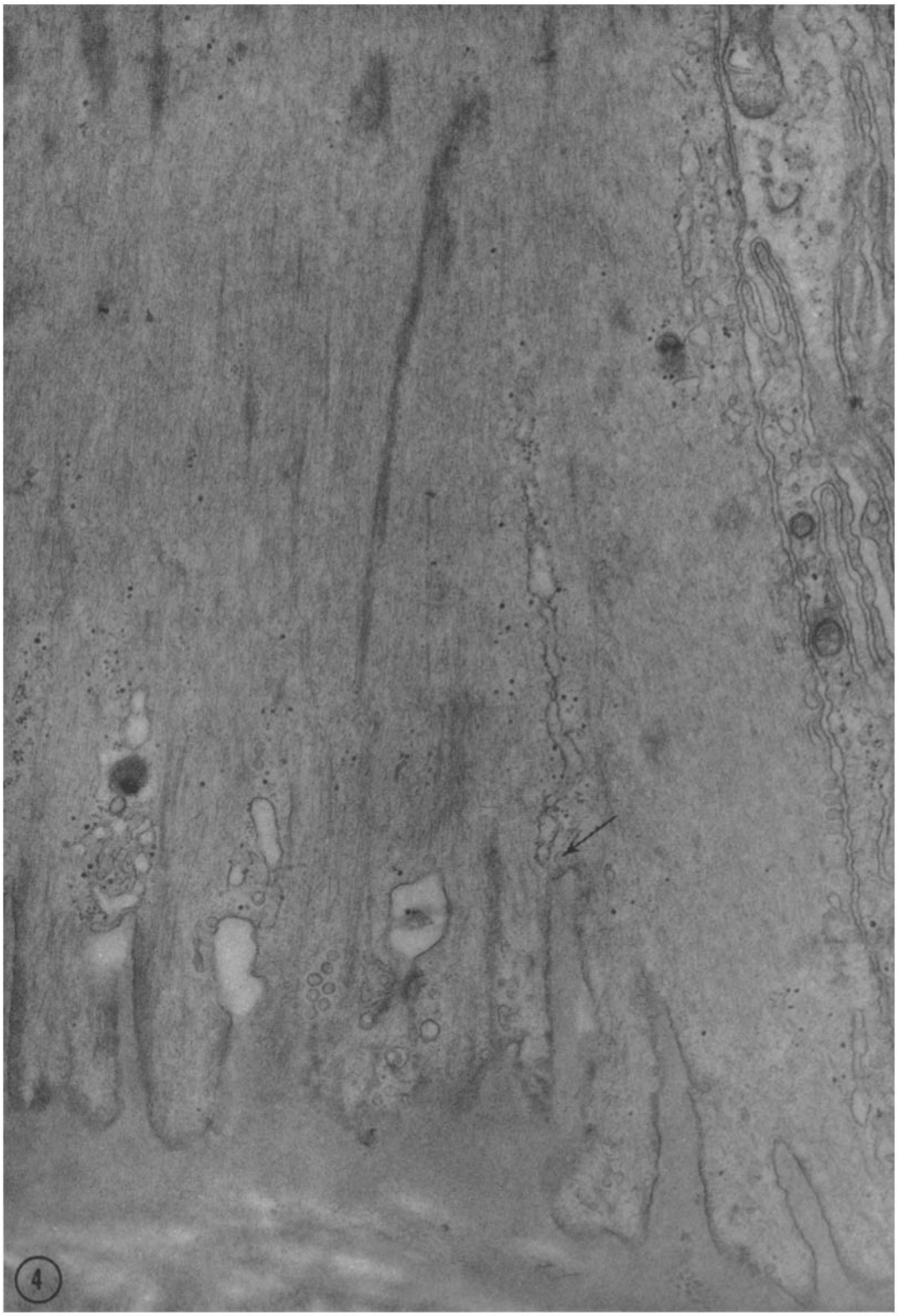


FIGURE 4 This section of the base of a myoepithelial cell is nearly parallel to the long axis of most of the myofilaments. Some filaments may be followed for some distance and seem to be finely beaded; others seem to branch or have a wavy appearance. The dense zones are irregular in form and in this plane may be very long. A column of smooth-surfaced endoplasmic reticulum, that seems to take its origin at the plasma membrane (arrow), follows the same course as the myofilaments. The amorphous adepithelial membrane varies in thickness and does not fill completely all the incursions of the cell surface. Pits alternate with dense zones along the inner surface of the plasma membrane; the latter seem to serve as insertion points for myofilaments. An occasional microtubule is seen in longitudinal section. Lead citrate stain. × 16,500.

