In ictu oculi

An atlas of blinking across the species

from the perspective of a neurologist

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Volume 1. Introduction, Fish, Frogs, Turtles, Lizards, Crocodiles, Birds (Accipitriformes, Charadriiformes, Anseriformes, Bucerotiformes)

Foreword

This is not a book of pretty pictures. Many of the photographs were taken through bars in cages in zoos in poor light. The animal was often moving causing blurring of the image. Rather, this a record of a blinking in a large number of species. The photo is included if it shows something about blinking. That said, I have to confess that some pictures were only included because they were pretty!

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Summary

Blinking, which occurs in almost all terrestrial creatures, has received little or no attention in the scientific literature. Yet the requirement to keep the eye moist, allowing oxygen in the atmosphere to reach the corneal cells which have no blood supply, was as important in its way as developing lungs and limbs, to fishes adopting a terrestrial lifestyle. The present study is an attempt to capture the diversification which has occurred across the species. Video recordings were made of blinking in 2 species of fishes, 5 species of frog, 15 species of turtle, 20 species of lizard, 8 species of crocodile, 545 species of birds and 89 species of mammals. Blinking in two species of mudskipper involved retraction of the globes through skin slits into the skull. In frogs, blinking involved retraction of the globes with elevation of the lower lids, a transparent part of which (the nictitating membrane) lay behind the lids, only appearing during a blink and rising vertically to cover the corneas. Two types of blink were observed in turtles. One involved unfurling and vertical movement of opaque lower lids, and retraction of the globes. In the other, a nictitating membrane arose from the inner canthus of the eye, moved horizontally and operated independently from the lower lid blink. In both, there was retraction of the globes. Blinking in lizards involved retraction of the globes, horizontal movement of the nictitating membranes and independent elevation of the lower lids. In one there was an upper lid blink. Crocodiles had a similar blink with, in some species, heavily armoured upper lids sinking into the orbits as the globes retracted. Nictitating membrane blinks with no globe retraction or lower lid elevation also occurred. The commonest blink in birds comprised horizontal movement of nictitating membranes arising from the inner canthus, on head turns. In some orders of birds, this was accompanied by an upper eyelid blink. Preening and drowsiness were associated with elevation of the lower eyelids. In some species blinks occurred with pecking. There was no globe retraction in birds and most had no visible eye movements. Blinking occurred with eye movement in those species where this was preserved. Globe retraction was a major feature in the blinking of most species of mammals. This was associated with horizontal movement of the nictitating membrane arising in the inner canthus and closure of the eyelids. The latter made it impossible to see the nictitating membrane without prising the eyes open. In the meerkat, okapi and rock hydrax, blinking involved the nictitating membrane without eyelid closure. In hominids, both globe retraction and nictitating membrane blinks have been lost. The diversification of blinking in terrestrial animals lends itself to further studies on its origins.

Introduction

Anyone who has observed birds at close quarters cannot fail to be struck by how frequently they blink. Why do they do this? I started to video birds to see if I could shed light on this curious phenomenon. Then I moved onto other creatures and more questions arose. Why do some creatures blink with their upper lids, others with their lower? Why do some have nictitating membranes? Why do some retract their eyeballs? Rabbits and guinea pigs hardly blink at all. In cats, you may get a glimpse of the 'third' eyelid, or nictitating membrane. Blinking can be so brief it can only be caught on video. It is in birds that blinking really comes into its own.

So many questions! I started to read what had been written on the subject but could find very little. There were tomes on vision and on eyes, but eyelids tended to be relegated to afterthoughts on 'adnexae' (the parts adjoining the organ of main interest). Much of the anatomical work had been done, not in the last century but the one before! This book catalogues the ways in which blinking has diversified since fishes left water behind and established themselves on land.

Blinking is something that we all do, an unconscious action of little apparent significance or importance. Yet blinking is not only essential for the health of our eyes, it played a key role in the emergence of our ancestors from the sea and in their adoption of a terrestrial lifestyle. The cornea and lens focus light on the photoreceptors of the retina. They are transparent and have no blood vessels passing through them, though curiously, light has to pass through layers of cells and blood vessels to reach the photoreceptors in the deepest part of the retina. In fish, oxygen dissolved in water diffuses into the cornea and then across the aqueous fluid in the anterior chamber of the eye, to the lens. Once fishes began to venture onto land, they faced the problem that the surface of the cornea dries out in air. Atmospheric oxygen cannot diffuse into the cornea unless it is wet. And so, anatomical structures - eyelids and secretory glands - evolved which allowed the cornea to remain moist at all times. These structures also assumed other functions like protection of the eyes, which were now more vulnerable to injury as particles tend to travel faster in air than in water. Eyelids, being soft structures, might shut out dust or wind but provide little protection from mechanical pressure or blows. Blinking in many species thus came to involve retraction of the eyeball into the relative safety of the orbit, where the bony skull could take the impact. In other species, prominent eyebrow ridges evolved under which the eyes could shelter.

Blinking involves transient eye closure. Sustained eye closure occurring during sleep poses a problem as the cornea, moist or not, no longer has access to atmospheric oxygen. This problem has been dealt with by providing both the conjunctival surface of the eyelids and nictitating membranes with a rich blood supply from which oxygen can diffuse into the cornea.

Upper eyelids, lower eyelids, nictitating membranes, globe retraction and provision of moisture are the available components of blinks. There are also fast blinks and slow blinks which is discussed in the section entitled 'Tonic and phasic blinks' on the website (see below). The method of blinking varies from species to species. Particular attention is given to birds, of which there are about 10,000 species, as these vary markedly in the way they blink.

Most of the blinks demonstrated are spontaneous - recorded while observing animals without in any way interfering with them. Reflex blinking, in response to the cornea being touched was observed in one bird. In some birds, blinking also occurs during pecking.

Discussion of the anatomy of blinking borrows heavily from the classic monograph of Gordon Lynn Walls, *The vertebrate eye and its adaptive radiation* (1943).

This monograph is the written and greatly expanded version of the website: 'Winks-and-blinks' where many of the videos used to produce the stills in this book may be seen.

For about 30 years, I practiced as a clinical neurologist at Westmead, a Sydney teaching hospital. Neurology is a discipline which relies on observation of the clinical features and signs of patients and, when video cameras became available in the early 1980s, I began to video my patients, particularly those with interesting physical signs or those where there might be doubt about the diagnosis. Many of these videos are published online by Oxford University Press as a Manual of Neurological Signs, which I did with my colleague Paddy Grattan-Smith. When I retired 14 years ago, my interest turned to birds and other animals. I have tried to bring the same discipline I followed in neurological practice, that of careful observation coupled with a review of the literature, to the study of blinking.

John Morris

Methods

Since 2015, video recordings have been made of blinking in mudskippers, frogs, turtles, lizards, crocodiles, birds and mammals. This was mainly done in zoos where animals could be approached close enough to gain adequate detail, but also in the wild. Videoing was done using a Panasonic Lumix DMC FZ2500 digital single-lens reflex camera and a Sony FDR–AX53 camcorder. The zoom on these cameras allowed close-up views of the eyes even when the animal was more than 5 metres away. There was no intervention such as making a noise, gesticulating or using flash photography. Most filming was carried out at 25 frames/second and in some settings at 100 frames/second. While they remained in view, animals were videoed until they blinked. With frogs, turtles, lizards and crocodiles, 30 minutes or longer might pass between blinks and sometimes the opportunity passed without seeing one. With birds, blinks were frequent but often the bird did not stay in sight for more than a few seconds unless it was sleepy or preening. When the opportunity arose, the same animal might be videoed repeatedly. Wild birds were studied in Sydney, Australia, and to a small extent in the UK and the Netherlands. Captive birds and other animals were filmed at zoos in Australia: Taronga and Featherdale Park in Sydney, the Reptile Park in Gosford and zoos in Canberra, Melbourne, Adelaide, Launceston and Queensland (Australia Zoo, Lone Pine and Currumbin); Singapore: the Jurong Bird Park; UK: London Zoo, Whipsnade, Barnes Wetlands, Torquay, Woburn Abbey, Bristol, Crocodiles of the World in Carterton, Oxfordshire and the Suffolk Owl Sanctuary; Ireland: Dublin; Belgium: Pairi Daiza Zoo; France: ZooParc de Beauval; Netherlands: Rotterdam Zoo, the Avifauna Park; USA: Bronx Zoo in New York, San Diego Zoo; South Africa: Pretoria, Hout Bay and Stellenbosch; New Zealand: Auckland; Greece: Athens. Sampling was opportunistic depending on which species the zoos happened to have. Common species were often videoed multiple times. Rare species might be videoed only once.

Digital video files were analysed using Movavi Video Editing software [Versions 12.1 to 15.4.1] (which is easy to use and not overly expensive), made in Novosibirsk, Russia, with a Dell laptop (XPS 15 9560), made in Longhua, China, and later a MacBook Pro (2.6 GHz Processor and 16 GB memory), US Apple Company, manufactured in China. Video files could be viewed frame by frame in order to follow the position of the eyelids and nictitating membrane during the course of a blink. An estimate of the time course of a blink was made in some situations by counting the frames. At 25 frames/second, the duration of each frame Is 40ms.If a species was of particular interest but not accessible, videos on internet sites were viewed. The sample was opportunistic and limited by availability.

For the purposes of the study, the nictitating membrane is defined as a fold in the conjunctival mucous membrane, arising either from the inner surface of the lower eyelid as in the frog, or from the bulbar conjunctiva in the region of the medial canthus as in most other terrestrial vertebrates. It comprises stratified, non-keratinised cuboidal and columnar cells interspersed with mucus secreting goblet cells. The membrane is thin, often transparent, but may also be pigmented. In many species, the inner and outer layers of the leading edge of the membrane are separated by a thin layer of cartilage. Tubules arising from the harderian gland enter the membrane and open onto its inner surface allowing it to spread its secretions over the cornea. Nictitating membranes are made to move across the cornea by globe retraction or by being pulled by tendons connected to muscles which usually lie behind the eye. In species where the membrane is still visible but immobile the term vestigial nictitating membrane is used. Eyelids differ from the nictitating membrane in having an outer layer of (keratinised) skin as well as hair (with sebaceous and Meibomian glands) in mammals, or feathers in birds. The distinction however is not absolute. In the frog, while the bulbar surface of the membrane comprises mucoid epithelium like the conjunctival membrane, the outer layer is stratified epithelium like frog skin (Lande & Zadunaisky, 1970).

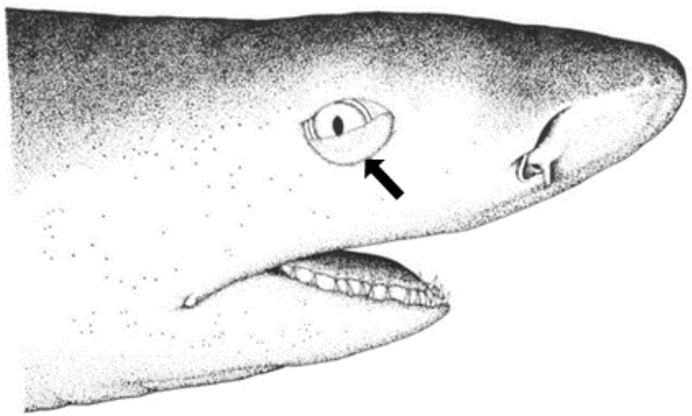
Stills from the videos, together with tracings to illustrate their key features, are shown of blinking in mudskippers, frogs, turtles, lizards, crocodiles, birds and mammals. These are followed by a brief illustrated review of the postulated mechanisms by which the membrane is made to move across the eye or vice versa. The chapter on this in Wall's influential monograph (Walls, 1943) predicts whether movement of the nictitating membrane can occur in isolation or is invariably accompanied by globe retraction or elevation of the lower lid. This study provides an opportunity to see how well the models proposed by Walls stand up. Of note is how mobility of the membrane has been lost in many species.

The results begin with a study of mudskippers which can be regarded as having a prototype or precursor of a nictitating membrane where the eyeball is cleansed and moistened by brushing against a static membrane.

Fishes

Fishes are aquatic vertebrates which have gills and fins. 99% of the extant 32,000 species are ray-finned fish in the Class Actinoptergii, so-called because they have bony or horny spines (rays) in their fins. Their vertebrae are also made of bone. Ray-finned fishes appeared 400Mya. Teleosts, a sub-class of ray-finned fishes, account for 96% of extant species. Chondrichthyes is a class of fish where the skeleton is made of cartilage. Sharks, rays and skates belong to a subclass of cartilaginous fish called Elasmobrachii. Cartilaginous fish first appeared about 430Mya.

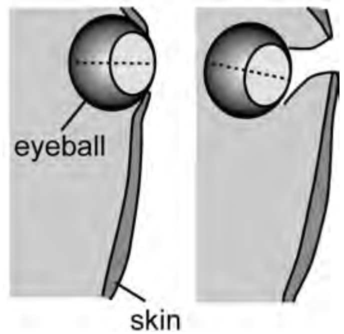
Some sharks have well-formed upper and lower eyelids which



Nictitating membrane (arrow) in a Lemon shark (Negaprion brevivirostris) from Gruber 1977.

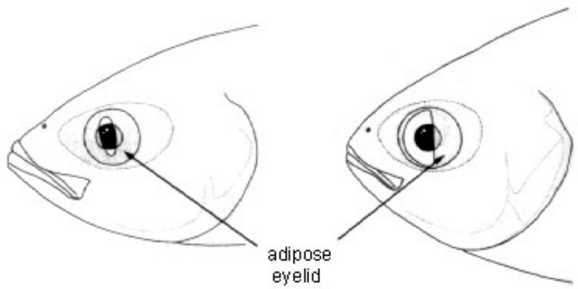
are mobile. Some also have a nictitating membrane, consisting of a fold in the lower eyelid which is drawn upwards and backwards across the eye by levator palpebrae nictitans, a muscle behind the eye innervated by the oculomotor (IIIrd cranial) nerve (Gruber S. , 1977). The membrane is dense, opaque, covered by tiny tooth-like scales, and only protective, there being no requirement to moisten the cornea.

In the whale shark, *Rhincodon typus* (Elasmobranchii, Rhincodontidae), the eyeball can rotate and retract, protecting it from injury. During this process, white connective tissue from the retrobulbar space is displaced around the eyeball and partially fills the space where the eye used to be (Tomita & al., 2020).



Schematic representation of rotation and retraction of the eyeball in a whale shark.

Most bony fish do not blink; some have transparent ‘adipose eyelids’ which may cover most or all of the eye. These are immobile.



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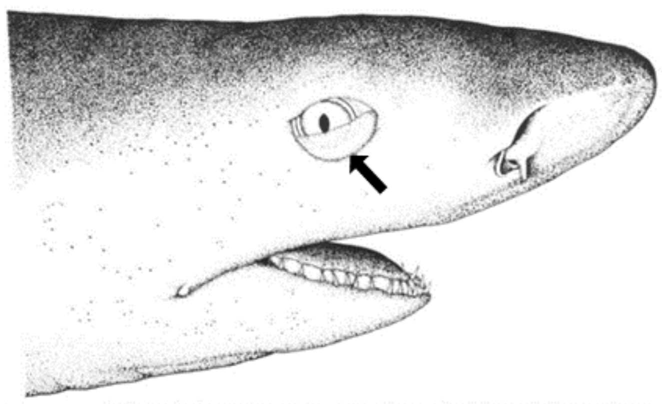

Nictitating membrane (arrow) in a Lemon shark (Negaprion brevivirostris) from Gruber 1977.

Elasmobrachii. Cartilaginous fish first appeared about 430Mya.

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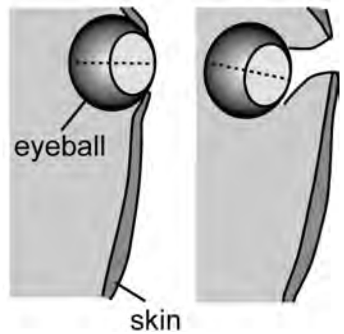

Schematic representation of rotation and retraction of the eyeball in a whale shark.

