Electron Microscopic Observations on Avian Esophageal Epithelium*

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Summary. The stratified squamous epithelium of the chicken and pigeon esophageal mucosa was studied mainly with the electron microscope.

1. The basal and spinous cells contained well-developed Golgi complexes, many mitochondria and multivesicular bodies. In the chicken basal cell a centriole and a single cilium were found. Both cells were rich in free ribosomes; the cisternae of the granular endoplasmic reticulum were sparse though tending to increase towards the spinous cells. The tonofilament bundles conspicuously increased towards the spinous cells.

2. In the chicken spinous cells some dilated cisternae of the granular endoplasmic reticulum contained a filament bundle. The “intracisternal filament bundles” were more frequent in the stratum granulosum, but became indistinguishable in the stratum corneum where the membranes of the cisternae disappeared.

3. In the desmosomes which were most frequent in the stratum spinosum followed by the granulosum, the “intercellular contact layer” (ODLAND) was indistinct in chickens but distinct in pigeons; tight junctions were frequent. A quintuple-layered structure in the tight junctions and a “fusion line” showing a periodical fibrillar substructure were demonstrated.

4. The flattened granulosum cells were filled with tonofilaments. Some mitochondria were degenerated but the Golgi complex was often well-preserved.

5. A few keratohyalin granules in the nucleus and cytoplasm occurred in the chicken granulosum cells. They were round, dense bodies with a fingerprint-like and/or a granular structure. The intranuclear granules seemed to be discharged into the cytoplasm.

6. Membrane-coating granules (MCG) were round, electron lucent bodies limited by a smooth membrane and seemed to be formed in the Golgi complex. They were rare in the stratum basale but numerous in the spinosum. In the stratum granulosum they reached their maximal number and were gathered beneath the upper plasma membrane to be released by emiocytosis.

7. The stratum corneum cells retained altered nuclei and cell organelles but none of the Golgi complexes, MCG and intracisternal filament bundles. Typical “keratin pattern” was not seen.

The stratified squamous epithelium is the most wide-spread epithelial type in higher vertebrates, covering the skin as the epidermis and the mucous membranes of several organs such as the oral cavity, a part of the pharynx, esophagus, vagina, portio vaginalis of the cervix uteri, etc. Recently, the stratified squamous epithelium has become an interesting research subject in electron microscopy. Especially the epidermis of the human and vertebrate skin has most frequently been studied to learn about the fundamental features of the ultrastructure in the stratified

*This study was directed by Prof. emer. Toshio Ito, former director of this department.
squamous epithelium and several morphological aspects of the keratinization mechanism.

On the other hand, it is also an important morphological problem to observe comparatively the stratified squamous epithelia lining the mucous membranes of different regions and organs, but electron microscopic studies on this subject have been less numerous than those on epidermis. The ultrastructures of the epithelia of the oral mucosa including the gingiva have been observed by Sognnaes and Albright (1956), Fasske and Themann (1959), Albright and Listgarten (1962), Gibbins (1962), Zelickson and Hartmann (1962), Farbman (1964), Frithiof and Wersäll (1965), Gavin (1968) and others. The human cervical epithelium has been studied by Karrer (1960) and Singleton et al. (1968), the epithelium of an anterior part of the mouse stomach by Pipan (1968) and the epithelium of cornified patches of the urinary bladder of vitamin A-deficient rats by Hicks (1968). Some authors have observed the ultrastructures of the esophageal epithelium (Ohmke, 1964; Ohmke and Petry, 1964; Oláh and Rhölich, 1966; Parakkal, 1967 etc.), but electron microscopic study on the avian esophageal epithelium has been carried out only by Hinsch (1967), who described the differentiation of the esophageal epithelium and mucous glands in the chick embryo. The present study in the chicken and pigeon is, as far as the author knows, the first electron microscopic study dealing with the fine structure of the adult avian esophageal epithelium.

**Materials and Methods**

Small blocks of esophageal mucosa including the epithelial lining were excised from adult pigeons and domestic fowls and cut into small pieces to be immersed for about 1–2 hours in an ice-cold, modified Caulfield's solution containing 0.5% glutaraldehyde, and in a 2.5% solution of glutaraldehyde buffered at pH 7.4 with 0.1 M phosphate buffer containing 4.5% sucrose. In the latter case, after this initial fixation the pieces were washed in the same buffer containing 5% sucrose and postfixed in an ice-cold, 1% solution of phosphate-buffered osmium tetroxide containing 4.5% sucrose. Following rapid dehydration in a graded series of cold ethanol and treatment with propylene oxide, the tissue pieces were embedded in Epon 812. Ultrathin sections were cut with glass knives on a Porter-Blum ultramicrotome and mounted on copper grids without supporting film. The sections were stained with uranyl acetate followed by lead acetate, and examined with electron microscopes of JEM-5G, JEM-7 and JEM-7A type.

**Observations**

In light microscopic observation the stratified squamous epithelia of the chicken and pigeon esophagus are not conspicuously different. They are composed of piles of numerous epithelial cells which are reduced gradually in thickness toward the luminal surface of the epithelium. The basal layer is represented by a row of relatively high epithelial cells whereas the uppermost layer by strongly flattened cells. Between these layers there exist layers of polygonal and spindle-shaped epithelial cells. The intercellular spaces and bridges are not conspicuous in light microscopy. The flattened cells of the superficial layers scarcely show exact histological signs of cornification. By light microscopy keratohyalin granules have been
Fig. 1. A basal cell in chicken esophageal epithelium. A relatively large nucleus (N) contains two conspicuous nucleoli (NL). On the basal plasma membrane facing a basement membrane (BM) half-desmosomes (HD) are seen. Numerous slender microvilli protrude from this and adjacent cells into a wide intercellular space (IS). Desmosomes (D) are not numerous. The cytoplasm contains mitochondria (M) some of which contain intramitochondrial granules, scanty rough endoplasmic reticulum (ER), Golgi complexes (G), a centriole (C) and bundles of tonofilaments (TF). The cytoplasmic matrix is filled with free ribosomes aggregated into polysomes. In the neighborhood of the centriole a cross-section of a single cilium (CL) is seen surrounded by a light space. Along the plasma membrane lining the intercellular space many pinocytotic vesicles are seen, some of which are bristle-coated. CN connective tissue, VP virus particles. × 15,200
demonstrated in the epithelial layer subjacent to the superficial layer in neither the chicken nor pigeon esophageal epithelium. In spite of these histological findings the electron microscopic observation on the chicken and pigeon esophageal epithelium has been carried out by dividing it, merely for convenience's sake in accordance with the case of the epidermis, into four layers, namely the stratum basale, stratum spinosum, stratum granulosum and stratum corneum.

