



Morphological properties and musculature of the eyelids of the Egyptian agama, *Trapelus mutabilis*

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Abstract

This study provides a comprehensive anatomical and histological description of the eyelids of the Egyptian agama, *Trapelus mutabilis*. Both the movable upper and lower eyelids, as well as the thin and reduced third eyelid, represent distinctive features of the Egyptian agama's eye. The upper eyelid appears shorter than the lower one; furthermore, the cranial skin above the upper eyelid extends laterally to form a superior projection. Micro-ornamentations and sensory organs are located at the tips of the eyelid scales, which are arranged in an imbricated pattern. The histological structure of the upper eyelid closely resembles that of the lower eyelid. The external surface of both eyelids consists of keratinized stratified squamous epithelium composed of two to four cell layers, while the internal surface is lined with stratified cuboidal epithelium. Melanophores and iridophores constitute the principal pigment cells in both eyelids. The third eyelid is a reduced fold with a concave surface that connects posteriorly with the lacrimal gland at the medial canthus of the eye. Its external surface is covered by stratified squamous epithelium, whereas the internal surface is lined with one or two layers of cuboidal cells with rounded nuclei that are continuous with the conjunctival epithelium. Video recordings of the species under laboratory conditions demonstrated synchronization between eyelid and eyeball movements. Based on these observations, the present authors propose that this species possesses multiple structural and functional adaptations that enhance ocular protection. Protection against ultraviolet radiation is reinforced by two types of pigment cells, while the hard eyelid scales, superior extensions of wide scales, and the presence of sensory organs at the scale tips collectively enhance the protective reflex against external stimuli. These features represent morphological adaptations to the harsh environmental conditions in which this species lives.

Keywords *Trapelus mutabilis* · Eyelids · Eye morphology · Sensory organs · Histology · Ocular adaptation · Video recordings

Introduction

In many vertebrates, the eyes represent the most important sensory organs. The visual capacities of an animal are adaptive responses to its specific lifestyle and habitat, both of which are closely linked to maintaining optimal visual function. Anatomically, the eyes are supported by protective and accessory structures collectively known as the adnexa, which include the eyelids, orbital glands, and extraocular muscles (Guerra-Fuentes et al. 2014). These adnexal structures exhibit varying degrees of modification among different reptilian taxa, reflecting the diverse ecological and behavioral demands of these taxa.

Species-specific variations in eyelid morphology and mobility often correspond to ecological adaptations,

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particularly in reptiles with aquatic or fossorial lifestyles. Both upper and lower eyelids are present in most lizards, as well as in turtles, tuataras, and crocodylians. However, in some species, the eyelids have undergone modification resulting in partial fusion, as observed in chameleons, where a circular aperture remains around the corneal region, or in the development of transparent eyelids, as seen in many geckos and snakes (Schwab 2012). In snakes, a transparent scale derived from the skin remains permanently fused over the cornea, forming a spectacle. Similarly, some skinks, lacertid lizards, and iguanine lizards possess a transparent lower eyelid composed of clear scales (Lawton 2006; Schwab 2012).

Various forms of eye mobility have been documented among reptiles. These movements are highly specialized and, in certain taxa such as chameleons, occur independently in each eye, a feature that has attracted considerable scientific interest. Pettigrew et al. (1999) examined the convergence of visual optics, ocular motility, and behavioral specialization in chameleons (Reptilia) and sand lances (Teleostei). El Hassni et al. (2000) identified the localization of the motor neurons controlling extraocular muscles in *Chamaeleo chamaeleon*, while Ott (2001) demonstrated that chameleons exhibit independent eye movements that become synchronized during saccadic prey tracking.

Previous studies have also explored the frequency-domain characteristics of reflexive and conditioned eyelid responses in various vertebrates, for instance, in cats (Domingo et al. 1997) and rabbits (Gruart et al. 2000), suggesting that a comprehensive analysis of eyelid reflexes and conditioned responses can provide insight into the functional organization of neural circuits underlying ocular motion. Xu et al. (2023) further hypothesized that a chameleon-inspired, active-vision perception strategy based on shifty behavioral patterns could enable mobile robots to achieve rapid visual search and target tracking. Although several studies have described eye mobility across various vertebrate groups, few have examined the morphological characteristics of eyelids and their impact on ocular movement. More recently, anatomical investigations in wild bird species (Al-Nefei et al. 2022; Mahmoud et al. 2022) have examined the relationship between eyelid structural features and kinetic performance.

The demanding desert environment inhabited by the Egyptian agama has drawn the attention of the present authors, particularly regarding how these lizards maintain effective visual performance under harsh ecological conditions. The Egyptian agama (*Trapelus mutabilis*) is a small diurnal lizard distributed in North Sinai, Egypt (Baha El Din 2006; Wagner et al. 2011). Understanding the detailed structure of the eyelids provides valuable insight into the visual adaptations of this species. In the present study, the

ocular eyelids and associated musculature of *T. mutabilis* were examined using scanning electron microscopy (SEM), histological analysis, and anatomical dissection. Additionally, the dynamic movements of the eyelids and eyeballs were recorded under laboratory conditions to assess potential synchronization between them, similar to that observed in chameleons.

Materials and methods

Specimen collection

During April and May, ten adult Egyptian agama lizards (*Trapelus mutabilis*) were collected from North Sinai, Egypt. All procedures adhered to the guidelines of the Research Ethics Committee (Approval number: ASWU/05/SC/ZO/23–03/01). Live specimens were transported to the Comparative Anatomy of Vertebrates Laboratory for subsequent dissection and analysis.

Recording of eye movements

Specimens were evenly allocated into two cages, each measuring 50 × 100 × 50 cm (width × length × height), and equipped with feeding and drinking stations. Cameras were installed at each corner of the cages to record ocular activity. Lizards were allowed a two-day acclimatization period before eye-movement recording. Animals were fed small pieces of commercially available cow liver. Video recordings were converted into sequential still images using software available at <https://www.dvdvideosoft.com/products/dvd-free-video-to-jpg-convert.htm>.

Five specimens were anesthetized via intramuscular injection of a combination of xylazine (5 mg/kg), acepromazine (0.3 mg/kg), and ketamine (35–50 mg/kg) for anatomical, scanning electron microscopy (SEM), and histological investigations. The remaining specimens were returned to their natural habitat to preserve ecological balance.

Anatomical and Scanning Electron Microscopy Investigations.

For anatomical analysis, the heads were fixed in 10% formalin for two weeks and subsequently stored in 2% phenoxyethanol. Images were captured using an Olympus SZ61 stereomicroscope connected to a TouPCam XCAM full HD camera. Anatomical terminology followed the *Nomina Anatomica Veterinaria* (2017) for consistent description of the skull and orbital structures.

