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THE MORPHOGENESIS OF CIRCUMVALLATE PAPILLAE AND DIFFERENTIATION OF TASTE BUDS IN SHEEP ONTOGENY

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Abstract

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This report deals with the morphogenesis of circumvallate papillae and the distribution and differentiation of taste buds in the lingual epithelium of sheep during ontogeny.

Tongues were collected from ovine foetuses at 50, 55, 60, 65, 76, 85, 93 and 128 days after fertilization and from adult sheep. They were examined for the appearance of lingual mucosal structures with special concern for the morphogenesis of circumvallate papilae and the differentiation of taste buds in their epihelium. Attention was also paid to the development and formation of gll. gustatoriae and their ducts, the development of the furrow encircling the circumvallate papilla, and the differentiation of other types of lingual papillae.

Taste buds are formed in the epithelium before the papillae take shape, and are first located on the dorsal surface of the papillae, descending later into the epithelium of papilla walls. The number of buds gradually increases during foetal development. The foundation of the taste bud is soon followed by differentiation of its cells into two types.

Circumvallate papillae attain their typical shape before the surrounding furrow is laid down.

Ducts of gll. gustatoriae are iniciated concurrently with shape differentiation of the circumvallate papilla while their lumina are completed when the furrow is developing.

Lingua, circumvallate papilla, taste bud, differentiation, sheep.

Taste buds were first described in fish (Schulze 1863) and later in mammals (Loven 1868, Schwalbe 1868). In the following period many studies based on light microscopic observations were published the results of which gave an essential insight into the structure of taste organs in various species,

particularly in mammals and man (Kolmer 1910; Retzius 1912; Heidenhain 1914 and others).

Studies of the ultrastructure of taste buds in different animal species provided more detailed information that has led to the understanding of mechanisms governing the registration of taste sensation (De Lorenzo 1958; Farbman 1965a; Uga 1966; Murray and Murray 1967; Murray 1969; Murray et al. 1969; Murray 1971, 1973).

The ultrastructure of taste organs in man and farm animals is now well understood and published in current standard textbooks of anatomy (Krolling and Grau 1960; Banks 1981; Maršala 1983). The function of taste organs, based on morphological observations, has been studied by several authors (Zotterman 1959; Beidler 1970; Ganong 1978).

General information on the development of taste organs in man, laboratory and farm animals are provided by standard textbook (Michel 1983); more detailed data can be found in papers by Beidler and Smallman (1965) and Farbman (1971). No data, however, are available on the process of differentiation of taste buds during ontogeny in mammals. This fact made us undertake investigations into the foundation, development and distribution of taste buds and related structures in ontogeny, using sheep as experimental animals.

Materials and Methods

Tongues were collected from ovine foetuses at 50, 55, 60, 65, 76, 85, 93 and 128 days after fertilization, and from two adult sheep. The foetal age was determined on the basis of crown-rump length according to Evans (1973) (Table 1). From each age category two samples were collected, sections being excised from the area of the tongue at the junction between its body and root, and immediately fixed in 10% neutral formaldehyde.

Table 1

Age and Size of Ovine Foetuses

Serial number	Age after fertilization in days	Number of animals in experiment	Crown-rump length in mm
1	50	2	70
2	55	2	85
3	60	2	105
4	65	2	130
5	76	2	200
6	85	2	240
7	93	2	260
8	128	2	403
9	Adult animal at 450 days post partum	2	1 200

Samples for light microscopic examination were prepared in a routine manner with one modification - the graded alcohol series started with a concentration of 10% alcohol. This approach ensured mild and gradual dehydration and prevented the occurrence of artifacts due to shrinking of embryonic tissue rich in water.

The sections were treated with hematoxylin-eosin and Gomori's stains followed by nuclear red staining. For some sections green trichrome stain, Masson, was used.

Results

Foetus, 50 days of age (Fig. 1)

At this foetal age the tongue surface has an uneven appearance. Primitive papillae like dome-shaped protrusions are localized along the lateral margins of the dorsum linguae, but are absent in the middle part of it. The lingual mucosa consists of several layers of epithelial cells with a distinct bottom layer. This has a palisade-like arrangement and is attached to the basal membrane. The cells of the layer have clear, well-stained nuclei. Above the cells, towards the surface, there are one or two layers of cells irregular in both size and shape, with conspicuously light cytoplasm. The cells in the apical part of the papilla are unevenly distributed in several layers (Fig. 1).

The epithelium has an almost uniform structure all over the lingual surface including the tape of the papillae where nothing indicates the beginning of taste bud formation.

The dome-shaped bodies on the lingual surface are supported with connective tissue stroma originating in the lamina propria mucosae richly supplied with veins, particularly in the area below the bases of the primitive papillae. The lamina propria mucosae has a relatively thin homogenous texture (Fig. 1).

Foetus, 55 days of age (Figs 2 and 3)

The dome-shaped protrusions, seen at the previous stage, are smoothed by proliferating epithelial cells, which results in a mildly undulating appearance of the lingual surface (Fig. 2). Cross-sections show foundations of papillae with first signs of shape and size differentiation. The spaces between the papillae are filled with compact epithelial bands. The bottom part of the epithelium attached to the basal membrane is discernible by its palisade-shaped cells, with well-staining nuclei, arranged in several layers. Cells located near the lingual surface and those found between the developing papillae are characterized by polyedric shape and light-staining cytoplasm (Fig. 3).

The superficial epithelial layer of some of the founded papillae show taste buds at varying stages of differentiation. Most frequently seen formations were clusters of cells derived from the bottom epithelial layer (Fig. 2). Occasionally, taste buds in more advanced stages of differentiation were seen (Fig. 3).

The cells of the lower epithelial part adjacent to the developing taste bud became elongated and flattened; similar changes in shape were also seen in their nuclei (Fig. 3).

In the lamina propria mucosae, connective tissue below the bases of developing papillae grows denser; this is where the aponeurosis linguae will later develop (Fig. 3).

Foetus, 60 days of age (Figs 4 to 6)

The epithelium of the lingual surface has a mildly undulating appearance with occasional shallow and narrow depressions indicating where the developing papilla will later separate from the surrounding tissue. The overal appearance and structure of the epithelium is similar to that seen at the previous stage (Fig. 6).

A cross-section of the dorsum linguae shows that the amount and size of the developing papillae are similar to those found in the 55-day-old foetus. However, changes can be seen in the shape of circumvallate papillae which begin to attain their typical configuration (Fig. 6). Their foundations form two parallel rows along each lateral edge of the dorsum linguae. The papillae of the medial row are less differentiated. The encircling cuts, clearly outlined in lateral rows, are markedly shallower, the developing papillary stroma is lower. The stroma of the developing circumvallate papilla is encompassed with a deeply grounded, compact cell band. The bottom part of this projection is made up by accumulation of cells derived from the basal epithelial layer (Fig. 6).

The epithelium of the dorsal surface of the circumvallate papilla contains taste buds at varying stages of differentiation. Cells observed most frequently have oval shapes and passed through nearly the entire thickness of the epithelium. Their texture is considerably thinner than that of the surrounding epithelium and two types of nuclei can be discerned: small oval hyperchromatic nuclei and large oval nuclei with diffuse chromatin. The taste buds are covered with two or three layers of flat epithelial cells that prevent the bud from communicating with the lingual surface (Fig. 6).

Formations characteristic of the previous stage are observed only occasionally (Fig. 5).

The foundations of the aponeurosis linguae is more marked (Fig. 5).

Foetus, 65 days of age (Figs 7 to 10)

The structure of the dorsum linguae resembles that of the previous stage (Fig. 7). The developing stromata of the circumvallate papillae mildly broaden and elongate. The other papillae, however, do not show any changes in either number or shape as compared with those of the 60-day-old foetus.

The epithelium of the dorsum linguae is more compact in structure. The top epithelial cells get gradually flatter, as do their nuclei, and form several continuous layers on the mucosal surface (Fig. 10). The epithelium projects between the papillae forming compact cell bands. These are particularly marked in circumvallate papillae where they indicate the future encircling trench (Fig. 7). The lower part of the band forms a pestle-like base which penetrates deep into the lamina propria mucosae, later giving rise to ducts of the gustatory glands (Fig. 10).

Taste buds at different stages of differentiation are seen in increasing numbers largely in the epithelium of the dorsal surface of circumvallate papillae. The inner structure is similar to that of the 60-day-old foetus, but the shape is elongated and narrower. Taste buds are also found on the dorsal surface of still undifferentiated papillae near to the medial line of the dorsum linguae (Fig. 9). Foundations of taste buds in the form of cell clusters are occasionally observed. They are totally different from the structures described above but already had two differentiated types of nuclei (Fig. 8). The buds appear to have more nuclei with diffuse chromatin than polychromatic ones. The basal parts of the buds partly get into the stroma of the papilla. The basal membrane under the bottom of the bud forms an extrusion and separates the bud from the papillary stroma. The cells of the basal layer of the epithelium attached to the taste bud elongate in shape and their nuclei become rod-like. The cells gather tightly along the sides of the taste bud (Fig. 9).