by invaginations of irregular size and shape, and the basement membrane is quite irregular along its inner, adepithelial surface while its outer border is usually smooth (Figs. 2 and 4). It, therefore, varies greatly in thickness. Where the incursions of the basal surface of the myoepithelial cell are deepest, the amorphous basement membrane may not fill the crevice completely, and a clear space may be evident (Fig. 4). At these sites the plasma membrane is frequently populated with pits or pinocytotic vesicles, and profiles of the endoplasmic reticulum lie close to the cell surface (Fig. 4). Occasionally, small membranous profiles may be embedded in the basement membrane, but their identification as nerve terminals or as processes of fibroblasts or other connective tissue elements is uncertain. Nerve fibers were never observed terminating directly on either myoepithelial or secretory cells.

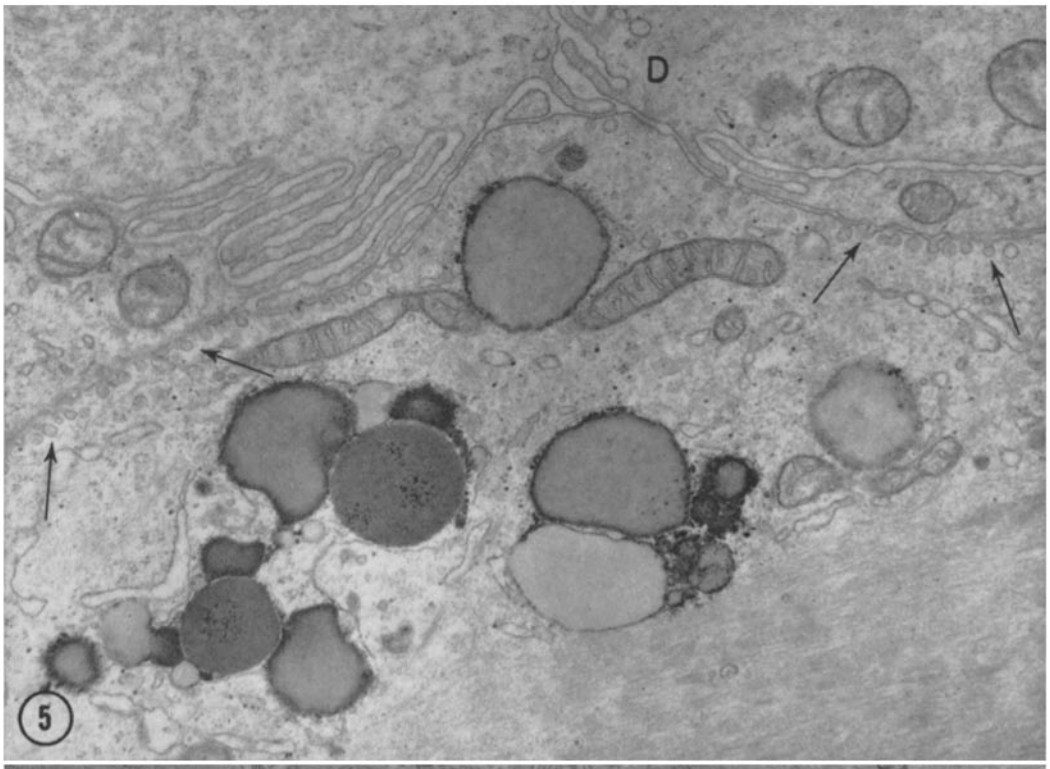
The plasma membrane of the myoepithelial cell has a different character at different regions of the cell surface. Where the plasma membrane adjoins the basement membrane and where it limits areas of cytoplasm containing myofilaments, its inner surface is associated with a cytoplasmic zone of high electron density (Figs. 2 and 4). The dense zone is more or less homogeneous along the base of the cell, and it may serve as an attachment site for myofilaments since many of the filaments seem to terminate in these regions (Fig. 4). The dense zones are interrupted wherever pits or caveolae appear along the basal plasma membrane (Fig. 4).

