Title:

Tongue microarchitecture and functional characterization of the lingual papillae in the desert hedgehog (*Paraechinus aethiopicus*)

Authors & Affiliations:

Diaa Massoud[1], Mervat A. AbdRabou[1], Maged Fouda[1], Fayez Shaldoum[1], Barakat M. Alrashdi[1], Mousa O. Germoush[1], Haifa E. Alfassam[2], Aljohara M. Al- Otaibi[2], Soha A. Soliman[3], Hanan H. Abd-Elhafeez[4], Mervat Hassan[5], Ayman M. Mahmoud[6,7]*

[1]Department of Biology, College of Science, Jouf University, Sakaka, Al-Jouf, 72341, Saudi Arabia

[2]Biology Department, College of Science, Princess Nourah Bint Abdulrahman University, Riyadh 11564, Saudi Arabia

[3]Department of Histology, Faculty of Veterinary Medicine, South Valley University, Qena, Egypt

[4]Department of Cell and Tissues, Faculty of Veterinary Medicine, Assiut University, Assiut, 71526, Egypt

[5]Department of Theriogenology, Faculty of Veterinary Medicine, New Valley University, Elkharga, Egypt

[6]Department of Life Sciences, Faculty of Science and Engineering, Manchester Metropolitan University, Manchester, UK.

[7]Physiology Division, Zoology Department, Faculty of Science, Beni-Suef University, Beni-Suef, Egypt.

***** Corresponding author:

Ayman M. Mahmoud
Department of Life Sciences, Faculty of Science and Engineering, Manchester Metropolitan University, Manchester M1 5GD, UK. E-mail: a.mahmoud@mmu.ac.uk

ABSTRACT

The present work attempted to provide a comprehensive description of the morphoanatomical, histological, and ultrastructural characteristics of the tongue in the desert hedgehog (*Paraechinus aethiopicus*), and to correlate lingual modifications to the feeding lifestyle. Five adult male hedgehogs were utilized in our investigation. The macroscopic observations revealed elongated, with a moderately pointed apex, tongue and the tongue dorsum lacks both lingual prominence and median sulcus. The main subdivisions of the tongue are radix linguae (root), corpus linguae (body), and apex linguae (apex). The tongue dorsum carries two types of mechanical (conical and filiform) and gustatory (fungiform and circumvallate) papillae. The lingual apex is characterized by the existence of a unique encapsulated muscular structure. Additionally, the lingual glands were interposed between the muscular strands and no lingual glands were detected on the lingual apex. The dorsal surface of the lingual apex exhibited the highest level of keratinization as revealed by histochemical staining while the root showed moderate staining. The topography of the tongue was investigated by scanning electron microscopy (SEM). The obtained results are important to provide basic knowledge that can contribute to better understanding of the nourishment, feeding habits and behavior in this species. Furthermore, the addition of the newly investigated species may help us to determine the evolutionary relationships among species.

Keywords: Desert hedgehog; Tongue adaptation; Feeding habit; Keratinization; Lingual papillae.

1. INTRODUCTION

The animal feeding mechanism is an essential factor in determining the adaptation of an individual to the surrounding environment to maximize survival chances (Goodarzi & Azarhoosh, 2016). The tongue is the key player in this mechanism as it facilitates food processing and manipulation inside the buccal cavity (Hiiemae & Crompton, 2013; Sakr, 2022). It also contributes to chemical perception due to the existence of taste receptors embedded in the lingual epithelium (Dando et al., 2015), and may participate in the vocalization and grooming of the body (Levin & Pfeiffer, 2002). It is generally known that there is a direct connection between the anatomical features of the tongue and feeding preferences (M. M. A. Abumandour & El-Bakary, 2017; Massoud & Abumandour, 2020). Hence, the mammalian tongue exhibits great diversity among species. It differs mainly in shape, length, lingual glands, and the type of papillae that covers the dorsal epithelium. Although this variation is highly remarkable at different taxonomic levels, inter- and intraspecific variations are also frequently noticed (Gregorin, 2003).

Anatomically, the tongue of mammals is a highly movable organ that rests on the floor of the buccal cavity (Pastor et al., 2021). The mobility of the tongue is connected to the presence of both extrinsic and intrinsic muscle bundles as well as a dense innervation of the overlying mucosa (Merlino et al., 2022). The tongue dorsum is shielded by squamous striated epithelium (Gewily et al., 2021). In between, the lingual papillae are intercalated and their type and location are subject to great variation depending on the nature of the foodstuffs the animal consumes (Sadeghinezhad, Tootian, & Javadi, 2018). Functionally, there are two primary types of lingual papillae, gustatory and nongustatory (M. M. Abumandour & El-Bakary, 2013). The gustatory papilla encloses taste buds which contain taste cells that transfer chemical signals to the central nervous system (CNS). The nongustatory papillae may protect the tongue surface from abrasion during feeding against hard food materials (Igbokwe & Mbajiorgu, 2019). Therefore, their distribution and structure are of great importance in understanding the feeding habits (Mahdy, Abdalla, & Mohamed, 2021).

Mammals are an important partner in all ecosystems and play a crucial role in biological balance and sustainability (Altaf et al., 2023). Hedgehogs are small mammalian species with spiny coats and tiny eyes. Hedgehogs belong to the family *Erinaceidae* and their populations are widely distributed in Europe, Africa, and Asia (Bazm, Goodarzi, Abumandour, Naseri, & Hosseinipour, 2020). The Desert hedgehog (*Paraechinus aethiopicus*) is a nocturnal animal with a weight ranges between 280 and 510 g. It is frequently seen in arid and semiarid deserts because of its ability to adapt to the harsh environmental conditions (Massoud, 2020). It has been documented in the Middle East and North African deserts. In the Arabian Peninsula, it inhabits many localities except for the Hijaz/Asser mountains (Alagaili, Bennett, Mohammed, & Hart, 2017). Several investigations have discussed the lingual morphoanatomy and feeding habits in small mammals, including hedgehogs (Akbari, Babaei, & Hassanzadeh, 2018; Cizek, Hamouzova, Goździewska-Harłajczuk, Klekowska-Nawrot, & Kvapil, 2020). For instance, The Ethiopian hedgehog has an insectivorous feeding lifestyle and mainly consumes insects and small invertebrates (Mohamed, 2021). The tongue topography and microanatomy of *P. aethiopicus* have not been examined yet and there is no information discussing the lingual adaptation to feeding habits in thit species. Hence, the current work was designed to explore morphoanatomical, histological, and ultrastructural characteristics of the tongue in *P. aethiopicus*, and to correlate lingual modifications to the feeding lifestyle.

2. MATERIALS AND METHODS

2.1. Collection site and animal handling

Five adult male desert hedgehogs (*P. aethiopicus*) were included in this investigation. The animals were collected from the rural area surrounding Sakaka, (Aljouf, Saudi Arabia; 29°54'29.0"N 40°12'14.5" E) during the spring season (March – June) where the animals become active after the long period of hibernation during the winter. The current work was approved and conducted under the guidelines of the local Committee of Bioethics at Jouf University (No. 6/08/44). Physical examination was carried out to ensure that all collected animals were healthy. The maturity of the animals was also checked by recording the body weight which ranged between 450 and 520 gm. The animals were anesthetized and tongues were excised and immersed in the appropriate fixative for microscopic and macroscopic analysis.

2.2. Gross anatomy

The excised tongues were assessed macroscopically using a Boeco stereomicroscope. The length and width of the tongue and its three main subdivisions were measured. The macroscopic measurements were obtained from digital photos captured by the microscope supplied with the camera. The measurements were recorded and expressed as the means ± standard deviation (SD).

2.3. Tissue processing

For light microscopic investigations, the excised tongues were immersed in Serra's fixative (ethanol, formalin, and glacial acetic acid mixed 6:3:1 by volume) for 48 h at 4°C. The tissue samples were dehydrated in a graded series of ethanol and clearing was performed through three changes of xylol for 20 min each, and the last change was performed in an oven at 59°C. The samples were embedded in paraffin wax with a melting point of 59°C overnight. Six hours later, the samples were oriented vertically in paraffin wax. Using a Leica Biosystems RM 2155 automated microtome, 7 µm thick sections were cut.

2.4. Histological and keratin examination

The sections were dewaxed in xylol and hydrated in a descending alcohol series. Thereafter, the sections were stained with hematoxylin for 15 min followed by washing and blueing in running water. The intensity of staining was adjusted, and the excess staining was removed using 1% acid alcohol. Counterstaining was performed using 1% eosin for 60 sec and the sections were then dehydrated using an ascending series of alcohol, cleared in xylol for 10 min, mounted in DPX and covered with coverslips.

