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# Histochemical Study of the Posterior Lingual Glands of the Large Bamboo Rat (*Rhizomys sumatrensis*) and the Lesser Bamboo Rat (*Cannomys badius*)

## Estudio Histoquímico de las Glándulas Linguales Posteriores de la Rata de Bambú Grande (*Rhizomys sumatrensis*) y la Rata de Bambú Menor (*Cannomys badius*)

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**WANNAPRASERT, T.** Histochemical study of the posterior lingual glands of the large bamboo rat (*Rhizomys sumatrensis*) and the lesser bamboo rat (*Cannomys badius*) *Int. J. Morphol., 43(3)*:993-1000, 2025.

**SUMMARY:** The von Ebner's and Weber's glands are lingual salivary glands located at the posterior part of the mammalian tongue. In the present study, histochemical features of glycoconjugates secreted by both glands were examined in the large and lesser bamboo rats, fossorial herbivorous rodents distributed in Indochina. The results revealed that the posterior lingual glands of these two bamboo rat species consisted of serous von Ebner's glands and mucous Weber's glands. The histochemistry using periodic acid-Schiff (PAS), alcian blue (AB) pH 1.0 and 2.5, AB pH 2.5/PAS, aldehyde fuchsin (AF) pH 1.0 and AF pH 1.0/AB pH 2.5 staining demonstrated that the secretion of von Ebner's glands contained neutral glycoconjugates without acidic forms, whereas that of Weber's glands included mainly acidic glycoconjugates (probably mucins), which were predominantly sulfated forms. Small amounts of neutral glycoconjugates were detected in the Weber's glands of the large bamboo rat but were lacking in the lesser bamboo rat. The glycoconjugate content in saliva from these lingual glands may have a taste-related function associated with the taste buds of the vallate papillae. Beyond protection against irritating factors, the presumed sulfated mucins secreted by Weber's glands may improve the antimicrobial properties of the mucus. Subtle differences in histochemical staining between the two bamboo rats are possibly related to their different diet specificity.

**KEY WORDS: Histochemistry; Histology; Minor salivary glands; Mucins; Rodents.**

## INTRODUCTION

The mammalian tongue performs the vital functions of food manipulation, gustatory perception, grooming and vocalization. This organ consists of complex core muscles covered by connective tissues and mucosal epithelium. Numerous surface projections of a stratified epithelium with a connective tissue core form the lingual papillae. Extensive information about the lingual papillae has been published and revealed considerable variations in their microanatomy and distribution, especially among rodents, which constitute the largest mammalian order. However, less attention has been paid to analyses of the lingual glands lying in the muscular layers.

Lingual glands are recognized as a set of the minor salivary glands. Mammalian lingual glands are generally classified into three types: glands of Blandin-Nuhn at the tongue apex, von Ebner's glands related to the vallate and foliate papillae, and Weber's glands at the tongue radix. However, lingual glands in the body part of the tongue have recently been reported in the Persian squirrel (Akbari *et al*., 2024). For the three general types, the glands of Blandin-Nuhn are not common in all mammals (Tandler *et al*., 1994), but the other two types are unanimously found. von Ebner's glands typically consist of purely serous acini, whereas Weber's glands show a purely mucous or mixed seromucous type. The seromucous glands typically exhibit predominantly mucous acini, some of which are capped with serous demilunes (Nagato *et al*., 1997; Paliwal *et al*., 2006; Gozdziewska-Harlajczuk *et al*., 2018). The histological appearance of Weber's glands, even with the serous parts, essentially resembles that of the sublingual gland (Harrison, 2021).

Secretory products produced by serous and mucous acinar cells have a different chemical composition. Serous acini secrete a watery product containing digestive enzymes, proteins and glycoproteins with taste-related roles (Hand *et al*., 1999; Redman, 2012). Mucous cells secrete mucus, which is a slimy material that lubricates the oral cavity and

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forms a protective biofilm over the oral mucosal surfaces (de Paula *et al*., 2017). The principal components of mucus are mucins, heavily glycosylated glycoproteins responsible for its viscous and gel-forming properties. The different secretory products made by these two acinar cells reflect fundamental differences in their cell architecture and intracellular mechanisms (de Paula *et al*., 2017; Gozdziewska-Harlajczuk *et al*., 2018). The relative distribution of serous and mucous acinar cells in each salivary gland is species-specific (Melvin *et al*., 2005). The histochemical properties of saliva, particularly the carbohydrate component of glycoconjugates (including glycoproteins), secreted by lingual glands vary among different species, depending on the distribution of these two cell types. Differences in their secretion are thought to in turn relate to the diet type and developmental change of the animal (Youn & Jo, 1998; Levin & Pfeiffer, 2002).

