AN ELECTRON MICROSCOPIC STUDY OF ECCRINE SWEAT GLANDS OF THE CAT FOOT AND TOE PADS— EVIDENCE FOR DUCTAL REABSORPTION IN THE HUMAN

BRYCE L. MUNGER, M.D., and SAUL W. BRUSILOW, M.D.

From the Armed Forces Institute of Pathology, Washington, D. C., and the Department of Pediatrics, The Johns Hopkins Hospital, Baltimore. Dr. Munger's present address is Department of Anatomy, Washington University School of Medicine, St. Louis

ABSTRACT

The eccrine sweat glands of the cat foot and toe pads have been studied by light and electron microscopy before and after stimulation with mecholyl. The ultrastructure of these glands in the cat is found to be entirely comparable to that in the human (13). The ultrastructure and staining properties of the secretory segment of the two species are identical. The ductal part of the feline gland is shorter and the ductal cells have only scant mitochondria as compared with the human. Since Brusilow *et al.* (1) have observed that the secretion of the cat foot pad is isotonic as compared with human sweat, which is hypotonic, and since the secretory segments of the two species are structurally identical, the striking difference in the morphology of the duct is regarded as being responsible for the difference in the chemistry of the secretion of the two species. Thus the duct in the human is capable of reabsorbing sodium and chloride.

INTRODUCTION

Two distinct types of cells are present in the secretory segment of human eccrine sweat glands. It has been postulated that each cell type secretes a different product. Mucoid (dark) cells upon stimulation liberate secretory vacuoles, containing at least an acid mucopolysaccharide, into the glandular lumen (13). Clear cells are thought to deliver a predominantly watery fluid into intercellular canaliculi which convey this fluid to the gland lumen. The combined secretion of these two cells traverses a long duct which presumably reabsorbs sodium and chloride from the precursor sweat solution (19, 23). The resultant solution delivered to the skin surface is hypotonic with respect to sodium and chloride (17) and contains small amounts of other ionic and organic constituents.

Brusilow et al. (1) have observed that sweat collected from foot or toe pads of the cat is isotonic rather than hypotonic. The sweat which is secreted by the cat foot pad after stimulation with mecholyl or pilocarpine contains amounts of sodium and chloride almost identical with those in normal serum. The glands which secrete this sweat have been regarded as eccrine in type (6, 22), but Montagna (9) believes that they are in no way comparable to human eccrine sweat glands. The present study was undertaken to examine the eccrine sweat glands of cat foot and toe pads by light and electron microscopy and to try to determine (a) whether these glands are comparable to those of the human, and (b) if so, why the cat produces an isotonic sweat whereas the human secretes a hypotonic sweat.

MATERIALS AND METHODS

The foot and toe pads of six adult cats of both sexes and of two 3-month-old male kittens were studied by light and electron microscopy. The cats were anesthetized by intraperitoneal injection of Nembutal. The specimens were removed by cutting with scissors down to the bone of the phalanx or metacarpal. Thin slices of tissue were cut for fixation in 10 per cent neutral formol or formol-Zenker solution. Small cylinders, 1 mm in diameter, were cut perpendicular to the skin surface and fixed in Dalton's chromeosmium fixation (2) for electron microscopy. The formol-fixed tissue was embedded in paraffin, sectioned at 5 μ , and stained with hematoxylin and eosin, the colloidal iron stain (12) and Alcian blue stain (11) for acid mucopolysaccharides, the PAS stain (8) for glycogen, before and after diastase treatment, and the toluidine blue stain at pH 5.6 for basophilia and metachromasia (10).

