JJBS

Volume 17, Number 1,March 2024
ISSN 1995-6673
Pages 99 – 108
https://doi.org/10.54319/jjbs/170109

Jordan Journal of Biological Sciences

The Salivary Glands of the Camel: An Element of Adaptation to Desert Conditions and Mitigation of Climate Change Impacts

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Received: March 5, 2023; Revised: June 29, 2023; Accepted: July 26, 2023

Abstract

The one-humped camel is well-adapted to low nutritive resources, arid environments and desert ecosystems. Salivary glands have an essential role in moistening and swallowing the ingested food and forestomach digestion regulation and in water body homeostasis. The present study aims to find out the morphological, histological and histochemical characterization of the salivary glands of the dromedary camel concerning the salivation process's role in challenging the arid conditions and to mitigate the climate change impacts. Representative samples of the salivary glands of healthy 16 adult one-humped camel **(**Camelus dromedaries) of both sexes were tested including mandibular glands, parotid glands, sublingual glands, buccal glands, lingual glands, labial glands and palatine ones. The samples were processed according to the following handling: gross examination, fixation, dehydration, clearing, wax impregnation, embedding, trimming, sectioning, slide mounting, hematoxylin-eosin (H&E) and a battery of histological and histochemical staining. The salivary glands demonstrated variable types of tubule-acinar and tubule-alveolar secretory portions surrounded by numerous myoepithelial cells and armed with interlobular and intralobular ducts rich with goblet cells. In addition, the glands showed variable secretory cells (mucous, serous, mucoserous and mixed seromucous) with variable secretory products mainly mucusubstances, neutral mucin, acidic mucosubstances, sialomucins, sulphomucins, and glycoproteins. Moreover, the glands collectively demonstrated activities for the following enzymes: dehydrogenases, phosphatases, esterases, carboxylases, aminopeptidases, peroxidases, cytochrome oxidases and carbonic anhydrases. furthermore, the glands exhibited alcianophilia and metachromasia. The findings of the present study indicate that the structure and the secretion of the salivary glands of the camel support an efficient salivation process and represent a strong challenge to growing water scarcity and expansion of xerophytes as the main pastoral resources for camels. In that sense, salivary glands in camels are one of the elements of his panoply adaptation to arid conditions and to mitigate the climate change impacts.

Keywords: Camel, salivary glands, histochemistry, mucosubstances, mitigation, adaptation, climate change

1. Introduction

The one-humped camel is living in a specific environment characterized notably by the low nutritive value of the pastoral resources and the aridity of the ecosystems. Many studies showed that the dromedary camel is physiologically adapted to such conditions (Yagil, 1985; Wilson, 1989; Bengoumi and Faye, 2002). The ability of the camel to survive in such environments is based on his unique anatomical and physiological particularities including salivation which could play an eminent role in the current context of climatic changes (Faye et al., 2012). Indeed, due to the arid environment, the plants grazed by camels are mainly xerophytes, characterized by small leaves often covered by wax, more or less spinous and usually rich in lignin (Fahn and Cutler, 1992). To consume such vegetation, the camel had to develop mastication, salivation and swallowing mechanisms based anatomically on tough and mobile lips together with a unique tongue able to pick desert plants small leaves (Taib and Jarrar, 1989). In addition, the dromedary has buccal internal dermis lined by compound keratinized epithelium covering a loose connective dense fibrous connective tissue (Tayeb 1950; Al-Asgah et al., 1990). Moreover, the cheek of this animal is lined by crowded thick papillae, together with sharp teeth, muscular esophagus and efficient salivary glands (Nadipour et al., 2001). These unique anatomical features, enable the camel to ingest and feed on xerophytes that require a large amount of saliva as a lubricant and on grasses that are not eatable by other animals of the same arid environment.

Camel saliva plays an essential role in moistening and swallowing the ingested food, and in oral hygiene maintaining the gastrointestinal canal regulation of digestion and absorption (Jarrar and Faye, 2012). In addition, camel saliva demonstrates buffer power in the

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stomach due to the specific richness of camel saliva by bicarbonates (Al-Razaiki et al., 2023).

The camel lives in an environment characterized by the scarcity of water and suffering from being irregularly watered. The dromedary camel can produce daily about 12-21 liters of saliva with respect to diet components and can be 150 liters under the toughest conditions (Kay et al., 1980; Kay and Maloiy, 1989). The dromedary camel relies on well-sophisticated salivary glands scattered around the oral cavity enabling him to produce large quantities of saliva. The salivary glands battery includes large parotid glands and well-developed mandibular glands located obliquely to the parotid ones and having less than half of their size (Nawar and Khaligi, 1977). The mandibular glands of the one-humped camel could produce rapid saliva secretion during feeding with a slower rate of salivation during rumination (Hoppe et al., 1975). Moreover, the camel possesses a well-developed pair of polystomatic sublingual glands covered by the mylohyoid muscle and situated under the epithelial lining of the tongue root. In addition, the camel has a set of minor salivary glands that support the process of salivation. Of these are scattered buccal glands situated in the buccinators where the ventral buccal salivary glands are embedded anterior to the masseter muscle in the lateral sides of the mandibular epithelium (Jarrar and Faye, 2012). Moreover, the camel possesses scattered lingual Von Ebner's salivary glands open in the trench surrounding the lingual circumvallate papillae (Jarrar and Taib, 1989). Furthermore, labial glands are situated in the lamina propria of the inner labial epithelial lining located just above the labial muscularis together with palatine salivary glands embedded in the palatine epithelial lining (Jarrar and Taib, 1989).

