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Prenatal Development of Palatal Surface Structures

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Abstract

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The aim of this study was to determine the beginning development of palatal surface. The surface structures were studied by scanning electron microscopy in foetuses and embryos of European pine vole (*Microtus subterraneus,* Arvicolidae, Rodentia). The estimated age of the subjects ranged from 13 to 21 days (pregnancy period is 21 days).

The palatal surface is characterised by ridges (rugae palatinae), the number of which is species-specific (in adult European pine voles 7 to 8). For the purpose of this study, the palate was divided into the rugal area (zone of palatal ridges) and the interrugal area (zone between the individual palatal ridges).

The formation of surface structures in apical parts of epithelial cells was observed in the late embryonic period at ontogenesis days (OD) 12.5 to 13.5, when the lateral palatal processes were still oriented vertically. The cell surface was characterised by rarely dispersed minute cytoplasmic projections, sometimes arranged into rows along cell borders. In the early foetal period (OD 17 to 18), when the palatal processes were fused, the surface structures formed irregular lines (microplicae) particularly in rugal areas, and numerous short microvilli in the interrugal areas. Later, the individual microvilli merged into lines, which increased and formed a dense tangle of microvilli. Hence, before birth the surface pattern was similar to that seen in adult individuals. The microplication proceeded in adults to the extent that borders of the individual lines became indistinct and the palatal surface attained a pitted appearance.

SEM, microplicae, microvilli, rugae palatinae, palate

Scanning electron microscopy was used to study epithelial surfaces of various mammalian organs by a number of authors. The respiratory epithelium was studied by Lenz (1973), Greenwood and Holland (1972), and Andrews (1979), the corneal epithelium by Blümcke and Morgenroth (1967) and Goller (1990), and the vaginal epithelium by Parakkal (1974). The studies demonstrated the presence of surface cytoplasmic folds on numerous cells, which were termed cytoplasmic folds (Merrilees 1974), microvillar ridges (Harris and Hunt 1975), microridges (Sperry and Warsersug 1976), microrugae (Bánóczy et al. 1980), or microplicae (Blümcke and Morgenroth 1967).

The surface structure of the oral epithelium during the prenatal development was studied in various animal species. Waterman et al. (1973) described progressive changes in the palatal fusion area of mice. Peterková et al. (1987) and Sakamoto et al. (1989) concentrated on the development of palatal ridges in mice.

Schüpbach et al. (1983) monitored the development of the secondary palate of rat including changes in palatal ridge patterns and the fate of the fusion line on the hard and the soft palates.

Meller et al. (1980) described changes in surface topography in pre-fusion stages of the secondary palate development in rabbit embryos, concentrating on changes in surface epithelial cells along the medial edges of palatal processes.

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England et al. (1979), who studied the development of the palate by scanning electron microscopy in the fitch (*Mustela putorius)*, found in the fusion region a surface coating rich in glycoprotein staining positively with ruthenium red. Gulamhusein et al. (1982), who studied palatogenesis in fitch foetuses from OD 27 to OD 29, described two phases of palate fusion: the first was the initial contact of lateral palatal processes associated with the production of cell residues, and the second was cell migration outside the epithelial seam.

Waterman and Meller (1974) investigated pre-fusion changes in the human palatal epithelium, that were similar to those seen in mice, but differed morphologically.

Appleton and Heaney (1977) found distinct among-area differences in the surface pattern of the oral mucosa of adult pig.

Andrews (1976) published a SEM study of surfaces of stratified squamous epithelia of various regions of the digestive tract, cornea, and conjunctiva of macaque, domestic cat, and domestic rabbit. A common feature of all the surfaces under study was the presence of partly keratinised or non-keratinised areas and of characteristic ridged microplicae forming a wide variety of patterns.

Nair and Schroeder (1981) in their comparative study of the epithelial surface of the buccal and labial areas in macaque demonstrated only inconsiderable differences in the density of microplication and described eight patterns of surface structures including (1) the bifurcating type of microplication, (2) the bridge-like type (short links between two microplicae), (3) the ring-like type, (4) simple endings, (5) U turn endings, (6) looped endings, (7) hooked endings, and (8) microvilli.

Cleaton-Jones (1972) in his SEM study of the soft palate epithelium of African green monkeys (*Chlorocebus aethiops*) found among-area differences and attributed them to the degree of keratinisation. In subsequent study Cleaton-Jones (1975) found structural analogy between the surfaces of the buccal and the soft palate mucosae.

Matravers et al. (1982) confirmed his findings by computer analysis, but classified the differences as faint.

Several hypotheses of the function of microplicae have been propounded.

Cleaton-Jones (1972; 1975) and Andrews (1976) suppose that microplicae of the free surface of epithelial cells are inactive residues of cytoplasmic fields that were responsible for interdigitation and adhesion between the stratified cells in the earlier developmental phase. Andrews (1976) attributes them a protective role, because they reduce surface contact areas and minimise frictional resistance between the two opposite surfaces. Nair et al. (1981) confirmed that cell surfaces with microplicae can be found in areas exposed to a higher pressure of the opposite tissue surface or foreign body. Blümcke and Morgenroth (1967) suppose that microplication facilitates laminar flow of secretions. Wassersug and Johnson (1976) hold the opinion that microplication provide a reserve for the expansion of surface cells.