Bamboo rats are fossorial rodents of the family Spalacidae, subfamily Rhizomyinae, tribe Rhizomyini. There are four known species placed in two genera, *Rhizomys* and *Cannomys*. *Rhizomys* consists of the large bamboo rat (*R. sumatrensis*), the hoary bamboo rat (*R. pruinosus*) and the Chinese bamboo rat (*R. sinensis*); while *Cannomys* includes only a single species, the lesser bamboo rat (*C. badius*) (Norris, 2017). The bamboo rats are spread across the Indochinese peninsula, and three species of them exist in Thailand (i.e., all of them except for *R. sinensis*) (Lekagul & McNeely, 1988; Naksatit & Rojanadilok, 1988). They inhabit a wide range of habitats from bamboo thickets in high-altitude mountainous areas to cultivated gardens and grassy areas (Lekagul & McNeely, 1988; Norris, 2017). They usually stay underground during the day and surface at night to forage for food. Besides eating bamboo material, as their name suggests, their diet includes various plant roots and tubers, grass seeds and fallen fruits. Of noted is that the lesser bamboo rat is more variable in its habitat and feeds on a wider variety of plants (Naksatit & Rojanadilok, 1988; Norris, 2017). The skull morphology, body size and color, and the pattern of footpads are physical characteristics which distinguish one species from the others (Lekagul & McNeely, 1988; Norris, 2017).

Although the composition and chemical features of secreted glycoconjugates from the lingual glands have been evaluated in several rodents, this information is still lacking in the bamboo rats. Due to encounters with habitat loss and difficulties in animal tracking, the only specimens from Thailand obtained herein were the large and lesser bamboo rats. Therefore, the purpose of the present study was to determine the histochemical properties of the lingual gland secretions in these two species. To facilitate understanding, the general histology of the lingual glands is preliminarily described. The results of histochemistry are compared with previous reports on rodents and other mammals, deepening the understanding of lingual glands in relation to food-manipulating functions in both bamboo rats.

## MATERIAL AND METHOD

Four large bamboo rats (one female and three males; average body mass of 1.48 ± 0.17 kg) and five lesser bamboo rats (four females and one male; average body mass of 274.68 ± 37.51 g) from Thailand were used as the study material. The large bamboo rats died of natural causes and were obtained from Surat Thani and Uthai Thani provinces. The lesser bamboo rats were obtained from local markets in Sukhothai province, except for one that was a natural death in Chiang Rai province. All animals were fresh adult corpses with intact tongues. After removal from the oral cavity, the tongues were washed gently with distilled water to remove debris.

For histological processing, the posterior part of each tongue from the vallate papillae to the radix was sectioned into small pieces of appropriate dimensions and fixed in 10 % (v/v) neural buffered formalin for 48–72 h. Fixed specimens were dehydrated in a graded series of ethanol from 25 % to 100 % (v/v) and then embedded in paraffin. The paraffin blocks were cut into 5-µm-thick sections and stained with haematoxilin–eosin (H&E) to observe general tissue characteristics.

To analyze the histochemical properties of glycoconjugates secreted by lingual salivary glands, selected sections were stained with periodic acid-Schiff (PAS) to demonstrate neutral glycoconjugates, alcian blue (AB) at pH 2.5 to detect acidic glycoconjugates (carboxylated and sulfated glycoconjugates), AB at pH 1.0 and aldehyde fuchsin (AF) at pH 1.0 to assess sulfated glycoconjugates, AB pH 2.5/PAS to distinguish neutral glycoconjugates from acidic glycoconjugates, and AF pH 1.0/AB pH 2.5 to compare the nature of the acidic glycoconjugate types (carboxylated or sulfated). Details of the staining techniques are shown in Table I. Mounted slides were observed and imaged using a light microscope (Olympus U-TV0.5XC-3, Japan).

