ELECTRON MICROSCOPY OF THE DUCT, AND ESPECIALLY THE "CUTICULAR BORDER" OF THE ECCRINE SWEAT GLANDS IN *MACACA MULATTA*

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Previous electron microscopic studies on the coiled duct of the eccrine sweat glands have described the luminal cells as having "a cuticle of fibrous texture" (1) or "osmiophilic bands" (2). These terms were apparently used to describe a structure which we have now resolved to be a highly developed terminal web associated with an elaborate system of desmosomes.

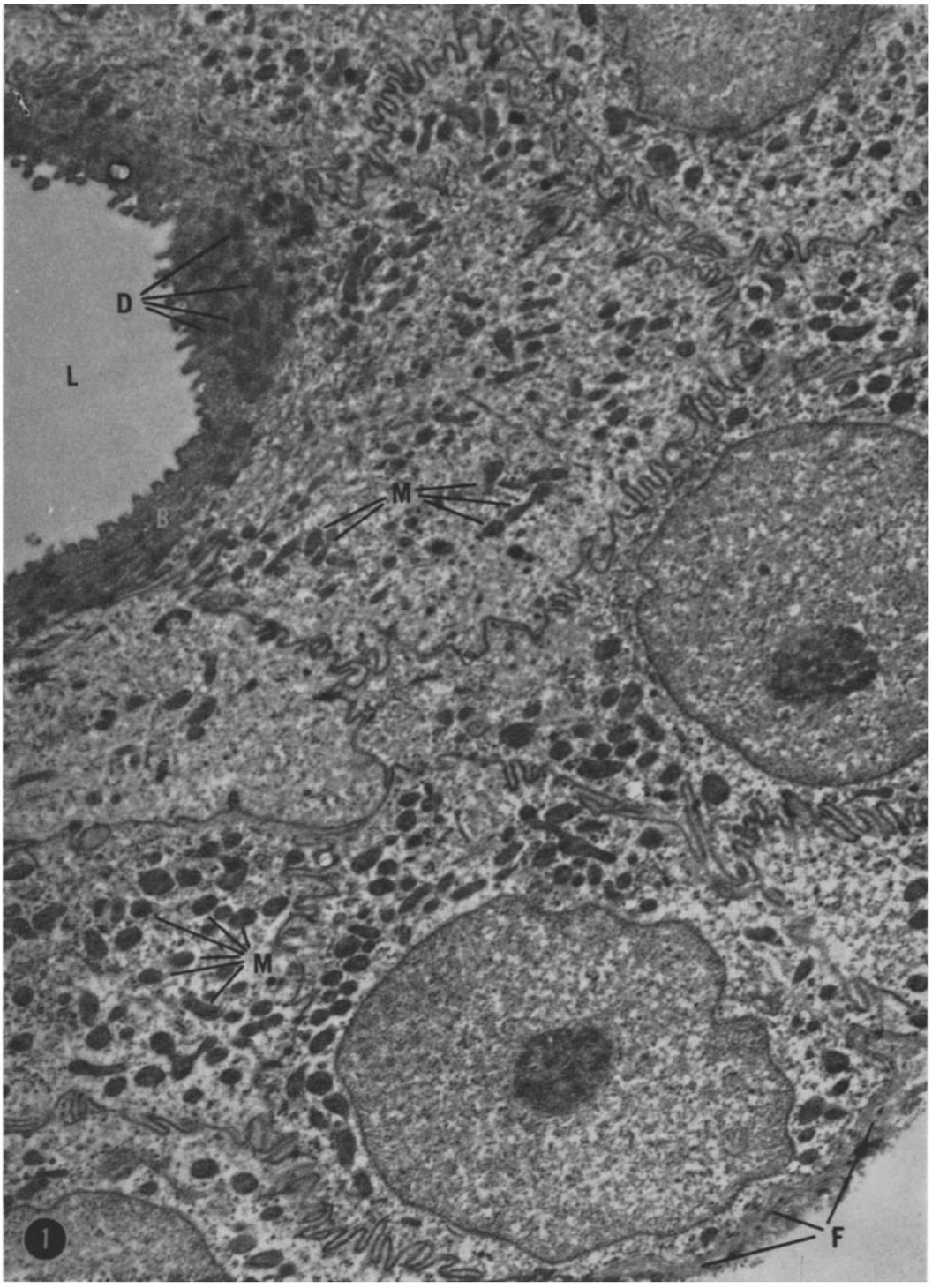
OBSERVATIONS

The coiled duct of the eccrine sweat glands consists of two or three layers of epithelial cells concentrically arranged around the lumen (Fig. 1). The *superficial cells* have a fibrous luminal border; the *peripheral cells*, usually contain moderate amounts of glycogen and rest on a poorly developed basement membrane. Numerous blood vessels and unmyelinated nerves adhere to the coiled duct.

The Luminal Border: The low microvilli on the inner surface of the luminal cells are surrounded by a plasma membrane composed of two adielectronic lines separated by a light band. The outer dense line is ~50 A thick, the thinner one ~20 A; the light band between them is about 25 A wide. A few smooth surfaced vesicles in the cytoplasm beneath the microvilli may result from

FIGURE 1

A low power electron micrograph through the coiled eccrine sweat duct of the rhesus monkey. A small portion of the lumen (*L*) of the gland is visible. Low microvilli surmount the luminal border (*B*), where several large dense desmosomes (*D*) are visible joining the plasma membranes of two adjacent luminal cells. Numerous small mitochondria (*M*), agranular and granular membranes appear in the cytoplasm of the superficial and the peripheral cells. Organized Golgi elements and ergastoplasm have not been observed in the duct cells. The opposed plasma membranes of these cells are elaborately folded. A peripheral cell is shown in the lower left corner opposed to a layer of fine fibrils (*F*). × 9,000.


D
L
M
M
F
1

pinocytotic activity at the surface of the cell. Occasionally, partially closed vesicles are found in the crypts between the short microvilli. The cytoplasm of the microvilli just beneath the plasma membrane is filled with moderately dense tonofilaments. Similar filaments are inserted on the attachment plaques along the lateral borders of adjoining luminal cells.

