Original Article

Morphological study of the Lingual papillae of Jentink's flying squirrel (*Hylopetes platyurus*)

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Abstract

This study describes the anatomy and histology of the tongue in the Jentink's flying squirrel (*Hylopetes platyurus*), a rodent native to Indonesia (Borneo and Sumatra). We examined the characteristics of the tongue using scanning electron microscopy (SEM) and light microscopy (LM). Macroscopic observations revealed three distinct regions: the apex, corpus (body) and radix (root). The dorsal surface of the apex was characterized by a median groove and lacked the lingual prominence that is common in many rodents. SEM and LM revealed the distribution of papillae over the dorsal surface of the tongue. The papillae could be categorized as mechanical papillae (filiform, conical, large conical) and gustatory papillae (fungiform, foliate, and vallate). Filiform papillae covered the apex and the anterior two-thirds of the corpus. Fungiform papillae were distributed among the filiform papillae from the apex to the corpus, whereas the foliate papillae were present only on the apex. Conical papillae were located on the posterior of the corpus, and the large conical papillae were on the lateral surface of the lingual radix. Three vallate papillae were arranged in a "V" pointing toward the larynx on the posterior part of the radix. This research provides the first detailed observations of the lingual papillae in *Hylopetes platyurus*. The shape, structure and distribution of papillae are described and compared with those in other rodent species.

Keywords: *Hylopetes platyurus*, lingual papillae, light microscopy, scanning electron microscopy

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Introduction

The Jentink's flying squirrel, also known as the gray-cheeked flying squirrel, (*Hylopetes platyurus*) is a mammal of the order Rodentia (Fig. 1). Eight to nine small flying squirrel species of the genus *Hylopetes* are native to southeast Asia (Thorington *et al*., 1996; Rasmussen and Thorington 2008). *H. platyurus* is distributed throughout the Malay Peninsula and on the islands of Borneo and Sumatra, Indonesia (Amr *et al*., 2006). Although *H. platyurus* is native to Indonesia, there are also increasing numbers held in captivity as pets.

H. platyurus is nocturnal and omnivorous and this species actively feeds on fruit, fungi, nuts and birds' eggs at night. The tongue is an essential organ of the digestive system and plays a major role in food transportation, swallowing and vocalization. The tongue can also perceive taste stimuli due to the presence of gustatory papillae on the tongue. Several morphological studies have used scanning electron microscopy (SEM) and light microscopy (LM) to examine the dorsal surface of the tongue in rodents – mainly laboratory animals, including the guinea pig (Kobayashi 1990; Ciena *et al*., 2017), BALB/c mouse (Toprak 2006; Toprak and Yilmaz 2016), the Wistar rat (Picoli *et al*. 2006; Verli *et al*., 2008; Costa *et al*., 2013), Sprague–Dawley rats (Costa *et al*., 2013; Reginato *et al*., 2014; Davydova *et al*., 2017), and hamsters (Whitehead and Kachele 1994; Parks and Whitehead 1998). However, fewer studies have examined the tongue in wild rodents, such as the bank vole (Jackowiak and Godynicki 2005), nutria (Emura *et al*., 2011), agouti (Ciena *et al*., 2013) and the mole-rat (Kilinc *et al*. 2010). There are a wide variety of rodent species and subspecies among mammals; the morphological variation in rodents represent adaptations to different habitats and feeding behavior (Shindo *et al*., 2006; Wannaprasert 2017). Thus, it is critical to conduct morphological research on the tongues of mammals, especially rodents.

Despite the wide distribution of *Hylopetes* spp. across Southeast Asia, the lingual morphology of this genus has not been thoroughly investigated. A few studies have examined other species of flying squirrels, such as *Petaurista leucogenys* (Emura *et al*., 1999), *Pteromys momonga* (Emura 2019), and *Sciurus anomalus* (Sadeghinezhad *et al*., 2016); however, there are no detailed reports on the anatomical and histological features of the tongue in *H. platyurus*. The present study was designed to observe the features of the tongue of *H. platyurus* by LM and SEM. We also compared our findings with those of other rodent species and mammals described in the literature.

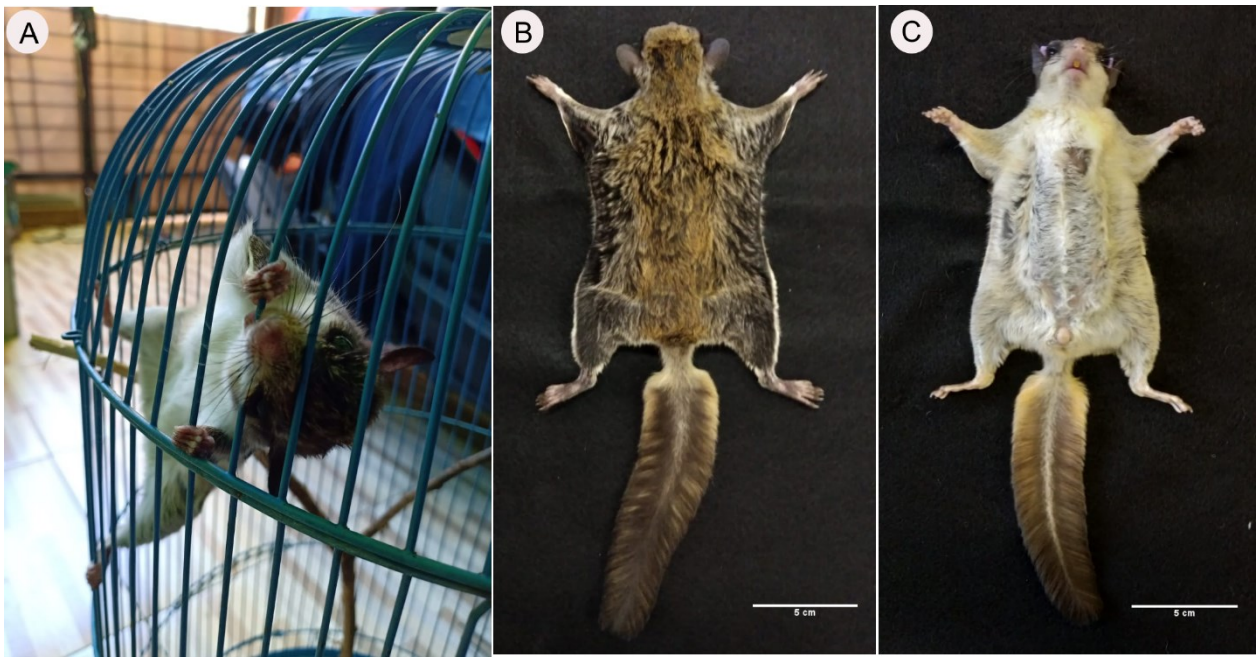

Figure 1 (A) The Jentink's flying squirrel, also known as the gray-cheeked flying squirrel. Based on observation, (B) on its middle back, the Jentink's flying squirrel has reddish-brown fur while on the side area it has grey fur. (C) In addition, white fur totally covers the ventral area of the Jentink's flying squirrel.