Some morphometric studies, and to a lesser extent histological ones, investigated the major salivary glands of the one-humped camel (Nassar, 1971; Nawar & Khaligi, 1975; Nawar and Khaligi, 1977, Abdalla, 1979, Mosallam et al., 1983), and to lesser extent the minor ones (Fahmy and Dellman, 1968; Jarrar and Taib, 2005, Taib and Jarrar, 1998). However, beyond the anatomical dispersion of the salivary glands, their performance in terms of quantity and quality of saliva production is related to their anatomic-physiological structure. The present work was undertaken to provide morphometric, histological and histochemical description and characterization for the salivation battery of the dromedary camel as a tool of adaptation to arid environments.

2. Materials and Methods

Representative biopsies of major (mandibular, parotid and sublingual) and minor (buccal, lingual, labial and palatine) salivary glands were collected from 16 healthy adult one-humped camels of both sexes with the age of 5-6 years old (body weigh 470-560 kg) of Majaheem breed obtained from the main slaughterhouse in Skaka city of Saudi Arabia. The tissue blocks were subjected to detailed anatomical, histological and histochemical investigations including gross anatomy, fixation by buffered neutral formalin (BNF), dehydration by ascending concentration of ethanol, clearing in chloroform, impregnation and embedding by paraffin wax (melting point 58 C).

Paraffin sections (4-5 πm thickness) of all samples under study were subjected to hematoxylin and eosin (H&E) and trichrome stains (Jarrar and Taib, 2018). In addition, paraffin and frozen sections (8-10 πm thickness) were subjected to the following battery of histochemistry techniques (Pearse, 1992; Jarrar and Taib, 2016 and 2018; Survarna et al., 2019): Periodic acid Schiff (PAS) reaction, amylase digestion-PAS for glycogen and neutral mucosubstances characterization, alcian blue (AB) at pH 2.5 and 1.0 for acid mucosubstances, PAS-AB (pH 2.5) and PAS-AB (pH 1.0) for distinction between neutral and acid mucosubstances, aldehyde fuchsin (AF) and AF-AB (pH 2.5 and 1.0) for the distinction between sulphomucins and sialomucins. Other paraffin sections were exposed to the following enzymatic digestion tests: amylase-PAS, neuraminidase-AB (pH 2.5), hyaluronidase-AB (pH 2.5), neuraminidase-TB (pH 3.7) and hyaluronidase-TB (pH 2.0). In addition, proteins were detected by ninhydrin-Schiff, mercuric bromophenol blue (MBP) and trypsin digestion-PAS. Moreover, the enzyme histochemical activity was determined for the following enzymes: alkaline phosphatase, acid phosphatase, mitochondrial adenosine triphosphatase, non-specific esterases, succinic dehydrogenase, carbonic anhydrase and aminopeptidase.

All conducted experimental procedures were approved by the Ethics Committee for the use of experimental animals at Jerash University (approval number JU/17/05/2019).

3. Results and Discussion

The dromedary camel has a thick upper lip divided by a fissure of two mobile parts. This fissure is continuous with a lateral nose external wing. On the other hand, the lower lip demonstrates hanging with an apparent chin and becomes more pointed. However, both lips are covered by hairy skin with long tactile hairs covering the external superficial surface (Figure 1a-c). A previous study reported that both lips have scattered labial glands in grey-blue labial epithelial lining (Taib and Jarrar, 1987).

The lips guard the entrance of the oral activity and each consists anatomically of three anatomical zones: cutaneous, transitional and mucosal zone (Figure 2a). Histologically, the cutaneous of the lip consists of two layers, an outer epidermis and deeper dermis. The dermis is embedded with scattered sweat and sebaceous glans together with the roots of the tactile hairs (Figure 2b). The labial transitional area is covered by a thin skin and extends up to the oral mucosa. This zone lacks sweat glands and hair roots. The labial mucosal zone includes three sublayers: Mucosa, submucosa and muscularis. The mucosa consists of compound squamous epithelium while the submucosa is formed of connective tissue rich in blood vessels and collagenous fibers together with tubule-alveolar labial glands (Figure 2c). The muscularis of the mucosal zone consists of skeletal muscle fibers making the core of the mucosal sublayer (Figure 2d).

The one-humped camel has an elongated mobile tongue consisting mainly of obliquely arranged skeletal muscle bulk (Figure 3b-c). The tongue is about 40 cm long and is attached to the hyoid bone. Filiform, fungiform and circumvallate papillae cover the upper surface of the dorsum of the tongue and its lateral edges. Some studies reported that the tongue of the camel is highly innervated containing numerous ganglia and nerve fibers (Qayyum et al., 1991). In addition, the tongue of the one-humped camel is covered with a variable thickness of cornified compound squamous epithelium. The lingual lamina propria is narrow and continuous with the muscularis mucosa lining the submucosa sublayer (Figure 4a). The dorsal lingual epithelium of this animal demonstrates filiform, fungiform, circumvallate papillae together with wart-like papillae (Figure 4b). Bundles of thick connective tissue are seen along the ventral lingual surface. The filiform papillae are conical in shape with variable thickness and height and are scattered mainly in the dorsum and the lateral edges of the tongue. On the other hand, the rounded fungiform papillae together with the taste pores are seen in the anterior lingual surface. However, the circumvallate papillae are restricted to the posterior portion of the tongue (Figure 3c).

The inferior lingual surface lacks cornification and is lined with squamous epithelium. Two types of minor salivary glands are situated in the lamina propria: Von Ebner's glands and Weber's glands which are superficially embedded amongst dense connective tissues and surrounded by bundles of lingual striated muscle. The lingual core exhibits a bundle of skeletal muscles arranged variably in transverse and oblique arrangements (Figure 4c). The stroma of the tongue contains numerous ganglia and nerve fibers.

