Principal ocular glands in the desert rodent *Gerbillus tarabuli*: morpho-functional adaptive analysis

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**Abstract**

**Background**: Desert rodent, *Gerbillus tarabuli*, is a seed-eating animal and do not require drinking water. It depends upon metabolic water. Understanding the functional characteristics of ocular glands which produce a watery lacrimal fluid is of interest. In the present study, we described the macroscopic anatomy and microscopic structure of the paraarorbita glands in *tarabuli*'s gerbil.

**Results**: There are up to four distinct orbital glands: lacrimal (LG), Harderian (HG), Meibomian (MG), and conjunctival mucous glands. Each eye has three eyelids, the main upper and lower lids and a third lid hidden between them in the inner corner of the eye. The LG is bipartite, situated on the dorsolateral aspect of the eyeball. The HG is large and localized deep in the orbit. The MG is found in the dense connective tissue plate. Upon light microscopic examination, the LG is an acinar gland; its secretory cells have mucous and serous granular cytoplasm. The endpieces of HG consist of tubuloalveoli, with two cellular types: prismatic vacuolated cells and pyramidal basophilic cells. The MG acini are closely arranged one after another. Each acinus contains a basal layer of myoepithelial cells and a mass of rounded, vacuolated cells. The nictitating membrane is formed by a semilunar fold of conjunctiva, supported by a hyaline cartilage. Numerous goblet cell clusters are detected in the covering conjunctiva particularly in the bulbar conjunctiva. Mucin glycoproteins appear to be abundant in the precorneal tear film, probably acting against desiccation stress.

**Conclusions**: Based on the data from this study, it could be concluded that the orbital glands of gerbil are well-developed, similar to other mammals.

**Keywords**: Anatomy, Histology, *Gerbillus tarabuli*, Ocular glands

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**Background**

Rodents from arid and semiarid habitats are faced with a dry, dusty, and windy climate. They are adapted to arid conditions, where the spatial and temporal availability of free water is limited or scarce. *Gerbillus tarabuli* (tara buli’s gerbil) which belongs to the family Muridae (subfamily Gerbillinae) is a nocturnal species independent of any free water or even of moist food. It eats primarily dry, high carbohydrate seeds.

Tears secreted by the ocular glands have an important role in maintaining the integrity of the ocular surface and the preservation of visual acuity. The ocular glands as well as secretory components of the ocular surface, including the conjunctiva goblets cells, act as a functional unit (Stern et al., 2004). They produce the ocular tear film which is complex containing multiple layers (Argüeso & Gipson, 2001; Bron et al., 2004). Its major function is to provide an optically smooth surface over the cornea and retarding evaporation from the eye (Bron et al., 2004; King-Smith et al., 2008; Rantamaki et al., 2012).
In addition, it was reported that the tear layer maintains the health of the cells on the ocular surface by providing nourishment and removal of waste products and also protects them from environment. Studies of the orbital glands were earlier conducted in many species of animals (Abou-Elmagd, 1992; Djeridane, 1992; Gargiulo et al., 1999; Kleckowska-Nawrot & Dziegiel, 2007; Martin et al., 1988; Mohammadpour, 2009; Rehorek et al., 2010; Sakai, 1989). It was revealed that the anatomical structure of these glands is characterized by great variability (Chieffi et al., 1993; Dimitrov, 2011; Dimitrov & Genchev, 2011; Payne, 1994; Rehorek et al., 2005). In all mammalian species, the lacrimal gland (LG) is located in the outer canthus while the Harderian gland (HG) is situated in the inner canthus of the orbit. The LG as was reported by Gargiulo et al. (Gargiulo et al., 1999) and Aldana Marcos, Cintia Ferrari, Cervino, and Affanni (Aldana Marcos et al., 2002) is a mixed gland consisting of tubulo-acinar units. On the other hand, the HG in mammals is defined as a lipid-secreting tubulolacceolar ocular gland (Payne, 1994; Sakai, 1981) and similarly in desert rodent by Djeridane (Djeridane, 1992) and Saadi-Brenkia, Haniche, and Bendjelloul (Saadi-Brenkia et al., 2013). According to Leeson (1963), the MGs have been described by Duke-Elder and Wybar (Duke-Elder & Wybar, 1961) as consisting of long tubes embedded in the tarsal plate and opening onto the surface at the lid margin.

Methods

This study was carried out on ten adult gerbils (five males and five females), ranging in weight from 23 to 45 g each. They were trapped in the desert of Beni-Abbes, region distant of 1250 km from the capital Algiers. They were housed in the animal facility of the Research Unit of dry area (URZA). The animals were cared for in accordance with the criteria outlined in the “Guide for the Care and Use of Experimental Animals” prepared by the National Academy of Sciences and published by the National Institute of Health. Gerbils were anesthetized by intraperitoneal (i.p.) injection with 10 mg/kg of ketamine hydrochloride then sacrificed by decapitation. The eyes with surrounding eyelids were dissected and fixed in 10% buffered formalin overnight. The samples were rinsed in water, dehydrated in ethanol, and embedded in paraffin. Five- to 7-μm-thick serial longitudinal sections from each sample were cut with a microtome (Leica RM2125RT). The sections were deparaffinized and stained with hematoxylin-eosin for morphological description and Masson trichrome and Van Gieson for connective tissue and collagen fiber identification. The Periodic acid-Schiff procedure was used to stain for mucosubstances contained in goblet cells. They were evaluated using a Zeiss light microscope and images obtained using a Canon camera. Histological auto fluorescence studies were performed in unstained paraffin sections using a fluorescence microscope (450–490-nm filter) (Ortiz et al., 2001).

