A macroscopic and microscopic study of the development of the rat palate including the soft palate

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SUMMARY

The development of the hard and soft palates in rat foetuses was studied macroscopically and microscopically. The development of the hard palate followed generally accepted lines and the development of the rat soft palate was described for the first time. This resembled that of the hard palate except that there was no rotation of the posterior part of the palatal shelf. Closure of the soft palate was very rapid occurring between 16,16 and 17,16 days p.i. Keratinization of palatal epithelium was present from the 18th day p.i. as were taste buds and developing mucous glands in the soft palate. The adult configuration of the soft palate oral epithelium had not been attained by day 21 p.i. suggesting that a further postnatal period of development or adaptation occurs.

OPSOMMING

Ontwikkeling van die harde- en sagte-verhemeltes in fetusse van rotte is makroskopies en mikroskopies bestudeer. Die ontwikkeling van die harde verhemelte het 'n normale verloop gehad. Die ontwikkeling van die sagte verhemelte van die rot word vir die eerste keer beskryf. Die ontwikkeling van die sagte verhemelte het ooreengekom met die van die harde verhemelte, behalwe dat daar geen rotasie van die posterieur deel van die palatale rif was nie. Sluiting van die sagte verhemelte het vinnig geskied, d.w.s. tussen 16,16 en 17,16 dae p.i. Keratinisering van die palatale epiteel, asook die teenwoordigheid van smaakknoppies sowel as ontwikkelende mukus-kliere in die sagte verhemelte, is vanaf die 18de dag waargeneem. Volwasse voorkoms van die mondepiteel sagte verhemelte is teen die 21ste dag p.i. nog nie behaal nie. Dit dui op 'n verdere postnatale periode van ontwikkeling of aanpassing.

INTRODUCTION

The development of the secondary palate has been of interest to many scientists. Among the studies reported are included those of Peter (1924), Pons-Tortello (1937), Lazzaro (1940), Walker and Fraser (1956), Zeiller, Weinstein and Gibson (1964), Coleman (1965), Hughes, Furstman and Bernick (1967), Nanda (1969), Wragg *et al* (1970), Mistretta (1972), Pourtois (1972), Wragg, Diewert and Klein (1972), Cox (1973), Diewert (1974) and Shah and Chaudhry (1974). Only in 2 of these studies was attention paid to the soft palate. Mistretta (1972) described the formation of taste buds including those in the soft palate, while Shah and Chaudhry (1974) described the formation of the hard and soft palates in the Golden Syrian hamster.

The study reported was undertaken to:

- (i) describe the formation of the soft palate and to correlate this with the formation of the rest of the secondary palate in the Wistar strain albino rat;
- (ii) determine when taste buds are first recognizable in the developing soft palate.

MATERIALS AND METHODS

In all embryological studies it is essential to know, as accurately as possible, the ages of the embryos, but there is no agreement on the time of onset of pregnancy (Kalter 1968). Accordingly in this study, the following technique was used.

Two female Wistar albino rats were placed in a cage together with a Wistar male rat, from 16h00-08h00 the following day. The female rats were then removed and the vaginal plug looked for. Vaginal smears were also made. The finding of either a vaginal plug or spermatozoa in a vaginal smear was taken as a sign of copulation. In such cases it was assumed that conception had taken place at midnight. The following day was designated day O post insemination (O d.p.i.) and subsequent days as I d.p.i., 2 d.p.i. and so on. The pregnant rats were kept in individual cages until required.

Macroscopic studies

A total of 183 foetuses, between the ages of 14 and 21 days p.i. were examined. At least 12 foetuses were evaluated at each time interval. The two times at which foetuses were killed were indicated by the figures 9 (09h00) and 16 (16h00) placed after the age in days e.g. 15,9 and 17,16 d.p.i.

All were fixed in 10 per cent neutral buffered formol saline after which they were decapitated and their tongues and mandibles removed with the aid of a Zeiss operating microscope. During this removal the relationship of the tongue to the palatal shelves and palate was noted. Drawings of the developing palates were made using a Wild dissecting microscope fitted with drawing tube and, where deemed necessary, photographs were taken with a Canon macrophotography apparatus.