Tissue for electron microscopy was fixed for 1 hour in Dalton's fixative (2) dehydrated through a graded series of alcohols, and embedded in Epon 812 (Shell Chemical Company) according to procedures

FIGURE 1

Phase contrast micrograph of kitten toe pad. A portion of a secretory segment (SS) has been cut tangentially. The cells surrounding the lumen (L) are cuboidal, and a suggestion of vacuolization can be seen in the cytoplasm of some cells. A portion of eccrine duct (DU) is also cut in section, and a double layer of cuboidal cells surrounds the duct lumen (L). The duct cells appear relatively flat, but the extent of the cytoplasm of various cells is impossible to determine at this magnification. Immediately adjacent to the duct lumen is a zone of increased contrast which represents the "cuticular border" seen in routine preparations. Numerous capillaries (C) and fat cells (F) are present in the connective tissue which surrounds the gland. \times 900.

FIGURE 2

Phase contrast micrograph of kitten toe pad secretory segment. All components of the secretory segment can be identified in this micrograph. Surrounding the lumen (L) are two types of secretory cells. Mucoid (dark) cells (Nm) can be identified by the presence of numerous secretory vacuoles (s) present in the apical sytoplasm. Between groups of mucoid cells are clear cells (Nc) which lack secretory vacuoles, and intercellular canaliculi (IC) course between adjacent clear cells. All cells which can be positively identified in this micrograph are labeled Nc for clear cells and Nm for mucoid cells in the appropriate nuclei. Myoepithelial cells (y) can be identified as small cells of uniform contrast situated beneath the mucoid and clear cells. \times 900.

FIGURE 3

Gallocyanin chrome alum-stained sections of secretory segment. The lumen (L) is surrounded by intensely stained nuclei indicating the presence of the various cells. The cytoplasm of some cells stains with the dye; these are the mucoid or dark cells (Nm). Other cells lack coloration of the cytoplasm, and these are the clear cells (Mc). The general appearance is identical with that in man (13). The apical cytoplasm of mucoid cells appears reticulated in this stain; the reticulation is due to the negative staining of the secretory vacuoles as seen in Fig. 2. \times 900.

FIGURE 4

Cross-section of secretory segment stained with the modified Hale colloidal iron stain for acid mucopolysaccharides. Areas appearing black and gray in the micrograph appear blue in the microscope. In the apical cytoplasm of some cells are numerous discrete, round, stained bodies (arrows) which are identical in form and distribution with the secretory vacuoles seen in Fig. 2. The lumen (L) also stains positively. Intercellular canaliculi cannot be identified with certainty. The surrounding connective tissue is also intensely colored. Cells lacking intracellular mucopolysaccharide are considered to be clear cells. \times 900.



B. L. MUNGER AND S. W. BRUSILOW Eccrine Sweat Glands of Cat Foot Pads 405

devised by Luft (7). Sections of the Epon-embedded material were cut with glass knives on a Porter-Blum microtome, mounted on Formvar-coated grids, and examined in an RCA EMU-3D electron microscope. Some sections were stained with saturated aqueous uranyl acetate (24) to increase electron contrast. Osmium-fixed tissue was also embedded in methacrylate according to routine procedures, but the preservation was not satisfactory for electron microscopy. One micron sections of methacrylate-embedded osmium-fixed tissue were cut on a Porter-Blum microtome for light microscopy, and these sections were stained with gallocyanin chrome alum, PAS, and the Hale colloidal iron stains as described previously (13). For phase microscopy the methacrylate was removed by soaking in xylene, and the sections were mounted directly in oil of refractive index 1.460 (3).

The secretion of sweat was stimulated by the injection of 0.1 cc of a 0.05 per cent solution of mecholyl in normal saline into the foot and toe pads. Specimens were removed 5, 15, and 30 minutes after stimulation and prepared as described above. Prior to injection one foot pad and one toe pad of each animal had been removed for controls.