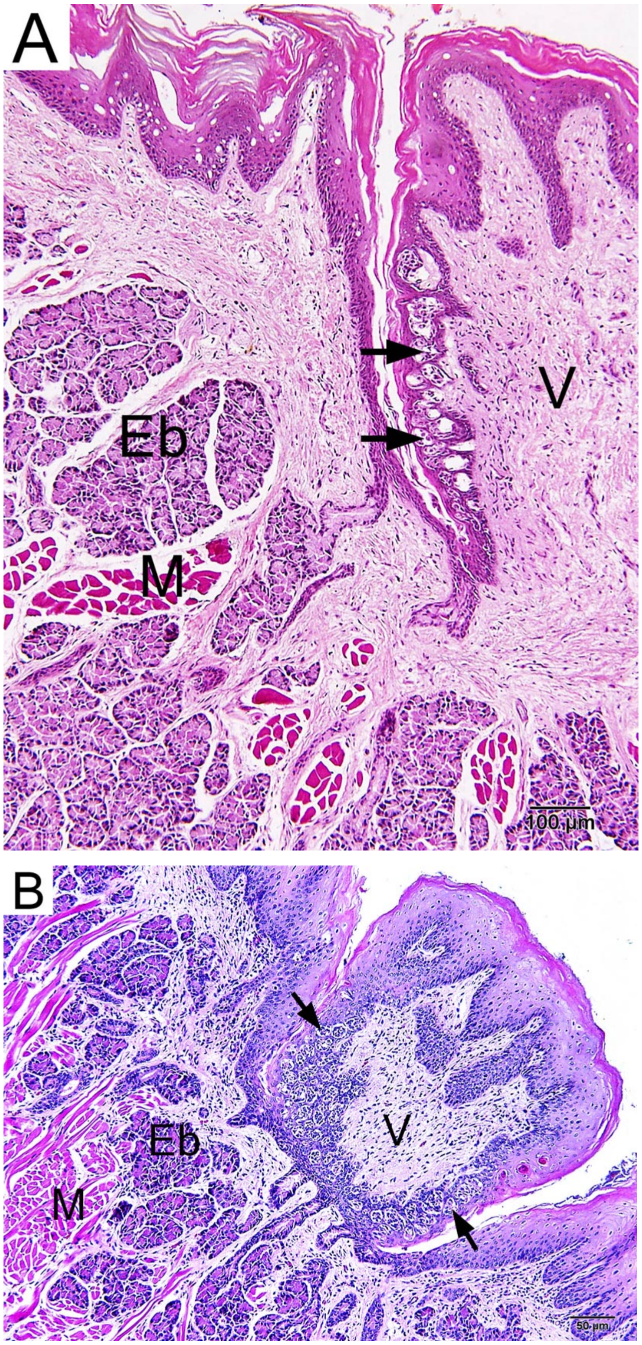
Table I. Histochemical staining techniques used to identify different types of glycoconjugates (Luna, 1968; Kuru *et al*., 2017).

| Staining | Glycoconjugates |
|---|---|
| PAS | Neutral glycoconjugates |
| AB pH 2.5 | Both carboxylated and sulfated acidic glycoconjugates |
| AB pH 1.0 | Sulfated glycoconjugates |
| AB pH 2.5/PAS | Comparison of neutral and acidic glycoconjugates |
| AF pH 1.0 | Sulfated glycoconjugates |
| AF pH 1.0/AB pH 2.5 | Comparison of carboxylated and sulfated glycoconjugates |

Abbreviations: PAS, periodic acid-Schiff; AB, alcian blue; AF, aldehyde fuchsin.

## RESULTS

Two types of lingual salivary glands, von Ebner's glands and Weber's glands, were found at the posterior tongue in both bamboo rat species. These glands started to appear at the front of the vallate papillae. The von Ebner's glands, located medial to Weber's glands, were restricted around the vallate papillae (Fig. 1A, B). Weber's glands occupy a wider area from the



