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The development of palatal rugae in the European pine vole, *Microtus subterraneus* (Arvicolidae, Rodentia)

Marcela BUCHTOVÁ*, František TICHÝ, Iveta PUTNOVÁ and Ivan MÍŠEK

*Department of Anatomy, Histology and Embryology, Faculty of Veterinary Medicine, University of Veterinary and Pharmaceutical Sciences, Palackého 1-3, 612 42 Brno, Czech Republic; *e-mail: buchtovam@vfu.cz*

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A b s t r a c t . In the European pine vole (*Microtus subterraneus*, Arvicolidae, Rodentia) eight palatal rugae are formed, three of them are located in the antemolar, five in the intermolar area. The development of these rugae was studied in staged and aged embryos and fetuses using light and scanning electron microscopy. In 12.5 to 13.5 DO (days of ontogeny) embryos, epithelial thickening of ruga 1 was observed, whilst rugae 2 to 4 appeared as epithelial buds in rostral parts of the palatal processes; in their caudal parts, epithelial thickening was discernible (future rugae 5 to 8). The cell surface was characterised by rarely dispersed minute cytoplasmatic projections, sometimes arranged into rows along cell borders. In embryos at 14 to 16 DO, the secondary palate was closed and eight rugae were observed as in newborn voles. Rugae 1 to 3 distinctly protruded into the oral cavity. In fetuses at 17 to 18 DO, formation of the mesenchymal core in palatal rugae occured in rostro-caudal direction. SEM revealed simple-shaped microvilli and microplicae on the epithelial surfaces. In fetuses at 18 to 18.5 DO, the shape of the epithelial base was changed beneath ruga 2 to 6. The rugal core was distinctly developed in all rugae. The microplicae were thicker, acquired more complex shape and became interlaced. In fetuses at 19 to 19.5 DO, the special formation of the epithelial base beneath ruga 2 to 6 continued. The cell surface was covered by a dense network of microplicae the mass of which considerably increased.

Key words: palatal ridge, prenatal development, secondary palate

Introduction

Palatal rugae in mammals are transversally running crests, which are exclusively formed by the mucosa of the hard palate except where an ossified base can be distinguished. It is assumed that the rugae facilitate food transport through the oral cavity (Z i e t z s c h m a n n et al. 1943), prevent loss of food from the mouth (S c o t t & S y m o n s 1967), and participate in food crushing (E i s e n t r a u t 1975). Because of the presence of tactile and gustatory receptors, rugae contribute to perception (S c o t t & S y m o n s 1967) of taste, mechanical food qualities, and tongue position (H a l a t a & B a u m a n n 1999). Finally, P o u r t o i s (1972) suggested that palatal ridge could participate in prenatal stiffening of the oral epithelium by thickening of lateral palatal processes during the development of the secondary palate.

The occurrence, number and arrangement of palatal rugae in mammalians are species–specific. Data on the number of rugae in Sciuridae, Muridae, primates, and man were published by E i s e n t r a u t (1969), E i s e n t r a u t (1975), and S c h u l t z (1949, 1958), respectively. Individual variations in the number and morphology of palatal rugae in man were described in detail by C a r u s o (1969). To facilitate inter–species comparison,

Kutuzov & Sicher (1952) divided the hard palate into a rostral zone with antemolar rugae (AMR), a medial zone with intermolar rugae (IMR), and a caudal postrugal field (PRF). The first significant attempt to classify palatal rugae was that by Lysell (1955), who discerned primary, secondary, and fragmentary rugae. A more detailed description of human palatal rugae was published by Thomas & Kotze (1983) who also considered size, specific shape details, and size of rugal patterns and dental arches.