Materials and Methods

Animal Specimens: Eight Jentink's flying squirrel (*Hylopetes platyurus*) adult individuals were randomly selected from a collection of flying squirrels in captivity in Surabaya, Java Island, Indonesia, without regard to gender or age. The species identity was verified in the Laboratory of Animal Systematics at the Faculty of Biology, Universitas Gadjah Mada. The study was conducted in the Laboratory of Microanatomy and Macroanatomy, Department of Anatomy, Universitas Gadjah Mada; SEM was performed in the Integrated Laboratory for Research and Testing, Universitas Gadjah Mada. The capture process and research methods were approved by the Ethical Committee of the Faculty of Veterinary Medicine, Universitas Gadjah Mada, Yogyakarta, Indonesia (approval number 0007/EC-FKH/int./2020).

Conservation Status: According to the International Union for Conservation of Nature (IUCN)'s Red List of Threatened Species, the conservation status of

Hylopetes platyurus is Data Deficient (DD), i.e., the information available is insufficient to assess the risk to the species. There is no information regarding *H. platyurus* in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

Gross Macroscopy Analysis: The eight *H. platyurus* individuals were anesthetized using 10 mg/kg corpus weight (BW) ketamine and 2 mg/kg BW xylazine; then euthanized with a combination ketamine and xylazine overdose. The oral cavity was dissected and the tongue was removed by separating the occipito-mandible joint. Each sample was rinsed with 0.9% NaCl for 5 mins five times. Macroscopic observations were performed using a camera (Canon EOS 7000D, Tokyo, Japan). The samples were randomly divided into two groups and four samples were prepared for SEM, while four samples were stained with hematoxylin and eosin (HE) for LM analysis.

Scanning Electron Microscopy: Four *H. platyurus* tongues were examined using an SEM. The tongues were placed in a fixation solution of 0.5% glutaraldehyde (Chem Cruz, Texas, USA), 1.5% formaldehyde (Nacalai Tesque, Kyoto, Japan) and 100 g hydroxyethyl piperazineethanesulfonic acid (HEPES; Chem Cruz, Texas, USA) in 100 mL phosphate-buffered saline. The tongues were then washed with 0.9% NaCl (Nacalai Tesque, Kyoto, Japan) and gradually dehydrated using an ethanol series from 70% to absolute ethanol (KgaA, Darmstadt, Germany). Next, the samples were critical point dried using a castable vacuum system (25 °C, 4 Pa; Buehler 1000 Vacuum System, Stuttgart, Germany), then coated with platinum (JEOL JEC-3000FC, Tokyo, Japan) before examination under SEM (Jeol JSM6510LA, Tokyo, Japan) at an accelerating voltage of 10 kV.

Hematoxylin and Eosin Staining: Four tongues were fixed in 10% formalin and then gradually dehydrated using an ethanol series (KgaA) from 70% to 100% concentration. The samples were then cleared in xylene (KgaA, Darmstadt, Germany) and embedded in paraffin (Leica Biosystems, Wetzlar, Germany). Sections 8 µm in thickness were cut using a rotary microtome (Yamato RV 240, Asaka, Japan) from the apex, corpus and radix parts of the tongue. Following routine histological processing, the tissue samples were stained with HE (Bio-optica, Milano, Spain) and observed under a light microscope (Olympus BX51, Tokyo, Japan). Photographs were taken using Optilab software (Optilab, Yogyakarta, Indonesia).

Results

Gross Morphology of the Tongue: The *H. platyurus* tongue has three distinct regions: the apex, which is the most rostral part; the corpus, known also as lingual body; and the radix or lingual root, which is the most caudal part attached to the larynx. Macroscopic examination revealed a groove in the center of the dorsal surface of the tongue, extending from the apex to the corpus; this is called the median groove (Fig. 2A). The apex of the tongue can move freely in all directions (Fig.2B).

The lingual corpus (body) is located immediately adjacent to the apex rostrally and the radix (root) caudally (Fig. 2C). The border between the apex and corpus can be identified from the type of papillae and the change in direction at the end of the median groove. There is no clear border between the lingual corpus and radix. There are three vallate papillae on the radix, forming a "V" shape pointing toward the larynx (Fig.2D).