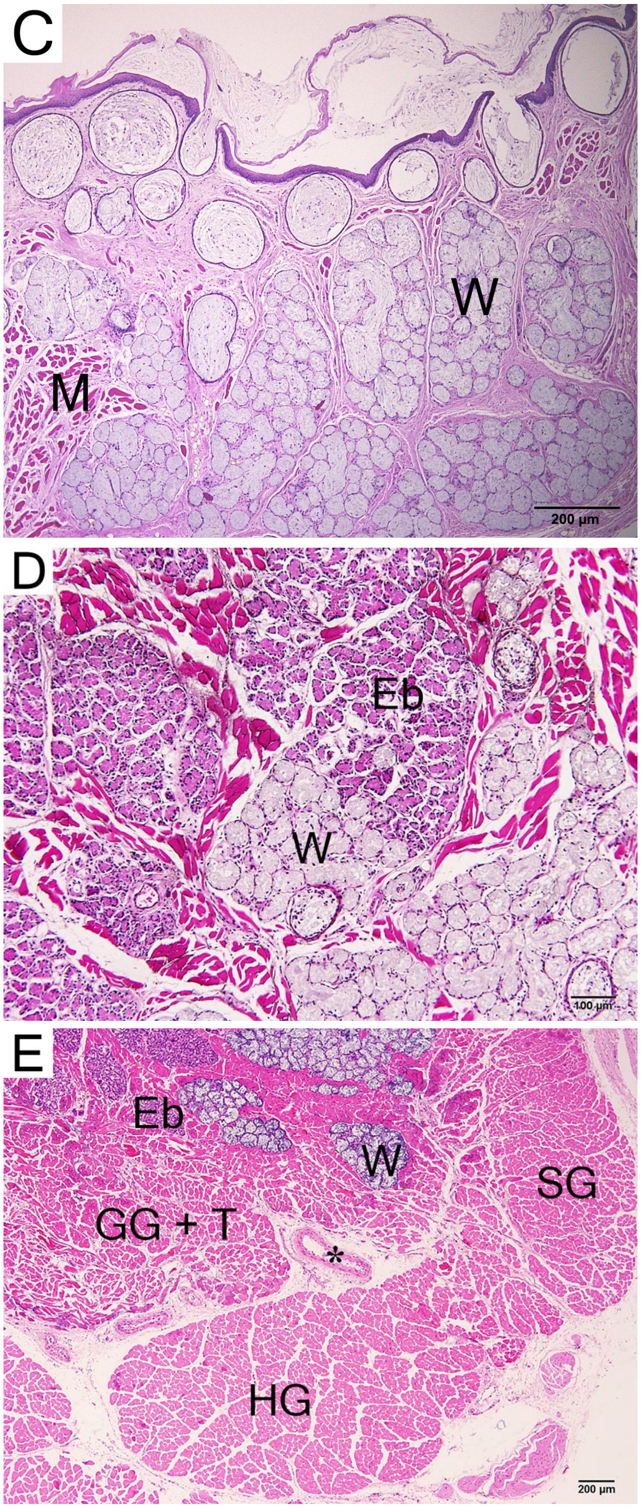




Fig. 1. Photomicrographs of the posterior lingual salivary glands stained with H&E of the large bamboo rat and the lesser bamboo rat. (A, B) Serous von Ebner's glands (Eb) beneath the vallate papilla (V) of the large bamboo rat and the lesser bamboo rat, respectively. (C) Mucous Weber's glands (W) at the tongue radix. (D) A combination of Ebner's glands and Weber's glands within the same glandular lobules. (E) Mixed fibers of the genioglossus (GG) and the transversus (T) muscles beneath the lingual glands. The lingual artery is indicated with an asterisk. Arrows, taste buds; HG, hyoglossus; M, muscles; SG, styloglossus.

vicinity of the vallate papillae to the tongue radix (Fig. 1C). A combination of these two glands within the same glandular lobules was occasionally found at their interface (Fig. 1D). With respect to their orientation to tongue muscles, the lateral sides of the lingual glands were sandwiched between the paired styloglossus muscles. Beneath the glands was mixed fibers of the transversus and the genioglossus muscles (Fig. 1E).

In both species, von Ebner's glands and Weber's glands were tubuloacinar glands. The former were located beneath the lamina propria of the vallate papillae and drained via ducts into the base of the vallate trench (Fig. 1A, B), and were typically composed of serous acini. On the other hand, Weber's glands consisted of purely mucous acinar cells, and their secretions were conveyed to the epithelial surface at the side and back of the vallate papillae. The striated ducts of both lingual glands were absent. The excretory ducts of von Ebner's glands were lined by a bistratified epithelium that consisted of inner (luminal) columnar or cuboidal cells and outer flat basal cells. In Weber's glands, the secretory acini drained into dilated tubules that combined to form excretory ducts lined by a stratified squamous epithelium (Fig. 1C).

For the histochemistry of glycoconjugates, von Ebner's glands of both bamboo rat species showed similar staining results (Table II). The serous acini of von Ebner's glands stained positively with PAS and exhibited a reddish-purple color, indicating the production of neutral glycoconjugates (Figs. 2A, 3A). They also reacted to AB pH 2.5/PAS staining with a pinkish-purple color, indicating predominantly neutral glycoconjugates (Figs. 2B, 3B). Staining levels were relatively weak in the glands of the