The basis of the aponeurosis linguae is narrower, cells are packed together and the whole layer resembles a connective tissue band (Fig. 8).

Foetus, 76 days of age (Figs 11 and 12)

The dorsum linguae does not differ significantly from that seen at the previous stage. The foundations of the papillae are slimmer and taller the spaces between them are filled with epithelial projections and the surface epithelial layer is thicker (Fig. 11). The epithelium contains numerous cells which, towards the surface, get flatter. Their nuclei gradually lose the ability to stain.

The projections surrounding the circumvallate papillae are particularly large and prominent. Their lower regions penetrate beneath the papillary, producing the reduced base characteristic of the circumvallate papillae (Fig. 11). Below the projections in the lamina propria mucosae, glandular ducts with first signs of lumina were apparent; their secretory regions begin to develop deeper in the lingual musculature (Fig. 11).

Taste buds were observed ont only in the dorsal epithelium of the circumvallate papillae but also in the epithelium of their walls. Apart from it, more taste buds were seen in the epithelium of still undifferentiated papillae situated near the central part of the tongue. The buds were round in shape with the nuclei of the two types described before accumulated in the upper half of the bud. As before, the large nuclei with diffuse chromatin are prevalent (Fig. 12). The buds are covered with several layers of epithelial cells preventing contact with the mucosal surface. The base of the taste bud is embedded in the lamina propria mucosae and separated from it by a fold of the basal membrane.

In the dorsal epithelium of some papillae found in the medial third of the tongue, taste buds had the forms of cell clusters similar in distribution and appearance to those seen at the previous stage.

The developing aponeurosis linguae is similar in appearance to that in the 65-day-old foetus (Fig. 11).

Foetus, 85 days of age (Fig. 13)

Growing papillae are beginning to protrude above the surface of the tongue. The pattern of irregularities is in accordance with the stage of differentiation (Fig. 13). The surface epithelium is similar in both appearance and structure to that of the previous stage. In the surface cells, however, the ability of nuclei to stain is further reduced.

At this stage the shape of the papillary stroma enabled us to distinguish some other papillary types, particularly the conical or fungiform ones. Each epithelial projection has a very fine line running through the middle part of it, composed of flat cells with rod-like nuclei. This line indicating a future trench reaches up to the middle of the papilla (Fig. 13).

The circumvallate papillae of this stage are the largest structures in the lingual epithelium. They have already attained the typical shape and, from the basal region of encircling projections, they send out luminized and branched ducts of the gustatory glands that penetrate through the aponeurosis linguae and join with numerous secretory regions situated among muscle fasciculi.

The papillary stroma contains a great numbers of veins which, in some instances, penetrate under the basal membrane.

Taste buds are located in the epithelium of the dorsal surface and the walls of the circumvallate papillae (Fig. 13). They are most frequently oval in shape and are distributed in a manner similar to that found in the 76-day-old foetus (Fig. 13). The buds having this structure, however, are completely limited to the epithelium. Spherical buds occur less frequently and were observed mainly on the dorsal surface of the circumvallate papillae.

The aponeurosis linguae acquires the definite structure.

Foetus, 93 days of age (Figs 14 to 16)

The mucosa of the dorsum linguae is broken into papillae separated by narrow clefts of varying depths produced by cleavage of compact epithelial projections (Fig. 14). The papillae are differentiated into three types: fungiform, conical and circumvallate (fig. 14).

The circumvallate papillae are separated from the surrounding mucosa by deep furrows the bottoms of which are the starting points of distinct luminized and branched ducts of the gustatory glands. The ducts pass through the aponeurosis linguae and get inserted deep into the lingual musculature where they make contact with numerous secretory regions (Fig. 14).

The epithelium of both the dorsal surface and the walls of the circumvallate papillae bears taste buds (Fig. 15). Their shape as well as cell composition resemble those of the 85-day-old foetus. The buds on the dorsum of the papilla reach with their convex surfaces the underside of the epithelium and are covered with only a single layer of very flat cells - the site of a future porus gustatorius (Fig. 16). The bases of the buds push the basal membrane against the lamina propria mucosae (Fig. 16). Buds in the walls of the circumvallate papilla do not go through the whole thickness of the epithelium and are situated closer to the basal epithelial layer; they may even penetrate into the papillary stroma (Fig. 15).

The stroma of the papillae is supplied with numerous richly branched veins (Fig. 16).

Compared with the previous stage, the aponeurosis linguae is more marked but its structure remains unchanged (Fig. 14).

Foetus, 128 days of age (Figs 17 and 18)

The papillae on the tongue surface are clearly separated with deep trench and can be distinguished as circumvallate, fungiform and conical (Fig. 17).

The epithelium has an appearance similar to that in the 93-day--old foetus. The lamina propria mucosae extends against the epithelium on the papillary surface forming fine secondary papillae.

The circumvallate papillae, in comparison with the previous stage, are larger in size, with deep encircling trenches reaching down to the papillary base. The trench bottom gives rise to branched ducts of the gustatory glands that are connected with the secretory regions situated among muscle fasciculi (Fig. 17).

Numerous taste buds are found in the epithelium of both the dorsal surface and the upper part of the walls of the circumvallate papillae (Fig. 18). The buds have a shape of elongated oval and, similarly to the previous stage, their convex bases push the basal membrane against the lamina propria mucosae (Fig. 18). The bud passes through the whole thicknes of the epithelium reaching with its upper pole the level of surface cells. In some buds the porus gustatorius can clearly be seen. The buds are composed of spindle-shaped cells with the nuclei as characterized before (Fig. 18).

The lamina propria mucosae is reduced to the papillary stroma whose lower margin is formed by the distinct aponeurosis linguae (Fig. 17).

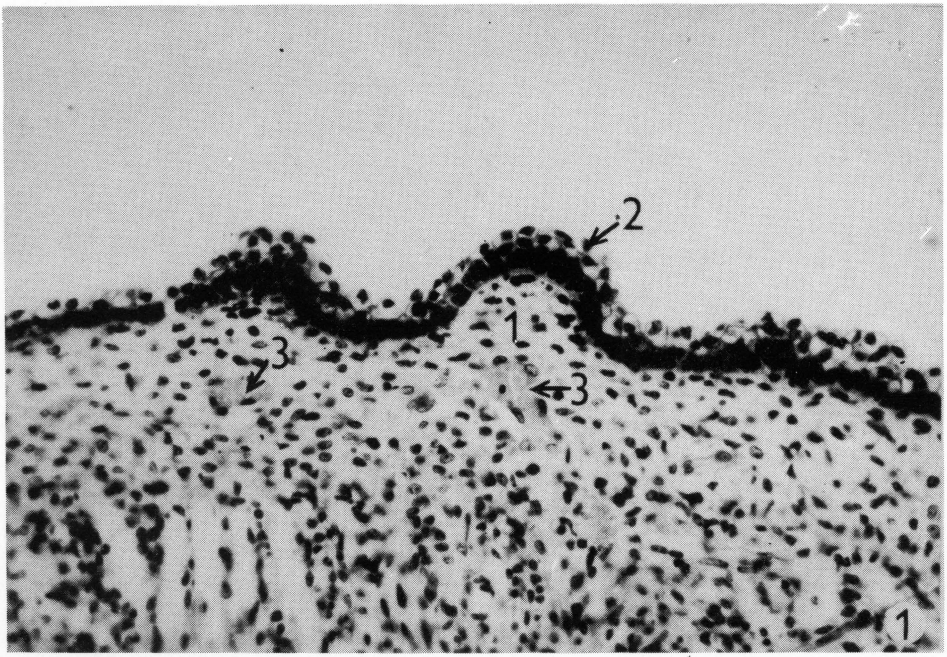
Adult animal, 450 days of age (Figs 19 and 20)

The mucosa of the dorsum linguae in the adult animal bears papillae whose type, shape, structure and size are typical of the species.

The surface epithelium does not differ in structure from that found in the 128-day-old foetus. The fine secondary papillae stretching from the lamina propria mucosae against the epithelium are longer and occur in greater numbers than in the foetus mentioned (fig. 19).

We were interested particularly in the appearance of the circumvallate papilla - the most important carrier of taste buds. The papilla has the typical shape, the encircling trench is widely open and its bottom gives rise to ducts of the gustatory glands (Fig. 19). The secretory regions of the glands are situated in clusters near the base of the circumvallate papilla.