The prenatal development of palatal rugae was investigated in mice by Luke (1984), Luke (1988), Peterková et al. (1987), Peterková (1985), and Sakamoto et al. (1989), in rats by Thomas & Roussow (1991), and in man and pig by Thomas (1984). The increasing number of palatal rugae during prenatal development was described in rabbits (Meller et al. 1980). The development of rugae in mice starts at day 13 (Peterková et al. 1987) when proliferating epithelium forms three anlagen in the cranial part of the developing lateral palatal processes. Additional anlagen are formed at day 14 and anlagen of all rugae are present at the stage of palatal fusion. Supernumerary R8 may be observed in some individuals at day 15 (the numbers of AMR and IMR in adult mice are 3 plus 5 to 6, respectively). Peterková et al. (1987) also defined six stages of individual development of palatal rugae as follows: 1) thickening of epithelium, dipping into mesenchyme – the rugal anlage; 2) levelling of basement membrane and protrusion of epithelium above the surface – the primitive ruga; 3) condensation of mesenchymal cells beneath the top of rugae; 4) formation of bulged fibrous stroma beneath the rugae – the rugal core - covered by thinning epithelium; 5) epithelium of uniform thickness similar to that covering the interrugal areas – definitive ruga, initial keratinization; 6) the ruga as in adults. Thomas & Roussow (1991) observed in rats the first rugae to rise at the time when the vertical growth of palatal processes changed to horizontal (days of ontogeny 14 = DO 14). Definitive rugal patterns (3 AMR and 5 IMR) became apparent as the secondary palate fused (DO 16). Meller et al. (1980) found three rostral rugae on vertical palatal processes at day 15, four to five rugae in the front half of horizontal palatal processes at day 16, and seven to eight rugae at day 17. The fusion and formation of the secondary palate in rabbits was completed at day 18. The total number of palatal rugae in adult rabbits is 15 (Weber 1927). The first rugae in human embryos were distinguished at 32 mm CRL i.e. at or after palatal fusion (Thomas 1984). The number of rugae in adult humans, which never extend beyond the 2nd molar, varies between 2 and 8 (Schultz 1949). The first rugae in pig become apparent at 20 mm CRL, i.e. before palatal fusion begins (Thomas 1984).

All these reports concerned development of palatal rugae in farm animals and man, using largely light microscopic techniques. Others authors attempted to study the development of palatal rugae by scanning electron microscopic (SEM). SEM pattern of the oral mucosa surface was described by Schüpbach et al. (1983), who followed the development of the secondary palate in rats, and by Meller et al. (1980) who conducted a similar study in rabbits. McMillan et al. (1982) studied the surface epithelium of cheek pouches in hamsters. Matravers & Tyldesley (1978) compared morphological characteristics of the surface of normal and malignant oral epithelium in man. Appleton & Heaney (1977) published an SEM study of the porcine oral mucosa and Matravers et al. (1982) studied the effect of keratinization on the general pattern of epithelium in the same species. Nair & Schroeder (1981) dealt with surface density of microplicae and regional variations in buccal and labial mucosae. The density varied between 120 and 550 per 100 μm^2 of cell surface. Lack of information on the

occurrence of microplicae and their surface density in the prenatal period encouraged us to the present study we are reporting on.

This study was made in the line of our interest to look for relationships between palatal rugae formation and tooth primordial development. We focused on the European pine vole (*Microtus subterraneus*, Arvicolidae) who represents a small herbivor free living rodent.

Material and Methods

The development of palatal rugae was studied in twenty embryos and fetuses of the European pine vole using preparative, light microscopic and electron microscopic techniques. The estimated age of the subjects varied between 13 and 20 days of gestation (gestation period is 21 days), CRL (crown-rump length) between 5.9 and 21.0 mm (birth length varied between 23 and 27 mm), and SCS (Štěrba's comparable stages, Štěrba 1975, Štěrba 1995) between 5 and 9. All the specimens were from the Embryological Collection of the Institute of Anatomy, Histology, and Embryology of the University of Veterinary and Pharmaceutical Sciences, Brno, Czech Republic. Series of sagittal histological sections of the region head were cut at 5 μm thickness and stained with haematoxylin–eosine (HE).

The height of rugal and interrugal oral epithelium and total height of rugae was measured for each developmental stage to define the growth of individual components of the rugae.

To facilitate the orientation, the rugae were numbered RP1 (RP - ruga palatina) to RP8 starting with most rostral one. The development of palatal rugae was described using the nomenclature suggested by Peterková et al. (1987), where:

rugal anlage = epithelial thickening dipping into mesenchyme

primitive ruga = epithelial thickening bulging over the surface, levelling of the basement membrane

rugal core = fibrous stroma with condensed mesenchymal cells beneath the ruga; rugal mesenchyme protrudes over the palatal (interrugal) level

definitive ruga = extensive epithelium–covered ridge of connective tissue with well formed rugal core distinctly bulging into the oral cavity.