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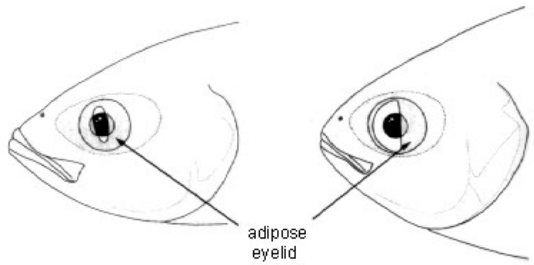
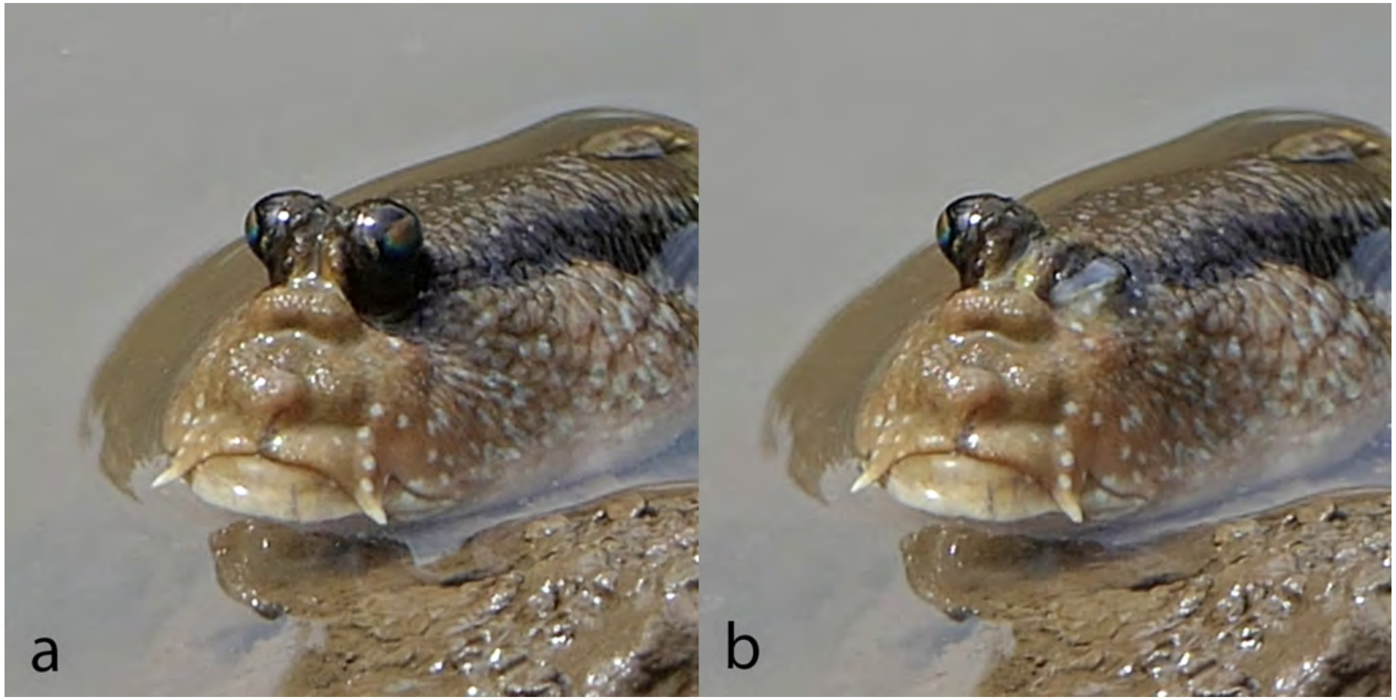


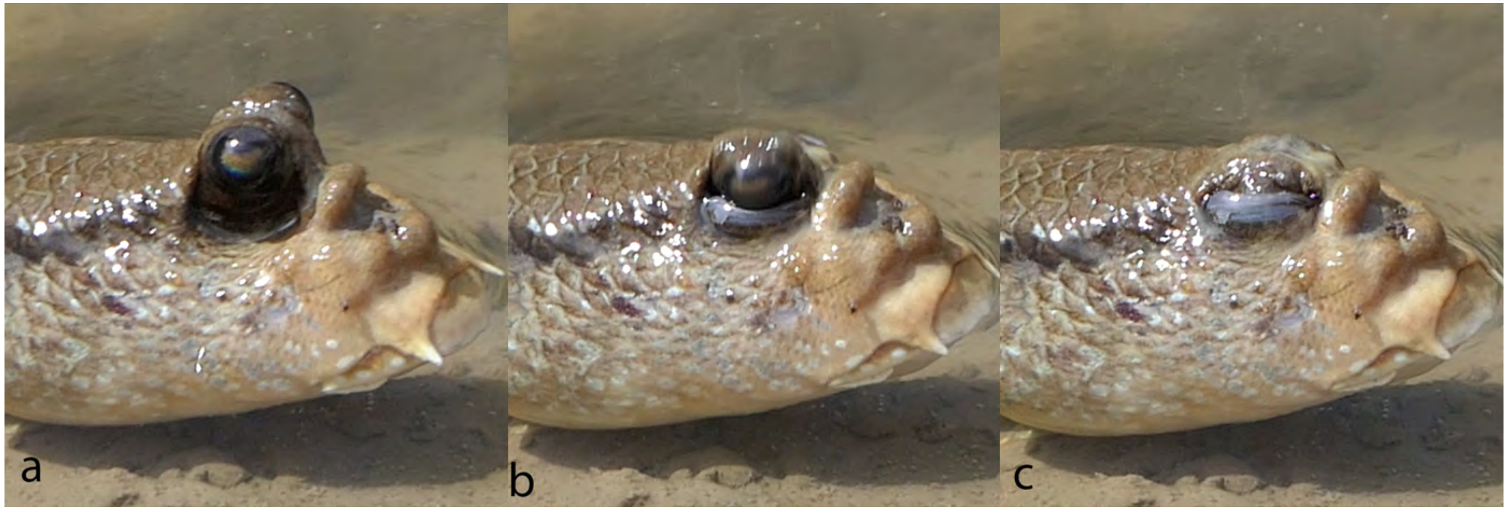
One bony fish which can blink is the mudskipper, an amphibious goby which spends much of its time on exposed mudflats in the Tropics (Takita, Larson, & Ishimatsu, 2011). There are 10 genera and 32 living species of mudskipper. In the pictures below, blinks and winks (unilateral blinks) are seen in two Australian species.

Giant mudskipper (*Periophthalmodon freycineti*)

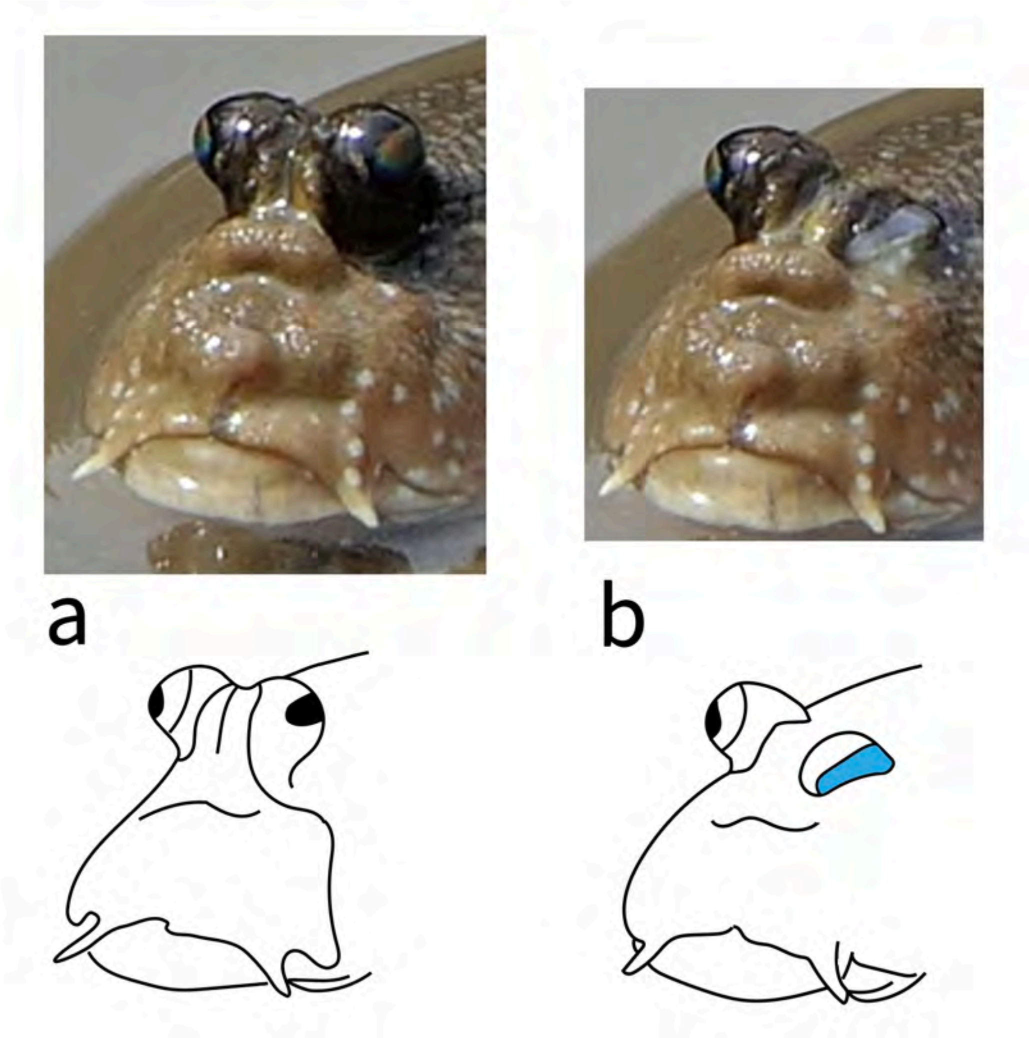
Globe retraction



Left sided wink: a) eyes open b) left eye retracted behind the dermal cup.



Side view of a blink in a specimen in a tidal creek in the Botanical Gardens in Cairns. a) The globe with a horizontally elongated pupil sits partially embedded on the top of a black pigmented turret with no obvious separation into upper or lower (medial or lateral) lids. b) During the blink, the globes retract into the head of the fish. c) As the globe retracts it disappears behind the lower 'lid' or dermal cup. The upper lid sinks with the eyeball during retraction. The dermal cup contains water and each time the globe retracts, the cornea is moistened. Identified by Dr Helen Larson, Curator Emeritus, Fishes, Museum and Art Gallery of the Northern Territory.

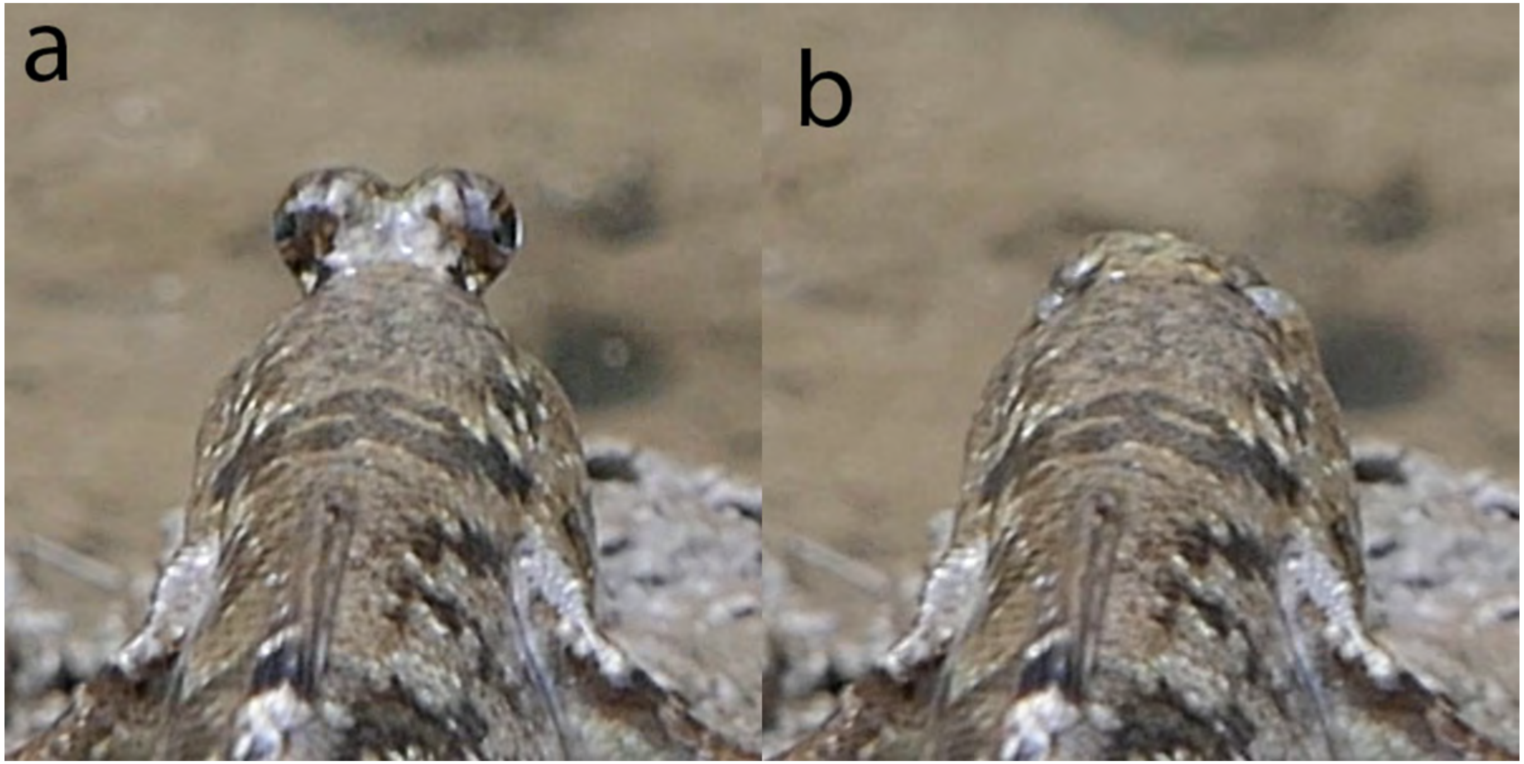


Globe retraction wink with stationary membrane: a) Pre-blink, the eyes are elevated on stalks and pointing laterally in opposite directions. b) The left eye has retracted past a semi-translucent membrane, the dermal cup membrane (blue), into the skull.

Movement of the dermal cup membrane is passive, brought about by the retraction of the globe. The eye returns to its resting position by elastic recoil.

Barred mudskipper (*Periophthalmus argentilineatus*)

Globe retraction



Blink in a specimen, also in Cairns. Identified by Dr Helen Larson, Curator Emeritus, Fishes, Museum and Art Gallery of the Northern Territory.

Mechanism of global retraction in mudskippers

Globe retraction is achieved by contraction of the six extraocular muscles common to all vertebrates (Young GC, 2008). The muscles are supplied by the IIIrd, IVth and VIth cranial nerves.

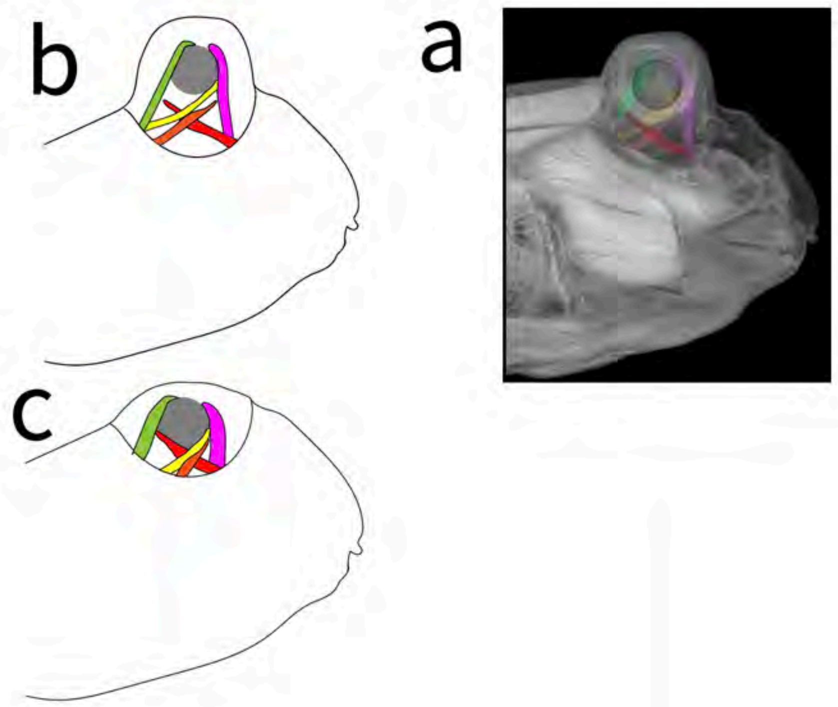


Figure a from the paper by Aiello et al (Aiello BR, 2023) *shows some of the extraocular muscles (colored) in an African mudskipper (Periophthalmodon Barbary's) and Figures b and c depict the shortening of the extraocular muscles which causes globe retraction*

Movement of the dermal cup membrane is passive, brought about by the retraction of the globe. The eye returns to its resting position by elastic recoil. There is no evidence of orbital glands such as the harderian or lacrimal gland.

Comments

The dorsal position of the eyes and their elevation on turrets, suggests that the transition mudskippers made from water to land involved acquiring aerial vision while remaining partially submerged in water. This would enable them to prey on flying insects while lessening their chance of being preyed on themselves. As their pectoral fins evolved, allowing them to walk, they were able to make sorties onto land – mainly mudbanks, rocky shores and sandy beaches. Unless these sorties were brief, they now had to deal with corneas which were drying out and, as a result, unable to absorb atmospheric oxygen. There were of course, many other adaptations to a terrestrial life such as absorbing oxygen through the skin and gills, but these are not the subject of this book.