OBSERVATIONS

Light Microscopy

The foot pad of a mature cat as seen in crosssections stained with hematoxylin and eosin or in

unstained osmium-fixed tissue by phase microscopy is composed of a thick epidermis, a dense, discrete dermis, and a thick layer of adipose tissue interlaced by bands of connective tissue. The bulk of the pad is composed of a 1 to 1.5 cm thick layer of adipose tissue which extends from the dermis to the fascia overlying the metacarpal bones. Tubular structures identified as eccrine sweat glands extend from the epidermis, course through the dermis and mass of adipose tissue, and terminate just above the fascia that forms the base of the pad. Thus the glands are not coiled at the dermosubcutaneous junction as are human eccrine sweat glands, but rather they extend as slightly undulating tubes through the dermis and massive fat pad. The duct can be identified as having a double layer of cuboidal cells lining the lumen (Fig. 1). The duct extends only from the skin surface to the zone at the base of the dermis. The remainder of the gland extending through the fatty tissue of the foot pad is the secretory segment (Figs. 1 and 2). Toe pads differ from foot pads in having less adipose tissue; as a result the sweat glands are more closely packed in toe pads, facilitating electron microscopic study.

The cytology of the gland as seen by light microscopy is identical with that in the human (13). The duct is composed of a double layer of cuboidal cells: a layer of surface cells bordering

FIGURE 5

Secretory segment of adult cat foot pad. The lumen (L) of this secretory segment is present in the upper part of the micrograph. Secretory vacuoles (S) indicate the presence of mucoid (dark) cells and appear to be similar to those indicated in Fig. 2. The nuclei of clear cells (Nc) are indistinct owing to the uniformity of density of the nucleus and cytoplasm. Between adjacent clear cells is an intercellular canaliculus (IC) which is difficult to resolve in detail at this magnification. Scattered mitochondria (M) can be seen in both cell types, but those in the clear cells blend with the background of cytoplasmic density at this magnification. A myoepithelial cell (Y) forms a thin band surrounding the secretory cells. \times 7000.

FIGURE 6

Clear cells surrounding an intercellular canaliculus in secretory segment of cat foot pad, 5 minutes after stimulation. Numerous microvilli (V) project into the intercellular canaliculus (IC). Terminal bars (T) are formed by the cell membranes of adjacent clear cells as they abut on the canaliculus. The cell membranes interdigitate as they surround the canaliculus, forming a lamellar system of apposed cell membranes (I). Numerous mitochondria (M) are scattered throughout the cytoplasm. Dense material thought to represent lipid (F) is also present in the cytoplasm. A portion of one clear cell nucleus (N) is present. An area of decreased density (arrow) is seen in the matrix of one mitochondrion. The background cytoplasm is predominantly granular. $\times 25,000$.



B. L. MUNGER AND S. W. BRUSILOW Eccrine Sweat Glands of Cat Foot Pads 407

the lumen, and a layer of basal cells resting on the basement membrane. The luminal edge of surface cells appears homogeneous and of dark contrast; this zone corresponds to the hyaline appearing "cuticular border" seen in routine hematoxylin and eosin-stained preparations.

Two types of secretory cells are present in the secretory segment surrounded by myoepithelial cells. As in the human, mucoid cells (dark cells of Montagna (10)) have a basophilic cytoplasm (Fig. 3) containing the secretory vacuoles (Fig. 2) in the apical part of the cell which stain selectively for acid mucopolysaccharide (Fig. 4) with the modified Hale colloidal iron stain. These secretory vacuoles are also faintly metachromatic, but are PAS-negative. The other cell type of the secretory segment is the clear cell, which lacks cytoplasmic basophilia (Fig. 3) and intracellular mucopolysaccharide (Fig. 4). Between adjacent clear cells are intercellular canaliculi (Fig. 2) which course from the lumen to the base of the gland. The contents of the intercellular canaliculi and the glandular lumen also contain mucopolysaccharide (Fig. 4). The clear cells contain PAS-positive, diastase-digestible material presumed to be glycogen.

Following stimulation the only change visible by light microscopy is a diminution of cytoplasmic glycogen in clear cells.

