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SCANNING ELECTRON MICROSCOPIC STUDIES OF THE ORAL MUCOSA AND ITS MICROVASCULATURE: A REVIEW OF THE PALATINE MUCOSA AND ITS MICROVASCULAR ARCHITECTURE IN MAMMALS

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Abstract

The present paper deals with the microvascular architecture of the palatine mucosa in primates, carnivorae, and rodentia utilizing microvascular corrosion castings and epithelium-separated specimens.

The submucous vascular network is under-developed since the hard palatine mucosa was designated the mucoperiosteum, except some areas. The palatine venous plexus appears to show regional differences with animal species differences. The well-developed plexus is observed to be two-layered and may contribute to the process of regurgitation of rough food and assist in mastication with the palatine plicae. Formation and patterns of the arterial network in the lamina propria are in a close relation with connective tissue elements. The subepithelial capillary network constitutes an advanced base for the ascending crus of the capillary loop and its pattern is affected by the properties of the connective tissue papillae and the diverging fashion of the capillary loops.

Capillary loops of the transverse palatine plica are arranged parallel to the sagittal axis and at right angles to the top line of each plica. Features of the capillary loops are characteristics in the top, the anterior and posterior slopes of the plica, respectively. High connective tissue papillae in both the anterior slope and plical top may be of a resistant form for mollifying exhaustion, affected by the periodicity and mastication function. Although it is difficult to elucidate the lamination of the palatine mucosa in histological slides, it was resolved by examination on its vascular architectures.

Key Words: Microvascular architecture, palatine mucosa, transverse palatine plica, scanning electron microscope, vascular corrosion castings, mammals.

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Introduction

Three-dimensional observation of microvascular corrosion casts under a scanning electron microscope (SEM) is most helpful for understanding the microvascular arrangements and has now become a routine technique. For this purpose, micro-casting and appropriate observation methods are required.

The acrylic plastic injection method for gross and approximate-microscopic examinations of vascular and duct systems was described by Taniguchi, Ohta *et al.* (1952, 1955). They performed three-dimensional studies of blood vessels and glandular ducts in normal structures. Vascular casting methods and three-dimensional findings of vascular system utilizing plastic castings have been reported by other authors (Murakami 1971; for detailed reviews see, Lametschwandtner *et al.*, 1984, 1990). We have attempted to develop micro-casting for SEM studies by modifying the above, original acrylic injection method, in association with the gradual advance and wider use of SEM. The first publication from our department concerned the "Splenic sheathed vessel of the pig" employing a micro-casting method for SEM (Ohta *et al.*, 1977). Subsequently, we have continued SEM investigations of micro-castings of various organs and tissues, and summarized the findings in a recent publication (Ohta *et al.*, 1990). Reviewing the history of this research, we strongly feel that all studies using light microscopy and macroscopic methods should be re-investigated by SEM.

The histology of the oral mucosa is considered to be that of a general laminar formation except for the absence of the lamina muscularis mucosae. However, Schroeder (1981) classified the oral mucosa into three types: lining, masticatory and specialized mucosae, according to regional differences reflected in the histological structures and functions. Based on the topographic coverings of the oral cavity, he assigned the hard palatine mucosa and attached gingivae to the masticatory mucosa, and explained the differences in lamina formation, function and properties of each type.

We examined the microvasculature of the palatine mucosa from the comparative anatomical standpoint, and how it contributes directly to the function of the relevant prehensile organ, masticatory or mashing apparatus. Detailed descriptions are presented from our previous findings and unpublished data.

Materials and Methods

For this paper, various mammalian species belonging to different families in terms of their comparative anatomy were selected, as follows: Primates - Japanese monkeys (*Macaca fuscata*), common squirrel monkeys (*Saimiri sciureus*) and humans, Carnivorae - cats (*Felis domestica*) and dogs (*Canis*), Rodentia - Wistar rats, and Lagomorpha - rabbits.

Acryl plastic injection was performed according to our published method (Ohta *et al.*, 1990). The ultimate target of this research has been narrowed down morphologically to the elucidation of the interrelations between the connective tissue papilla (in the lamina propria) and the capillary loop based on the characteristic histological structures of the palatine mucosa. To this end, we prepared epithelium-separated materials as follows. Epithelium-periosteum dissected out from the palatine mucosa was subjected to separation of its epithelial layer from the lamina propria by treatment with 2 N sodium bromide (12～24 hours at room temperature) according to the method of Felsher (1947) and Ooya and Tooya (1980). This material was fixed in 2% glutaraldehyde, post-fixed in 1% osmium tetroxide, and freeze-dried in t-butyl alcohol (Inoue and Osatake, 1988). Samples were coated with gold and then observed by SEM (JEOL JSM-T300, operating at 5 and 10 kV, working distances 40～45 mm).

Results and Review of the literature

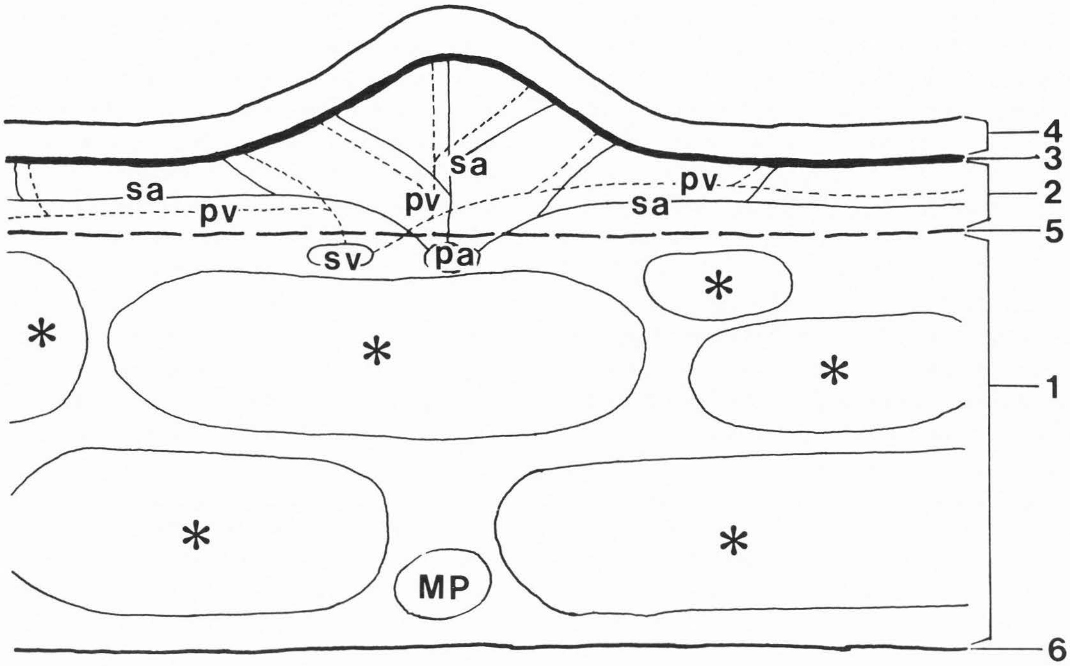
The vascular architecture of the oral mucosa has long been described to consist of three vascular networks: a network in the lamina propria, and two others in submucosa and subperiosteum (in human adults and fetuses by Swindle, 1963, Suzuki, 1964; and in dogs by Sayo, 1985). In fact, the former two networks represent a characteristic feature as the palatine mucosa with wide variations. These variations are observed in the formation of the transverse palatine plicae, the morphology and density of the connective tissue papillae and regional differences with diversity among animal species. Based on comparative and detailed observations, the framework of the classifications made so far is adequate in terms of the functional anatomy. Toda (1986) attempted to elucidate the laminar formation of the palatine mucosa based on the laminar formation of its vascular architecture, and finally obtained satisfactory results.