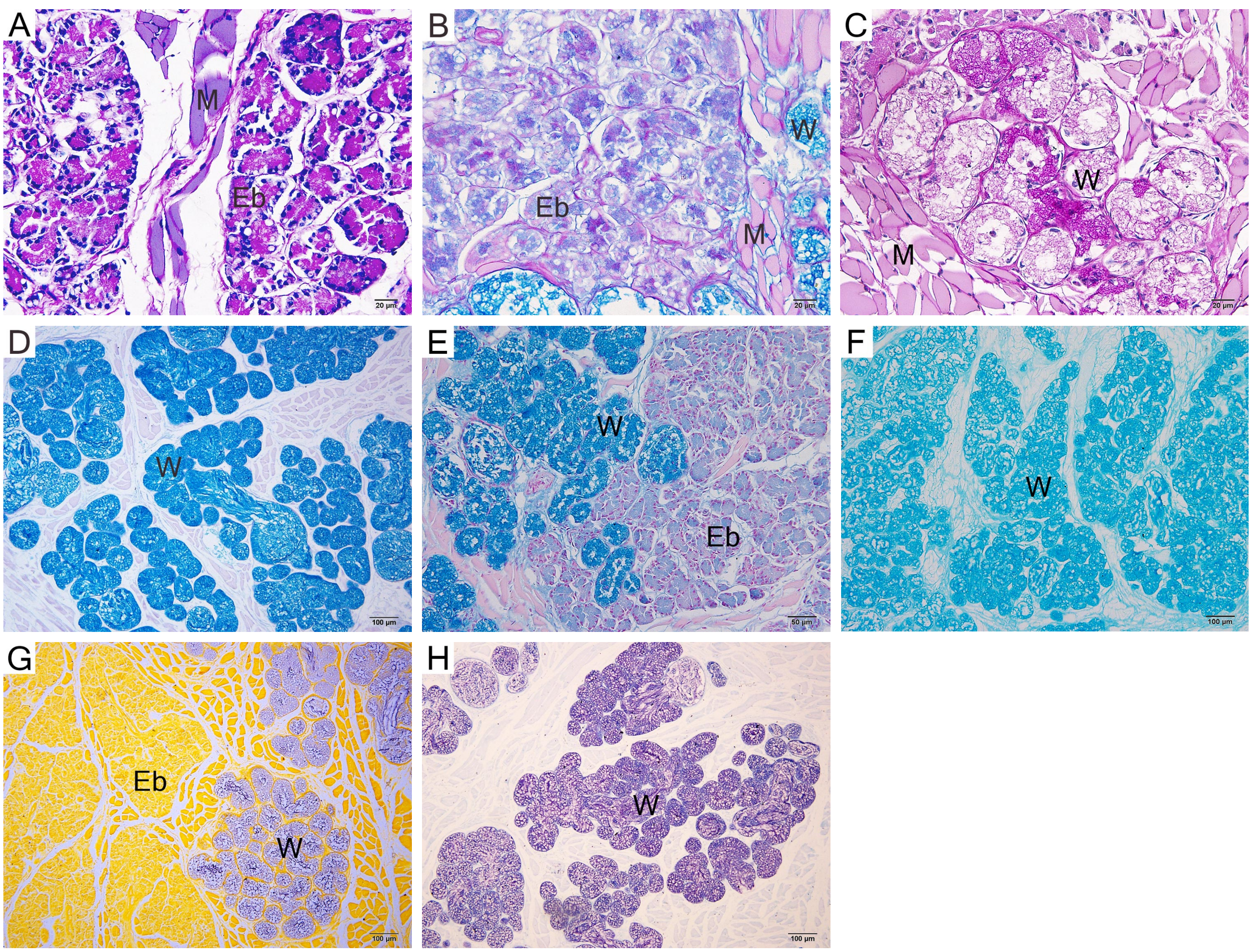



Fig. 2. Photomicrographs of the large bamboo rat's posterior lingual glands showing positive histochemical staining. (A) Positive PAS staining with a reddish-purple color in the acini of von Ebner's glands (Eb). (B) Positive AB pH 2.5/PAS staining with a pinkish-purple color in the acini of von Ebner's glands. (C) Positive PAS staining with a reddish-purple color in some acini of Weber's glands (W). (D) Positive AB pH 2.5/PAS staining with a strongly blue color in Weber's gland cells. (E, F) Strong positive AB pH 2.5 and 1.0 staining, respectively, with a blue color in Weber's glands' acini. (G) Positive AF pH 1.0 staining with a purple color in Weber's gland cells. (H) Positive AF pH 1.0/AB pH 2.5 staining with a purple color in the acini of Weber's glands. M, muscles.

large bamboo rat. The glands of both species showed no positive reactions to AB pH 1.0 and 2.5, AF pH 1.0 and AF pH 1.0/AB pH 2.5 staining, confirming the absence of acidic glycoconjugates in their cells.

Histochemical characteristics of the mucous Weber's glands were slightly different between the two species (Table II). Weber's glands of the large bamboo rat showed PAS-positive reactions with a reddish-purple color in a few acini, indicating the sparse presence of neutral glycoconjugates in their secretion (Fig. 2C), whereas there were no positive reactions in the lesser bamboo rat. In both species, AB pH 2.5/PAS staining imparted a strongly blue color to Weber's gland cells, demonstrating the overwhelming majority of acidic glycoconjugates compared to neutral glycoconjugates (Figs. 2D, 3B). The glands stained strongly with AB and showed a blue color at both pH conditions, indicating the presence of acidic glycoconjugates with carboxyl and sulfonic groups (Figs. 2E, 2F, 3C, 3D). As a purple coloration was seen with AF pH 1.0, highly acidic sulfated glycoconjugates were considered to be present (Figs. 2G, 3E). The positive combined AF pH 1.0/AB pH 2.5 staining, showing a purple color in most mucous acini in comparison to a blue color, confirmed a mixture of both acidic glycoconjugates but with a higher content of the sulfated forms than the carboxylated forms (Figs. 2H, 3F).