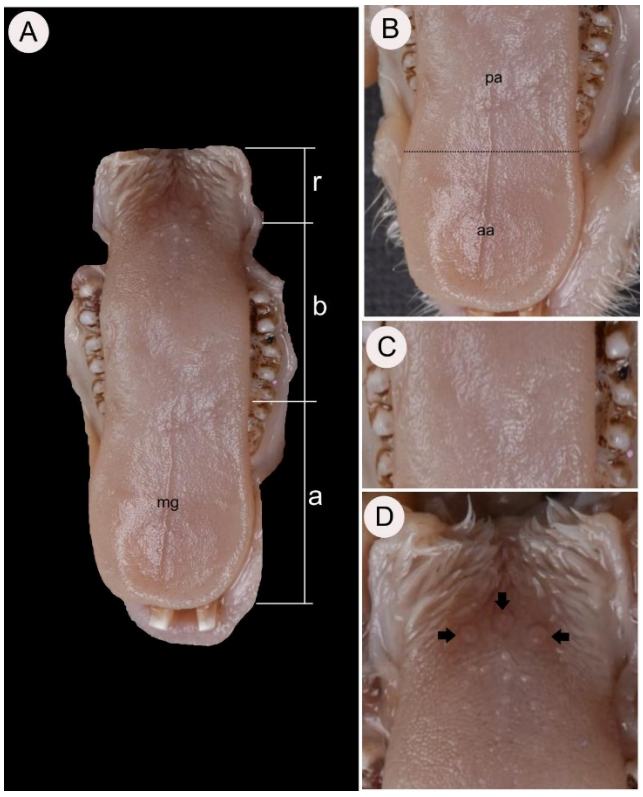

Figure 2 (A) Macroscopic depiction of the tongue of the Jentink's flying squirrel: (a) apex; (b) body (corpus); (r) root (radix); (mg) median groove. (B) Macroscopic dorsal view of the apex of the tongue of flying squirrel: aa (anterior apex); pa (posterior apex). (C) Macroscopic dorsal view of the corpus of the tongue of flying squirrel. (D) Macroscopic dorsal view of the radix of the tongue of flying squirrel. Black arrow indicates vallate papilla.

Scanning Electron Microscopy: SEM revealed the distribution of papillae on the dorsal surface of the tongue. Five types of papillae were observed: two types of mechanical papillae (filiform and conical) and three gustatory papillae (fungiform, foliate and vallate) (Fig. 3, Table 1). Filiform papillae were distributed along the surface of the tongue from the apex to part of the radix. Fungiform papillae were found among the filiform papillae from the apex to the radix. Meanwhile, the foliate papillae were only on the apex. Large conical papillae were distributed over the dorsolateral surface of the radix. The vallate papillae were located only on the posterior part of the radix.

Apex: Short filiform papillae were directed caudally on the apex and characterized by a single-pointed triangular top edge pointing upward, with a blunt, serrated lateral edge (Fig. 4A, 4B). These papillae covered the anterior half of the apex, while long filiform papillae covered the posterior half. The long filiform papillae were similar in structure to the short filiform papillae but significantly longer (Fig. 4D). Among the filiform papillae, there were fungiform papillae, which were rounded or oval, resembling a mushroom head (Figure 4A, 4C). Additionally, foliate papillae were located among the filiform papillae on the apex; these papillae had the fold-like tridimensional structures of which had rougher surfaces compared to the fungiform papillae (Fig. 4B).

Corpus (Lingual body): Long filiform and conical papillae were distributed on the tongue corpus (Fig. 5). The conical papillae form a radiating pattern in different directions but symmetrical positions; they were pointed cranially, caudally and medially (Fig. 5A, 5B). The conical papillae were triangular, with a blunt tip (Fig. 5B, 5C). Fungiform papillae were distributed among the long filiform and conical papillae in this area (Fig. 5C). The long filiform papillae, located on the posterior of the lingual corpus, point cranially rather than caudally (Fig. 5D) and were irregular in shape and width.

Radix (Root): Three types of papillae were distributed on the lingual radix. Conical filiform papillae with teardrop-like shapes were distributed in a unique radial pattern on the anterior apex. Fungiform papillae were scattered among the conical filiform papillae (Fig. 6A). The large conical papillae filled both lateral sides of the radix, while three vallate papillae occupying the posterior part of the radix, forming a "V" shape with two papillae on the anterior side and the third on the posterior side, close to the larynx (Fig. 6B, 6C).

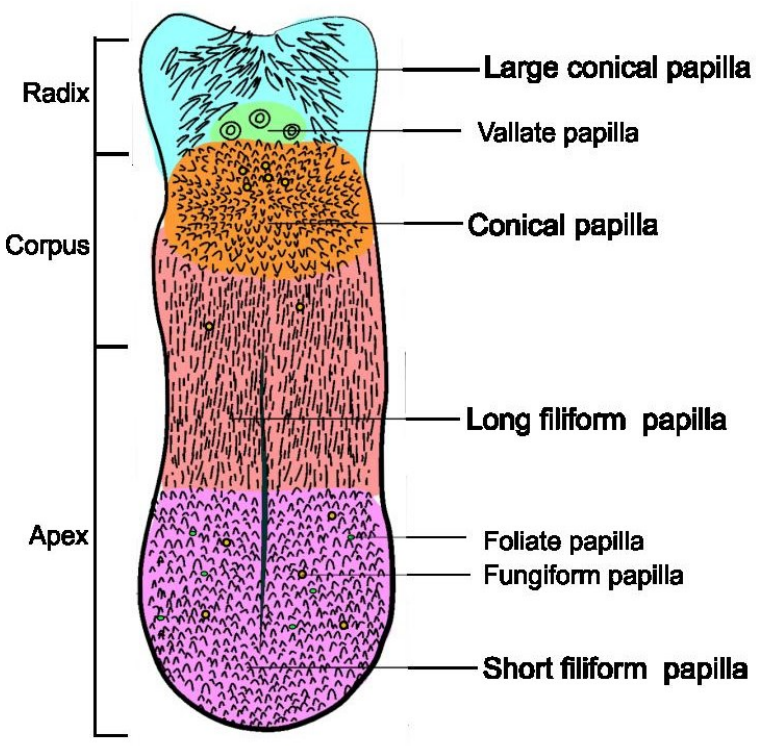

Figure 3 Schematic dorsal view of the tongue of Jentink's flying squirrel, with papilla distribution and region.

Table 1 Distribution and measurements of the lingual papillae on the tongue of *Hylopetes platyurus*.