Microscopic studies

Six foetuses at each of the time intervals evaluated macroscopically were prepared for histological examination. Four of the specimens in each age group were serially sectioned in the coronal plane and the remaining 2 in the sagittal plane. Sections were stained with haematoxylin and eosin, Masson's trichrome or Picro-Mallory.

To ensure as wide a selection of foetuses as possible, each foetus examined histologically was taken from a different mother.

RESULTS

Macroscopic observations

- 14 days p.i.
- (i) *Foetus:* The foetus had an average crown-rump length of 11 mm with a straight back and notch between the shoulder and occiput. The head was inclined downwards and forwards in relation to the back and showed a short snout as well as an easily recognizable eye.
- (ii) Palate: The primary palate was already formed anteriorly while posterior to this the 2 secondary palatal shelves were visible, widely separated from each other (Fig. 1). In this gap was the tongue which was closely applied to the cranial base. The palatal shelves extended posteriorly from the lateral part of the primary palate, almost parallel to each other to end in a rounded free standing ledge. The anterior one third of the shelves was bulbous and showed 2 rudimentary rugae. The posterior two thirds had a sharper edge directed vertically into the oral cavity. The junction between these areas was easily seen. Between the roof of the future nasal cavity and the palatal shelves was a very narrow space.

Animals killed 7 h later showed a similar picture.

- 15 days p.i.
- (i) Foetus: Crown-rump length was now about 13,5 mm and the back was no longer straight but curved convexly. The head was still inclined towards the tail but the notch in the occipital region was shallower.
- (ii) Palate: The tongue was still situated between the palatal shelves in contact with the cranial base. The palatal shelves had increased in length but were still widely separated (Fig. 1). In the anterior third 2 rugae were present and the bulbous shelves seen at 14 days had now become sharper with an inferomedial inclination of about 45° . The middle and posterior thirds also had a sharpish edge but this was directed vertically into the oral cavity. A posterior ledge was still present and fairly closely applied to the cranial base. In the anterior third the palatal shelves had a slight medial protrusion. Two bulges were present in the cranial base, one on either side of the midline

just distal to the posterior end of the palatal shelves. These showed the area of the future nasopharyngeal hiatus.

The only demonstrable differences between foetuses of 15,9 d.p.i. and 15,16 d.p.i. was a slight increase in palatal shelf length in the older animals.

16 days p.i.

- (i) Foetus: Growth had increased the crown-rump length to 15 mm. The occipital notch was shallower and the snout had lengthened.
- (ii) Palate: This appeared to be a period of intense activity and differences were seen between the 16,9 and 16,16 d.p.i. foetuses. The anterior third had become horizontal and was approaching the midline in the area between the anterior and middle thirds. Of the 30 foetuses examined at this stage one had already fused across the midline. Twelve had shelves in contact but not yet fused (Fig. 2) while 17 were almost touching across the midline. On the average, 4 rugae were seen. Two of these were opposite the point of contact at the posterior end of the anterior third of the shelves, and the other 2 were anterior to this i.e., opposite an area neither in contact nor fused.

The middle and posterior thirds were still vertically directed and had the tongue between them. The posterior ends were also directed slightly towards each other and were still anterior to the pharyngeal bulges.

In the 16,16 d.p.i. specimens, in all the 23 foetuses examined, the palatal shelves were in contact across the midline, and all still had an unfused area in the anterior one third (Figs. 1, 2). Seven or 8 rugae were present and fusion had proceeded as far posteriorly as the most posterior ruga. The posterior one third was still fairly widely separated and the shelf edges were directed medially at about 45° . The tongue no longer lay between these. The pharyngeal bulges were present but the posterior end of the palatal shelves i.e. the forming soft palate had not yet reached this.

In none of the specimens were the opposite palatal shelves alternately vertical and horizontal.

- 17 days p.i.
- (i) *Foetus:* The crown-rump length had increased to 20 mm and the head resembled more the newborn rat shape. The snout was longer and the head was less flexed although it was still inclined towards the tip of the tail.
- (ii) Palate: Fourteen foetuses were examined in the 17,9 d.p.i. group. In all of these the anterior onethird but not the posterior two thirds of the soft palate were fused (Figs 1, 2). The palatal shelves were horizontal and ended in a posterior free end which was still a little anterior to the pharyngeal bulges.