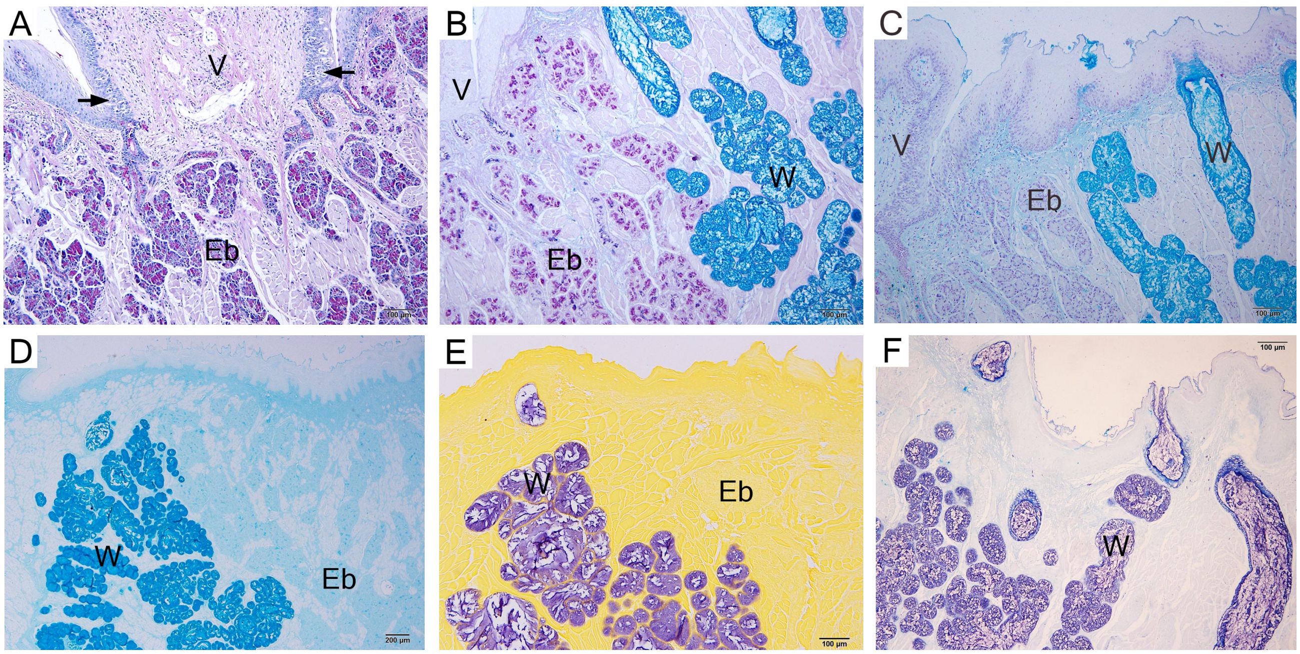



Fig. 3. Photomicrographs of the lesser bamboo rat's posterior lingual glands showing positive histochemical staining. (A) Positive PAS staining with a reddish-purple color in the acini of von Ebner's glands (Eb). (B) Positive AB pH 2.5/PAS staining with a pinkish-purple color in the acini of von Ebner's glands and a strongly blue color in Weber's gland cells (W). (C, D) Strong positive AB pH 2.5 and 1.0 staining, respectively, with a blue color in Weber's gland cells. (E) Positive AF pH 1.0 staining with a purple color in Weber's gland cells. (F) Positive AF pH 1.0/AB pH 2.5 staining with a relatively purple color in the acini of Weber's glands. Arrows, taste buds; V, vallate papilla.

Table II. Distribution and reaction levels of glycoconjugates in the lingual glands of the bamboo rats.

| Staining techniques | Large bamboo rat | | Lesser bamboo rat | |
|---|---|---|---|---|
| | VEG | WG | VEG | WG |
| PAS | ++ | + | ++ | - |
| AB pH 2.5 | - | ++ | - | ++ |
| AB pH 1.0 | - | ++ | - | +++ |
| AB pH 2.5/PAS | + $^{PAS}$ | ++ $^{AB}$ | ++ $^{PAS}$ | ++ $^{AB}$ |
| AF pH 1.0 | - | ++ | - | +++ |
| AF pH 1.0/AB pH 2.5 | - | ++ $^{AF}$ | - | ++ $^{AF}$ |

Abbreviations: PAS, periodic acid-Schiff; AB, alcian blue; AF, aldehyde fuchsin; VEG, von Ebner's gland; WG, Weber's gland. Reaction levels: -, negative; +, weak; ++, strong; +++, very strong. Superscript letters indicated the dominant stains.