Except for Cleaton-Jones (1972), who propounded the hypothesis that microplication results from denudation of common cellular interdigitations, none of the authors referred to above studied the development of microplication.

The development of palatal ridges has been described in several animal species (Peterková et al. 1987; Sakamoto et al. 1989; Thomas and Rossouw 1991) including the European pine vole (Buchtová et al. 2001; Buchtová et al. 2002 in press), but little attention has been paid to the development surface structures during the prenatal period. Meller et al. (1980) observed microvilli on the surface of some cells in 15- and 16-day-old rabbit embryos and Sakamoto et al. (1989) described microvilli arranged in rows along cell margins and occasionally also in centres of cells of vertical palatal processes in mouse embryos aged 14 days.

The objective of this study was to describe differences in the occurrence of microplication in the prenatal period of which only little is known.

Materials and Methods

Samples for the study were collected from embryos and foetuses of European pine vole (*Microtus subterraneus*, *Arvicolidae, Rodentia*) kept in the embryological collection of the Institute of Anatomy, Histology, and Embryology of the University of Veterinary and Pharmacological Sciences, Brno. Their age was estimated using the "Staging and Ageing" method (Štěrba 1975; 1995). The classification of the embryos and foetuses in terms of Štěrba's comparable stages (SCS) was done on the basis of the crown - rump length (CRL) and external characters. The age estimate varied between 12.5 and 20 days and CRL between 6.8 and 23.0 mm. Gestation period and CRL at birth of this species are 21 days and 23.0 to 27.0 mm).

The material was fixed in 10% formol, washed in distilled water, dehydrated through a graded series (30-100%) of ethanol solutions, dried to critical-point method, coated with gold, and viewed and photographed in the scanning electron microscope Tesla BS 300. The appearance and total length of the surface structures were assessed in the rugal and the interrugal areas. Total lengths of microplicae were measured in areas of 100 μm^2 always in 5 photographs of the area of each comparable stage.

In this study, the surface structures are termed microvilli if their length and width were equal and microplicae if the length exceeded the width.

Results

SCS 5: CRL 6.0 to 7.0 mm, DO 12.5 to 13.5

The secondary palate has not yet fused. Lateral palatal processes were short and vertical. Three rudiments of palatal ridges were distinguished in rostral parts of palatal processes.

The plan view of surface cells was polygonal and their diameter varied between 7.5 and 11.5 μm. Minute cytoplasmic projections, which were apparent at the free cell surface, were more numerous at the cell borders (Plate XI, Fig. 1).

SCS 6: CRL 8.1 to 12.0 mm, DO 14.0 to 16.0

Eight palatal ridges were apparent on the already fused secondary palate (Fig. 2). This pattern of the palatal ridges corresponded to findings in adult individuals. A protruding strip of cells in the area of the palatal seam was an evidence of union of lateral palatal processes and proceeding fusion into a unified secondary palate (Plate XII, Fig. 3).

The cell surface was irregularly undulated and covered by numerous microvilli. The mean cell size was the same as in the preceding stage.

SCS 7: CRL 13.0 to 16.0 mm, DO 17.0 to 18.0 (first foetal stage)

Surface cell structures in the rugal areas had the shape of microvilli (Fig. 4) or irregular lines (microplicae), in which segmentation was still apparent (Plate XIII, Fig. 5). The total length of the microplicae varied between 150 and 180 μm per 100 μm^2. Microplicae in the interrugal areas were arranged into aggregated segmented lines (Fig. 6) with a total length of 200 to 230 μm per 100 μm^2.

SCS 8: CRL 16.0 to 19.5 mm, DO 18.0 to 18.5

Concentric lines around the protruding nucleus (Plate XIV, Fig. 7) or solitary reticulate areas (Fig. 8) of microplicae developed in numerous cells in rugal areas. The total length of microplicae varied between 170 and 230 μm per 100 μm^2.

The initially segmented lines in the interrugal areas changed into continuous microplicae, which begun to interconnect (Plate XV, Fig. 9). The total length of the microplicae varied from 210 to 310 μm per 100 μm^2.

The size of surface cells varied from 15.5 to 22 μm.

SCS 9: CRL 19.0 – 21.0 mm, DO 19.0 - 19.5

The cell surface in the rugal and the interrugal areas was covered with a dense network of microplicae. Individual microplicae were no more distinguishable. The width of microplicae increased considerably and only very narrow spaces were left between the individual branches

(Fig. 10). In the rugal areas the total length of microplicae varied from 230 to 290 μm per 100 μm^2 and in the interrugal areas from 250 to 300 μm per 100 μm^2 (Plate XVI, Fig. 11).

Cell size was the same as in SCS 8 (varied from 15.5 to 22 μm).

Adult

The microvilli increased in size to the extent that their demarcation became indistinct. Advanced fusion made the density determination impossible. Sharply demarcated depressions were formed between the aggregations of microplicae (Fig. 12).

Discussion

Surface structures on palatal epithelial cells in European pine vole began to develop in the late embryonic stage, i.e. at OD 12.5 to 13.5, corresponding to SCS 5. At this time, the lateral palatal processes are directed vertically and the cell surface is covered with scarce cytoplasmic projections. This finding corresponds to observations of Meller et al. (1980) in rabbits. Meller et al. (1980) described microvilli on the surface of boulder-shaped cells at OD 15 and 16, corresponding to SCS 5 (Štěrba 1995). The occurrence of microvilli in mouse embryos at OD 14 (= SCS 5 to 6, Štěrba 1995) was also reported by Sakamoto et al. (1989). In this study, I have not labelled the projections as microvilli, because their exact structure is not apparent from SEM imaging. Therefore, I intend to use transmission electron microscopy to describe the ultrastructure of these projections exactly.