Electron Microscopy of Unstimulated Secretory Segment

Mucoid (dark) cells have numerous secretory vacuoles in the apical cytoplasm (Fig. 5). These vacuoles are round to oval in outline and are bounded by an incomplete limiting membrane as seen in section (Fig. 7). They contain fibrillar material of low electron opacity. The cytoplasm of mucoid cells is predominantly granular, consisting largely of dense 150 A granules thought to represent ribonucleoprotein (15). Only a few granules are associated with membrane profiles. Scattered mitochondria are present throughout the cytoplasm (Fig. 7).

The Golgi apparatus of mucoid cells is prominent, with many flattened, agranular membranous sacs, arranged in lamellar form, associated with numerous vacuoles and vesicles. A continuity can be traced between dilatations of Golgi sacs and secretory vacuoles. The small vacuoles in intimate association with the Golgi apparatus are considered to be prosecretory vacuoles, that is, secretory vacuoles in the process of formation (Fig. 7).

Clear cells are identified in electron micrographs as being associated with intercellular canaliculi (Figs 5 and 6). Their cytoplasm is predominantly granular. While it is impossible to determine with accuracy the nature of the individual granules, many of them resemble glycogen units (Fig. 14). Numerous mitochondria containing occasional dense granules are present in the cytoplasm of clear cells. A very small Golgi apparatus is present in some cells, and only a few agranular membranous profiles are scen scattered throughout the cytoplasm.

Numerous closely packed microvilli (Fig. 6) project into the intercellular canaliculi which course between adjacent clear cells. The cell membranes of adjacent clear cells interdigitate with one another, producing lamellar arrays of membranes which radiate from the intercellular canaliculi (Fig. 6). Adjacent cell membranes are thickened to form terminal bars as they abut on the canaliculi (Fig. 6).

Surrounding both mucoid and clear cells are myoepithelial cells (Fig. 13). A more detailed account of the ultrastructure of myoepithelial cells and the changes accompanying stimulation will be the subject of another report.

In adult cats many eccrine glands appear dilated and have cyst-like lumens. In such a situation the cells surrounding the secretory lumen are relatively undifferentiated; only occasional cells contain secretory vacuoles, and intercellular canaliculi are rare. The majority of the cells are cuboidal and lack cytologic specialization. Such dilated glands are seldom found in kittens, however. Langley (5) noted that kittens sweat much more profusely than adult cats, and he attributed this difference to obstruction of glands by the thick cornified epidermis in older animals. While many of the eccrine glands from adult cats observed in the present study were normal in appearance, consistent observations were impossible because many were dilated. Therefore, the remaining observations were made on kittens exclusively.

A relatively thick basement membrane surrounds the secretory segment (Fig. 13), and in some areas collagen fibers appear to be inserted into the substance of the basement membrane. Numerous small processes of fibroblasts are disposed circumferentially around the secretory



FIGURE 7

Mucoid cell cytoplasm from secretory segment of kitten toe pad 5 minutes after stimulation. Numerous secretory vacuoles (S) are present, surrounded by a distinct limiting membrane (arrow). In some places the limiting membrane appears incomplete. The mitochondria (M) demonstrate occasional vacuoles similar to those of the mitochondria of clear cells following stimulation. The Golgi apparatus (G) is prominent, and numerous small vacuoles are intimately associated with it. Some of the vacuoles in association with the Golgi apparatus are considered to be prosecretory vacuoles (P), that is, vacuoles in the process of formation. A few ergastoplasmic membranes (ER) with associated granules and isolated granules are present in the background cytoplasm. $\times 19,000$.

B. L. MUNGER AND S. W. BRUSILOW Eccrine Sweat Glands of Cat Foot Pads 409

segment. Occasional bundles of unmyelinated nerve fibers embedded in Schwann cells are present in the connective tissue surrounding the gland, but no nerve endings have been seen within the substance of the basement membrane or in contact with secretory cells or myoepithelium. Mast cells have not been seen in the connective tissue surrounding the cat eccrine glands, although they are numerous in man. Numerous capillaries are embedded in the connective tissue surrounding the glands.