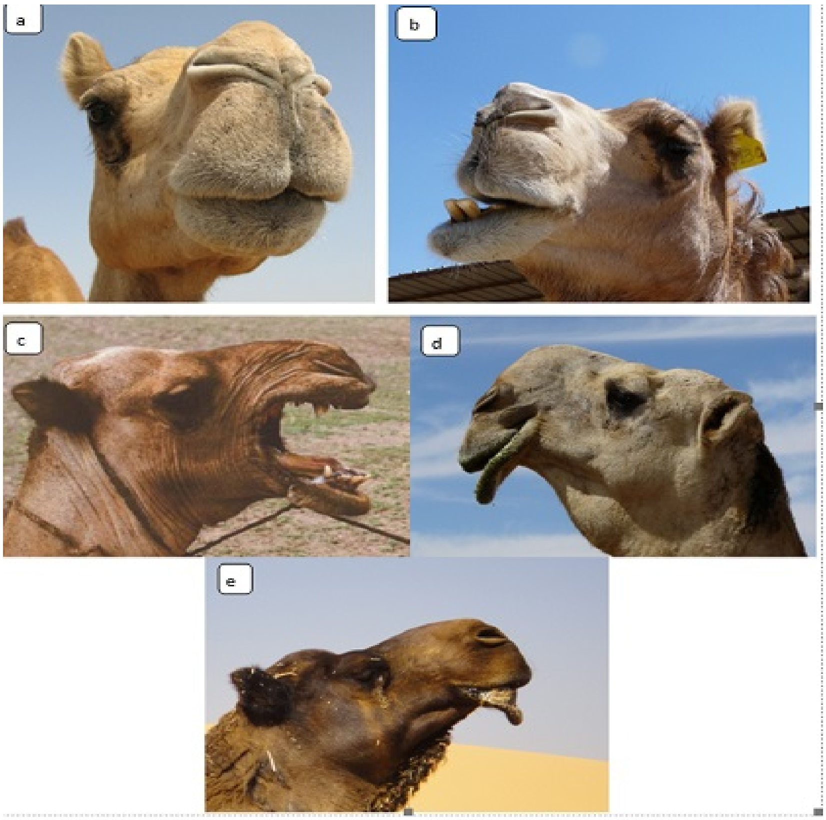

Figure 1. Photographs on libs of the one-humped camel demonstrating: (a) The external surface of the lip covered by long tactile hairy skin, (b) Tactile hairs covering both libs, (c) Sharp teeth, (d) Mobile rubbery lip (e) Hanging lip in an old camel

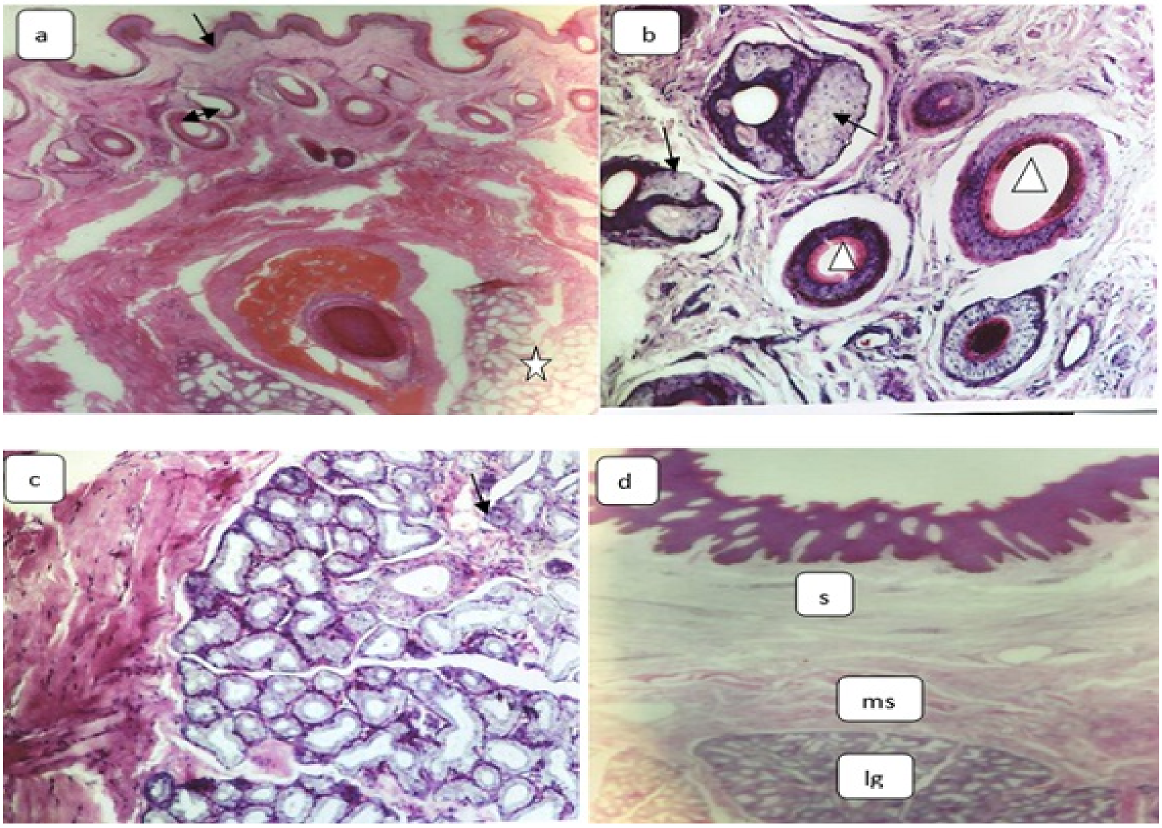

Figure 2(a-d). Micrographs through in the cutaneous zone of the camel lip demonstrating (a) The epidermis (arrow), hair roots (double arrow) and labial glands (star), (b) Sebaceous glands (arrows) and hair follicles (triangles), (c) The tubule-alveolar nature of the labial salivary glands, (d**)** The mucosal zone sublayers: submucosa (s), muscularis (ms) and labial glands (lg).