Type of Papillae	Apex	Corpus	Radix	Length (μm)	Width (μm)
Short filiform papilla	+	-	-	60±4	50±6.4
Long filiform papilla	+	+	-	409±54	115±18
Conical filiform papilla	-	+	+	135±13	77±5
Large conical papilla	-	-	+	612±60	125±12
Fungiform papilla	+	+	+	92±5	92±5
Foliate papilla	+	-	-	90±3	90±3
Vallate papilla	-	-	+	202±18	202±18

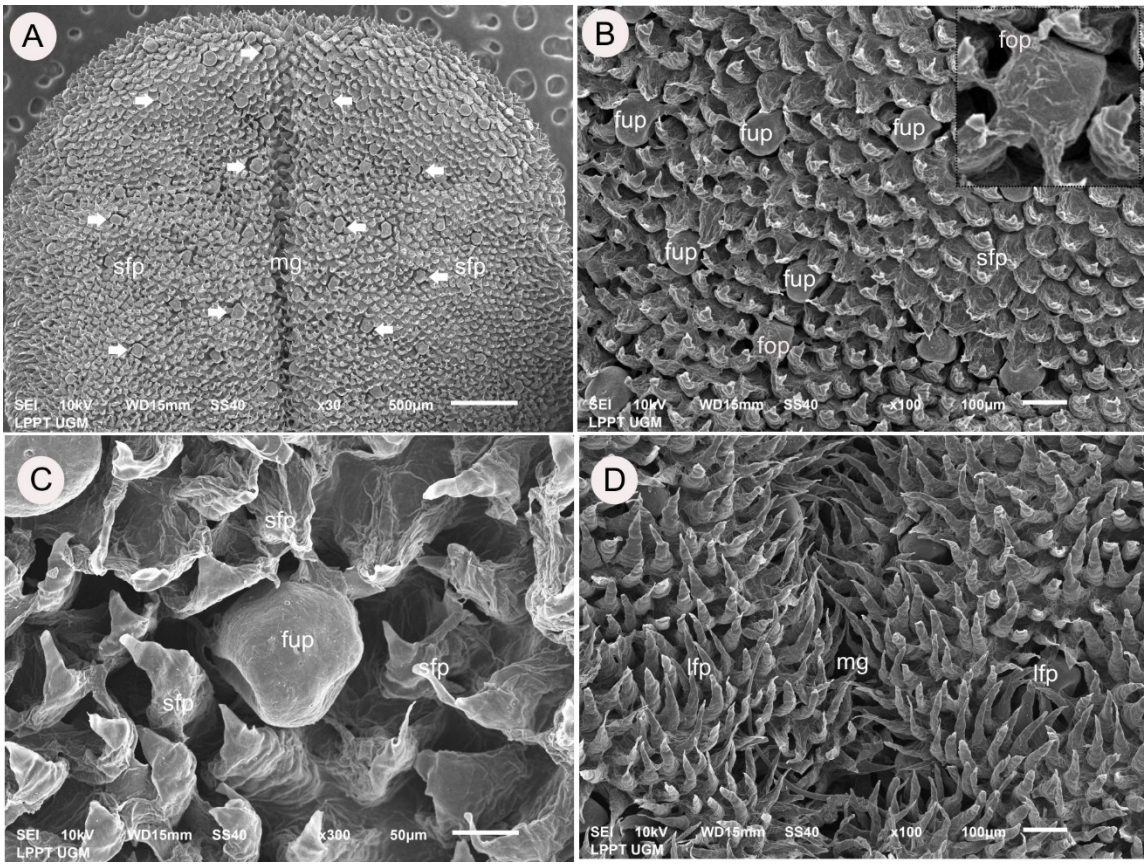

Figure 4 Scanning electron microscopy (SEM) images of the apex region of the tongue of Jentink's flying squirrel. (A) Anterior apex; short filiform papilla (sfp); median groove (mg); fungiform papilla (white arrow). (B) Short filiform papilla on the anterior apex at high magnification (200 x); fungiform papilla (fup). (C) Fungiform papilla on the anterior apex at high magnification (300x); (D) Posterior apex; long filiform papilla (lfp); median groove (mg).

Histological Observation: HE staining revealed three tissue layers in the tongue, namely, the lamina epithelialis mucosae, lamina propria mucosae and lamina muscularis mucosae. The lingua mucosa papillae were identical to those observed with SEM, i.e., fungiform, foliate, filiform, conical and vallate papillae. These papillae were bound by complex squamous epithelium and a layer of keratin. The lingual mucosa also included the lamina propria mucosae, a thick tissue that enters the papillae. The lamina muscularis mucosae consisted of a layer of muscle fibers.

Apex: Histological study of the apex revealed three types of papillae, namely, filiform (long and short), fungiform and foliate (Fig. 7). The filiform papillae, which were distributed all over the apex surface, were highly keratinized, with sharp and thin edges. There were far fewer fungiform papillae scattered among the filiform papillae (Fig. 7C, 7D). The fungiform papillae were spherical in shape and thinly keratinized, bearing taste buds that function as taste receptors. Foliate papillae were also observed among the filiform papillae on the apex (Fig 7A, 7B).

Corpus (Lingual Body): Histological study of the lingual corpus revealed long filiform, conical and fungiform papillae. The long filiform and fungiform papillae of the corpus had the same characteristics as those of the apex. The conical papillae had thick keratinization, a conical shape and a blunt tip (Fig. 8). Fungiform papillae were spread evenly between the long filiform and conical papillae (Fig. 8A, 8B).

Radix (Root): Histological study of the radix revealed conical, large conical and vallate papillae (Fig. 9). The vallate papillae were round and bound with walls and trenches created by epithelial invagination (Fig. 9B). The vallate papillae were larger than the other papillae and covered with a thin layer of keratin. These papillae also had many more taste buds compared to the fungiform papillae (Fig. 9B). The large conical papillae were triangular with sharp edges and a thick layer of keratin. The large conical papillae of the radix had the same characteristics as those of the corpus but a larger size (Fig. 9C).