**Stratum basale**

The basal cells are cuboidal to cylindrical in shape and contain a relatively large nucleus with conspicuous nucleoli in which granular and fibrillar parts are discernible (Fig 1). The cytoplasmic layer around the nucleus protrudes numerous irregular-shaped, slender microvilli into the wide intercellular space where they are intermingled with those projected from adjacent basal cells and spinous cells bordering the basal layer (Fig. 1–3). There occur desmosomes between apposed cell membranes of two bulky cytoplasmic processes projected face to face into the intercellular space (Fig. 1, 3), but they are not numerous in the basal layer. Along the basal plasma membrane of the basal cells facing the connective tissue of lamina propria mucosae a basement membrane is observed. Several thickened areas of high electron density found along the basal plasma membrane are half-desmosomes (Fig. 1, 3). Many pinocytotic invaginations and vesicles are found on and along the plasma membranes lining the surfaces facing the connective tissue and the intercellular spaces; bristle-coated vesicles are frequently mixed (Fig. 1–3).

![Fig. 2. A portion of a basal cell of chicken esophageal epithelium. Multivesicular bodies (MB) are numerous near the Golgi complex (G) in the close proximity of the nucleus (N). Around the multivesicular bodies smooth vesicles are accumulated, some of which adhere to a limiting membrane of the bodies. Along the cell surface facing the intercellular space (IS) numerous pinocytotic vesicles are seen, some of which are bristle-coated. D desmosome, M mitochondria, MV microvilli, TF bundles of tonofilaments. ×29,800](image-url)
The cytoplasm of the basal cells is characterized by abundant free ribosomes. They are mostly aggregated into rosette-like clusters (polysomes) which are closely packed and almost evenly distributed throughout the entire cytoplasm (Fig. 1–3). The tendency of the polysome formation may be more prominent in the fowl than in the pigeon. On the other hand, the cisternae of the granular endoplasmic reticulum are only sparsely scattered in random places (Fig. 1–3). Golgi complexes are found close to the nucleus and consist of stacks of flattened parallel cisternae, numerous vesicles and vacuoles probably produced by dilations of the flattened cisternae (Fig. 1, 2). Round, oval and elongated profiles of mitochondria found around the nucleus contain sometimes electron dense intramitochondrial granules and are frequently associated with flattened cisternae of the granular endoplasmic reticulum elongated along their surface. In a basal cell illustrated in Figure 1 a centriole is demonstrated.

![Fig. 3. A basal portion of a basal cell in pigeon esophageal epithelium. Around the nucleus (N) there are seen mitochondria (M), scanty rough endoplasmic reticulum (ER), bundles of tonofilaments (TF) and a large amount of free ribosomes which show no pronounced tendency to be grouped in polysomes. Along basal plasma membrane facing the basement membrane (BM) half-desmosomes (HD), pinocytotic vesicles and invagination are seen. In a cytoplasmic area near the intercellular space (IS) some smooth membrane-bounded bodies are seen which probably correspond to membrane-coating granules (MCG). CN connective tissue, MV microvilli. ×36,000](image-url)
on one side of the nucleus and in its neighborhood a cross-section of a probable single cilium appears surrounded by a light halo. Within the electron lucent matrix of the cilium several round profiles of filaments or microtubules are detectable. The topographical relationship between the centriole and Golgi complexes is unknown.

Multivesicular bodies occur in the basal cells, occasionally concentrated near the Golgi complex. Figure 2 shows, in the close proximity of multivesicular bodies, accumulated vesicles of variable sizes, some of which adhere to the limiting membrane of the multivesicular bodies. No dense bodies (probable lysosomes) are observed in the basal cells. Sometimes in the pigeon and rarely in the chicken, the basal cells of the esophageal epithelium contain a few so-called membrane-coating granules (MCG), which are round or oval in shape and consist of a distinct smooth limiting membrane and a homogeneous or flocculent matrix of low electron density (Fig. 3).

The basal cells generally contain a small amount of tonofilaments 75 to 80 Å thick. The great majority of the tonofilaments form compact bundles of variable thickness running in different directions (Fig. 1–3). In the bundles, individual filaments are distinguishable, which are closely packed in parallel (Fig. 2, 3). The bundles of tonofilaments, namely tonofibrils, exist usually in the cytoplasm without being bounded by the limiting membrane, and numerous clusters of free ribosomes occur closely around them (Fig. 2, 3). Some tonofibrils run toward and terminate on the desmosomes (Fig. 1). The same relationship is also seen between the tonofibrils and the half-desmosomes along the basal plasma membrane (Fig. 1).

Occasionally minute spherical particles have been sporadically found in the connective tissue just beneath the basal cells and in the intercellular space of the esophageal epithelium of normal adult chickens (Fig. 1). These particles measuring about 1,000–1,300 Å in diameter are composed of a smooth limiting membrane and a very dense spherical core about 300 Å in diameter, and an electron lucent halo between both components is divided into an outer and an inner space by a dense line or membrane around the core. The nature of these minute particles is unknown, but they most likely correspond to virus particles.

**Stratum spinosum**

Morphological differences between the cells of different layers are gradual and the spinous cells lying immediately above the basal layer resemble the basal cells in ultrastructure. The spinous cells, whose typical forms are found in more upper layers of the stratum spinosum, are generally polygonal in shape and contain a round or oval nucleus profiled by a somewhat indentd nuclear envelope roughly in the center of the cytoplasm (Fig. 4). The intercellular spaces are narrower than those between the basal cells. Between apposed plasma membranes of bulky cytoplasmic processes projected from neighboring spinous cells into the intercellular space there appear desmosomes which are characterized by a convergence of tonofilaments (Fig. 4). In the intercellular space between the bulky cytoplasmic processes connected by desmosomes, numerous slender microvillous cytoplasmic processes protrude from bordering spinous cells (Fig. 4). Tight junctions found between the microvilli and/or the bulky processes are much less numerous than desmosomes (Fig. 4, 6). In the cytoplasm of spinous cells the tonofilaments remarkably increase
in amount as compared with basal cells. Upwards in the spinous cell layer, the bundles of tonofilaments tend to increase gradually and occupy often a greater part of the cytoplasm (Fig. 4). In the bundles of tonofilaments the individual filaments, 75-80 Å in thickness, are apparently distinguished from each other, though they are closely packed in parallel (Fig. 5). The tonofibrils ramify frequently in simple fashion. Thus, the cytoplasm is divided into irregular compartments and a round area surrounding the nucleus (Fig. 4).

