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Fine structure of the horny teeth of the lamprey, *Entosphenus japonicus**

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Summary. The fine structure of the horny teeth of the lamprey, *Entosphenus japonicus*, was examined by light- and electron-microscopy. Most of the horny teeth consisted of two horny and two nonhorny layers. The primary horny layer was well keratinized, and the cells were closely packed and intensely interdigitated, being joined together by many modified desmosomes. The plasma membrane of the horny cell, unlike the membranes of other vertebrates, was not thickened. The intercellular spaces were filled with electron-dense material. Microridges were seen on the free surface. Structures resembling microridges were found on the underside of the primary horny layer. The secondary horny layer displayed various stages of keratinization. The keratinization started at the apex and developed toward the base. In the early stage of keratinization, the superficial cells became cylindrical and were arranged in a row forming a dome-shaped line. Their nuclei were situated in the basal part of the cells. The appearance of the nonhorny layers varied according to the degree of keratinization of the horny layers beneath them. The nonhorny cells were joined together by many desmosomes and possessed many tonofilament bundles. The replacement and keratinization of the horny teeth are discussed in the light of these results.

Key words: Lamprey – Horny teeth – Keratinization – Oral mucosa – Microridges

The lamprey has horny teeth on both its buccal funnel and tongue. These structures, considered to be a primitive stage in the evolution of vertebrate

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teeth, play an important role in feeding. They enable firm attachment to the prey while rasping off muscle tissue therefrom. The number, arrangement, and external shape of horny teeth differ among the various species (Berg 1962; Trott and Lucow 1964). However, all have the same histological structure, consisting of cornified squamous epithelium and a horny layer beneath which lies a nonhorny layer. The primary horny layer is a functional horny plate; the subsequently formed layers are successive additional plates (Sognnaes and Lustig 1955; Manion and Piavis 1977).

Sognnaes and Lustig (1955), who investigated histologically by light microscopy, the horny teeth of *Petromyzon marinus* reported them to consist of three horny layers, with an increasing degree of keratinization being demonstrated from the young tertiary layer to the primary layer. Trott and Lucow (1964) investigated by light-microscopic histochemistry two species, *Petromyzon marinus* and *Polistotema stoutii* and that the horny teeth of *Petromyzon marinus* consist of three horny layers. These layers were stained with equal intensity by the performic acid Shiff reaction for keratin. However, the horny teeth of *Polistotema stoutii* consist of only one horny layer. In recent papers, Saegusa et al. (1977) reported the results of investigations by light and scanning electron microscopy on *Entosphenus mitsucrii*, a non-parasitic species which remains in rivers without migrating to the sea, in which they found that the horny teeth are located in three horny layers and that the contours of the epithelial cells become increasingly obscure from the tertiary layer to the primary layer. From investigation light- and scanning electron-microscopy on *Entosphenus japonicus*, which phylogenetically degenerated into *Entosphenus mitsucrii*, Yoshie and Honma (1979) reported that the horny teeth consist of two horny layers and a precornified cell layer and that the two horny layers show the same stainability during routine staining with Azan.

To elucidate the nature of the replacement teeth and of the keratinization process in the horny teeth of *Entosphenus japonicus* we have examined their fine structure by light and electron microscopy.

Materials and methods

Adult lampreys, *Entosphenus japonicus*, about 60 cm in length, were captured in the Shinano River (Japan) during their winter migration from the sea.

For light- and scanning electron-microscopy, the lampreys were fixed by perfusion in 3% glutaraldehyde in 0.1 M phosphate buffer (pH 7.4) using an aortic bulb. The upper labial teeth were cut away from the buccal funnel. For light microscopy, the teeth were dehydrated and embedded in celloidin using conventional methods. The teeth were then sectioned and stained with hematoxylin and eosin. For scanning electron microscopy, the teeth were post-fixed for 2 h in 1% OsO_4 with the same buffer, dehydrated through a series of graded ethanol baths, and then transferred into iso-amylacetate. The specimens were then critical point-dried using liquid CO_2, coated with gold, and examined in JSM T-20 and JSM 50-A scanning electron microscopes.

For transmission electron microscopy, the horny teeth were cut away from the buccal funnel and cut into pieces. The specimens were fixed in 3% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.4) for 2 h and post-fixed in 1% OsO_4 with the same buffer for 2 h. The specimens were block-stained in 2% uranyl acetate for 40 min and then dehydrated in