In the 17,16 day p.i. group which consisted of 16 foetuses, 11 had fully formed soft palates. The posterior free ledges were now fused in the midline with each other and also with the postero-lateral pharyngeal wall just ventral to the pharyngeal bulges. The nasopharyngeal wall was thus formed, of which the palatal shelves appeared to contribute the anterior third. Of the remaining 5 foetuses, in 3 the palatal shelves were in contact but not yet fused; while the other 2 were not yet in contact in the posterior third. At high magnification 2 or 3 of the papillae seen in the central area (Cleaton-Jones 1971) were discerned. These were seen only in the anterior third. The 3 zones of epithelium seen in the adult were not yet recognizable.

18 days p.i.-21 days p.i.

- (i) *Foetus:* There was a continuous increase in size accompanied by an unflexing of the head which was no longer directed towards the tip of the tail but horizontally forwards.
- (ii) Palate: Apart from one partially unfused specimen at 18.9 days p.i., all the soft palates were fully fused. From the 18th day p.i. onwards 2 zones of epithelium could be distinguished macroscopically on the surface at high magnifications. These were a central zone containing papillae and an outer zone having none of these. The number of papillae seemed to increase only slightly by the 21st day p.i. The most obvious feature was an increase in length of the soft palate. The anterior unfused area was fused in one third of the rat foetuses by 18,9 days p.i. and fully fused by 18,16 days p.i.

Microscopic observations

14 days p.i.

In the sagittal sections the primary palate was present and the cranial base was very convex in shape with the tongue closely applied to it.

In the anterior third, the palatal shelves were bulbous. Towards the posterior part of this anterior third a groove appeared approximately midway across the convex medial surface of the shelves. This twisted in a spiral pattern from medial to lateral to delineate a ventrally directed edge to the shelves.

In the middle third of the palatal shelves, they were almost triangular in cross section and projected vertically downwards. Towards the posterior third the shape of the shelves changed becoming more bulbous with a flattened medial edge directed at about 45° towards the midline. A cleft separated the dorsal surface of this from the cranial base.

At the posterior end of the shelves they were directed almost horizontally medially from the lateral walls of the oral cavity.

The tongue was closely applied to the cranial base throughout but the shape varied. Anteriorly both the tongue and cranial base were U shaped with parallel sides. The shape was more rounded in the middle third and flattened posteriorly.



Fig. 1. Diagram showing various stages in palatal development. The numbers indicate the days post insemination.



Fig. 2. Photographs of the developing palate. A. 16,9 days p.i. the secondary palatal shelves have just established contact. x 4.

B. 16,16 days p.i. the area of contact has extended posteriorly. x 4. C. 17,9 days p.i. the future hard palate is fully formed and formation of the soft palate has begun. x 4.

The substance of the shelves consisted of closely packed mesenchyme with a covering epithelium. This epithelium was a cuboidal type 1-3 cells thick over the apex and a thicker stratified squamous epithelium over the medial and lateral surfaces.

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15 days p.i.

In the sagittal sections the cranial base was still very convex with the tongue closely applied to it. The tongue and mandible had grown forward (Fig. 3).



Fig. 3. Sagittal section through a 15,9 day p.i. foetus. The tongue (T) is closely applied to the cranial base. H & E x 30.

The shape of the anterior one third of the palatal shelves had altered from being bulbous to more conical in cross section. The shelves were demarcated from the cranial base by a small notch (Fig. 4). In this area the tongue appeared less closely applied to the cranial base. The orientation of the rest of the palatal shelves was similar to that seen at 14 days p.i. In the middle third the shelves were fairly triangular in cross section (Fig. 5) with the tongue applied to the cranial base.



Fig. 4. Coronal section through a 15,9 day p.i. foetus showing the ventrally directed palatal shelves in the anterior one-third of the developing secondary palate. The notch demarcating the cranial base and palatal shelf is arrowed. H & E x 50.



Fig. 5. In the middle third of the developing palate, the shelves are more triangular in cross section. 15,9 days p.i. H & E x 50.

At the junction between the middle and posterior thirds the shelves were directed medially at about 45° with a flattened medial surface (Fig. 6). This changed to a horizontal medially directed shelf at the posterior end (Fig. 7). The mesenchyme of the shelves was still undifferentiated and the overlying epithelium appeared unchanged to that at 15 d.p.i. The foetuses at 15,16 d.p.i. were essentially the same. The nasal septum was situated well above the palatal shelves.