Fig. 1. Schematic illustrations demonstrating the microvascular architecture of the palatine mucosa and transverse plica; the submucous vascular network, lamina propria vascular network, subepithelial capillary network and capillary loops. **(a)** General scheme; **(b)** cat and dog; **(c)** rabbit and rat; **(d)** Japanese monkey; **(e)** human and common squirrel monkey. **1**: Submucous vascular network; **2**: Lamina propria vascular network; **3**: Subepithelial capillary network; **4**: Capillary loops; **5**: Boundary between lamina propria and submucous layer; **6**: Periosteum. **pa**: Primary arterial network; **pv**: primary venous network; **sa**: secondary arterial network; **sv**: secondary venous network; **MP**: major (hard) palatine artery; *****: palatine venous plexus.

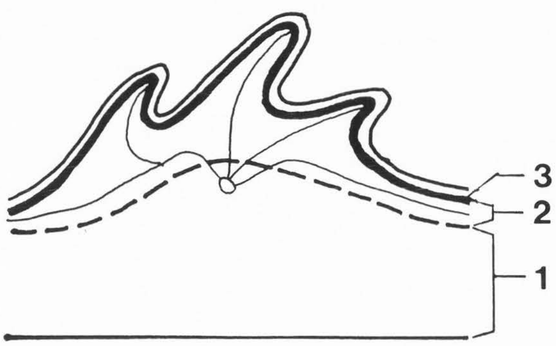
The present paper deals with the fine vascular layer architecture (Fig. 1) of the hard palatine mucosa, especially the transverse palatine plicae or ridges as characteristics in mammalian species, the subepithelial capillary network and the construction of the capillary loop, and discusses the interrelations between the forms of the connective tissue papillae and capillary loop formation.

1. Submucous vascular network (Fig. 1)

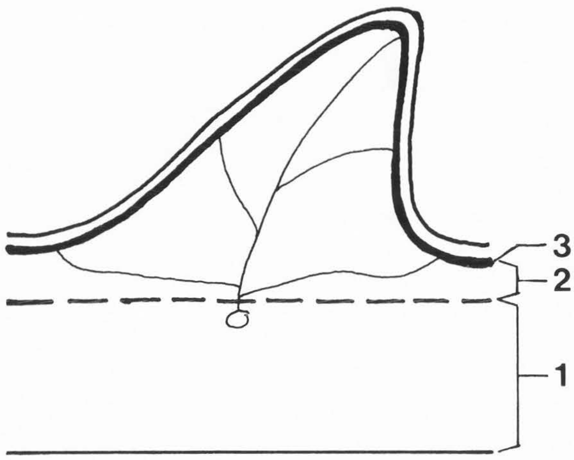
a. Submucous arterial network The primary arterial network originates from the submucous layer. The original arteries which contribute to the formation of this network are as follows: numerous primary ramifications, the medial and lateral branches diverging from the major hard palatine artery, e.g., dogs, cats and rabbits (Sawa, 1961), and the major palatine artery like in human adults and fetuses (Sawa, 1961), Japanese monkeys (Kajiwara, 1989), and common squirrel monkeys (Inoue and Toda, 1991), respectively. Each of the medial and lateral branches generally runs in accordance with the passage of the transverse palatine plica or ridge, in the basis of each of which it passes medially or laterally. In some species, such as the common squirrel monkey, Japanese monkey and man, in all of which the plicae are not well-developed, the medial and lateral branches are not often situated on the base line of the plica. Both branches give rise to abundant plical branches (Sawa, 1961), which participate directly in the formation of the primary or submucous arterial network in cats (Toda, 1986) and rabbits (Ike, 1990). This network is formed by numerous twigs from the plical branches in Japanese monkeys (Kajiwara, 1989), common squirrel monkeys (Inoue and Toda, 1991) and man. The depth of passage of the medial and lateral branches has been examined. Their parent arteries pass forwards in the submucous tissue, although a well-developed palatine or secondary venous plexus is formed there in cats, rabbits and Japanese monkeys. The palatine mucosa is often present as mucoperiosteum or palatine aponeurosis. However,