Figure 3(a-c). Photographs showing (a) The muscle mass of the camel tongue, (b)The hole-elongated tongue. Note the situation of the papillae at the base of the tongue, (c) The circumvallate and wart-like papillae.

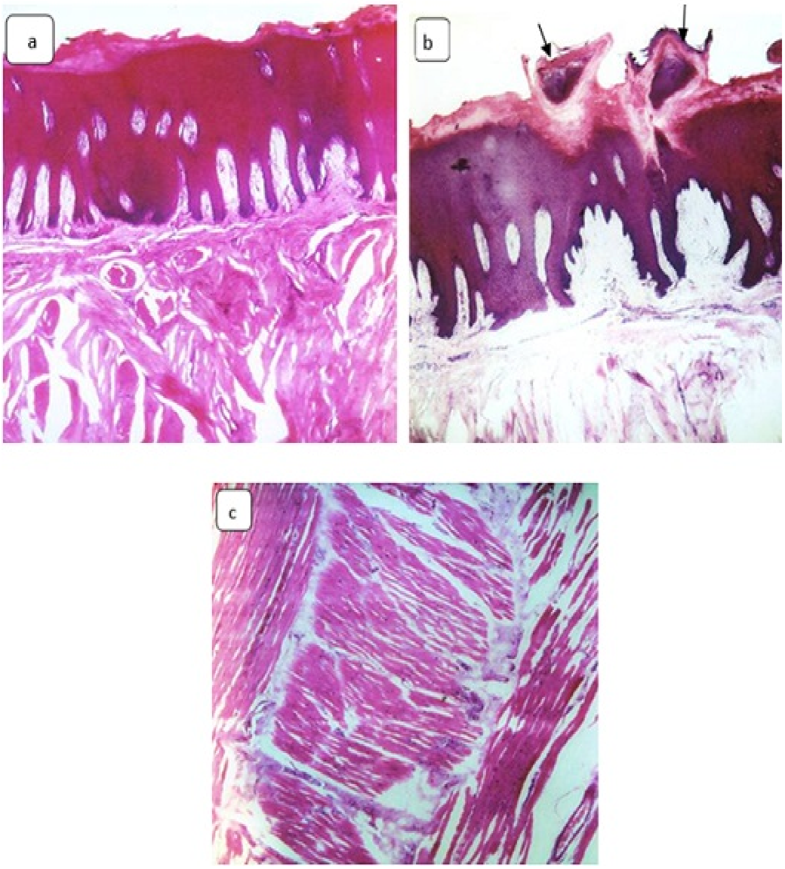

Figure 4(a-c). Micrographs in the tongue of the one-humped camel demonstrate (a) The lingual dorsum with the lamina propria, (b) The lingual dorsum with two fungiform papillae (arrows), (c) Muscle bundles of the lingual core.

3.1. The parotid glands

This major salivary gland is the largest in the dromedary camel with a four-sided shape and brown-red color, located between the ramus of the mandible and the atlas wing (Figure 5a). It demonstrates an average weight of 0.005% of live body weight and up to 145 gm in the adult animal (Kay et al., 1980). Also, this gland shows an average dimension of 13.8 cm x 5.7 cm x 2.5 cm. The parotid gland of the camel has a ductal system lined by cuboidal epithelium with occasional goblet cells and ambulated narrow intercalated ducts can. This gland can produce up to 21 liters of saliva depending on the type of diet (Nawar and El-Khaligi, 1975; Kay and Maloiy, 1989).

The parotid gland of the camel is of serous compound tubule-acinar type, covered by a capsule of fibrous and connective tissue. This gland demonstrates three variable end pieces of storage, secretory and exhaustion but lacks glycogen. The parotid gland of a one-humped camel has a large duct with folded lumen lined by compouned columnar epithelium with a large number of goblet cells (Figure 5b).

3.2. The mandibular glands

The mandibular gland of the camel is oval in shape and located obliquely under the parotid gland and covered by a layer of fibrous connective tissue surrounded by a collagenous capsule (Figure 5c). This gland demonstrates an average dimensions of 9.5 cm x 3.6 cm x 1.9 cm and an average weight of 52 gm (Nawar and Khaligi, 1977). Moreover, the salivation of the mandibular glands of the camel is rapid during ingestion and slow during rumination (Hoppe et al., 1975).

The secretory portion of the mandibular glands of the camel is tubuloacinar type consisting of mucous and seromucous cells with seromucous cells embedded between the mucous ones. The former cells are made of the secretory tubules and acini, while the seromucous one form acini and demilunes filled with variable types of secretory granules (Figure 5e). In addition, the duct of this gland has folded lumen lined by stratified columnar epithelium rich in goblet cells. However, goblet cells are also seen in the epithelium of the interlobular ducts.

3.3. The inferior molar glands

These glands are also called the ventral buccal glands and are embedded in the buccinators anterior to the masseter muscle and lateral to the mandibles (Taib and Jarrar, 1989). The dorsal part of this gland consists of large lobules while the ventral part demonstrates a dark brown layer in the form of a pyramid. The ventral portion of this gland consists of serous acini surrounded by numerous myoepithelial cells, while the dorsal part of the gland is composed of mucoserous acini. The serous acini of the ventral buccal gland are devoid of mucosubstances of any type while mucouserous ones demonstrate carboxylated mucosubstances and glycoproteins but are devoid of glycogen and sulphated mucosubstances. Moreover, this gland shows enzymatic activity for adenosine triphosphatase, nonspecific esterase, α-amylase, succinic dehydrogenase and alkaline phosphatase. However, the ventral buccal gland of the dromedary does not have enzymatic activity for lipase, aminopeptidase, beta-glucuronidase and cholinesterase.