For SEM, small ocular specimens were excised and fixed in 5% glutaraldehyde in cacodylate buffer for 48 h at 4 °C. Specimens were washed thrice in 0.1% cacodylate buffer, post-fixed in 1% osmium tetroxide for 2 h at 37 °C, and



Fig. 1 Photomicrograph of the eye of the Egyptian agama, *Trapelus mutabilis*, showing the upper eyelid (Ue) with superior extension (star) and lower eyelid (Le)

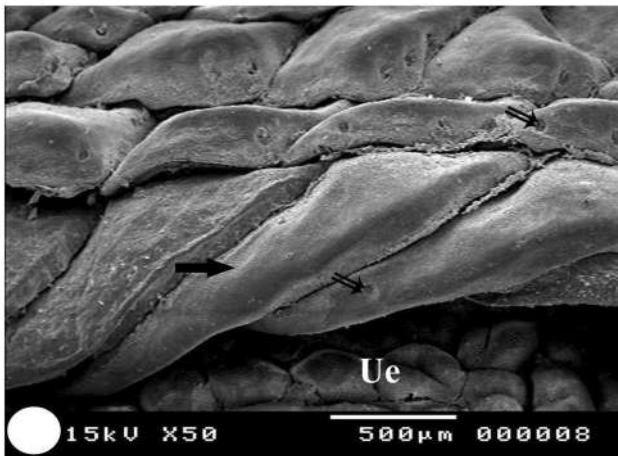


Fig. 2 Scanning electron micrograph of the superior extension of the Egyptian agama, *Trapelus mutabilis*, showing the plate-like scales (arrow) with skin sense organs (double arrow)

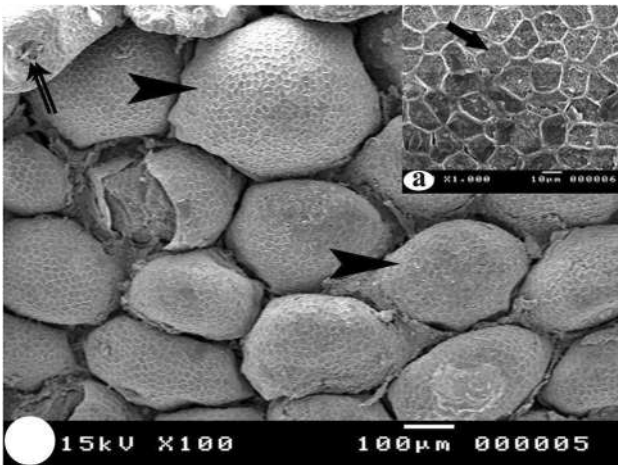


Fig. 3 Scanning electron micrograph of the upper eyelid of the Egyptian agama, *Trapelus mutabilis*, showing the polygonal scales on the external surface of the upper eyelid (arrowhead) and the sense organ on the tip of the upper eyelid scale (double arrow). (a) High magnification of the scale surface showing the micro-ornamentation resembling a honeycomb (arrow)

washed again three times in the same buffer. Dehydration was performed through a graded ethanol series, followed by infiltration in amyl acetate for two days. Samples were then dried using critical point drying with liquid CO₂, sputter-coated with gold, and examined using a JEOL JSM-5400IV SEM at 15 kV.

Histological investigation

For light microscopy, specimens were bisected longitudinally, and the lower jaw was removed. Samples underwent decalcification in EDTA for two weeks, dehydration through a graded ethanol series, clarification in methyl benzoate for three days, and paraffin embedding. Serial sections of 7 µm thickness were obtained and fixed in 10% neutral formalin for a period of three days. Sections were stained with hematoxylin and eosin and Masson's trichrome (Drury & Wallington 1980), and then imaged using an Olympus DP74 camera mounted on an Olympus BX43 microscope.

For semithin sectioning, ocular samples (~1 mm³) were fixed in 5% glutaraldehyde in cacodylate buffer for 2 h, rinsed repeatedly in the same buffer (pH 7.2) for 1 h, and post-fixed in 1% osmium tetroxide at 4 °C for 2 h. Following multiple washes, specimens were dehydrated through a graded alcohol series, embedded in epoxy resin, and sectioned at a thickness of 1 µm. Semithin sections were stained with toluidine blue and analyzed under light microscopy.

Results

Morphological investigation of the eyelids

Trapelus mutabilis, an Egyptian agama, possesses three eyelids: the movable upper and lower eyelids and a thin, reduced third eyelid (NM). Compared to the lower eyelid, the upper eyelid is shorter (Fig. 1). The superior extension of the head's skin, which extends laterally above the upper eyelid, is characterized by large, plate-like scales containing skin sense organs at their terminal points (Fig. 2). Highly variable polygonal scales are distributed on the external surface of both eyelids, with approximately ten scales at the edges of the upper and lower eyelids, as observed by scanning electron microscopy (Fig. 3). The orientation of the scales on the upper eyelid is similar to that on the lower eyelid; these scales are arranged in an imbricate order, and their surfaces feature micro-ornamentation and Oberhäutchen with honeycomb-like structures (Fig. 3a). These honeycomb-like structures consist of numerous tiny honeycombs. Additionally, the tips of these scales possess skin sense organs (Fig. 4).

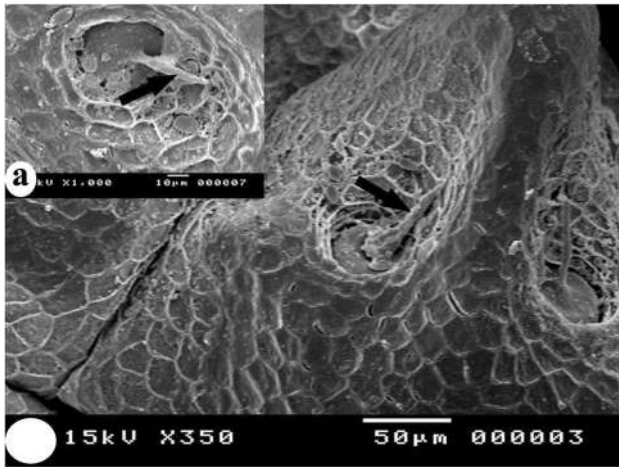


Fig. 4 Scanning electron micrograph of the edge of the upper eyelid of the Egyptian agama, *Trapelus mutabilis*, showing the sense organs on the tips of the scales (arrow). (a) High magnification of the sense organ (arrow)