Mudskippers moisten their eyes by retracting them into their head where the equivalent of a lower lid, the dermal cup, contains a water reservoir – topped up while the fish is in water. Such a system will only work while the fish spends part of its time in water. In order to venture afield, creatures exchanging a marine environment for a terrestrial one had to evolve another means of producing moisture for the corneas.

Retracting the eyes into the head also affords them some protection, important for example in species preying on potentially injurious creatures such as crabs.

The extraocular muscles of mudskippers are similar to, although longer (due to the turret) than other fish. Indeed, the pattern of four rectus and two oblique muscles innervated by cranial nerves, III, IV and VI is common to all jawed vertebrates (Fritzsch, 2024). According to Walls (Walls, 1943), fish do not have retractor muscles and there is little information available on how mudfish retract their eyes. How this is done varies from species to species. For example, the giant guitarfish uses the inferior oblique extra-ocular muscle to retract the eye (Tomita T. , 2015). Nor is there information on how mudskippers unretract their eyes.

Mudskippers often blink with one eye only (winking) which allows them to lubricate that eye while still keeping the other eye out for prey or predators.

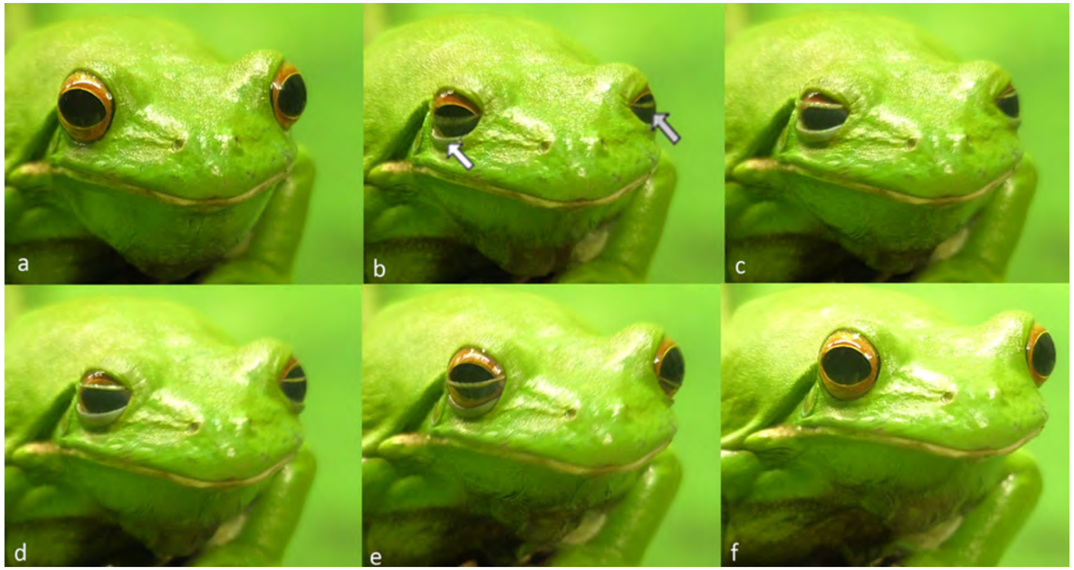
While in water, the cornea exerts no refracting power, as the refractive indices of the cornea and water are the same. In most fishes, focussing on the retina is done by an almost spherical lens. Accommodation is done by to and fro movement of the lens. A spherical lens is less amenable to changes in shape, which is the means by which accommodation occurs in, for example, reptiles (Duke-Elder., 1958). In air, the addition of refraction by the fish cornea would cause myopia. The myopia has been corrected for in mudskippers by flattening of the lens

Frogs (Order Anura)

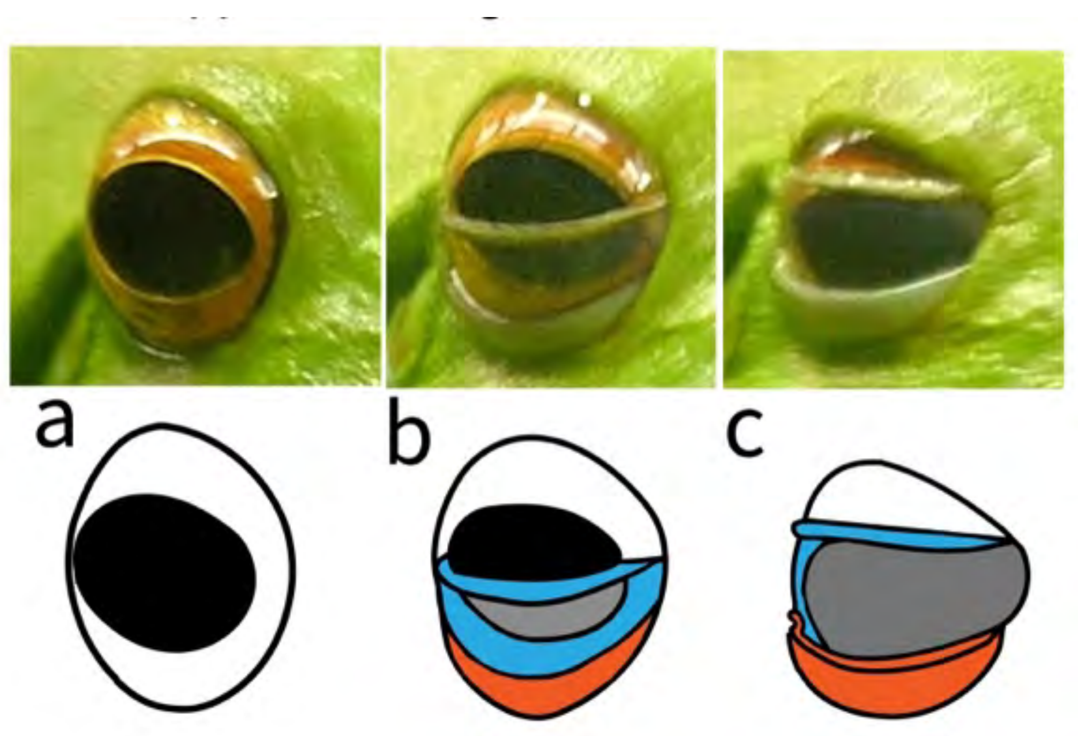
Most living frogs arose from lineages originating at the time of the Cretaceous-Paleogene mass extinction 66Mya. Their closest relatives are salamanders. Frogs are an order within the class of amphibia comprising over 7,000 species. Despite the name, only a minority of frogs are truly amphibious after they cease to be tadpoles. The majority are wholly terrestrial, and a few are wholly aquatic. Wholly aquatic anurans such as aglossal toads, never develop eyelids**.** No taxonomic distinction is made between frogs and toads. Tadpoles, the larval stage of frogs, have no eyelids. Frogs have slit-shaped pupils elongated in the horizontal axis. Examples of blinking in adult frogs follow:

White-lipped tree frog (*Nyctimystes infrafrenatus*)

Globe retraction with elevation of lower lid nictitating membrane



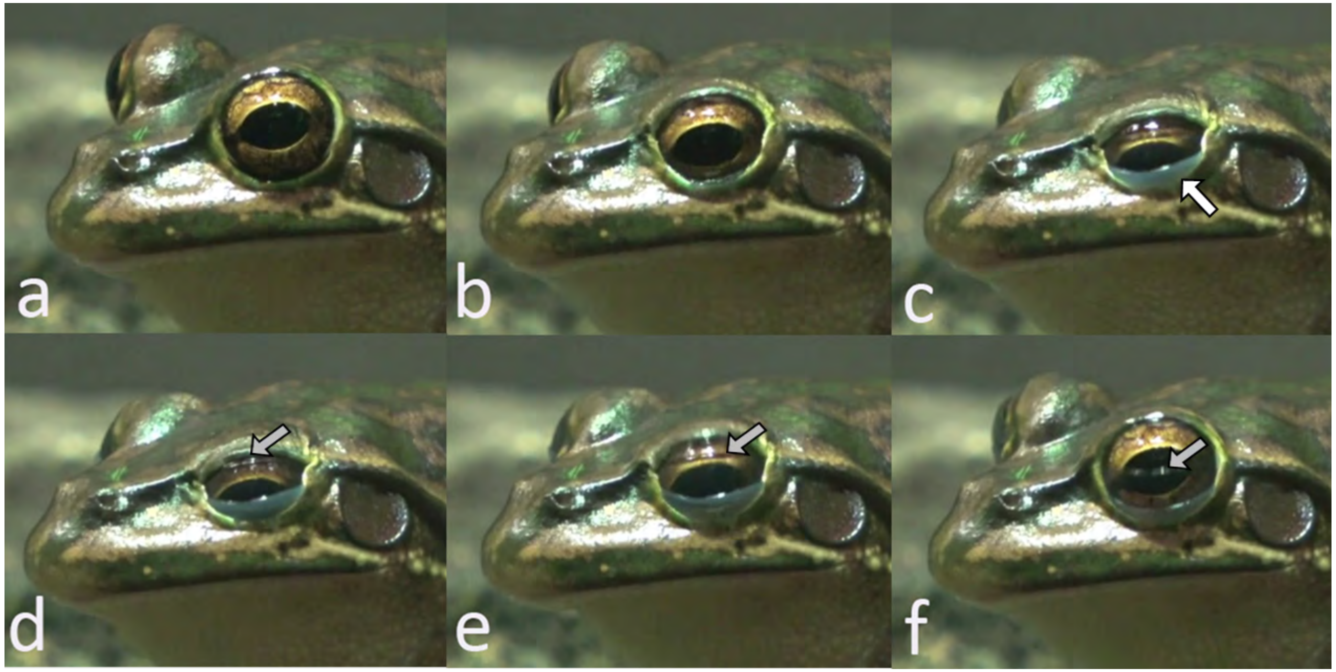
Blink during a slight left head turn: a) At rest with protruding eyes and horizontally elongated pupils. b) Eyeball retraction, elevation of lower lid ⬉ and elevation of a translucent nictitating membrane ⬉ c) Maximal blink. d) The eyeballs start to unretract. e) The nictitating membranes descend. f) Back to resting position.



Lower lid nictitating membrane blink with globe retraction, right eye: a) Pre-blink showing a horizontally elongated oval pupil. b) Blink involving the nictitating membrane (blue), partly covering the pupil, with the pupil visible behind it, and the lower lid (orange). c) Maximum excursion of the lower lid - covering the pupil. The narrowing of the palpebral fissure is due to retraction of the globe.

Green and golden bell frog (*Litoria aurea*)

Globe retraction with elevation of lower lid nictitating membrane

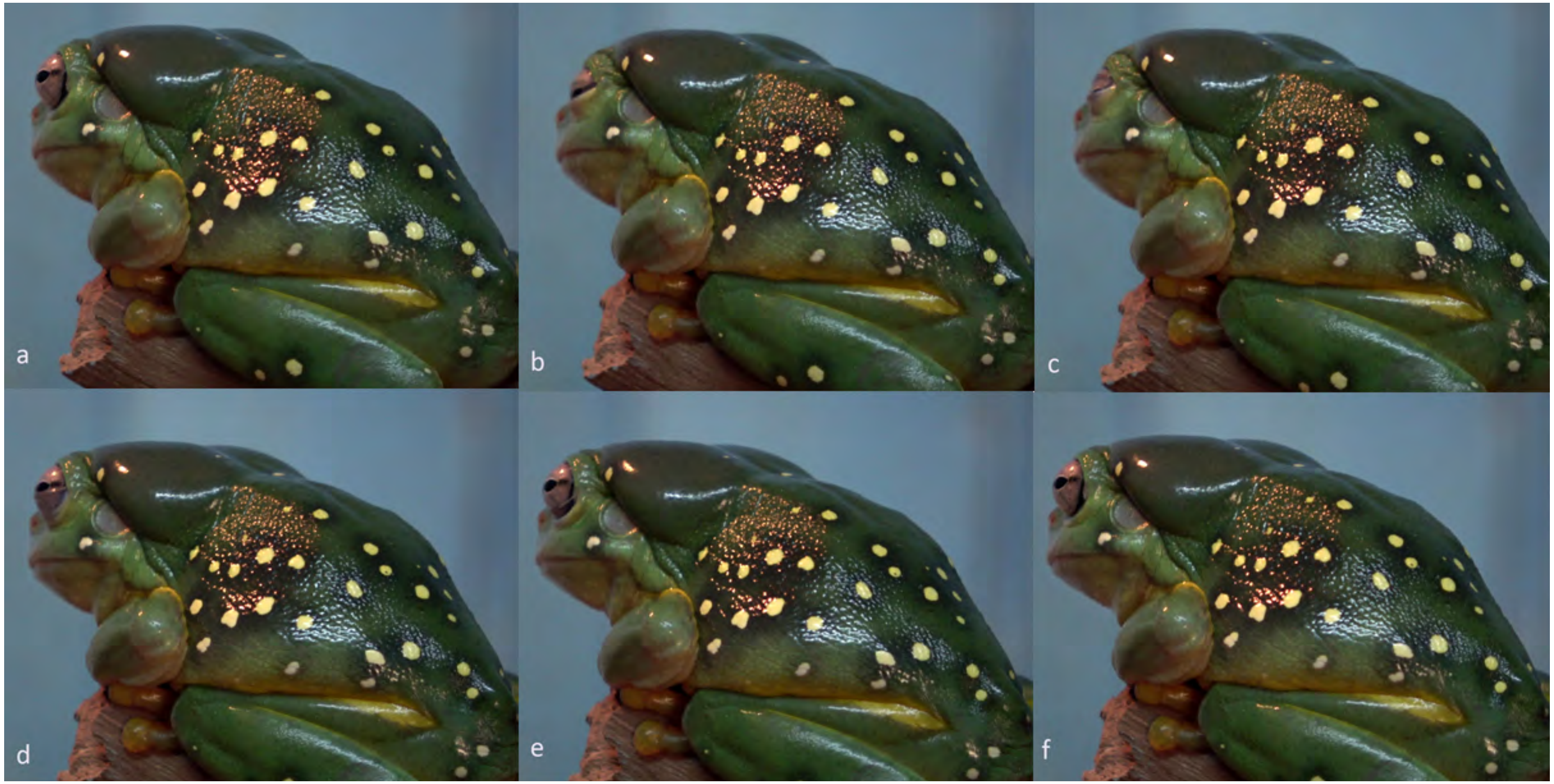


Blink seen from the left side. a) At rest. Horizontally elongated pupils. b) Eyeballs start to retract. At this time the left palpebral fissure narrows and the 'rims' around its edge become more prominent. c) The pale green semi-translucent left lower lid rises to partially cover the pupil (arrow). What is harder to see is that a translucent nictitating membrane has covered the eye d) The top edge of the left nictitating membrane, marked by arrow, here and in e) and f), is seen descending down the cornea.

Magnificent or splendid tree frog (*Ranoidea splendida*)

Globe retraction with elevation of lower lid nictitating membrane

Blink during mouth opening in a magnificent tree frog (Ranoidea splendida): a) At rest. b) and c) Onset of blink during mouth opening. d) and e) Edge ↙ of descending transparent nictitating membrane as blink ends. f) End of blink



Note prominence of eye. a) Pre-blink. b) Globe retracts. c) Lower lid elevates. d) and e) Globe unretracts. Nictitating membrane and lower lid descend. f) Post-blink.

Sleeping splendid tree frog with the edge of the lower lid at mid-pupil level and nictitating membrane fully elevated.