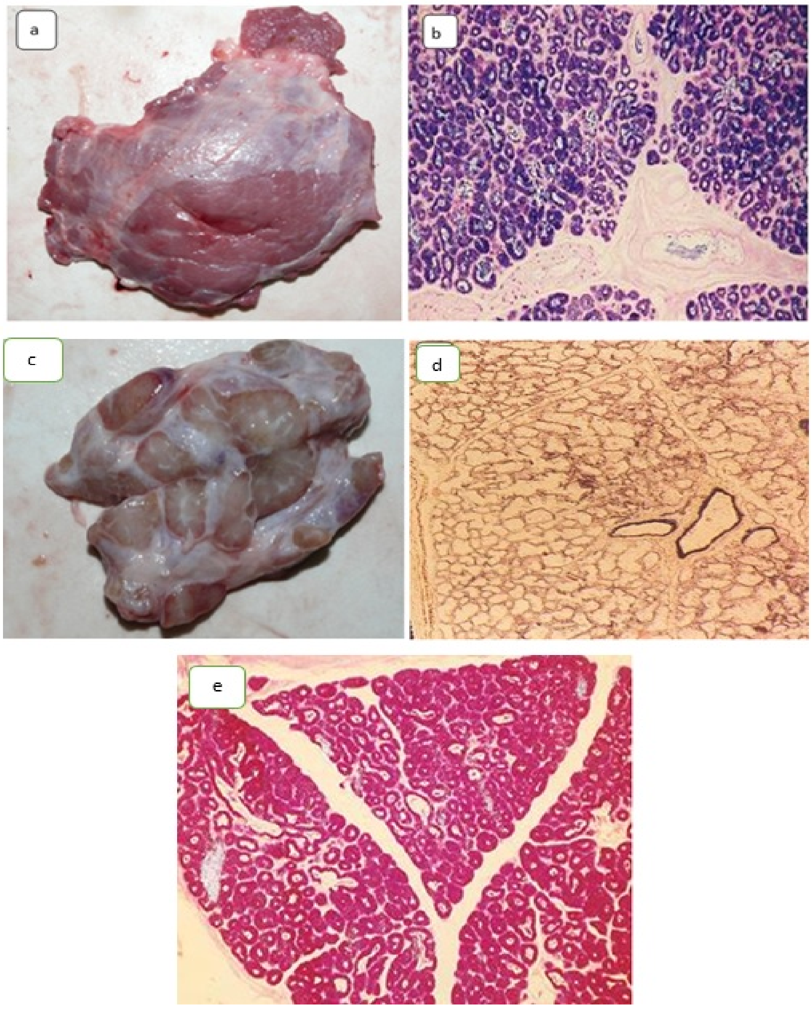

Figure 5(a-f). Micrographs show (a) Gross view of the parotid gland, (b) Parotid gland section stained with alcain blue-Aldehyde fuchsin stain demonstrating acid mucosubstances. (c) Gross examination of the mandibular gland demonstrates lobulation of the gland, (d) Section through the mandibular salivary gland demonstrates succinate dehydrogenase activity, (e) Section through the mandibular salivary glands stained with PAS method.

3.4. The sublingual glands

The sublingual glands of the camel are located along the root of the tongue under the mucous membrane (Jarrar and Faye, 2012). These glands are polystomatic in nature, small in size, pale yellow in color, flat in shape and covered by the mylohyoid muscle. These glands open separately in the floor of the buccal cavity via 16-20 excretory ducts and are embedded in dense fibrous connective tissue rich with adipose tissue and scattered in between smooth muscle bundles. The sublingual glands have numerous excretory ducts that open on the floor of the cavum oris proprium in both sides.

These glands are compound tubulo-acinar ones composed of many lobules made of two types of cells: seromucous and mucoserous (Figure 6a). The mucoserous cells constitute the main secretory portion of the glands and to a lesser extent the seromucous part. However, the mucoserous portion is distributed in the surrounding connective tissue while the seromucous excretory cells are seen embedded between the mucoserous ones. The mucoserous cells secrete neutral mucosubstances, sialomucins and to less extent sulphomucins (Figure 6b). On the other hand, the seromucous cells elaborate moderate quantity of neutral and acid mucosubstances but lack glycogen (Figure 6c).