The distribution of tate buds, as compared with the foetus at 128 days, is limited to the epithelium of the papillary walls. The buds run through the whole epithelium and have the pori gustatorii open. The structure, shape and appearance of taste buds in adult animals are similar to those in the foetus at the previous stage of development (Fig. 20).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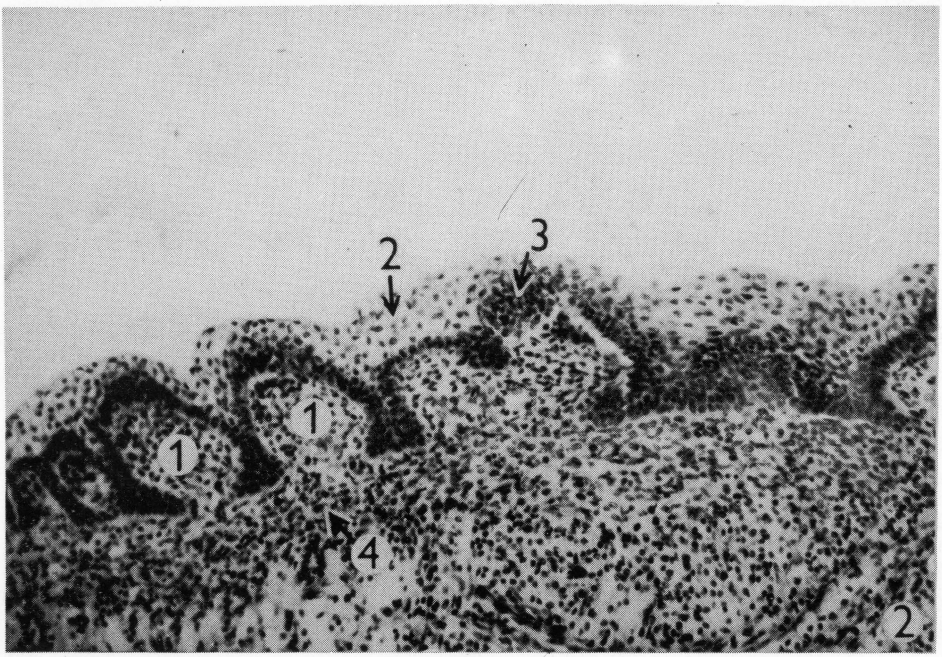
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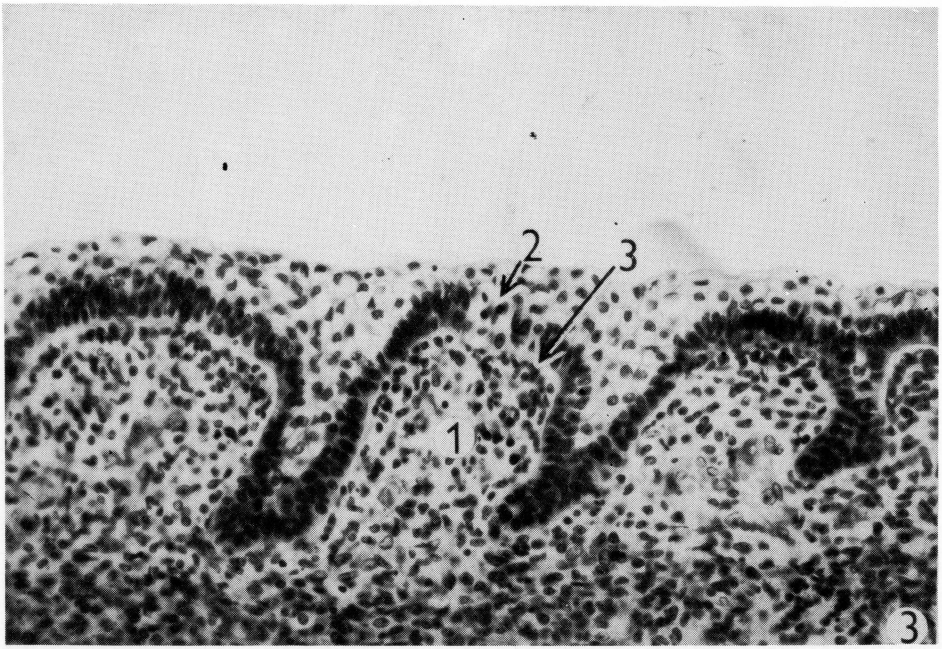