The extent of keratinization was investigated in the main subdivisions of the tongue as previously described (Ayoub, 1963). The sections were deparaffinized, rehydrated, washed in tap water for 10 min and then immersed in 5% acid-fuchsin solution for 3 min. The sections were then incubated in aniline blue and orange-G solution for 30 min, dehydration, cleared, mounted in DPX and covered.

Digital micrographs were utilized to measure the total thickness of the lingual epithelium and correlate it to the keratinized layer. The thickness was recorded at regular intervals in the tongue regions using ImageJ. Ten measurements perpendicular to the surface were used to calculate the mean thickness of the three sections.

2.5. Scanning Electron Microscopy (SEM)

Two of the five tongues were rinsed in 0.1 M phosphate buffer (pH 7.2) and then fixed in 2.5% glutaraldehyde for 24 h. Sodium tetroxide (1%) was used for postfixation for 2 h at 4°C. The fixed samples were washed once more in 0.1 M phosphate buffer, dehydrated in increasing grades of ethanol followed by critical drying in liquid carbon dioxide. Each specimen was mounted on an aluminum stub covered with carbon tabs. The prepared specimens were examined and photographed using JEOL SEM.

3. RESULTS

3.1. Macroscopic examination

P. aethiopicus tongue appeared to be elongated with a moderately pointed apex and can move freely for food capture. The optical observations showed that there was no lingual prominence detected on the tongue dorsum (Fig. 1). The lingual root is characterized by the existence of two lateral ridges on both sides and the median sulcus was not observed. The tongue consists of the root (*radix linguae*) (Fig. 1A), the body (*corpus linguae*) (Fig. 1B), and the free apex (*apex linguae*) (Fig. 1C). A variety of lingual papillae were found on the tongue dorsal epithelium. Filiform papillae were very common with fungiform types scattered among them. The tongue root carried distinct circumvallate papillae arranged in the three corners of a triangle, two lateral and one located at the pharyngeal entrance (Fig. 1A). A frenulum situated at the corpus radix border connects the ventral side of the tongue to the mandible. Morphometric analysis of the tongue revealed that it measures 3.11 ± 0.19 cm in length and 0.78 ± 0.08 cm in width at the apex and broadens toward the radix to record 1.28 ± 0.11 cm. The width of the lingual body was found to be 1.1 ± 0.13 cm.

3.2. Microscopic observations

Histological analysis of the tongue sections stained with hematoxylin and eosin (H&E) revealed that the architectural arrangement of the tongue can be categorized into three distinct layers; mucosa, submucosa, and muscular layer, which ran from the outside to the inside. The tongue dorsum has an outer covering consisting of stratified squamous epithelium (Fig. 2). A highly keratinized layer protected the underlying epithelium and connective tissue cores, especially in the lingual body and apex (Fig. 2B & C). In between, numerous forms of lingual papillae of both types (mechanical and gustatory) were dispersed. On the dorsal surface, filiform, conical, fungiform, and circumvallate papillae were distinguished. Filiform papillae with multiple spikes were the most noticeable kind. Conical-shaped papillae existed in the lateral margins of the lingual body and the spaces between three circumvallate papillae (Fig. 3A & B). The lingual apex and body were the only locations where the filiform type existed. The circumvallate papillae had a discoid shape and existed only on the radix linguae *(*Fig. 2A). These types of papillae were characterized by their large form and well-observed circumpapillary sulcus that encircled them completely (Fig. 2A). Numerous taste buds were found on the papillae lateral wall, near the circumpapillary sulcus and a stratified squamous thinly cornified epithelium covered them. The fungiform papillae were dispersed along the three subdivisions of the tongue. Taste buds in this form of papillae were primarily found in the apical region of the papilla rather than on its lateral surfaces. The lingual papillae were invaded by a core of connective tissue in which numerous blood vessels are located. Foliate papillae were not recognized in this species. The lamina propria was a loose connective tissue layer that invaded the core of the lingual papillae and was found just beneath the lingual epithelium (Fig. 2B & C).

The submucosa consisted of a connective tissue layer containing blood and nerve supply. The tongue appeared highly muscular and very rich with numerous skeletal bundles that run in all directions (Fig. 3). Underneath the connective tissue layer is a thick core of striated muscles consisting of longitudinal and transverse muscle strands. The lingual apex is characterized by the presence of a pear shaped encapsulated structure consisting of transverse muscle bundles and a base of longitudinal muscle fibers (Fig. 3C). The lingual glands were intercalated between the skeletal muscles and were not detected in the lingual apex (Fig. 3C). The glands were detected in the lingual body and existed only toward the ventrolateral boundaries just beneath the non-keratinized squamous epithelium (Fig. 3B). The gland population with serous secretions (Von Ebner's glands) increased intensively at the lingual root toward the pharyngeal entrance and took a superficial position, especially under the circumvallate papilla (Fig. 3A).

The histochemical determination of tongue keratinization was performed using Ayoub-Shklar staining (Fig. 4). The tongue dorsum is characterized by the existence of stratified squamous epithelium that is intensely keratinized. The filiform papillae-covering epithelium exhibited the highest level of keratinization, but keratinization exists also in the epithelium positioned between the papillae, making the entire epithelium on the dorsal side of the tongue highly keratinized. The radix linguae were covered with a very thin keratinized layer, especially on the dorsal surface of the circumvallate papilla (Fig. 4A). The corpus linguae and apex linguae were intensely stained, reflecting a higher extent of keratinization (Fig. 4B & C), whereas the ventral side of the tongue displayed a moderate degree of keratinization of the epithelium.

3.3. Ultrastructure examination

SEM analysis of the dorsal epithelium of the tongue of *P. aethiopicus* enabled us to identify and differentiate the main types of papillae. Filiform papillae were abundant on the lingual mucosa and dome-shaped fungiform papillae were dispersed among them (Fig. 5). At high magnification, the filiform type carried two or three flattened spikes with desquamating scales on the dorsal surface (Fig. 5C). The enlarged portion of the fungiform papilla exhibited a dorsal taste pore on the dorsal surface surrounded by a papillary ridge and the stratified scales exhibited desquamation (Fig. 5D). The radix linguae revealed three circumvallate papillae positioned on the three corners of the triangle with conical papillae in between (Fig. 6A). The conical-shaped papillae had multiple projections (Fig. 6 B). At higher magnification, the circumvallate papillae and several openings of the lingual glands were identified (Fig. 6C). A distinct complete shallow groove was observed, a circumferential groove, an annular pad surrounding the papilla, and several taste pores were also recognized on the apical surface of the papilla (Fig. 6C).

3.4. Morphometric analysis

The morphometric measurements of the thickness in the total tongue epithelium vary greatly in the three main subdivisions as shown in Table 1. Comparing the lingual apex to the lingual body and lingual root, the lingual apex had the thickest epithelium. Additionally, the thickness in the keratinized epithelium for the three subdivisions was measured. The lingual apex exhibited the greatest degree of keratinization (Table 1).

4. DISCUSSION

The current study described the lingual topography of the desert hedgehog (*P. aethiopicus*) using histological, histochemical, and ultrastructral approaches to link the feeding habits to the tongue architecture. The morphometric and anatomical analyses of the tongue permit better understanding of the functional microanatomy of the alimentary canal in various vertebrates. The proper manipulation of foodstuff in the stomach and intestine of a particular species allows better absorption of nutrients. However, food preprocessing in the buccal cavity plays a crucial role in this process (Goździewska-Harłajczuk, Klećkowska-Nawrot, Hamouzová, & Čížek, 2022). The desert hedgehog mainly consumes insects and small invertebrates (Massoud, 2020). The macroscopic observations showed that there was no lingual prominence detected on the tongue dorsum. The emergence of this part in the tongue dorsum was detected in several species, including Sulawesi bear (Goździewska-Harłajczuk et al., 2022), koala (Kobayashi et al., 2003), Egyptian water buffalo (Farrag et al., 2022), lowland tapir (Goździewska-Harłajczuk, Hamouzová, Klećkowska-Nawrot, Barszcz, & Čížek, 2020), barking deer (Adnyane, Zuki, Noordin, & Agungpriyono, 2010), Wistar rat (Huțanu et al., 2022) and Nile grass rat (Massoud & Abumandour, 2019). It appears that the existence of lingual prominence is closely linked to herbivorous feeding habits to grind grass and hard food materials against the hard palate and crush teeth (Haggag, Mahmoud, Salem, & AbuBakr, 2020). Additionally, the median sulcus was not observed in the desert hedgehog. A similar observation was recorded in the long-eared hedgehog (Massoud & Abumandour, 2019), Brandt's hedgehog (Goodarzi & Azarhoosh, 2016), and the African pygmy hedgehog (Cizek, Hamouzova, Goździewska-Harłajczuk, Klekowska-Nawrot, & Kvapil, 2022). However, it was recorded in rodents (Davydova et al., 2017), Nile grass rat (Massoud & Abumandour, 2019), agouti (Ciena et al., 2013), Pampas deer (Erdoğan & Prez, 2013), and Persian squirrel (Sadeghinezhad et al., 2018). It appears that this feature is very common in plant-eating habituated animals (Massoud & Abumandour, 2019). Therefore, the tongues of members of the family *Erinaceidae* generally lack the median sulcus and lingual prominence which seems to be a conserved feature of that family. Additionally, the lingual root is characterized by the existence of two lateral ridges on both sides. This feature was also documented in the long-eared hedgehog (Parchami, Salimi, & Khosravi, 2018). The existence of these folds may help prevent saliva accumulation in the buccal cavity and facilitate its flow toward the pharyngeal entrance.