**DISCUSSION**

Based on previous studies, the large and lesser bamboo rats have neither Blandin-Nuhn glands at the tip of the tongue nor lingual glands, in the lingual body, but von Ebner's glands and Weber's glands are present at the posterior tongue (Wannaprasert, 2018; Wannaprasert *et al*., 2020). Herein, the histochemical analysis of these posterior lingual glands was carried out and the histochemical features of their secreted glycoconjugates are discussed in comparison with those of other mammals.

The present study revealed that the von Ebner's gland secretion in both bamboo rats lacked acidic glycoconjugates but contained neutral glycoconjugates, although in relatively small amounts in the large bamboo rat. This neutral serous secretion is similar to that reported in many mammals, e.g. the cat, ferret, gray short-tailed opossum, Persian squirrel, plantain squirrel and sugar glider (Sozmen *et al*., 1999; Triantafyllou *et al*., 2001; Okada *et al*., 2013; Damia *et al*., 2021; Megawati *et al*., 2023; Akbari *et al*., 2024). However, it differs from the glands of the mole rat and Patagonian mara, which produce a mixture of neutral and acidic mucosubstances (Kuru *et al*., 2017; Cízek *et al*., 2023), and the glands of the rabbit, one-humped camel and WWCPS rat, which are free from glycoconjugate contents (at least based on their negative AB/PAS staining) (Abou-Elhamd *et al*., 2018; Gozdziewska-Harlajczuk *et al*., 2018; Nabil & Tawfiek, 2020).

As seen in other mammals, the von Ebner's glands of the large and lesser bamboo rats emptied serous saliva into the vallate trench that surrounded and abutted the taste buds. Because most of the lingual taste buds are located in the side wall of the vallate papillae (no foliate papillae in the bamboo rats), the secretion of von Ebner's glands is largely involved with taste transduction in the majority of lingual taste buds (Gurkan & Bradley, 1987; Zhang *et al*., 2022). Standard histochemical staining methods, as used in this study, can be used to determine whether glandular acinar cells synthesize glycoconjugates, but do not determine the specific carbohydrate residues that constitute such glycoconjugates (Pinkstaff, 1993). According to the definition of serous secretion, von Ebner's glands are assumed to produce a watery, protein-rich fluid with a low viscous character due to a lack of mucins (de Paula *et al*., 2017; Pedersen *et al*., 2018). In the Wistar rat, PAS-positive substances in the acini of von Ebner's glands were not identified as neutral mucins but as other glycoproteins based on a structural appearance of the cytoplasm (Hutanu *et al*., 2022; Florin *et al*., 2024). Perhaps the PAS-positive glycoconjugates detected in von Ebner's glands of these two bamboo rat species are proteoglycans or other glycoproteins instead of neutral mucins. Further investigation using other biochemical methods, e.g. lectin-binding analysis, is needed to identify the specific structural types of glycoconjugates. This work can only estimate that the neutral glycoconjugate components of saliva from von Ebner's glands may participate in supplying the microenvironment of the vallate taste buds and facilitating taste receptor activation.

Weber's glands of the large and lesser bamboo rats were of the purely mucous type and produced predominantly acidic glycoconjugates, the majority of which were sulfated forms. The large bamboo rat also contained small amounts of neutral glycoconjugates in their secretion, in contrast to the lack of any neutral ones in the lesser bamboo rat. Purely mucous Weber's glands are also found in the camel, mole rat, Patagonian mara, plantain squirrel, rabbit and Wistar rat (Kuru *et al*., 2017; Nabil & Tawfiek, 2020; Cízek *et al*., 2023; Megawati *et al*., 2023; Almansour *et al*., 2024; Florin *et al*., 2024). These glands secrete both neutral and acidic mucins, except for those of the rabbit that lack neutral mucins. Mixed seromucous Weber's glands have been reported in the gray short-tailed opossum, Persian squirrel, sugar glider and WWCPS rat (Okada *et al*., 2013; Gozdziewska-Harlajczuk *et al*., 2018; Damia *et al*., 2021; Akbari *et al*., 2024). Secretory endpieces of the seromucous glands commonly produce both types of mucins.