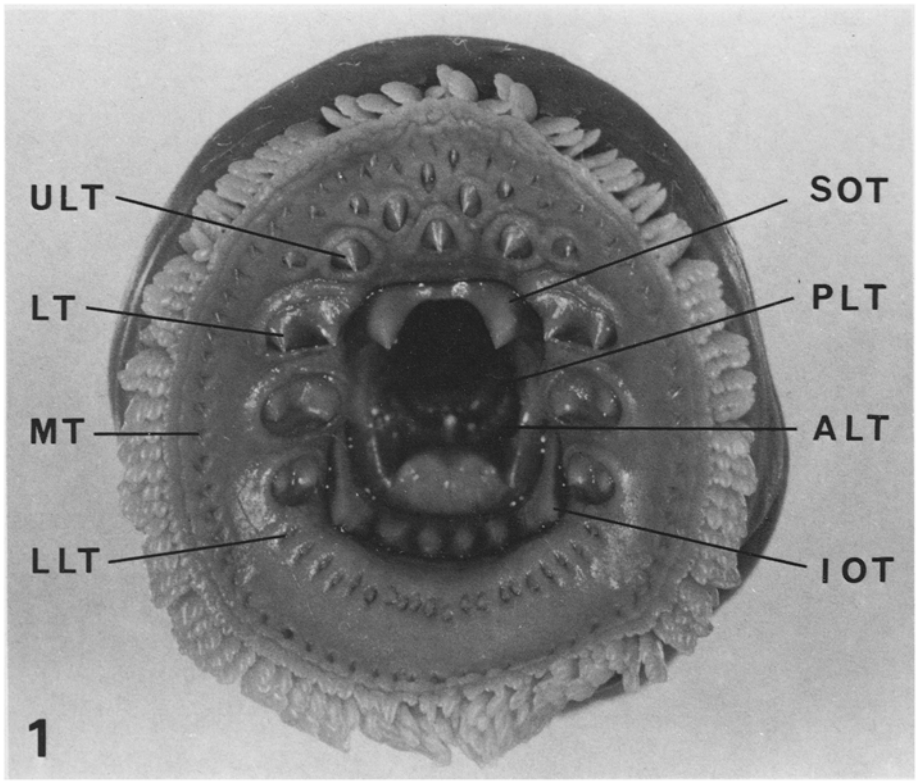


Fig. 1. Gross anatomy of the lamprey mouth. *ALT* anterior lingual tooth; *PLT* posterior lingual tooth; *SOT* supraoral tooth; *IOT* infraoral tooth; *LT* lateral tooth; *ULT* upper labial tooth; *LLT* lower labial tooth; *MT* marginal tooth. × 4

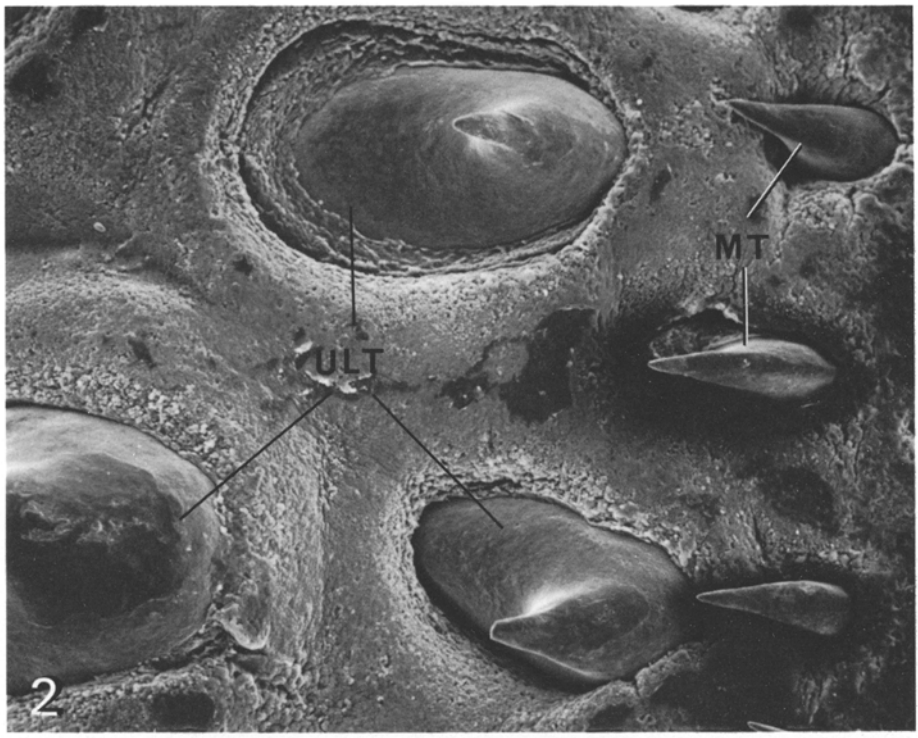
a series of graded ethanol baths. After being embedded in Epon 812 and sectioned, the specimens were finally stained with uranyl acetate and examined in a JEM 100B transmission electron microscope.

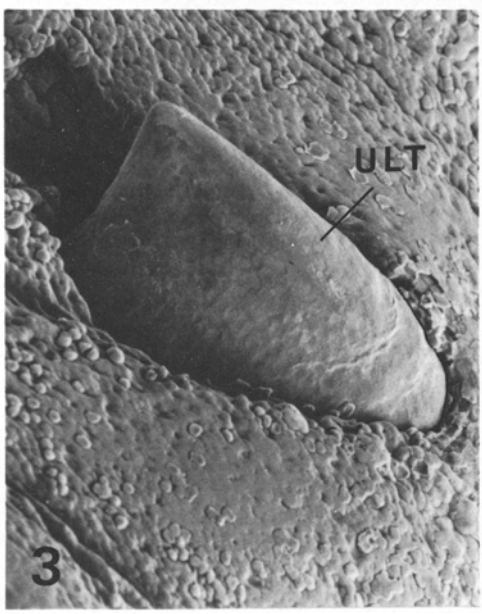
Results

Gross anatomy

The horny teeth, which exist in various sizes and shapes, depending on their location, may be designated as posterior or anterior lingual, supra- or infraoral, lateral, upper or lower labial, or marginal teeth (see Fig. 1).

The anterior lingual tooth, situated on the periphery of the tongue, is U-shaped and subdivided into 15–16 sharp sawtooth-like cusps. The two posterior lingual teeth, situated on the dorsal surface of the tongue, are subdivided into 10 to 12 cusps. The large and wide supraoral tooth on the upper plate of the mouth is subdivided into two large cusps. The infraoral tooth, which is opposite the supraoral, has 6 to 7 cusps. Two of these cusps on each side of the buccal funnel are enlarged and bifurcated.