The plasma membrane abutting the overlying epithelial cells is nearly smooth and bears very few villous folds or processes (Figs. 1 to 6). This feature of the myoepithelial cell contrasts strikingly with the elaborately folded surface of the adjacent secretory or clear cells that rests on the myoepithelium but seldom interdigitates with it (Figs. 1, 2, 4 to 6). Pits or caveolae of uniform size characteristically line the apical surface of the myoepithelial cell (Figs. 2 to 6). They are cup-shaped with a central cavity nearly twice the diameter of the apical opening, and they seem to be identical with similar structures found in smooth muscle and endothelial cells. The presence of pits on the surfaces of myoepithelial cells has been reported by Takahashi (44), Matsuzawa and Kurosumi (30), Kurosumi *et al.* (19), and Scott and Pease (40), but many investigators seem to have overlooked them. Pits are never seen on the plasma membranes of the clear or dark secretory cells of the eccrine sweat glands; so this character alone distinguishes between the myoepithelial and secretory elements. Desmosomes are sparse but they are observed occasionally joining the myoepithelium to the secretory cells (Fig. 5).

In the eccrine sweat glands myoepithelial cells seldom contact one another directly. Where two myoepithelial cells do contact one another, the cell surfaces may be bonded by a tight junction or nexus for a short distance. Spaces usually separate the cells, and the basal processes of one or more clear cells usually fill the gaps thus formed and contact the basement membrane (Fig. 1). In these regions the surfaces of the clear secretory cells are elaborately folded and intermeshed; here also a highly developed system of intercellular canaliculi (Figs. 1, 5 to 7) takes its origin. There is, therefore, a close relationship between the basal, absorptive surfaces of the clear cells and the interposed myoepithelium.

FIGURE 5 The contours of the apical plasma membrane of the myoepithelial cell are regular and lined with pits (arrows) while the adjacent clear cells bear long villous processes. In a rare instance, a desmosome (*D*) is seen between a clear cell and a myoepithelial cell. Globules of variable size, shape, and electron opacity, that are interpreted as lipofuscin, lie in the cytoplasm above the massed myofilaments. Lead citrate stain. × 24,000.