Electron Microscopy of Eccrine Duct

Surface cells of the eccrine duct have large nuclei of irregular outline and scant cytoplasm (Fig. 8). The luminal edge of these cells is thrown into numerous small, blunt microvilli (Figs. 8 and 10). Beneath the microvilli is a dense zone of filamentous and granular material termed the "cuticular border" (Figs. 8 and 10). The "cuticular border" is thin as compared with that in man, and no mitochondria have been observed embedded in its substance, as frequently seen in man. The general structure of the "cuticular border" is identical with that in the human, consisting of masses of tonofilaments (terminal web) and small granules (Fig. 10). The tonofilaments insert into numerous desmosomes between adjacent duct cells (Fig. 12). These desmosomes are identical with pairs of structures described by Odland (14) as

"attachment plaques" is squamous epithelia (Fig. 11).

Basal cells appear similar in structure to surface cells. The numerous mitochondria which are present in basal cells of the duct in humans are conspicuously absent in the cat. In many sections studied, only very occasional mitochondria are present in the cytoplasm (Fig. 9), and they contain virtually no mitochondrial granules. The cell membrane of basal cells abutting onto the basement membrane is focally specialized into disc-like attachment plates (Fig. 9). These attachment plates resemble half of a desmosome, consisting of a thickened cell membrane into which tonofilaments insert, and a zone of density between the thickened cell membrane and the basement membrane. This dense zone would appear to correspond to the intermediate dense layer of the attachment plates between the cells of stratified squamous epithelium (14). These basal attachment plates are more pronounced in the cat than in man and resemble the basal attachment plates of stratified squamous epithelium (20).

Electron Microscopy of Secretory Segment after Stimulation

Mucoid cells demonstrate active extrusion as early as 5 minutes after stimulation by the subcutaneous injection of mecholyl. Numerous secretory vacuoles bulge into the lumen, and other

FIGURE 8

Eccrine duct from kitten toe pad. The duct wall is composed of a double layer of cells: surface cells (Ns) and basal cells (Nb), labeled in the appropriate nuclei. A zone of irregular density surrounding the lumen (L) is the "cuticular border" (CB) of light microscopy. Blunt microvilli (V) project into the lumen from the cytoplasm of the surface cell. Numerous desmosomes (D) are seen between adjacent cells. A distinct basement membrane (BM) surrounds the duct. \times 11,700.

FIGURE 9

A portion of the cytoplasm of two basal cells of the eccrine duct stained with uranyl acetate The nuclei (N) of two adjoining basal cells are present at the extreme edges of the micrograph. The cytoplasm contains only a few ill defined structures that could represent mitochondria (M). Arrays of filaments that can be identified as tonofilaments (arrows) are scattered throughout the cytoplasm. Numerous desmosomes (D)lie between adjacent cells. The basement membrane (BM) shows enhanced contrast following uranyl acetate staining, as compared with Fig. 8. The cell membrane at the base of the cell is focally differentiated into plate-like densities, resembling half of a desmosome (A). These are dermal attachment plates which consist of a thickened cell membrane and a dense band (toward the basement membrane) which would correspond to the intermediate dense layer of the desmosome. \times 45,600.



B. L. MUNGER AND S. W. BRUSILOW Eccrine Sweat Glands of Cat Foot Pads 411

vacuoles show fusion of their limiting membranes with the cell membrane (Fig. 13). Bits of cytoplasmic and membranous debris are present in the glandular lumen. The Golgi apparatus is more prominent than it is in unstimulated mucoid cells, and prosecretory vacuoles can be easily identified (Fig. 7). Some of the mitochondria are vacuolated (Fig. 7) in a manner similar to that seen in clear cell mitochondria of human eccrine glands following stimulation (13). After stimulation the secretory vacuoles remain decreased in number for 15 to 30 minutes.