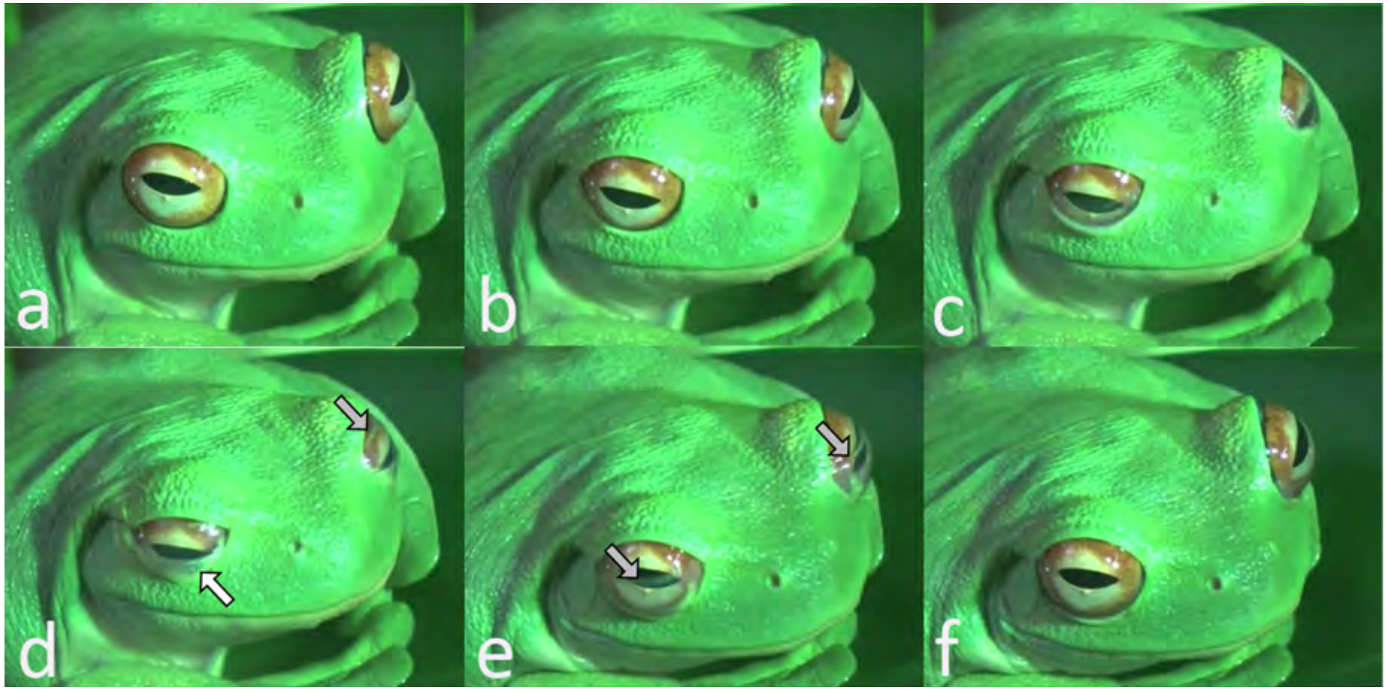
Yellow spotted tree frog (*Litoria castanea*)

Globe retraction with elevation of lower lid nictitating membrane

Yellow spotted bell frog (Litoria castanea): a) At rest b) Partial blink showing edges of lower lid ⇖ and nictitating membrane ⇙ c) Lower lid now descended leaving just the nictitating membrane

Red-eyed tree frog (*Litoria chloris*)

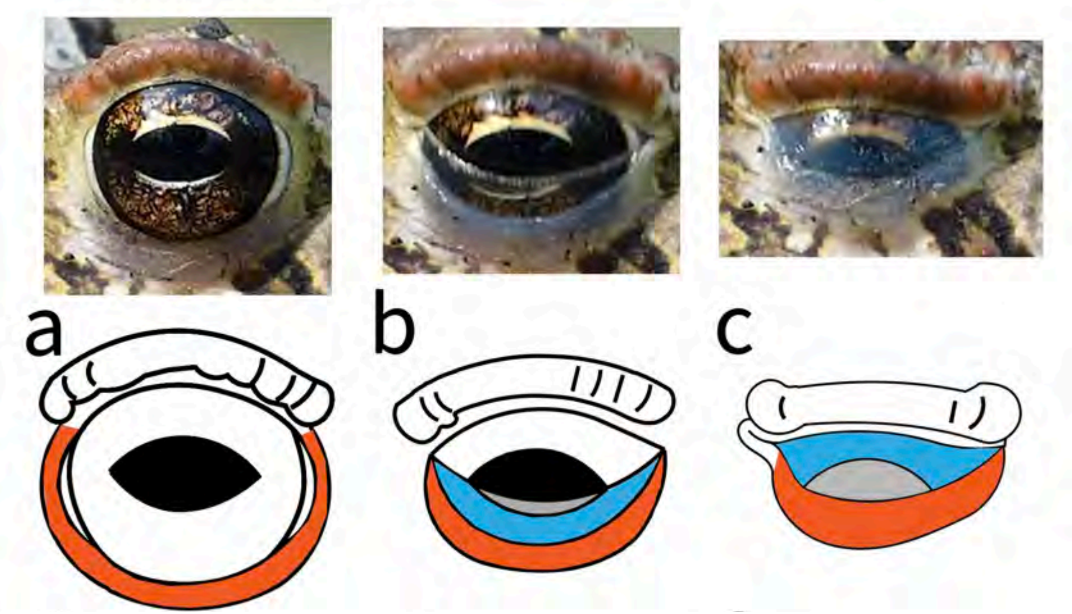
Globe retraction with elevation of ‘lower lid nictitating membrane’



a) Pre-blink. Horizontally elongated pupils. b) Both globes retract causing narrowing of the palpebral fissures. c) The eyes retract further. d) and e) A semi-translucent lower lid (white arrow) is seen rising in the right eye and the edge (grey arrow) of a translucent nictitating membrane is seen rising in the left eye. f) Post-blink.

Cane toad (*Rhinella marina*). Source: internet.

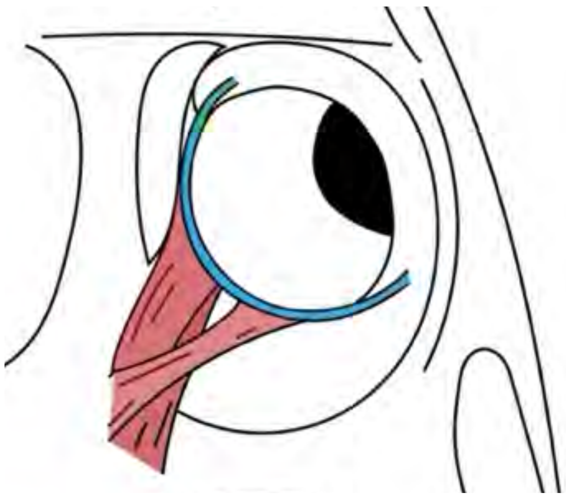
Lower lid nictitating membrane blink with globe retraction



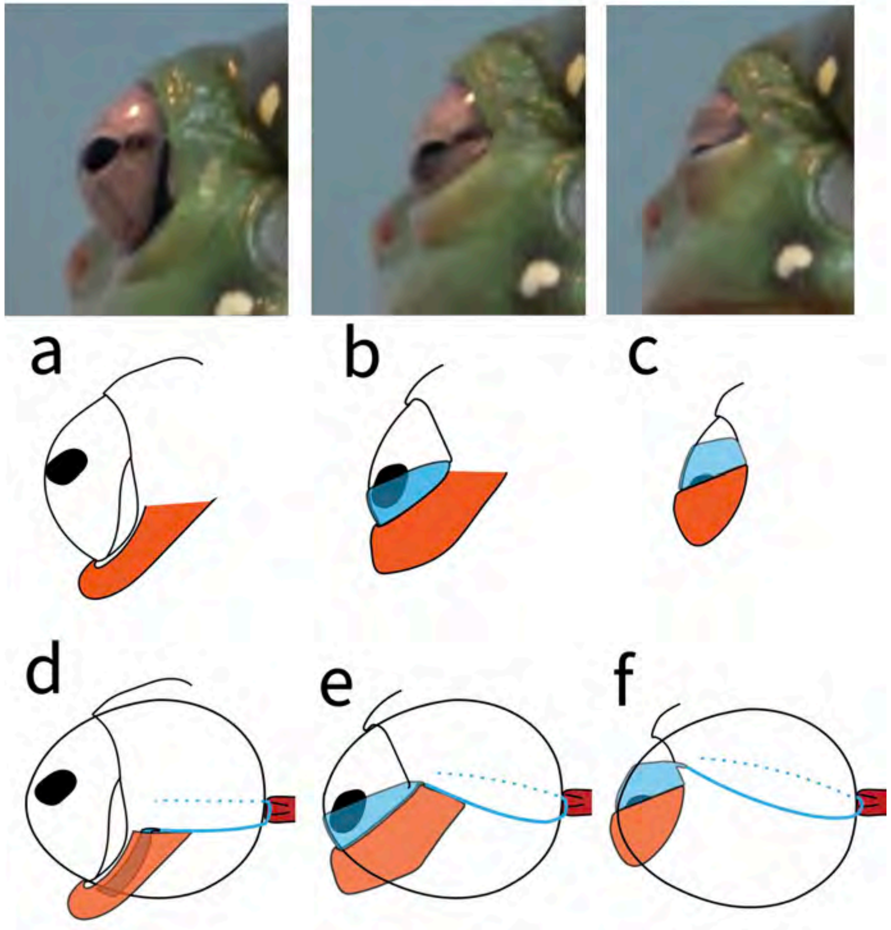
a) Pre-blink showing a horizontally elongated pupil and lower eyelid (orange). b) Blink involving nictitating membrane (blue) and lower lid (orange) rising and partly covering the pupil. c) Maximum excursion of the nictitating membrane and lower lid covering the cornea. The narrowing of the palpebral fissure is due to retraction of the globe.

Mechanism of elevation of the nictitating membrane and lower lid in frogs.

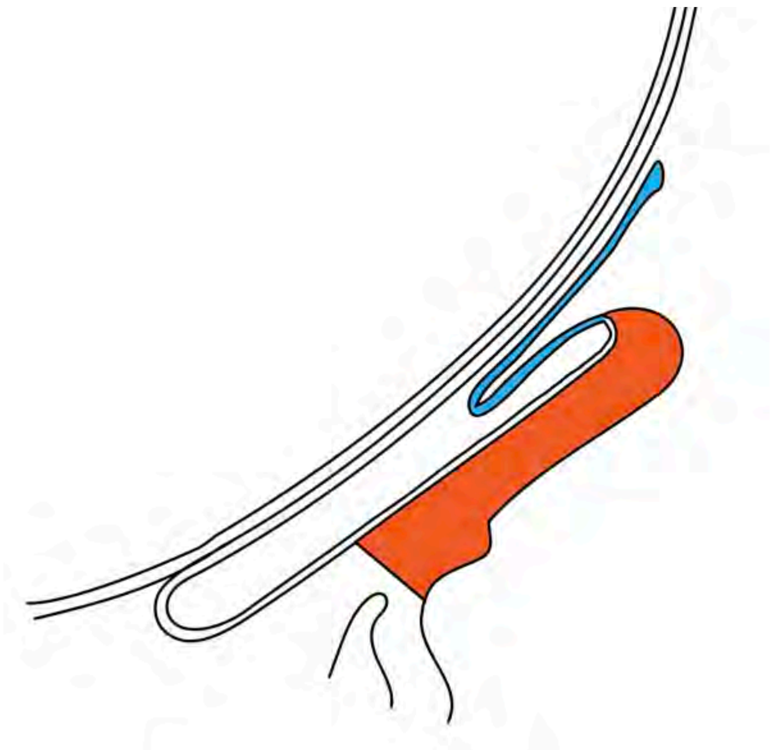
It is difficult to find current studies of the muscles involved in moving the nictitating membrane and lower lid in frogs. According to Ecker (Ecker, 1889) and Walls (Walls, 1943) the two upper ends of the nictitating membrane are connected to each other by a tendon.



This figure adapted from Ecker (Ecker, 1889)*, provides a view from below of the coronal plane of a frog's head showing the bellies of the retractor bulbi muscle (brown) inserting onto the globe. The tendon of the nictitating membrane (blue) encircles the globe. According to Ecker* (Ecker, 1889)*, the tendon of the nictitating membrane pulls the membrane up over the cornea when the globe is retracted into the orbit by the bellies of the retractor bulbi muscle. At the end of the blink, the globe pushes the membrane and lower lid aside as the retractor bulbi muscle relaxes and the levator bulbi muscle, which sits under the globe like a hammock, contracts. The lower lid is folded again by the action of a slip of the levator bulbi muscle* (Duellman & Trueb, 1994)



This figure shows a lower lid nictitating membrane blink with globe retraction (left eye from the side) in a magnificent tree frog (Ranoidea splendida) together with a drawing of the proposed mechanism of the blink a) Pre-blink showing prominence of the globe and a horizontally elongated pupil. b) The globe retracts and the nictitating membrane (blue) and lower lid (orange) rise. c) Maximum excursion of the nictitating membrane and lower lid with marked retraction of the globe. d) Pre-blink, showing the nictitating membrane (blue shadow) behind the lower lid (orange) and the tendon of the nictitating membrane (blue line) forming the medial part of the tendon circling the globe. It is attached to the lower surface of the retractor bulbi muscle behind the eye. e) Blink, showing the nictitating membrane and lower lid being drawn over the eye as the globe is pulled into the orbit by the retractor bulbi muscle.



Sagittal section of the eye and lower lid showing the nictitating membrane (blue) arising from the conjunctival membrane inside the lower lid (orange).

The retractor bulbi muscle is supplied by the VIth cranial nerve and the levator bulbi muscle by the Vth cranial nerve (Duellman & Trueb, 1994).

Comments

As with mudskippers, frog's eyes sit on the dorsum of the skull and in some species are elevated above the skull allowing aerial vision for the detection of prey and predators, while the rest of the animal remains submerged in water. And, as with mudskippers,

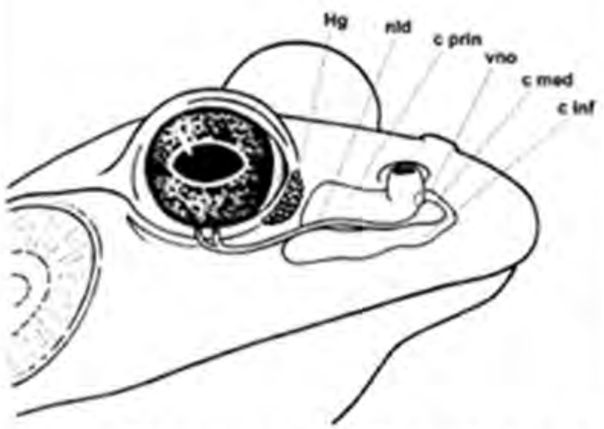


FIG. 1. Schematic diagram of the nasal cavity of a frog in right anterolateral view. Abbreviations: c inf, cavum inferius; c med, cavum medium; c prin, cavum principale; Hg, Harderian gland; nld, nasolacrimal duct; vno, vomeronasal organ.

Nasolacrimal duct (nld) connecting the conjunctival space with the nasal cavity (Hillenius, 2001)

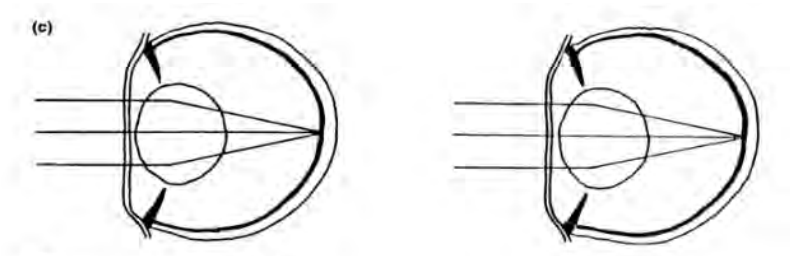
blinking involves retraction of the globes into the skull. Frogs have upper and lower eyelids, although the upper one appears to have no movement independent of the eyeball – sinking a little as the eyeball retracts. The lower lid rises a little on globe retraction but the nictitating membrane, which is a fold arising from the inner surface of the lower lid, rises to fully cover the cornea in a full blink and during sleep. The membrane is usually semi-transparent, preventing complete loss of vision during a blink, an advantage in the presence of predators or prey. Winking has a similar benefit. The nictitating membrane moistens the surface of the cornea by spreading oily secretions from a gland present in all vertebrates with a nictitating membrane, the Harderian gland, which fills most of the orbit (while also providing cushioning behind the eye). The secretions of the Harderian drain from the lacrimal duct, which opens in the middle of the lower eyelid (unlike mammals where the duct opens in puncta on the medial end of the upper and lower eyelids), into the nasal cavity (Duellman & Trueb, 1994). There is a circulation of secretions from the gland into the conjunctival space and then into the nasal cavity via the nasolacrimal duct (Figure below). The nictitating membrane probably also protects the cornea from floating debris when the eye is open. Retraction of the globe into the skull protects the eye from mechanical injury from pressure or from a blow, an important function as frogs lack a neck and can jump but cannot turn their heads to avoid injury. Uniquely, blinking in frogs also aids in swallowing as the retracted eyes project into the throat.

In summary, frogs have the following features of blinking which are additional to those seen in mudskippers: a mobile lower lid, a semi-transparent nictitating membrane and a gland which lubricates the cornea. Blinking in frogs is initiated by retraction of the globe by the retractor bulbi muscle. This causes elevation of the nictitating membrane by pulling on its tendon, which circles the globe. The nictitating membrane is an extension of the lower eyelid. There is no muscle pulling on the nictitating membrane tendon other than the retractor bulbi muscle to which it is attached, so movement of the nictitating membrane/lower eyelid and retraction of the globe cannot occur independently of each other. The upper eyelid has no muscles or tendons attached to it. Any movement of the upper eyelid which occurs is therefore passive, caused by the eyeball on which it rests, retracting into the skull and then protruding at the end of the blink.