Meller et al. (1980) described the presence of lameliform or filiform cell projections on medial borders of palatal processes at the time of fusion. No such projections were observed in this study, but their existence cannot be denied because of a small number of samples collected immediately before palatal fusion. Cumulation of cell remnants in the fusion area and migration of cells outside the epithelial seam was observed in my study in samples collected at OD 17 to 18. Similar findings in mice were reported by Waterman et al. (1973) and in rabbits by Meller et al. (1980).

Meller et al. (1980) showed not only microvilli, but also short microplicae in rabbits at OD 17 (= SCS 5 to 6, Štěrba 1995) in his pictorial documentation, but did not mention them in comments thereto. Unlike these authors, I did not observe in European pine vole distinct surface structures in the form of microplicae until OD 17, which corresponds to SCS 7 (1st foetal stage).

At the time when the secondary palate was completely developed (1st foetal period, OD 17 to 18), the surface structures in the rugal areas were characterised by irregularly arranged lines (microplicae) and in the interrugal areas by numerous short microvilli or segmented lines. Subsequently, the microvilli amalgamated into lines. Microplicae increased in size and became interconnected by transversal bridges to form a dense network. Rapid development of surface structures in the rugal areas in the prenatal period resulted in their amalgamation and the areas acquired pitted appearance similar to that seen in adults. Such appearance is typical of areas exposed to increased mechanical strain (Cleaton-Jones 1975). In keeping with these findings, I observed the typical pitted appearance of mucosal surface immediately before birth. After birth, the rugal area is exposed to a higher pressure due to milk sucking than the interrugal areas, in which crested arrangement was observed before birth.

Nair and Schroeder (1981) allege that microplicae develop at sites exposed to pressure. My observations indicate that larger numbers of microplicae develop in interrugal areas, where the pressure strain is much weaker, or even zero (prenatal period). The large number of microplicae and their perfect arrangement during the prenatal period are indicative of their probable participation in processes associated with laminar flow of surface secretions (Blümcke and Morgenroth 1967).

The hypothesis of microplicae as a reserve for cell expansion (Wassersug and

Johnson 1976) seems to be unlikely, because their proportion increases during the development. If it were correct, abnormal formation of microplicae should be expected at the beginning of the foetal period when the growth activity in this area culminates. Therefore, our observations do not support the hypothesis.

Nair and Schroeder (1981) observed only sporadic parallel plicae on the surface of buccal and labial mucosae of macaque. My findings shows that parallel microplicae, arranged concentrically around the protruding nucleus as a rule, were very frequent in the rugal areas.

Cleaton-Jones (1975) described microplicae on the surface of cells of non-kretinised oral mucosa and pitted appearance or individual microvilli on the surface of keratinised epithelium. One can speculate on causes of differences in surface patterns between the rugal and the interrugal areas. One of possible explanations is that kratinisation goes on more rapidly in the rugal areas, and therefore the epithelial surface attains pitted appearance, which is typical of adults, before birth already. However, the appearances of the two areas differ entirely. Also unclear are mechanisms of the development of complex surface patterns during the prenatal period. My observations support the hypothesis of progressive amalgamation of microvilli into microplicae which subsequently become interconnected and increase in size. Such hypothesis is opposed by the findings of Cleaton-Jones (1975), who regards microplicae as remnants of interdigitation which earlier provided adhesion among cells of a stratified epithelium. That would mean that the development of the surface structures begins at the time of cell renewal by desquamation of superficial layers. My observations indicate, however, that distinct microplicae were developed already towards the end of the embryonic period and at the beginning of the foetal period, which is the time of increased proliferative activity of the epithelium. Light microscopy shows a significant increase in the number of cell layers (Buchtová et al. in press 2002), but no massive desquamation. Demonstration of an abnormal increase in the renewal of surface cells of the oral epithelium requires an in-depth immunohistochemical study focused on the detection of keratinisation.

Prenatální vývoj povrchových struktur patra

Vývoj povrchových struktur patra byl studován u embryí a fétů *Microtus subterraneus* (Arvicolidae, Rodentia) metodou rastrovací elektronové mikroskopie. Odhadnutý věk vzorků kolísal od 13 do 21 dní (doba březosti je 21 dní).

Na povrchu patra se vyskytují patrové stupně (rugae palatinae), jejichž počet mezidruhově kolísá (u dospělce hrabošíka podzemního je 7-8 rugae palatinae). Pro studium byla oblast patra rozdělena na dvě oblasti: rugální oblast (zóna patrových stupňů) a interrugální oblast (zóna mezi jednotlivými patrovými stupni).