Results

We did not observe gender differences anatomically or histologically in samples.

Macroscopic analysis

The lids are composed of different layers which are superimposed from the conjunctiva to the external integument. MGs (tarsal glands) are located on the inner aspect of the main eyelids, and their orifices are visible along the free lid margin (Fig. 1a, b).

*Gerbillus tarabuli* has a transparent or translucent third eyelid or nictitating membrane, underneath the other two eyelids. The HG is a deep structure, connecting to the deep aspect of the nictitans membrane, filling the medial and posterior aspect of the orbit (Fig. 1c).

The gerbil contains a bipartite dorsal lacrimal gland. It appears as a pale structure, which was macroscopically difficult to distinguish from the surrounding adipose tissue (Fig. 1d).

Microscopic analysis

Conjunctiva and MGs

The conjunctiva is a thin continuous mucous membrane lining the inner surface of the eyelids and much of the anterior surface of the eye. Three distinct areas of the conjunctiva are recognized: the bulbar conjunctiva, the palpebral conjunctiva, and the conjunctiva lining the fornix. The bulbar surface possesses a stratified epithelium and a lamina propria formed by dense connective tissue (Fig. 2A). The palpebral surface is composed of a columnar prismatic epithelium rich in clusters of goblet cells (Fig. 2B, B’). The eyelid skin is supported by connective tissue that constitutes the tarsal plate. It contains tarsal glands or MGs, orbicularis muscle, and Muller muscle. MGs are sebaceous glands embedded within the tarse plate of the upper and lower lids. The glandular units consist of acini arranged tightly in spherical shape; the acinar cells are completely occupied by lipid droplets (Fig. 2B, C).
Third eyelid
Near the corner of the eye, the conjunctiva forms a large fold and constitutes then a third eyelid or nictitating membrane. The central axis of the third eyelid contains a band of hyaline cartilaginous tissue. On both sides of this cartilaginous plate, there is a cellular conjunctive tissue (Fig. 2D).

Harderian gland
The gerbil HG is surrounded by a thin connective tissue capsule which sends septa dividing the gland into lobules of varying size. The endpieces of the gland are tubuloalveolar with a wide central lumen, lined by a pseudostratified columnar epithelium (Fig. 2D, D'). Two glandular cell types can be distinguished: Prismatic cells account for the majority of cells, which are characterized by a highly vacuolated cytoplasm. Pyramidal cells are less common; they have a basophilic cytoplasm with numerous granules PAS+. There are no recognizable excretory ducts in the glandular parenchyma. Often, the glandular lumen contains pigment accretions. Fluorescence microscopy has confirmed the presence of porphyrins (Fig. 2E, F).

Lacrimal gland
The LG is surrounded by fibrous tissue. It is a compact structure, organized in acinar units, which are separated into lobules by a thin connective tissue (Fig. 3a). The interstitium is rich in blood vessels, nerves, and excretory ducts. The lumen of each acinus is lined by columnar epithelial cells. Two types of secretory cells are observed, according to their morphologic appearance. Serous cells have a basophilic cytoplasm containing rounded nuclei and mucus-producing cells with flattened nuclei basally located. Thus, the gland is seromucous, but the mucous acini make up the largest part (Fig. 3b).

Discussion
Desert-dwelling rodents display physiological features that favor body water conservation, such as efficient kidney function, low fecal water content, and comparatively low evaporative water loss (Degen, 1997). Thus, for the optical integrity, they must keep the eye wet and clean in this dry environment.

Conjunctiva and Meibomian glands
The conjunctival epithelium forms a physical protective barrier through goblet cell secretions. It contributes to the formation and maintenance of a “tear film,” which produces protective scaffolding over the ocular surface (Chen Wensheng et al., 2003). In gerbils, goblet cells in the conjunctiva are numerous and gathered in clusters in the bulbar side, as was reported in rat by Setzer,
Fig. 2  (A) Light micrograph of gerbil bulbar conjunctiva: stratified epithelium (E) with clusters of goblet cells (arrows) and lamina propria (asterisk). H/E stain. (B) Meibomian glands embedded within the tarsal plate, central duct (arrow), palpebral conjunctiva (double arrow), and Muller muscle (asterisk). H/E stain; (B’) inset box, goblet cells (double arrow) interspersed amongst epithelial columnar prismatic cells of palpebral surface. Masson’s trichrome stain. (C) A portion of Meibomian glands (MG) displaying the acinar cells entirely full by lipid droplets. H/E stain. (D) A micrograph showing the Harderian gland (HG) and third eyelid (arrow) closely fastened. Masson’s trichrome stain. (D’) inset box, the presence of central hyalin cartilaginous tissue (arrow). Van Gieson stain. (E, F) Sections of HG, two secretory cells form the tubuloalveoli. (E) Pyramidal cells (arrowhead), prismatic cells (blue arrow), lumen (L). Van Gieson stain. (F) Section under a fluorescence microscope showing porphyrin (P) and pyramidal cells (arrowhead).