FIGURE 6 Portions of two myoepithelial cells and four clear cells are shown in this electron micrograph. The columns of smooth-surfaced endoplasmic reticulum and associated mitochondria that course through the masses of myofilaments are shown in section. The surfaces of the myoepithelial cells are regular except where one interdigitates with two adjoining clear cells (arrow). The clear cells intermesh with each other, form intercellular canaliculi, and contain abundant profiles of the smooth-surfaced endoplasmic reticulum. Lead citrate stain. × 13,000.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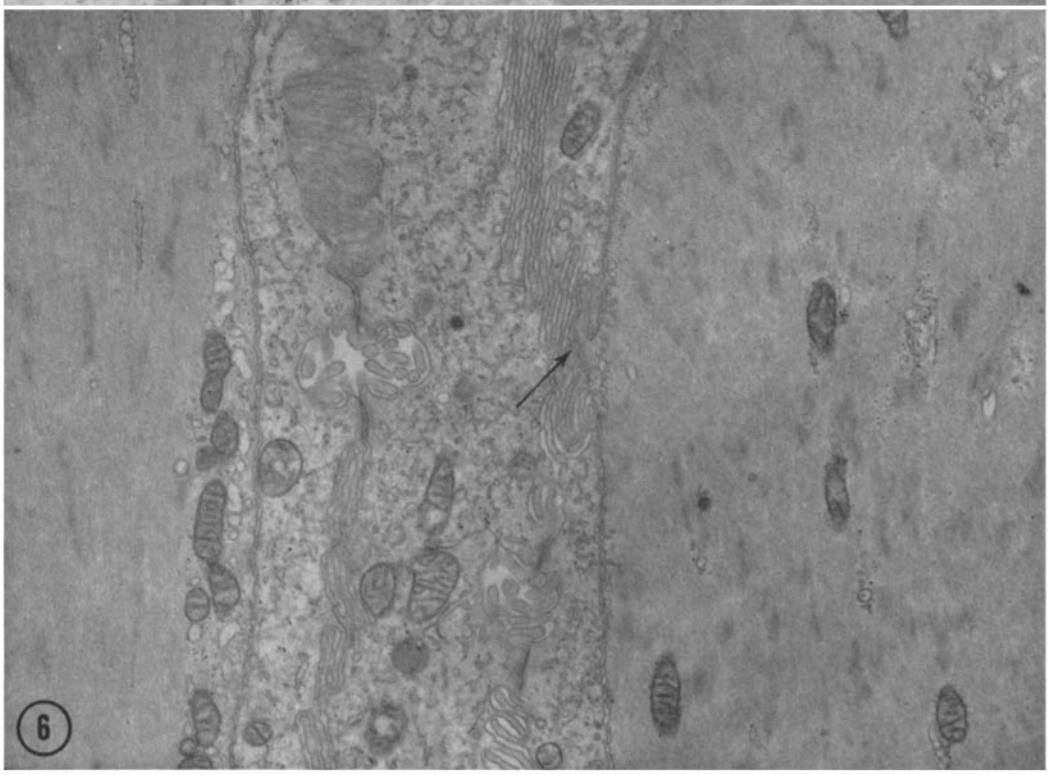
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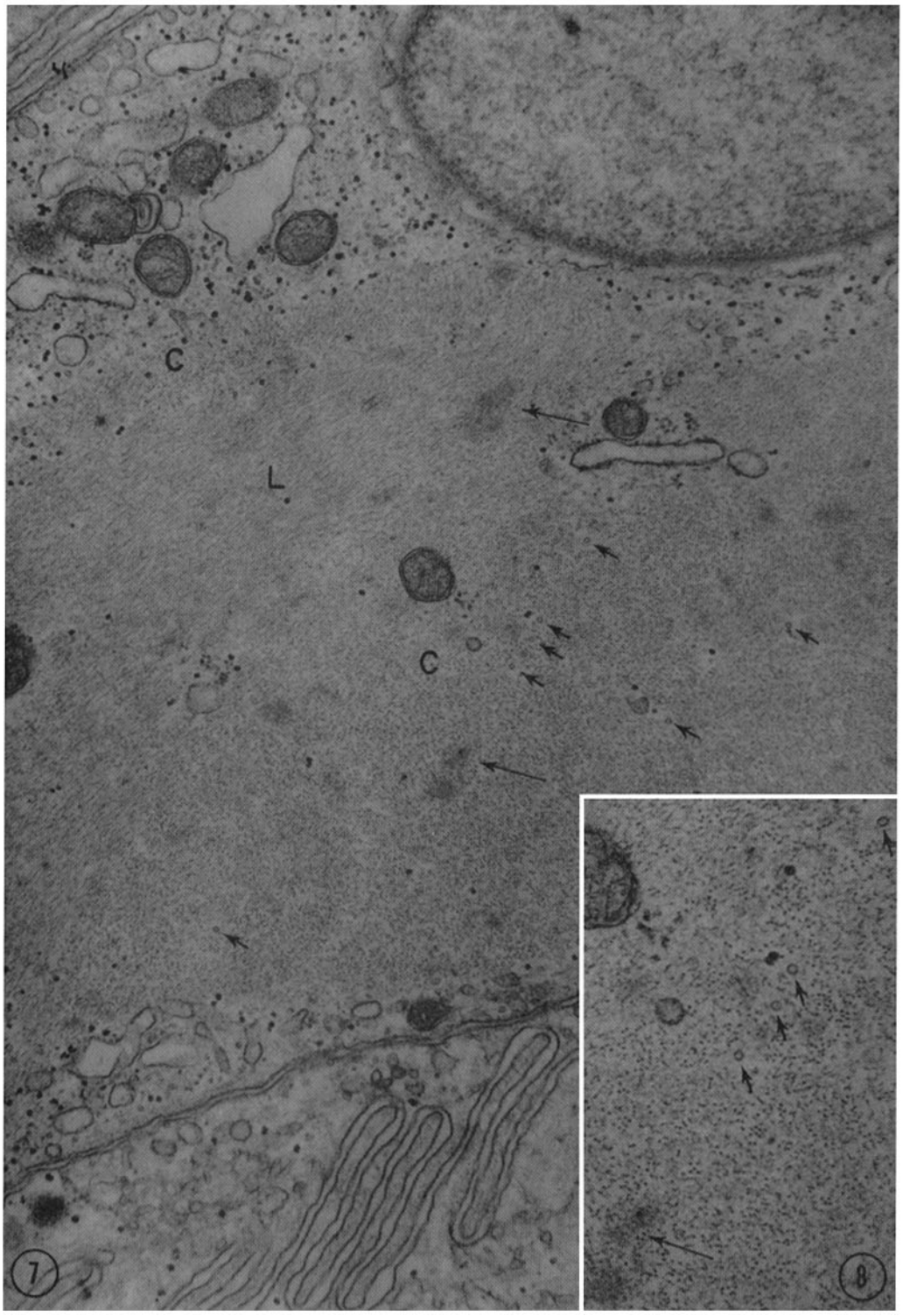