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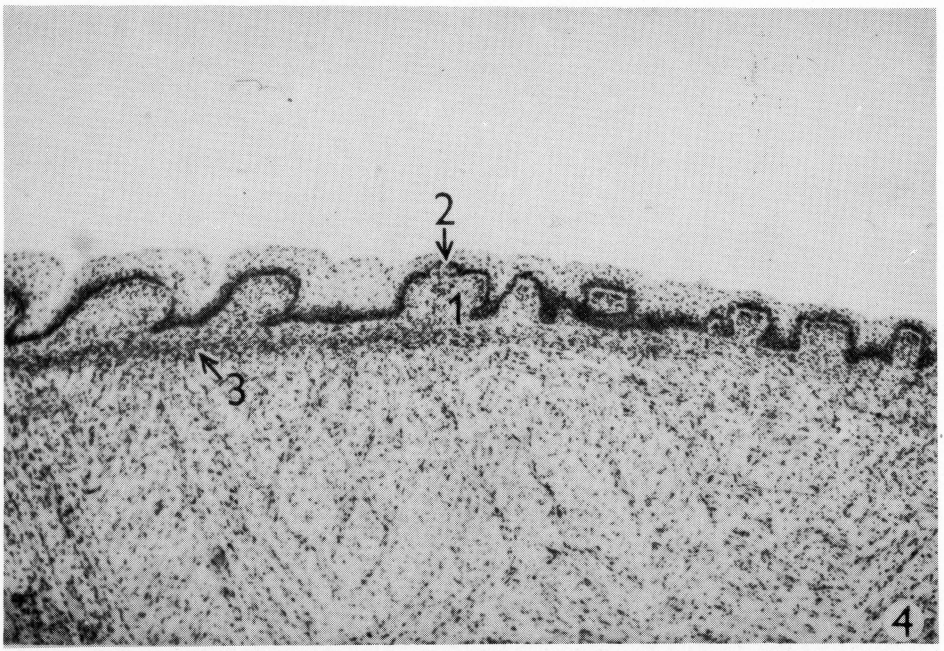
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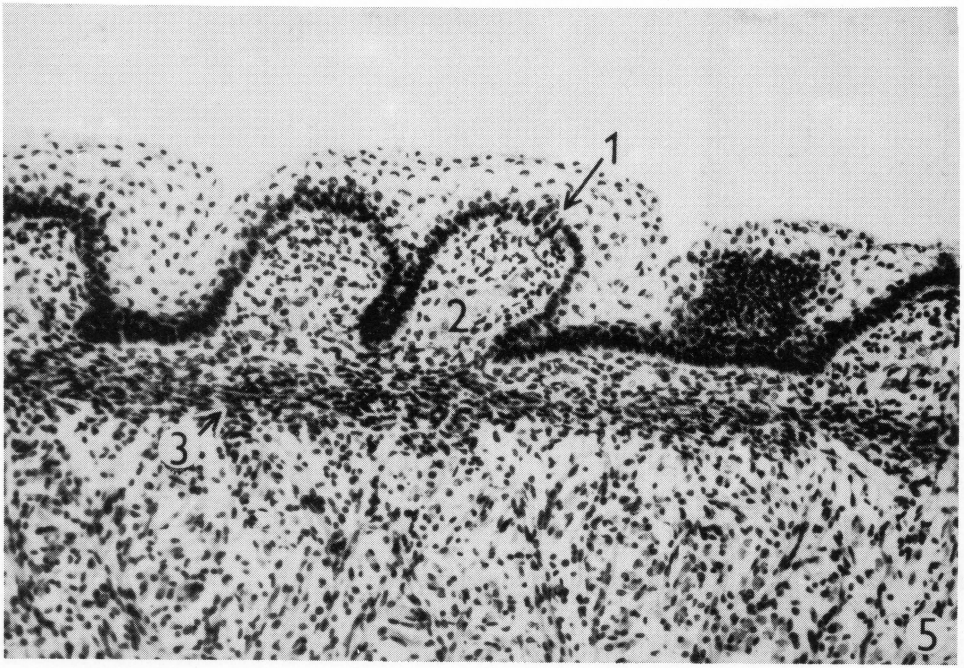
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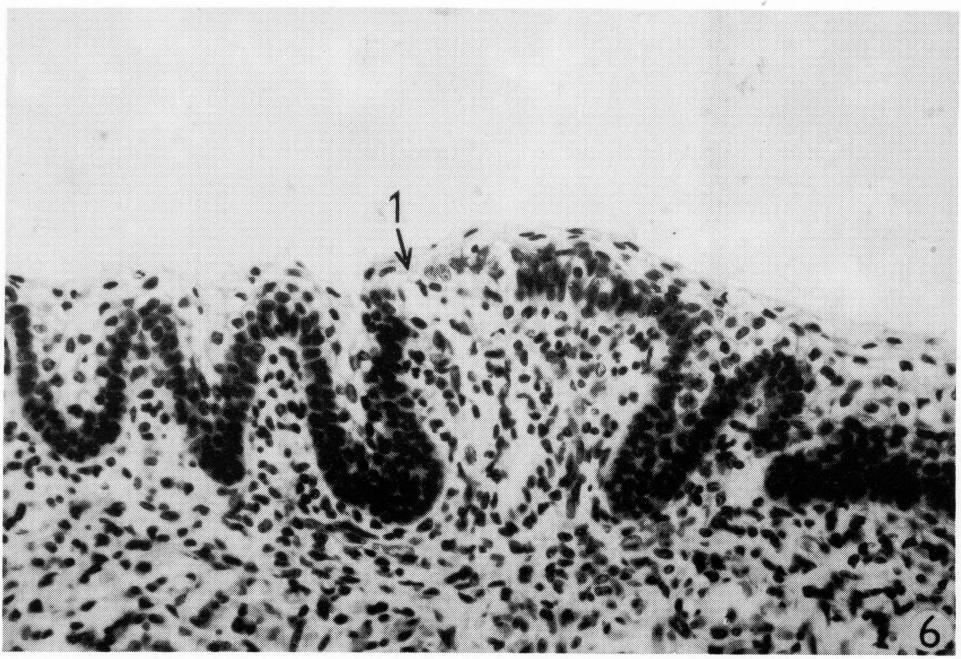
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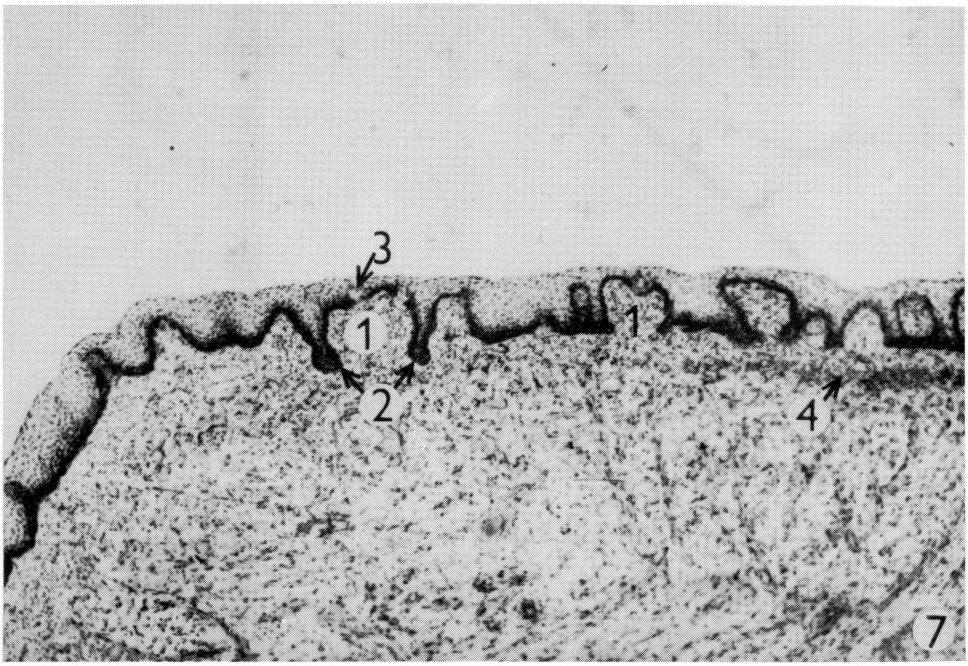
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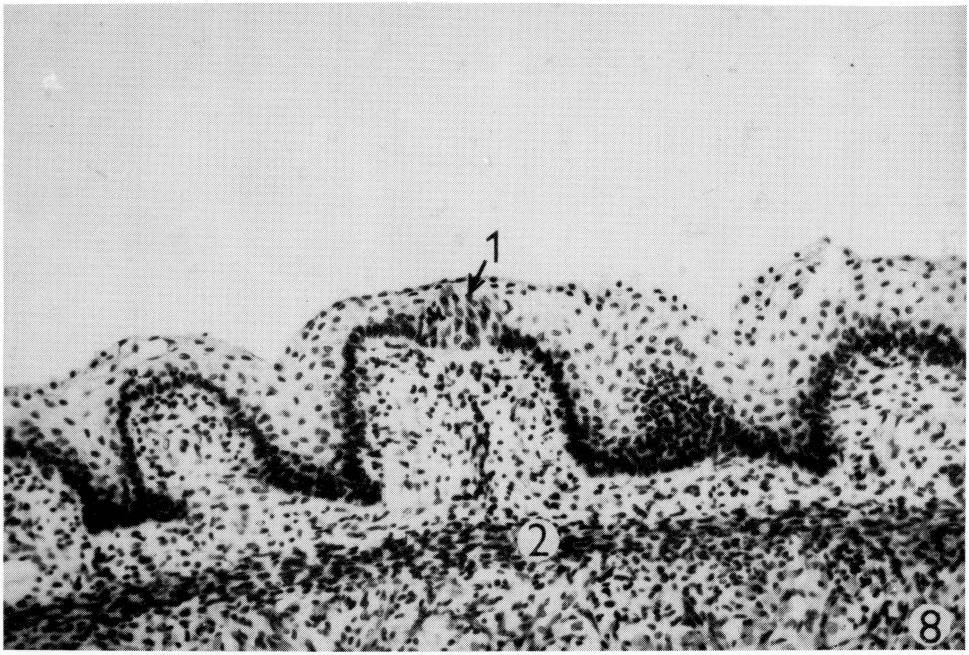
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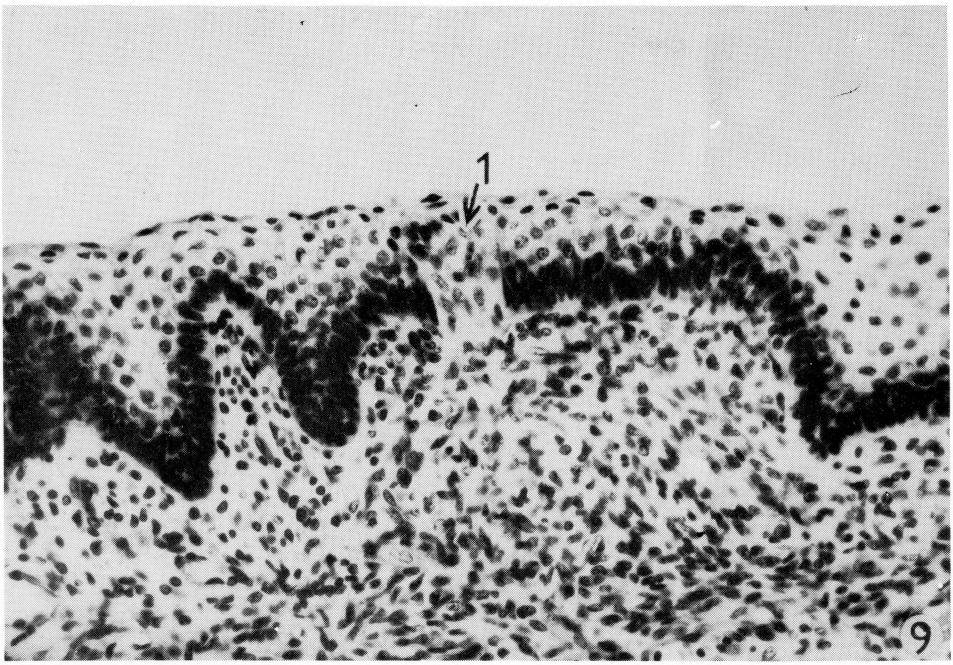