Similar to other mammals, the tongue dorsum of the desert hedgehog carries numerous forms of mechanical and gustatory lingual papillae. The mechanical forms were represented by the conical and filiform types. The filiform type may be simple, bidentate or multidentate. The spines are tilted posteriorly toward the pharyngeal entrance to facilitate food processing, chewing, and aboral shifting of the food (Akbari et al., 2018). The spines of the filiform papilla have been suggested to be related to facilitating the movement of foodstuffs and retaining them inside the buccal cavity by increasing friction (Taiwo et al., 2009). The gustatory types were represented by the fungiform and circumvallate types. The dome-shaped fungiform appears to be distributed densely on the lingual apex and body between the filiform papillae. While the lingual root was devoid of the fungiform type, similar observations were recorded in the long-eared hedgehog (Parchami et al., 2018). Similar papillary arrangements were reported in rabbits even though they are herbivores (Beraldo-Massoli et al., 2013). The spatial distribution of fungiform papillae varies among mammalian species. In gerbils, it is distributed on the lingual body and root, while the lingual apex lacks it (Grandi, Arcari, & Azalli, 1994). In ocelots, fishing cats, and leopards, fungiform papillae are densely distributed on the lingual apex (Freire et al., 2019). It is assumed that the spatial arrangement of this type of papilla is not correlated with the nature of the food ingested. No foliate type was recognized in our investigation. Similarly, foliate papillae were not recognized in Brandt's hedgehog and the long-eared hedgehog (Goodarzi & Azarhoosh, 2016; Massoud & Abumandour, 2019), Javan mongoose (Kusuma et al., 2022), common opossum (Okada & Schraufnagel, 2005), and ocelot (Freire et al., 2019).

The circumvallate papillae, on the other hand, were found only on the lingual radix. Similar findings were reported in other hedgehogs (Cizek et al., 2022; Massoud & Abumandour, 2019). They were three in number and arranged in the corners of a triangle. Previous studies reported that the number of circumvallate papillae varies among species depending on the nature of food materials that animals consume (M. M. A. Abumandour, Morsy, & Elghoul, 2022; Akbari et al., 2018; Nasr, Gamal, & Elsheikh, 2012). It was not recognized in guinea pigs and has the foliate type instead (Kobayashi, 1990), single in rats (Humphries, Seow, Danee, Ness, & Warburton, 2023), two in the bamboo rat (Wannaprasert, Phanthuma-opas, & Jindatip, 2020), three in most carnivores such that documented in the Javan mongoose (Kusuma et al., 2022), opossum [54], two in silver fox (Freire et al., 2019), two in insectivorous bats (Massoud & Abumandour, 2020), and three in the fruit-eating bat (M. M. Abumandour & El-Bakary, 2013). The ruminants such as goats, sheep, and cattle, possess greater numbers ranging from 12-18, 18-24, and 16-34, respectively (Selim & Samir, 2018). In the family *Erinaceidae*, three were found in the European hedgehog

(Akbari et al., 2018), the lesser hedgehog tenrec (Cizek et al., 2020), Brandt's hedgehog (Goodarzi & Azarhoosh, 2016), the African pygmy hedgehog (Cizek et al., 2022), and the long-eared hedgehog (Massoud & Abumandour, 2019). In our study, the same number of circumvallate papillae were recognized. The fungiform and circumvallate papillae contain numerous taste buds that aid in taste perception (Hino et al., 2022).

Both microscopic and ultrastructural analyses revealed that the lingual papillae could be differentiated according to their function. The mechanical and the gustatory represent the main forms and similar arrangement was recognized in several mammalian species such as the European hedgehog (Akbari et al., 2018), Horsfield's tree shrew (Gartiwa et al., 2021), the gray mongoose (Al-Arubaye, 2022), the Egyptian long-eared hedgehog and the Nile grass rat (Massoud & Abumandour, 2019), Wistar rat (Huțanu et al., 2022), common opossum (Okada & Schraufnagel, 2005), the Egyptian fruit bat and the Egyptian tomb bat (El-Mansi, Al-Kahtani, & Abumandour, 2019), lowland tapir (Goździewska-Harłajczuk et al., 2020), African pygmy hedgehog (Cizek et al., 2022), rakali and the greater stick-nest rat (Humphries et al., 2023). Fork filiform papillae carrying two or three spines were described previously in other hedgehogs, including the long-eared hedgehog (Massoud & Abumandour, 2019) and Brandt's hedgehog (Goodarzi & Azarhoosh, 2016). However, this type of papilla was also recorded in other insectivorous mammals unrelated to hedgehogs such as anteater (Casali et al., 2017), Laxmann's shrew (Park & Lee, 2009), and Japanese shrew-mole (Kobayashi et al., 2003). On the other hand, the conical-shaped papillae of the desert hedgehog were distributed on the distal part of the tongue in the small triangular area between the linguae radix inbetween the three circumvallate papillae, while the distal part was devoid of that type. Similar observations were reported in the lowland paca (Beraldo-Massoli et al., 2013), leopard (Sadeghinezhad, Sheibani, Memarian, & Chiocchetti, 2017), and ocelot (Freire et al., 2019). However, the conical-shaped papillae in desert hedgehogs undergo numerous processes and this feature is unique and has not been described before. Previous reports speculated that the conical shape papillae may be considered a structural modification of the filiform type that exists on the caudal region of the tongue (Freire et al., 2019). Further investigation on this type may be required to know more about the ontogeny and its correlation to the feeding habit. Some reports claimed that this position protects the oral mucous membrane from mechanical injury and prevents the retraction of the processed food during its passage toward the pharyngeal entrance (Iwasaki, 2002; Sharma et al., 1999; Wolczuk, 2014). Conclusively, the morphological and anatomical differences relate to the functional role they play.

Histochemical detection of keratinization of the tongue dorsum revealed a higher extent of staining in the apex linguae and corpus linguae than in the radix linguae. This feature may be correlated with the fact that the lingual tip is subject to a greater extent of abrasion and dehydration than the lingual root during food manipulation (Taiwo et al., 2009). Additionally, the filiform papillae exhibit dense staining when compared with the fungiform and circumvallate papillae. The greater extent of keratinization could reflect structural adaptation to protect the tongue dorsum against abrasion caused by tough food materials. Hence, the lingual surface is more suited for the manipulation and crushing of hard foodstuffs, such as insects and small invertebrates. The existence of a thick keratinized layer over the filiform papillae and the apparent loss of taste buds strongly suggest its mechanical role. Similar structural adaptations have been reported in the rakali and greater stick-nest rat (Humphries et al., 2023), the lesser bamboo rat (Wannaprasert et al., 2020), the Javan mongoose (Kusuma et al., 2022), the Nile grass rat and the Egyptian long-eared hedgehog (Massoud & Abumandour, 2019). The thickness of the keratinized covering and its proportion to the total thickness of the tongue epithelium is the highest at the lingual apex. Hence, the degree of keratinization in the lingual epithelium is closely related to the nature of foodstuffs and becomes greater in those areas particularly subjected to mechanical friction (Iwasaki, 2002). Consequently, it can be assumed that the anterior portion of the tongue is responsible for the mechanical handling of foodstuffs, while the posterior portion is responsible for taste perception.