Počátek tvorby povrchových struktur na apikálních částech epitelových buněk byl sledován v pozdní embryonální periodě - v 12,5 až 13,5 den ontogeneze (DO), kdy laterální patrové výběžky ještě směřují vertikálně. Na povrchu buněk se vyskytovaly řídce roztroušené drobné cytoplazmatické výběžky, místy uspořádané do řad podél buněčných hranic.V ranné fetální periodě (v DO 17 - 18), kdy sekundární patro bylo již vytvořeno a zcela uzavřeno, měly povrchové struktury vzhled nepravidelně uspořádaných linií (mikroplik) zejména v rugálních oblastech, a krátkých četných mikroklků v interrugálních oblastech. Později došlo k postupnému splývání jednotlivých mikroklků do linií, jejich mohutnění a tvorbě husté sítě mikroplik, takže již před narozením byl povrch obdobného vzhledu jako u dospělců. U dospělých jedinců rozvoj mikroplik natolik pokročil, že hranice jednotlivých linií byly nezřetelné a povrch patra měl jámovité vzezření.

Acknowledgement

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References

ANDREWS PM 1976: Microplicae: Characteristic ridge-like folds of the plasmalemma. J Cell Biol **68**: 420-429

ANDREWS PM 1979: The respiratory system. In. Hodges, GM, Hallowes, RC: Biomedical research applications of scanning electron microscopy. Academic Press, pp. 177-202

APPLETON J, HEANEY TG 1977: A scanning electron microscope study of the surface features of porcine oral mucosa. J Periodont Res **12**: 430-435

BÁNÓCZY J, LAPIS K, ALBRECHT M 1980: Scanning electron microscopic study of oral leukoplakia. J Oral Path **9**:145-154

BLÜMCKE S, MORGENROTH K 1967: The stereo ultrastructure of the external and internal surface of the cornea. J Ultrast Res **18**: 502-518

BUCHTOVÁ M, PUTNOVÁ I, TICHÝ F, MÍŠEK I 2001: Prenatal development of rugae palatinae in *Microtus subterraneus*. J Morph **248**: 212

BUCHTOVÁ M, TICHÝ F, PUTNOVÁ I, MÍŠEK I 2002: Development of rugae palatinae in *Microtus subterraneus* (Arvicolidae, Rodentia). Acta Zool (in press)

CLEATON-JONES P 1972: Surface ultrastructure of the mucosa of the soft palate in the vervet monkey. S Afr J Med Sci **37**: 101-104

CLEATON-JONES P 1975: Surface characteristics of cells from different layers of keratinized and non-keratinized oral epithelium. J Periodont Res **10**: 79-87

CLEATON-JONES P, FLEISCH L 1973: A comparative study of the surface of keratinized and non-keratinized oral epithelium. J Periodont Res **8**: 366-370

ENGLAND MA, GULAMHUSEIN A, McTURK GLC 1979: The developing ferret palate studied by Ruthenium red staining and scanning electron microscopy. J Anat **129**: 216

GOLLER T 1990: Lichtmikroskopische, raster- und transmissionelekronenmikro- skopische Untersuchungen der Konjunktiva des Hundes. Dissertation, Berlin, pp. 115

GREENWOOD MF, HOLLAND P 1972: The mammalian respiratory tract surface. SEM study. Lab Invest **27**: 296-304

GULAMHUSEIN AP, ENGLAND MA 1982: The developing ferret palate—a scanning electron microscope study: I. Primary palate and secondary palatal shelves. J Craniofac Genet Dev Biol **2**: 107-23

HARRIS JE, HUNT S 1975: The fine structure of the epidermis of two species of salmonid fish, the Atlantic salmon (*Salmo salar L.*) and the brown trout (*Salmo trutta L.*) I. General organization and filament-containing cells. Cell Tissue Res **157**: 553-565

HAWKES JW 1974: The structure of fish skin. I. General organization. Cell Tissue Res **149**: 147-58

LENZ H 1973: Tree-dimensional surface representation of the cilia-free nasal mucosa of man. SEM study. Acta Otolaryng **76**: 47-57

MATRAVERS JM, HEANEY TG, APPLETON J 1982: Computer analysis of the surface ultrastructural features of porcine oral mucosa. Archs Oral Biol **27**: 481-485

McMILLAN MD, KERR MA 1990: A light and scanning electron microscope study of epithelial thickenings and rete ridges in the adult hamster cheek pouch. Archs Oral Biol **35**: 235-240

MELLER SM, PAOLA DP, BARTON LH, MANDELLA RD 1980: Secondary palatal development in the New Zealand white rabbit: a scaning electron microscopic study. Anat Rec **198**: 229–244

MERRILEES MJ 1974: Epidermal fine structure of the teleost *Esox americanus* (Esocidae, Salmoniformes). J Ultrastruct Res **47**: 272-283

NAIR PNR, SCHROEDER HE 1981: Variation and density of microplications in superficial cells of the normal oral lining mucosa in the monkey *Macacus fascicularis*. Archs Oral Biol **26**: 837-843

PARAKKAL PF 1974: Cyclical changes in the vaginal epithelim of the rat seen by scanning electron microscopy. Anat Rec **178**: 529-37

PETERKOVÁ R, KLEPÁČEK I, PETERKA M 1987: Prenatal development of rugae palatinae in mice: scanning electron microscopic and histologic studies. J Craniofac Genet Dev Biol **7**:169-189

SAKAMOTO MK, NAKAMURA K, HANDA J, KIHARA T, TANIMURA T 1989: Morphogenesis of the secondary palate in mouse embryos with special reference to the development of rugae. Anat Rec **223**: 299-310