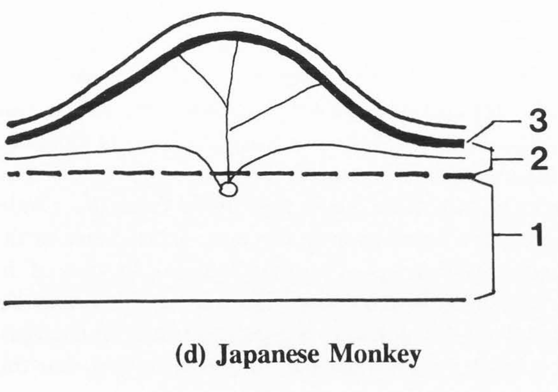
(a) General Scheme



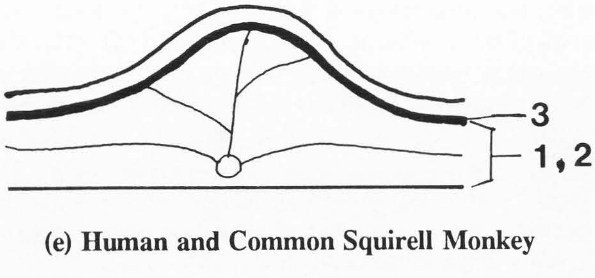
(b) Cat and Dog



(c) Rabbit and Rat



(d) Japanese Monkey



(e) Human and Common Squirell Monkey

such a presence should be restricted to regions where the above venous plexus is absent as judged from the laminar formation of the vascular networks. It should be mentioned that regions to which the venous plexus spreads, do not have the properties of a mucoperiosteum, although the palatine arteries pass forwards. Viewed from this standpoint, areas having characteristics of the mucoperiosteum may be restricted to the median palatine suture in the intermolar area in rabbits and the median palatine raphe and the palate-gingival junction (Zona fibrosa) in common squirrel monkeys, Japanese monkeys and man. No venous plexus is found in these restricted areas, but they are filled densely and tightly with collagen fibers down to the periosteum.

The topographic relations between the major (hard) palatine artery, the medial and lateral branches and mucosal layers have been examined. In rabbits and cats, arterial vessels pass forwards on the periosteum deeply in the hard palate and gradually superficially into the boundary between the submucous layer and lamina propria. Accordingly, the medial and lateral branches located in the posterior area of the palate pass through a meshwork composed of thick venous vessels to form the submucous arterial network (Fig. 1), which is superficial to the venous plexus. A complete, two-dimensional meshwork of the arterial network is observed only within a thin submucous layer, being filled densely with collagen down to the periosteum without any glands or venous plexus area, as noted along the median suture of the intermolar and an expansion towards the posterior teeth gingivae. This structure may be termed the periosteal arterial network. Sayo (1985) reported that, in dogs, vascular networks were formed in the lamina propria, the supra- and infraosseous layers, respectively. We have made considerable efforts to detect and identify each vascular layer mentioned by Sayo using microvascular corrosion casts. However, it was difficult to clarify the respective components, and more precise analysis of this problem is clearly necessary.

b. Submucous or palatine venous plexus Venous blood emanating from the lamina propria drains into a venous network in the submucous layer. This can be designated the secondary venous plexus (Fig. 1) and is comparable with the primary arterial network. In this venous network, it is important and interesting to observe the developmental differences by species as well as regional differences in the palate (Fig. 1). The network in common squirrel monkeys is usually undeveloped in its two-dimensional expansion. In Japanese monkeys, it is also undeveloped over the entire palate, scarce in the posterior area of the median region, but exceptionally well-developed in the anterior region as well as around the major palatine artery as observed in man. On the other hand, the venous plexus in rabbits and dogs is well-developed, spreading over most of the entire hard palate. Miller (1979) stated that the venous palatine plexus was unevenly distributed in dogs. His observations might not have been made by means of a three-dimensional approach. The venous plexus in man is well-developed within the incisive region, undeveloped or absent in the molar region but well-developed towards the soft palate. In general, this plexus is composed of thicker, sagittally passing venules which are connected with thinner frontally or obliquely passing venules. The submucous tissue cannot be separated histologically into superficial and deep layers. However, the deep network of the palatine venous plexus is located in the median one third, consisting of thicker sagittally passing venules, while the superficial network is located in the median network, being composed of radially spreading venules towards the posterior teeth. It can thus be said that the components of the submucous two-layered tissue do, as a double vascular structure, overlap each other, although they are out of position in part. In other words, regions constituting a two-layered vascular architecture are restricted to areas beneath the transverse palatine plicae and in the posterior half of the median one third, but never in the posterolateral region. In the region lacking the venous plexus, the superficial layer of the submucous tissue directly becomes component fibers of the periosteum, with no interpositioning of any deep layer. In rabbits, the venules passing in the median one third of the superficial layer are thick but those in the deep layer are fine. Also, the plexus is fairly thin in both the incisive papillary and intermolar areas. Ike (1990) paid special attention to the mode of expansion of this plexus in the rabbit. The diastema of this species is extremely elongated in the sagittal direction so as to occupy 80% of the antero-posterior length of the palate, and a pair of elongated palatine fissures are positioned just at the level of the diastema. On the fissures, all osseous elements are defective, showing separation by a connective tissue membrane from the nasal bottom with a perpendicular median septum, by means of which the nasal mucosa is connected tightly with the lamina propria of the oral mucosa. Under these conditions, the palatine venous plexus is so well-developed that it covers the non-osseous area, and bilateral margins expand beyond the long rim of the diastema. The anterior ends flow together in several veins towards the face. One other characteristic feature is that the plexus is separated completely into right and left halves by the perpendicular membrane. Most of the venous blood from this plexus finally drains backwards to the deep facial veins at the posterolateral corners of the bony palate. In view of the fact that the position where the venous plexus is extremely well-developed in a regular form is situated just at the level of the diastema, Ike emphasized that this plexus may contribute to the process of regurgitation of rough food and further assist in mashing or mastication with the plicae as well as the cheek teeth. Simultaneously, as an additional useful function, it may contribute by acting as a cushion for rough food in rodentia. Sayo (1985) reported venous valves in the venous channels of the palatine venous network in the boundary area between the hard and soft palates of the dog, and indicated that one function of the plexus may be as a reservoir of blood and heat ventilator. It is rather difficult to assess whether Ike's cushion theory or Sayo's ventilator theory is appropriate. Nevertheless, such structures of the hard palate should, in terms of both their histology and angiology, be reflected in the food habits and mode of mastication or chewing of the animal species concerned. A role as a cushion for rough and unmashed food may thus sometimes be necessary. In any case, further detailed examinations are required, especially of the comparative functional anatomy.