The lingual muscles of the desert hedgehog were composed of striated muscular bundles that ran in diverse directions, playing a vital role in modeling the lingual profile, as seen in other vertebrate mammals. It is highly adapted for food manipulation and procession inside the buccal cavity. Interestingly, the lingual apex is characterized by the existence of a unique pear-shaped-encapsulated structure consisting of a transverse muscle bundle and a base of longitudinal muscle fibers. This feature may be related to the self-anointing behavior of hedgehogs (Akbari et al., 2018). When an animal encounters a strange object, the animal starts to lick it, creating foamy salivary secretion. However, the purpose of this behavior is still unknown. Many hypotheses propose that this behavior is related to masking the animal's odor against predators (Massoud et al., 2023). Salivary glands were seen intercalated between the muscular strands. Its main purpose is to keep the mouth moist, lubricate food materials, and facilitate food movement and manipulation inside the buccal cavity. The lingual apex is devoid of salivary glands. It was situated on the marginal boundaries of the tongue body far from the highly keratinized lingual epithelium. In contrast, the lingual glands occupied a more superficial position in the tongue root just beneath the circumvallate papillae. The absence of the lingual gland from the tongue apex may be correlated to the fact that it is more susceptible to dehydration than other parts (Taiwo et al., 2009). The lingual glands are categorized into Weber’s glands and von Ebner’s glands. The seromucous secretions of Weber's glands aids in the mobility of the tongue and swallowing of hard food materials. Von Ebner's glands with serous secretions were found beneath the circumvallate papillae, implying a role in taste perception (Anjani, Saragih, Wihadmadyatami, & Kusindarta, 2023; Haddao & Yasear, 2018).

5. CONCLUSION

The current work represents the first description of the lingual anatomy and microanatomy of the desert hedgehog (*P. aethiopicus*). The tongue of desert hedgehog does not exhibit great differences among other members of hedgehogs. Hence, the lingual features seem to be conserved among the family *Erinaceidae* as the feeding habits are more or less the same. The obtained results are important to provide basic knowledge that can contribute to better understanding of the nourishment, feeding habits and behavior in this species. Furthermore, the addition of the newly investigated species may help to determine the evolutionary relationships among species. Our study aims to attract attention to the fauna of Saudi Arabia and provides more detailed information regarding the anatomical adaptation of the tongue to feeding preferences. Additionally, it may pave the way for the diagnosis of many pathological conditions of the tongue in this species as a companion animal.

Authors contribution

Conceptualization: D.M., and A.M.M.; Methodology: D.M., M.A.A., M.F., F.S., B.M.A., M.O.G., H.A., A.M.A., S.A.S., H.H.A, and A.M.M.; Investigation: D.M., M.A.A., M.F., F.S., B.M.A., M.O.G., and H.H.A; Data analysis: D.M., F.S., B.M.A., M.O.G., and A.M.M.; Resources: H.A., A.M.A., and S.A.S.; Writing-Original draft: D.M. and A.M.M.; Writing-Review and editing: D.M. and A.M.M.; Funding acquisition: D.M.; Validation: A.M.M.. All authors agreed to the submission of the final version of the manuscript.

Acknowledgments

The authors extend their appreciation to the Deanship of Scientific Research at Jouf University for funding this work through research grant No. DSR2022-RG- 0116.

Funding

The authors extend their appreciation to the Deanship of Scientific Research at Jouf University for funding this work through research grant No. DSR2022-RG- 0116.

Conflict of interest

The authors declare no conflicts of interest.

Ethics declarations

The study was conducted according to the guidelines of the Declaration of Jouf University and approved by the local Committee of Bioethics of Jouf University (No. 6/08/44).

Availability of data and material

The manuscript contains all data supporting the reported results.

References

Abumandour, M. M., & El-Bakary, R. M. (2013). Morphological and scanning electron microscopic studies of the tongue of the Egyptian fruit bat (Rousettus aegyptiacus) and their lingual adaptation for its feeding habits. *Vet Res Commun, 37*(3), 229-238. doi:10.1007/s11259-013-9567-9

Abumandour, M. M. A., & El-Bakary, N. E. R. (2017). Morphological features of the tongue and laryngeal entrance in two predatory birds with similar feeding preferences: common kestrel (Falco tinnunculus) and Hume's tawny owl (Strix butleri). *Anatomical Science International, 92*(3), 352-363. Retrieved from https://doi.org/10.1007/s12565-016-0339-9

Abumandour, M. M. A., Morsy, K., & Elghoul, M. (2022). *Morphological features of the Egyptian Ossimi sheep tongue: New scanning electron microscopic insights into its papillary system adaptations to Egyptian ecological conditions*. Histologia, Embryologia: Anatomia.

Adnyane, I. K. M., Zuki, A. B., Noordin, M. M., & Agungpriyono, S. (2010). Histological study of the parotid and mandibular glands of barking deer (Muntiacus muntjak) with special reference to the distribution of carbohydrate content. *Anatomia, Histologia, Embryologia, 39*(6), 516-520.

Akbari, G., Babaei, M., & Hassanzadeh, B. (2018). Morphological study of the European hedgehog (Erinaceus europaeus) tongue by SEM and LM. *Anatomical Science International, 93*(2), 207-217. Retrieved from https://doi.org/10.1007/s12565-017-0391-0

Al-Arubaye, N. (2022). Anatomical assessments for grey mongoose tongue by scanning electron microscope (Herpestes edwardsii) in Iraq. *Archives of Razi Institute, 77*(1), 129.

Alagaili, A. N., Bennett, N. C., Mohammed, O. B., & Hart, D. W. (2017). The reproductive biology of the Ethiopian hedgehog, Paraechinus aethiopicus, from central Saudi Arabia: the role of rainfall and temperature. *Journal of Arid Environments, 145*, 1-9.

Altaf, M., Javid, A., Khan, A. M., Nazer, S., Irfan, I., Iqbal, K. J., . . . Ashraf, S. (2023). Habitat Preferences of Wild Mammalian Species around River Chenab in Sialkot, Gujrat and Gujranwala Districts, Punjab, Pakistan. *Pakistan Journal of Zoology, 55*(6). doi:10.17582/journal.pjz/20190922190944

Anjani, A. K., Saragih, G. R., Wihadmadyatami, H., & Kusindarta, D. L. (2023). Lingual morphology of domesticated Asian small-clawed otters in Yogyakarta, Indonesia. *Vet Med-Czech, 68*, 91-105.

Ayoub, P. (1963). A modification of the Mallory connective tissue stain as a stain for keratin. *J. Oral Surg., 16*, 580-581.

Bazm, M. A., Goodarzi, N., Abumandour, M. M. A., Naseri, L., & Hosseinipour, M. (2020). Histological characterisation of the skin of the Paraechinus hypomelas, Brandt, 1836 (Erinaceidae: Eulipotyphla). *Folia Morphologica, 79*(2), 280-287.

Beraldo-Massoli, M. C., Ribeiro, P. R. Q., Vieira, L. G., Menezes, L. T., Lima, M. O., Souza, R. R., & Santos, A. L. Q. (2013). Morfologia da l}ngua e caracter}sticas das papilas linguais de Cuniculus paca (Rodentia: Cuniculidae). *Biotemas, 26*, 167-177.

Casali, D. M., Martins-Santos, E., Santos, A. L. Q., Miranda, F. R., Mahecha, G. A. B., & Perini, F. A. (2017). Morphology of the tongue of Vermilingua (Xenarthra: Pilosa) and evolutionary considerations. *Journal of Morphology, 278*(10), 1380-1399.

Ciena, A. P., Bolina, C. d. S., de Almeida, S. R. Y., Rici, R. E. G., de Oliveira, M. F., Silva, M. C. P. d., . . . Watanabe, I.-s. (2013). Structural and ultrastructural features of the agouti tongue (Dasyprocta aguti Linnaeus, 1766). *Journal of Anatomy, 223*(2), 152-158. doi:https://doi.org/10.1111/joa.12065

Cizek, P., Hamouzova, P., Goździewska-Harłajczuk, K., Klekowska-Nawrot, J., & Kvapil, P. (2020). Microscopic structure of the tongue in the lesser hedgehog tenrec (Echinops telfairi, Afrosoricida) and its relation to phylogenesis. *Anatomical Science International, 95*(3), 313-322.

Cizek, P., Hamouzova, P., Goździewska-Harłajczuk, K., Klekowska-Nawrot, J., & Kvapil, P. (2022). Ultrastructure of the tongue in the African pygmy hedgehog (Atelerix albiventris), comparison within the family Erinaceidae. *Acta Zoologica, 103*(4), 442-452.

Dando, R., Pereira, E., Kurian, M., Barro-Soria, R., Chaudhari, N., & Roper, S. D. (2015). A permeability barrier surrounds taste buds in lingual epithelia. *American Journal of Physiology-Cell Physiology, 308*(1), C21-C32.