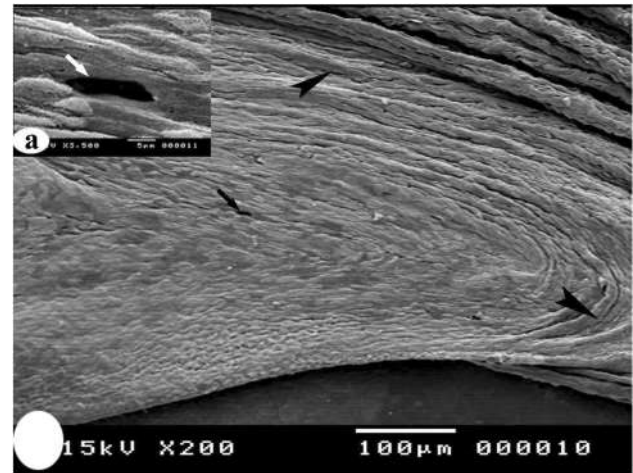


Fig. 6 Scanning electron micrograph of the external surface of the third eyelid of the Egyptian agama, *Trapelus mutabilis*, showing a few folds (arrowhead) and many orifices of the lacrimal glands (arrow). (a) High magnification of the orifices of the lacrimal glands (arrow)

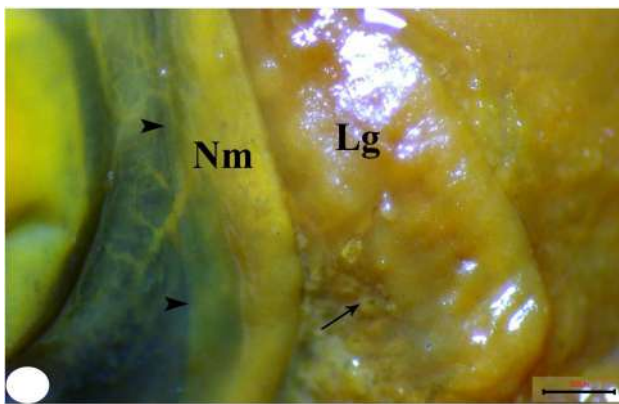


Fig. 5 Photomicrograph of the eye of the Egyptian agama, *Trapelus mutabilis*, showing the reduced third eyelid (Nm) with a delicate free end (arrowhead), and the position of the lacrimal gland (Lg) and its pores at the base of the third eyelid (arrow)

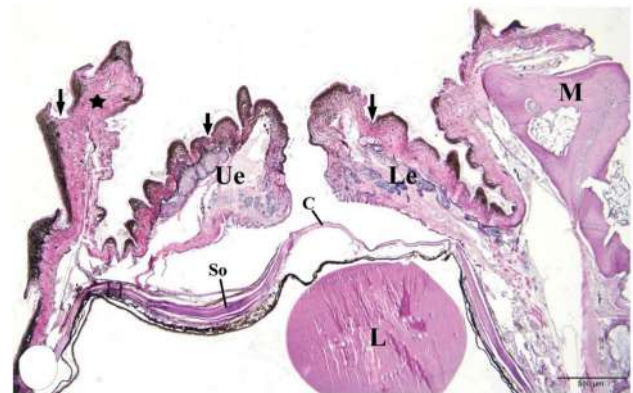


Fig. 7 Photomicrograph of a complete cross-section of the eye of the Egyptian agama, *Trapelus mutabilis*, showing the upper eyelid (Ue), lower eyelid (Le), superior extension (star) with scales linked by a hinge area (arrow), scleral ossicle (So), cornea (C), lens (L), and maxillary bone (M)

The anatomical investigation of the NM of *T. mutabilis* revealed it to be a concave and reduced membrane. It appears as a small projection connected to the lacrimal gland at the medial canthus of the eye (Fig. 5). SEM investigation of the NM revealed that its surface has few folds with a delicate free edge, as well as the orifices of the lacrimal gland in the medial canthus (Fig. 6).

Histological investigation of the eyelids

Histological examination of the upper and lower eyelids of *T. mutabilis* demonstrated that the histological architecture of the external and internal surfaces of both eyelids is analogous (Fig. 7). The histological composition of the upper and lower eyelids, along with the superior extension of *T. mutabilis*, revealed that both the superior extension and the

external surface of the upper eyelid consist of keratinized stratified squamous epithelium featuring 2–4 layers of nucleated cells, encased by a rigid keratin layer that forms horny epidermal scales with sense organs at their tips (Fig. 8). The horny scales are linked by wrinkled hinge areas formed of transitional epithelium (Figs. 9 and 12). The internal surface of the upper eyelid consists of stratified cuboidal epithelium with 2–5 layers of nucleated cells containing oval and rounded nuclei. The superficial cells exhibit apical cytoplasmic protrusions (Figs. 10, 11).

The dermal layer (stroma) located between the external and internal surfaces is composed of fibrous connective tissue filled with densely packed collagen fibers of varying orientations, blood vessels, muscle fibers, and two types of pigment cells: iridophores and melanophores. Iridophores,

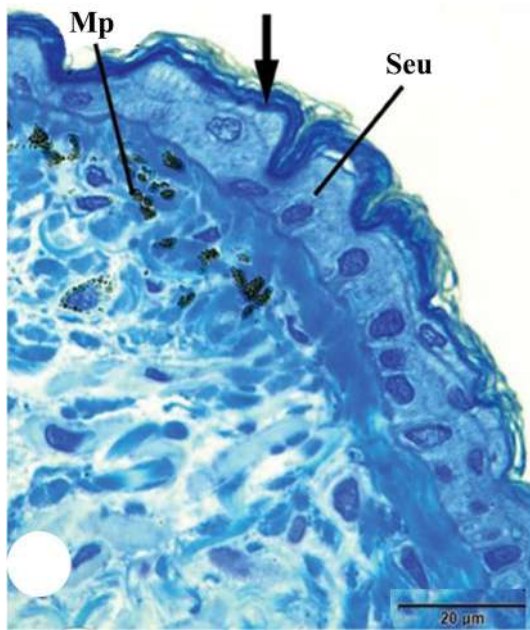


Fig. 8 Photomicrograph of a semithin section of the upper eyelid of the Egyptian agama, *Trapelus mutabilis*, showing the epithelium of the external surface of the upper eyelid (Seu), composed of 2–4 nucleated cell layers covered by a thick keratin layer (arrow), and the pigmented cells beneath the epithelium (Mp)

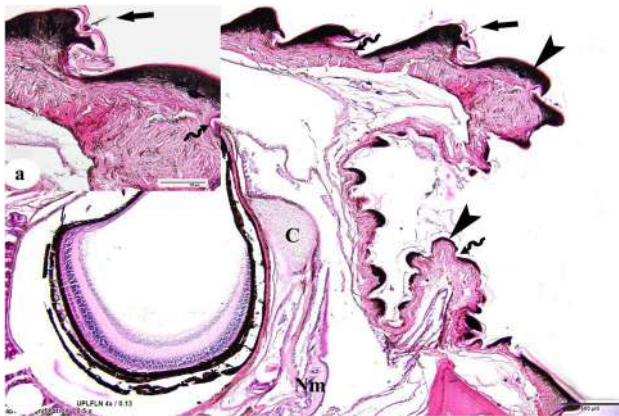


Fig. 9 Photomicrograph of a complete cross-section of the eye of the Egyptian agama, *Trapelus mutabilis*, showing the horny scales of the upper and lower eyelids (arrowhead) with the sense organ on their tips (arrow) linked via a wrinkly hinge area (zigzag arrow), the reduced third eyelid (Nm), and its conjunctival cartilage (C). **a** High magnification of the horny scales (arrowhead) with the sense organ on their tips (arrow)

which contain brownish-yellow granules, are located beneath the basement membrane of the keratinized stratified squamous epithelium. Melanophores appear as black cells with dendrite-like extensions scattered within the stroma (Figs. 12, 13).