Turtles (Order Testudines)

Turtles are reptiles with a bony carapace. They are of the order Testudines, also known as Chelonia. DNA sequencing places turtles close to Archosaurs (birds, crocodiles and dinosaurs) (Crawford, Parham, & al, 2014). The clade which includes Testudines and Archosaurs is called Archelosauria. Turtles are further subdivided into Cryptodira which can retract the head directly into the shell, and Pleurodira which fold their necks to the side to protect their heads.

Turtles have diversified little since ancestors of the 348 extant species first appeared 220mya, except for a period when continental coastal margins appeared 30mya increasing the size of their potential habitat (Thompson, 1961). No taxonomic distinction is made between turtles, tortoises and terrapins. Turtles have round pupils. As with mudskippers, turtles which are primarily aquatic have had to deal with changes in the focussing properties of the cornea depending on whether they are looking through water or air. This problem has been dealt with in sea turtles by evolving flat corneas which do not refract light (figure below).



Refraction with a flat cornea in sea turtles (left water; right air)

Blinks are shown in a number of turtles:

The study

31 species of turtle were studied (Table below). All turtles blinked with their lower lids. Most had 2-3 ridges in the lower lid which pulled apart as the lid rose to cover the eye and the globe retracted. Some turtles had movement of the nictitating membrane during a lower eyelid blink though often the excursion of the membrane across the eye was incomplete. In others, there appeared to be a nictitating membrane in the medial canthus when the eye was open, but it was not possible to see whether it moved, as the lower lid closed so rapidly during a blink. Sometimes it could be seen withdrawing as the lower lid descended at the end of the blink. So, turtles were classified into having a resting/vestigial nictitating membrane, or a mobile nictitating membrane. 1 of 7 species of the sub-order Pleurodira had mobile nictitating membranes. 16 of 24 species of the sub-order Cryptodira had mobile nictitating membranes and in 5 the nictitating membrane was visible before the blink.

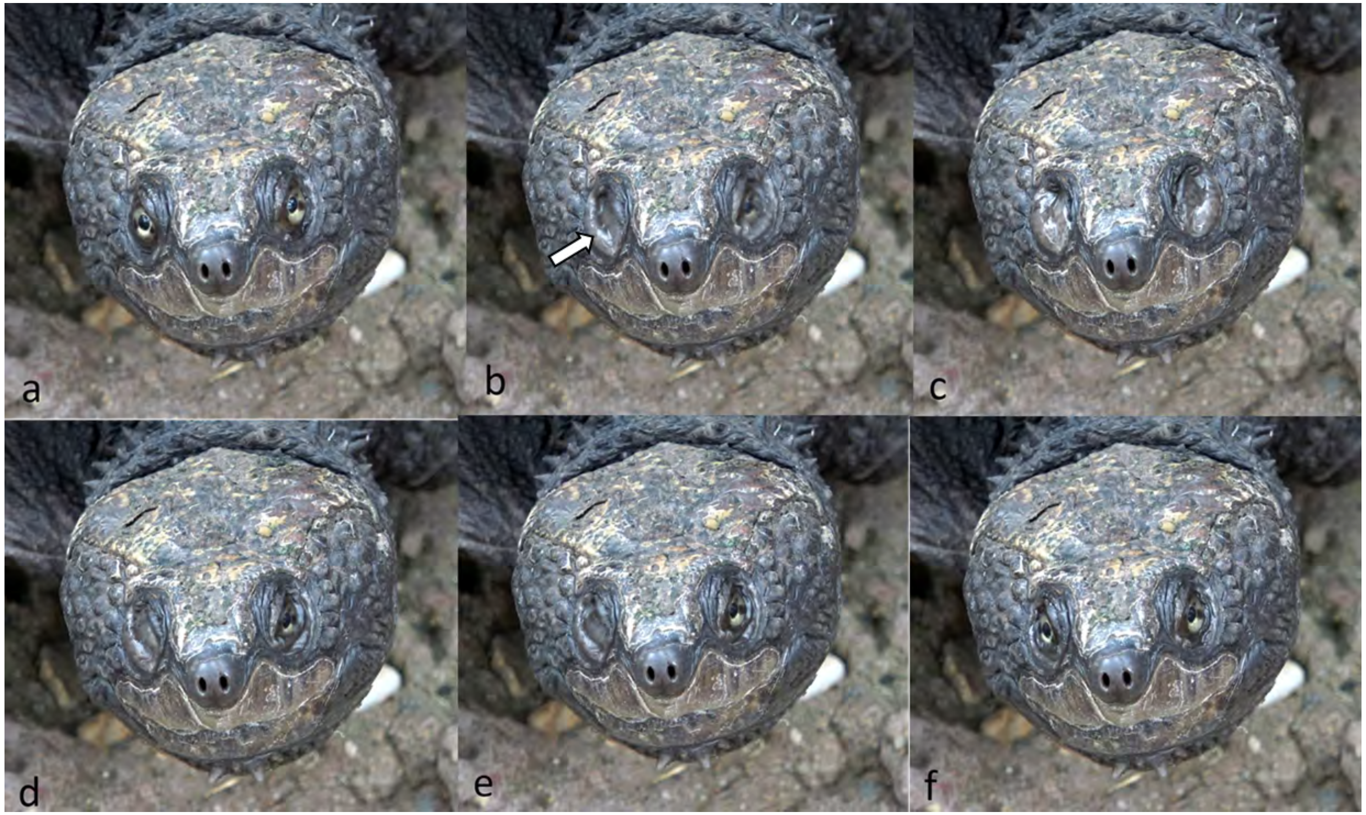
Suborder	**Family**	***Species/Genus/Family***	**Common name**	**Source**	**Vestigial/resting**	**Mobile nictitating**	**Globe retraction**	**Freshwater**	**Terrestrial**	**Marine**
Pleurodira	Chelidae	*Chelodina longicollis*	Eastern long-necked turtle	Video			Y	Y		
Pleurodira	Chelidae	*Emydura macquarii*	Murray River turtle	Video			Y	Y		
Pleurodira	Chelidae	*Emydura subglobosa worrelli*	Diamond head turtle	Video				Y		
Pleurodira	Chelidae	*Myuchelys latisternum*	Saw shelled turtle	Video			Y	Y		
Pleurodira	Pelomedusidae	*Pelomedusa subrufus*	African helmeted	Video			Y	Y		
Pleurodira	Podocnemididae	*Erymnochelys madagascariensis*	Madagascan big-headed turtle	Video		Y	Y	Y		
Pleurodira	Podocnemididae	*Podocnemis expansa*	Arrau turtle	Internet			Y	Y		
Cryptodira	Carettochelyidae	*Carettochelys insculpta*	Pig nosed turtle	Video		Y	Y	Y		
Cryptodira	Chelydridae	*Chelydra serpentina*	Common snapping turtle	Internet		Y		Y		
Cryptodira	Cheloniidae	*Caretta caretta*	Loggerhead turtle	Internet		Y	Y			Y
Cryptodira	Cheloniidae	*Chelonia mydas*	Green sea turtle	Internet		Y	Y			Y
Cryptodira	Cheloniidae	*Natator depressus*	Flatback sea turtle	Internet	Y		Y			Y
Cryptodira	Cheloniidae	*Eretmochelys imbricata*	Hawksbill sea	Internet		Y				Y
Cryptodira	Cheloniidae	*Lepidochelys olivacea*	Olive ridley sea turtle	Internet	Y					Y
Cryptodira	Dermochelyidae	*Dermochelys coriacea*	Leatherback sea	Internet		Y	Y			Y
Cryptodira	Emydidae	*Pseudemys concinna*	River cooter	Video			Y	Y		
Cryptodira	Emydidae	*Trachemys scripta scripta*	Yellow belled	Video	Y			Y		
Cryptodira	Emydidae	*Trachemys scripta elegans*	Red eared slider	Video	Y			Y		
Cryptodira	Geoemydidae	*Mauremys sinensis*	Chinese stripe necked turtle	Video	Y		Y	Y		
Cryptodira	Kinosternidae	*Sternotherus odoratus*	Eastern musk	Internet			Y	Y		
Cryptodira	Testudinidae	*Chelonoidis niger*	Galápagos tortoise	Video		Y	Y		Y	
Cryptodira	Testudinidae	*Chelonoidis denticulatus*	Yellow footed tortoise	Video		Y	Y		Y	
Cryptodira	Testudinidae	*Indotestudo elongata*	Elongated tortoise	Video		Y	Y		Y	
Cryptodira	Testudinidae	*Geochelone elegans*	Indian star tortoise	Video		Y	Y		Y	
Cryptodira	Testudinidae	*Geochelone gigantea*	Aldabra giant	Video		Y	Y		Y	
Cryptodira	Testudinidae	*Stigmochelys pardalis*	Leopard tortoise	Video		Y	Y		Y	
Cryptodira	Testudinidae	*Centrochelys sulcata*	African spurred tortoise	Video		Y			Y	
Cryptodira	Testudinidae	*Manouria emys*	Asian forest	Video		Y	Y		Y	
Cryptodira	Testudinidae	*Asrochelys radiata*	Radiated tortoise	Video		Y	Y		Y	
Cryptodira	Testudinidae	*Chelonoidis carbonaris*	Red footed	Video		Y	Y		Y	
Cryptodira	Trionychidae	*Apalone spinifera*	Chinese softshell turtle	Internet	Y			Y		

Freshwater turtles

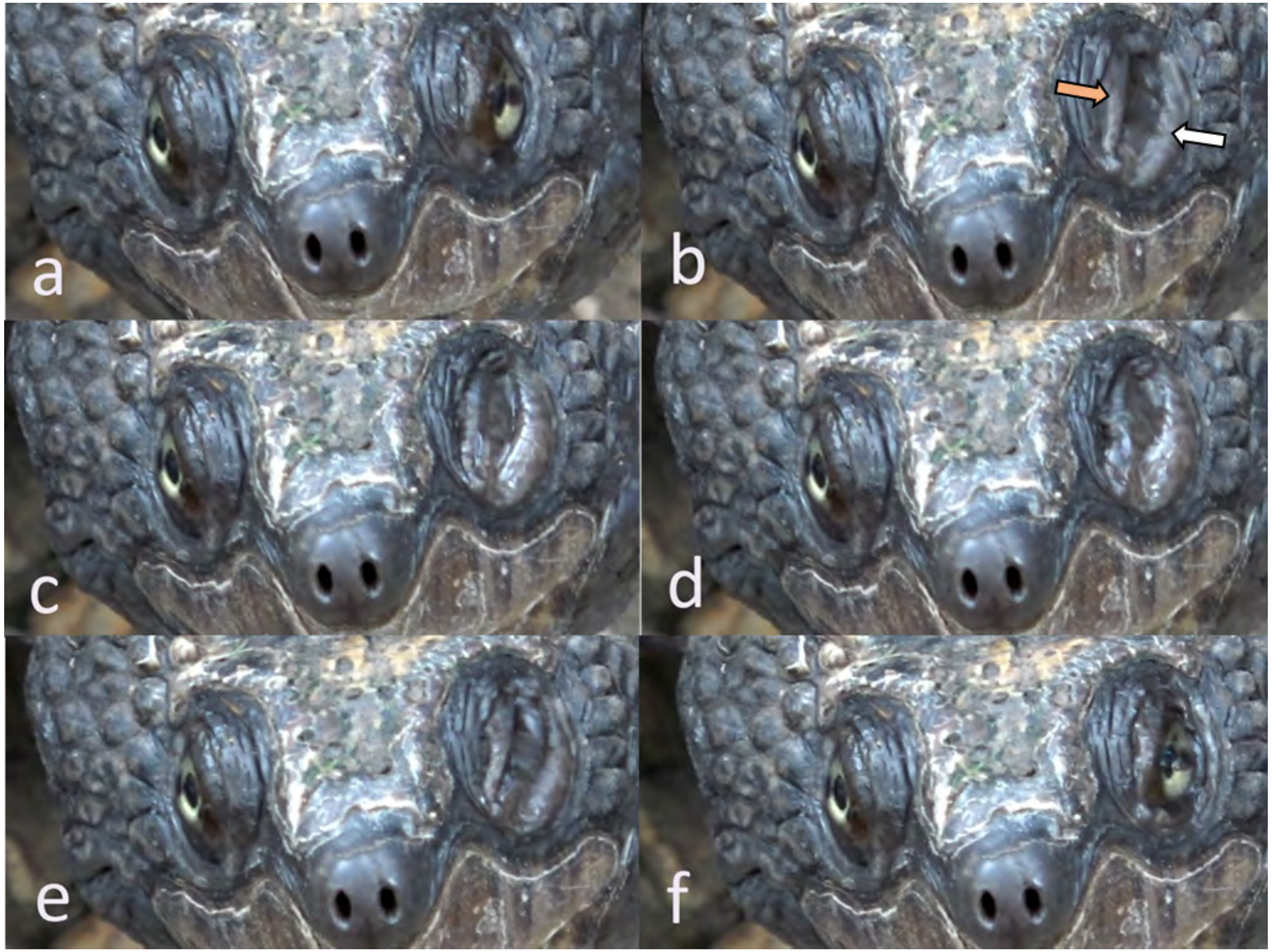
Family Chelidae

Saw shelled turtle (*Myuchelys latisternum*)

Globe retraction with elevation of lower lid nictitating membrane



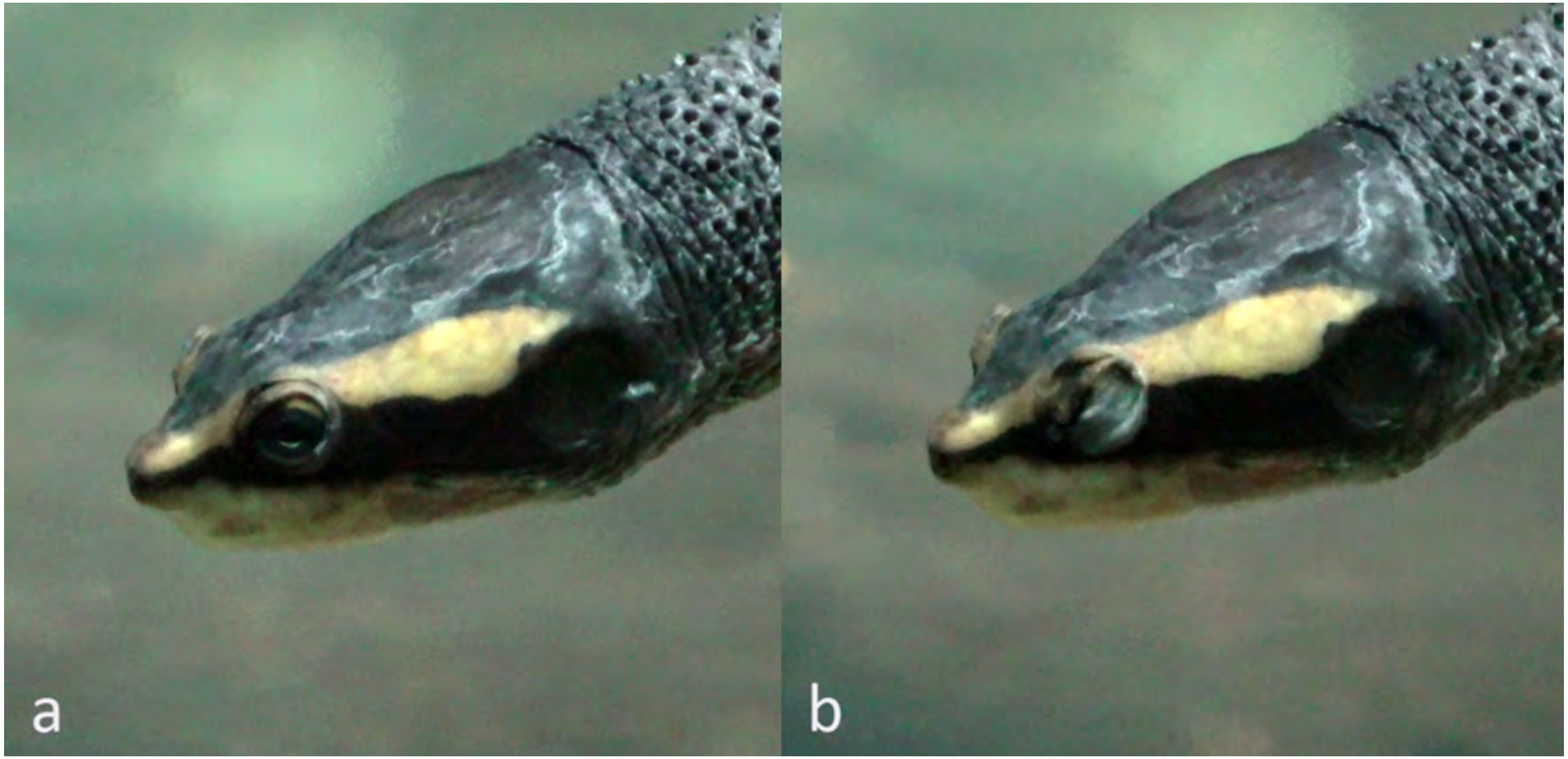
a) Pre-blink. b) Both eyes are retracted and the right covered. The left eye is still visible. The inferior part of the right lower lid (white arrow) is thicker than the superior part which covers the eye. c) Both eyes are covered by the lower lids. d) and e) The left eye opens. f) Post-blink.