Davydova, L., Tkach, G., Tymoshenko, A., Moskalenko, A., Sikora, V., Kyptenko, L., . . . Suchonos, O. (2017). Anatomical and morphological aspects of papillae, epithelium, muscles, and glands of rats' tongue: Light, scanning, and transmission electron microscopic study. *Interv Med Appl Sci, 9*(3), 168-177. doi:10.1556/1646.9.2017.21

El-Mansi, A. A., Al-Kahtani, M. A., & Abumandour, M. M. A. (2019). Comparative phenotypic and structural adaptations of tongue and gastrointestinal tract in two bats having different feeding habits captured from Saudi Arabia: Egyptian fruit bat (Rousettus aegyptiacus) and Egyptian tomb bat (Taphozous perforatus). *Zoologischer Anzeiger, 281*, 24-38.

Erdoğan, S., & Prez, W. (2013). Anatomical and scanning electron microscopic characteristics of the tongue in the pampas deer (Cervidae: Ozotoceros bezoarticus, Linnaeus 1758). *Microscopy Research and Technique, 76*(10), 1025-1034.

Farrag, F. A., Mahmoud, S. F., Kassab, M. A., Hassan, A., Abdelmohdy, F., Shukry, M., . . . Fayed, M. (2022). Ultrastructural features on the oral cavity floor (tongue, sublingual caruncle) of the Egyptian water buffalo (Bubalus bubalis): gross, histology and scanning electron microscope. *Folia Morphol (Warsz), 81*(3), 650-662. doi:10.5603/FM.a2021.0061

Freire, E. C. B., Moreira, L. G. d. S., Giese, E. G., Branco, É., da Silva, L. M., & de Lima, A. R. (2019). Papillary architecture of the Leopardus pardalis tongue. *Anatomia, Histologia, Embryologia, 48*(5), 421-428. doi:https://doi.org/10.1111/ahe.12462

Gartiwa, G., Damia, U., Megawati, E. I., Pradipta, S. I. D., Gunawan, G., Karnati, S., . . . Kusindarta, D. L. (2021). Morphological characterization of Horsfield's treeshrew Tupaia javanica lingual papillae: Light microscopy and scanning electron microscopy studies. *Anatomia, Histologia, Embryologia, 50*(5), 801-811. doi:https://doi.org/10.1111/ahe.12724

Gewily, D. I., Mahmoud, F. A., Saber, S. A., ElSalkh, B. A., El-Dahshan, A. A., Abumandour, M. M. A., . . . Gadel-Rab, A. G. (2021). Ultrastructural comparison between the tongue of two reptilian species endemic in Egyptian fauna; Bosc's fringe-toed lizard Acanthodactylus boskianus and Sinai fan-fingered gecko Ptyodactylus guttatus. *Microsc Res Tech, 84*(9), 1977-1991. doi:10.1002/jemt.23753

Goodarzi, N., & Azarhoosh, M. (2016). Morpholoical study of the brandt's hedgehog, paraechinus hypomelas (Eulipotyphla, Erinaceidae), Tongue. *Vestnik Zoologii, 50*(5), 457-466. Retrieved from https://doi.org/10.1515/vzoo-2016-0052

Goździewska-Harłajczuk, K., Hamouzová, P., Klećkowska-Nawrot, J., Barszcz, K., & Čížek, P. (2020). Microstructure of the Surface of the Tongue and Histochemical Study of the Lingual Glands of the Lowland Tapir (Tapirus terrestris Linnaeus, 1758) (Perissodactyla: Tapiridae). *Animals, 10*(12). doi:10.3390/ani10122297

Goździewska-Harłajczuk, K., Klećkowska-Nawrot, J., Hamouzová, P., & Čížek, P. (2022). Microstructure of the tongue surface and lingual glands of the Sulawesi bear cuscus, Ailurops ursinus (Marsupialia: Phalangeridae)—A light and scanning electron microscopic study. *Acta Zoologica, 103*(3), 259-281. doi:https://doi.org/10.1111/azo.12367

Grandi, D., Arcari, M. L., & Azalli, G. (1994). Ultrastructural aspects of the lingual papillae in the gerbil (Meriones unguiculatus). *Ital J Anat Embryol, 99*, 201-217.

Gregorin, R. (2003). Comparative morphology of the tongue in free-tailed bats (Chiroptera, Molossidae). *Iheringia. S{\'e}rie Zoologia, 93*(2), 213-221.

Haddao, K. M., & Yasear, A. Y. (2018). Weber's Salivary Glands Of Rabbit: Histological And Histochemical Studies''. *Biochemical and Cellular Archives, 18*(5), 557-560.

Haggag, T., Mahmoud, E. F., Salem, Z. A., & AbuBakr, N. (2020). Comparative evaluation of the ultrastructural morphology and distribution of filiform and fungiform tongue papillae in Egyptian mice, fruit bats and long-eared hedgehogs. *Anatomy & Cell Biology, 53*(4), 493-501.

Hiiemae, K. M., & Crompton, A. W. (2013). Mastication, food transport, and swallowing. In *Functional vertebrate morphology* (pp. 262-290).

Hino, K., Hirashima, S., Tsuneyoshi, R., Togo, A., Hiroshige, T., Kusukawa, J., . . . Ohta, K. (2022). Three-dimensional ultrastructure and histomorphology of mouse circumvallate papillary taste buds before and after birth using focused ion beam-scanning electron microscope tomography. *Tissue and Cell, 75*, 101714. doi:https://doi.org/10.1016/j.tice.2021.101714

Humphries, A., Seow, B., Danee, S., Ness, B., & Warburton, N. M. (2023). *Comparative tongue anatomy of the rakali (Hydromys chrysogaster) and greater stick-nest rat (Leporillus conditor) (Rodentia; Muridae)*: Australian Mammalogy.

Huțanu, E., Damian, A., Micluș, V., Rațiu, I. A., Rus, V., Vlasiuc, I., & Gal, A. F. (2022). Morphometric Features and Microanatomy of the Lingual Filiform Papillae in the Wistar Rat. *Biology, 11*(6), 920. Retrieved from https://doi.org/10.3390/biology11060920

Igbokwe, C. O., & Mbajiorgu, F. E. (2019). Anatomical and scanning electron microscopic study of the tongue in the African giant pouched rats (Cricetomys gambianus, Waterhouse). *Anat Histol Embryol, 48*(5), 455-465. doi:10.1111/ahe.12467

Iwasaki, S. (2002). Evolution of the structure and function of the vertebrate tongue. *Journal of Anatomy, 201*(1), 1-13.

Kobayashi, K. (1990). Three-dimensional architecture of the connective tissue core of the lingual papillae in the guinea pig. *Anatomy and Embryology, 182*(3), 205-213.

Kobayashi, K., Kumakura, M., Yoshimura, K., Nonaka, K., Murayama, T., & Henneberg, M. (2003). Comparative morphological study of the lingual papillae and their connective tissue cores of the koala. *Anatomy and Embryology, 206*(4), 247-254. Retrieved from https://doi.org/10.1007/s00429-002-0296-z

Kusuma, I. F., Damia, U., Megawati, E. I., Saputra, F. C. E., Karnati, S., Kusindarta, D. L., & Wihadmadyatami, H. (2022). Morphology of lingual papillae in the Javan mongoose (Herpestes javanicus) by scanning electron microscopy and light microscopy. *Anatomia, Histologia, Embryologia, 51*(6), 756-768.

Levin, M. J., & Pfeiffer, C. J. (2002). Gross and microscopic observations on the lingual structure of the Florida Manatee Trichechus manatus latirostris. *Anatomia, Histologia, Embryologia, 31*(5), 278-285.

Mahdy, M. A. A., Abdalla, K. E. H., & Mohamed, S. A. (2021). Morphological and scanning electron microscopic studies of the lingual papillae of the tongue of the goat (Capra hircus). *Microsc Res Tech, 84*(5), 891-901. doi:10.1002/jemt.23649

Massoud, D. (2020). Regional differences in the skin of the desert hedgehog (Paraechinus aethiopicus) with special reference to hair polymorphism. *Zoologischer Anzeiger, 289*. Retrieved from https://doi.org/10.1016/j.jcz.2020.10.004

Massoud, D., & Abumandour, M. M. A. (2019). Descriptive studies on the tongue of two micro-mammals inhabiting the Egyptian fauna; the Nile grass rat (Arvicanthis niloticus) and the Egyptian long-eared hedgehog (Hemiechinus auritus). *Microscopy Research and Technique, 82*, 9. Retrieved from https://doi.org/10.1002/jemt.23324

Massoud, D., & Abumandour, M. M. A. (2020). Anatomical features of the tongue of two chiropterans endemic in the Egyptian fauna; the Egyptian fruit bat (Rousettus aegyptiacus) and insectivorous bat (Pipistrellus kuhlii). *Acta Histochemica, 122*(2), 151503.