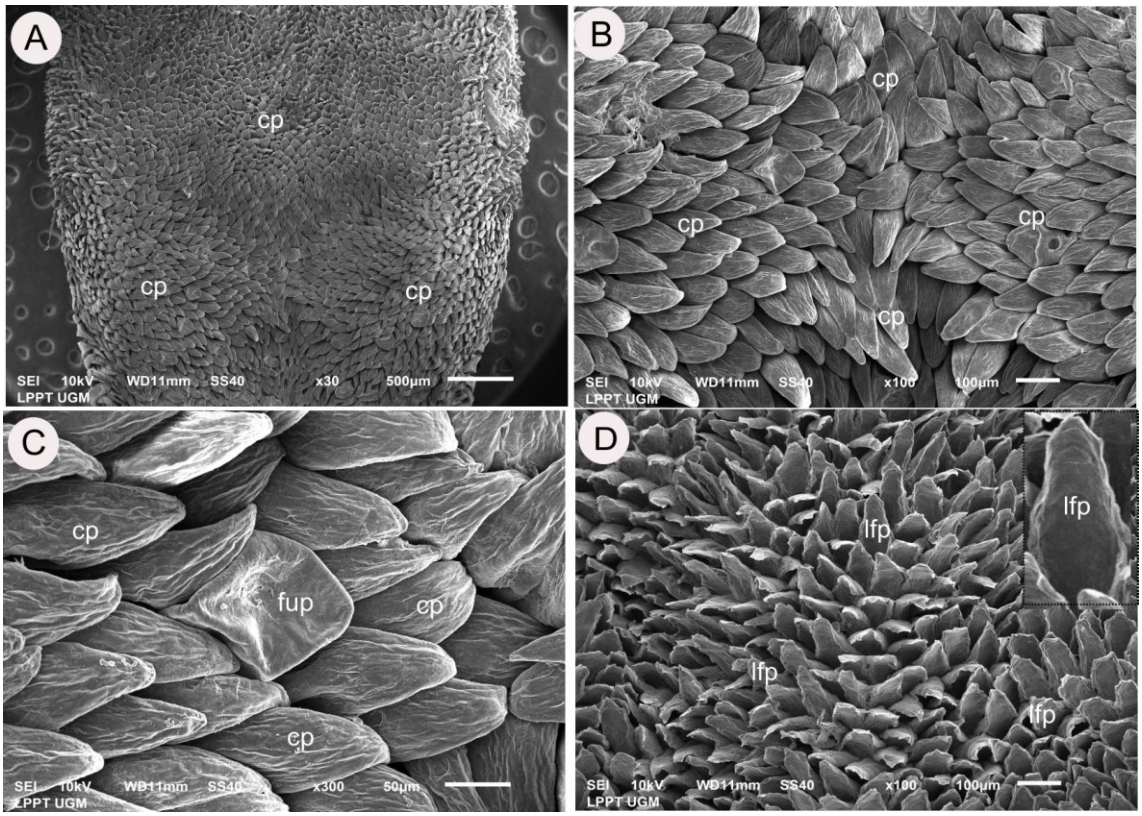

Figure 5 Scanning electron microscopy (SEM) images of the corpus of the tongue of Jentink's flying squirrel. (A) conical papillae (cp), shows conical papillae in a radiating symmetrical pattern. (B) High magnification conical papillae in a radiating symmetrical pattern. (C) The conical papillae (cp), between which papillae the fungiform papillae (fup) are present. (D) The long filiform papillae (lfp) on the anterior part of the corpus.

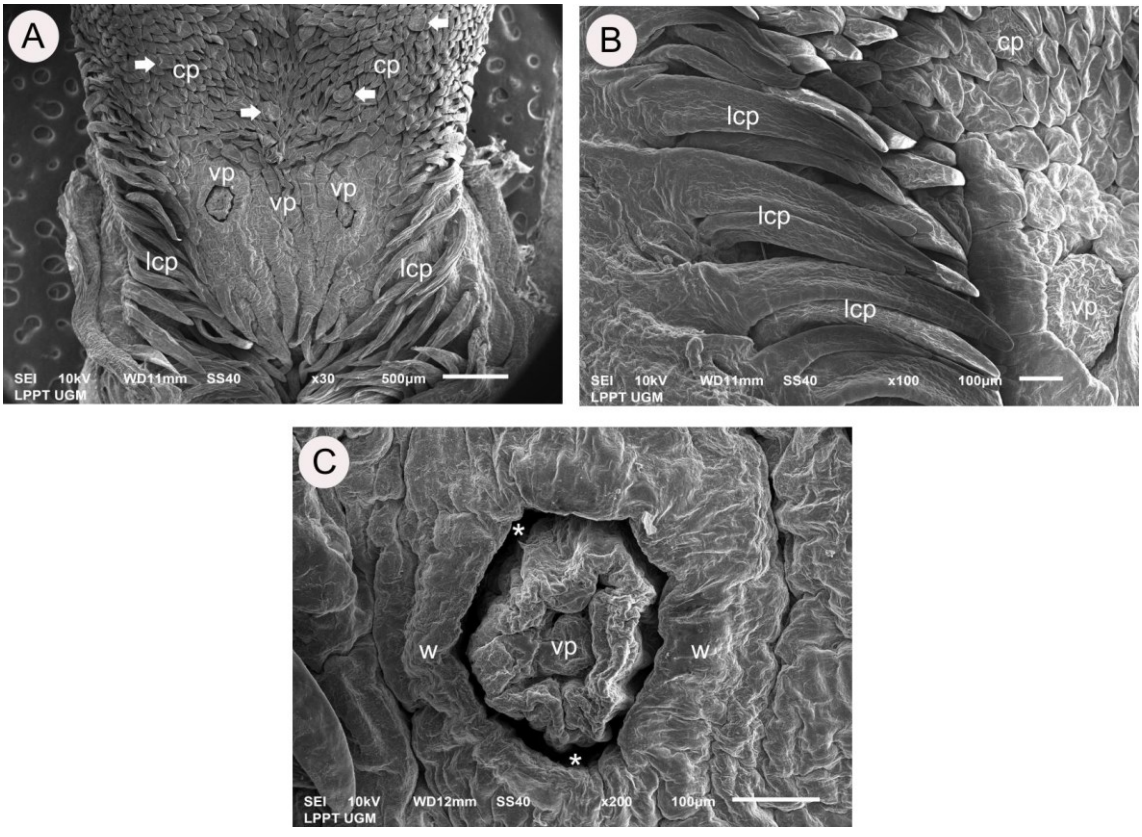

Figure 6 Scanning electron microscopy (SEM) images of the radix of the tongue of Jentink's flying squirrel. (A) On the radix, the conical papillae (cp), large conical papillae (lcp), fungiform papillae (white arrow), and vallate papillae (vp) are distributed. (B) High magnification of the large conical papillae (lcp) on the lateral side of the vallate papillae (vp) and conical papillae (cp). (C) Photograph of a vallate papilla (vp) surrounded by one layer of wall (w) that forms a circular groove (*) around the papilla.