In these compartments the cytoplasmic organelles of spinous cells are mainly distributed. Numerous free ribosomes tending to aggregate into rosette-like clusters are distributed in all cytoplasmic areas. In the spinous cells the development of the granular endoplasmic reticulum is more marked than in the basal cells. The ribosome-studded cisternae have increased in number, being distributed in random

Fig. 4. A polygonal spinous cell in pigeon esophageal epithelium. Around the nucleus (N) numerous mitochondria (M), a large amount of free ribosomes, elongated cisternae of the rough endoplasmic reticulum (ER) and a Golgi complex (G) are seen. Tonofilament bundles (TF) fill up a great part of the cytoplasm. Besides numerous desmosomes (D) formed between the microvilli (MV) protruded from this and the adjacent cells, a few tight junctions (TJ) participate in the spinous cell connection. ×13,200
locations (Fig. 4), and some of them show intensive dilations. The spinous cells contain relatively numerous mitochondria scattered in cytoplasmic areas between bundles of tonofilaments, and as shown in Figure 4 they are sometimes accumulated around the nucleus. Intimate topographical relationship between mitochondria and ribosome-studded cisternae is frequently observed. The intramitochondrial granules are rare. Golgi complexes of the spinous cells are similar in ultrastructure to those of the basal cells (Fig. 4, 6) and are found near the nucleus. Multivesicular bodies are extremely rare (Fig. 6). Dense bodies are found neither in chicken nor in pigeon spinous cells.

It is a noteworthy finding obtained in the present study that in the spinous cells

![Figure 5](image_url)

**Fig 5.** A portion of a spinous cell of chicken esophageal epithelium. Abundant free ribosomes aggregated into rosette-like clusters (R) and numerous tonofilament bundles (TF) are seen. In the right bottom a dilated cisterna of the rough endoplasmic reticulum (ER) contains a tonofilament bundle ("intracisternal filament bundle," arrow) and a flocculent fibrillar material. An outer membrane of the nuclear envelope bulges in several portions into the cytoplasm. Two tangentially sectioned nuclear pores (NP) are seen. MCG membrane-coating granules, N nucleus. ×35,800
of the chicken esophageal epithelium there appear “intracisternal filament bundles” (Fig. 5). The filaments, 75-80 Å thick, occur in dilated cisternae of the granular endoplasmic reticulum, forming bundles of variable thickness. The cisternae may contain, besides a filament bundle, a flocculent or fibrillar material. The intracisternal filaments may agree in thickness and in ultrastructural appearances with tonofilaments present in the cytoplasmic matrix.

The membrane-coating granules (MCG), which occurred rarely in the basal cells, increase in number in the spinous cells and are distributed randomly in cytoplasmic areas. In the relatively flattened spinous cells near the stratum granulosum numerous MCG occur, often distributed widely in the cytoplasm but occasionally

![Fig. 6. Flattened spinous cells in the upper stratum spinosum of pigeon esophageal epithelium. The cytoplasm is rich in tonofilament bundles and free ribosomes, and between them mitochondria (M), cisternae of the rough endoplasmic reticulum (ER), a Golgi complex (G) and a multivesicular body (MB) are seen. Numerous microvillous processes (MV) in the narrow intercellular space are connected by a few tight junctions (TJ) and many desmosomes (D) where the tonofilaments terminated. Membrane-coating granules (MCG) show a tendency to concentrate in the peripheral cytoplasmic layer just beneath the plasma membranes lining the distal surfaces of epithelial cells. N nucleus ×20,900](image-url)
tending to be concentrated in the upper periphery of the cells (Fig. 6). They are round or oval bodies 900-2,200 Å in diameter and are bounded by a distinct smooth limiting membrane (Fig. 6). The matrix of the membrane-bounded MCG is of low electron density and appears almost homogeneous or flocculent, but the electron density of the matrix is generally much lower in the pigeon than in the fowl and it

Fig. 7. Several tight junctions (TJ) and desmosomes (D) between the spinous cells located at the transitional region between the stratum spinosum and granulosum in chicken esophageal epithelium. Longitudinal and cross sections of microvillous processes (MV) are seen in the narrow intercellular space (IS). In the plasma membrane a trilaminar structure is apparent and the outer leaflets of juxtaposed plasma membranes fuse with each other to make a single fusion line in the tight junctions. In the part of a tight junction indicated by an arrow a periodic fibrillar structure in place of a fusion line is recognized. In the desmosomes an intercellular contact layer is indistinct. ER dilated cisternae of rough endoplasmic reticulum, R free ribosomes, TF tonofilament bundles. × 47,600
appears frequently vacuolar, as if empty (Fig. 6, 9, 14, 15). The distinct characteristic lamellar structure of the matrix as described by the authors in the MCG of several mammals including man has not been recognized in the chicken and pigeon. The MCG may be formed in the Golgi complex from the dilated portions of the Golgi cisternae or vacuoles as suggested in Figures 6 (pigeon) and 13 (chicken).

The tight junctions, which have been rarely found between spinous cells as described above, increase in number in the flattened cells near the stratum granulosum. Between such epithelial cells as illustrated in Figures 7 and 8 a number of tight junctions are found together with desmosomes; sometimes both types of the cell junction occur continuously as seen in Figure 8. In Figure 7 many tight junctions are formed between closely apposed plasma membranes of the juxtaposed microvilli which are cut transversely in this figure. As shown in these figures, especially in Figure 8, a quintuple-layered structure of the tight junctions is evident; the thinner and less-dense outer leaflets of closely apposed plasma membranes fuse with each other to make a "fusion line" where the intercellular space is completely closed. On detailed observations, the fusion line appears as if dotted, and a tangential section of the fusion line shows a periodical, finely fibrillar structure which

Fig. 8. A tight junction (TJ) and a desmosome (D) are seen continuously between the spinous cells located at the transitional region between the stratum spinosum and granulosum of chicken esophageal epithelium. A unit membrane is distinct. In the desmosome the apposed plasma membranes retain a trilaminal unit membrane structure, and attachment plaques are separated from inner leaflets by a narrow electron lucent layer. An intercellular contact layer is indistinct. In the tight junction a fusion line is apparent which shows partially a periodic fibrillar structure (arrow). ER cisternae of the rough endoplasmic reticulum. ×74,000
consists of fine parallel filaments of about 40 Å in thickness repeated at intervals of approximately 70 Å (Fig. 7, 8).