Massoud, D., Bin-Meferij, M. M., El-Kott, A. F., El-Maksoud, A., M., M., & Negm, S. (2023). Histology and histochemistry of the major salivary glands in the southern white-breasted hedgehog (Erinaceus concolor). *Anatomia, Histologia, Embryologia, 52*(2), 254-261.

Merlino, D. J., Vander Wert, C. J., Peraza, L. R., Howlett, L., Yin, L. X., Moore, E. J., . . . Van Abel, K. M. (2022). The oral tongue and floor of mouth in three dimensions (3D): A digital anatomical model derived from radiology, peer-reviewed literature, and medical illustration. *Operative Techniques in Otolaryngology-Head and Neck Surgery, 33*(4), 259-271. doi:https://doi.org/10.1016/j.otot.2022.10.006

Mohamed, W. F. (2021). *Changes in the feeding behavior and habitat use of the desert hedgehog Paraechinus aethiopicus (Ehrenberg 1832, Eulipotyphla: Erinaceidae)*. 82: in Saudi Arabia. Brazilian Journal of Biology.

Nasr, E. S., Gamal, A. M., & Elsheikh, E. H. (2012). Light and scanning electron microscopic study of the dorsal lingual papillae of the rat Arvicanthis niloticus (Muridae, Rodentia). *J. Am, 8*(4), 619-627.

Okada, S., & Schraufnagel, D. E. (2005). Scanning Electron Microscopic Structure of the Lingual Papillae of the Common Opossum (Didelphis marsupialis). *Microscopy and Microanalysis, 11*(4), 319-332. Retrieved from https://doi.org/10.1017/S1431927605050257

Parchami, A., Salimi, M., & Khosravi, M. (2018). Tongue structure in the long-eared hedgehog (Hemiechinus auritus): A scanning electron microscopic study. *Veterinary Research Forum, 9*, 3.

Park, J.-W., & Lee, J.-H. (2009). Morphological study on the dorsal lingual papillae of Sorex caecutiens Laxmann. *Applied Microscopy, 39*(2), 101-106.

Pastor, J. F., Muchlinski, M. N., Potau, J. M., Casado, A., Garca-Mesa, Y., Vega, J. A., & Cabo, R. (2021). The tongue in three species of lemurs: Flower and nectar feeding adaptations. *Animals, 11*(10), 2811.

Sadeghinezhad, J., Sheibani, M. T., Memarian, I., & Chiocchetti, R. (2017). Morphological study of the Persian leopard (Panthera pardus saxicolor) tongue. *Anatomia, Histologia, Embryologia, 46*(3), 240-248.

Sadeghinezhad, J., Tootian, Z., & Javadi, F. (2018). Anatomical and histological structure of the tongue and histochemical characteristics of the lingual salivary glands in the Persian squirrel (Sciurus anomalus). *Anat Sci Int, 93*(1), 58-68. doi:10.1007/s12565-016-0367-5

Sakr, M. F. (2022). Physiology of the Tongue. In *Tongue Lesions* (pp. 25-32).

Selim, A., & Samir, R. (2018). Light and scanning electron microscope studies of the tongue of the Egyptian Mongoose (Herpestes ichneumon). *J Cytol Histol, 9*(499), 2.

Sharma, R. S. K., Vidyadaran, M. K., Zulkifli, I., Azlan, J. M., Sumita, S., Azilah, A. J., & Ho, O. K. (1999). Ecomorphological implications of the microstructures on the tongue of the fawn roundleaf bat, Hipposideros cervinus (Chiroptera: Hipposideridae). *Australian Journal of Zoology, 47*(4), 405-409.

Taiwo, A. A., David, A. O., Oladele, A. A., Samson, A. O., Emmanuel, O. O., Frank, O. A., . . . Oladele, P. O. (2009). A Comparative Histological Study of the Tongue of Rat (Rattus Norvegicus), Bat (Eidolon Helvum) and Pangolin (Manis Tricuspis). *International Journal of Morphology, 27*(4), 1111-1119. doi:10.4067/S0717-95022009000400026

Wannaprasert, T., Phanthuma-opas, P., & Jindatip, D. (2020). Morphology and microstructure of the tongue of the lesser bamboo rat (Cannomys badius). *Acta Zoologica, 101*(3), 282-291.

Wolczuk, K. (2014). Dorsal surface of the tongue of the Hazel Dormouse Muscardinus Avellanarius: Scanning electron and light microscopic studies/Grzbietowa Powierzchnia Jezyka Orzesznicy Muscardinus Avellanarius: Badania Z Wykorzystaniem Mikroskopu Skaningowego I Swietlnego. *Zoologica Poloniae, 59*, 35.

Tables:

Table 1. Thickness of the lingual total epithelium and keratinized epithelium in the desert hedgehog *P. aethiopicus*. Values in the table are expressed as the means and standard deviations.

	Apex	**Body**	**Root**
Total epithelium thickness	89.978 ± 6.46	74.173 ± 10.82	23.702 ± 7.09
Keratinized epithelium thickness	65.865 ± 6.62	49.013 ± 5.9	8.655 ± 1.15

Figure legends

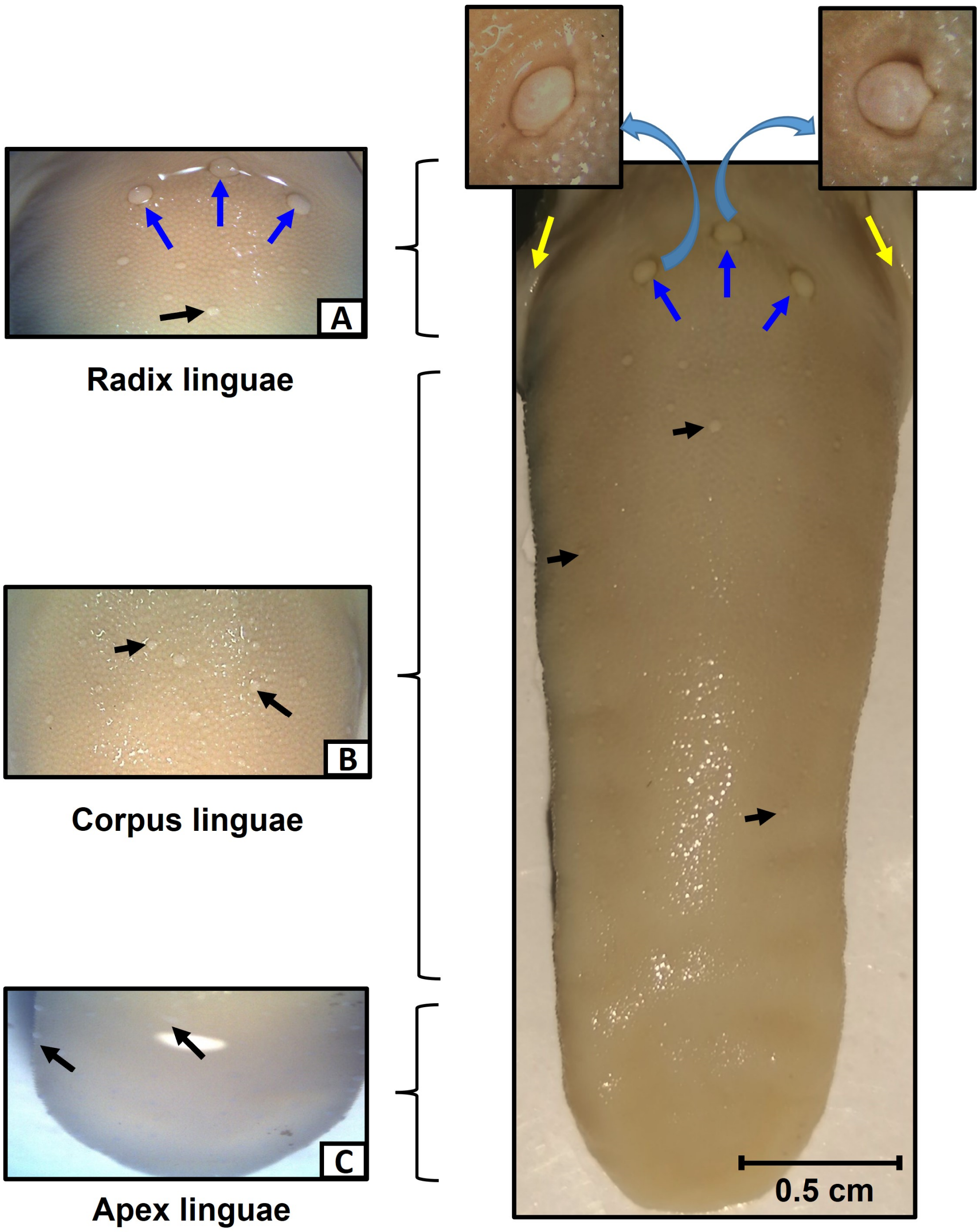

Figure 1. Macroscopic observations of the tongue dorsal epithelium in the desert hedgehog (*P. aethiopicus*) showing the three main subdivisions: radix linguae (root) (A), corpus linguae (body) (B), and apex linguae (apex) (C). The root of the tongue carries three circumvallate papillae arranged in the three corners of a triangle (blue arrows). The lingual body and apex carry filiform- and conical-shaped papillae. The dome–shape of fungiform papillae is scattered among the dorsal epithelium of the three subdivisions. The lingual root is characterized by the existence of two lateral ridges on both sides (yellow arrows).