Samples for scanning electron microscopy were collected at 6.8 to 23.0 mm CRL. The arrangement according to Štěrba's "Staging and Ageing" method was used for age determination on the basis of CRL and morphological features. Specimens were fixed in 10% formaldehyde, critical point dried, spittered with gold, and viewed and photographed in a TESLA BS 300 scanning electron microscope.

Abbreviations:

AMR - antemolar rugae, CRL - crown-rump length, DO - days of ontogeny, E - epithelium, HE - haematoxylin-eosine, IMR - intermolar rugae, M - mesenchyme, O - oral cavity, RC - rugal core, RP - ruga palatina, SCS - Štěrba's comparable stages, SEM - scanning electron microscopy.

Results

SCS 5: CRL 6.0 to 7.0 mm; estimated age DO 12.5 to 13.5

The secondary palate was not yet closed at this stage. Anlagen of RP2 to RP4 were distinguished in the rostral part of vertical palatal processes as epithelial thickening protruding from the palatal surface in form of primitive rugae (Fig. 1). The epithelial

thickening consisted of a basal layer of high cylindrical cells, two intermediate layers of lower cylindrical cells, and a superficial layer of cuboid cells. The basal membrane beneath the epithelial thickening was levelled. The height of the epithelium at the top of the rugae measured from 22 to 30 µm. Eighteen to nineteen µm thick anlagen of RP1 in the form of an epithelial thickening dipping into mesenchyme could be seen in the rostral segments of both palatal processes next to the orifice of the ductus incisivus. The interrugal epithelium consisted of one layer of basal cuboid cells and one layer of flat superficial cells. The thickness of the interrugal epithelium varied from 9 to 11 µm. The caudal palatal area (Fig. 2) was covered by an wide 30 to 32 µm high four–layered epithelial thickening dipping into mesenchyme; the stratum basale was formed by cylindrical cells.

Scanning electron microscopy showed polygonal cells; their diameters varied between 7.5 and 11.5 µm. Minute cytoplasmatic projections, which were apparent at the free cell surface, were more numerous at the cell border.

SCS 6: CRL 8.1 to 12.0 mm; estimated age DO 14.0 to 16.0

Eight palatal rugae were apparent on the already formed secondary palate (Fig. 7). Number and arrangement of the palatal ridges corresponded to the pattern seen in adult voles. Three transversal rugae (RP1 - RP3) fused in the palatal midline of the antemolar area. RP1 was situated in close proximity to the papilla incisiva. Five pairs of intermolar rugae converged caudally towards the midline without joining each other.

Sagittal histological sections showed the bulging of RP2 and RP3 into the oral cavity to be formed by epithelial thickening consisting of two layers of cylindrical and two to three layers of polygonal cells (Fig. 3). The epithelial thickness of the primitive rugae varied between 26 and 30 µm. Distinctive accumulation of concentrically arranged mesenchymal cells was apparent beneath the epithelium. The basal lamina was convex and formation of a rugal core was starting. The epithelium covering RP4 to RP7 consisted of three to four layers and its height varied from 19 to 23 µm. Accumulation of mesenchymal cells was not observed at this stage and the basal lamina was flat (Fig. 4). The epithelium in the caudal palatal area, corresponding to RP8, was thickened: it consisted of two to three layers of cylindrical basal cells, covered by two layers of polygonal superficial cells. Generally, the area of RP8 closely resembled the caudal thickened area dipping into mesenchyme described in the preceding stage. The 9 to 13.5 µm high interrugal epithelium was formed by two layers of cuboid cells.

SEM revealed irregularly undulating cell surface, which was covered by numerous mikrovilli. The cell size was similar as at the preceding stage.

SCS 7: CRL 13.0 to 16.0 mm, estimated age DO 17.0 to 18.0 days.