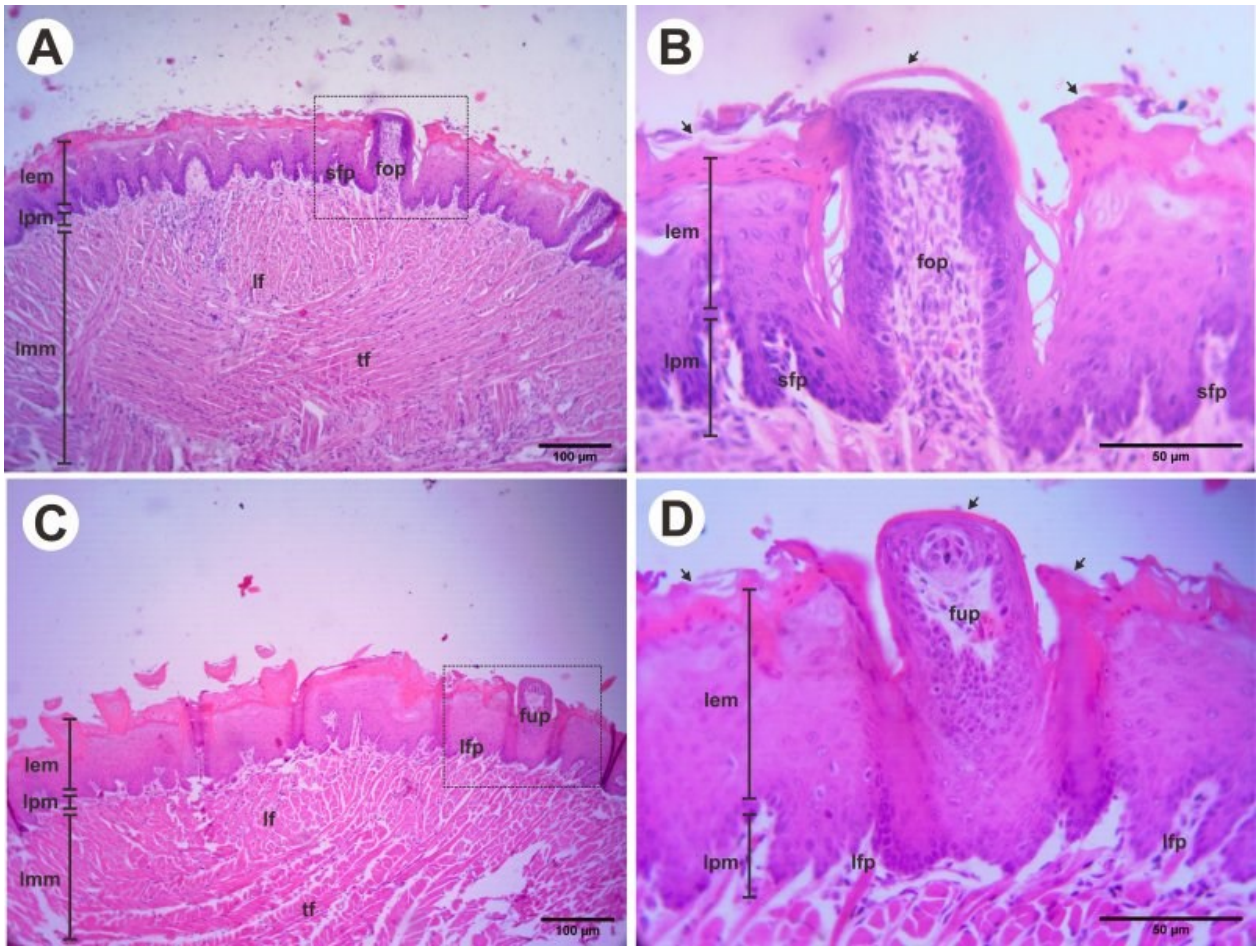

Figure 7 Photomicrograph of the Jentink's flying squirrel tongue with hematoxylin and eosin staining. (A) The histology of the anterior apex. The apex is histologically divided into three layers: (lem) lamina epithelialis mucosae, (lpm) lamina propria mucosae, and (lmm) lamina muscularis mucosae. The muscularis layer includes the transversal fibers (tf) and longitudinal fibers (lf). The foliate papilla (fop) observed between short filiform papillae (sfp). (B) High magnification foliate papillae (fop) between short filiform papillae (sfp). Keratinization of the epithelium appears thick in short filiform papilla and thin in foliate papillae (black arrow). (C) The histology of the posterior apex. Fungiform papillae (fup) between long filiform papillae (lfp). (D) High magnification of fungiform papillae (fup) can be observed between long filiform papilla (lfp). Keratinization of the epithelium appears thick in long filiform papillae and thin in fungiform papillae (black arrow).

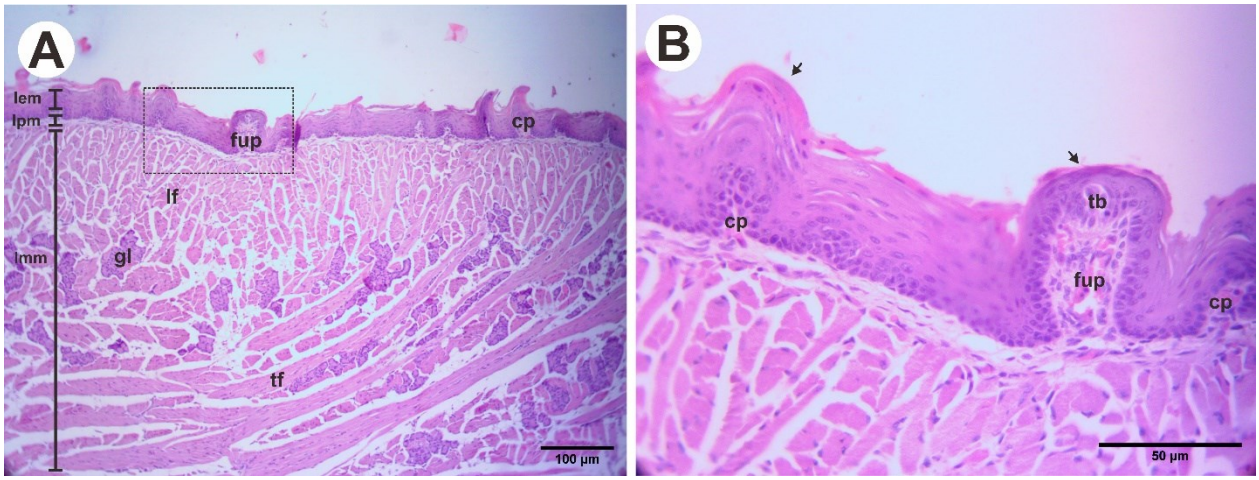

Figure 8 The histology of the corpus of the tongue Jentink's flying squirrel. (A) The conical papillae (cp) and fungiform papillae (fup) are present. The corpus is histologically divided into three layers: (lem) lamina epithelialis mucosae, (lpm) lamina propria mucosae, and (lmm) lamina muscularis mucosae. In addition, on the lingual muscle the transversal fibers (tf), longitudinal fibers (lf) and lingual glands (gl) can clearly be seen. (B) High magnification of the conical papillae (cp) and fungiform papilla (fup). Conical papillae have thick keratinization (black arrow). The fungiform papilla has a taste bud (tb) and a thin layer of keratin (black arrow).