The tonofilaments are wavy, rarely straight, and measure 35 to 70 A in diameter (Fig. 2). The filaments are loosely organized and give a spongy appearance to the terminal web. Some filaments appear to be continuous with the inner adielectronic line of the plasmalemma. Near the attachment zones, the filaments are oriented parallel to one another (Figs. 2 and 3). In the immediate vicinity of the attachment plaques, they become closely aggregated and form compact, moderately adielectronic zones. Deeper in the cell, just above the level of the nucleus, the tonofilaments are straighter and less numerous. This zone also contains a few small mitochondria, some smooth surfaced vesicles, and strands of agranular reticulum. The more basal cytoplasm of the superficial cells contains randomly scattered mitochondria of various shapes and sizes, some granular and agranular reticulum, and a few granules of glycogen. Organized ergastoplasm and Golgi elements have not been observed.

The nuclei of the luminal cells occasionally have irregular boundaries. They may be somewhat flattened on a plane parallel to the long axis of the duct, and the nuclear envelope may be slightly irregular.

The Attachment Zones: The plasma membranes of adjoining superficial cells are extensively and elaborately interdigitated, and have numerous attachment zones. In between attachment zones the plasma membranes of the luminal cells are separated by a dense line, thus forming quintuple-layered cell interconnections (3). The attachment zones are larger and more numerous near the luminal surface and are usually oriented more or less parallel to it. There are no visible morphological landmarks where the luminal and lateral surfaces of the cell meet. The largest attachment zone observed in a single section was 55 mμ in section (Figs. 2 and 3). The attachment plaques of opposed cells are ∽120 to 140 A wide and they are separated by a gap ∽200 to 220 A wide. Within this gap are distinguished three dense lines which correspond to the intermediate dense layers and the intercellular contact layer described by Odland (5) in epidermal cells. In the cells of the duct these layers appear as moderately dense lines ∽20–30 A wide, separated by electron light bands of about the same width.