The number of epithelial cell layers covering RP1 to RP3 remained unchanged, the epithelium was 26 to 31.5 µm thick. Condensation of mesenchymal cells and formation of bulging connective tissue (rugal core) was observed beneath the rugae (Fig. 5). The total height of the rugae increased to 33 to 45 µm. Accumulation of mesenchymal cells was apparent beneath RP4 to RP7 but initial formation of rugal cores was apparent only beneath RP4 and RP5. The area of RP8 was still covered by an up to 40 µm thick epithelium that protruded into mesenchyme with a markedly undulating basis (Fig. 6).

SEM revealed linear, arch–shaped or circular microplicae on the surface of some cells of the hard palatal mucosa. However, most of the surface structures appeared as individual microvilli or segmented lines (Fig. 8).

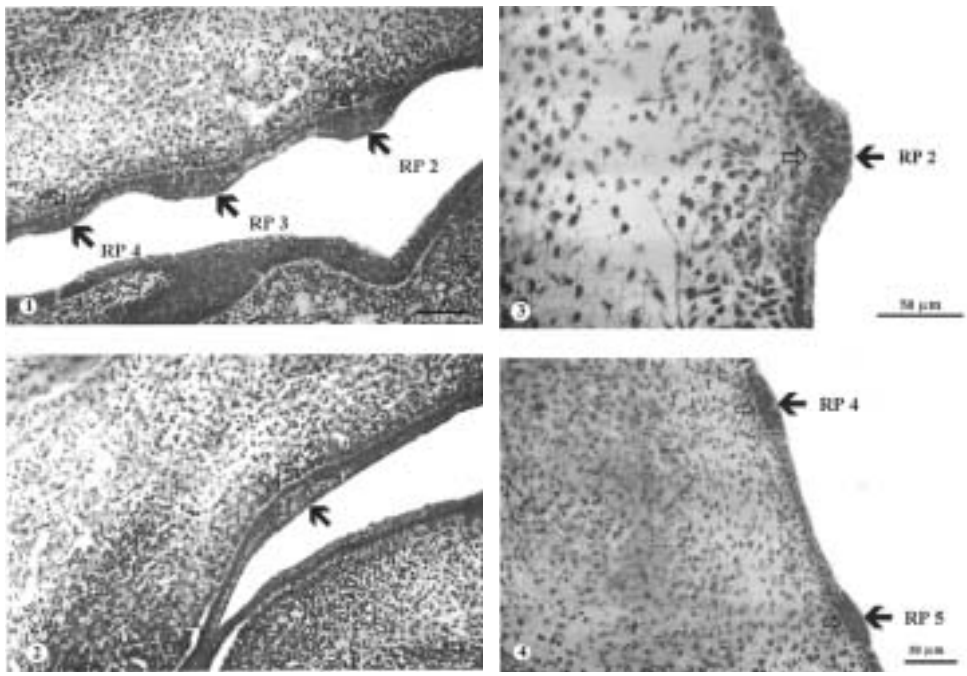

Fig. 1. Palatal ridges 2 to 4 in rostral parts of lateral palatal processes representing epithelial thickening (🡐). The basal lamina is levelled (⇨). SCS 5, CRL 6.5 mm, DO 13.0, sagittal section, HE, x375.

Fig. 2. Extended area of epithelial thickening in caudal parts of lateral palatal processes (⇨) Epithelium is dipping into mesenchyme (🡐). SCS 5, CRL 6.3 mm, DO 13.0, sagittal section, HE, x375.

Fig. 3. Palatal ridge 2 bulging into the oral cavity (🡐) with accumulation of mesenchyme beneath it. There is uneven lamina basalis (⇨) with starting formation of rugal core. SCS 6, CRL 10.1 mm, DO 15.0, sagittal section, HE, x600.

Fig. 4. Ruga 4 and ruga 5 seen as epithelial nodules at this stage (🡐). Lamina basalis is flat, rugal cores are missing (⇨). SCS 6, CRL 10.1 mm, DO 15.0, sagittal section, HE, x375.