Wink in the same species at higher magnification: a) Pre-blink. b), c) and d) Left eye is retracted and both upper (orange arrow) and lower lids (white arrow) are prominent as they sink into the orbit. The thinner superior part of the lower lid has covered the left eye. e) The lower lid is descending. f) Post-blink.

Red-bellied short-necked turtle (*Emydura subglobosa*)

Globe retraction with elevation of lower lid nictitating membrane

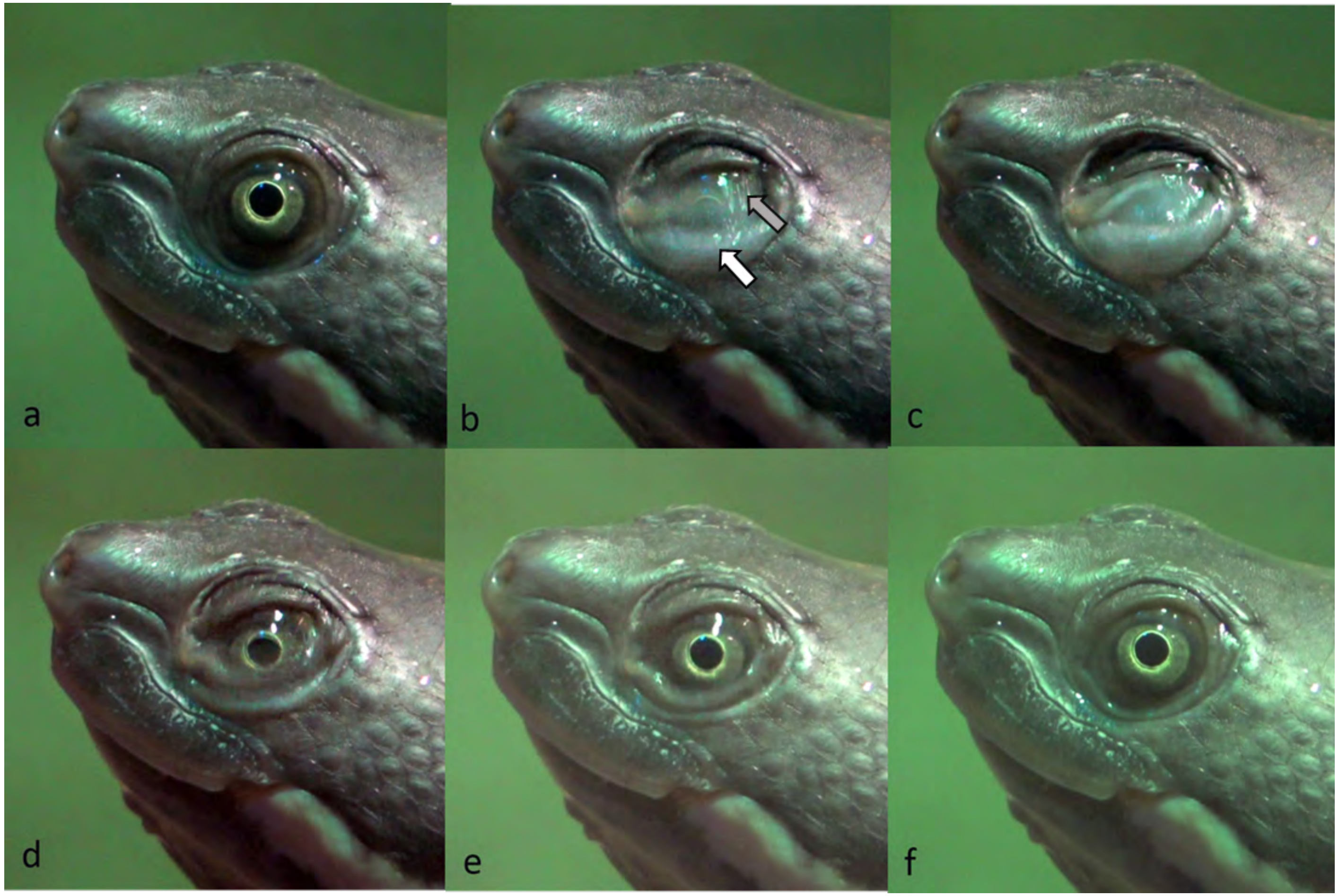


Swimming underwater. a) Pre-blink. b) Lower lid elevated during a blink.

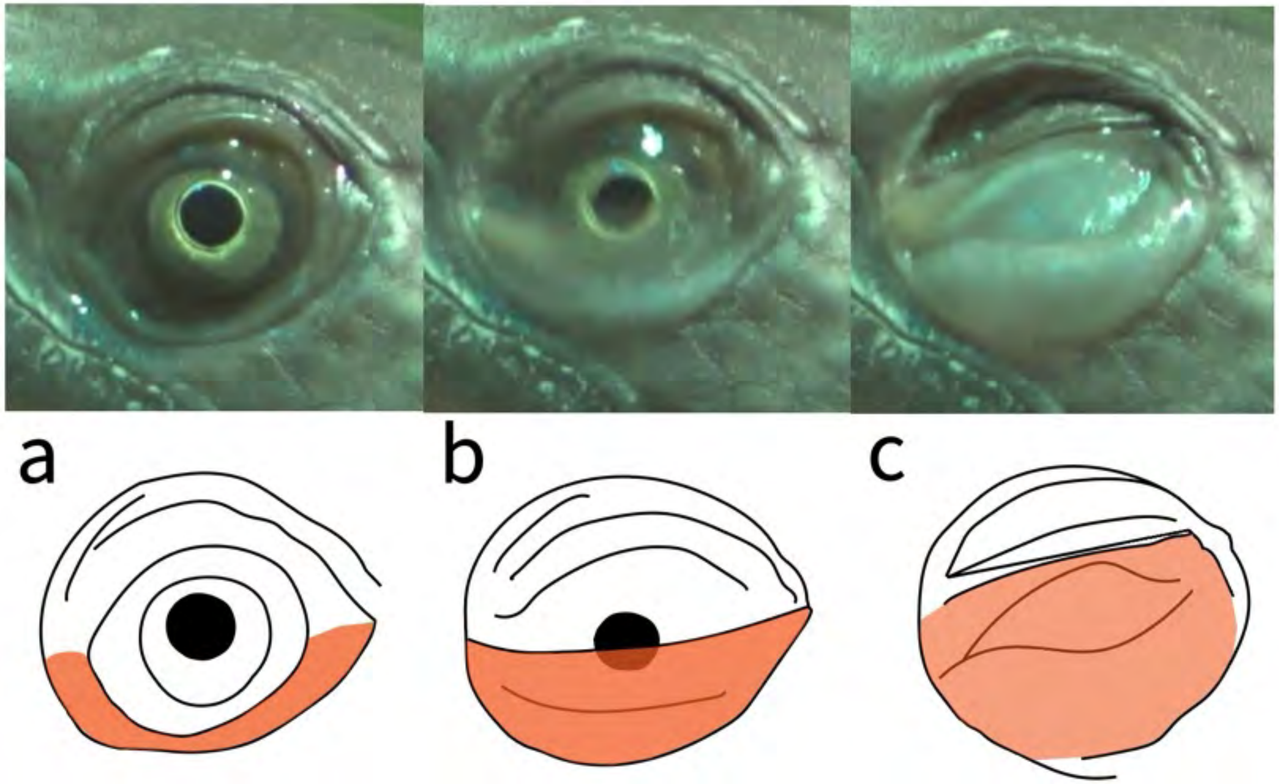
Murray River turtle (*Emydura macquarii*)

Globe retraction with elevation of 'lower lid nictitating membrane'

a) Pre-blink. b) Maximal blink. The upper lid has lowered slightly due to globe retraction. The eye is covered by the lower lid which comprises two parts: a semi-translucent upper section (grey arrow) and an opaque lower section (white arrow). c) Post-blink.



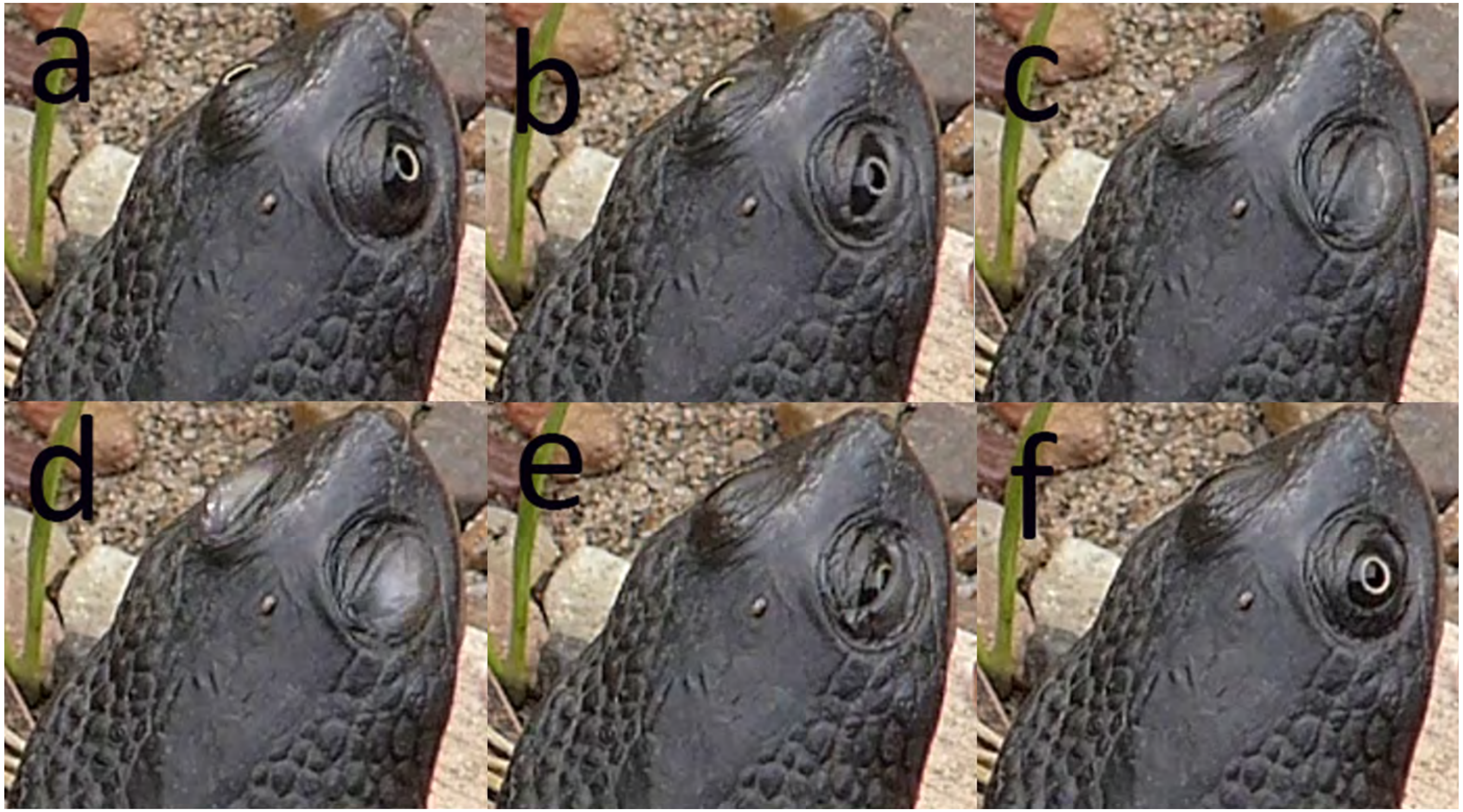
Murray River turtle underwater: a) Pre-blink. b) Upper lid sinks as globe retracts. Eye covered by semi-translucent upper section of the lower lid (grey arrow) and opaque lower section (white arrow). c) Maximal blink. d) and e) Lower lid descends. f) Post-blink



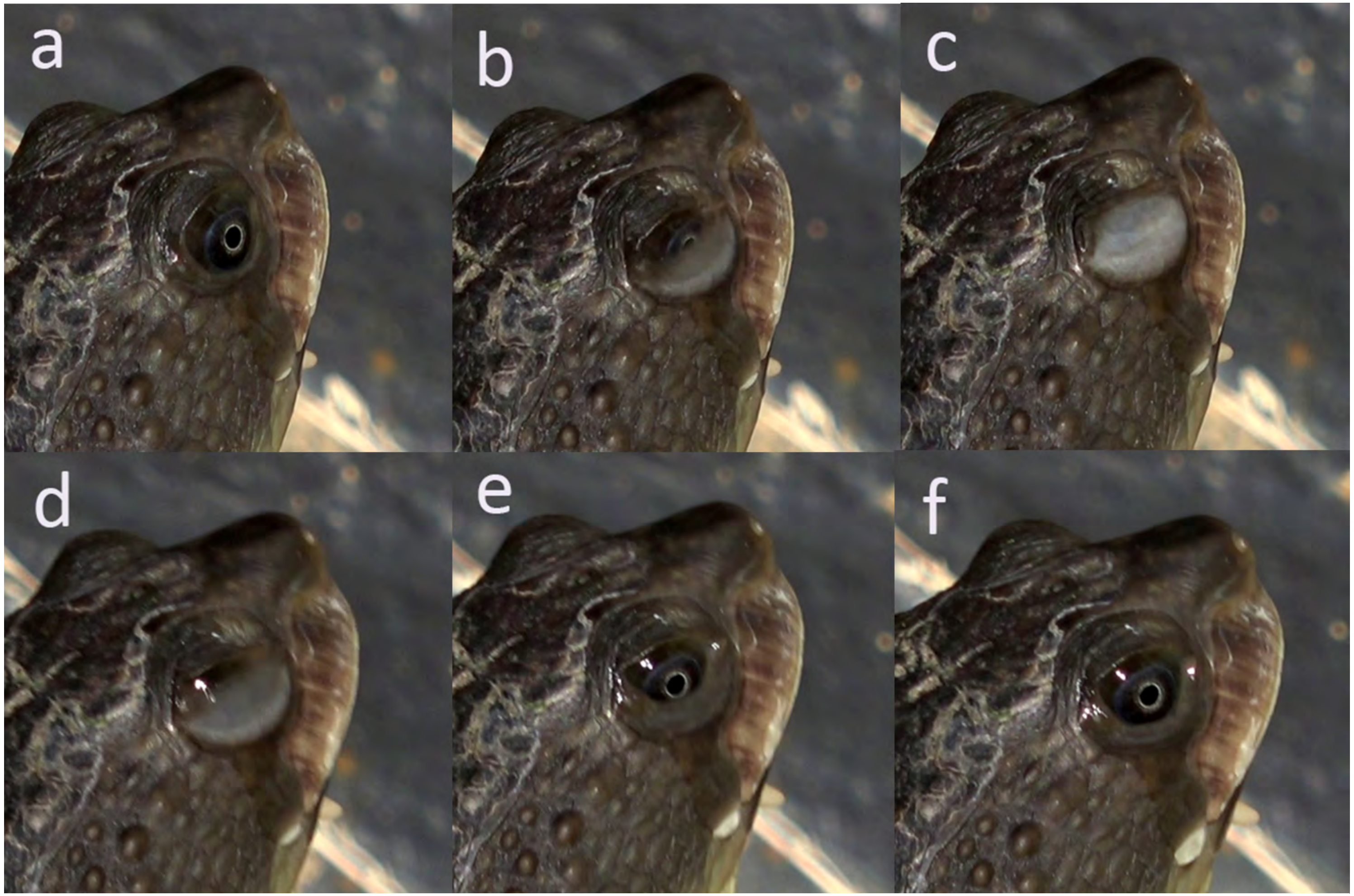
Lower lid blink with globe retraction in the right eye: a) Pre-blink showing no evidence of a nictitating membrane. b) Blink involving elevation of the upper and lower segments of the lower lid to the level of the pupil. c) Maximum excursion of the lower lid, covering the eye. The upper and lower segments of the lower lid are separated by a crease.