The matrix of the mitochondria of clear cells, 5 minutes after stimulation, shows areas of decreased density, similar to that described for the human (Fig. 6). This change is more pronounced 15 minutes after stimulation (Fig. 14). In all cells of the secretory segment, dense masses of material resembling lipid (21) are present after stimulation (Fig. 13). Lipid droplets are only rarely seen in unstimulated cells. Masses of glycogen (Figs. 13 and 14) are clearly demarcated from the general cytoplasm in clear cells 15 and 30 minutes after stimulation, whereas in unstimulated glands the glycogen appears to be dispersed. These glycogen accumulations are conspicuously rimmed by mitochondria. In some areas the mitochondrial limiting membrane cannot be resolved and the substance of the mitochondrion appears to merge with the glycogen mass (Fig. 14), but in these areas the mitochondrial membrane may have been sectioned tangentially. A given cell often contains more than one such glycogen accumulation.

DISCUSSION

On the basis of the above description, the sweat glands of the cat foot and toe pads are found to be eccrine glands directly comparable to human eccrine sweat glands as described previously (13). In the two species, the cytology, staining characteristics, and ultrastructure of the secretory segment are identical, both in the unstimulated and stimulated states.

The structure of the eccrine duct, however, is markedly different in the two species. The eccrine duct of the cat is shorter and smaller than it is in man, and the ductal cells contain far fewer mitochondria and a much thinner "cuticular border." The length of this duct in the cat is estimated to be one-tenth the length of the gland, whereas in the human it is one-third to one-half the length of the gland (9). The prominence of mitochondria in the basal cells of the duct in humans has been emphasized (13), and the paucity of mitochondria in comparable cells in the cat is striking by comparison.

Sweat secreted by the cat foot pad is always

FIGURE 10

FIGURE 11

A desmosome between two basal cells, at higher magnification, in the eccrime duct of kitten toe pad stained with uranyl acetate. At the desmosome the cell membranes are visibly double (a), but the upper membrane is cut tangentially and so appears as one. Between the cell membranes are three dense zones. The vague central dense band (c) is the intercellular contact layer as defined by Odland (14). The other dense bands, on either side of it, are the intermediate dense layers (b). The dense regions on both sides of the desmosome represent tonofilaments cut tangentially (TF). \times 130,000.

FIGURE 12

A desmosome between two basal cells of an eccrine duct stained with uranyl acetate. The desmosome (D) is cut in such a plane that the tonofilaments (TF) are cut in predominantly longitudinal section. Similar masses of tonofilaments are also seen in the cytoplasm of the basal cells in Fig. 9. \times 46,000.

412

THE JOURNAL OF BIOPHYSICAL AND BIOCHEMICAL CYTOLOGY · VOLUME 11, 1961

Luminal part of a surface cell of an eccrine duct stained with uranyl acetate. Microvilli (V) project into the lumen (L). In the cytoplasm of the surface cell between the nucleus (N) and the lumen is a zone of filamentous and granular material that comprises the "cuticular border" (CB). \times 45,600.



B. L. MUNGER AND S. W. BRUSILOW Eccrine Sweat Glands of Cat Foot Pads 413

iso-osmolar (1), whereas human eccrine sweat is hypotonic with respect to sodium and chloride (17). The small size and paucity of cell organelles of the cat eccrine duct is considered to be responsible for the difference in the secretory product, since the secretory segments of the two species are identical in morphology. This conclusion is entirely consistent with the physiologic interpretations of Thaysen and coworkers (19, 23). Schwartz and Thaysen (19) believe that the increasing osmolarity of sweat with increasing rate of secretion is due to the limited capacity of ductal reabsorption. Furthermore, on the basis of their arguments, the initial secretion product is most likely to be isotonic (23), and ductal secretion of water is not consistent with the concentration of urea in the delivered product (23). The human eccrine duct thus reabsorbs sodium and chloride from an isotonic precursor solution.