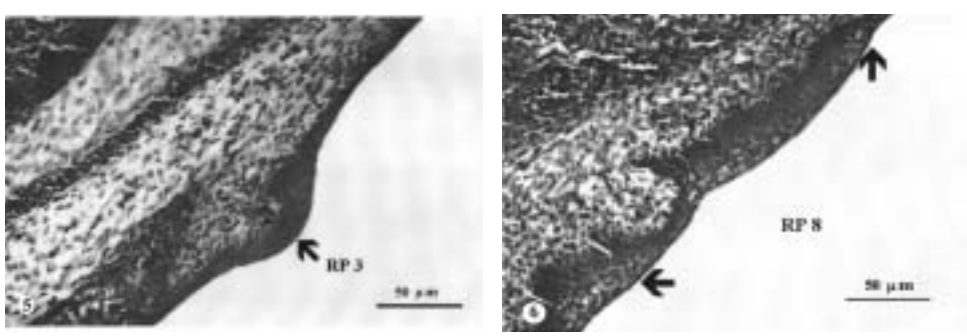

Fig. 5. Ruga 3 (🡐) with well developed rugal core bulging into the oral cavity (⇨). SCS 7, CRL 16.0 mm, DO 18.0, sagittal section, HE, x600.

Fig. 6. Ruga 8 formed by an extended area of epithelial thickening (🡐). SCS 7, CRL 16.0 mm, DO 18.0, sagittal section HE, x600.

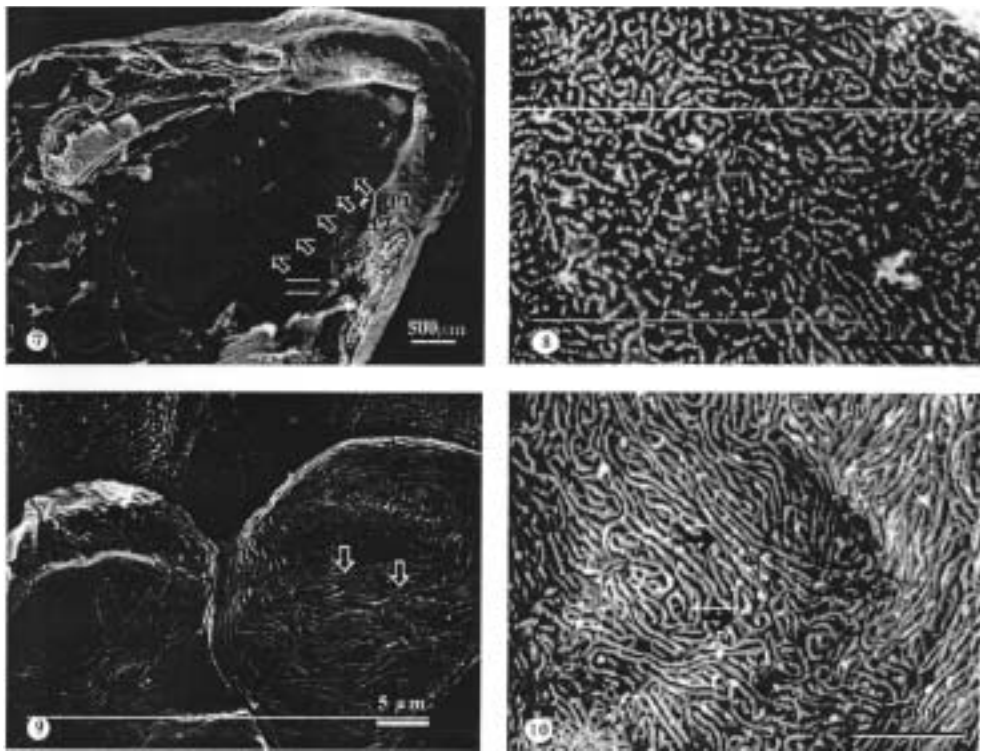

Fig. 7. The palate after the fusion of palatal processes and formation of the secondary palate. Three AMR (rugae 1 to 3) joining in the palatal midline and five pairs of IMR (rugae 4 to 8) can be seen. SCS 6, CRL 10.2 mm, DO 15.0, SEM, x30.

Fig. 8. Detailed view of a cell of the RP2 to RP3 interrugal epithelium. Microplicae are apparent on the cell surface (←). SCS 7, CRL 13.8 mm, DO 17.0, SEM x6000.