SCHÜPBACH PM, CHAMBERLAIN JG, SCHROEDER HE 1983: Development of the secondary palate in the rat: a scanning electron microscopic study. J Craniofac Genet Dev Biol **3**: 159-77

SPERRY DG, WASSERSUG RJ 1976: A proposed function for microridges on epithelial cells. Anat Rec **185**: 253-257

ŠTĚRBA O 1975: Prenatal growth of the mole, *Talpa europaea*. Folia Morphol Praha **23**: 282-285

ŠTĚRBA O 1995: Staging and ageing of mammalian embryos and fetuses. Acta Vet Brno **64**: 83-89

THOMAS CJ, ROSSOUW RJ 1991: The early development of palatal rugae in the rat. Austral Dent J **36**: 342-348

WASSERSUG RJ, JOHNSON RK 1976: A remarkable pyloric caecum in the evermannellid genus *Coccorella* with notes on gut structure and function in alepisauroid fishes (Pisces, Myctophiformes). J Zool, Lond **179**: 273-289

WATERMAN RE, MELLER SM 1974: Alternations in the epithelial surface of human palatal shelves prior to and during fusion: A scanning electron microscope study. Anat Rec **180**: 111-136

WATERMAN RE, ROSS LM, MELLER SM 1973: Alterations in the epithelial surface of A/Jax mouse palatal shelves prior to and during palatal fusion. A scanning electron microscope study. Anat Rec **176**: 361-376

Plate XI
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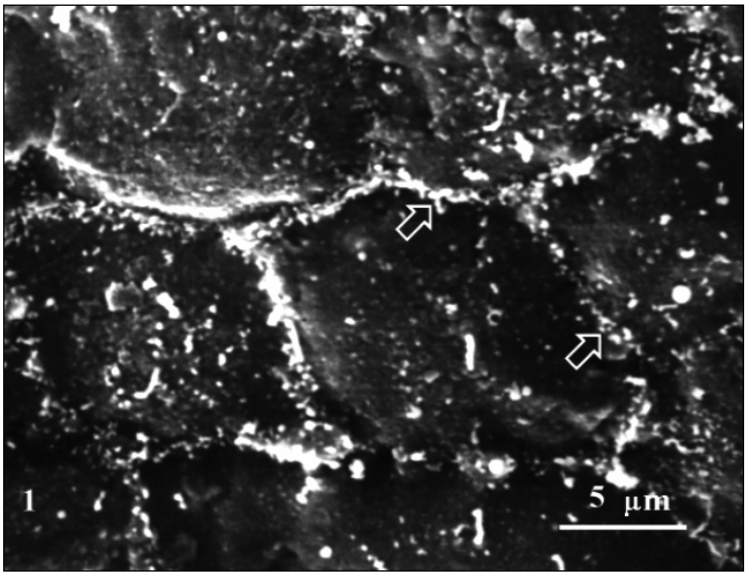

Fig. 1. Rugal area R1. Small cytoplasmic projections on cell surface (➪). SCS5, CRL = 6.8 mm, DO 13.0. SEM × 8 000.

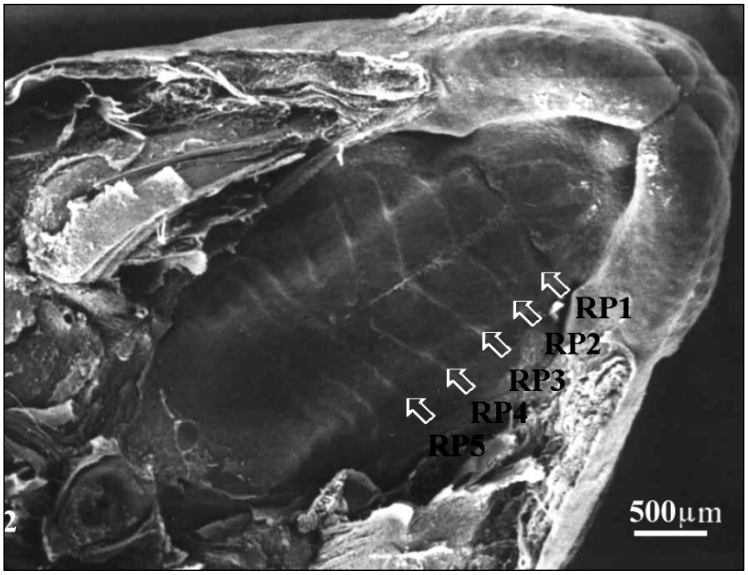

Fig. 2. A view of the whole palate of European pine vole after fusion of palatal processes and development of secondary palate. Arrows show five rostral palatal ridges (RP), which are numbered rostrocaudally. SCS 6, CRL = 10.2 mm, DO 15.0. SEM × 45.