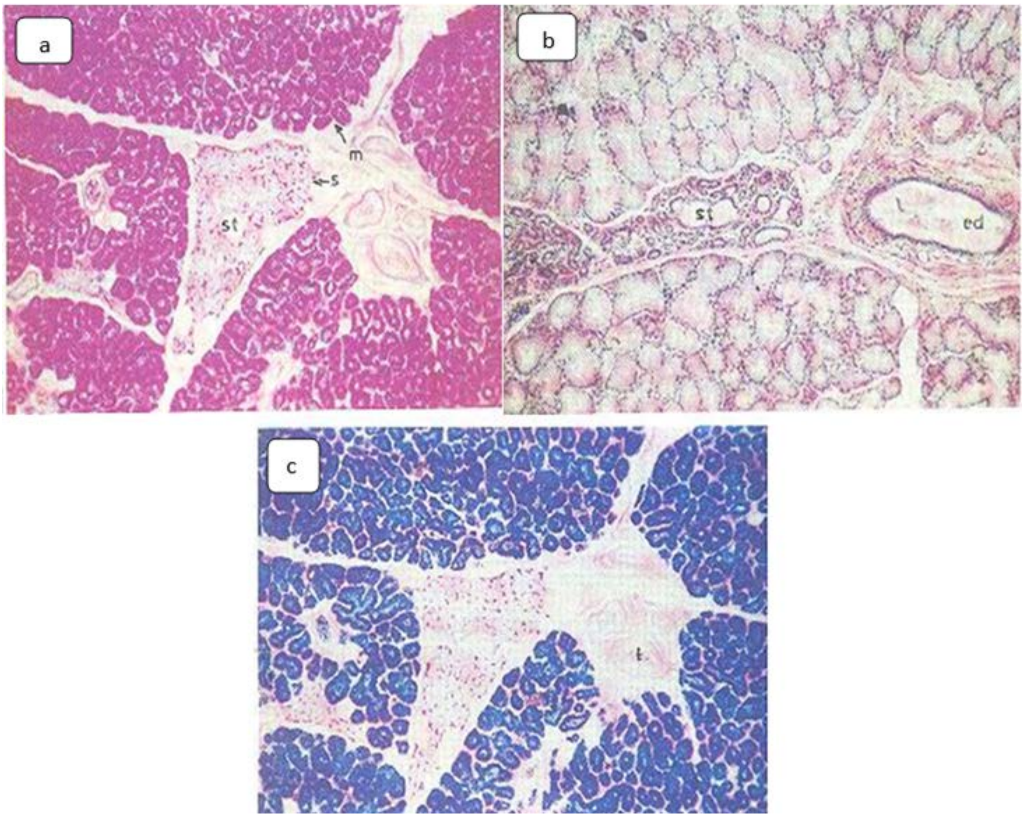

Figure 6(a-c). Micrographs show sections in the sublingual salivary gland of a camel demonstrating (a) Sublingual gland lobulation, (b) The sublingual salivary gland stained with PAS demonstrating neutral mucosubstances, (c) The sublingual salivary gland stained with alcian blue.

The sublingual glands of the dromedary camel glands demonstrate the activity of succinic dehydrogenase, alkaline phosphatase, non-specific esterase and aminopeptidase and to lesser extent activities of peroxidase and cytochrome oxidase with no beta-glucoronidase, lipase and amylase activities. The intralobular and striated ducts are lined with simple cuboidal cells with flattened epithelium seen in the intercalated ducts with no goblet cells.

3.5. The lingual salivary glands

The dromedary camel has two groups of lingual salivary glands, the Von Ebner's and Weber's glands with the following anatomical presentation:

3.5.1. The Von Ebner's lingual glands

These glands are situated in the lingual connective tissue under the circumvallate papillae. Studies indicated that these glands open mainly in the trench that surrounds the circumvallate papillae and are deeply located in the lingual adipose tissues (Jarrar and Taib, 1989). The Von Ebner's glands are a holocrine tubuloalveolar type and seromucous in nature with a branch of intercalated ducts (Figure 7a). The endpieces of these lingual glands rest on a delicate thin basement membrane. The striated ducts are lined by simple cuboidal epithelium while the cells of the secretory portion have prominent large nuclei and are filled with eosinophilic granules in their apical. Moreover, the histochemical characterization reveals that Von Ebner's glands contain a mixture of neutral mucosubstances, carboxylated and sulphated acidic mucosubstances together with orthochromatic materials. In addition, these glands demonstrate activity for the following enzymes: acid phosphatases, alkaline phosphatase, carbonic anhydrase, adenosine triphosphatase, amylase, succinic dehydrogenase and non-specific esterase (Figure 7b).

3.5.2. The Weber's lingual glands

The Weber's glands of the camel are located under the scattered thin papillae located at the tongue base. These glands consist of branched secretory tubules lined by a simple columnar epithelium with cells having alveolar cytoplasm and elongated nuclei located at the base of the cells (Figure 7c). These glands have conspicuous interlobular excretory and striated ducts lined by pseudostratified epithelium. These glands are embedded in vascularized dense connective tissue in between the bundles of muscles. However, Weber's glands demonstrate neutral mucosubstances, carboxylated and sulphated mucosubstances together with the activity of dehydrogenases and phosphatases (Figure 7d).

3.6. The labial glands

The lips of the dromedary camel are covered with hairs except for the contact area between the skin and the epithelial lining of the oral cavity which constitutes a keratinized stratified squamous epithelium covering the orbicularis muscle and the underneath collagenous connective tissues.

The labial glands of the dromedary camel are situated deeply in the lamina propria and in between the labial striated muscles. These glands are tubule-alveolar mucoserous ones in both the infra- and supra-labial libs (Figure 8a). The acini of these glands are capped by serous demilunes separated from each other by interlobular ducts and to a lesser extent in the intertubular ones. The secretory cells of the labial glands demonstrate variable shapes containing cytoplasmic granules with eosinophilic granules filling the cytoplasm of the demilunar cells. Moreover, these glands exhibit neutral mucosubstances, alcianophilia and metachromasia (Figure 8b). In addition, the mucoserous cells of these glands reveal enzymatic activity mainly for acid phosphatase, ATPase, alkaline phosphatase, succinic dehydrogenase, non-specific esterase, carbonic anhydrase, aminopeptidase and amylase (Figure 8c).