2. Lamina propria arteriole network (Fig. 1)

When compared to the connective tissue or lamina propria papillae of the lining (ordinary) oral mucosa, that of the masticatory mucosa connected by highly dense fibrous connective tissue has nearly twice the density (Schroeder, 1981). There are no differences in the thickness of the lamina propria and submucous layer among animal species, although the regional differences are distinct and serve to delineate the boundary between the two layers. Further, obscurity of the boundary between the submucous or primary arterial network and the arteriole network in the lamina propria is reflected by the original histological structure. In particular, such obscurity is considerably more pronounced in common squirrel monkeys (Inoue and Toda, 1991) and Japanese monkeys (Kajiwara, 1989) (Fig. 1), but there is no obscurity in cats and rabbits. This is one reason why the superficial-most, thick component venous channels of the well-developed venous plexus are located tangentially just at the level of the boundary zone. The bony palate of Japanese monkeys reveals a deep curvature in frontal sections and bilateral protrusions along the median line, so that the areas between the convex and concave parts appear as pan-shaped recesses, which are filled with connective tissue between the lamina propria and periosteum. In the case of the above obscure boundary, as observed in common squirrel monkeys and in the interplical area of Japanese monkeys, abundant arterioles diverging from the secondary arteriole network extend epithelialwards arborizing into ramifications like bushes.

The primary venule network develops in the lamina propria. Its general aspect is similar to that of the arteriole network. Venules draining from the capillary loops are usually accompanied by arterioles except for the smaller caliber venules.

3. Subepithelial capillary network (Fig. 1)

This network constitutes an advanced base, from which the ascending crus of the capillary loop protruding into each connective tissue papilla diverges. If all the loops could be reaped on the corrosion cast, the subepithelial capillary network may appear as a two-dimensional meshwork. In other words, the "bushes of capillary loops" can be designated a subepithelial capillary plexus. Such ramifications are observed in primates. Topographic protrusions of the subepithelial capillary network are demonstrated in accordance with the elevations of the transverse palatine plicae with elongation at right angles to the plical top. In the cat capillary network, rough meshworks are observed in places, and from these meshworks, capillary loops sprout into the connective tissue papillae. Sayo (1985) demonstrated a hexagonal meshwork in the lamina propria, although there has been no description of the subepithelial capillary network.

The original subepithelial capillary network is essentially observed as a capillary meshwork within a single plane (Fig. 1). However, this mode of occurrence is effectively influenced by the morphological characteristics of the connective tissue papillae and the diverging form of the capillary loops. Again, this is one reason why the present authors prefer to regard this network as an advanced base.

4. Capillary loops of the transverse palatine plica

The transverse palatine plicae are formed by elevations of the lamina propria (Fig. 1) in common squirrel monkeys, Japanese monkeys, man, rabbits and rats, and by elevations of the submucous tissue in cats. One plica in the cat consists of one ridge and characteristic small processes on both the anterior and posterior slopes of the ridge (Fig. 2). The plicae of rabbits are well-developed and mostly uniform, appearing as a continuous, serrated elevation with a posterior inclination in sagittal sections. The general view of the plicae resembles one of remnants. The plicae of rats are not tall, with a sagittally chopped edge at the plical top, and filiform-shaped processes grow in the median one third of the anterior soft palate.

In all the species examined, each capillary loop in the connective tissue papilla is positioned at right-angles to the transverse plica, forming regular lines parallel to the antero-posterior axis of the palate, that is, in the sagittal plane. It can be said that this linear arrangement in sagittal sections may be related to the developmental direction of the secondary palate.

In common squirrel monkeys (Inoue and Toda, 1991), the capillary loop in the plical top appears as a simple hair-pin (about 200 μm in height) with a slightly anterior inclination. The loops are observed as part of the elevations of the subepithelial capillary network itself. The loops in the interplical region are similar in height to the plical top with slight opening between the ascending and descending crura.

In Japanese monkeys (Kajiwara, 1989), the subepithelial network is elongated sagittally, that is, perpendicularly to the top line of the plicae. This arrangement is observed more distinctly in the slopes of the plicae. Capillary loops are also lined up perpendicularly to the plical top in each segment even if the plica is strongly curved. The loops (200 μm in height) appear as hair-pins with a minimal inclination but are rarely twisted and branched.

In cats (Toda, 1986) and rabbits (Ike, 1990), the plicae are quite different in form from those of the above species. In cats, the plica is much larger along the antero-posterior axis in a sagittal direction, since it is formed by an elevation of the submucous layer, so facilitating its distinction into the anterior and posterior slopes and plical top. The following processes are observed: anterior conical processes, numbering 7 on average, aligned on the anterior slope; small digital-form processes (700 μm in height and 500 μm in base diameter) on the plical top; and posterior conical processes (700 μm in height and 500 μm in base diameter), numbering 8 on average, on the posterior slope (Fig. 2). All these processes are formed as protrusions of the lamina propria. The anterior slope is not steep and postero-inferiorly has the highest connective tissue papillae; however, the posterior slope is steep, with the lowest and smallest number of papillae. The arterioles from the incomplete arterial network in the lamina propria are continuous with the adjacent ones, superficial to the venous plexus to form a shelf-like network, from which capillary loops sprout to the processes and plical top. One arteriole is provided with one process as a rule. Capillary loops entering one process in the form of a bundle give rise to one ascending crus entering one connective tissue papilla. Each loop appears as a hair-pin, sometimes with a slightly posterior inclination. The arrangement of the capillary loops is always parallel to the sagittal direction. The loop of the interplical area has bridges between its crura or with more than one descending crus in some cases.