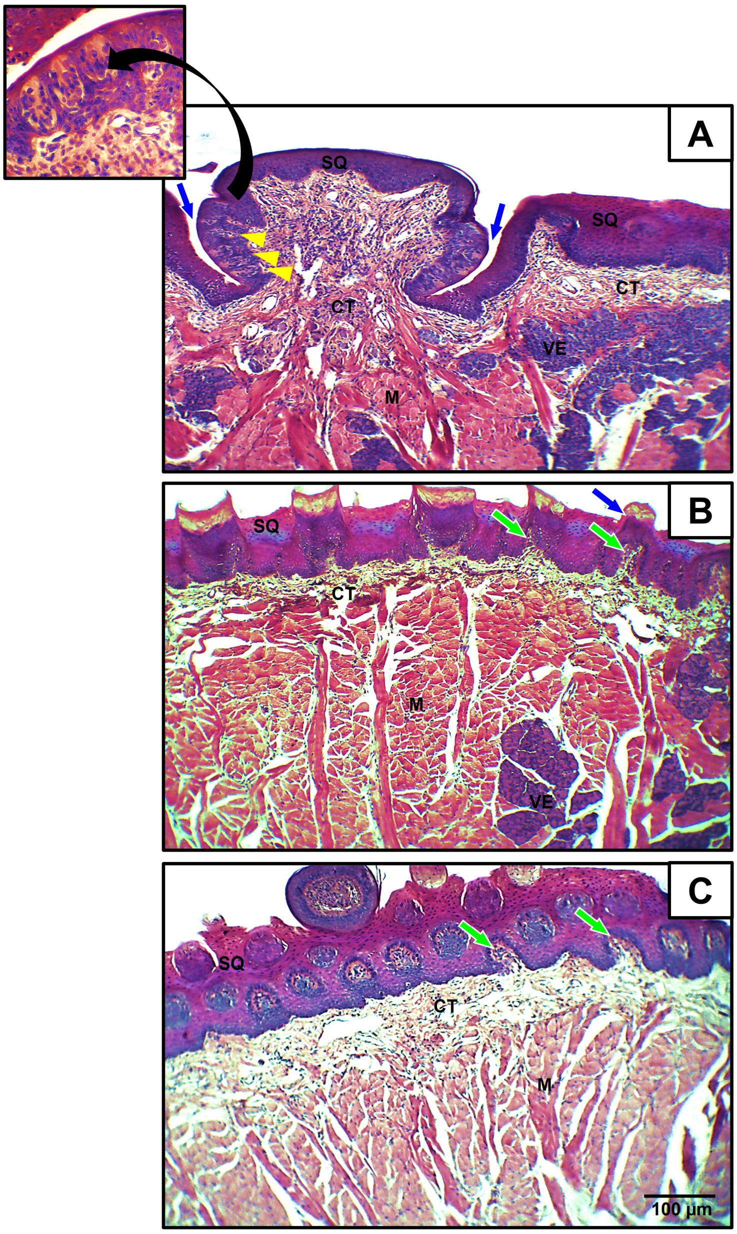

Figure 2, Photomicrograph of the histological analysis of the desert hedgehog (*P. aethiopicus*) stained with H&E showing the general architecture of the three main subdivisions: radix linguae (root), corpus linguae (body), and apex linguae (apex). The tongue dorsum is covered with stratified squamous epithelium (SQ), underneath is the underlying connective tissue layer (CT), and the muscular core (M). (A) The lingual root with the circumvallate papilla and surrounding circumferential groove (blue arrow) and the underlying Von Ebner's glands (VE). Additionally, the taste buds are shown in the enlarged box. (B) The lingual body carrying filiform papillae with numerous spikes and the invading lamina propria (green arrows). Additionally, conical-shaped papillae are shown on the lateral boundary (blue arrow). (C) The lingual apex with filiform papillae and dome-shaped fungiform papillae is also shown.

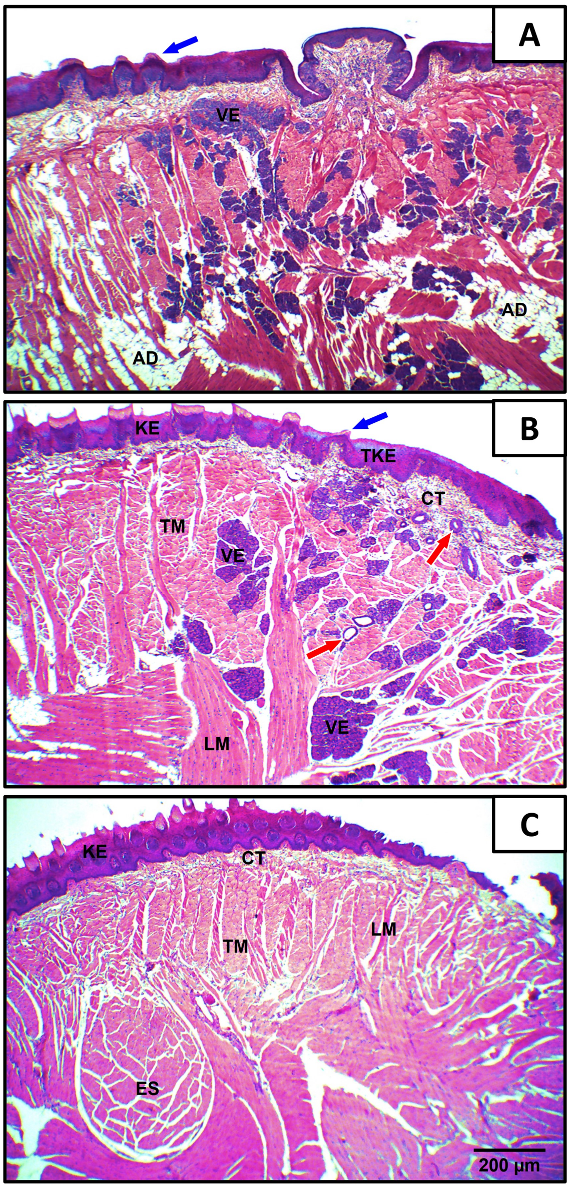

Figure 3. Photomicrograph of the histological analysis of the desert hedgehog (*P. aethiopicus*) stained with H&E showing the general architecture of the three main subdivisions: radix linguae (root), corpus linguae (body), and apex linguae (apex). (A) The tongue root with circumvallate papillae and conical papillae is also shown (blue arrow). the lingual glands (VE) were densely distributed in the lingual root and intercalated between the muscle strands. Additionally, numerous clusters of adipose tissue (AD) are shown between the muscle strands. (B) The section shows the body of the tongue with intensely keratinized squamous epithelium (KE) devoid of the lingual glands and was localized on the lateral boundaries of the tongue where keratinization is very thin (TKE). (C) The section shows the apex of the tongue, which is completely devoid of the lingual glands. The pear-shaped encapsulated muscular structure (ES) is situated only in the lingual apex. The muscular core consists of transverse strands (TM) and longitudinal strands (LM).