The histological examination of the third eyelid (NM) of *T. mutabilis* demonstrated that it has two surfaces: an external (upper) and an internal (basal) surface (Figs. 14,

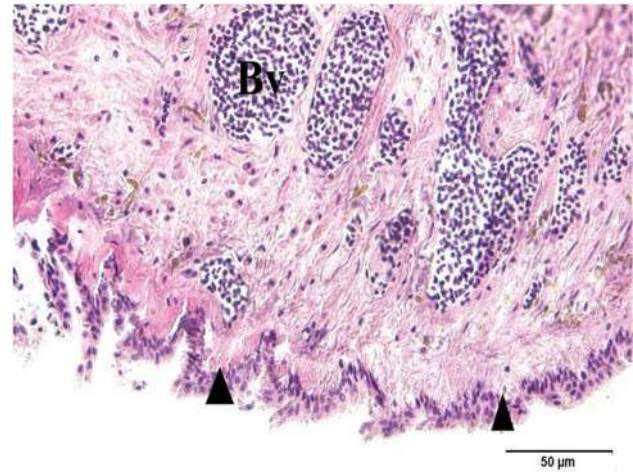


Fig. 10 Photomicrograph of a transverse section of the upper eyelid of the Egyptian agama, *Trapelus mutabilis*, showing its internal surface consisting of stratified cuboidal epithelium (arrowhead), and the stroma filled with large blood vessels (Bv)

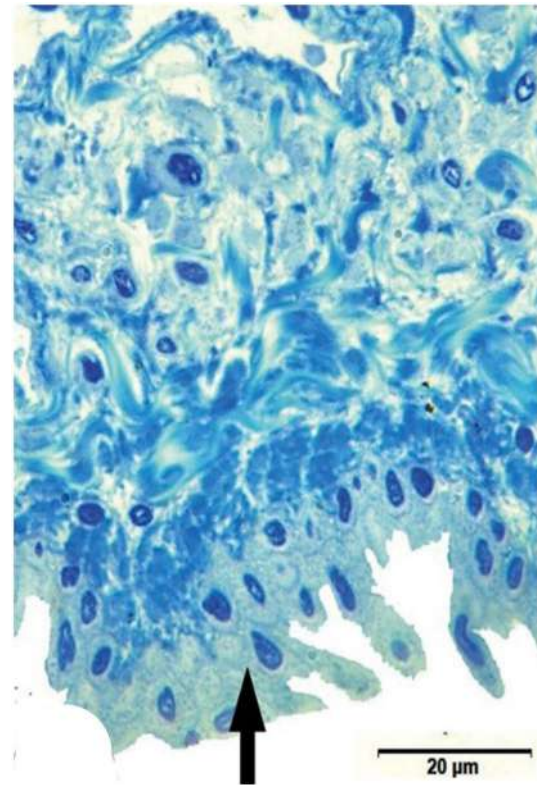


Fig. 11 Photomicrograph of a semithin section of the internal surface of the upper eyelid of the Egyptian agama, *Trapelus mutabilis*, showing the stratified cuboidal epithelium with apical cytoplasmic small protrusions (arrow)

15). The NM is formed by stratified squamous epithelium on the external surface, and one or two nucleated cell layers with rounded nuclei, continuous with the conjunctival epithelium, constitute the internal surface. The epithelium of the internal surface of the third eyelid contains goblet

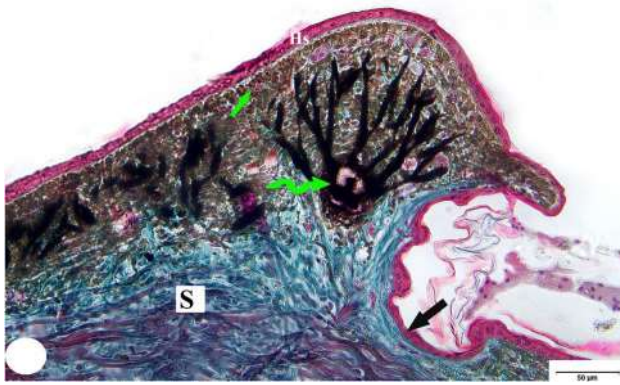


Fig. 12 Photomicrograph of a transverse section of the upper eyelid of the Egyptian agama, *Trapelus mutabilis*, showing the horny scales (Hs) with wrinkly hinge area (arrow). The stroma (S) is filled with densely packed collagen fibers, melanophores with dendrite-like extensions (zigzag arrow), and iridophores (arrow) beneath the basement membrane of the external epithelium of the eyelid

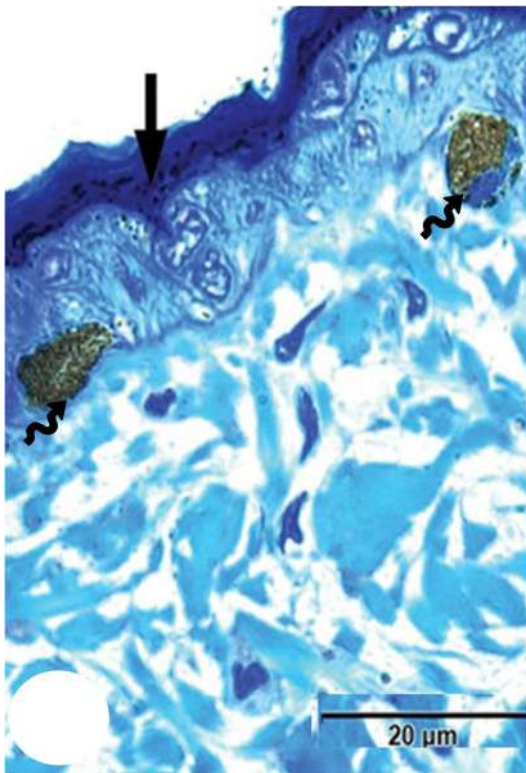


Fig. 13 Photomicrograph of a semithin section of the lower eyelid of the Egyptian agama, *Trapelus mutabilis*, showing the shape of iridophores (zigzag arrow) beneath the basement membrane of the external epithelium of the eyelid, which is covered by a thick keratin layer (arrow)

cells (Fig. 14). In addition, the connective tissue stroma of the NM is primarily composed of collagen fibers running transversely and containing blood vessels (Fig. 14). The conjunctival epithelium consists of one to three nucleated