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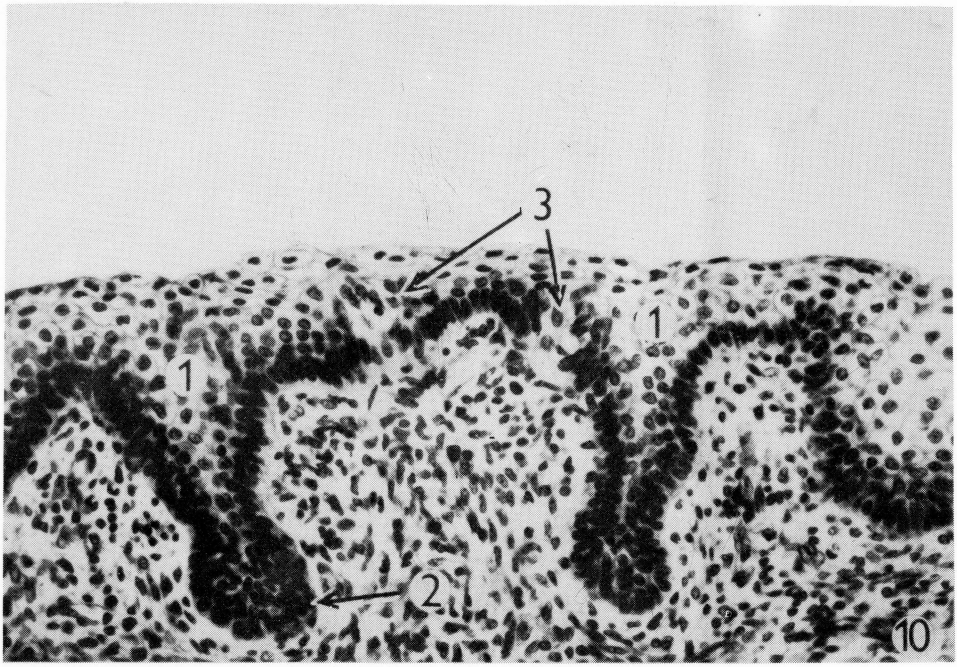
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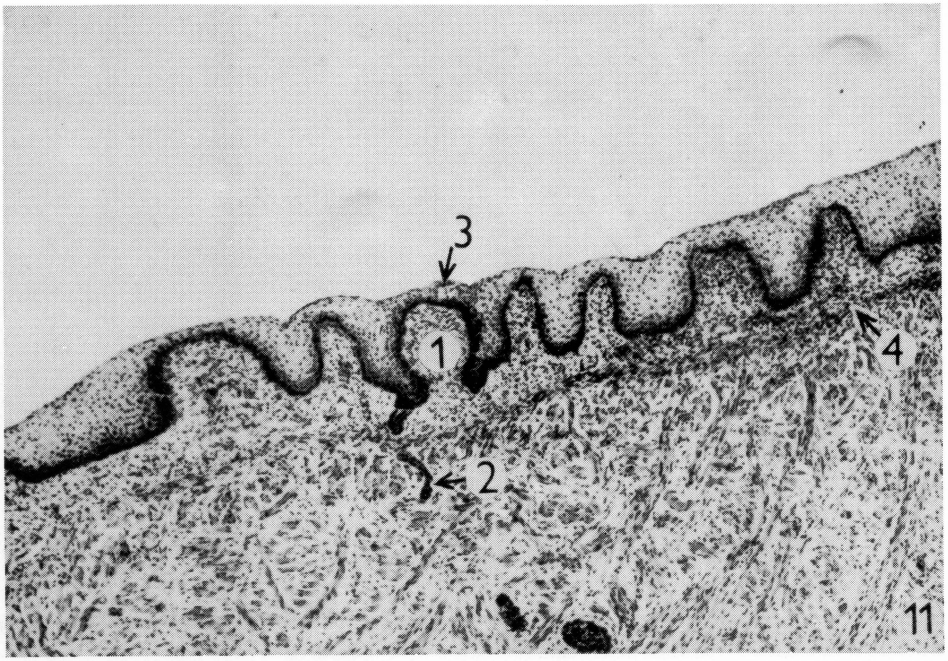
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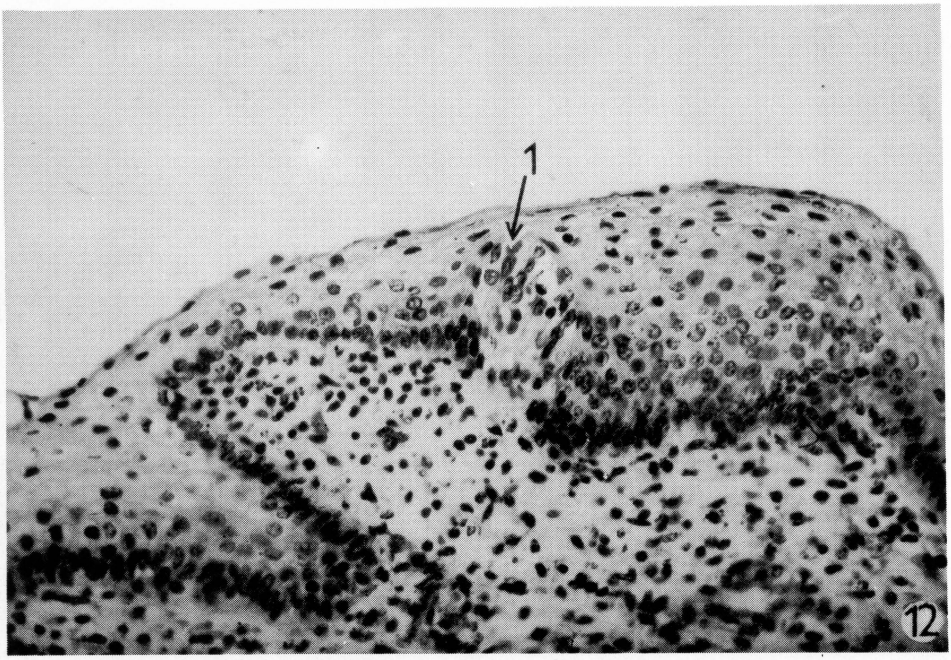
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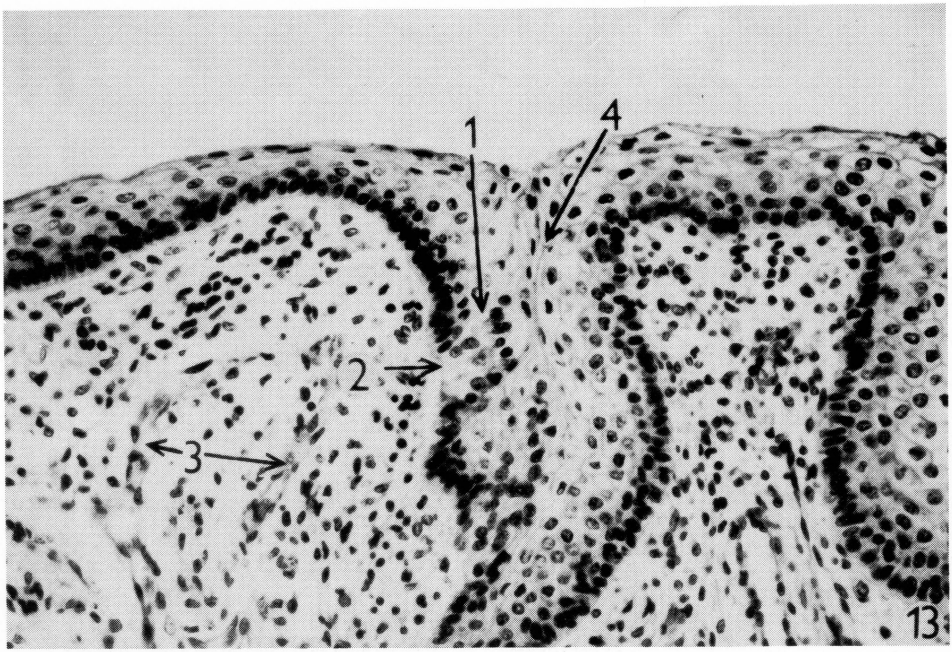
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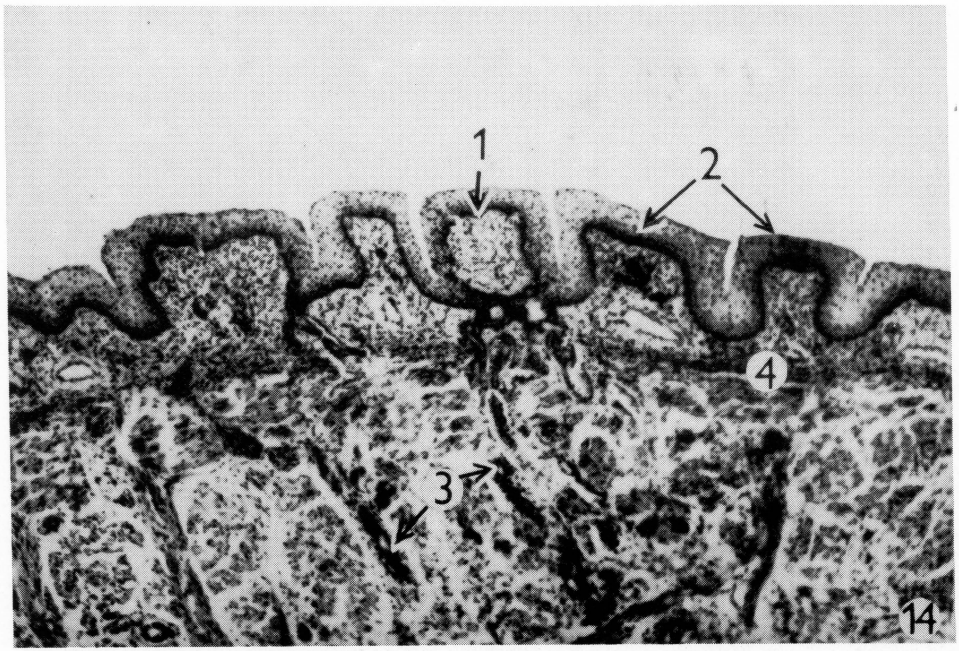
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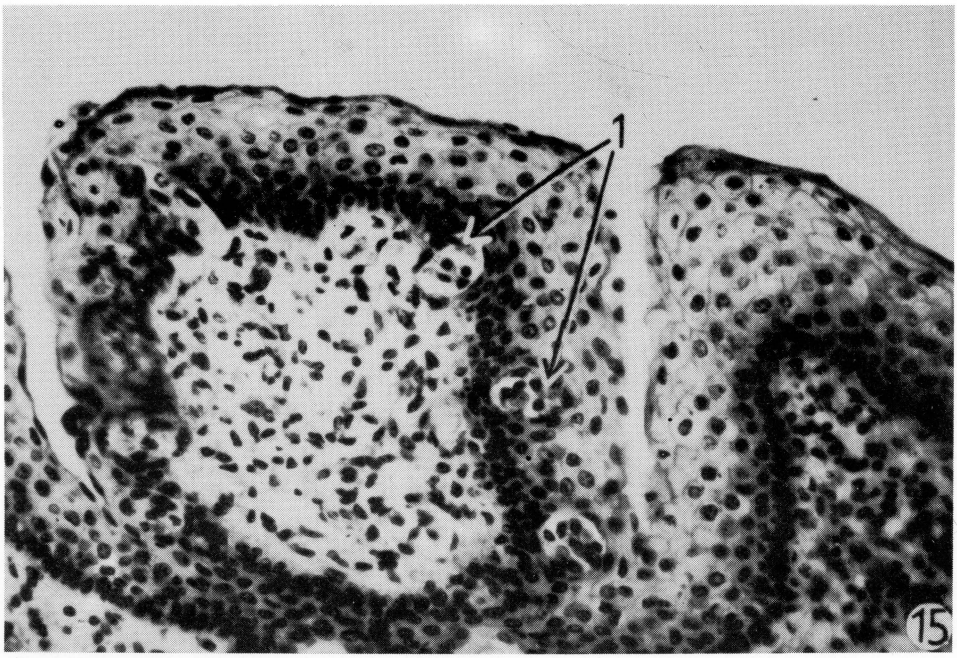