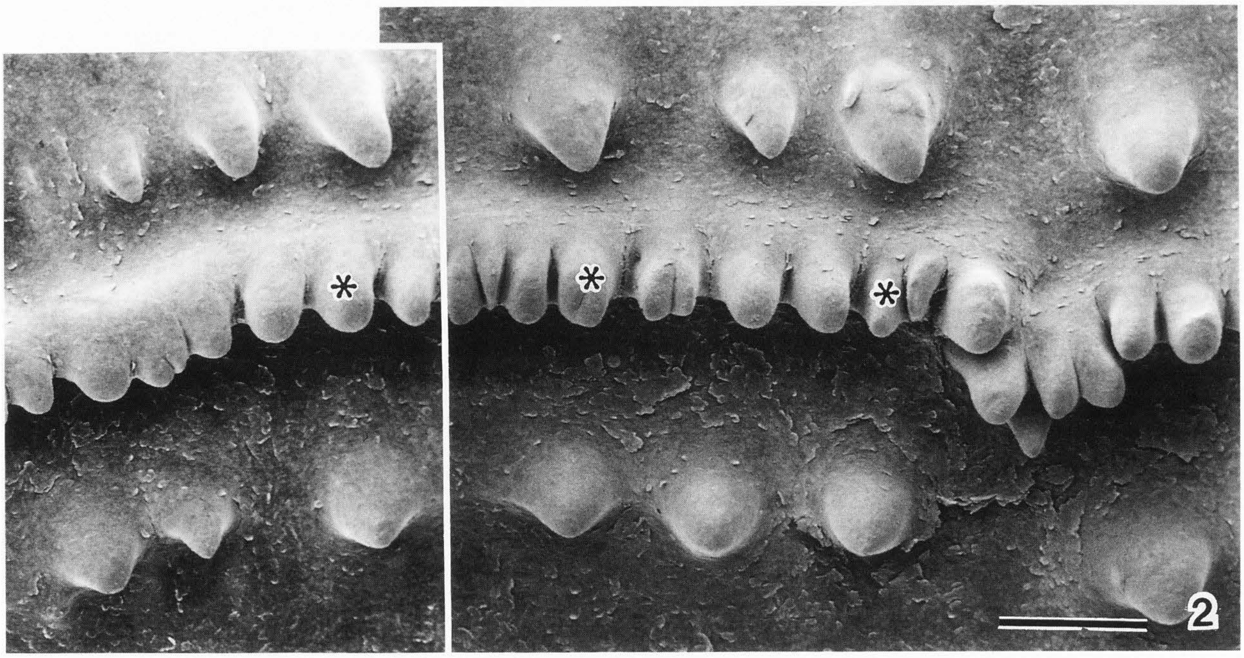
In rabbits (Ike, 1990), the plicae show regional differences which are so marked that a division can be made into the incisive papillary, palatine fissure and intermolar regions. Ike undertook precise and detailed investigations of the interrelations between the morphology of the connective tissue papillae and capillary loops. The findings are summarized in Table 1. The general aspect of the plicae is briefly as follows: the anterior slope is long with a loose postero-inferior inclination, while the posterior slope is in the form of a cleft-cut and no interplical area exists as such. In sagittal sections through the entire hard palate, the continuation of the plicae resembles a saw blade. Furthermore, each plical (arterial) branch is always located immediately anterior to the posterior cleft-cut slope. The findings of Ike are summarized in Table 2. Throughout the hard palate, the following features are evident. In the anterior slope, the papillae are slender and long cones grow densely with a regularly sagittal arrangement. The capillary loop is tall in the form of typical hair-pin, sometimes with slight opening of the intercrura. At the plical top, the papilla consists of a thick cone with an obscurely sagittal arrangement in the posterior area, and the loop has an opened intercrura and bridges between the crura. On the posterior slope, the papilla forms a cone and the loop displays obscurely sagittal arrangements with an opened intercrura. In the extremely narrow interplical area, the papilla is low and variable in form (cone or cylinder) in a coarse arrangement and the loop also has a variable form (arcade, tightly closed at its tip, etc.).

The incisive papilla of cats (Toda, 1986) is observed as a typical pentagonal plate, where capillary loops are formed very densely (Fig. 3) but without the characteristics seen in the transverse palatine plicae mentioned above. The papilla of Japanese monkeys (Kajiwara, 1989) is observed as an arrowhead with a sharp anterior tip (Fig. 4). The papilla of common squirrel monkeys (Inoue and Toda, 1991) consists of a flat, unswollen plate. In all the species examined, the density of loop distribution is somewhat higher than that in other areas of the palate.

In rats, one plica is composed of numerous small wedge-like processes (Iwaku, 1976), each of which is compressed in a right-left direction and resembles a sagittally-elongated nipple. One connective tissue papilla corresponds to one nipple. It displays a cleft-cut in its anterior slope but is not steep in its posterior slope in epithelium-separated specimens (Fig. 5). The capillary loops in one nipple are not simple as in the hair-pin type, but the tips of the loops are connected with a capillary running along the sagittally-elongated plical top, so that the ascending and descending cura number more than two appearing a small meshwork (Fig. 6).

A general view of the plicae in man (Figs. 7 and 8) reveals them to be underdeveloped, although they are developed in the incisive region. The capillary loop in the plica appears wide at each basis and is twisted 2 or 3 times at its tip, but there is no hair-pin type in other areas.

For all the species examined, it can be said that the high connective tissue papillae in both the anterior slope and plical top may be of a resistant form for mollifying exhaustion, affected by the periodicity and mashing or masticatory function. In other words, these topographic