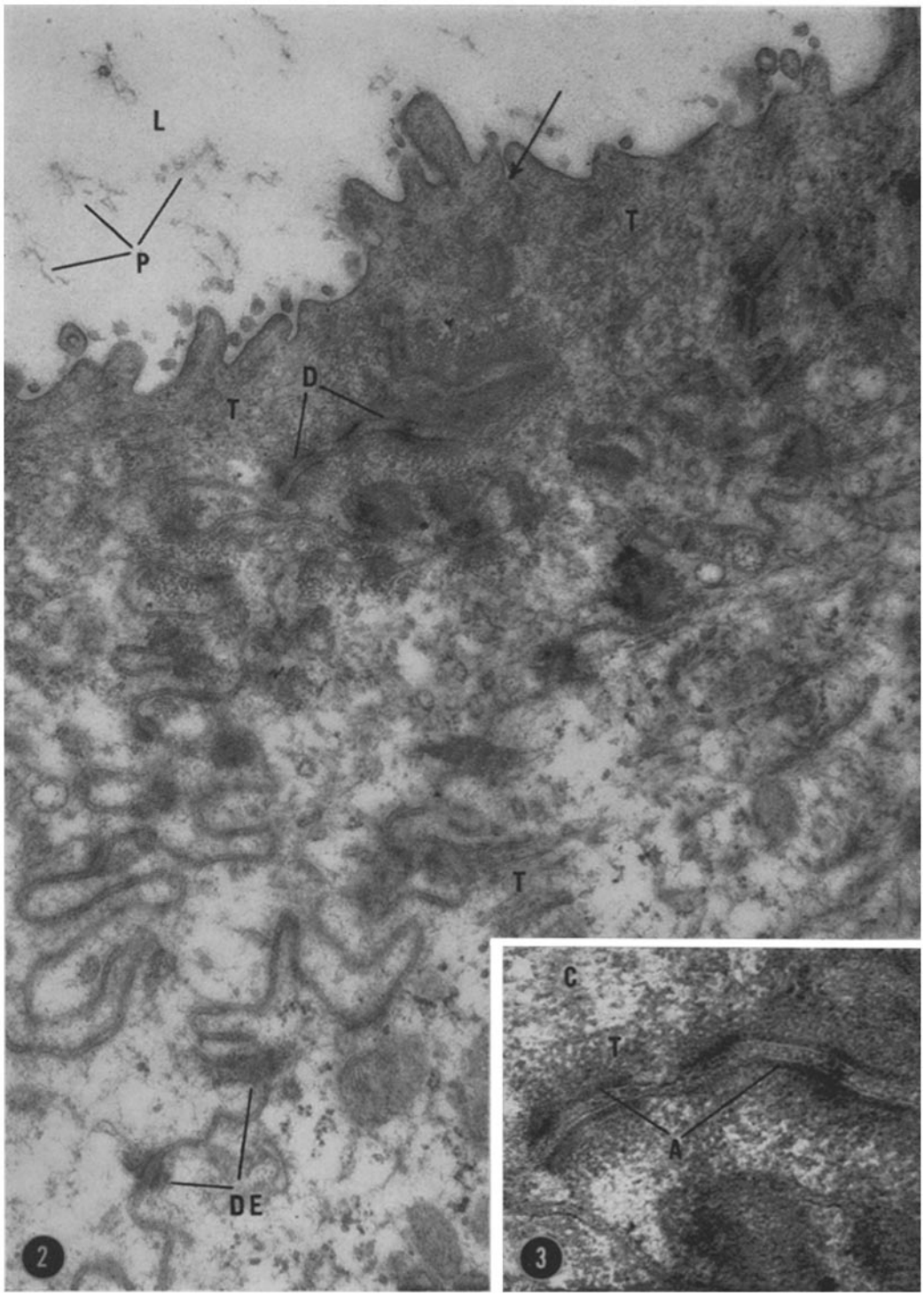
An irregular line of moderate density separates the surrounding tonofibrils from the attachment plaques. The tonofibrils are composed of numerous, oriented, irregular tonofilaments that radiate out from the attachment zone for a distance of at least 45 mμ.