Electron microscopic histochemistry has revealed that the mucous acinar cells are replete with mucin-containing storage granules accumulated in the apical cytoplasm (Pinkstaff, 1980; de Paula *et al*., 2017; Harrison, 2021). Mucins are considered as the main glycoconjugates in the saliva produced from the minor salivary glands (Pedersen *et al*., 2018; Zhang *et al*., 2022). The glycoconjugates in Weber's glands detected by histochemical techniques are accordingly referred to as mucins. Although contributing little to whole salivary flow, minor glands, including Weber's glands, are significant in maintaining a mucin-rich protective fluid (Benn & Thomson, 2014; Zhang *et al*., 2022) to provide lubrication of the oral cavity for ease of swallowing hard, abrasive food particles and facilitation of tongue movement. Sulfated glycoconjugates (mucins) predominated in these two bamboo rat species as well as in the mole rat in the same Spalacidae (Kuru *et al*., 2017). Mucin sulfation contributes to the negative surface charge of the mucus that confers more resistance to degradation of the mucus layer by bacterial enzymes (Amerongen *et al*., 1998; Placet *et al*., 2021). It has also been suggested that sulfated mucins offer additional protection from luminal lesions by increasing the mucus viscosity and potential resistance to microbial attachment (Croix *et al*., 2011; Xia *et al*., 2021). Beyond protective properties against irritating factors, Weber's glands' saliva of these spalacid rodents probably has an important antimicrobial action to help control oral microflora.

From another functional perspective, the muco-adhesive property of mucins is proposed to be a factor affecting taste function. Hydrophobic and lipophilic compounds, such as phytosterols in plants, can be emulsified by the mucins. The dissolution of tastants may facilitate retention of these taste molecules on the tongue, prolonging access to taste receptors (Pedersen *et al*., 2018; Pushpass *et al*., 2019). In the bamboo rats as well as many mammals, Weber's glands secreted saliva drained onto the tongue surface in the vicinity of the vallate papillae. Thus, the mucins secreted by Weber's glands may aid in the interaction between tastants and taste receptors in the vallate papillae, enhancing the gustatory capacity.

## CONCLUSIONS

The present study provided the first information on the histochemistry of the posterior lingual salivary glands in the large and lesser bamboo rats. The histochemical analysis revealed that the serous saliva of von Ebner's glands of both species contained neutral glycoconjugates without acidic forms. Weber's glands consisted of mucous acini secreting mainly acidic glycoconjugates (probably mucins) of predominantly sulfated forms. Due to the location of these lingual glands being closely associated with the vallate taste buds, the secreted glycoconjugates are speculated to have taste-related roles. The presence of sulfated groups in the Weber's gland secretion may increase the mucin backbone to be more resistant to attachment and enzymatic degradation by bacteria. The subtle differences in histochemical staining between the large and lesser bamboo rats may reflect their different feeding habits, in that the large bamboo rat is more specific to a bamboo diet, whereas the lesser bamboo rat feeds on a wider variety of vegetation (Naksatit & Rojanadilok, 1988; Norris, 2017). It has also been proposed previously to be related to various stages of the secretory cycle of the lingual glands (Pinkstaff, 1980; Akbari *et al*., 2024). The findings on the two bamboo rat species in this study and comparative data with other species could contribute to a better understanding of histology and functions of the lingual salivary glands in mammals.

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**WANNAPRASERT, T.** Estudio histoquímico de las glándulas linguales posteriores de la rata de bambú grande (*Rhizomys sumatrensis*) y la rata de bambú menor (*Cannomys badius*). *Int. J. Morphol., 43(3)*:993-1000, 2025.

**RESUMEN**: Las glándulas de von Ebner y de Weber son glándulas salivales linguales ubicadas en la parte posterior de la lengua de los mamíferos. En el presente estudio, se examinaron las características histoquímicas de los glicoconjugados secretados por ambas glándulas en las ratas de bambú grande y menor, roedores herbívoros fosoriales distribuidos en Indochina. Los resultados revelaron que las glándulas linguales posteriores de estas dos especies de ratas de bambú consistían en glándulas de von Ebner serosas y glándulas de Weber mucosas. La histoquímica utilizando tinción de ácido peryódico de Schiff (PAS), azul alcián (AB) pH 1.0 y 2.5, AB pH 2.5/PAS, aldehído fucsina (AF) pH 1.0 y AF pH 1.0/AB pH 2.5 demostró que la secreción de las glándulas de von Ebner contenía glicoconjugados neutros sin formas ácidas, mientras que la de las glándulas de Weber incluía principalmente glicoconjugados ácidos (probablemente mucinas), que eran formas predominantemente sulfatadas. Se detectaron pequeñas cantidades de glicoconjugados neutros en las glándulas de Weber de la rata grande del bambú, pero faltaban en la rata menor del bambú. El contenido de glicoconjugados en la saliva de estas glándulas linguales puede tener una función relacionada con el gusto asociada con las papilas gustativas de las papilas valadas. Más allá de la protección contra factores irritantes, las presuntas mucinas sulfatadas secretadas por las glándulas de Weber pueden mejorar las propiedades antimicrobianas del moco. Las sutiles diferencias en la tinción histoquímica entre las dos ratas de bambú posiblemente estén relacionadas con la distinta especificidad de su dieta.

**PALABRAS CLAVE: Histoquímica; Histología; Glándulas salivales menores; Mucinas; Roedores.**

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