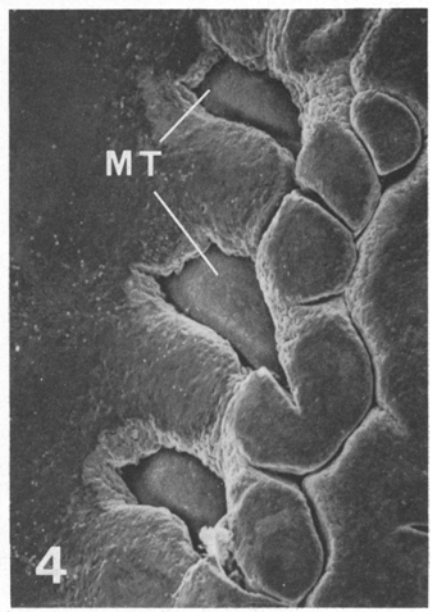


Fig. 2. Scanning electron micrograph of the sharp upper labial (*ULT*) and sharp marginal teeth (*MT*). ×42

Fig. 3. Scanning electron micrograph of a blunt upper labial tooth (*ULT*). ×72

Fig. 4. Scanning electron micrograph of blunt marginal teeth (*MT*). ×42

The three lateral teeth, located in three rows on each side of the buccal funnel, are bifid and curved towards the pharynx. The 10–15 upper labial teeth, situated in a radial row above the supraoral tooth, are sharp, cone-shaped, and curved towards the pharynx (Figs. 2, 3). Those at the periphery of the mouth are small. About 20 small, slender cone-shaped lower labial teeth, situated on the side of the infraoral tooth, form an arched row oriented towards the opening of the mouth. The marginal teeth are situated along the margin of the round mouth (Figs. 2, 4). Occasionally observed are degenerate horny teeth which are shorter and blunter than most horny teeth.

Light-microscopic observations

Most of the horny teeth that we studied are comprised of two horny and two nonhorny layers; a few contain only one horny and one nonhorny layer. All of these layers are dome-shaped (Fig. 5).

The primary horny layer is the most keratinized. This layer is yellow and is not stained by hematoxylin and eosin. Most of the cells in this layer are flattened and closely packed. Nuclei are not visible. In the lower part of the apex, the cells are not flattened and are stained only slightly by eosin.

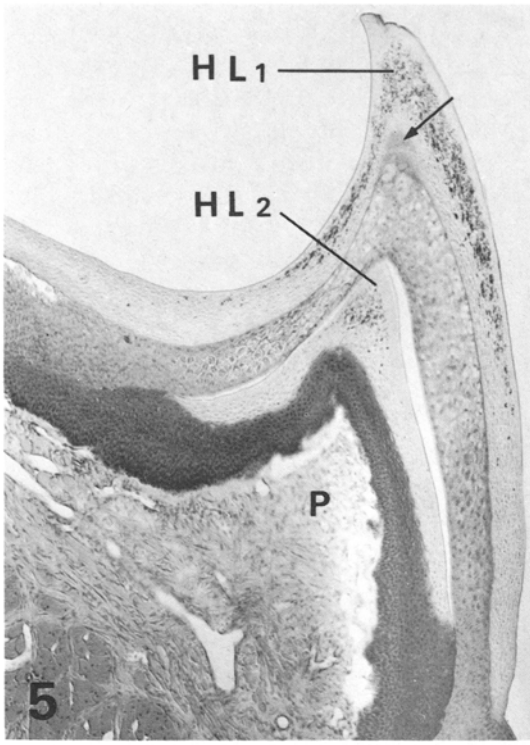
The secondary horny layer shows various stages of keratinization. In some specimens, the keratinized layer is yellow and dome-shaped and does not stain with hematoxylin and eosin. In other specimens, keratinization occurs only at the apical cone, with all except the cells strongly stained by hematoxylin. Judging from the appearance of these secondary horny layers, keratinization seems to proceed from the apex to the base. In the early stages of keratinization, the superficial cells of this secondary layer become cylindrical and are arranged in a dome-shaped row. Their nuclei are situated in the basal part of the cells, and their upper portions are strongly stained by hematoxylin (Fig. 6).

The nonhorny layer lies beneath the horny layer. The structure of the nonhorny cells is altered according to the degree of keratinization of the secondary horny layer. The nonhorny cells underlying an incompletely keratinized horny layer are stained by eosin and are similar in size to the oral mucosal epithelial cells. These transformed into enlarged cells lightly stained by eosin and then become stellate as the keratinization process of the secondary horny layer proceeds.

Scanning electron-microscopic observations

In a vertically cut surface of the horny layer, the cells appear flattened and the intercellular spaces are narrow and long. However, in the lower part of the apex, where the cells are lightly stained by eosin, they are neither closely packed nor flattened and the intercellular spaces are large and round (Fig. 7).