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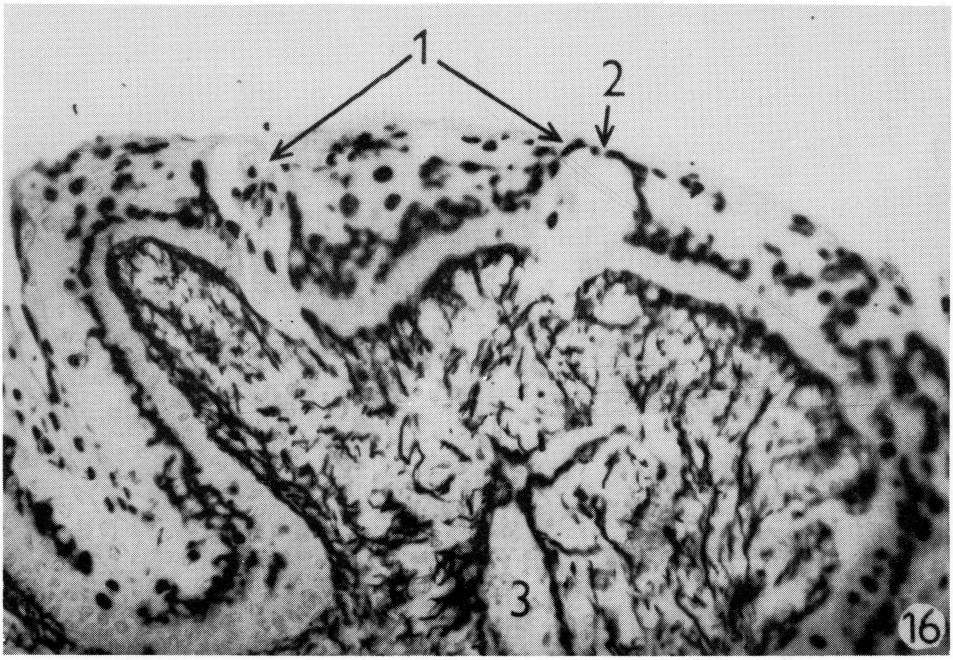
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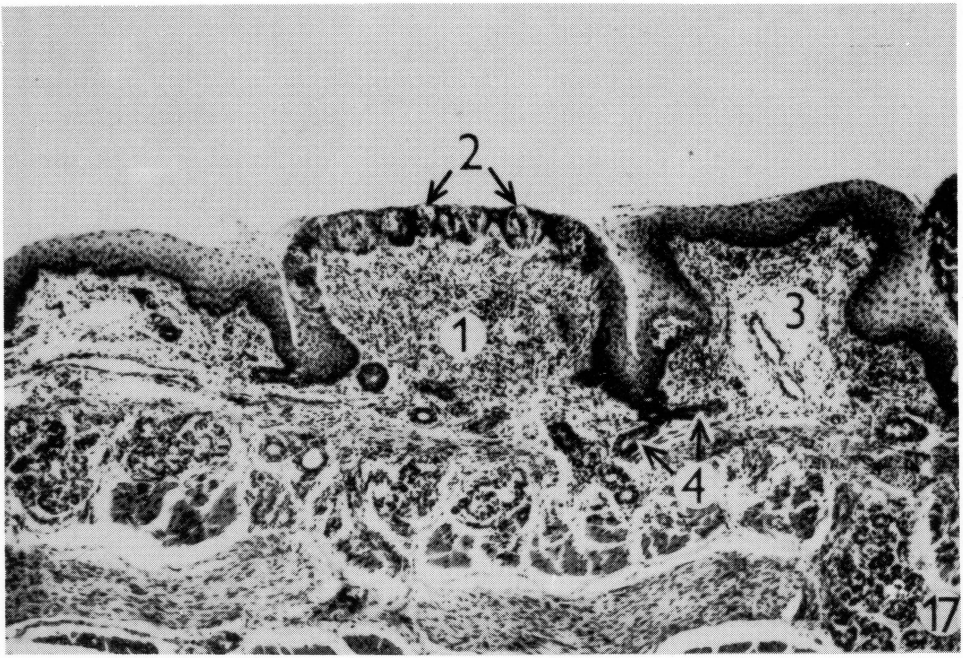
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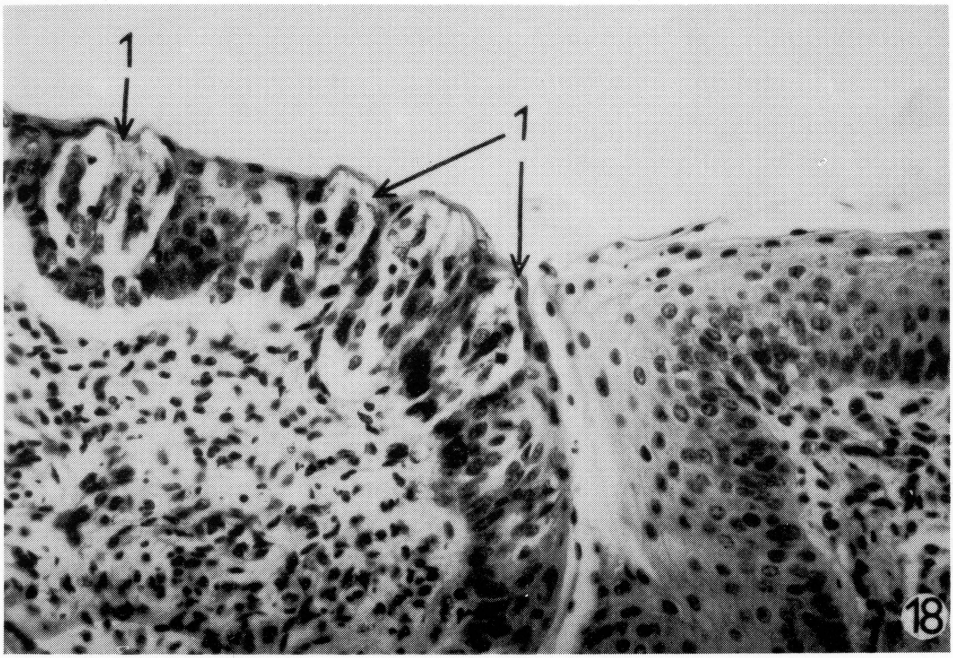
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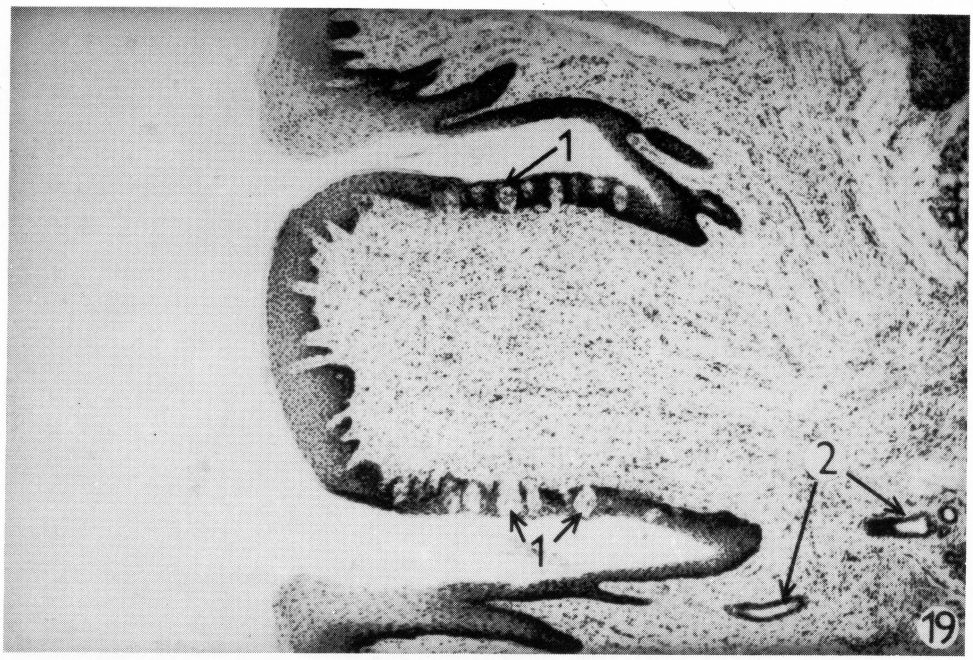
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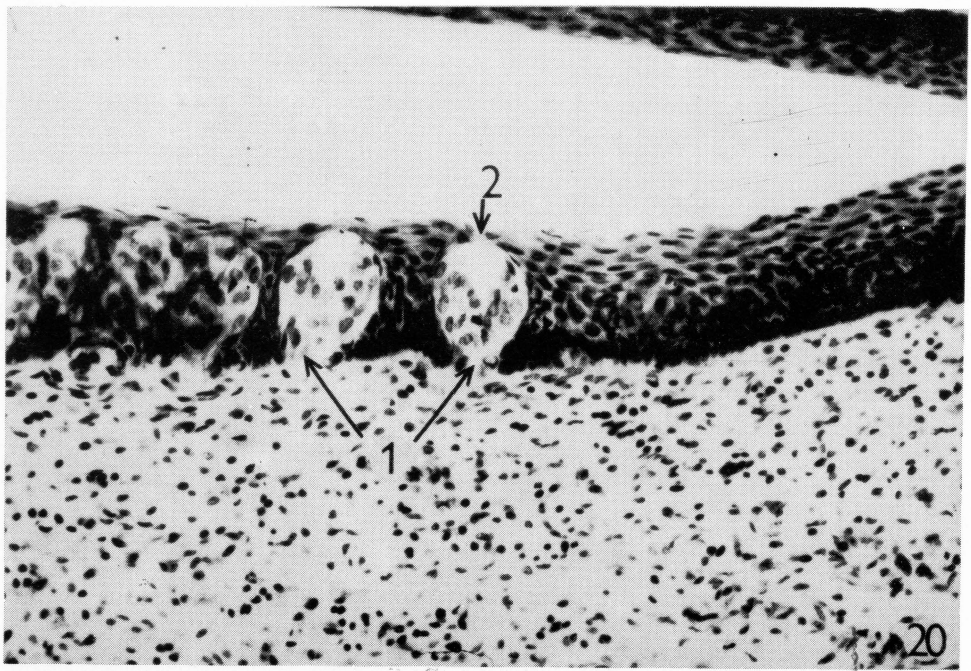
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Discussion