FIGURES 7 and 8 In this section the myofilaments of the myoepithelial cell are cut in cross-section in two zones (*C*) and longitudinally in one area (*L*). In cross-section the filaments are dense spots approximately 50 A in diameter; they are associated with a somewhat less dense material that interconnects many of the filaments. Occasional glycogen granules and randomly spaced microtubules (small arrows) appear among the myofilaments. The latter are not perfectly symmetrical in cross-section but vary somewhat in thickness at their perimeter. All of these components are surrounded by a pale matrix. In the dense zones (large arrows) the myofilaments are still evident, but the associated dense material is in high concentration to the almost total exclusion of the pale matrix. These features are best seen in the enlarged inset, Fig. 8. In longitudinal section the myofilaments form a fine anastomosing reticulum. Lead citrate stain. Fig. 7, × 34,500. Fig. 8, × 64,000.

Coarse glycogen granules, separate or clumped in rosettes, are abundant near the nucleus and scattered throughout the myoepithelial cell (Figs. 2, 4, and 7). Glycogen is more commonly associated with the mitochondria and with the profiles of the SSER than with the rough-surfaced endoplasmic reticulum (RSER) of the cell.

Profiles of the SSER appear both as irregular dilated cisternae and as small vesicles. The SSER is well developed in the perinuclear cytoplasm, and its reticular structure is visualized best there. Profiles of the SSER are the most common components of the cytoplasmic cores penetrating the masses of myofilaments (Figs. 3, 4, and 6).

The RSER is highly variable. Some myoepithelial cells contain abundant rough-surfaced membranes, while others have little or none. In cells containing RSER the membranes are usually restricted to the perinuclear and apical cytoplasmic zones (Fig. 2). The cytoplasmic cores penetrating the fibrillar areas do not characteristically bear profiles of the RSER. In all cases, the ribonucleoprotein particles appear clustered in rosettes along the surfaces of the membranes. Free ribosomes, usually in clusters, may be scattered through the cytoplasm, but they are rarely found among the masses of myofilaments.

A Golgi apparatus with typical fine structure is often associated with neighboring profiles of the endoplasmic reticulum (Fig. 3). The Golgi membranes are not pervasive, being restricted principally to the apical and supranuclear cytoplasmic zones.

The mitochondria of the myoepithelium vary in size and shape according to their disposition within the cytoplasm of the cell, and they differ noticeably from those in neighboring clear cells (Fig. 2). In the apical cytoplasmic rim, the mitochondria are small spheres or short rods scattered among the other cytoplasmic organelles without apparent orientation. In the cores of the cytoplasm that run among the masses of myofilaments, especially toward the base of the cell, the mitochondria are long and slender. In both sites, these organelles are similar in their internal structure; they have a very dense matrix and the cristae are usually oriented at right angles to the long axis. The cristae are somewhat dilated and the pseudomatrix is not so electron-opaque as the true matrix. Intramitochondrial granules are seldom present.

Irregularly shaped spherules of lipid and pigment are also found in myoepithelial cells (20, 31). These are not bounded by membranes and are highly variable in their size, shape, and electron opacity (Fig. 5). Small membrane-bounded vesicles containing a dense granular substance are also occasionally encountered (Figs. 4 and 5).

The bulk of the cytoplasm of the myoepithelial cell is filled with oriented myofilaments. These elements may be inserted at dense zones on the inner surface of the plasma membrane (Fig. 4), or they may terminate without obvious attachment sites in the cytoplasm bordering the plasma membrane (Figs. 3 and 6). Neighboring myofilaments share a common orientation, but in a single thin section different masses of myofilaments may be oriented in different planes with no sharp separation or boundary between the individual masses (Fig. 7). Within the filamentous masses small irregular dense zones appear intermittently (Figs. 1 to 6, and 7).