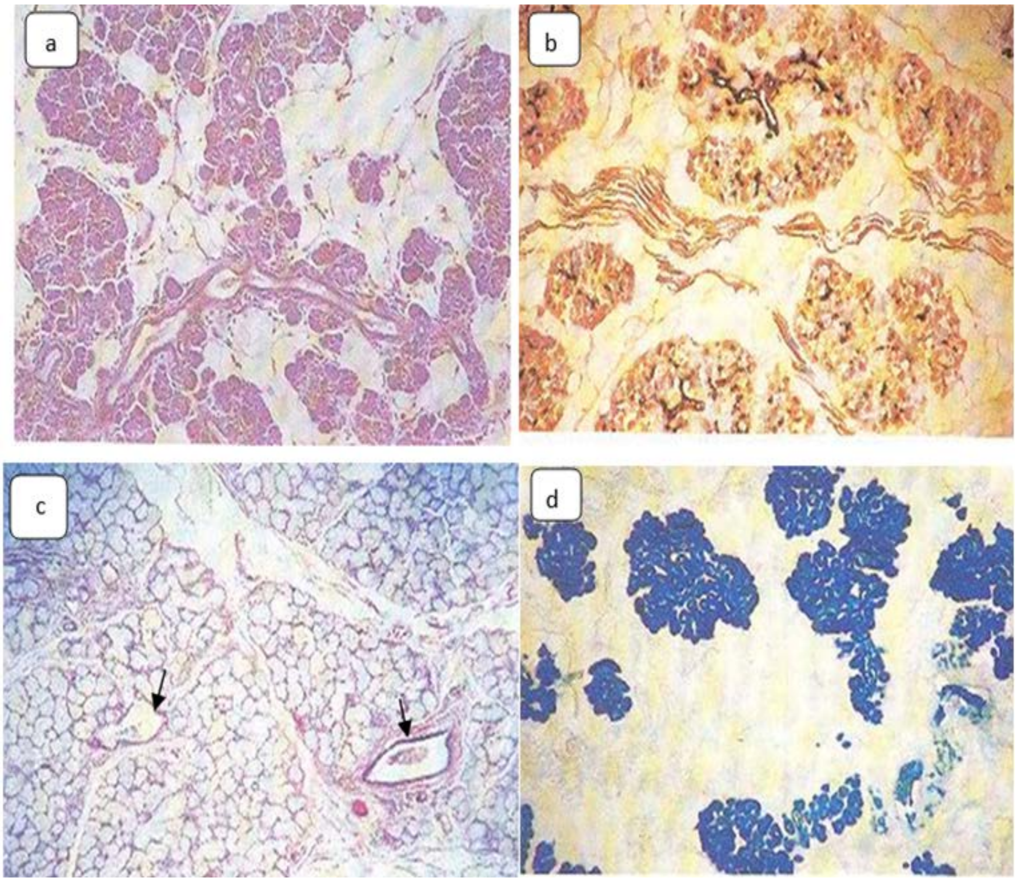

Figure 7(a-d). Micrographs illustrate sections demonstrated in the tongue of the one-humped camel: (a) The secretory portion of Von Ebner's glands, (b) Von Ebner's glands demonstrating alkaline phosphatase activity, (c) Secretory portion and the striated duct of the Weber's glands, (d) The Weber's lingual salivary gland stained with alcian blue (pH = 1.0) demonstrating sulphated mucosubstances

3.7. The palatine glands

These glands are located mainly in the soft palate but not in the hard one. The lining of the plate consists of stratified squamous epithelium forming ridges in the hard palate but not in the soft one. The stroma of the palatine glands is rich in muscle fibers, fat cells and interlobular ducts (Figure 8d). The lining of both the interlobular and intralobular ducts consists of simple cuboidal epithelium with secretory cells open in the striated ducts. However, the palatine glands of the camel are devoid of intercalated ducts. Moreover, these glands elaborate sialomucins, sulfomucins and neutral mucosubstances (Figure 8e). In addition, these glands demonstrate activity for dehydrogenases, phosphatases, and carboxyhdrases.

Thus, salivary glands in camels are characterized by their wide physiological functions, not only acting as a lubricant of the alimentary bowl in dry conditions), but also in many enzymatic activities contributing to the better valorization of a diet characterized in desert conditions by its dryness, poor nutritive value and low-absorbable components. In a context of climatic changes and living in an ecosystem facing one major hot spot of the interaction livestock-environment (i.e. desertification), the camel is showing his remarkable ability to not only survive but to valorize such a growing ecosystem (Steinfeld et al., 2003; Faye et al., 2012). The one-humped camel demonstrates anatomical, physiological and behavioral features adaptable for desert ecosystems that are not seen among other livestock (Yagil, 1985; Bengoumi and Faye, 2002; Jarrar 2006; Jarrar and Faye, 2012). The salivation function based on the specific structure of salivary glands is one element of the expected ability of the camel to be adapted to this transitional period toward a warmer and dryer world as we can experience with the growing presence of large camelids over the world (Faye, 2022). Notably, the expansion of dromedary camels in Africa following the recent droughts that have affected the margin of Sahara supports this evidence (Thornton et al., 2009). Moreover, the implementation of camel farming in desert areas of Southern Africa and North America (Faye, 2020) could be indirectly considered as a consequence of the ability of camels to occupy and valorize all arid lands of the world. Furthermore, in more favorable environments as in Western Europe, the newly implemented camels showed their ability to clear the ground by consuming nettles, brambles or rumex, plants that are neglected by other herbivores.