Microridges are observed on the free surface of horny teeth and vary in appearance from apex to base. At the apex, the microridges are wide and shallow and the spaces between the ridges contain micropores (Fig. 8a).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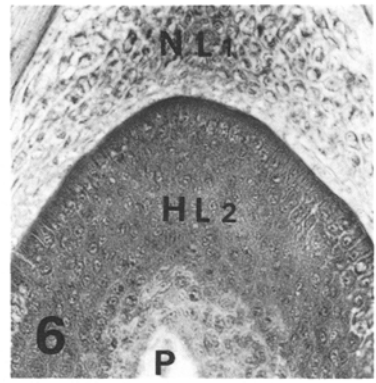
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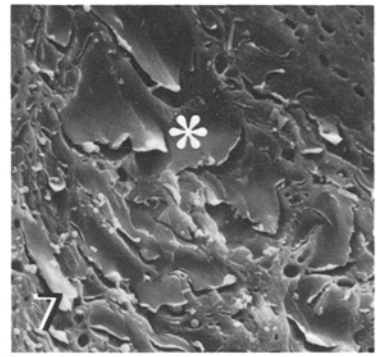
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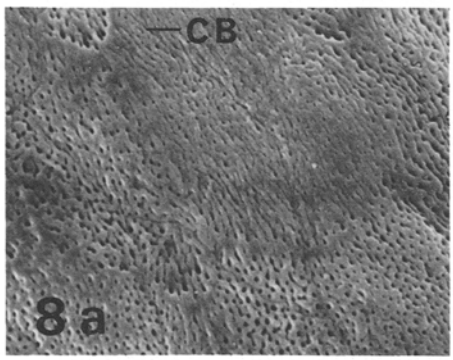
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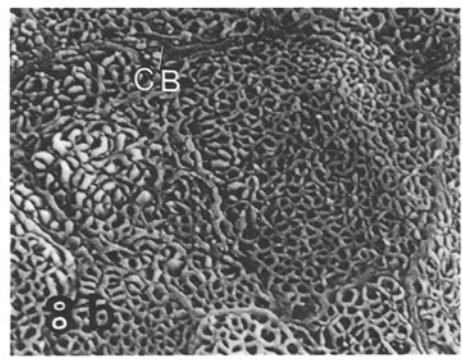
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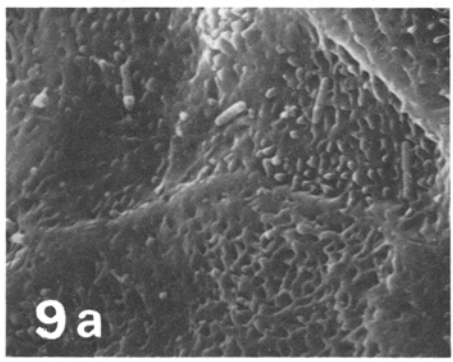
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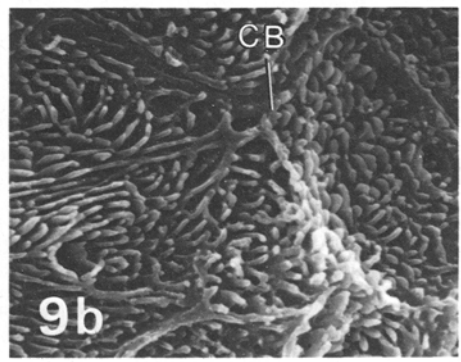
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At the base, the microridges appear as threadlike projections and form a dense network. The spaces between ridges are irregularly shaped deep holes. Occasionally, the microridges appear swollen, so that the spaces between ridges are narrow or absent. Large microridges are observed at the cell boundaries (Fig. 8b).

Commonly, microridges on the oral mucosa of fish are seen only on the free surface (Ryuta and Miyoshi 1978). However, when the primary horny layer is stripped off, cytoarchitectures resembling microridges are observed on the undersurface. At the apex they appear as short knoblike and threadlike projections (Fig. 9a), whereas at the base they are long and threadlike projections forming a dense network. Along the cell boundaries long and swollen threadlike projections are seen (Fig. 9b).

Transmission electron-microscopic observations

The primary horny layer. The primary horny layer consists of 10–15 layers of horny cells. These cells are flattened and closely packed together with intense interdigitations. All of the cellular organelles including nuclei have disappeared. The cells are filled with striae of electron-dense and slightly dense consolidated material which forms a horny plate. However, an occasional cell possesses a shrunken nucleus (Fig. 10).

The superficial horny cells have microridges on their free surfaces. These microridges are cornified and filled with the same electron-dense material as the other parts of the cytoplasm. No glycocalyces are present (Fig. 13).

At the sites of interdigitation there are a large number of desmosomes whose structure differs strikingly from that of desmosomes in nonhorny cells. The attachment plaques in the cytoplasm are fairly dense and the intermediate lines in the intercellular spaces are thin and electron-dense; but the intercellular spaces themselves are electron-lucent. Electron-dense bands are seen in place of the tonofilament bundles converging on the attachment plaques. The unit membrane of the horny cells is approximately

Fig. 5. Light micrograph of a vertical section of an upper labial tooth. The lower part of the primary horny layer (*HL1*) is lightly stained by eosin (*arrow*). Hematoxylin and eosin staining. × 100

Fig. 6. Light micrograph of the secondary horny layer during an early stage of keratinization. The uppermost cells of this layer are conically arranged in a row. *NL1* primary nonhorny layer; *HL2* secondary horny layer; *P* connective tissue papilla. × 190

Fig. 7. Scanning electron micrograph of the vertically cut surface of the primary horny layer. The lower part of this layer is slightly flattened (*). × 700

Fig. 8. Scanning electron micrograph of the free surface of an upper labial tooth; **a** apical portion; **b** basal portion. *CB* cell boundary. × 3300

Fig. 9. Scanning electron micrograph of the under surface of the primary horny layer; **a** apical portion; **b** basal portion. *CB* cell boundary. × 3300