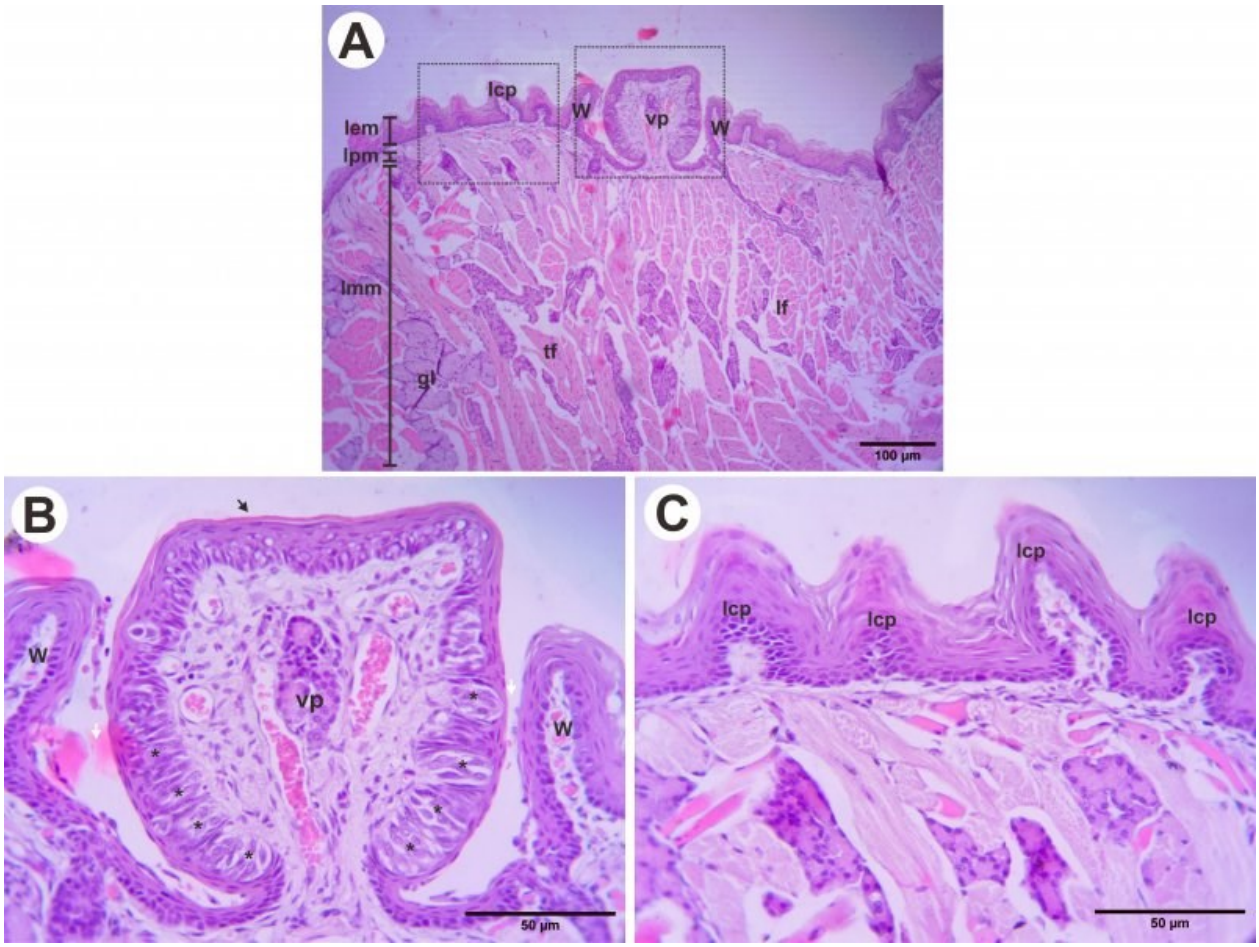

Figure 9 The histology of the radix of the tongue Jentink's flying squirrel. (A) On the surface there are large conical papillae (lcp) and a vallate papilla (vp). The radix region histologically consists of three layers (as do the apex and corpus): (lem) lamina epithelialis mucosae, (lpm) lamina propria mucosae, and (lmm) lamina muscularis mucosae. In addition, the transversal fibers (tf), longitudinal fibers (lf) and some lingual glands (gl) can be seen on the muscularis layer. The vallate papilla has an outer wall (w) that follows the path surrounding the papillae. (B) High magnification of a vallate papilla (vp) in the radix; in the mucosa of the vallate papillae, abundant taste buds can be found (*). Vallate papillae have thin epithelial keratinization (black arrow). Vallate papillae were limited by a sulcus (white arrow) and walls (w) formed from epithelial invaginations. (C) High magnification of the large conical papilla (lcp) in the radix.