Fig. 9. Detailed view of a RP5 cell. Microplicae form concentric lines around the protruding nucleus. SCS 8, 18.3 mm CRL, DO 18.5, SEM, x4500.

Fig. 10. Detailed view of two cells of the interrugal epithelium between RP4 and RP5. Microplicae form a dense interlocked network (←). SCS 9, CRL 20.0 mm, DO 19.5, SEM, x6000.

SCS 8 : CRL 16.0 to 19.5 mm; estimated age DO 18.0 to 18.5

Continuous thickening of the basal epithelial layers was observed in sagittal histological sections of RP2 to RP6. At the cranial margin of each rugae, the number of epithelial layers increased to 5 to 7 and simultaneously the basement membrane was markedly undulated. In contrast to previous stages, rugal cores now increased also in the caudal rugae (RP6 - RP8) which now reached the shape of definite ruga. Total height of individual rugae palatinae reached 35 to 50 µm, thickness of apical epithelium varied from 26 to 31.5 µm. No changes in shape of the RP1 base was observed.

SEM showed successive interlacing of microplicae in the interrugal zone. Most cells belonging to rugae were devoid of microplicae in the area of protruding nuclei (Fig. 9). The cell size varied from 15.5 to 22 µm.

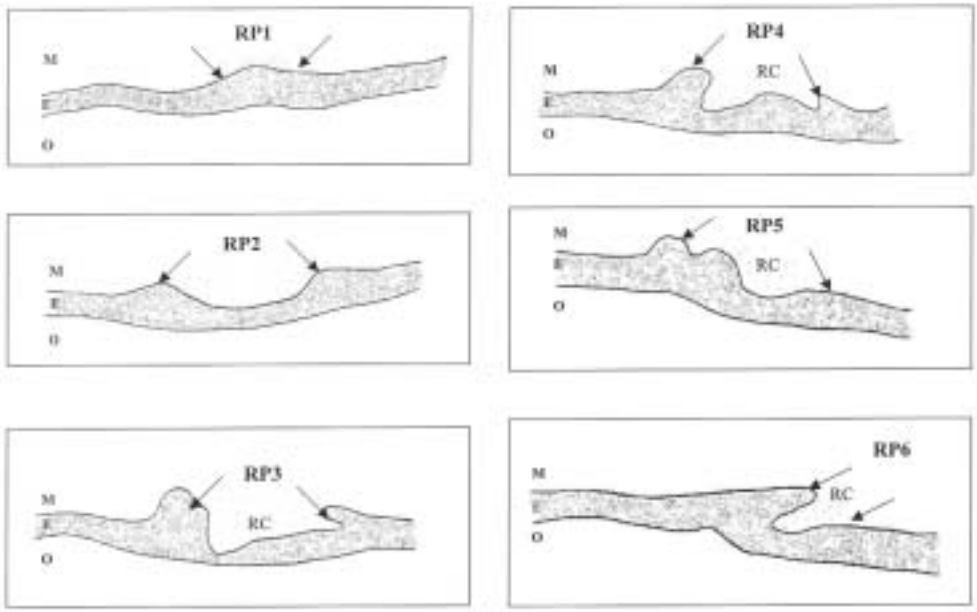

Fig. 11. The shape of palatal rugae as seen in sagittal sections in SCS 9. Mesenchyme (M), epithelium (E), oral cavity (O). The rostral end of the oral cavity is to the left of the picture. Rostral and caudal end of individual rugae (⋋⋌). Area of rugal core (RC). SCS 9, CRL 21.0 mm, DO 19.5, x400.

SCS 9: CRL 19.0 to 21.0 mm; estimated age DO 19.0 to 19.5

Distinctive changes at the epithelial base were observed in RP2 to RP6. The basement membrane became markedly undulated (Fig. 11). The epithelium was thickened mostly at the cranial and caudal margins of the rugae where its height reached up to 60 μm. On the other hand, epithelial thickness was reduced to 7 to 10 μm on the top of all rugae. Cores were formed beneath all the rugae.

SEM showed a regular dense network of interconnected microplicae on the epithelial surface. Individual microplicae were no longer distinguishable. The microplicae were considerably thickened and only narrow spaces were left among their individual branches. Cell size was the same as at SCS 8 (Fig. 10).