Plate XII

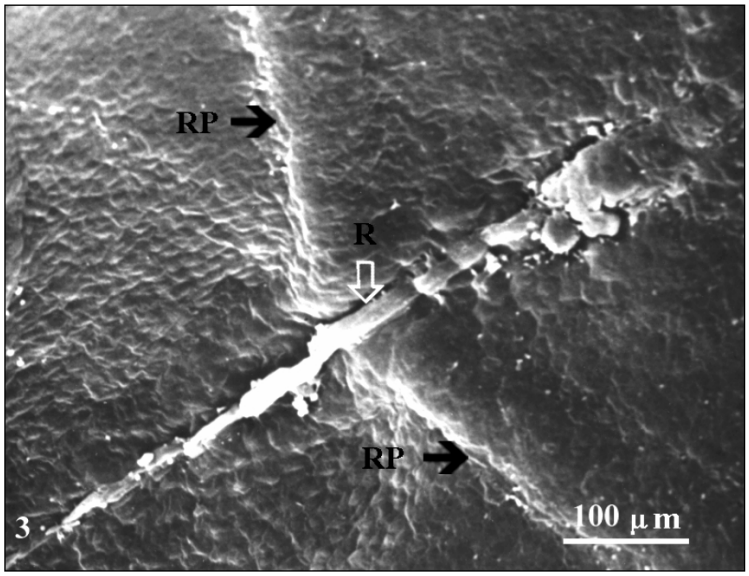

Fig. 3. Palatal seam (R- future raphe palati) and palatal ridge 3 (RP = rugae palatinae) at the time of fusion of lateral palatal processes. Cell remnants (⇨) cells protruding above the surface can be seen in the area of palatal seam. SCS 6, CRL = 10.2 mm, DO 15.0. SEM × 400.

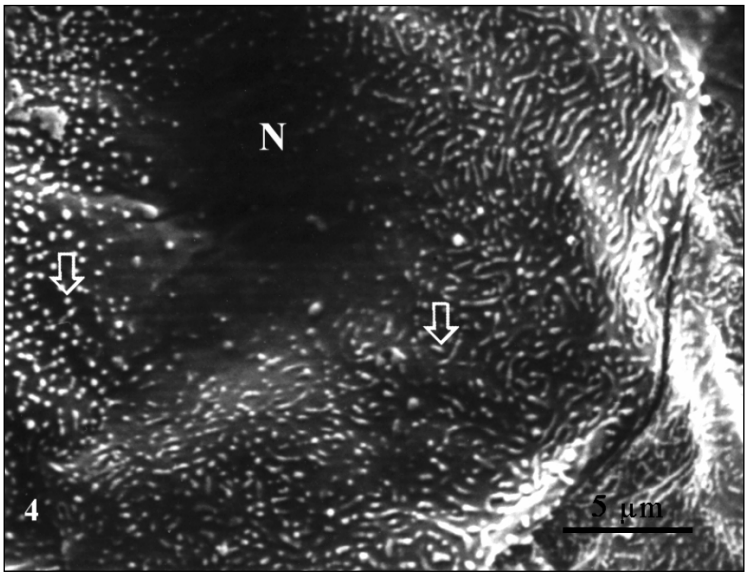

Fig. 4. Rugal area RP 2. Surface structures with the appearance of microvilli (⇨), situated around the nucleus (N). SCS 7, CRL = 15.5 mm, DO 18.0. SEM × 8 500.

Plate XIII

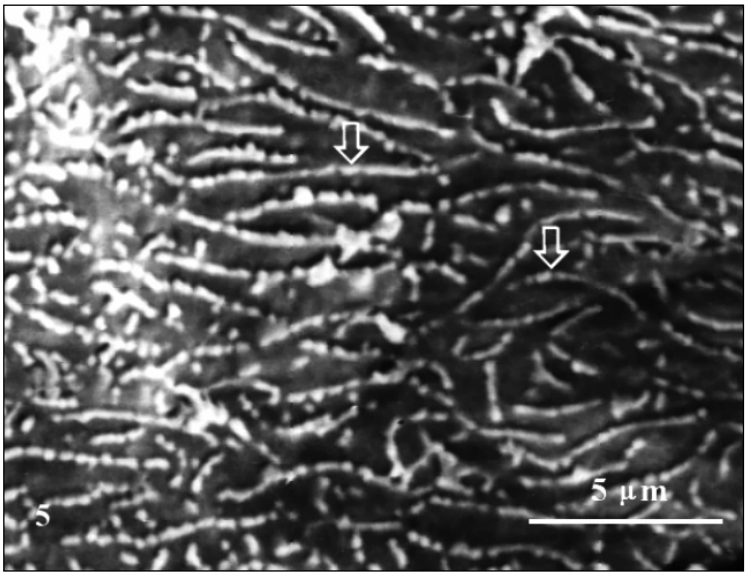

Fig. 5. Rugal area RP 2. Surface structures are arranged into irregular lines - microplicae (⇨). SCS 7, CRL = 15.5 mm, DO 18.0. SEM × 12 000.