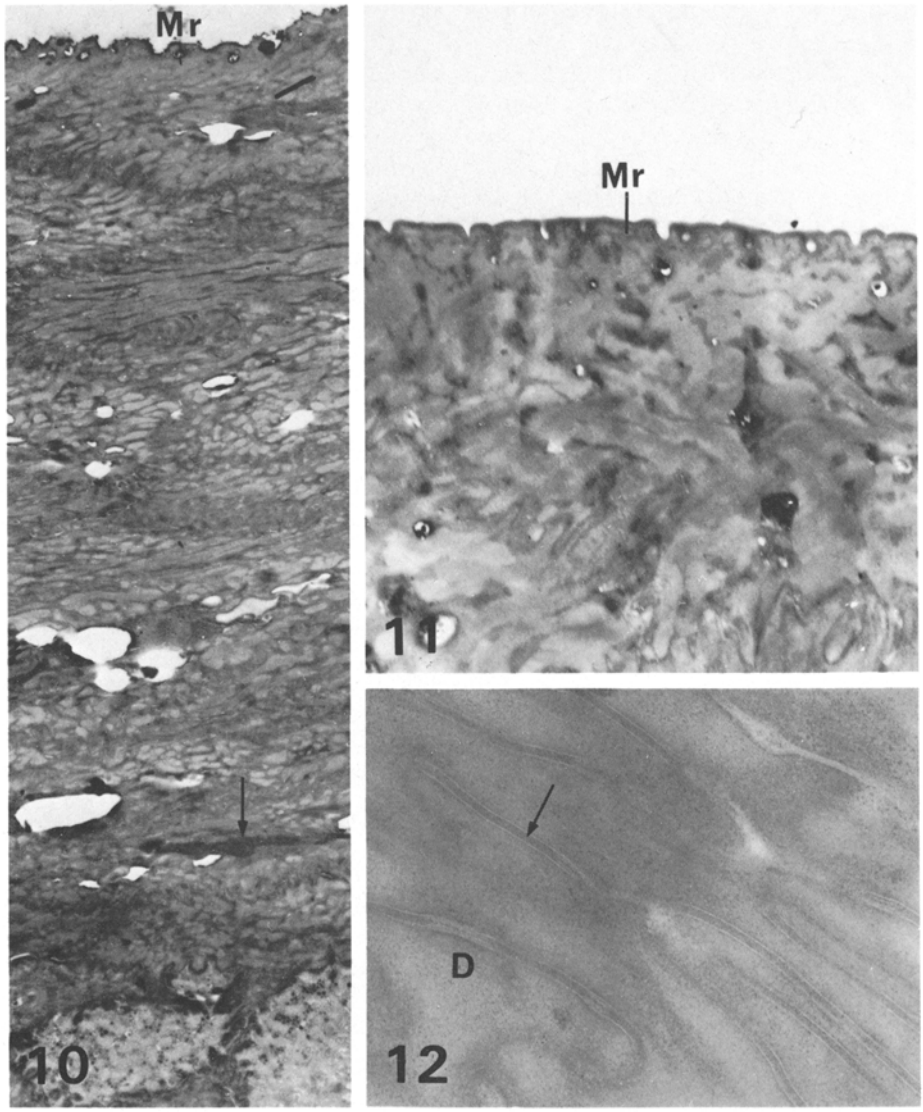


Fig. 10. Transmission electron micrograph of the primary horny layer. The electron-lucent area in the lower part photograph is the primary nonhorny layer. An occasional horny cell possesses a shrunken nucleus (*arrow*). Microridges (*Mr*) are seen at the free surface. × 6000

Fig. 11. High-magnification view of superficial horny cells. *Mr* microridges. × 10100

Fig. 12. Interdigitation and adhesion between primary horny cells. Intercellular spaces are filled with electron-dense material (*arrow*). Modified desmosomes (*D*) are seen. × 63800

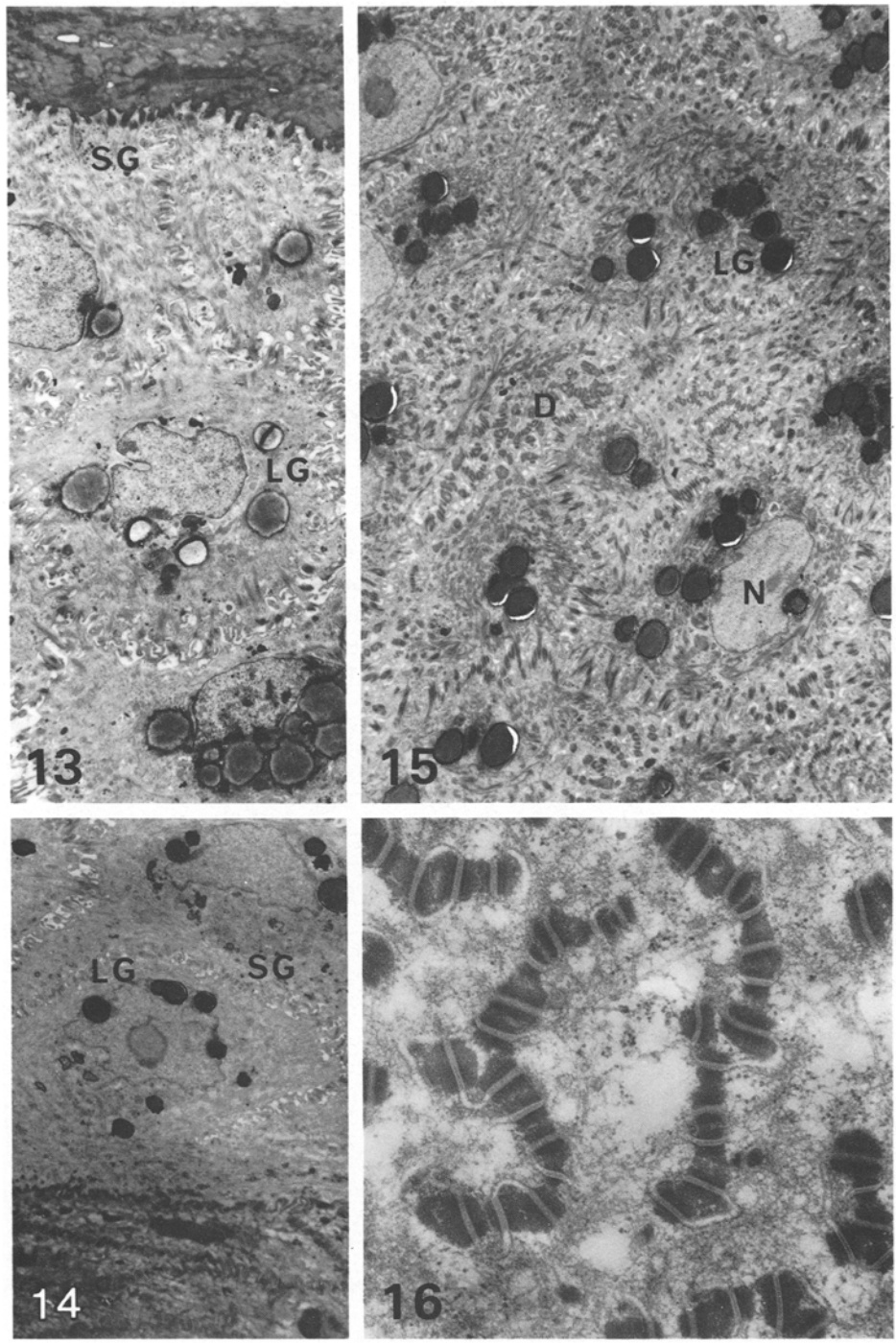


Fig. 13. Junction between the primary horny and nonhorny layers. *LG* large granules; *SG* small granules. × 3500