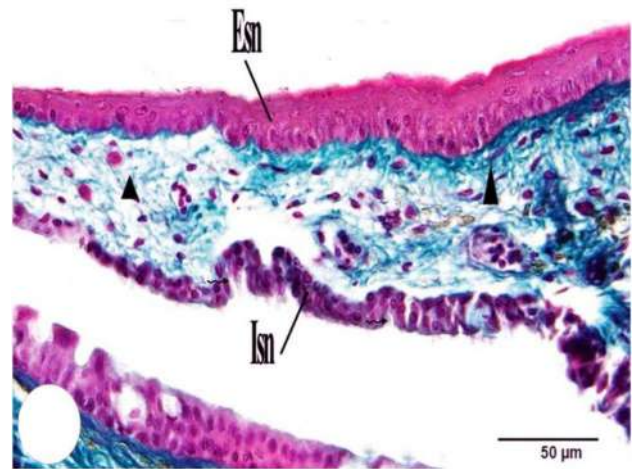


Fig. 14 Photomicrograph of a transverse section of the third eyelid of the Egyptian agama, *Trapelus mutabilis*, showing the stratified squamous epithelium of the external surface (Esn), which is continuous with one or two nucleated cell layers forming the internal surface (Isn) with goblet cells (zigzag arrow), and collagen fibers within its stroma (arrowhead)

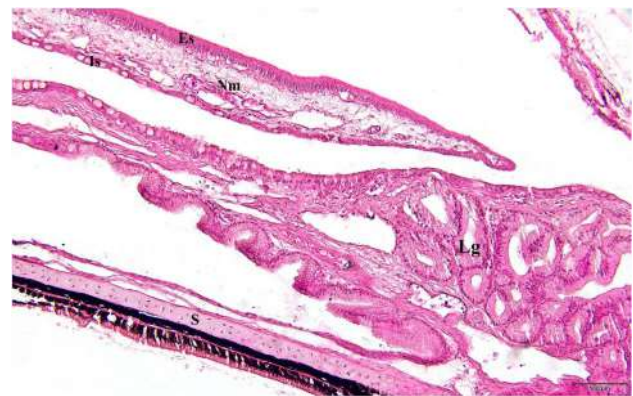


Fig. 15 Photomicrograph of a transverse section of the third eyelid of the Egyptian agama, *Trapelus mutabilis*, showing the location of the third eyelid (Nm) related to the lacrimal gland (Lg), its external surface (Es), and internal surface (Is)

layers, and the connective tissue is composed of collagen fibers, blood vessels, and hyaline cartilage (Fig. 16).

Anatomical investigation of the ocular muscles

The ocular muscles include extraocular and accessory ocular muscles (Figs. 17, 18).

A. Extraocular muscles

Dorsalis rectus muscle (DRM): The DRM is a sheet-like muscle composed of parallel fibers that run dorsal to the dorsalis oblique muscle (DOM) and ventral to the medialis rectus muscle (MRM). It originates fleshy from the orbitosphenoid bone, spreading out to form two aponeurotic

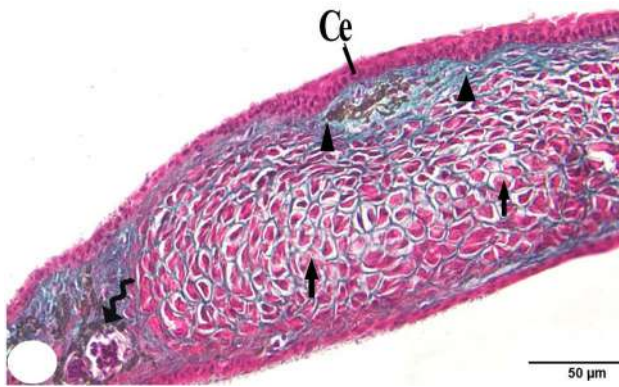


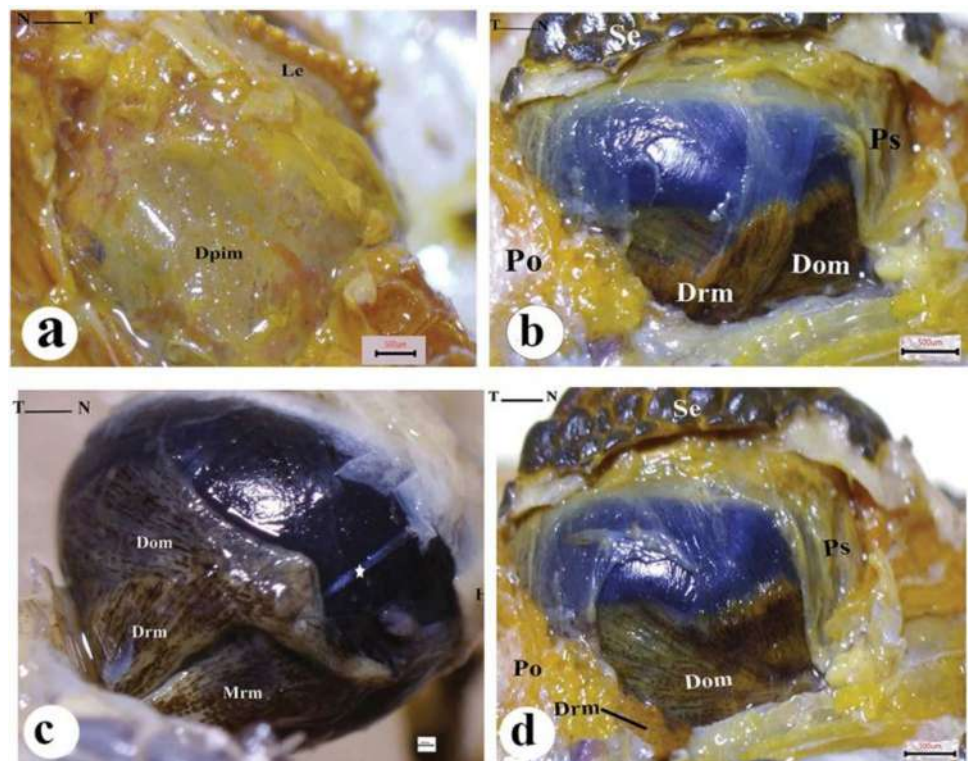
Fig. 16 Photomicrograph of a transverse section of the eye of the Egyptian agama, *Trapelus mutabilis*, showing the conjunctival epithelium (Ce) with its cartilaginous support (arrow), scattered collagen fibers (arrowhead), and blood vessels (zigzag arrow) in its stroma

branches that insert on the scleral cartilage and the superior extension of the upper eyelid. This aponeurosis passes over the dorsal surface of the aponeurosis of the DOM. The origin of the DRM lies dorsal to the optic nerve, posterodorsal to the origin of the ventralis rectus muscle (VRM), and anterodorsal to the origin of the lateralis rectus muscle (LRM). The insertion site of the DRM is dorsal to the insertion site of the DOM.