Fig. 3  a The gerbil lacrimal gland covered by a capsule (Cp) composed mainly of dense collagenous connective. The connective tissue septa (S) divide the gland into lobes and lobules (arrow). H/E stain. b Higher magnification of acini endpieces with central canal (C). H/E stain.
Nichols, and Dawson (Setzer et al., 1987) and in Mongolian gerbil by Micali et al. (Micali et al., 1998). The MGs lie inserted in the conjunctival side of the tarsal plate, and histologically, they confirmed the description of the tarsal glands set by Duke-Elder and Wybar (Duke-Elder & Wybar, 1961) based on light microscopy. As reported by Tiffany (Tiffany, 1987), the eyelid margin is the source of physiologically important lipid secretion, meibum. These lipids must be an effective barrier to tear evaporation in this species.

**Third eyelid**

The gerbil’s third eyelid or nictitating membrane appears well-developed. In agreement with Sisson and Grossman (Sisson & Grossman, 1974), the third eyelid is a semilunar fold of the conjunctiva in the medial angle of the eye. It is supported by a piece of cartilage. Our study shows a hyaline cartilage and many goblet cells at the bulbar surface of the membrane. The same findings were described in albino rat, cattle, and small ruminants (Bisaria & Bisaria, 1978; Dellmann & Eurell, 1998; Schlegel et al., 2001). According to Saito, Watanabe, and Kotani (Saito et al., 2004) and Umeda et al. (Umeda et al., 2010), beside its function as a mechanical protection barrier for ocular surface, the third eyelid is important for the distribution of tears and contributes to their production through mucin cells.

**Harderian gland**

The HG is the largest among ocular glands in gerbil. In all rodents studied, the HG is a well-developed gland situated behind the ocular globe (Brownscheidle & Niuwenhuis, 1978; Johnston et al., 1985; Lopez et al., 1993; Watanabe, 1980). The glandular parenchyma is organized in lobules and the secretory units are tubuloalveolar. The epithelium is pseudostratified with two cell types, columnar acidophilic cells, analogous to single cells in other desert rodents (Djeridane, 1996; Johnston et al., 1983; Sabry et al., 2000), and pyramidal basophilic cells remarkable by their aspect and their situation in the secretory epithelium. They have many PAS+ granules indicating glycoprotein storage (Saadi-Brenkia et al., 2013). All their histological characteristics are comparable to those observed in cell type III in desert rodents by Djeridane (Djeridane, 1996). But glycoprotein granules encountered in the *Gerbillus tarabuli* gland have not previously been detected in these species. They were described in HG cells of dolphin (Bodyak & Stepanova, 1994), in tree shrew (Pradidarcheep et al., 2003), and in armadillo of South America (Aldana Marcos & Affanni, 2005). The presence of porphyrins in the glandular lumina as solid accretions was previously indicated by Chieffi et al. (Chieffi et al., 1996) in other species of rodents.

**Lacrimal gland**

The principal lacrimal gland of desert rodents has not been previously investigated. The gerbil possesses a bipartite dorsal lacrimal gland; it appears as a pale structure. These findings agree with those of Sinha and Calhoun (Sinha & Calhoun, 1966) in ruminants and Veiga Neto, Tamaga, Zorzetto, and Dalpai (Veiga Neto et al., 1992) in primates. Our histological analysis shows that the lacrimal gland is organized in lobules separated by septa of connective tissue sent from the capsule that surrounds the gland. Serous and mucous acini are present. The gland is predominantly mucous. These mixed glands have been described in many mammals (Allen et al., 1972; Gargiulo et al., 1999; Kühnel & Scheele, 1979). In contrast, rat lacrimal glands are defined as being purely serous (Lorber, 1989).

**Conclusion**

To conclude, there seems to be nothing unusual in the morphological aspect of gerbil’s orbital glands; thus, the current work has provided normative data on the main ocular glands of this desert species, which are represented by Meibomian glands and Harderian gland. They constitute the principal source of the lipid layer; that must be an effective barrier to avoid water evaporation from dry air of arid environment. The aqueous layer is formed by the lacrimal glands. Mucin glycoproteins seem to be a major functional constituent of the precorneal tear film in gerbil. They are produced by conjunctival goblet cells, Harderian glands, and lacrimal glands. It could be suggested that more research should be performed for future comparative studies with rat and human. This is particularly important as there is growing evidence of the link between lowered levels of mucins and pathologic features of dry eyes.

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**Authors’ contributions**

OS-B conceived and designed the study, NH prepared the figures, and SL revised the manuscript. All authors have participated in the elaboration of this work and have approved for this submission.

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**Availability of data and materials**

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

**Ethics approval and consent to participate**

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