Fig. 14. Junction between the primary nonhorny and secondary horny layers. *LG* large granules; *SG* small granules. × 3500

Fig. 15. The middle part of the primary nonhorny layer. The cells are intensely interdigitated and joined together by a great number of desmosomes (*D*). *LG* large granules; *SG* small granules; *N* nucleus. × 3400

Fig. 16. High magnification view of desmosomes seen in Fig. 15. × 27300

6 nm in thickness, and the intercellular spaces themselves are approximately 17 nm thick and are filled with electron-dense material. Intercellular spaces in the desmosomes are approximately 18 nm in thickness (Fig. 12).

The primary nonhorny layer. The primary nonhorny layer is electron-lucent and clearly distinguishable from the horny layer. The cells bear many short processes from adjacent desmosome-rich cells. In section, several adjacent desmosomes appear like striped belts. The cytoplasm contains many randomly oriented bundles of tonofilament, numerous free ribosomes, and large and small granules. The large granules are situated in the perinuclear area, whereas the small granules are located at the periphery of the cell (Figs. 13, 14, 15, 16). The nonhorny cells in horny teeth are different from those in the oral mucosal epithelium. Tonofilaments are less abundant in the oral mucosal epithelial cells, which also have granules and vesicles quite different in appearance from those in the nonhorny cells of horny teeth (Fig. 19).

The cells at the junction between the primary horny and nonhorny layers are interdigitated and joined together by well-developed desmosomes. These desmosomes are attached to tonofilament bundles which run vertically in the cytoplasm of the nonhorny cells. Among the tonofilament bundles, numerous free ribosomes, vesicles, and small granules are observed. The intercellular spaces are filled with fibrous material (Fig. 17). The junction between the primary nonhorny layer and the secondary horny layer is very similar to the primary horny-nonhorny junction just described (Fig. 18).

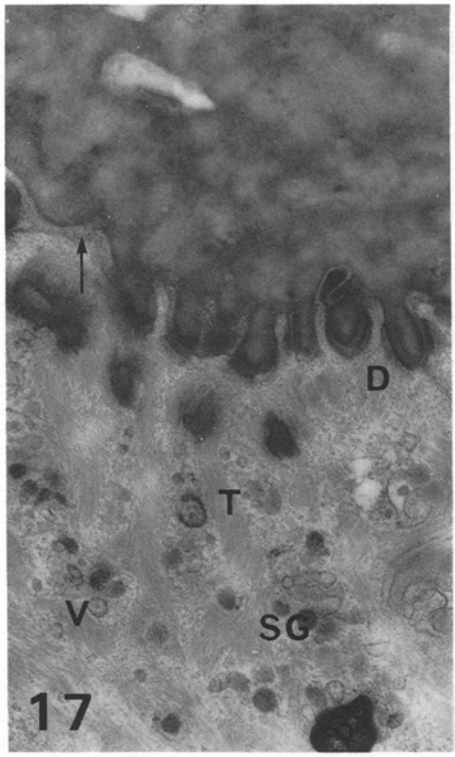
The secondary horny layer. In the beginning stages of keratinization in the secondary horny layer, the junction between the horny and nonhorny layers is not obvious. Most of the prehorny cells in the secondary horny layer are long and slender and possess keratohyalin granules. However, the round cells beneath them possess these same dense granules (Fig. 21).

The secondary horny layer succeeds the primary horny layer and displays various stages of keratinization. Figure 20a–c show these different stages and the cell transformations which occur during the process. In Fig. 20a, electron-dense bundles are seen. They are not limited by membranes and often have ribosomes and filaments attached to them. In Fig. 20b, the cells appear flattened and their organelles are not visible; only their remnants are seen. The intercellular spaces are electron-lucent. In Fig. 20c, the rem-

Fig. 17. Junction between the primary horny and nonhorny layers. Fibrous material is seen in the intercellular space (*arrow*). Junction between the primary nonhorny layer's bottommost cell and the secondary horny layer's uppermost cell. *T* tonofilaments; *SG* small granules; *V* vesicles; *D* desmosomes. × 24000

Fig. 18. Junction between the primary nonhorny and secondary horny layers. Fibrous material is seen in the intercellular space (*arrow*). *R* free ribosomes. × 25000