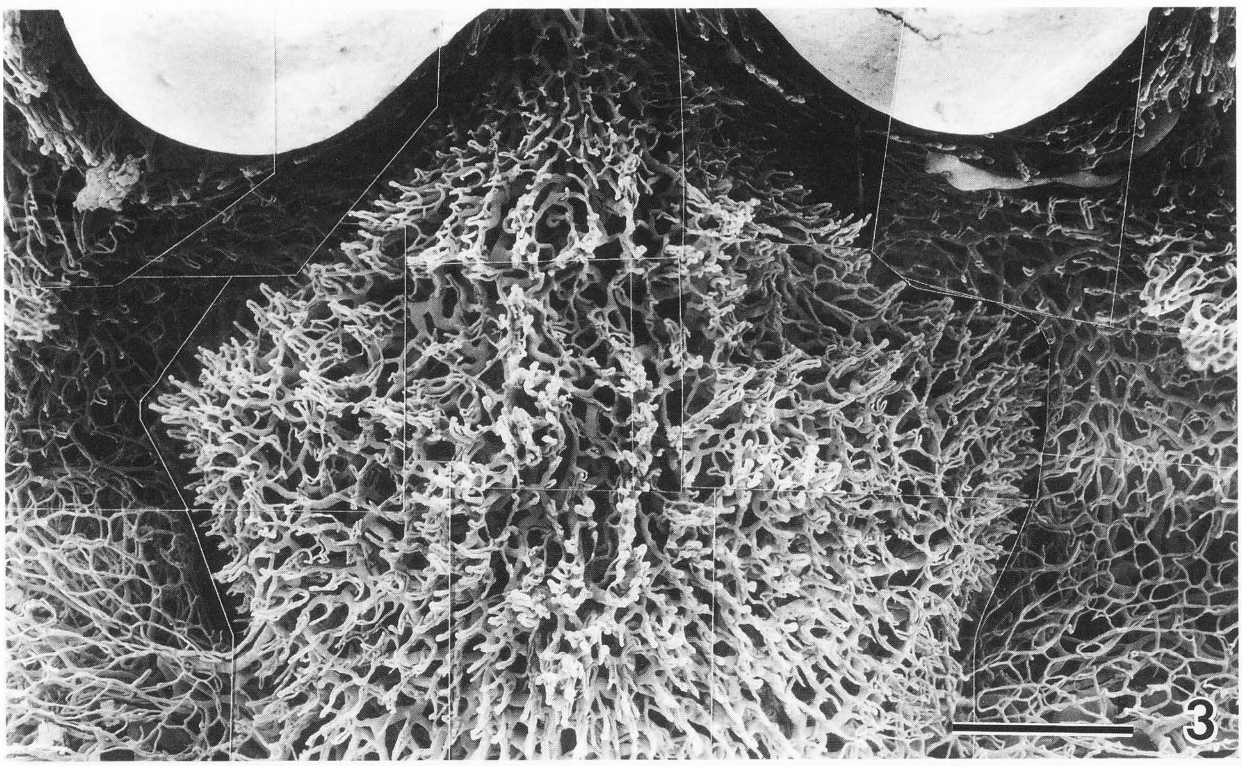
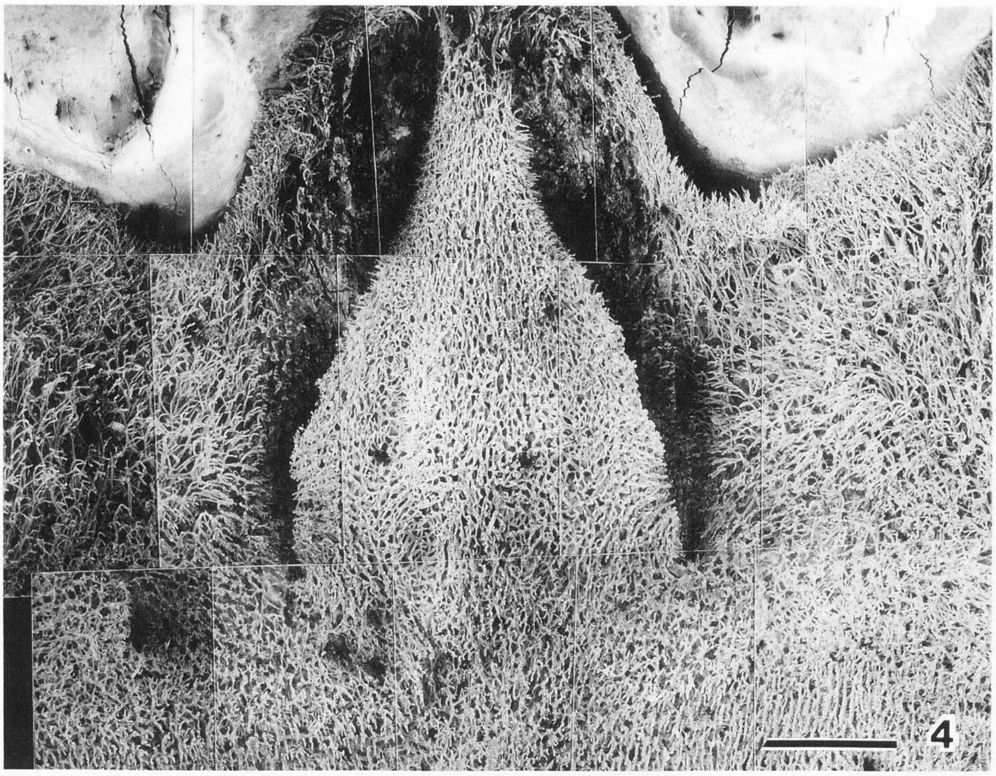
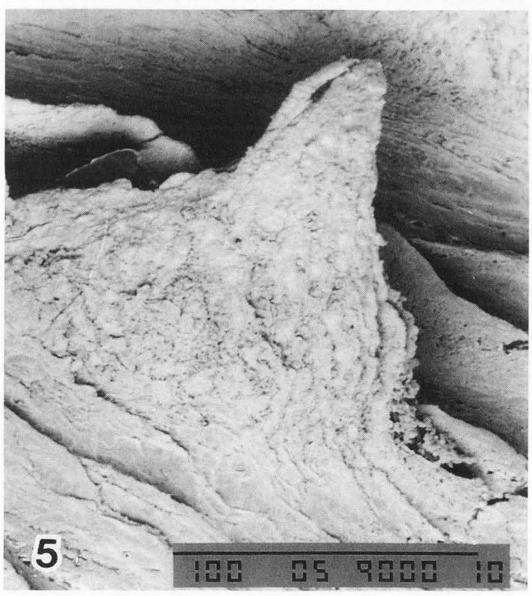


Fig. 2. A close-up of a transverse palatine plica in the cat. The small digitiform processes (*) are observed in a line. The anterior and posterior conical processes are located in the anterior (above) and posterior slopes, respectively. Calibration bar = 1 mm.

Fig. 3. Microvasculature of the incisive papilla in the cat. A subepithelial capillary network is observed all over the pentagonal incisive papilla. Capillary loops sprout from this network. Calibration bar = 1 mm