FIGURE 2

The "cuticular border" of a luminal duct cell. The lumen of the duct (*L*) contains many filamentous or possibly membranous structures (*P*) evidently associated with the secretory product. The short microvilli are surrounded by a plasmalemma consisting of two adielectronic lines separated by a light layer. At the luminal interface the junction between two duct cells (arrow) show no special structure. Close to the luminal border, however, the membranes of adjacent cells are connected by large desmosomes (*D*). Fine tonofilaments (*T*) fill the apical cytoplasm of the luminal cells, but are more sparse basally. Both longitudinal and transverse sections of the tonofilaments are apparent. Dense aggregates of tonofilaments insert on the attachment plaques of the desmosomes. Toward the base of the cell the desmosomes (*DE*) are smaller. Quintuple-layer interconnections are also apparent between the cells. × 56,000.

FIGURE 3

The large desmosomes in Fig. 2 are shown at higher magnification. These are identical in their fine structure with the desmosomes observed in human cervical epithelium (3). Oriented tonofilaments (*T*) are aggregated at the attachment plaques (*A*) while loosely organized tonofilaments form a sponge-like mesh in the apical cytoplasm (*C*). × 107,000.


L
P
T
D
T
T
DE
2
C
T
A
3

The Peripheral Cells: The outer cells of the duct have a plasma membrane ~50 A thick, and they are separated one from another by an intermembranous space about 120 A wide. This space, however, is variable and ranges from ~100 to ~170 A, even when sectioned in the same plane. The boundaries between adjacent cells are highly convoluted. The cytoplasm near the plasma membranes has a fibrous appearance and is considerably denser than that nearer the center of the cell. Small desmosomes, not nearly as numerous as those of the luminal cells, appear along the plasma membranes. The cytoplasm of the cells consists of membranous and granular components embedded in a predominantly amorphous matrix. Organized ergastoplasm and Golgi complex have not been observed. Glycogen granules observed in electron micrographs were verified by P.A.S. staining of adjacent thick sections. Numerous ubiquitous mitochondria in the shape of round granules or short rods have no particular orientation in the cytoplasm.

The nuclei of the basal cells frequently have deep invaginations and the cytoplasm in these infoldings usually contains mitochondria and ribonucleoprotein granules. Aside from this the nuclear envelope and the nucleoplasm show no peculiarity. Compared with the nuclei of the luminal cells, the nuclei of the basal cells have prominent nucleoli.

The basal borders of the peripheral cells are usually smooth, with an occasional in-pocketing. In marked contrast, the other borders of these cells have intricate convolutions (Fig. 1). The basement membrane is indistinct around the coiled duct; a thin, light line occasionally separates the plasma membrane from the underlying collagen.

DISCUSSION

With the light microscope the so called "cuticular border" of the superficial duct cells gives a moderate reaction for —SH groups and an intense reaction for S—S groups (4); it is birefringent under polarized light (7) and stains lightly with acid dyes (4). The electron microscope reveals that the "cuticular border" actually consists of a dense terminal web, composed of myriad intracellular tonofilaments, and an elaborate system of desmosomes. Published electron micrographs suggest that the luminal border of the coiled eccrine sweat duct of man (1, 2) is similar to that of the macaque. The morphology of both the tonofilaments and the attachment zones is identical to that described by Karrer (3) in human cervical epithelium.

These studies do not indicate the functional significance of the luminal border. The presence of microvilli and occasional smooth surfaced vesicles shows that some pinocytotic activity may occur here. Since neither a Golgi complex nor an organized ergastoplasm were observed, these are not primarily secretory cells. The most likely function of the tonofilaments is in the formation of a rigid ring to prevent the collapse and the occlusion of the lumen of the duct. The extended attachment plaques probably serve as buttressing and insertion points that strengthen the border architecturally. This thesis is supported by the fact that the cross-section of the lumen of the coiled duct is always circular, whereas that of the secretory coil, which has no cuticular border, is extremely variable in shape. A concept of architectural support does not necessarily negate a physiological function (6).

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