Discussion

The total number of palatal rugae in the adult European pine vole was eight (three antemolar and five intermolar). No data on the number of rugae in Arvicolidae was found in available literature but the same number of rugae was described in newborn rat by T h o m a s & R o s s o u w (1991). Although the number and arrangement of the rugae in rat and European pine vole are identical, their general shape in older fetuses, particularly that of IMR, was quite different resembling rather the patterns described in mice (P e t e r k o v á et al. 1987).

Similar to mouse (P e t e r k o v á et al. 1987) and rat (T h o m a s & R o u s s o w 1991), the palatal rugae in the newborn European pine voles consisted of lamina propria

mucosae covered by keratinised epithelium. A quite different arrangement was described for pig, in which bone tissue participates in the formation of eight rostral rugae. RP1 developed from protuberances on the palatal processes of incisor bones and RP2 to RP8 on palatal processes of the upper jaw. The total number of rugae in adult pig was found to vary between 20 and 23 (Weber 1927).

In rats, the beginning of palatal fusion and the appearance of the first rugal anlagen were apparent at gestation day 15 (Thomas & Rossouw 1995) and in mice at day 13 (Peterková et al. 1987) (SCS 5 - Štěrba 1995). Thomas (1984) observed the first rugal anlagen in pig at 20 mm CRL (SCS 5 - Štěrba 1995), i.e. before the beginning of palatal fusion, and in man somewhat later at 32 mm CRL, i.e. at the time of fusion of palatal processes (SCS 6 - Štěrba 1995). In our study on the European pine voles, the first anlagen were seen at 5.9 to 7.0 mm CRL (SCS 5 - Štěrba 1995), i.e. before the beginning of palatal fusion. These findings indicate that development of the first rugae in all mammals with distinct rugal patterns in adults precedes palatal fusion. Therefore, rugal anlagen could contribute to stiffen lateral palatal processes as suggested by Pourois (1972). Remarkably, the first rugae to develop were RP2 to RP4. These are the largest and most distinctly formed rugae in adult rodents. They are located in the antemolar zona (RP4 just between the antemolar and the intermolar area) at the level of the tooth-free segment of the margo interalveolaris of the upper jaw. Further rugae that are also distinctly developed in adults (RP1, RP5, RP6) begin to develop at the time of horizontalisation of palatal processes (Sakamoto et al. 1989). Hence, the most distinctive and extremely rostral rugae begin to develop before or during this growth reorientation. In our study, RP2 to RP4 were already apparent at the phase of lateral palatal processes (SCS 5). Moreover, a slight epithelial thickening was also observed histologically in sagittal sections at the level of the future RP1. An extensive area of epithelial thickening situated caudally to RP4 apparently provided material for the formation of RP5 to RP8. This situation occurred at the time of caudal extension of the palatal shelf, providing space for the development of RP5 to RP8. No such caudal extended area of epithelial thickening has been described as yet. The remaining rugae of the European pine vole developed during the subsequent stage (SCS 6). Rugal patterns corresponding to those observed in adult voles were apparent as soon as the secondary palate formed. No detailed studies on the number and pattern of rugae on palatal processes during horizontal reorientation were possible as material from this short period was missing. However, it can be concluded that establishing of rugal patterns in the European pine voles occurred at the same stage of development as in mice (Peterková et al. 1987, Sakamoto et al. 1989) and rats (Thomas & Rossouw 1991).

Unlike in small rodents, the palatal rugae in man begin to develop at the time of palatal fusion (SCS 6). Consequently, their stiffening role during palatal horizontalisation is therefore negligible. The same applies to the mechanical functioning of rugae in adult humans, as rugae phylogenetically are reduced to 2 to 8 indistinct palatal ridges (Schultz 1949, Schultz 1958).

No reduction of rugae (as described by Gegenbaur 1878 in man) or merging, division, or rise of new rugae after SCS 6 (as reported by Peterková et al. 1987 in mice) was observed during the prenatal development of European pine voles. The latter authors described the rise of a new ruga between RP7 and RP8 at SCS 8. As in the rat (Thomas & Rossouw 1991), RP1 of the European pine vole was incorporated into the papilla incisiva.

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