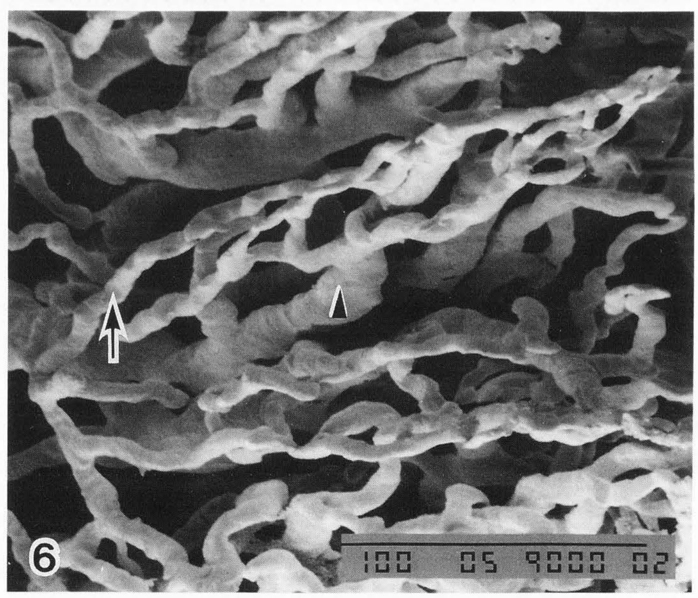
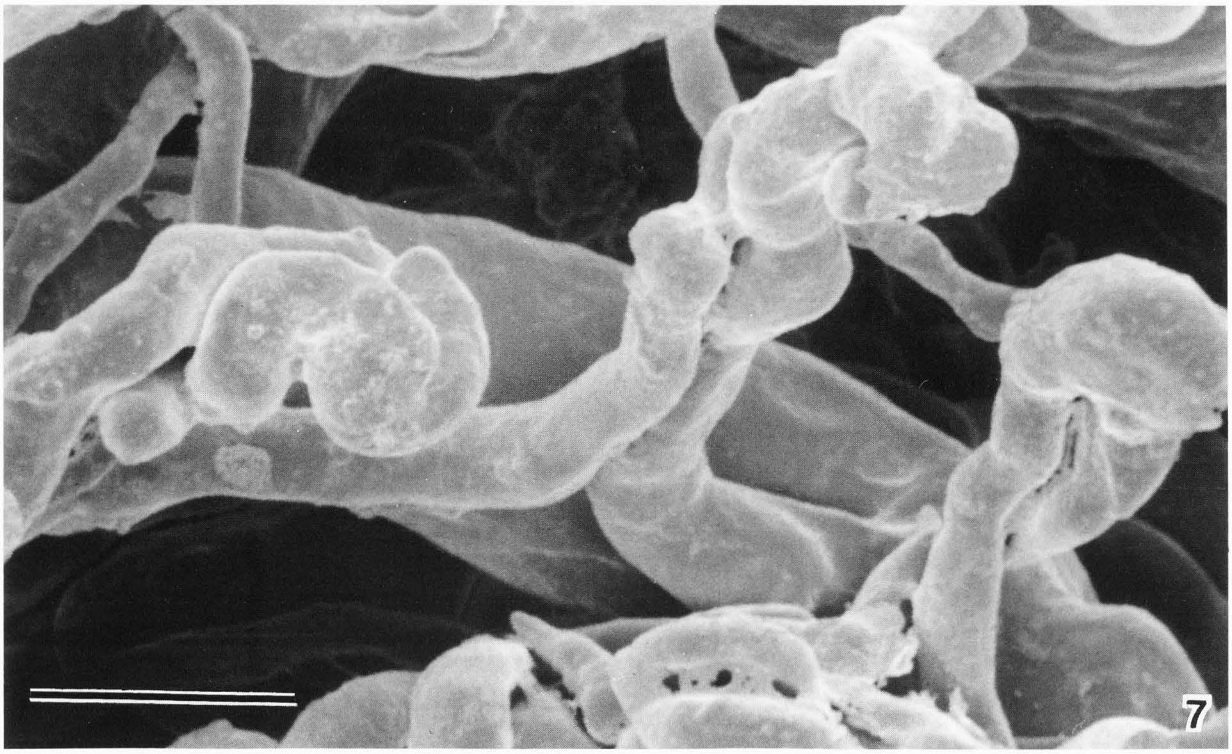


Fig. 4. Microvasculature of the incisive papillae in the Japanese monkey. The incisive papilla is observed in the shape of an arrowhead. Calibration bar = 1 mm.

Fig. 5. A connective tissue papilla on an epithelium-separated specimen in the rat. Each papilla is compressed in a right-left direction. A limited area is elevated to form a nipple corresponding to each connective tissue papilla. The anterior slope is usually steep in the shape of a cleft-cut. Generally, all papillae show an anterior inclination. Calibration bar = 100 μm.

Fig. 6. Capillary loops of the rat. The capillary loop in the papilla appears to be complicated, not in a simple hair-pin shape but like a small meshwork. An ascending (arrow) and descending crus (arrowhead). Calibration bar = 100 μm.



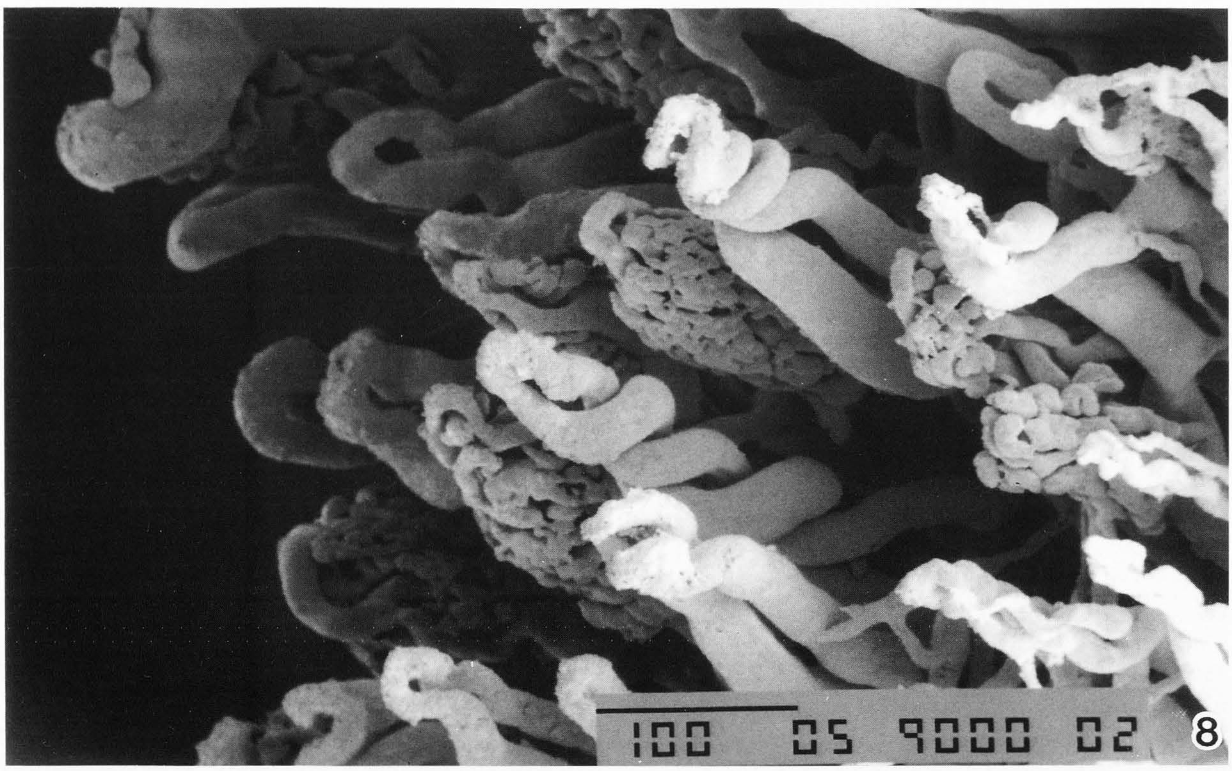


Fig. 7. Capillary loops in the molar region of man. The capillary loop is not observed to be a typical hair-pin loop, but similar to that in other oral mucosal regions. Calibration bar = 50 μm.