The "cuticular border" of surface cells of the duct in man must be capable of passive or active transport of ions. The ultrastructure of this border is markedly different from that of other known resorptive cell surfaces, such as those of epithelial cells of the intestine (26) and renal tubules (16). Since the "cuticular border" is birefringent (18), the masses of tonofilaments in this zone must be organized preferentially. Either the organization of these filaments or the nature of the proteins present in this zone (9) may account for the initial transfer of ions from the lumen to the cell interior. The numerous mitochondria in basal cells

of the duct are undoubtedly responsible for the transport of ions from the duct cells to the surrounding vascular supply. The peculiar prominence of mitochondrial granules in this zone is consistent with the untested hypothesis of Weiss (25) that these granules represent cation exchange resins.

Studies on the cat (4) and man (9) have reported that the amount of glycogen present in clear cells decreases following stimulation. In the present study similar changes were noted by light microscopy; however, discrete masses of glycogen are present following stimulation, whereas in unstimulated material only dispersed glycogen is seen. The discrete masses of glycogen may therefore represent areas of confluence of previously dispersed glycogen accentuated by a rim of mitochondria. Siekevitz and Palade (21) have described an intimate association of mitochondria and lipid droplets in pancreatic acinar cells following fasting. This association was interpreted as indicating that the pancreatic acinar cells had converted to fatty acid metabolism. The intimate association of mitochondria with glycogen following stimulation in the eccrine sweat gland might in the present case represent active metabolism of glycogen stores by secreting cells.

Dr. Brusilow is a Research Fellow of The National Foundation, Department of Pediatrics, The Johns Hopkins Hospital.

Received for publication, January 10, 1961.

BIBLIOGRAPHY

1. BRUSILOW, S. W., MUNGER, B. L., SHAVER, B., and COOKE, R. E., Comparative morphology and physiology of human and feline sweat glands, (abstract) Am. J. Dis. Child., in press.

FIGURE 13

Secretory segment of kitten toe pad 15 minutes after stimulation. A mucoid cell with nucleus (Nm) and numerous apical secretory vacuoles (S) is present at the left. Some of the secretory vacuoles appear to be in the process of being liberated from the cytoplasm (arrows), in that only a delicate membrane separates the substance of the vacuole from the lumen (L). A clear cell (Nc) is adjacent to the mucoid cell. The cytoplasm of both clear and mucoid cells contains dense lipid droplets (F), which were not present in the unstimulated cells. Masses of glycogen (GL) are present in the cytoplasm of clear cells, and these masses are rimmed by numerous mitochondria (M). Terminal bars (T) are present at the luminal edges of the adjoining clear and mucoid cells. A myoepithelial cell (Y) is present beneath the secretory cells. Surrounding the myoepithelial cell and clear cell is a basement membrane (BM). Only the mucoid cell borders on the myoepithelial cell. \times 14,000.



B. L. MUNGER AND S. W. BRUSILOW Eccrine Sweat Glands of Cat Foot Pads 415



FIGURE 14

Cytoplasm of clear cell in kitten toe pad 15 minutes after stimulation, stained with uranyl acetate. A mass of glycogen (GL) composed of small discrete units is surrounded by numerous mitochondria (M). A lipid droplet (F) is also present. At the arrows, the matrix of the mitochondria appears to be of less density than the surrounding matrix, a consistent finding in stimulated cells. A part of a myoepithelial cell (Y) is present in the lower part of the micrograph. \times 27,400.

- 2. DALTON, A. J., A chrome-osmium fixative for electron microscopy, *Anat. Rec.*, 1955, 121, 281.
- DAVIS, B. J., ORNSTEIN, L., TALEPOROS, P., and KOULISH, S., Simultaneous preservation of intracellular morphology and enzymatic or antigenic activities in frozen tissues for high resolution histochemistry, J. Histochem. and Cytochem., 1959, 7, 291.
- KAMMAMURA, S., A cytological study of cat sweat glands, Okajima Folia Anat. Japon., 1957, 30, 81.
- LANGLEY, J. N., The secretion of sweat. Part I. Supposed inhibitory nerve fibres on the posterior nerve roots. Secretion after denervation, J. Physiol., 1922, 56, 110.
- 6. LOVELL, J. E., and GETTY, R., The hair follicle,
- 416 The Journal of Biophysical and Biochemical Cytology · Volume 11, 1961

epidermis, dermis, and skin glands of the dog, Am. J. Vet. Research, 1957, 28, 873.