Fig. 6. At the posterior end of the middle third of the palatal shelves, these have a flattened surface directed inferomedially. 15,9 days p.i. H & E x 50.



Fig. 7. In their posterior third the shelves face medially 15,9 days p.i. H & E x 50.

16 days p.i.

In the 16,9 day p.i. foetus group, 2 had palatal shelves in the anterior two thirds that were in the process of becoming horizontal with a similar appearance in the middle third (Fig. 8). In both these areas the tongue was lower in the oral cavity but still lay between the palatal shelves. In the posterior third the shelves were now ventrally directed except for the most posterior end where they were bulbous and inferomedially directed.

In the remaining 16,9 d.p.i. specimens the shelves were horizontal in the area of junction of the anterior and middle thirds.

The rats sacrificed 7 hours later showed palatal shelves in contact but with no fusion across the midline in the region of the anterior and middle thirds of the secondary palate. The mesenchyme was still undifferentiated. In the sagittal sections the tongue was seen below the palatal shelves. The nasal septum was in contact with the nasal surface of the palatal shelves in the area, where they touched each other.

17 days p.i.

The tongue was seen in the sagittal sections to be protruding between the lips (Fig. 9) and was well below the secondary palate. The larynx was recognizable at the base of the tongue but was inferior to the posterior end of the palatal shelves.



Fig. 8. By the 16,9 day p.i. the palatal shelves are beginning to turn medially and the tongue is further away from the cranial base. H & E x 50.



Fig. 9. Sagittal section through a 17,9 day p.i. foetus. The developing tongue protrudes between the lips, the epiglottis (arrowed) is present and the developing secondary palate (P) is now above the tongue. H & E x 20.

In the anterior half of the secondary palate mesenchymal fusion had occurred across the midline, while in the posterior half the epithelia were still present in the midline (Fig. 10). Occasional gaps were seen between these epithelia which appeared joined by an eosinophilic material. Intra-membranous ossification was present in the lateral regions of the future hard palate.

In the posterior third of the secondary palate the soft palate was now developing. There was no nasal septum above the soft palate, only above the hard palate. In the 17,9 d.p.i. foetuses the anterior portion of the palatal shelves were directed medially towards each other (Fig. 11) and although in one foetus, they were in contact they were not yet fused. In the middle portion the shelves were more bulbous but still directed medially (Fig. 12). At the posterior end of the developing soft palate the palatal shelves were bulbous

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with a flattened medial surface directed towards its partner of the opposite side. They were fairly widely separated (Fig. 13).

By the 17,16 d.p.i. stage fusion had occurred across the entire soft palate. The mesenchyme was still undifferentiated.



Fig. 10. In this coronal section through the future hard palate the palatal shelves are in contact with each other but the epithelium here has not yet disappeared. 17,9 day p.i. H & E x 50.



Fig. 11. Shelves of the anterior end of the developing soft palate approaching the midline. 17,9 day p.i. H & E x 50.



Fig. 12. Middle third of the developing soft palate. There is a bulbous shelf on the left. 17.9 day p.i. H & E x 50.

18–21 days p.i.

By 18,9 days p.i. fusion was completed across the midline in all regions. In the sagittal sections the full lengths of both hard and soft palates were seen (Fig. 14) with the epiglottis protruding into the nasal cavity through the nasopharyngeal hiatus.



Fig. 13. In the posterior third of the developing soft palate, the shelves are widely separated and bulbous. 17,9 day p.i. H & E x 50.



Fig. 14. Sagittal section through an 18,9 day p.i. foetus. The palate is fully formed and the epiglottis (arrowed) protrudes into the nasal cavity through the nasopharyngeal hiatus. H & E x 50.

Bone formation was well advanced in the region of the hard palate and the epithelium covering both hard and soft palates was stratified. Keratinization had begun in the central area of the hard palate. Deep to the soft palate the medial pterygoid processes were beginning to form by endochondral ossification (Fig. 15), while in the soft palate itself, glands were also developing. These mucous glands began as a downgrowth of the oral epithelium into the underlying mesenchyme, which was at first solid, and later canalised (Fig. 16). Developing taste buds were observed in the soft palate epithelium. They consisted of 6-7 cells with a rather pale staining vacuolated cytoplasm grouped within the now stratified squamous epithelium (Fig. 16).