Fig. 8. Capillary loops at the transverse plica in the incisive region of man. Each of capillary loop has a wide basis and twists 2 or 3 times near its tip. Calibration bar = 100 μm.

Table 1. Morphology of the transverse palatine plicae or ridges (rabbit).

Incisive papillary region	1 or 2 in number, low, thick plate	anterior slope	postero-inferior inclination long, not steep
		top of plica	sharp
		posterior stope	antero-inferior cleft, short, overlapped by the anterior slope
		interplical	no flat area
Palatine fissure region	8 or 9 in number, tall and rectangle (typical)	anterior slope	postero-inferior inclination long, steep
		top of plica	somewhat round
		posterior slope	shorter than those of the anterior slope, a right angle to the interplical area
		interplical	slightly flat area
Between posterior teeth region	4 or 5 in number, lower than those of the palatine fissure region round triangle	anterior slope	equal to the posterior slope in length
		top of plica	round
		posterior slope	equal to the anterior slope in length
		interplical	slightly flat area

areas are actually organized and represent an activated interface.

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Table 2. Interrelations between the connective tissue papillae in lamina propria and capillary loops (rabbit).

		Connective tissue	Capillary loops
Incisive papillary region	anterior slope	sharp top, slender, tall cone	simple, tall, narrow intercrura (typical hair-pin)
	plica	round top, lower cylinder variably thick	lower, hair-pin with a little opened intercrura
	posterior slope	round top thick	opened at crura bases, lower some-times twisted
	interplical	sharp top slender tall needle-sharped	tall hair-pin with closing at at crura top but opened at bases
Palatine fissure region	anterior slope	somewhat sharp top tall cone with a wide opening	slender and tall hair-pin with opened at crura bases
	plica	round top, thick and tall cylinder with 2nd papillae frequently	irregular wavy, continuous loops, sometimes bridges between crura
	posterior slope	round top thick and tall cylinder	tall hair-pin, opened intercrura
	interplical	round top, low and large half-globe with irregular heights	arcade, opened intercrura in all length
Between posterior teeth region	anterior slope	round top, thick and tall cylinder[1]	hair-pin, slightly opened intercrura
	plica	round top, slender and tall cylinder[2]	slender, tall and simple hair-pin[2]
	posterior slope	resembling those of anterior slope	resembling those of the plical ridge in the incisive region
	interplica	somewhat round, taller cone or cylinder[3]	opened intercrura in all length[3]

[1]. resembling those of the posterior slope in the palatine fissure region.
[2]. resembling those of the ridge in the incisive region.
[3]. taller than those of the interplical area.

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Discussion with Reviewers

S. Yoshida: Please explain the relations between the linear arrangement of the capillary loops in sagittal sections and developmental direction of the secondary palate.

Authors: It can be considered that a serially undulating development directed toward the median line of the secondary palate may make the linear arrangement of the capillary loops.

S. Aharinejad: The submucosal venous plexus seems to be of particular significance. While Ike (1990) thought that this plexus may contribute to the process of regurgitation, Sayo (1985) suggested this plexus to be a blood reservoir and "heat ventilator". Have you ever seen conspicuous structural details on the wall of these veins? Do any valves and sphincter-like structures occur in the wall of these submucosal veins in the palate of rabbits? Do any histological findings exist on the wall composition of these submucosal veins? Does a particular neural supply of these veins exist?

Authors: We have just started to investigate particular structures on the venous wall comparatively, in order to elucidate Ike's food regurgitation or cushion and Sayo's blood reservoir and heat ventilator theories. Much more work is needed to answer to the questions you raise.

S. Aharinejad: I think that the following papers should be included and discussed in the paper: **a.** Jasinski A, Miodonski A (1981) Vascular arrangement in the oral mucosa of *Rana esculenta*. Scanning electron microscopy of corrosion casts. Arch. Histol. Jpn. **44**: 215-221. **b.** Sakamoto MK, Nakamura K, Handa J, Kihara T, Tanimura T (1991) Studies of variant palatal rugae in normal and corticosteroid-treated mouse embryos. Anat. Rec. **230**: 121-130.

Authors: Our work is concerned only with mammals and normal aspects, hence we have not discussed its relationship to the references you mentioned.

A. Lametschwandtner: Fig. 7 deserves special attention. The authors document and describe capillary loops whose tips are twisted 2 or 3 times. Close beside them vascular formations of nearly the same size but of entirely different structure are present, but not mentioned at all. The capillary loops described look very much like those described by Miodonski *et al.* (SEM studies on blood vessels in cancer of the larynx. Arch. Otolaryngol. **106**: 271-282, 1980), and Kus *et al.* (Morphology of arteries, veins and capillaries in cancer of the larynx. Cancer Res. Clin Oncol **100**: 271-282, 1981). Did the authors do histology to exclude pathological changes in the palatal mucosa?

In the second paragraph of results the authors state: "The present paper ... discusses the interrelations between the forms of the connective tissue papillae and capillary loop formation." This topic, not only during normal development but also under pathological conditions (see Miodonski *et al.*, 1980; and Kus *et al.*, 1981, above) is a very interesting one, but the authors do not refer to this. Both figures 7 and 8 cry for an explanation how this capillary loops are formed and what their physiological implications are.

Authors: Yes, we excluded any pathological aspects of the palatal tissue and its microvasculature. At this time we cannot give a reasonable answer to your second question since we do not have any findings on morbid aspects of capillary loops as you suggest.