As seen in Figures 7 and 8, in desmosomes of the chicken esophageal epithelium the “intercellular contact layer” (ODLAND), a dense midline found in the intercellular substance filling up the widened intercellular space at the level of desmosomes, is not very evident, but in desmosomes found in the pigeon esophageal epithelium its existence has surely been confirmed (Fig. 4, 9). The apposed plasma membranes in desmosomes retain a trilaminar structure (Fig. 8), and the so-called attachment

![Fig. 9. Strongly flattened epithelial cells of the stratum granulosum in pigeon esophageal epithelium. Intercellular spaces have become narrower and microvilli projected into them represent intercellular interdigitation. A considerable number of desmosomes (D) and a few tight junctions (TJ) connect the neighboring cells. The cytoplasm is densely packed with tonofilament bundles running in random directions. Membrane-coating granules (MCG) containing electron transparent content show a tendency to be concentrated along the plasma membrane lining the upper cell surface, and some of them show pictures suggesting the emiocytotic discharge of their content into the intercellular space (arrow). Free ribosomes and mitochondria (M) have decreased by far in number against those in the spinous cells. In the upper part of this figure a dense oval body similar to a keratohyalin granule (KG) is seen. N nucleus. ×25,200](image)
plaque is nothing but a dense cytoplasmic area contiguous to an inner leaflet of the plasma membrane from which it is separated by an extremely narrow, electron lucent layer. In the attachment plaque tonofilaments terminate in irregular fashion (Fig. 8).

**Stratum granulosum**

The boundary between the stratum spinosum and the stratum granulosum is not distinct. The epithelial cells of the stratum granulosum in the pigeon (Fig. 9, 14, 15) and chicken (Fig. 10-13) become more strongly flattened. The nucleus (Fig. 9, 10, 13) is also more or less flattened and contains a nucleolus. The intercellular spaces become narrower and microvilli projecting into the intercellular spaces form

![Fig. 10. Nucleated portion of an elongated flattened epithelial cell of the stratum granulosum in chicken esophageal epithelium. In the oval nucleus (N) a dense body (KG) with a fingerprint-like structure is present which is devoid of a limiting membrane and suggests the keratohyalin granule in the nucleoplasm. Near the nucleus are several dilated cisternae of rough endoplasmic reticulum (ER) some of which contain a tonofilament bundle (TF), intracisternal filament bundle. The cytoplasm is packed with tonofilament bundles running in random directions, among which free ribosomes are scattered. M mitochondria, MCG membrane-coating granules, NP nuclear pore. ×20,900](image-url)
the configuration of intercellular interdigitations which are much more prominent in the pigeon (Fig. 9, 14, 15) than in the chicken (Fig. 10, 12, 13). In the pigeon a considerable number of desmosomes and a few tight junctions are observed in this layer (Fig. 9, 14, 15).

The cytoplasm is occupied for the most part by abundant, densely packed tonofilaments running in random directions and showing less pronounced signs of the bundle formation. Free ribosomes are scattered and sometimes tend to aggregate into more or less well-defined clusters. Cisternae of the granular endoplasmic reticulum are identified in small numbers. Mitochondria have been reduced in number and especially in chickens they are frequently involved in changes of degeneration (Fig. 10, 11).

Membrane-coating granules are most numerous in the flattened epithelial cells

Fig. 11. A part of an epithelial cell of the stratum granulosum in chicken esophageal epithelium. A spherical electron dense body (KG) is shown which is devoid of a limiting membrane and shows mainly a granular, but partially lamellar structure. This intracytoplasmic keratohyalin granule is surrounded by ribosome-like particles (R). Besides the keratohyalin granule, there are seen some degenerating mitochondria (DM), lipid droplets (LP) and an intracisternal filament bundle (TF) where a ribosome-studded limiting membrane of cisterna has become faint and discontinuous. ×30,200
of the stratum granulosum, and they are much more numerous in the pigeon (Fig. 9, 14) and occasionally make a large accumulation (Fig. 15). The tendency of the membrane-coating granules to be gathered in a row along the plasma membrane of the upper surface of the cells is often confirmed also in the stratum granulosum both in the chicken and pigeon (Fig. 9, 14). In the stratum granulosum some of the MCG which closely approach the cell surface often come in contact with the plasma membrane (Fig. 9, 14). This may suggest the release of the content of the MCG into the intercellular spaces by means of emiocytotic or reversed pinocytotic process which may take place at a contact site of a limiting membrane. The minute invaginations frequently observed on the plasma membrane bordering dilated portions of the intercellular space may be induced by such a process of MCG release (Fig. 9). In the chicken stratum granulosum an electron opaque homogeneous material occurs in the intercellular space (Fig. 10, 13), suggesting a possible release of the contents of the MCG into the space. The Golgi complex occasionally remains almost unaltered near the nucleus (Fig. 13), and it consists of elongated flattened cisternae, vacuoles which are represented by dilated portions of the cisternae and vesicles. The Golgi complex shown in Figure 13 contains a few small membrane-coating granules suggesting their origin in Golgi vacuoles.

Fig. 12. A portion of an epithelial cell of the stratum granulosum in chicken esophageal epithelium. Among abundant tonofilament bundles closely packing the cytoplasm there appear an accumulation of mitochondria (M) and two intracisternal filament bundles (TF) where the ribosome-studded limiting membrane closely applied to the tonofilament bundles has become faint and discontinuous suggesting the beginning of its disappearance. ER cisterna of rough endoplasmic reticulum. IS intercellular space. R free ribosomes. ×31,000
As mentioned above, in both chickens and pigeons keratohyalin granules have seldom been identified by light microscopy in the layer corresponding to the stratum granulosum. By electron microscopy electron dense spherical bodies which presumably are referred to as keratohyalin granules have been very often detected in the nucleus and cytoplasm of the chicken cells. In the pigeon only one oval dense body resembling a keratohyalin granule has been encountered together with many MCG in a flattened epithelial cell of the stratum granulosum (Fig. 9), but it has not been exactly identified as the keratohyalin granule. The dense spherical bodies in the chicken stratum granulosum cell show peculiar ultrastructures. They are devoid of a limiting membrane both in the karyoplasm and in the cytoplasm, and exhibit

Fig. 13. Nucleated portion of an elongated flattened epithelial cell of the stratum granulosum in chicken esophageal epithelium. Near the nucleus (N) a Golgi complex composed of lamellae, vacuoles and vesicles is observed. In the Golgi area some membrane-coating granules (arrows) are present suggesting their origin from Golgi vacuoles. Besides the Golgi complex, abundant tonofilament bundles, clusters of ribosomes (R) and cisternae of the rough endoplasmic reticulum (ER) are seen. In the peripheral cytoplasm a few membrane-coating granules (MCG) are noticed. Narrow intercellular spaces (IS) contain a moderately electron dense homogeneous material resembling the contents of membrane-coating granules. ×20,900
either fingerprint-like or finely granular ultrastructures (Fig. 10, 11). Finely granular dense bodies composed of closely packed granules 100-160 Å in diameter have been more numerously found than the fingerprint-like dense bodies. A few dense bodies have shown both structures, the fingerprint-like pattern in their periphery and the finely granular one in their central part. As shown in Figure 11 the intracytoplasmic dense bodies are enveloped by an accumulation of ribosome-like particles. However, a small number of dense bodies, specially fingerprint-like ones are devoid of particle investment. A fingerprint-like dense body rarely is found in close proximity to the nucleus, being wrapped by membranes resembling the nuclear envelope.