Eastern long-necked turtle (*Chelodina longicollis*)

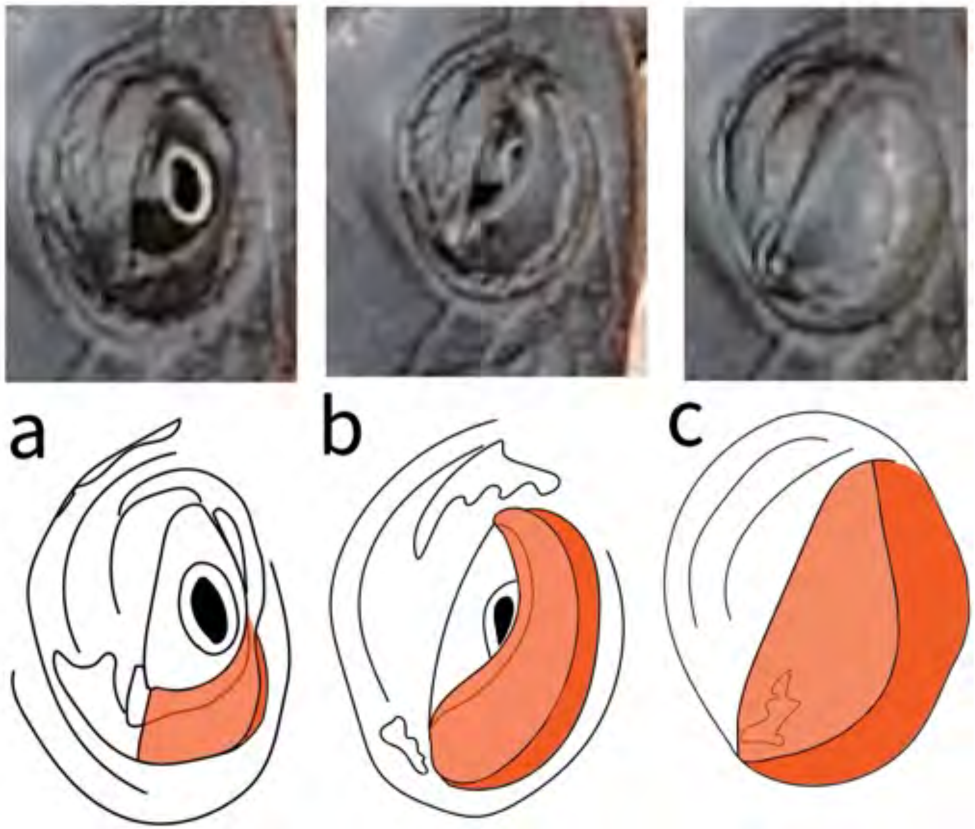
Globe retraction with elevation of 'lower lid nictitating membrane'



a) Pre-blink. b) Globes retract and right palpebral fissure narrows. c) and d) Lower lid, comprising thin upper and thicker lower sections, covers the eye. e) Lower lid descends. e) Post-blink.



Right eye of eastern long-necked turtle from side and at higher magnification. a) Pre-blink. b) Lower half of the eye covered by the lower lid, more opaque in the lower region than the upper. c) Full blink. d) Lower lid start to descend. e) Lower lid now looks brown, perhaps due to its upper part folding behind the lower part. f) Post-blink

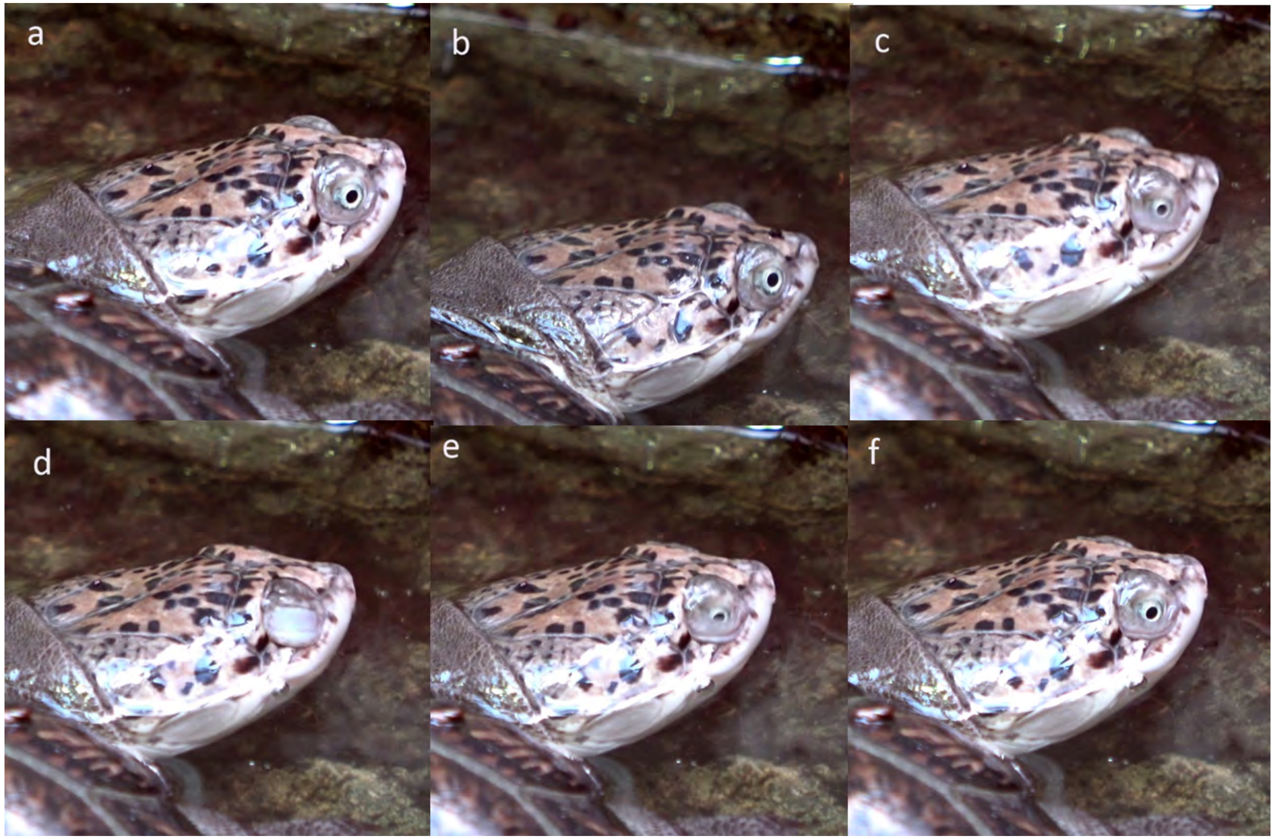


Lower lid blink with globe retraction in the right eye:
a) Pre- blink showing mainly the upper segment of the lower lid (orange). No nictitating membrane visible. b) Blink involving elevation of the upper and lower segments of the lower lid. Again, no nictitating membrane visible. c) Maximum excursion of the lower lid - covering the eye. The upper and lower segments of the lower lid are marked by a crease.

Family Pelomedusidae

African helmeted turtle (*Pelomedusa subrufus nigra*)

Globe retraction with elevation of 'lower lid nictitating membrane'

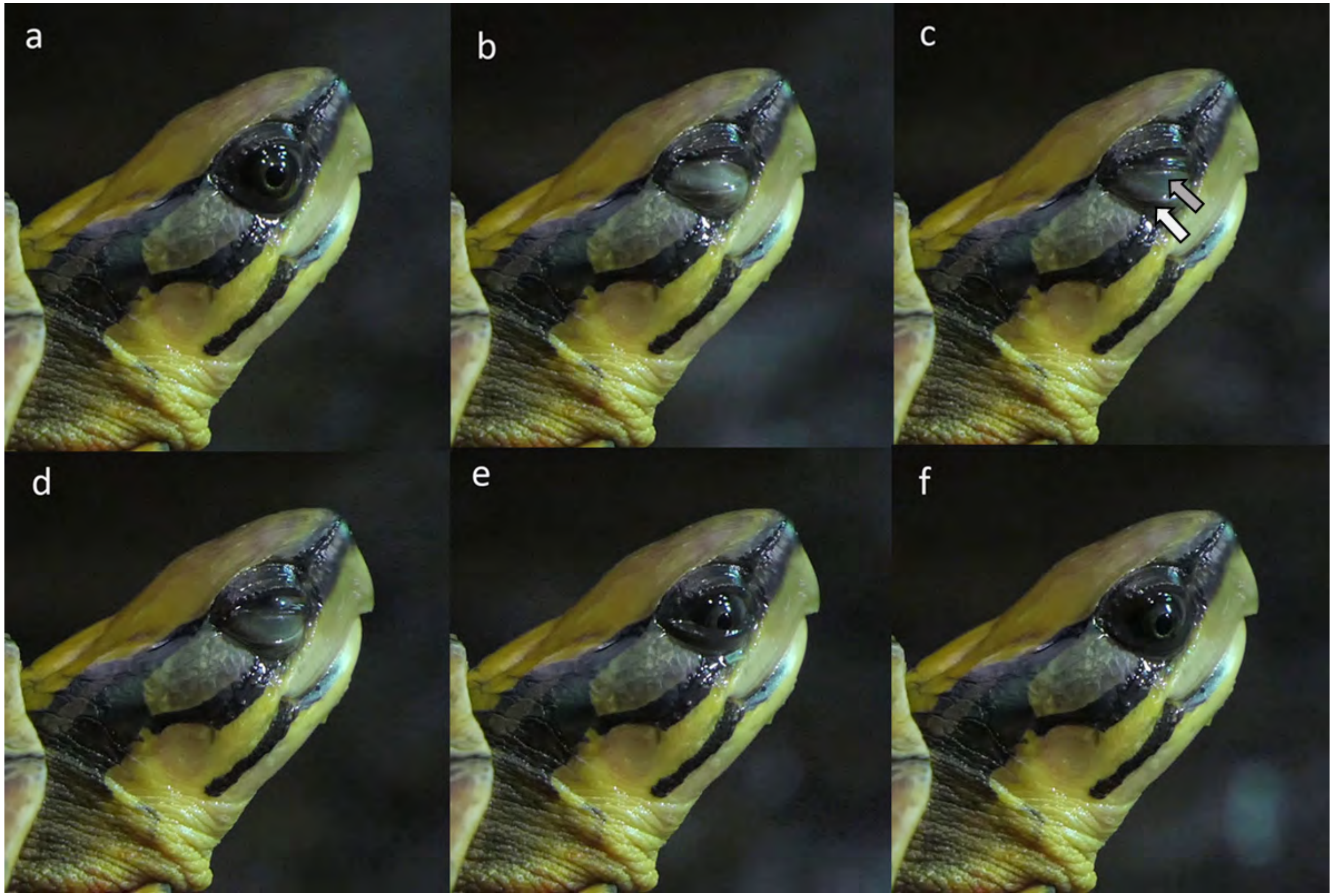


a) Before lowering head into water. b) Emerging from water. c) Lower lid rising. d) Lower lid maximally raised – appears to be in two parts. e) Lower lid descending. e) Post-blink.

Family Geoemydidae

Spiny turtle (*Heosemys spinosa*)

Globe retraction with elevation of 'lower lid nictitating membrane'

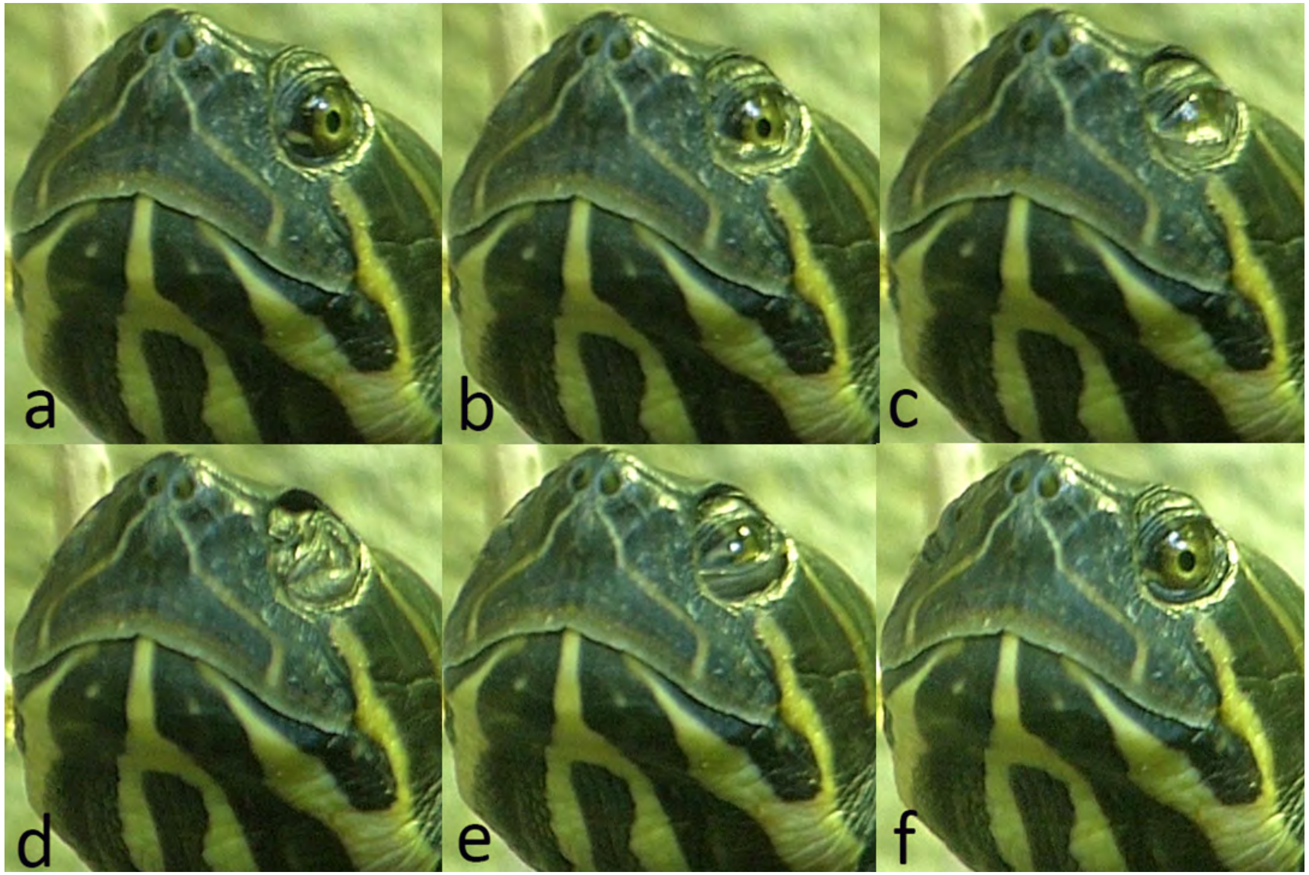


a) Pre-blink. b) Eye covered with lower lid with a paler upper section. c) and d) Semi-translucent upper section of lid (grey arrow) and brown opaque lower section (white arrow) descending. e) Semi-translucent section has now disappeared behind the lower section of the lower lid. f) Post-blink.