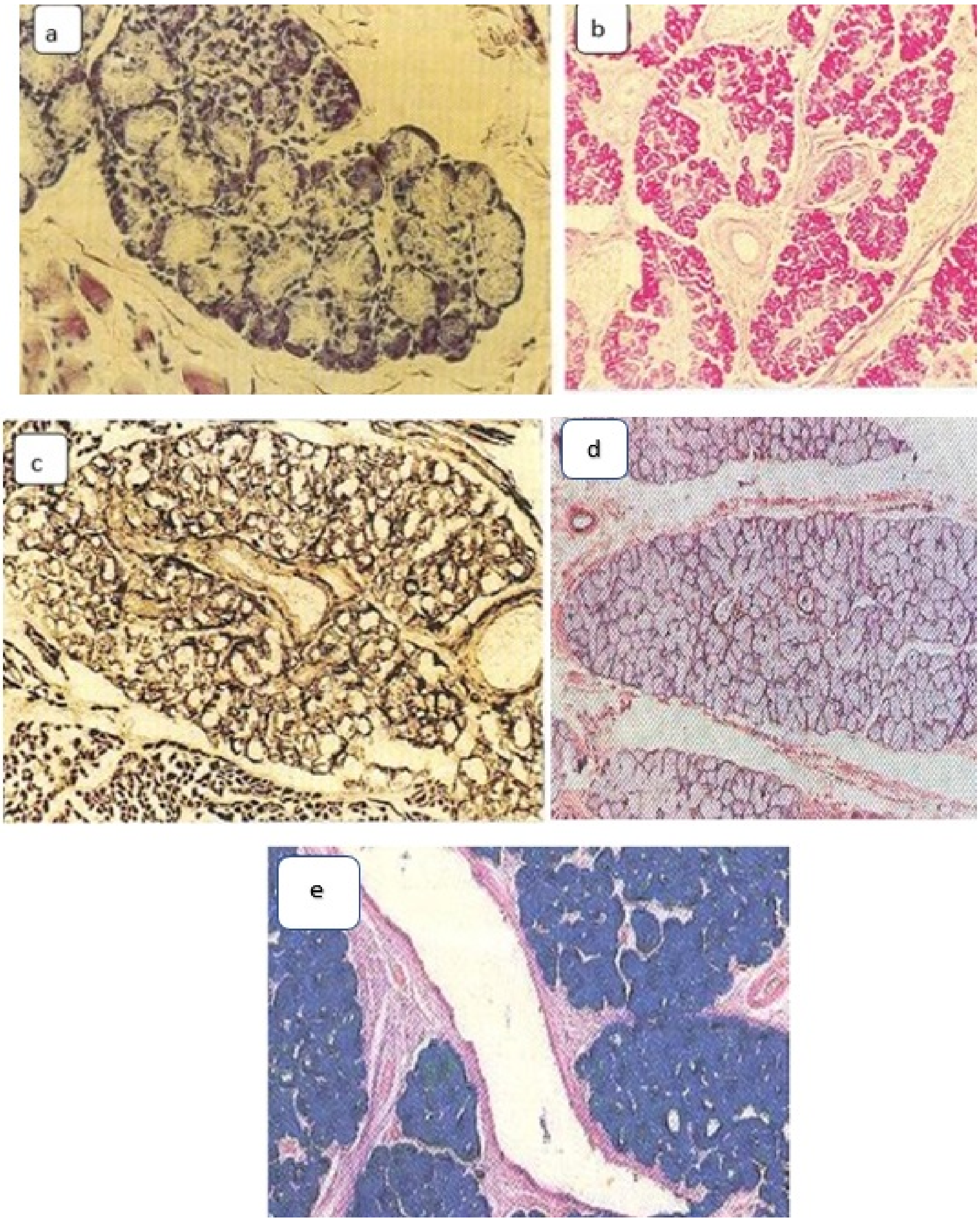

Figure 8(a-e). Micrograph sections in the labial salivary glands of the dromedary camel demonstrating: (a) Cluster of the labial gland acini, (b) Labial neutral mucosubstances, PAS stain, (c) Labial ATPase activity, (d) Palatine salivary glands stained with H&E stain, (e) Palatine salivary glands stained with PAS-alcian blue-(pH = 2.5).

The findings of the present work showed that camels have a complex salivary gland system consisting of three pairs of major salivary glands and several minor salivary glands. Adult camels can produce up to 150 liters of saliva per day, which is significantly more than other ruminants (cattle, ≥ 100 liters; sheep, ≥ 10 liters) (Al Razaiki et al., 2023). In addition, the findings indicate that camels' saliva contains a variety of proteins, electrolytes and enzymes. The sticky viscous saliva of camels helps them to retain mouth water, moist the food, prevent excessive water loss through evaporation and to reduce the amount of water needed for digestion. Moreover, the high concentration of electrolytes in camels' saliva helps to keep electrolytes homeostasis and prevent dehydration. Furthermore, the variable proteins and enzymes content of the camels' saliva have been found to offer antimicrobial and antifungal properties protecting the digestive system from harmful pathogens (Kay and Maloiy, 1989).

Collectively, the structure and the secretory contents of the camel salivary glands play an essential role in preventing dehydration and in breaking the tough fibrous plants they consume. Saliva helps to moisten the food, retain water in the mouth, moisten the nasal passage and enhance water reabsorption in the intestine. In addition, camels' saliva plays a vital role in their body's thermal regulation through panting where saliva evaporates to cool the inside of the mouth.

4. Conclusion

One may conclude from the findings that camels demonstrate an efficient salivation system contributing to better efficiency in the valorization of pastoral resources marked by the specific characteristics of the desert plants. The structure and the secretions of the salivary glands of the camel support an efficient salivation process and represent a strong challenge to the growing scarcity of water and the expansion of xerophytes as the main pastoral resources for camels. In that sense, salivary glands in camels are one of the elements of their panoply to resist harsh conditions and to mitigate the climate change impacts.

Acknowledgments

This project was supported by Researchers Supporting Project number (RSPD2024R900) King Saud University, Riyadh, Saudi Arabia. In addition, the authors greatly appreciate the help they got from Jerash University. The authors are thankful for the support they received from King Sau University and Jerash University.

Conflict of interest

The authors declare that they have no conflict of interests of any type.

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