Fig. 19. Oral mucosal epithelial cell. *Mr* microridges; *V* vesicles; *G* granules; *ER* endoplasmic reticulum; *Mt* mitochondria; *N* nucleus. × 6900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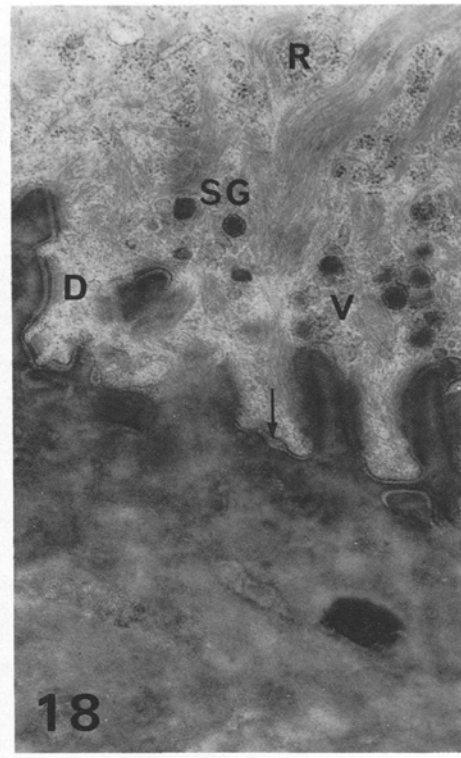
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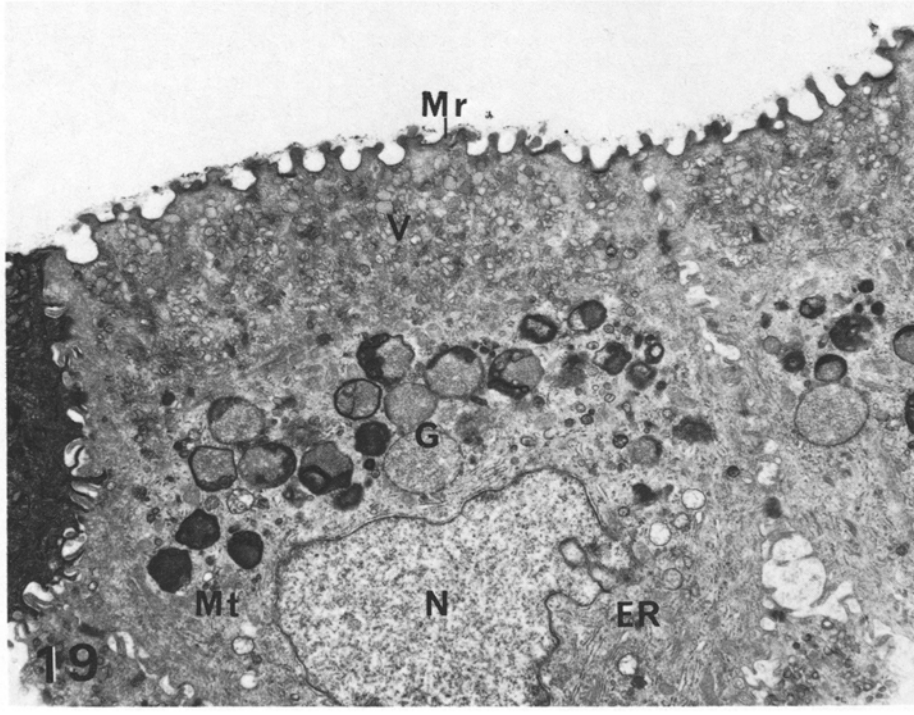
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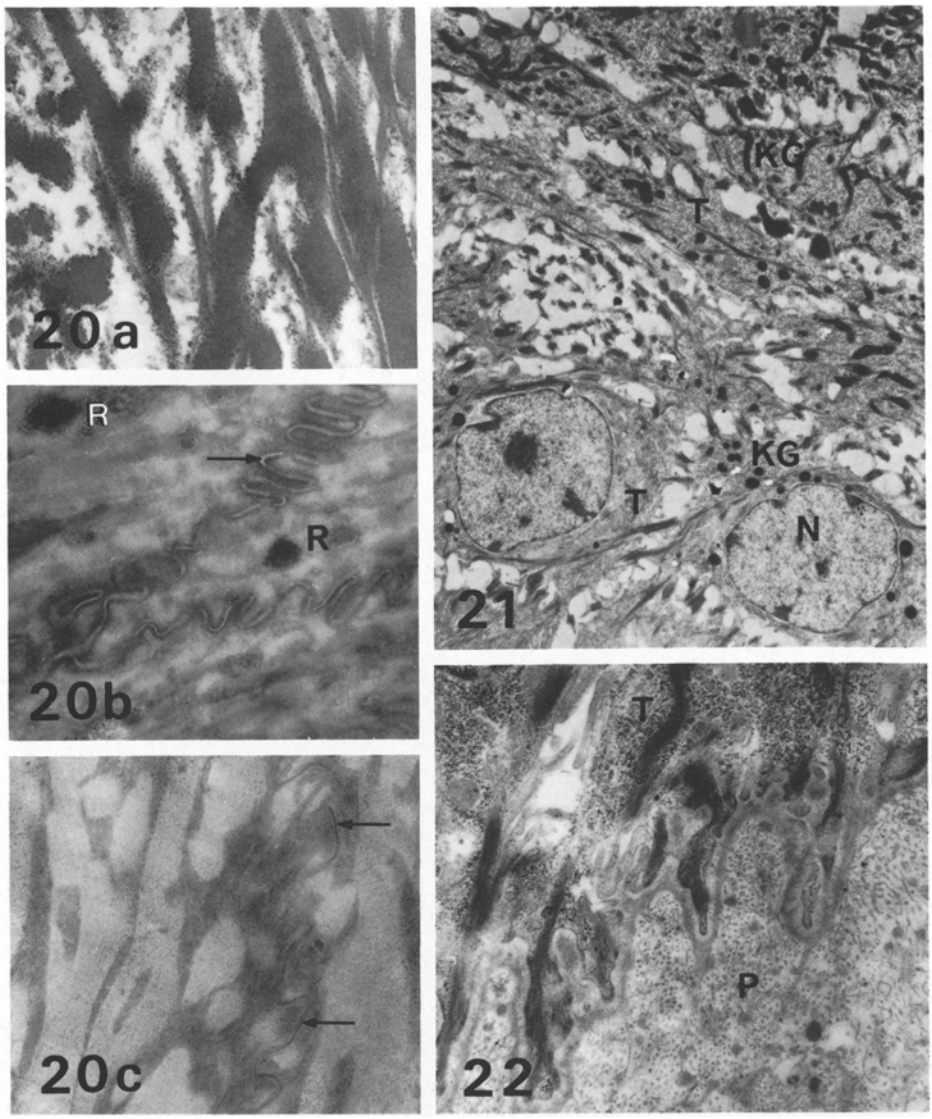