In the chicken esophageal epithelium the intracisternal filament bundles, which

**Fig. 14.** Portions of strongly flattened epithelial cells of the stratum granulosum in pigeon esophageal epithelium. Intercellular spaces are narrow and microvilli protruding there exhibit an intercellular interdigititation. A considerable number of desmosomes are found. The cytoplasm filled with tonofilament bundles contains a few cisternae of the rough endoplasmic reticulum (ER), free ribosomes (R), a Golgi complex (G), a few mitochondria (M) and a large number of membrane-coating granules (MCG) which are roughly concentrated on the upper side of the cells. A picture suggesting the emiocytosis of their content into the intercellular space is indicated by an arrow. ×35,500
have been detected for the first time in the stratum spinosum cells, increase in number in the stratum granulosum (Fig. 10). They are frequently encountered in random portions of the cytoplasm. However, in the epithelial cells of the upper layer of the stratum granulosum which are extensively filled with abundant tonofilaments, cisternae of the granular endoplasmic reticulum wrapping filament bundles have become faint and often discontinuous (Fig. 10, 12), and the tonofilaments come in contact with the filament bundles contained in the cisternae. These findings may indicate the gradual disappearance of the limiting membrane of the cisternae and the simultaneous appearance of naked filament bundles in the cytoplasm.

**Stratum corneum**

The strongly flattened epithelial cells of the stratum corneum in the chicken and pigeon esophagus are packed with compact bundles of abundant tonofilaments,

![Image](image_url)

**Fig. 15.** A large accumulation of membrane-coating granules (MCG) in the epithelial cells of the stratum granulosum in pigeon esophageal epithelium. Their content limited by a smooth membrane is characteristically electron lucent. Between adjacent epithelial cells there exist complex intercellular interdigitations and several desmosomes (D). In the upper left corner, a picture suggesting the emiocytec release of a membrane-coating granule into the intercellular space is noted (arrow). M mitochondria. ×35,600
the boundaries of which are not always distinct. Thus, the cells of this layer appear more electron dense than those of the stratum granulosum (Fig. 16). No intracisternal filament bundles remain in the cytoplasm. Intercellular spaces are generally wide. The epithelial cells protrude, as in other layers, numerous slender microvilli into the spaces, where, however, the configuration of intercellular interdigitations is not exhibited (Fig. 16). Desmosomes and tight junctions have decreased in number and the majority of them do not assume an original configuration.

**Fig. 16.** Stratum corneum and uppermost stratum granulosum in pigeon esophageal epithelium. In the lower part of the figure flattened epithelial cells of the uppermost stratum granulosum are seen packed with tonofilament bundles and containing dotted, aggregated free ribosomes (R). They send out slender microvilli into the intercellular spaces (IS) where the cell processes interdigitated in some places. Tight junctions are indicated by arrows. In an elongated nucleus (N) seen at the right bottom a double membrane structure of the nuclear envelope is not apparent. Flattened epithelial cells of the stratum corneum are closely packed by abundant tonofilament bundles and appear electron denser than those of the stratum granulosum. Among the tonofilament bundles there remain large degenerated mitochondria (DM) and free ribosomes (R). The cells project long microvilli (MV) into more dilated intercellular spaces. L Lumen of the esophagus. ×25,200
The nucleus of the cells is flattened and more or less intensively degenerated (Fig. 16). The Golgi complexes have completely disappeared, and mitochondria have been strongly reduced in number and are scattered randomly, being involved also in degeneration (Fig. 16, 17). Cisternae of the granular endoplasmic reticulum are rare. Free ribosomes which are scattered, mostly in small clusters, in the whole cytoplasm are reduced in number. The most striking cytological difference between the cells of the stratum granulosum and those of the stratum corneum is that the membrane-coating granules which are rather numerous in the former cells promptly disappear or are intensively reduced in number in the latter cells (Fig. 16).

As revealed in Figures 16 and 17, electron opaque tonofilaments, 75–80 Å thick, make bundles running in various directions and fill up the cytoplasm of the flattened epithelial cells of the stratum corneum. The filaments agree in electron density and thickness with those in the cells of other layers. An interfilamentous material is

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**Fig. 17.** Parts of two flattened epithelial cells in the uppermost layer of the stratum corneum of chicken esophageal epithelium. The cytoplasm is occupied by tonofilaments and electron transparent interfilamentous material. It further contains irregularly shaped light spaces, a small amount of free ribosomes (R) and probably degenerated mitochondria (DM). Thickened plasma membranes (horny cell envelope) are not identified. These corneum cells retain also microvilli protruding into the wide intercellular space (IS) and to the esophageal lumen (L). ×37,500
electron lucent in contrast to the electron dense tonofilaments. Brody's "keratin pattern" has not been confirmed in the stratum corneum of the avian esophageal epithelium examined in this study. The surface of the cell and its microvilli facing the intercellular space do not assume a "thickened plasma membrane" which may be comparable with the so-called "horny cell envelope" observed by the authors in the cornified cells of epidermis and cornified epithelia of mucous membranes of certain regions. Occasionally the cells of the uppermost layer of the stratum corneum facing the esophageal lumen appear electron transparent and edematous, and electron dense tonofilaments measuring 75-80 Å thick, are arranged very loosely and randomly without forming any bundles. It seems likely that these epithelial cells may have been highly altered by maceration. There appear frequently bacterioid profiles in the esophageal lumen.

Discussion

The previous authors of the light and electron microscopic studies on the stratified squamous epithelia covering the mucous membranes usually divided them into several layers. Some authors (Albright and Listgarten, 1962; Gibbins, 1962; Kurahashi and Takuma, 1962; Listgarten, 1964) divided them in agreement with the case of the epidermis, into four layers: the stratum basale, spinosum, granulosum and corneum, while others into only three layers: either into the basal or lower, middle or intermediate and upper or superficial layer (Oehmke and Petry, 1964; Gavin, 1968; Shingleton et al., 1968), or into the layer of basal cells, the layer of higher cells in the epithelium and the layer of cells closer to the surface (Zelickson and Hartmann, 1962). Zelickson and Hartmann electron microscopically observed the human oral lip epithelium where neither the presence of keratohyalin granules nor of horny cells were evident. By light microscopical investigations of the epithelium of the chicken and pigeon esophagus, the present author likewise could detect neither keratohyalin granules nor true horny cells. He further confirmed that the superficial layers consisting of intensively flattened, squamous cells retained small elongated nuclei. Nevertheless, the present author has designated four layers in accordance with Hioki (1941) who studied human esophageal epithelium light microscopically, the stratum basale, spinosum, granulosum and corneum—for merely convenience' sake.