- 7. LUFT, J. H., personal communication.
- MCMANUS, J. F. A., Histological and histochemical uses of periodic acid stain, *Stain Technol.*, 1948, 23, 99.
- 9. MONTAGNA, W., The Structure and Function of Skin, New York, Academic Press, Inc., 1956.
- MONTAGNA, W., CHASE, H. B., and LOBITZ, W. C., Histology and cytochemistry of human skin. IV. The eccrine sweat glands, J. Invest. Dermatol., 1953, 20, 415.
- MOWRY, R. W., Alcian blue technics for the histochemical study of acidic carbohydrates, J. Histochem. and Cytochem., 1956, 4, 407.
- 12. MOWRY, R. W., Improved procedure for the staining of acidic polysaccharides by Müller's colloidal (hydrous) ferric oxide and its combination with the Feulgen and periodic acid-Schiff reactions, *Lab. Invest.*, 1958, 7, 566.
- MUNGER, B. L., The ultrastructure and histophysiology of human eccrine sweat glands, J. Biophysic. and Biochem. Cytol., 1961, 11, 385.
- ODLAND, G. F., The fine structure of the interrelationship of cells in the human epidermis, J. Biophysic. and Biochem. Cytol., 1958, 4, 529.
- PALADE, G. E., and SIEKEVITZ, P., Pancreatic microsomes, J. Biophysic. and Biochem. Cytol., 1956, 2, 671.
- 16. RHODIN, J., Correlation of Ultrastructural Organization and Function in Normal and Experimentally Changed Proximal Convoluted Tubule Cells of the Mouse Kidney, Stockholm, Karolinska Institute, Aktiebolaget Godvil, 1954.
- 17. ROTHMAN, S., Physiology and Biochemistry of the

Skin, Chicago, University of Chicago Press, 1954.

- SCHMIDT, W. J., Doppelbrechung und Feinbau des Saumrohres (der sog. Cuticula) im Ausführgang der Schweissdrüsen des Menschen, Z. Zellforsch., 1959, 49, 711.
- SCHWARTZ, I. L., and THAYSEN, J. H., Excretion of sodium and potassium in human sweat, J. Clin. Invest., 1956, 35, 114.
- SELBY, C. C., An electron microscopic study of the epidermis of mammalian skin in thin sections. I. Dermo-epidermal junction and basal cell layer, J. Biophysic. and Biochem. Cytol., 1955, 1, 429.
- SIEKEVITZ, P., and PALADE, G. E., A cytochemical study on the pancreas of the guinea pig. II. Functional variations in the enzymatic activity of microsomes, J. Biophysic. and Biochem. Cytol., 1958, 4, 309.
- SPERLING, F., and KOPPANYI, T., Histophysiologic studies on sweating, Am. J. Anat., 1949, 84, 335.
- THAYSEN, J. H., Handling of alkali metals by exocrine glands other than the kidney, *in* The Alkali Metals in Biology, (H. H. Ussing, editor), *Handb. Exp. Pharmak.*, 1960, 13, 424.
- WATSON, M. L., Staining of tissue sections for electron microscopy with heavy metals, J. Biophysic. and Biochem. Cytol., 1958, 4, 475.
- WEISS, J. M., Mitochondrial changes induced by potassium and sodium in the duodenal absorptive cell as studied with the electron microscope, J. Exp. Med., 1955, 102, 783.
- ZETTERQVIST, H., The Ultrastructional Organization of the Columnar Absorbing Cells of the Mouse Jejunum, Stockholm, Karolinska Institute, Akticbolaget Godvil, 1956.