Studies on taste buds published up to now have provided comprehensive information on the shape, size, origin and development of the buds, on different types of cells involved and their ultrastructural characteristics, and on mechanisms governing perception of taste.

Only incomplete data, however, are available on exact timing of the foundation, distribution, development of shape and changes in topography of the taste buds of farm animals in relation to development of the tongue.

The surface epithelium of lingual mucosa in the sheep undergoes the most marked changes between 50 and 55 days of prenatal development. Our observations show that proliferating epithelial cells fill in the irregularities present on the 50th day and also produce aggregations of identical cells which give rise to taste buds. Some changes in shape can also be seen in the adjacent epithelial cells, which implies their association with the developing bud. These cells, referred to as pericalicular, serve as stock material, as suggested by Beidler and Smallman (1965) and Farbman (1965a), ready to replace or supplement cells of the developing bud, and they were found in all the stages studied. They ensure continuous regeneration of cells in the taste bud (Beidler and Smallman 1965, Farbman 1971).

The differentiation of a taste bud is triggered, according to some authors, by contact of epithelial cells with a nerve fibre (Farbman 1965a, 1971; Murray and Murray 1967). The place of contact also determines the site of a future bud. The buds, which were observed particularly in the epithelium of the developing circumvallate papillae, are primarily situated on the dorsal surface, later descending into the walls of the papilla. Since they were observed as late as on the 76th day it can be concluded that their migration is related to two factors: /1/ growth of the papillary connective tissue which, up to this day, has markedly gained in size and /2/ intensive proliferation of epithelial cells particularly on the dorsum of the papilla.

Growth of the papillary connective tissue and proliferation of epithelial cells result in shifting of buds in the epithelium from the surface to the walls of the papilla. It is of interest that the buds are detected before shape differentiation of the papilla is apparent (on days 55 and 60, respectively). An increase in the number of buds in the developing circumvallate papillae was recorded on the 65th day. If it is true that differentiation of the taste bud is induced by a nerve stimulus, then the lateral margins of the tongue with rows of developing circumvallate papilae are bound to have more intensive innervation.

Up to the 60th day, developing buds resembling clusters of cells occur concurrently with those having the typical elongated shape. Buds uniform in type, size and shape were seen on the 128th day, which implies that formation of buds and their differentiation have been finished by this age and further changes will involve only the size and position of the buds in the papilla.

Cells composing the taste bud begin to differentiate on the 60th day of intrauterine development when two cell types with markedly different nuclei can be distinguished. The detailed

structure of these cells in the taste buds of adults has been reported elsewhere (De Lorenzo 1958; Farbman 1965a; Murray et al. 1969; Murray 1973 and others).

At early stages of differentiation, taste buds are situated at the base of the epithelium. With changes in shape and size they also alter their position and appear in the surface epithelium on the 93rd day; the porus gustatorius is completed as late as on the 128th day of intrauterine development. In the following period the taste buds move from the dorsal surface of the papilla to the epithelium of its walls. These observations have not so far been reported in the literature and can, therefore, be considered original findings.

Shape differentiation of the circumvallate papillae begins at about 60 days and is finished by the 93rd day of intrauterine development. Growth of the circumvallate papilla and changes in its size are accompanied by development of an encircling trench and ducts of the gustatory glands. The latter begin to shape as compact epithelial projections on the 65th day, make contact with the secretory regions on the 76th day and are fully luminized by the 85th day of prenatal development. During the same period the cell projection providing the ground for the trench encircling the circumvallate papilla cleaves and gives rise to the complex of gustatory gland ducts opening at the base of the papilla.