In the chicken and pigeon the basal cells of the esophageal epithelium have wide intercellular spaces containing cytoplasmic processes or microvilli and show pictures indicating high pinocytotic activities. They contain in the cytoplasm Golgi complexes located near the nucleus, numerous mitochondria, abundant free ribosomes mainly in the form of polysomes, tonofilaments bundled into tonofibrils and a few cisternae of the granular endoplasmic reticulum. These cytological findings almost agree with the previous descriptions on the basal cells in the epidermis (Brody, 1960; Zelickson and Hartmann, 1961; Ofuji and Kawamura, 1966; Karásek and Oehlert, 1968a) and in the stratified squamous epithelia of mucous membranes (Albright and Listgarten, 1962; Kurahashi and Takuma, 1962; Zelickson and Hartmann, 1962; Listgarten, 1964; Oehmke, 1964; Oehmke and Petry, 1964; Parakkal, 1967; Gavin, 1968; Hicks, 1968; Shingleton et al. 1968). As emphasized by Ofuji and Kawamura (1966), Parakkal (1967), Gavin (1968) and Hicks (1968), the basal cells
contain abundant free ribosomes in contrast to the paucity of elements of the granular endoplasmic reticulum. A centriole in the stratified squamous epithelial cells has been reported only in the epidermis by a few authors; Zelickson and Hartmann (1961) revealed a centriole lying in a clear area (centrosome) at the upper pole of the nucleus of the human epidermal basal cells, and Karášek and Oehlert (1968a) found it in the basal cell of the guinea-pig epidermis. In the present study a centriole has been revealed on one side of the nucleus of basal cells of the chicken esophageal epithelium, and, in its vicinity, a single cilium has been found, presumably extending into a deep invagination of the plasma membrane continuous to the intercellular space. The basal body or another centriole from which the cilium may originate has not been detected.

As pointed out by Listgarten (1964), Parakkal (1967), Karášek and Oehlert (1968a), Singleton et al. (1968) and others in the studies on mammalian epidermis and stratified squamous epithelia, the spinous cells of esophageal epithelia of the chicken and pigeon are also characterized by the occurrence of numerous desmosomes and abundant tonofilament bundles. Free ribosomes have somewhat decreased in number but the development of the granular endoplasmic reticulum becomes more remarkable, as compared with the basal cells.

As one of the main findings obtained in the present study the “intracisternal filament bundles” have been revealed in the epithelial cells of the chicken esophageal epithelium. They appear first in the cytoplasm of the spinous cells and increase in number toward the stratum granulosum, but they are no longer detectable in the stratum corneum. In the “intracisternal filament bundles,” the filaments, which agree in thickness and in ultrastructural appearances with the cytoplasmic tonofilaments, are contained in dilated cisternae of the granular endoplasmic reticulum, making bundles of variable thickness. It thus seems reasonable to identify them as tonofilament bundles within cisternae of the rough-surfaced endoplasmic reticulum. In the upper layer of the stratum granulosum, the cisternae wrapping filament bundles are supposed to disappear and the naked bundles may be released in the cytoplasm to be mixed with the cytoplasmic tonofilament bundles. Thus, the tonofilament bundles derived from intracisternal filament bundles are no longer distinguishable in the stratum corneum. Thus, it seems likely that in the chicken esophageal epithelium two modes of the tonofilament formation might take place in the stratum spinosum and granulosum; in one, the tonofilaments might be formed in the cytoplasmic matrix and in the other in the cisternae of the granular endoplasmic reticulum.

Along with the descriptions in mammalian mucous membranes by Fasske and Themann (1959), Karrer (1960), Listgarten (1964) and others, the desmosomes in the epithelial cells of the avian esophagus coincide in ultrastructure with the desmosomes reported by Odland (1958) and Brody (1960) in their studies on the human epidermis. On the contrary to Odland’s view that the attachment plaque might be derived from the plasma membrane, Karrer (1960) considered this electron dense area as a condensed cytoplasm on the internal surface of the inner leaflet of the plasma membrane. The present author has also confirmed the latter view especially in the chicken esophageal epithelium. The intercellular contact layer (Odland), a dense midline found in the intercellular substance at the site of the desmosome, has not so
distinctly been demonstrated in the desmosomes of the chicken esophageal epithelium, but in the pigeon its constant existence has clearly been confirmed. Listgarten (1964) observed in the study on the keratinizing human gingival epithelium the disappearance of the intercellular contact layer in the desmosomes located in the upper layer of the stratum spinosum, and Gavin (1968) reported in the study on the non-keratinizing crevicular epithelium of the cat gingiva that the intercellular lamellae (intercellular contact layers) were often not so apparent. The occurrence of tight junctions together with desmosomes in the stratified squamous epithelia was reported by a number of investigators: by Karrer (1960) for the first time in the human uterine cervical epithelium, by Hicks (1968) in the cornified patches in the urinary bladder of vitamin-A deficient rats, by Bonneville (1969) in the periderm of the fetal rat epidermis and by Gavin (1968) in the non-keratinizing crevicular epithelium of the cat gingiva. Recently, Shibasaki (1970) observed many tight junctions together with numerous desmosomes between spinous cells in the normal human esophageal epithelium (personal communication, see also Ito and Ishii 1970). In the present study it has been elucidated that both chicken and pigeon esophageal epithelia possess tight junctions which occur mainly in the stratum spinosum and granulosum. The tight junctions have revealed a quintuple-layered structure as reported by Karrer (1960) and Gavin (1968). Especially in the chicken esophageal epithelium a fusion line of desmosomes has shown a substructure suggesting that it might have a periodical fibrillar structure oriented parallel to the cell surface.