In cross-section the myofilaments appear as discrete spots approximately 50 A in diameter (Fig. 8). They are spaced irregularly and are mingled with a somewhat less dense amorphous substance that connects the filaments randomly. These elements are, in turn, embedded in a matrix of low electron opacity. In some areas the amorphous substance predominates and the myofilaments are arranged in a pattern similar to that seen in the Z band of striated muscle (36) (Figs. 7 and 8). These areas appear at random and seem equivalent to the irregular dense zones, already mentioned.

In longitudinal section the myofilaments are usually aligned nearly parallel to each other throughout any single fibrillar mass (Figs. 3, 4, 6, and 7). The individual filaments may be followed only for a short distance before they pass out of the plane of the section, suggesting that they form a branching or anastomosing meshwork. Some myofilaments have a wavy appearance, and in some regions they may criss-cross randomly as in a felt-work (Fig. 4). The latter form is most frequently observed near the cell periphery, or in a zone in which filament masses showing different orientation converge on each other. Microtubules (6, 23) are present in the perinuclear cytoplasm and are scattered infrequently through the filamentous masses. In the latter zones, they are oriented with their long axis paralleling that of the myofilaments and are usually surrounded by a narrow zone of afilamentous cytoplasm. In cross-section they show some asymmetry, frequently being thicker on one axis than on the other (Fig. 8).

DISCUSSION

Relationship between Myoepithelial Cells and Secretory Cells

The myoepithelial cells are large and well differentiated in the secretory coil of the eccrine sweat glands of man. There is no indication that they are vestigal structures. Transitional forms between myoepithelial and secretory cells were not observed, and Hibbs' (13) suggestion that myoepithelial cells may develop into secretory cells is not supported by this study. Other investigators, including Kurosumi (19, 20), have also been unable to find such transitional cells in the sweat glands, and the bulk of the evidence indicates that the myoepithelium does not contribute cells to the secretory epithelium.

The close association between clear secretory cells and myoepithelial cells in human eccrine sweat glands suggests that the two cell types may function in concert. If, as Travill and Hill (46) have demonstrated in salivary glands, the myoepithelial cells decrease in diameter during contraction, their role as compressors in the secretory coil of the eccrine sweat gland may be a minor one, and their principal function may be in regulating the flow of metabolites to the secretory cells. The base of the clear cells, which most investigators consider to be the principal sweat-secreting cells (7, 8, 31–33), is elaborately folded and contacts the basement membrane only at the gaps in the myoepithelium. Contraction of the myoepithelial cells may force some sweat from the secretory coil initially (17), but it may also open wide gaps in the myoepithelial pavement. A much broader surface area of the highly folded plasma membrane at the absorptive base of the clear cell would then be exposed directly to the extracellular fluid. In this way, the myoepithelial cells would act as valves indirectly controlling the flow of sweat by regulating the surface area of the secretory cell that is exposed to the extracellular fluid. This suggestion seems to fit the physiological data on eccrine sweating and also offers an explanation for the latent or lag period observed between the time of stimulation of the gland and the production of sweat (28). It would also better explain the phenomena of maximal sweating and fatigue that have puzzled many physiologists (7, 39).

Differences between Myoepithelium and Smooth Muscle

Scott and Pease (40) have pointed out some of the differences between myoepithelial cells and smooth muscle cells. From this study, it is now possible to amplify and extend their observations. First, the myoepithelial cell is derived from the embryonic ectoderm, while smooth muscle cells have a mesodermal origin. This conclusion is supported by electron microscope studies, since the myoepithelium always lies on the epithelial side of the basement membrane while the smooth muscle cell is entirely surrounded by a homogeneous layer of basement membrane materials. Second, the myoepithelial cells are not sheathed by the delicate network of reticular fibers that envelops smooth muscle cells (1), but abut other epithelial elements directly. Third, the nucleus of the myoepithelial cell is displaced toward the apex of the cell while the nucleus of the smooth muscle cell is located near the center. Fourth, the plasma membrane of the myoepithelial cell shows regional specializations different from those of smooth muscle. The irregularly serrated cell membrane at the basal surface resembles that of smooth muscle in that dense thickenings alternate with regions of pinocytotic activity (3), but the apical surface of the cell is smooth, lacks dense thickenings, is studded with numerous pits, and is conjoined to the epithelial secretory cells by occasional desmosomes. Finally, at least in the eccrine sweat glands of man, the masses of myofilaments in the myoepithelial cells are penetrated by cytoplasmic cores bearing profiles of the SSER, filamentous mitochondria, and glycogen. Such structures have not been reported among the contractile elements of smooth muscle (3, 29).