Discussion

Morphological observation revealed that the wide, flat tongue of *H. platyurus* consists of three parts, namely, the apex, corpus (body) and radix (root). This three-part division has been observed in the tongue of other rodents, such as rats (Harłajczuk *et al*., 2018), Japanese giant flying squirrels (Emura *et al*., 1999), Persian flying squirrels (Sadeghinezhad *et al*. 2016), Patagonian cavy (Emura *et al*., 2011) and long-eared hedgehogs (Parchami *et al*., 2018). In *H. platyurus*, the tongue apex bears a median groove or sulcus medianus that divides the apex into two wide areas. Median groove formations are common among rodents, including *Clethrionomys glareolus* (Jackowiak and Godynicki 2005), *Hystrix cristata* (Karan *et al*., 2011), *Sciurus vulgaris* (Ünsaldi 2010), *Dasyprocta aguti* (Ciena *et al*., 2013), *Muscardinus avellanarius* (Wolczuk 2014), *Sciurus anomalus* (Sadeghinezhad *et al*., 2016), *Rhizomys sumatrensis* (Wannaprasert 2017),and *Octodon degus* (Cizek *et al*., 2016). Meanwhile, rodents such as the guinea pig (Kobayashi 1990), Patagonian cavy (Emura *et al*., 2011), capybara (Watanabe *et al*., 2013) and rock cavy (Santos *et al*., 2015) lack a sulcus medianus.

H. platyurus lack a lingual prominence on the posterior part of the corpus. This characteristic is also absent from the tongue of the long-eared hedgehog (Parchami *et al*., 2018; Jabbar 2019). The presence of a lingual prominence is regarded as an adaptation to herbivory, as the prominence—rich with muscle and filiform papillae—allows herbivores to grind food by crushing it between the tongue and the upper palate (Abumandour and El-Bakary 2013). In *H. platyurus,* the posterior part of the tongue, i.e., the radix (root), is characterized by the presence of vallate papillae.

SEM and LM observations revealed that the papillae of *H. platyurus* can be divided into two functional groups, mechanical and gustatory papillae. The filiform papillae and conical papillae can be categorized as mechanical, while the fungiform papillae, foliate papillae, and vallate papillae can be categorized as gustatory. The filiform papillae are predominant on the *H. platyurus* tongue, covering the apex and the anterior two-thirds of the corpus. The conical papillae, in contrast, are located partly on the corpus (body) and partly on the radix (root).

The distribution of the filiform papillae in *H. platyurus* is consistent with other members of the order Rodentia (Whitehead and Kachele 1994; Emura *et al*.,

1999, 2011; Jackowiak and Godynicki 2005; Nonaka *et al*., 2008; Cheng *et al*., 2009; Kilinc *et al*., 2010; Ünsaldi 2010; Ciena *et al*., 2013; Watanabe *et al*., 2013; Wolczuk 2014; Cizek *et al*., 2016; Sadeghinezhad *et al*., 2016; Wannaprasert 2017). The filiform papillae can be divided into two subtypes based on morphology: short and long filiform papillae. The short filiform papillae cover the majority of the apex and bear conical processes. In contrast, the long filiform papillae are located on the posterior part of the apex and the anterior two-thirds of the corpus; each bears a single triangular process, which is thicker and longer than those of the short filiform papillae. Similar types of filiform papillae have been observed in the guinea pig (Kobayashi 1990), American beaver (Shindo *et al*., 2006), capybara (Watanabe *et al*., 2013), and rock cavy (Santos *et al*., 2015). The filiform papillae may function as a supporting structure for food uptake, mastication and ingestion (Jackowiak and Godynicki 2005; Pastor *et al*., 2008). The conical papillae are found on the posterior third of the corpus and form a radiating symmetrical pattern, pointing cranially, medially and caudally. This pattern can also be observed on the tongue of the hazel dormouse (Wolczuk 2014). Conical papillae were also observed on the radix, whereas the large conical papillae were distributed on the lateral radix.

The gustatory papillae can be categorized as fungiform papillae, foliate papillae and vallate papillae. Morphologically, the fungiform papillae appear round in shape and are wider and shorter than the filiform papillae. The fungiform papillae are located among the filiform and conical papillae on the apex and corpus. In some rodents, such as the Patagonian cavy (Emura *et al*.. 2011), fungiform papillae are located on the lateral part of the apex. Our observations revealed that each fungiform papilla bears only one taste bud. This number varies among species, for example, the Persian flying squirrel has one to four taste buds per papilla (Sadeghinezhad *et al*., 2016).

Interestingly, unlike rodents such as the Patagonian cavy, capybara and rat (Emura *et al*., 2011; Watanabe *et al*., 2013; Harłajczuk *et al*., 2018), foliate papillae are present only between the short filiform papillae on the apex in *H. platyurus*. SEM and LM observations show that the foliate papillae in *H. platyurus* have the same structure as the fungiform papillae, but lack taste buds. In some mammalian species, such as koalas and common tree shrews, the foliate papillae also lack taste buds (Kobayashi and Wanichanon 1992; Kobayashi *et al*., 2003). In rodents, the foliate papillae are typically located on the radix of the tongue (Wolczuk 2014; Sadeghinezhad *et al*., 2016; Harłajczuk *et al*., 2018). However, blind mole rats (Kilinc *et al*., 2010) and large bamboo rats (Wannaprasert 2017) lack foliate papillae. According to Shindo *et al*., (2006), the development of foliate papillae is correlated with the type of food eaten and the way it is processed inside the mouth. In our study, the *H. platyurus* in captivity were fed a uniform food type, which may have restricted the development of the foliate papillae.

The presence of vallate papillae has been widely observed in rodents, with variations in number and morphology between species. This study demonstrates that *H. platyurus* has three vallate papillae on the posterior part of the radix. Guinea pigs (Kobayashi 1990), rabbits (Nonaka *et al*., 2008), blind mole rats (Kilinc *et al*., 2010), Patagonian cavies, capybara, nutria (Emura *et al*., 2011), and porcupines (Atalar and Karan 2011) bear two vallate papillae. The number of vallate papillae is reduced to one, which is centrally located in the caudal region, in rats (Harłajczuk *et al*., 2018), mice (Kobayashi and Wanichanon 1992) and bank voles (Jackowiak and Godynicki 2005). The Japanese flying squirrel (Emura *et al*., 1999), American beaver (Shindo *et al*., 2006), and Persian flying squirrel (Sadeghinezhad *et al*., 2016) have three vallate papillae. In *H. platyurus*, the vallate papillae are surrounded by a deep groove and a wall; histological examination shows that these papillae bear many taste buds on the lateral walls of the lamina epithelialis. The structure of the vallate papillae provides a wide taste area. Since *H. platyurus* is omnivorous, we can postulate here that the number of vallate papillae is important to improve food palatability.

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