The most conspicuous cytological characteristic of the granulosum cells is, as suggested by all previous investigators, that they contain keratohyalin granules. In the present study on avian esophageal epithelia the cytological evidence that they contain, in addition to keratohyalin granules, numerous so-called membrane-coating granules (MCG) has been admitted as the second important characteristic of the granulosum cells, though in the pigeon only one oval dense body resembling keratohyalin granules has been identified. As already known from light microscopic studies (Hioi, 1941; Kubota, 1943), the electron microscope observations indicate keratohyalin granules occurring in both the cytoplasm and the nucleus of the granulosum cells (Sognnaes and Albright, 1956, 1958; Oehmke, 1964; Oehmke and Petry, 1964; Parakkal, 1967; Hicks, 1968; Pipan, 1968). The keratohyalin granules are lacking in a limiting membrane. As to their internal fine structure, almost all electron microscopists have described it merely as a homogeneously electron opacity, while Kurahashi and Takuma (1962) have noted extremely dense minute particles in the keratohyalin granules of human gingival epithelium. Recently, Kobayashi (1970) has also confirmed in the esophageal epithelium of the guinea pig that the majority of keratohyalin granules are composed of electron dense minute particles about 165 Å in diameter which highly resemble ribosomes (personal communication, see also Ito and Ishii, 1970). Most investigators who studied electron microscopically mammalian stratified squamous epithelia including epidermis have recognized that keratohyalin granules in both the cytoplasm and the nucleus are closely surrounded by aggregated ribosomes (Brody, 1959b, 1960; Frei and Sheldon, 1961a; Gibbins, 1962; Oehmke, 1964; Oehmke and Petry, 1964; Snell, 1965; Parakkal, 1967; Hicks, 1968; Karasék and Oehlert, 1968b; Pipan, 1968; Bonneville, 1969 etc.). Many authors indeed came to the conclusion that the ribosomes may play a principal role in the
formation of keratohyalin granules. Although the present study indicates that the particle investment is an important ultrastructural characteristic of keratohyalin granules besides the high electron density and the lack of a limiting membrane, there have been recognized some dense bodies lacking the particle investment in both the cytoplasm and nucleoplasm and also those surrounded only by a granular structure resembling the material composing the bodies. The latter perhaps suggests breakdown in the periphery of the dense bodies. In this study the dense bodies found in the cytoplasm and the nucleus of the chicken granulosum cells have provisionally been considered as keratohyalin granules. The intranuclear dense bodies which agree in ultrastructure with the intracytoplasmic ones, especially, have not been associated with such a particle investment. A similar finding was reported by Oehmke and Petry (1964) in the study on the rat esophageal epithelium; according to them the cytoplasmic keratohyalin granules are provided with the halo of ribosomes, while the nuclear ones are surrounded merely by the clear halo. That both the nuclear and cytoplasmic keratohyalin granules are surrounded by the aggregate of ribosomes has been, however, reported by several authors like Oehmke (1964), Parakkal (1967) and Pipan (1968). The reason why several keratohyalin granules of the chicken esophageal epithelium were devoid of the particle investment is unknown, but it may be tenable that their breakdown had not yet begun in the periphery, since only keratohyalin granules surrounded by a finely granular material are associated with ribosome-like particles in variable numbers. The authors who observed the occurrence of keratohyalin granules within the nuclei of the granulosum cells believed that they might migrate through the nuclear membrane into the cytoplasm (Hioki, 1941; Kubota, 1943; Oehmke and Petry, 1964, etc.). In the present study a keratohyalin granule ensheathed by membranes resembling a nuclear envelope has been found in close proximity to the nucleus of a granulosum cell in the chicken esophageal epithelium. This feature may indicate the following mechanism of the release of the keratohyalin granule from the nucleus into the cytoplasm; the granule first migrates into the slender process protruding from the nucleus and then, as the process is pinched off, the granule encapsulated by the nuclear envelope may be liberated into the cytoplasm and finally becomes naked after the disappearance of the nuclear envelope. The present study has never demonstrated such an intimate topographical interconnection between the keratohyalin granules and the tonofilament bundles as suggested by Horstmann and Knoop (1958), Brody (1959b, 1960), Zelickson and Hartmann (1961), Frei and Sheldon (1961a), Snell (1965), Miyazaki (1966), Parakkal (1967), Hicks (1968), and Karasék and Oehlert (1968b).

As for the so-called membrane-coating granules (MCG), (small thick-walled vesicles, small lamellated bodies, keratinosomes, etc.), found by electron microscopy in the epidermis and the stratified squamous epithelia of the mucous membranes, their ultrastructure, origin and significance have been elucidated by numerous investigators to a large extent (Selby, 1955, 1957; Horstmann and Knoop, 1958; Odland, 1960; Frei and Sheldon, 1961b; Zelickson and Hartmann, 1961, 1962; Albright and Listgarten, 1962; Kurahashi and Takuma, 1962; Brody, 1962a; Farbman, 1964; Listgarten, 1964; Frithiof and Wersäll, 1965; Matoltsy and Parakkal, 1965; Rupec and Braun-Falco, 1965; Matolsty, 1966, 1969; Oláh and
Röhlch, 1966; Hashimoto et al., 1966; Miyazaki, 1966; Ofuji and Kawamura, 1966; Wilgram and Weinstock, 1966; Parakkal, 1967; Wolff and Holuber, 1967; Bonneville, Weinstock and Wilgram, 1968; Hicks, 1968; Karasék and Oehlert, 1967; Mandel, 1968; Pipan, 1968; Wilgram, 1968; Bonneville, 1969). The results obtained by these authors on the MCG are summarized as follows. The membrane-coating granules are round or oval granules measuring 0.1–0.5 μ or less in diameter and are bounded by a distinct smooth limiting membrane. Their matrix is relatively electron dense and exhibits a more or less conspicuous lamellar structure or a cross striation. They occur usually in the cells of the stratum spinosum and granulosum and tend to be concentrated beneath the plasma membrane on the upper side of the cell and after attachment of their limiting membrane to the plasma membrane they empty their contents into the intercellular space, so that the contents may participate in alteration or thickening of the plasma membrane of keratinizing cells by spreading over the cell surface (Farbman, 1964; Matoltsy and Parakkal, 1965; Oláh and Röhlch, 1966; Matoltsy, 1966; Parakkal, 1967; Karasék and Oehlert, 1968b). However, against this membrane-coating hypothesis of Matoltsy and Parakkal (1965), Wilgram and Weinstock (1966), Bonneville et al. (1968) and Wilgram (1968) presented the view that keratinosomes (MCG) do not participate in the thickening of the plasma membrane, but they may be associated with the rate of turnover of epithelial cells and appear to be related to the transformation of granulosum cells into horny cells. On the other hand, Wolff and Holuber (1967) revealed the acid phosphatase activity in both Odland bodies (MCG) and intercellular spaces and came to the conclusion that the Odland bodies might be nothing but lysosomes and might probably be discharged into the intercellular spaces to play a role not only in the epithelial keratinization but also in regulation of horny cell shedding. The membrane-coating granules observed in the chicken and pigeon esophageal epithelia highly resemble in ultrastructure those in the human esophageal epithelium and in the epithelium of the rabbit plica vocalis (Shibasaki, 1970 and Kobayashi, 1970; personal communications and see also Ito and Ishii, 1970). As pointed out by Farbman, 1964; Frithiof and Wersäll, 1965; Matoltsy, 1966; Oláh and Röhlch, 1966; Parakkal, 1968; Kobayashi, 1970 (personal communication) and others, the membrane-coating granules in avian esophageal epithelia also are concentrated along the upper plasma membrane of the cell. Some micrographs in this study suggest the release of the MCG into the intercellular spaces by means of emiocytosis and, further, a moderately electron dense material resembling the content of the MCG has been observed in the intercellular spaces between granulosum cells of the chicken. The fate and nature of the discharged MCG material remain unknown. As to the formation of MCG, various views have been proposed. The view postulating the MCG formation in the Golgi complex seems to be most predominant at present (Matoltsy and Parakkal, 1965; Oláh and Röhlch, 1966; Parakkal, 1966; Bonneville, Weinstock and Wilgam, 1968). In avian esophageal epithelia also the Golgi complexes found in the spinous and granulosum cells have shown pictures suggesting the origin of MCG from Golgi vacuoles. Frithiof and Wersäll (1965) and Oláh and Röhlch (1966) revealed that a highly electron dense lamellar material of MCG should be nothing but phospholipid. In the electron lucent MCG in avian esophageal epithelia the occurrence of a large content of such an osmiophilic material
as phospholipid is not expected.