Origin: Fleшы, from the orbitosphenoid bone.

Insertion: Aponeurotic on the scleral cartilage and superior extension of the upper eyelid.

Fig. 17 Photomacrograph of the eye dissection of the Egyptian agama, *Trapelus mutabilis*, after removal of the skin of the upper eyelid, showing the dorsalis rectus muscle (DRM), dorsalis oblique muscle (DOM), and depressor palpebrae inferioris muscle (DPIM)



Function: Elevation of the eyeball, elevation of the upper eyelid to help open the palpebral fissure, and extorsion.

Dorsalis oblique muscle (DOM): The DOM is a thin, wing-shaped muscle composed of oblique fibers that run dorsal to the MRM and ventral to the DRM. It originates fleshy from the parabasisphenoid bone, then fans out obliquely to form two aponeurotic branches that insert on the scleral cartilage and the superior extension of the upper eyelid. The origin of the DOM is located posterodorsally to the origin of the ventralis oblique muscle (VOM). The insertion site of the DOM is ventral to the insertion site of the DRM.

Origin: Fleшы, from the parabasisphenoid bone.

Insertion: Aponeurotic on the scleral cartilage and superior extension of the upper eyelid.

Function: Elevation of the eyeball, elevation of the upper eyelid, and intorsion.

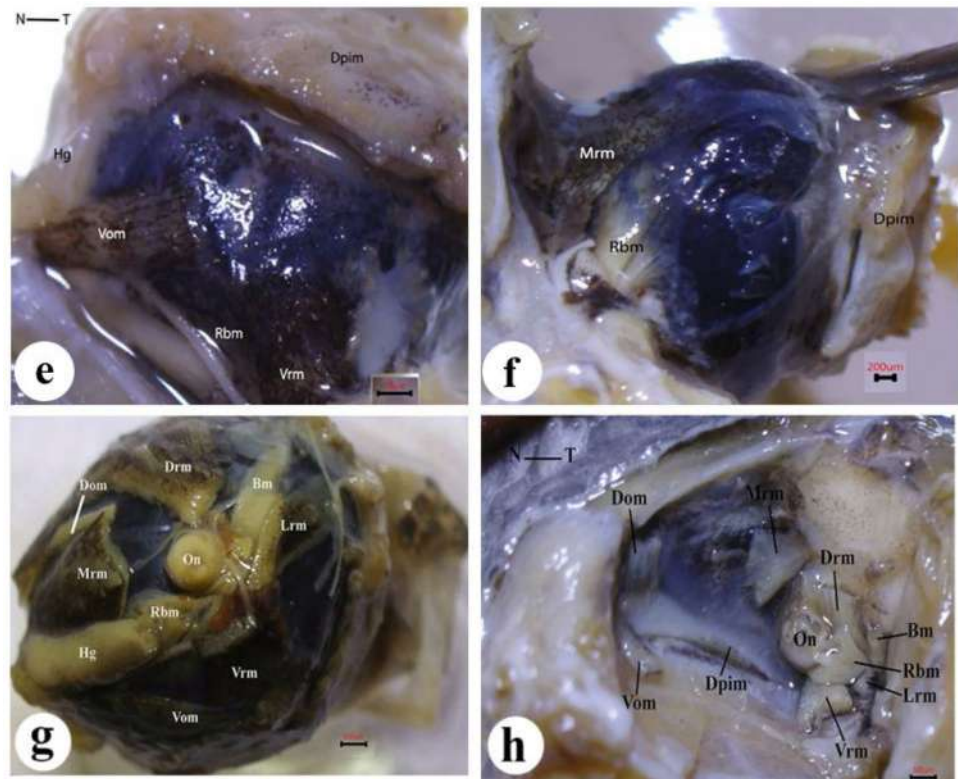
Medialis rectus muscle (MRM): The MRM is a sheet-like muscle composed of thin, parallel fibers located at the nasal pole of the eyeball, entirely covered by the DOM and the Harderian gland. It originates from the fleshy fibers of the orbitosphenoid bone. These muscle fibers turn obliquely toward the medial surface of the eyeball to insert into the scleral cartilage, positioned inferior to the Harderian gland.

Origin: Fleшы, from the orbitosphenoid bone.

Insertion: Aponeurotic on the scleral cartilage.

Function: Pulls the eyeball toward the anterior nasal pole (adduction).

Fig. 18 Photomacrograph of the eye dissection of the Egyptian agama, *Trapelus mutabilis*, after cutting the dorsalis rectus muscle (DRM), dorsalis oblique muscle (DOM), and depressor palpebrae inferioris muscle (DPIM), showing the medialis rectus muscle (MRM), the position of the Harderian gland (Hg), ventralis rectus muscle (VRM), ventralis oblique muscle (VOM), lateralis rectus muscle (LRM), and retractor bulbi muscle (RBM)



Ventralis rectus muscle (VRM): The VRM is a sheet-like muscle composed of parallel fibers that run ventrally to the depressor palpebrae inferioris muscle (DPIM). It originates from fleshy fibers of the parabasisphenoid bone, fanning out to insert as an aponeurosis on the scleral cartilage. Its insertion site is ventral to the insertion site of the VOM on the scleral cartilage. The origin of the VRM is located ventral to the optic nerve and anterodorsal to the origin of the LRM.

Origin: Fleshy, from the parabasisphenoid bone.

Insertion: Aponeurotic on the scleral cartilage.

Function: Depresses the eyeball and causes extorsion rotation.

Ventralis oblique muscle (VOM): The VOM is a sheet-like muscle with oblique fibers that run ventrally to the DPIM. It is situated on the anteroventral surface of the eyeball, oriented toward the nasal pole. It originates from fleshy fibers of the parabasisphenoid bone, fanning out to insert as an aponeurosis on the scleral cartilage. The aponeurosis of the VOM passes over the dorsal surface of the aponeurosis of the VRM. Its insertion site is dorsal to the insertion site of the VRM on the scleral cartilage. The origin of the VOM is located ventral to the optic nerve and anteroventral to the origin of the DOM.

Origin: Fleshy, from the parabasisphenoid bone.