Although the oral epithelium of the soft palate was now a stratified squamous epithelium there was, as yet, no keratinization. Finally at the tip of the soft palate some mesenchymal thickening suggested early muscle formation.

Over the period 19-21 days p.i. there was an advance in this pattern of development. Keratinization spread laterally from the centre of both the hard and soft palates and covered the surface of both by the 20th



Fig. 15. This cross section through the soft palate shows the forming medial pterygoid process (arrowed) and mucous glands. The posterior nasal cavity (NC) is separated from the oral cavity (OC) by the soft palate. The developing larynx (L) is situated below the oral cavity. 18,9 day p.i. H & E x 50.



Fig. 16. High magnification of A. developing mucous gland and B. developing taste bud in the soft palate (arrowed) 18,9 day p.i. Picro-Mallory x 250.

day p.i. No keratohyaline granules were seen, however, before birth.

The glandular tissue increased in amount in the soft palate and none was seen in the hard palate. By day 21 p.i. though there was still little glandular tissue present in comparison with the amount in the adult animal.

The 3 zones of epithelium seen histologically in the adult were not evident by day 21 p.i. The stratified squamous keratinized epithelium was about 4 cells thick with no stratum granulosum, no rete pegs and no connective tissue papillae. Taste buds had increased in number but still had the appearance seen at 18 days p.i. (Fig. 16). Fungiform papillae on the soft palate were not yet present although there was a one to two cell thickening in the region of the taste buds.

The epithelium at the junction of hard and soft palates was slightly thicker than elsewhere but the filiform papillae seen in the adult were not yet visible. Finally, despite there being some muscle fibres in the posterior third of the soft palate, the palatal aponeurosis could not be identified by the 21st day p.i.

DISCUSSION

In the Wistar strain albino rats studied, the sequence of closure of the secondary palate was the middle then the posterior portion of the hard palate followed by the soft palate and finally the anterior portion of the hard palate. This was the same order as seen in the Golden Hamster by Shah and Chaudhry (1974). A similar closure pattern in the hard palate only has been described in other rat studies, (Coleman 1965, Nanda 1969, Wragg *et al* 1970, Pourtois 1972) and in mice (Walker and Fraser 1956).

The timing of closure in the hard palate in this study was such that the hard palate was fully fused by 17,9 days p.i. in all specimens. In the 16,16 days p.i. specimens although the palatal shelves were all in contact in the hard palate region they could still be separated by gentle pressure. Wragg et al (1970) mentioned that all their foetal hard palates were closed at 16,17 days p.i. but did not say whether they meant they were in contact or firmly fused across the midline. Coleman (1965) also did not enlarge on what he meant by the hard palate being closed by the 16th day p.i. Even Zeiler et al (1964) in their extensive study of palatal development did not clarify this point. Thus the lag of 17 hours seen in this study before hard palate fusion was complete, may be due to confusion over interpretation of the term closure. If closure means contact between the palatal shelves then the hard palate was closed by 16,16 days p.i. If on the other hand closure means fusion then this was completed by 17,9 days p.i.

Whatever the definition of closure it is clear that the palatal shelves became upright and in contact with each other within a very short time. This agrees with the observation made in mice by Walker and Fraser (1956), human embryos (Lazzaro 1940) and in other rat studies (Zeiler *et al* 1964, Coleman 1965, Wragg *et al* 1970, Wragg *et al* 1972).

A similar finding of rapid closure was noticed in the present investigation in the case of the soft palate. The palatal shelves in this region were separated at 16,16 days p.i., closed in the anterior third by 17,9 days p.i. and completely fused by 17,17 days p.i. As this is the first such report of soft palate fusion in the rat, no comparisons with other workers are possible.

Confusion exists in the literature regarding the mechanism that leads to a change in position of the processes. Both Peter (1924) and Lazzaro (1940) considered that the ventrally directed palatal shelves achieved their horizontal position by undergoing medial rotation. A second viewpoint was that of Pons-Tortella (1937) who felt there was a new shelf growth from the medial surfaces of the shelves dorsal to the tongue. A similar theory was put forward by Walker and Fraser (1956) who wrote that this began at the posterior end of the shelves and moved anteriorly. Coleman (1965) believed 2 mechanisms were present which were active in different shelf areas. Anteriorly he felt that there was a rotation of the palatine processes, accompanied later at their posterior end by a horizontal extension of the medial surfaces of the shelves. In other words he stated that the anterior segment closed as suggested by Peter (1924) and Lazarro (1940) and the posterior according to the theory of Pons-Tortella (1937). There was no definition, however, of where the anterior segment ended or the posterior began. Nanda (1969) reported an inferior bulging in the anterior region of the shelves in 15 day p.i. rat foetuses which occurred on the 16th day p.i. posteriorly. He did not notice any medial outgrowths of tissue and felt that pure rotation occurred.