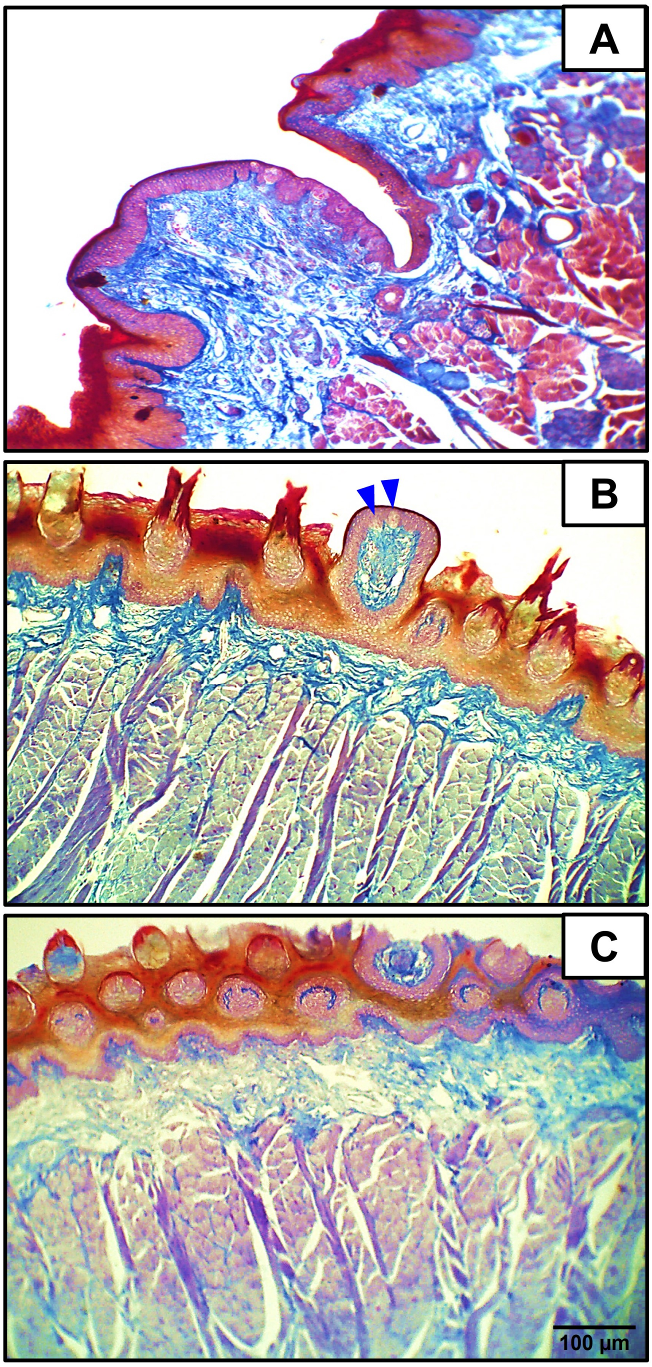

Figure 4. Histochemical detection of the extent of keratinization using Ayoub-Shklar staining for the three main subdivisions of the tongue: radix linguae (root), corpus linguae (body), and apex linguae (apex). (A) The tongue root shows very little staining, especially on the laterodorsal boundaries of the circumvallate papilla. (B) The lingual body with filiform papillae and dome-shaped fungiform papillae and intense keratinization on the lingual body epithelium. (C) Section of the lingual apex showing a high extent of staining.

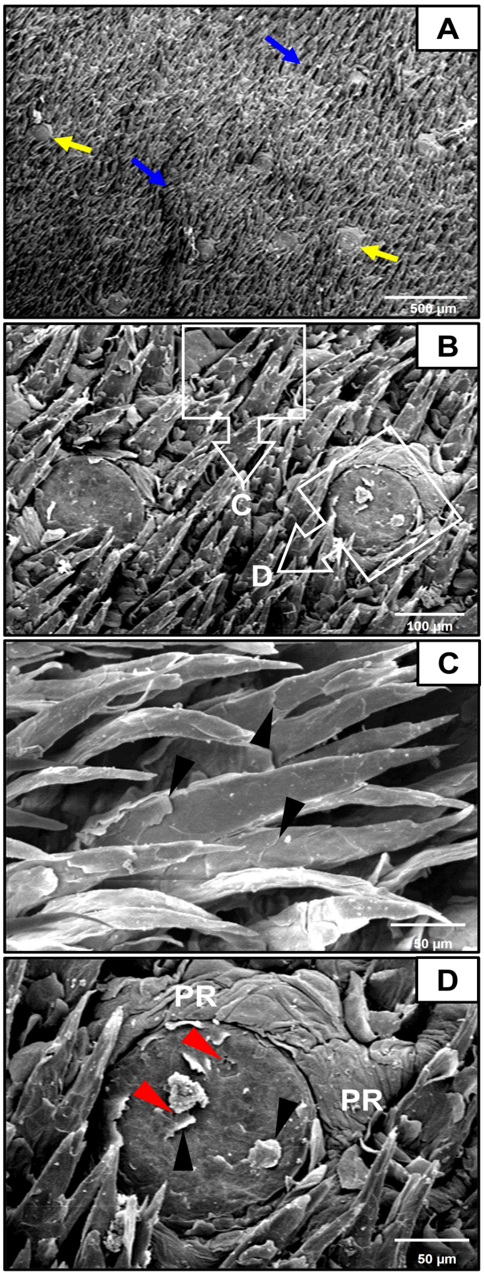

Figure 5. SEM of tongue dorsum in the desert hedgehog (*P. aethiopicus*) showing the filiform papillae that were densely distributed on the lingual mucosa. (A) The blue arrows show densely distributed filiform papillae, while dome-shaped papillae are indicated by yellow arrows. (B) An enlarged portion of (A). (C) Enlarged box of (B) showing the giant bifid and trifid filiform papillae with stratified scales on the dorsal surface. (D) Enlarged box of (B) exhibiting the dome-shaped fungiform papilla with a taste pore opening (red arrowheads) on the dorsal surface and surrounded by a papillary ridge (PR). The stratified scales were desquamating as shown by the black arrowheads.

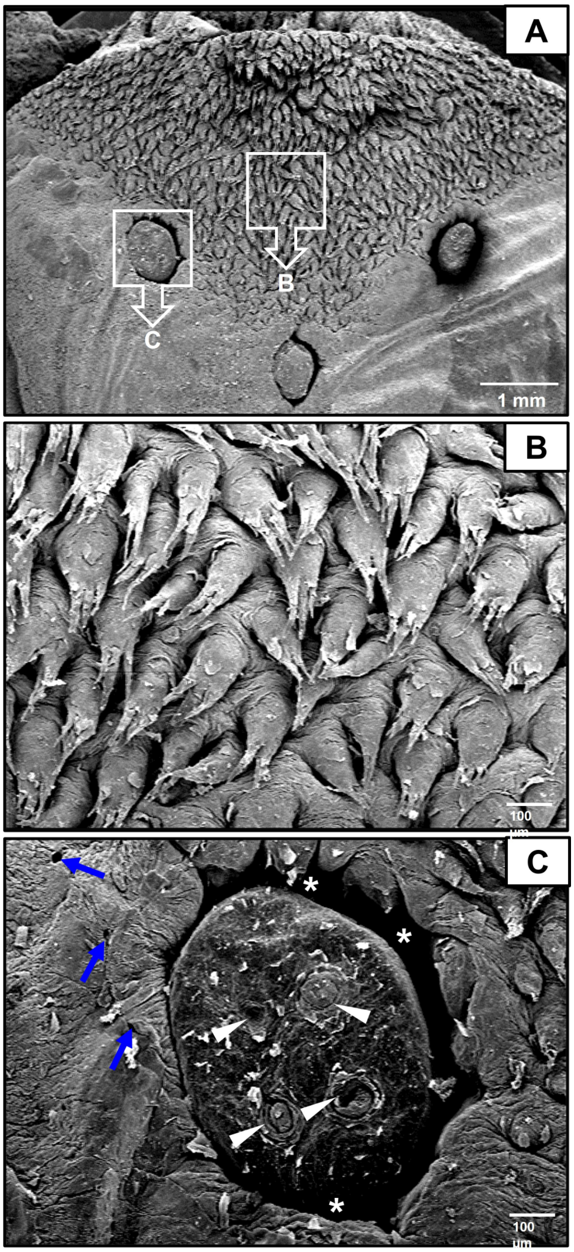

Figure 6. (A) SEM of the radix linguae of the desert hedgehog (*P. aethiopicus*) showing different forms of papillae. the circumvallate papillae were arranged in the corners of triangles and that the conical papillae were scattered in between. (B) Enlarged box of (A) showing conical-shaped papillae. (C) Enlarged box of (A) showing the circumvallate papillae and numerous openings of the lingual glands (blue arrows). A distinct complete shallow groove was observed, and a circumferential groove (asterisk), an annular pad (ap) surrounding the papilla, and several taste pores (white arrowheads) were also recognized on the apical surface of the papilla.