Most investigators have equated the masses of myofilaments in myoepithelial cells with those in smooth muscle cells, indicating that only a single size of myofilament is present (4, 11, 19, 44). Recent electron microscope studies on smooth muscle now indicate that two sizes of myofilaments may exist in these cells, although thin 50-A filaments predominate (34). Unless the larger filaments are equivalent to the microtubules reported in this paper, the large filaments seem to be lacking in the myoepithelium of eccrine sweat glands as well as in some other myoepithelial cells (45).

Correlations with Striated Muscle

The contractile apparatus of the myoepithelial cell is neither so complex nor so highly organized as that of striated muscle. In thin sections the fine structure of the masses that contain the myofilaments of the myoepithelial cell resembles that of the I band of striated muscle (11). The images in micrographs of glutaraldehyde-fixed material

seem identical with those in micrographs showing I-band structure in striated muscle after similar fixation (*e.g.*, Fig. 5, Franzini-Armstrong and Porter (9)). The 50-A filaments have the same density and diameter as the F-actin filaments present in all smooth and striated muscle cells that have been investigated (12). The dense zones that appear randomly within the filamentous masses share the characteristic density seen at the Z line of striated skeletal muscle. In the myoepithelium of the mammary gland Haguenau (11) has equated these densities with the Z line, and this study supports that conclusion although the pattern recently observed in the Z band of the striated muscle cell (36) has not been resolved clearly.

Microtubules in Myoepithelial Cells

Microtubules appear sparsely within the masses of myofilaments; and their long axes parallel those of the myofilaments. They apparently are not linked directly to the myofilaments, since pale areas of cytoplasm devoid of myofilaments sometimes surround them. The relationship of these structures to the contractile function of myoepithelial cells is not clear, but recent evidence from other cell types indicates that microtubules may be structural and/or contractile elements of the cell (6, 23). Their scant number in myoepithelial cells suggests, however, that they do not play a major role in the contractile function of these cells.

The Plasma Membrane and Phosphatase Activity

Alkaline phosphatase or adenosine triphosphatase (ATPase) activity has been demonstrated in the myoepithelium of salivary glands (41), prostate (38), Harderian gland (25), lacrimal glands (25), and in eccrine (2, 18, 30) and apocrine (2, 10) sweat glands. Goldstein (10) noted that the alkaline phosphatase activity was not localized within the contractile apparatus of myoepithelial cells since the end product of the histochemical reaction did not correspond to the birefringent areas of the cytoplasm that mark the myofilaments. In the sweat glands of the rat, Matsuzawa and Kurosumi (30) have shown by electron microscopic cytochemical methods that concentrations of both alkaline phosphatase and ATPase are localized along the folded basal membrane of the secretory cells rather than within the myoepithelial cells. The principal reactive sites in the myoepithelial cells were the pinocytotic vesicles or pits. These studies suggest that some of the earlier work in which the alkaline phosphatase reaction was used in identifying and studying myoepithelial cells should be reexamined. It also suggests that the phosphatases that have been demonstrated in these cells are probably engaged in transport phenomena in relation to the plasma membrane rather than in contractile mechanisms.

Variation among Myoepithelial Cells

The heterogeneity of structure observed among myoepithelial cells in human eccrine sweat glands indicates a high number of cell activities. Lining the plasma membrane of all the cells are small pits or caveolae that are usually associated with pinocytotic activity. Some cells have local concentrations of the RSER, suggesting the synthesis of proteins for export. In other cells the Golgi zone is very conspicuous, indicating perhaps its involvement in synthetic or secretory processes. Some cells are binucleate; others are interconnected by conjoined membranes. The cytoplasm in some cells is nearly completely filled with massed myofilaments, while in others as much as one-half of the cytoplasm is devoid of filaments. Such variation in the cell population shows that myoepithelial cells are probably engaged not only in contraction but also in other activities such as pinocytosis, cell division, the production of basement membrane or intercellular substances, and impulse transmission.

The author is indebted to Mrs. Lynne Farr and Mr. Winston Peak for their excellent technical assistance. The research was supported by a Career Development Award K3-AM-4938, Research Grant GM-08380, and Graduate Training Grant T1-GM-582 from the Public Health Service.

Received for publication, July 1, 1965.

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