In the present study the results obtained suggested a rotation of the shelves in all but the most posterior tip of the palatal shelves. Thus the observations of Peter (1924), Lazzaro (1940) and Nanda (1969) were upheld. The bulging noted by Nanda in the anterior region was a transient finding in 14 day p.i. foetuses in the present study, and appeared to play no role in palatal closure. The observations of Pons-Tortella (1937) and Walker and Fraser (1956) were not confirmed. There was no medial outgrowth from the shelves and rotation proceeded from anterior to posterior. On the other hand there was some agreement with Coleman (1965) in that the most posterior end of the palatal shelf did not undergo rotation but was always horizontal. This might possibly be tied up with the development of the nasopharyngeal hiatus.

The mechanism for rotation of the shelves seems generally accepted today to be due to an increase in sulpho-mucopolysaccharide ground substance (Larsson (1960, 1962a, 1962b)), but Orban (1957) felt it was due to an increase in cell numbers on the lateral side of the ventrally directed palatal shelves. This theory of Orban has been investigated and will be reported elsewhere (Cleaton-Jones, 1976).

Mato, Aikawa and Smiley (1972) described epithelial changes along the medial edge of human palatal processes just prior to fusion. This took the form of epithelial disarrangement accompanied by epithelial invaginations into the palatal mesenchyme. Shapiro and Sweney (1969) and Hudson and Shapiro (1973) among others also described cell degeneration in this region. No such changes were seen in the material examined nor in that examined with the scanning electron microscope (Cleaton-Jones, unpublished work).

In the present study, epithelial fragments were looked for in the soft palate following fusion but none were found. This agrees with the findings of Wood and Kraus (1962) in human embryos, and Mulvihill, Gamm and Ferm (1970) in hamsters, but is in contrast to the findings of Shah and Chaudhry (1974). Only occasional macrophages were seen after fusion. It is not possible to say whether the line of cell fusion was phagocytosed or displaced – the process called "mergence" by Burdi and Faist (1967).

The role of the change in position of the tongue in palatal closure which was suggested by Wragg *et al* (1972) to be an active process was not investigated in the present study.

An interesting observation is that the extension of the head on the neck which occurred with growth is only apparent. Wragg *et al* (1970) showed that when the angle between the posterior cranial base and cervical spine was measured there was actually an increase in flexion from days 14–17 p.i. Possibly then this apparent extension might be due to a straightening rather of the thoracic spine.

In the present study the epithelium overlying the hard and soft palates had become a stratified squamous epithelium by the 18th day p.i. and keratinization had begun in the central zone of the hard palate. This paralleled the keratinization of the skin in the same animals. Keratinization moved laterally and posteriorly from this initial site to cover the entire hard and soft palates by day 21 p.i. although no stratum granulosum was seen. This appears to be the first such description of initial keratinization in the rat oral cavity.

The mucous glands also began developing by day 18 p.i. but the soft palate was only partially filled by these glands by day 21 p.i. There must obviously then be a post-natal increase to reach the large amount present in the adult and this increase is possibly related to demand once eating has begun.

Similarly taste buds were first seen at day 18 p.i. This is the earliest yet described in the soft palate as Mistretta (1972) examined only post-natal rats. She reported a similar histological appearance of the taste buds one day after birth to that seen in this study at 18 days p.i. This is not the earliest that taste buds have been seen in the rat as Farbman (1972) has reported them in the tongue from 2–4 days p.i.

The arrangement of the soft palate mucosa into 3 epithelial zones as seen in the adult animals was not present by day 21 p.i. which suggests that it is possibly a post-natal functional modification. Also, the fungiform papillae had not yet appeared nor had the filiform papillae at the junction of hard and soft palates. Both must also be later functional adaptations.

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