Insertion: Aponeurotic on the scleral cartilage.

Function: Depresses the eyeball and causes rotation (intorsion/extorsion).

Lateralis rectus muscle (LRM): The LRM is a rectangular sheet composed of oblique muscle fibers. It originates from fleshy, narrow fibers of the parabasisphenoid bone and extends to insert into the scleral cartilage. The origin site of the LRM is ventral to the optic nerve and posteroventrally located relative to the origin site of the VRM. Its insertion site is dorsal to the insertion site of the bursalis muscle (BM) on the scleral cartilage.

Origin: Fleshy, from the parabasisphenoid bone.

Insertion: Aponeurotic on the scleral cartilage.

Function: Pulls the eyeball toward the posterior temporal pole (abduction).

Retractor bulbi muscle (RBM): The RBM is a sheet-like muscle composed of parallel fibers that run ventrally to the VRM. It originates from fleshy, narrow fibers of the parabasisphenoid bone, spreading out to form a broad aponeurosis that inserts on the scleral cartilage. The origin site of the RBM is ventral to the optic nerve and anterior to the origin site of the BM. Its insertion site is ventral to the insertion site of the VRM on the scleral cartilage.

Origin: Fleshy, from the parabasisphenoid bone.

Insertion: Aponeurotic on the scleral cartilage.

Function: Pulls the eyeball inward and outward within the socket.

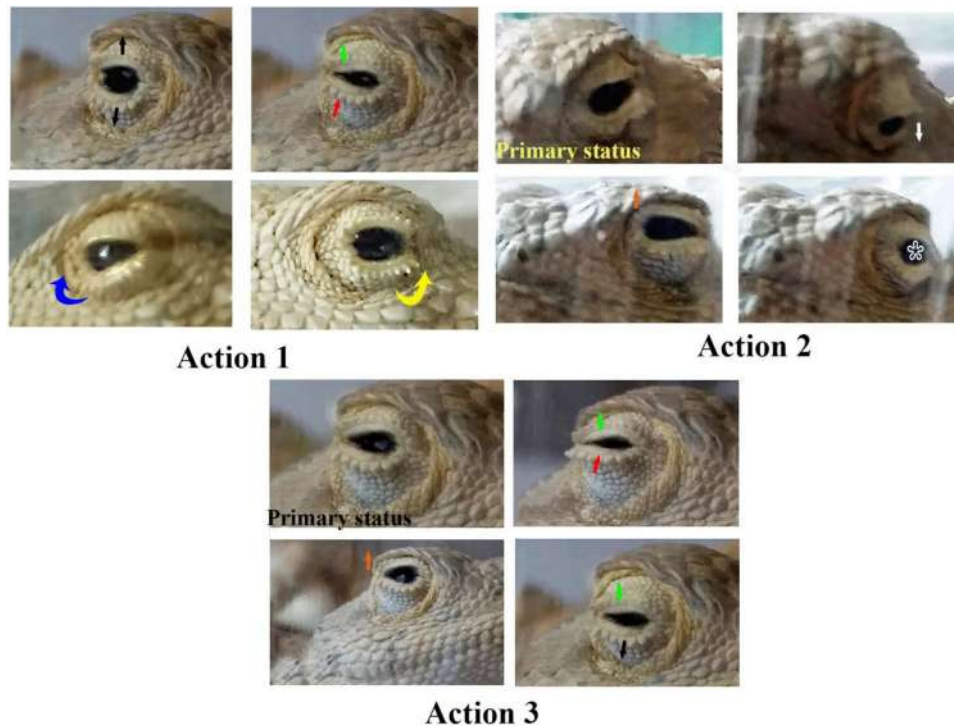


Fig. 19 Photograph of the eye of the Egyptian agama, *Trapelus mutabilis*, showing different actions: elevation and depression of the upper and lower eyelids, respectively (opening phase) (black arrow); downward movement of the upper eyelid (green arrow) and upward movement of the lower eyelid (red arrow) via contraction of the orbicularis oculi muscle (closure phase); adduction and rotation of the eyeball toward the nasal canthus (blue arrow) via contraction of the medialis

rectus muscle; abduction and rotation of the eyeball away from the nasal canthus (yellow arrow) via contraction of the lateralis rectus muscle; depression of the eyeball via contraction of the ventralis rectus and oblique muscles (white arrow); elevation of the eyeball via contraction of the dorsalis rectus and oblique muscles (orange arrow); and action of the retractor bulbi and bursalis muscles (star), pulling the eyeball inward into the socket

Bursalis muscle (BM): The BM is a sheet-like muscle composed of parallel fibers, appearing as a derivative of the RBM. It originates from fleshy, narrow fibers of the parabasisphenoid bone, spreading out to form an aponeurosis that inserts into the scleral cartilage. The origin site of the BM is ventral to the optic nerve and posterior to the origin site of the RBM. Its insertion site is ventral to the insertion site of the LRM. The tendon of the BM runs anteroposteriorly toward the upper eyelid and anteroventrally toward the lower eyelid.

Origin: Fleshy, from the parabasisphenoid bone.

Insertion: Aponeurotic on the scleral cartilage.

Function: Pulls the eyeball inward and outward within the socket.

B. Accessory Ocular Muscles

Depressor palpebrae inferioris muscle (DPIM): The DPIM is composed of tiny muscle fibers scattered within the periorbital fascia. It runs dorsally, covering the VRM and VOM. This muscle originates from its attachment on the fleshy parabasisphenoid bone, extending outward toward its insertion on the connective tissue of the lower eyelid.

Origin: Fleshy, from the parabasisphenoid bone.

Insertion: Aponeurotic on the connective tissue of the lower eyelid.

Function: Contraction of the depressor muscle pulls the lower eyelid, resulting in the opening of the palpebral fissure.

Orbicularis oculi muscle (OOM): The OOM is not visible during the dissection of the eye of the Egyptian agama, *Trapelus mutabilis*. Its fibers are located within the dermal layer of the eyelid stroma, adjacent to the internal surface of the eyelids.

Function: Contraction of the OOM results in the closure of the palpebral fissure.

Analysis of the video record of eye muscle action

The eye's motion was recorded via video in the laboratory (Fig. 19). Several recordings were analyzed to identify movements such as the opening and closing of the palpebral fissure and the elevation and depression of the upper and lower eyelids. However, identifying eyeball movements, such as elevation, depression, and rotation, proved to be a challenging task. The synchronization of eyelid movement

with eyeball movement facilitated more precise observation of these motions. This synchronization was particularly evident when the gaze was directed upward or downward, resulting in significant movements of the eyelids.