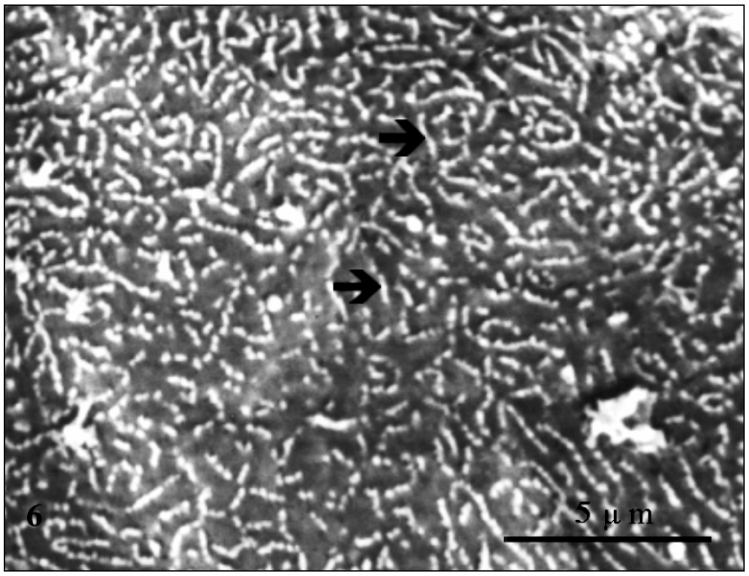

Fig. 6. Interrugal area RP 2-3. Densely aggregated microplicae in the form of short segmented lines (➜) surrounded by a large number of messy microvilli. SCS 7, CRL = 15.5 mm, DO 18. SEM × 12 000.

Plate XIV

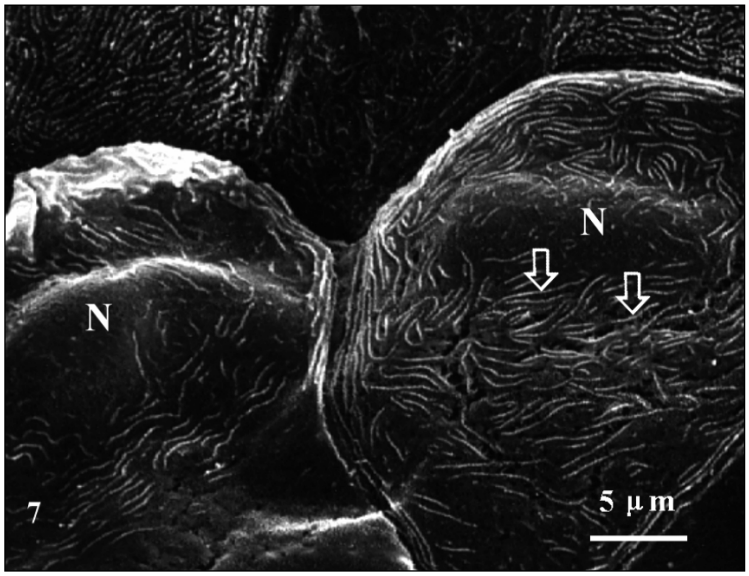

Fig. 7. Rugal area RP 5. Miocroplicae form concentric lines (⇨) around a protruding nucleus (N). SCS 8, CRL = 18.3 mm, DO 18.5. SEM × 6 000.

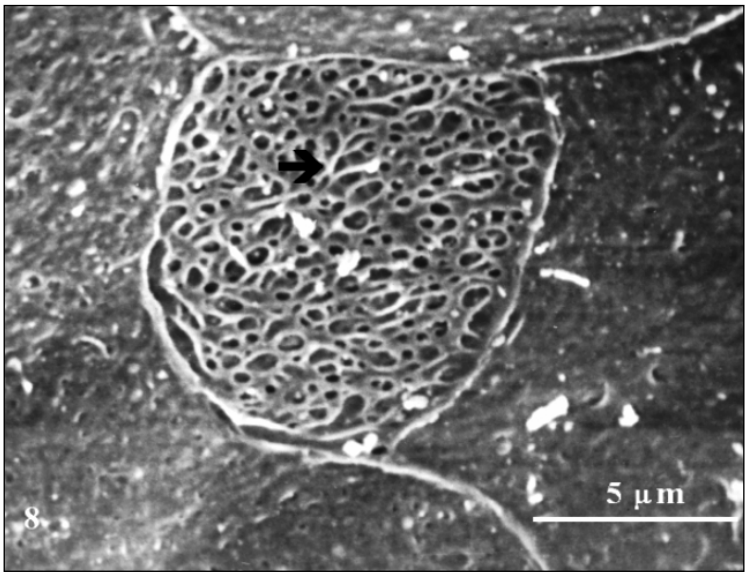

Fig. 8. Rugal area RP 5. A cell with a well developed network of microplicae (➜) is surrounded by surface structure-free cells. SCS 8, CRL = 18.3 mm, DO 18.5. SEM × 12 000.

Plate XV

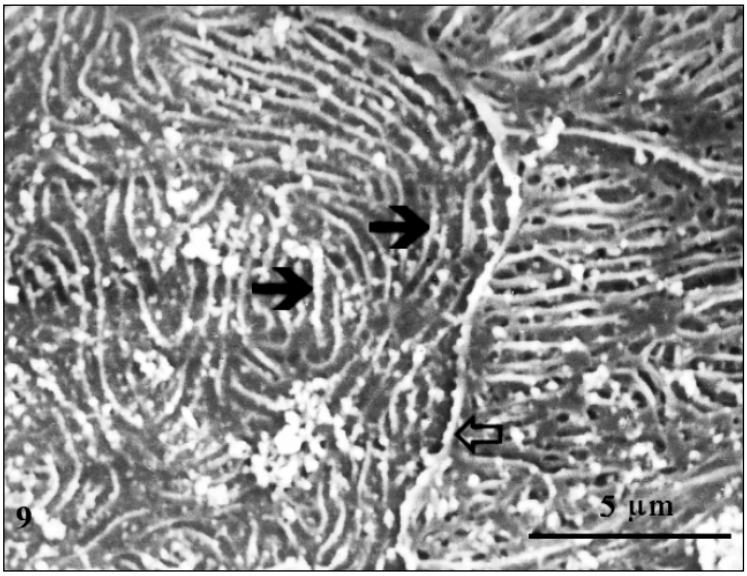

Fig. 9. Interrugal area RP 2-3. Segmented lines join into continuous microplicae (➜). (⇨ indicate cell borders). SCS 8, CRL = 18.3 mm, OD 18.5. SEM × 12 000.