On the 85th day of intrauterine development further types of lingual papillae can be distinguished. Our findings demonstrated that in foetal development of the sheep the time between the 76th and 93rd days is an important period during which the mucosa of the dorsum linguae is attaining its definite appearance.

No literature data describing the process of maturation of the lingual mucosa have been found; consequently, our results can be regarded as first of this sort.

Conclusions

In this paper we studied the differentiation of surface structures of the lingual mucosa in sheep with particular concern for the development and appearance of the circumvallate papillae and the morphogenesis and localization of taste buds and related structures. On the basis of our findings the following conclusions can be drawn:

1. Taste buds are first observed in the epithelium of the dorsal surface of papillae on the 55th day and their differentiation is completed by the 128th day of intrauterine development.
2. Taste buds increase in number from the 65th day of development.
3. At early stages, the buds are located to the epithelium of the dorsal surface of a circumvallate papilla. Later they move to the epithelium of papillary walls in the area of the encircling trench. This is first recorded on the 76th day of prenatal development.
4. The differentiation of various cell types within the taste bud can be followed from the 60th day of prenatal development.
5. The porus gustatorius opens on the 128th day.

6. Circumvallate papillae begin to develop on the 60th day and achieve their typical appearance on the 93rd day of intrauterine development.
7. Ducts of the gustatory glands are founded on the 65th day, they connect with the secretory regions on the 76th day and their luminization is completed by the 85th day of intrauterine development. They open into the trench encircling the circumvallate papilla, which has also been formed during this period.
8. The other types of lingual papillae differentiate in shape between the 85th and 93rd day of intrauterine development.

Morfogeneze hrazené papily a diferenciace chuťových pohárků u ovce v ontogenezi

V práci je popsána morfogeneze hrazených papil a diferenciace a distribuce chuťových pohárků v epitelu jazyka ovce během ontogeneze.

Byly odebrány jazyky fetů ovce ve stáří 50, 55, 60, 65, 76, 85, 93 a 128 dnů po oplození a jazyk dospělých jedinců. Byl sledován vzhled struktur sliznice jazyka se zaměřením na morfogenezi hrazených papil a na diferenciaci chuťových pohárků v jejich epitelu. Současně byla věnována pozornost vývoji a utváření gll. gustatoriae a jejich vývodů, vzniku brázdy, ohraničující hrazenou papilu, diferenciaci dalších typů jazykových papil.

Chuťové pohárky se zakládají v epitelu dříve, než dojde k tvarové diferenciaci papil a jsou lokalizovány nejprve na dorsální ploše papil a teprve později sestupují do epitelu jejich satěn. Počet pohárků se postupně zvyšuje během intrauterinního vývoje jedince. Krátce po vzniku pohárku dochází k diferenciaci jeho buněk ve dva typy.

Hrazené papily nabývají typického tvaru poněkud dříve, než dojde ke vzniku obkružující brázdy.

Základy vývodů gll. gustatoriae se objevují současně s tvarovou diferenciací hrazené papily a luminizují až se vznikající brázdou.

Морфогенез желобоватого сосочка и дифференциация вкусовых сосочков овцы в онтогенезе

В работе приводятся описание морфогенеза желобоватых сосочков, дифференциация и распределение вкусовых сосочков в эпителии языка в ходе онтогенеза.

Отбирали языки плодов овцы в возрасте 50, 55, 60, 65, 76, 85, 93 и 128 суток после оплодотворения и языки взрослых особей. Обследовали внешний вид структур слизистой языка с упором на морфогенез желобоватых сосочков и на дифференциацию вкусовых сосочков в их эпителии. Внимание одновременно уделяли развитию и формированию gll. gustatoriae и их выводным протокам, возникновению ограничивающей желобоватый сосочек борозды, дифференциации типов сосочков языка.

Вкусовые сосочку формируются в эпителии дифференциации формы сосочков и расположены сперва дорсальной плоскости сосочков и только немного позже доходят до эпителия их стенок. Численность вкусовых сосочков постепенно увеличивается в процессе внутриутробного развития индивида. Вскоре после возникновения сосочка происходит дифференциация его клеток на два типа.

Желобоватие сосочки приобретают форму несколько раньше возникновения окружающей борозды.

Основа протоков gll. gustatoriae появляется одновременно с дифференциацией формы желобогатого сосочка, люминизируя лищь с возникающей бороздой.

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Legends to Figures

Fig. 1. Part of the lingual surface in an ovine foetus 50 days old. Connective tissue of a primitive papilla (1) is covered with several layers of epithelial cells (2). Veins in thin connective tissue of the lamina propria mucosae (3). Stained with HE. x 160.

Fig. 2. Lingual surface of an ovine foetus 55 days old. Undifferentiated papillae (1) are covered with a thick epithelial layer (2). Developing taste bud (3). Aponeurosis linguae beginning to develop (4). Stained with HE. x 100.

Fig. 3. Detail of the lingual surface in a foetus 55 days old. Papilla (1) with foundations of a bud in the basal epithelial layer (2). Basal membrane (3). Stained with HE. x 160.

Fig. 4. Dorsum linguae in a 60-day-old ovine foetus. Circumvallate papilla begins to take shape (1). Developing bud (2). Aponeurosis linguae (3). Stained with HE. x 40.

Fig. 5. Lingual papillae without shape differentiation in a 60--day-old foetus. Developing taste bud (1). Vein (2) in connective tissue of the papilla. Aponeurosis linguae (3). Stained with HE. x 100.

Fig. 6. Developing circumvallate papilla at 60 days of prenatal development with a bud beginning to take form (1). Two types of nuclei can be distinguished. Stained with HE. x 160.

Fig. 7. Dorsum linguae in a foetus 65 days old. Developing circumvallate papillae (1). Ducts of the gustatory glands begin to form (2). Taste buds in the epithelium (3). Aponeurosis linguae (4). Stained with HE. x 40.

Fig. 8. Undifferentiated papilla on the lingual surface at 65 days. Foundations of a taste bud (1) in the epithelium. Connective tissue of the aponeurosis linguae is denser (2). Stained with HE. x 100.

Fig. 9. Differentiating papilla on the tongue of a 65-day-old foetus with a taste bud (1) in the epithelium. The bud is surrounded by elongated nuclei of the pericalicular cells of the basal epithelial layer. Stained with HE. x 160.

Fig. 10. Developing circumvallate papilla at 65 days. Compact cell bands as the origin of a papillary trench (1). Its pestle-shaped base will later give rise to ducts of the gustatory glands (2). Buds developing in the epithelium of the dorsal surface of the papilla (3). Stained with HE. x 160.

Fig. 11. Lingual surface in an ovine foetus 76 days old. Foundations of a circumvallate papilla (1). A section through a developing duct of the gustatory glands (2). Taste bud in the epithelium of the dorsal surface (3). Aponeurosis linguae (4). Stained with HE. x 40.

Fig. 12. Undifferentiated papilla on the lingual surface in an ovine foetus 76 days old. TasteTaste bud having a typical shape (1) with two kinds of nuclei. Stained with HE. x 160.

Fig. 13. Part of a circumvallate papilla in a 85-day-old ovine foetus. Taste bud (1). Basal membrane (2). Veins in connective tissue of the papillary stroma (3). Line indicating the future cleft of the cell band (4). Stained with HE. x 160.

Fig. 14. Lingual surface at 93 days of foetal development. Circumvallate papilla (1) with taste buds. Other types of lingual papillae (2). Sections through ducts of the gustatory glands (3) in connective and muscle tissue. Aponeurosis linguae (4). Stained with HE. x 40.

Fig. 15. Circumvallate papilla in a 93-day-old foetus with numerous taste buds (1) in the epithelium. Stained with HE. x 160.

Fig. 16. Circumvallate papilla in a 93-day-old foetus. Taste buds (1) in the epithelium of the dorsal surface. Developing porus gustatorius (2). Vein in the papillary stroma (3). Impregnated with Gomori's and nuclear red stains. x 160.

Fig. 17. Part of the lingual surface in a foetus 128 days old. Circumvallate papilla (1) with numerous taste buds (2) in the dorsal surface. Fungiform papilla (3). A section through ducts of the gustatory glands (4). Stained with HE. x 40.

Fig. 18. Part of a circumvallate papilla in a 128-day-old foetus. Taste buds (1) in the epithelium of both the dorsal surface and walls of the papilla. Note the two types of nuclei. Stained with HE. x 160.

Fig. 19. Circumvallate papilla in an adult sheep. Taste buds in the wall epithelium (1). Ducts of the gustatory glands (2). Stained with HE. x 40.

Fig. 20. Part of the papilla wall in an adult sheep. Taste buds in the epithelium (1). Open porus gustatorius (2). Stained with HE. x 160.