The elevation of the upper eyelid in *Trapelus mutabilis* is performed by the contraction of the DRM, which cooperates with the DOM that elevates the eyeball. Conversely, depression of the lower eyelid is performed by contraction of the DPIM. Simultaneous contraction of these upper and lower eyelid muscles expands the eye opening, opposing the action of the OOM responsible for closing the eyelids.

Observations showed that when the pupil moves anteriorly with a decrease in skin surface at the nasal canthus, it indicates rotation of the eyeball toward the anterior direction, which is performed by contraction of the medial rectus muscle. Conversely, when the eyeball abducts away from the nasal canthus, contraction of the LRM is responsible. Depression of the eyeball is achieved by contraction of the VRM and VOM, while the DRM and DOM perform elevation.

In an antagonistic dyad (lateralis–medialis, dorsalis–ventralis, and obliques), one muscle contracts while its partner relaxes; a muscle never acts independently of its partner. These three pairs execute the majority of movements simultaneously. Additionally, observations indicated that the eyeball is retracted further into the socket by the RBM and BM.

Discussion

Eyelids are integumentary duplications or folds of skin surrounding the eyes, functioning as a physical barrier in terrestrial vertebrates to protect against mechanical injury and desiccation, while also regulating light passage through the pupil (Johnson 1927; Walls 1942). Previous studies have confirmed that eyelids serve to safeguard the eyeball and maintain a moist ocular surface (Yasui et al. 2006).

In *Trapelus mutabilis*, the upper eyelid is anatomically similar to the lower eyelid; however, the lower eyelid exhibits greater mobility, descending through contraction of the dorsopalpebral inferior muscle (DPIM) attached at its base. Additionally, the lower eyelid is generally larger than the upper eyelid, a pattern commonly observed in reptiles and birds, in contrast to mammals, where the upper eyelid typically dominates in size and mobility (Wyneken 2012; Klećkowska-Nawrot et al. 2019).

The external surfaces of both eyelids in *T. mutabilis* are covered with highly polygonal scales of varying sizes and shapes. Large, plate-like scales dominate the superior extensions of the eyelids. These broad scales likely function as protective umbrellas for the eyes and as heat exchangers, contributing to water conservation in arid environments.

The presence of such scale diversity aligns with observations by Calsbeek et al. (2006) and Wegener et al. (2014), who noted that reptilian eyelid scales vary in pattern, shape, thickness, and degree of overlap, reflecting adaptations to environmental conditions.

The tips of these scales possess integumentary sense organs, featuring an Oberhäutchen with bristles. Leydig (1868) first described these organs in lizards (*Lacerta*, *Anguis*) and snakes (*Coronella*), identifying minute depressions on the scale surface, termed "organs of the sixth sense," comparable to taste receptors in amphibians and fish. Subsequent studies in agamids and other lizards distinguished two main types: one with Oberhäutchen bristles, typical of pygopodids, agamids, and gekkonids, and one without (Scortecci 1941; Landmann 1975). These organs likely integrate with visual and other sensory systems to detect, locate, and capture prey (MacLean 1980; Sherbrooke & Nagle 1996; Barrett et al. 1970). In *T. mutabilis*, the bristle-bearing sense organs may function as mechanoreceptors, facilitating environmental interaction.

Histologically, the epithelial structure of the upper and lower eyelids is similar; however, keratinization differs between them. The outer surfaces are covered with a thick keratin layer, whereas the inner surfaces are non-keratinized. This variation likely reflects functional demands: the keratinized exterior provides mechanical strength and durability, whereas the smooth inner surface reduces friction, allowing the eyelids to glide over the cornea.

Pigment cell distribution also varies within the dermis. Large black melanophores with dendritic extensions invaginate into the stratum basale of both eyelids, increasing in number within the superior extension of the upper eyelid. Brownish-yellow iridophores are scattered throughout the dermis of both eyelids and the upper eyelid extension. These pigment cells contribute to skin coloration and thermoregulation in reptiles (Saenko et al. 2013; Teyssier et al. 2015).

Anatomical analysis revealed that the nictitating membrane (NM) of *T. mutabilis* is thin and reduced, an unexpected trait for a terrestrial reptile. In species exposed to wind, dust, and sediment, the NM is typically well-developed (Schramm et al. 1994). Reduced NM has been documented in reptiles with spectacles, such as *Nothobachia ablephara* and *Calyptommatus sinebrachiatus* (Rehorek et al. 2000), and in burrowing squamates and other taxa where ecological conditions render the NM less critical (Caprette et al. 2004). In squamates, the NM normally functions as a movable pleat gliding over the cornea, assisted by exocrine secretions from the Harderian gland (Walls 1942; Payne 1994; Guerra-Fuentes et al. 2014). In *T. mutabilis*, the lacrimal gland opens near the NM surface, facilitating its limited movement. Due to the NM's reduced form, eyelid mobility is enhanced to remove foreign particles from the corneal

surface. The orbital gland secretions, along with conjunctival pleats and goblet cell mucus, further support corneal lubrication during eyelid movement (Mahmoud, 2022).

Observations also indicated synchronized movement between the eyelids and eyeball, mediated by extraocular muscles. The absence of a levator palpebrae superioris in *T. mutabilis* places responsibility for elevating the upper eyelid on the dorsorostral muscle (DRM) and dorsocaudal muscle (DOM), maintaining ocular surface moisture and reducing photoreceptor fatigue (Schwab 2012). Anatomical examination revealed that the DRM and DOM have dual origins on the orbitosphenoid and parabasisphenoid bones but share a common insertion on the sclera and upper eyelid, increasing contraction efficiency.

The retractor bulbi muscle (RBM) and bursalis muscle insert on the scleral cartilage, originating ventrally to the optic nerve, enabling inward and outward eyeball movements. In *Varanus*, similar protective retraction reflexes occur via simultaneous contraction of retractor and protractor muscles (El Hassni et al. 2000; Oelrich 1956; Tansley 1965; Wyneken 2012). RBMs are synapomorphic and have been lost in certain reptiles and birds; in snakes, this loss corresponds to a visual reduction similar to that in large-eyed raptors (Caprette et al. 2004). Supplementary muscles, such as the quadratus in lizards, assist in eye movement when RBMs are absent (Bour et al. 2000).

In summary, *T. mutabilis* exhibits multiple structural and functional adaptations that enhance ocular protection and visual performance. The eyelid scales, pigment cells, and mechanosensory organs provide defense against mechanical and UV damage. Enhanced eyelid mobility, in conjunction with specialized extraocular musculature, ensures effective corneal cleaning and optimal visual field. Collectively, these features demonstrate an integrated protective and sensory strategy, reflecting the species' adaptation to its harsh arid environment.

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Data availability All datasets generated and used in this study are available in the manuscript and Supporting Information.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This study complies with the Guidelines for Ethical Research of Aswan University (Approval number: ASWU/05/SC/

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