In the electron microscope study on the cornified cells of the stratum corneum in the human footpad epidermis, Selby (1957) recognized that the horny cells were composed exclusively of a homogeneous mass of transformed tonofibrils, and considered tonofilaments as the precursor of fibrous keratin; the tonofilaments formed in the stratum basale were believed to be transformed in the stratum granulosum into keratin. Brody (1959a, 1960) investigated the horny cells in the normal human and guinea pig epidermis and elucidated a fine structure of the homogeneous mass of transformed tonofibrils reported by Selby, and further proposed the structural pattern of keratin. The “keratin pattern” by Brody consists of bundles of less opaque (unstained) filaments (keratin filaments) and a highly opaque (stained) interfibrillar (amorphous) substance. At first he was doubtful about the direct transformation of tonofilaments into keratin filaments, because of the difference in thickness and electron opacity between both types of the filaments. This “keratin pattern” has been confirmed by several authors in the studies on the human and mammalian epidermis (Miyazaki, 1966; Karasek and Oehlert, 1968b). These investigators observed the disappearance of nuclei and cytoplasmic organelles and formation of thick plasma membranes (“horny cell envelope”) in the horny cells. Thereafter, in the studies on the epidermis in psoriasis vulgaris Brody (1962a, b) discovered the retention of nuclei in the stratum corneum (parakeratosis) and an abnormal horny substance exhibiting an “abnormal keratin pattern” which is composed of an electron opaque tonofibrillar material and an electron lucent homogeneous interfibrillar material.

The cells of the stratum corneum in the stratified squamous epithelia of mucous membranes have been observed under the electron microscope (Albright and Listgarten, 1962; Gibbins, 1962; Kurahashi and Takuma, 1962; Listgarten, 1964; Oehmke, 1964; Parakkal, 1967; Hicks, 1968) and disintegration or disappearance of nuclei and cell organelles such as Golgi complexes, mitochondria, endoplasmic reticulum and free ribosomes has been recognized in the strongly flattened cornified cells. The “keratin pattern” shown by Brody, however, has been confirmed by none of the above authors. According to Listgarten, the structural pattern of keratin in the human gingival keratinizing cells was similar to the abnormal keratin pattern observed by Brody. Kurahashi and Takuma (1962) maintained that the cornification of the human gingival epithelium might be evident, although they could not reveal the presence of the keratin pattern.

The epithelial cells of the stratum corneum of the chicken and pigeon esophagus show ultrastructural features similar to those of oral, gingival, palatal, esophageal and epidermal epithelia in humans and some mammals observed by the above-mentioned several authors. The remaining of nuclei, several cell organelles and microvilli and the lack of thickened plasma membranes (or horny cell envelope) seem to indicate an incomplete cornification of avian esophageal epithelia. The structural pattern of tonofilament bundles in the avian esophageal corneum cells agrees with that observed by Listgarten (1964) in the keratinizing cells of the human gingival epithelium, being composed of electron opaque tonofilaments and an electron lucent interfibrillar substance. Thus, the “keratin pattern” proposed by Brody has not been recognized in the avian esophageal epithelia. Therefore, on
the basis of numerous electron microscopic investigations carried out by many investigators including the present author it can be concluded that strongly flattened epithelial cells of the stratum corneum of the stratified squamous epithelia covering the mucous membrane, regardless of the presence or absence of histological signs for cornification, do not show any structure corresponding to the so-called “keratin pattern” by Brody (1959a, 1960), but they show a structure corresponding to the “abnormal keratin pattern” of Brody (1962a, b). Thus, in the studies of mucous membranes the “keratin pattern” of Brody seems invalid as a criterion of their keratinization.

Electron transparent, edematous, flattened epithelial cells with the electron dense tonofilaments running in random directions without forming bundles were occasionally found in the uppermost layer of the stratum corneum of chicken and pigeon esophageal epithelia. These cells may correspond to the electron lucent cells with sponge-like cytoplasm found on the surface of the stratum corneum of epidermis reported by Brody (1959a), Snell (1965), Miyazaki (1966) and Karasek and Oehlert (1968b). The edematous and sponge-like appearance of the cytoplasm may be caused by the maceration of the cells on the epithelial surface.

As to cornification of the esophageal epithelium in mammals the view has long predominated that the variety in the degree of cornification shown by this epithelium is correlated with the dietary habits of animals (Goetsch, 1910; Hioki, 1941; Parakkal, 1967; Hicks, 1968 and others). Especially, Parakkal (1967), who observed with the electron microscope the esophageal epithelium of adult mice, described in the introduction of his paper as follows: “In animals which eat coarse or hard food (rodents and ruminants) the epithelium undergoes a complete cornification, like mammalian epidermis, while mammals living on soft food (carnivores and man) lack a horny layer, because superficial cells of the epithelium retain their nuclei and contain occasionally a few keratohyalin granules.” The present finding that in chickens and pigeons living on coarse or hard food, the esophageal epithelia show incomplete cornification as in the case of “carnivores and man” speaks against the above hypothesis. At least it is concluded that this hypothesis is not applicable to the avian esophageal epithelia.
3. デスモソームは有棘層に最もしばしば、次いで顆粒層に多く現われる。タイトジャッショングも主に両層に多く現われ、その“融合線”がしばしば周期性をもつ細線維状構造を示す。

4. 強く扁平化した顆粒層細胞は張原線維束に富む。糸粒体のあるものは退化するが、ゴルジ装置はよく保持される。

5. ニワトリの顆粒層細胞の核と細胞質にはケラトヒアリン顆粒があり、これらは円く暗調で、指紋様および顆粒状構造を示す。核内のケラトヒアリン顆粒が細胞質へ放出される所見がある。

6. ゴルジ装置で形成されたメンプランコーティング顆粒（メ－顆粒）は円形で明るく、まれに基底層細胞にもあるが、顆粒層細胞で最多数に達し、細胞の上位形質膜下に集中して、開口分泌により細胞間腔に放出される。

7. 角化層細胞には強く変性した核があるが、ゴルジ装置、メ－顆粒および槽内線維束は完全に消失する。典型的なケラチン模様はない。

References