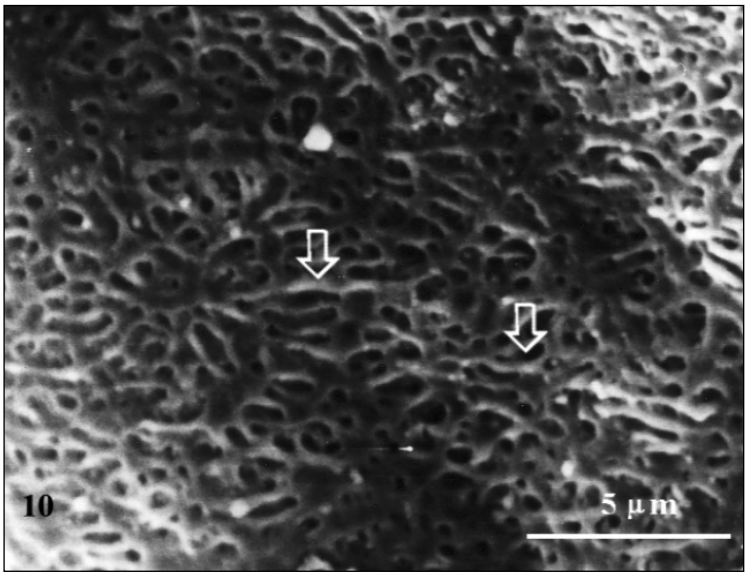

Fig. 10. Rugal area RP 2. Microplicae widen and amalgamate (⇨). SCS 9, CRL = 20.8 mm, OD 19.5. SEM × 12 000.

Plate XVI

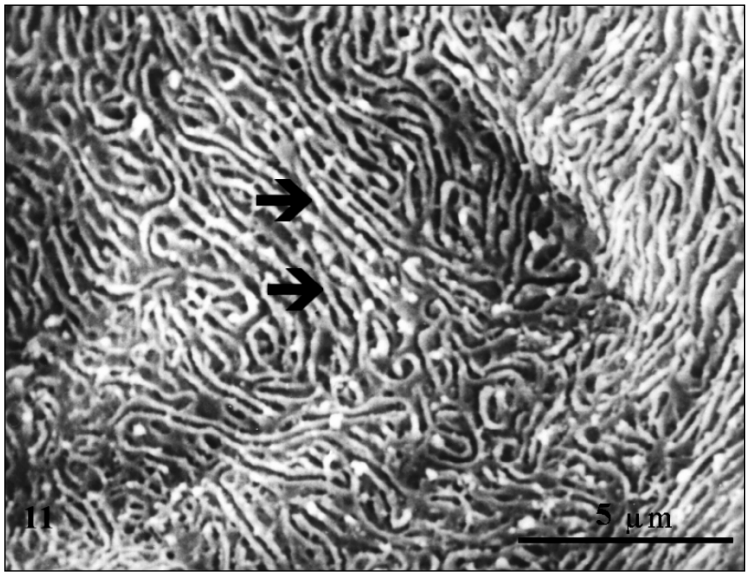

Fig. 11. Interrugal area RP 4-5. Microplicae form a network interlaced in a complex fashion. SCS 9, CRL = 20.8 mm, OD 19.5. SEM × 12 000.

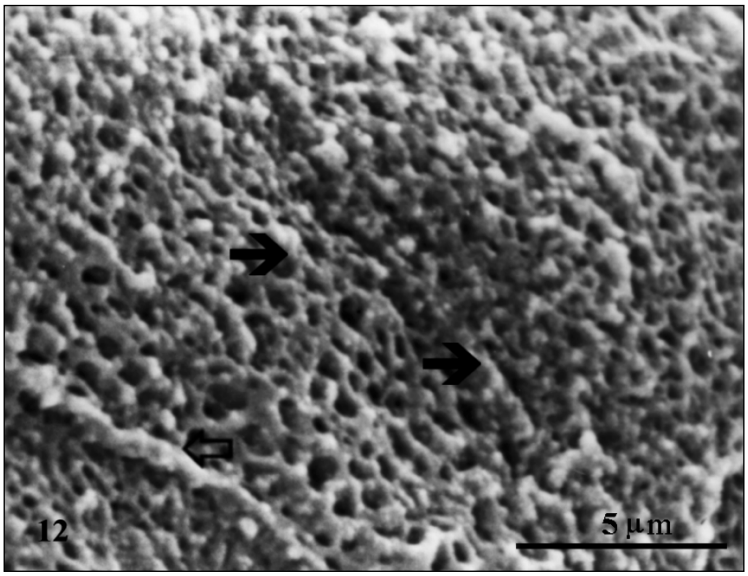

Fig. 12. Interrugal area RP 2-3. Microplicae form a massive dense interlaced network (➜). Free surface is reduced to individual loops. ⇨ indicates cell margin. Adult vole. SEM × 12 000.