Fig. 20. Transformation of the secondary horny cells during keratinization. Intercellular spaces are indicated (*arrow*). *R* remnant of an organelle. **a** ×20000; **b** ×25000; **c** ×24000

Fig. 21. Junction between young secondary horny and nonhorny layers. The young secondary horny cells are long and slender, whereas secondary nonhorny cells are round with the more superficial ones possessing keratohyalin granules. *KG* keratohyalin granules; *N* nucleus of a secondary nonhorny cell. *T* tonofilaments. ×4000

Fig. 22. Basal cell possessing many projections which are anchored in the connective tissue. Tonofilaments are found in these projections. *T* tonofilaments; *P* connective tissue papilla. ×13000

nants of organelles are gone and electron-opaque bands have appeared. The cells are filled with striae of electron-dense and slightly dense materials. The intercellular spaces are narrow than those in Fig. 20b and are filled with electron-dense material.

The secondary nonhorny layer. The secondary nonhorny layer lies beneath the secondary horny layer. The cells in this layer have round nuclei and abundant filaments. These cells are joined together by many desmosomes, though the latter are not so abundant as they are in the primary nonhorny cells.

The basal cells of this layer are possess many projections that anchor this layer to the connective tissue underlying the basal membrane. In the projections, tonofilaments are seen to run perpendicularly to the plane of the basal membrane (Fig. 22).

Discussion

The mechanism that creates the alternating arrangement of horny and nonhorny layers is not known. It is especially difficult to understand what mechanism arranges the superficial cells of the secondary horny layer in a row forming a dome-shaped line during the early stages of keratinization. Whatever the mechanism, the two-layered arrangement renews the lamprey's horny teeth. When succeeding teeth have become fully keratinized, the nonhorny layer degenerates and the primary horny layer easily falls off. The secondary horny layer then comes to occupy a surface position.

Intense interdigitation and the large number of desmosomes in all layers show that the horny teeth are subjected to violent forces from the environment. In particular, many more desmosomes are seen in the primary nonhorny layer than in the other layers. Desmosomes are well-known to serve as buttonlike connectors between the cytoskeletal system of individual cells, thereby distributing a shearing force on one cell to the tissue as a whole (Staehelin 1974). Therefore, shock absorbance is considered to have an important role of the nonhorny layer.

Whereas most of the keratinized epithelium scales off, the horny cells of the horny teeth do not but rather become a single horny plate. Modified desmosomes occur in both scaled-off epithelium and horny cells, although, in the former, the intermediate disk is electron-dense and thick and the epithelial cells are joined by desmosomes only whereas the other part lacking desmosomes is separated. On the other hand, in the horny layer of the horny teeth, the intermediate disk is electron-dense and thin with the intercellular space being approximately 18 nm. The intercellular spaces in areas without desmosomes are filled with an electron-dense material which is probably a cementing substance secreted by the horny cells during keratinization. The presence of this "cement" in the intercellular spaces along with the modified desmosomes may prevent the horny cells from being scaled off.

Takagi et al. (1976), who have classified microridges into five groups according to their developmental stages, state that in the process of epithelial keratinization, the microridges first become micropores and then progressively disappear. Uehara (1981) has suggested that the transformation of microridges may be related to the degree of epithelial keratinization. The microridges on the free surface (Figs. 8, 9) and the cytoarchitectures approximating the microridges on the under surface of the horny layer (Figs. 10, 11) vary from the apex to the base. Since keratinization proceeds from the apex downwards and the apex is more keratinized than the base, this spatial variation may be related to the keratinization process. The function of the microridges remains unknown even though many hypotheses have been suggested. Among these are a role in such as connection absorptive or secretory activities (Schliwa 1975), protection from environmental forces (Andrews 1976), a role in holding mucous secretion (Hughes and Wright 1970; Andrews 1974; Sperry and Wasserung 1976), helping to produce laminar flow (Juncqueira et al. 1970), and providing surface area for stretching (Sperry and Wasserung 1976). However, since the microridges on horny teeth are intensely keratinized, these hypotheses, except for the one suggesting protection from environmental forces, do not seem very plausible.

Keratinization of the epidermis has been studied in many of vertebrate classes – Mammalia (Lavker and Matoltsy 1970), Aves (Matoltsy 1969; Lavker and Matoltsy 1970), Reptilia (Maltoltsy and Huszar 1972; Landmann 1979), Amphibia (Farquhar and Palade 1965; Parakkal and Matoltsy 1964), Osteichthyes (Mittal and Whitear 1979). The horny cells of the horny teeth of lampreys are similar to the keratinized epithelial cells of other vertebrates in that they are filled with filaments. However, they differ in that the horny cells are filled with striae of electron-lucent and electron-dense materials and in that the plasma membranes are not thickened. The prekeratinous epithelium of frogs possesses large and small mucous granules; and furthermore, there are large granules in the perinuclear region and small granules in the cell periphery. The small granules are discharged into the intercellular spaces (Parakkal and Matoltsy 1964). In this regard, nonhorny cells of the horny teeth may be regarded as comparable to epidermal cells of frog. Keratohyalin granules are generally formed by the epidermis in mammals and birds but not in those of reptiles, amphibians, or fish (Matoltsy and Huszar 1972; Landmann 1979; Lavker and Matoltsy 1965; Matoltsy 1969; Mittal and Whitear 1979). However, in the keratinization process of lamprey teeth, keratohyalin granules are seen. Furthermore, the electron-dense bands (Fig. 20a) are not limited by membranes and are closely associated with ribosomes and cytoplasmic filaments. Therefore, they are considered to correspond to keratohyalin granules. In this regard, the horny cells of the horny teeth are similar to mammalian and avian epidermis.

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