Family Emydidae

River cooter (*Pseudemys concinna*)

Globe retraction with elevation of 'lower lid nictitating membrane'

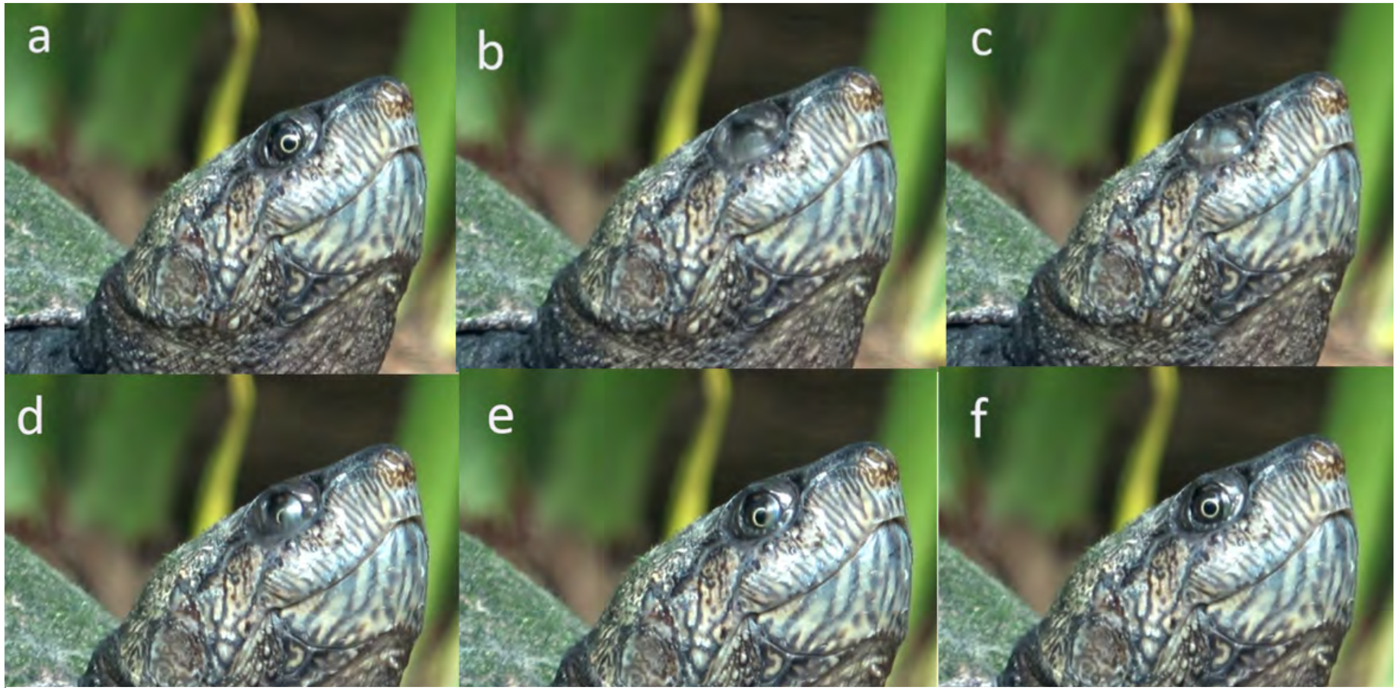


a) Pre-blink. b) Eye begins to retract and lower lid rises. c) Eye covered by lower lid, semi-translucent in the upper part, opaque and thicker in the lower part. d) Lower lid starts to fall. e) Upper section of lower lid tucks behind lower section revealing eye. f) Post-blink

Family Podocnemididae

Madagascan big-headed turtle (*Erymnochelys madagascariensis*)

Globe retraction, elevation of lower lid and horizontal movement of 'inner canthus nictitating membrane'



a) Pre-blink. b) Globe retracts and lower lid elevates. c) Lower lid descends but eye remains covered by semi-translucent nictitating membrane. d) Nictitating membrane can be seen half-way across the pupil withdrawing towards the inner canthus. e) More of the pupil is exposed as th membrane withdraws. f) Post-blink. The key observation here is that the nictitating membrane appears to move independently of globe retraction and lower lid movement.


d
e

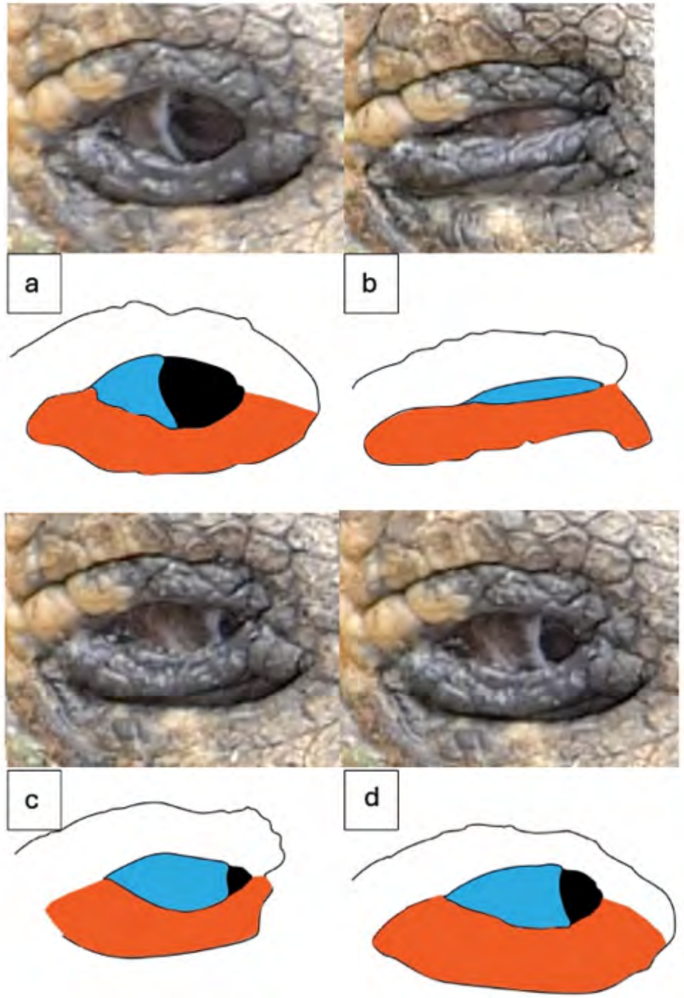
Terrestrial tortoises

Family Testudinidae

Galápagos tortoise (*Chelonoidis niger*)

Globe retraction, elevation of lower lid and horizontal movement of nictitating membrane

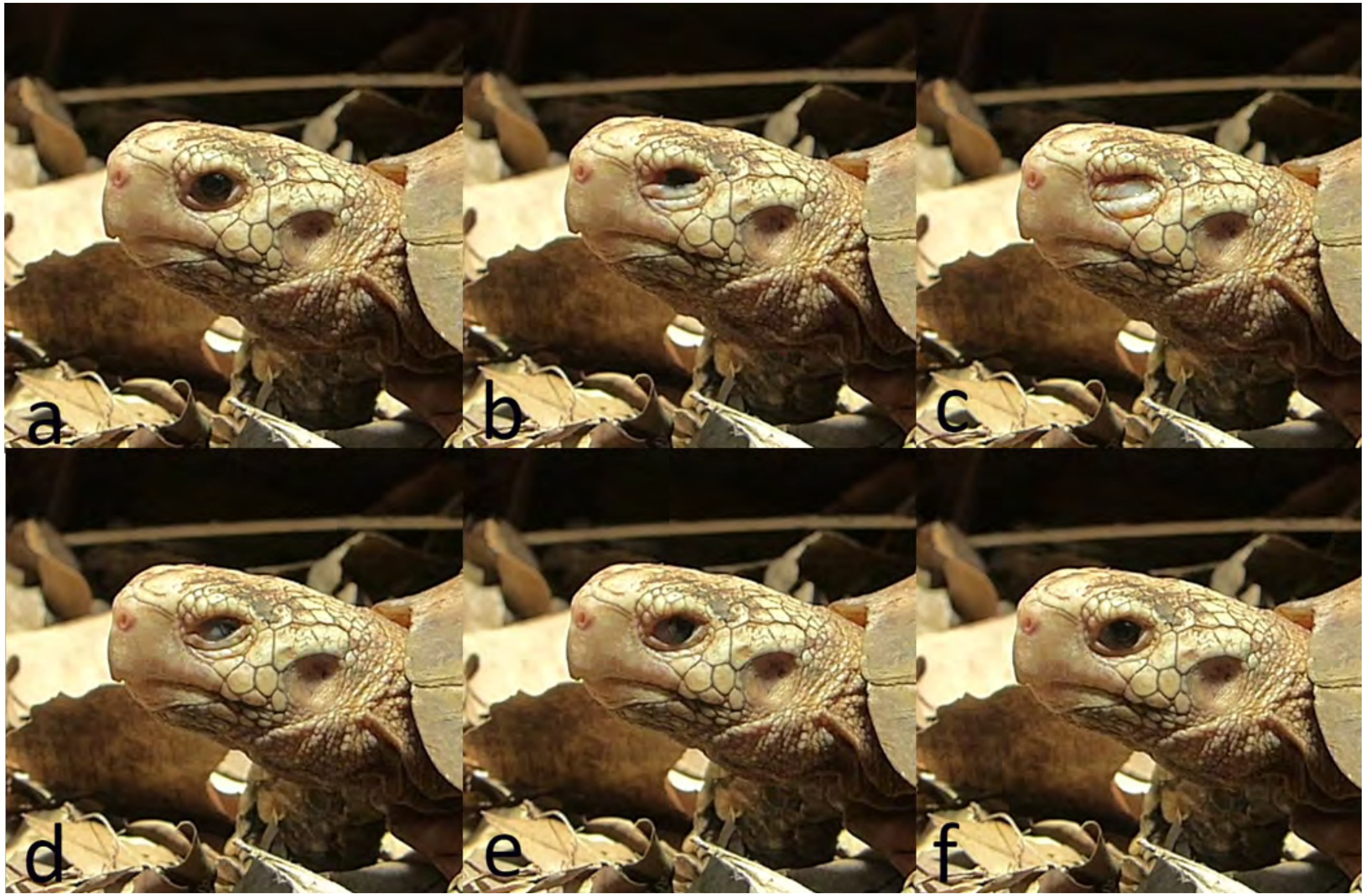
a) Pre-blink. b) Globe retraction begins. c) Full globe retraction causing lids to sink into the orbit. Lower lid elevation, closing the eye. d) Edge of nictitating membrane (grey arrow) visible as eye starts to open. e) Nictitating membrane moves back towards the inner fornix. f) Post-blink.



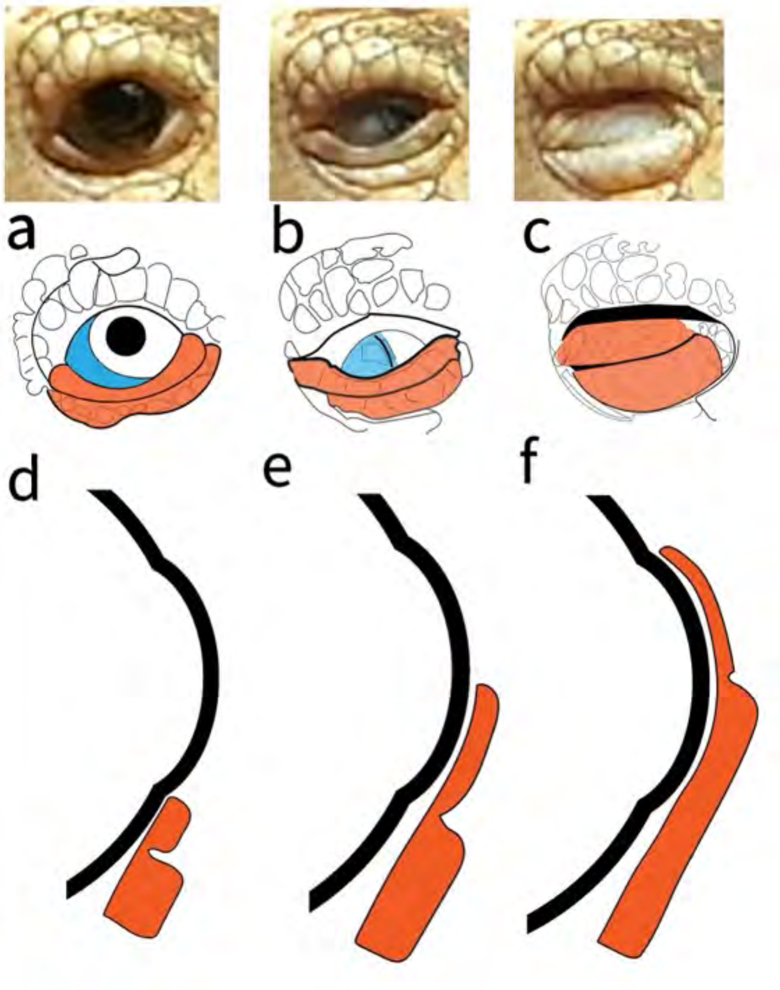
Nictitating membrane and lower lid blink with globe retraction, left eye: a) Pre-blink showing a resting nictitating membrane (blue) in the medial canthus. There is a clearly defined lower lid (orange) with no folds. b) Globe retraction and elevation of lower lid with full excursion of nictitating membrane. The upper lid has sunk into the orbit due to globe retraction. c) and d) Lower lid starts to fall and nictitating membrane begins to return to resting position.

Elongated tortoise (*Indotestudo elongata*)

Globe retraction, elevation of lower lid and horizontal movement of 'inner canthus nictitating membrane'



a) Pre-blink. b) Globe retraction and elevation of the lower eyelid c) Full elevation of the lower eyelid d) Lower lid descends revealing nictitating membrane halfway across the eye e) Lower lid descends further f) Post-blink.



Nictitating membrane and lower lid blink with globe retraction, left eye: a) Pre-blink showing the nictitating membrane (blue) in its resting position and the two segments of the lower lid (orange) separated by a crease. b) Partial blink involving the nictitating membrane covering the pupil and elevation of the lower lid. c) Maximum excursion of the lower lid, covering the eye. d) Pre-blink. Sagittal plane of the eye showing the two segments of the lower eyelid, e) The segments of the lower lid start to expand around the cornea. f) The lower lid covers the cornea.

Aldabra giant tortoise *(Geochelone gigantea)*

Globe retraction, elevation of lower lid and horizontal movement of ‘inner canthus nictitating membrane’

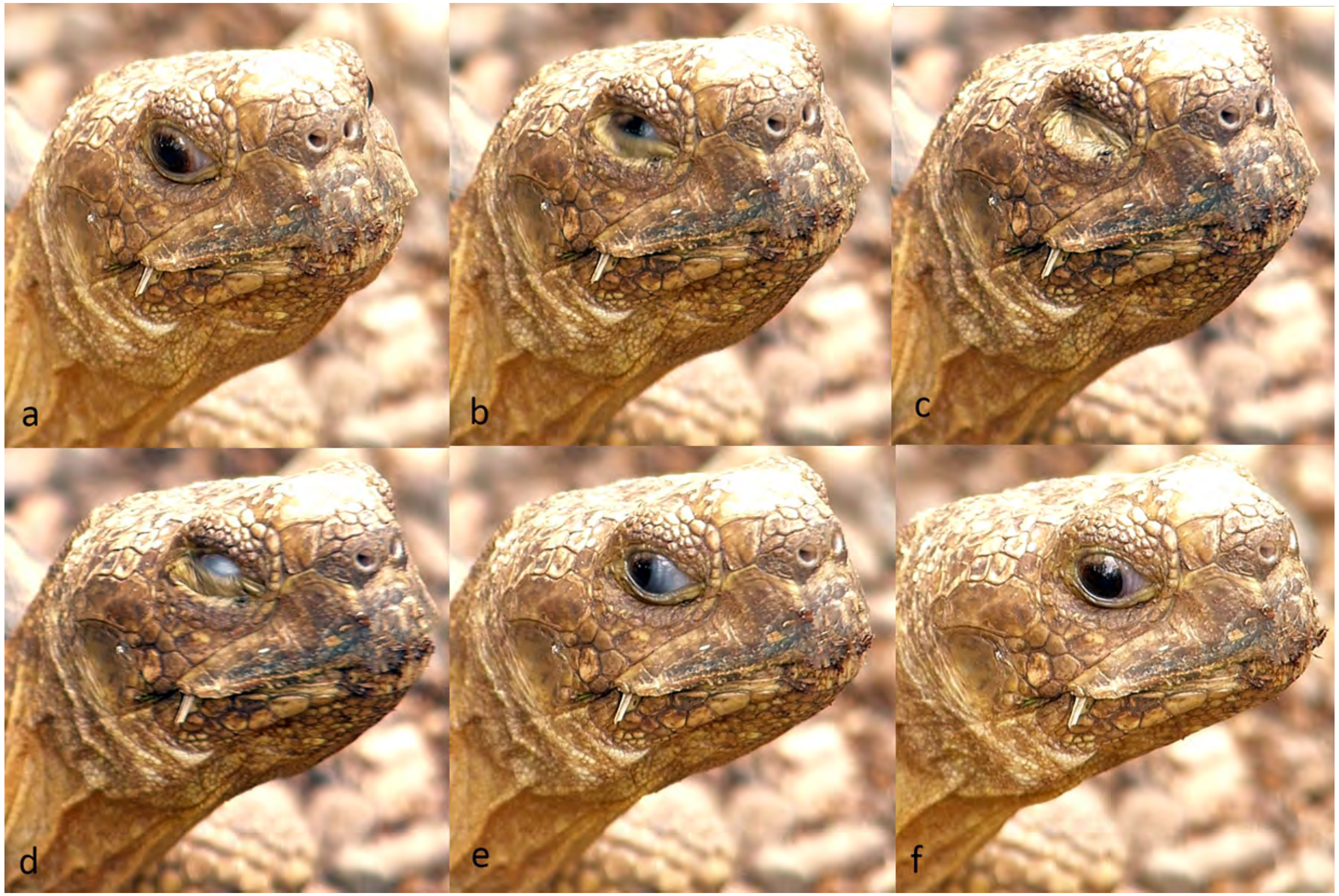
a) Pre-blink. b) Opaque nictitating membrane moves across the eye from the inner canthus. Lower lid elevates slightly. c) Maximal excursion of nictitating membrane and lower lid. d) and e) Nictitating membrane withdraws. f) Post-blink.

Aldabra giant tortoise (Geochelone gigantea) blink from a different angle; a) Pre-blink. b) Opaque nictitating membrane moves across the eye from the inner canthus. Palpebral fissure narrows probably due to retraction of the globe. Lower lid elevates slightly. c) Maximal excursion of nictitating membrane and lower lid. d) and e) Nictitating membrane withdraws. f) Post-blink.

Aldabra giant tortoise (Geochelone gigantea). a) Pre-blink. b) Lower lid rises, globe sinks into orbit. White nictitating membrane visible at inner canthus. c) Maximal excursion of lower lid. d) Lower lid starts to fall. Nictitating membrane visible again. e) Globe still retracted. f) Post-blink.

Leopard tortoise (*Stigmochelys pardalis*)

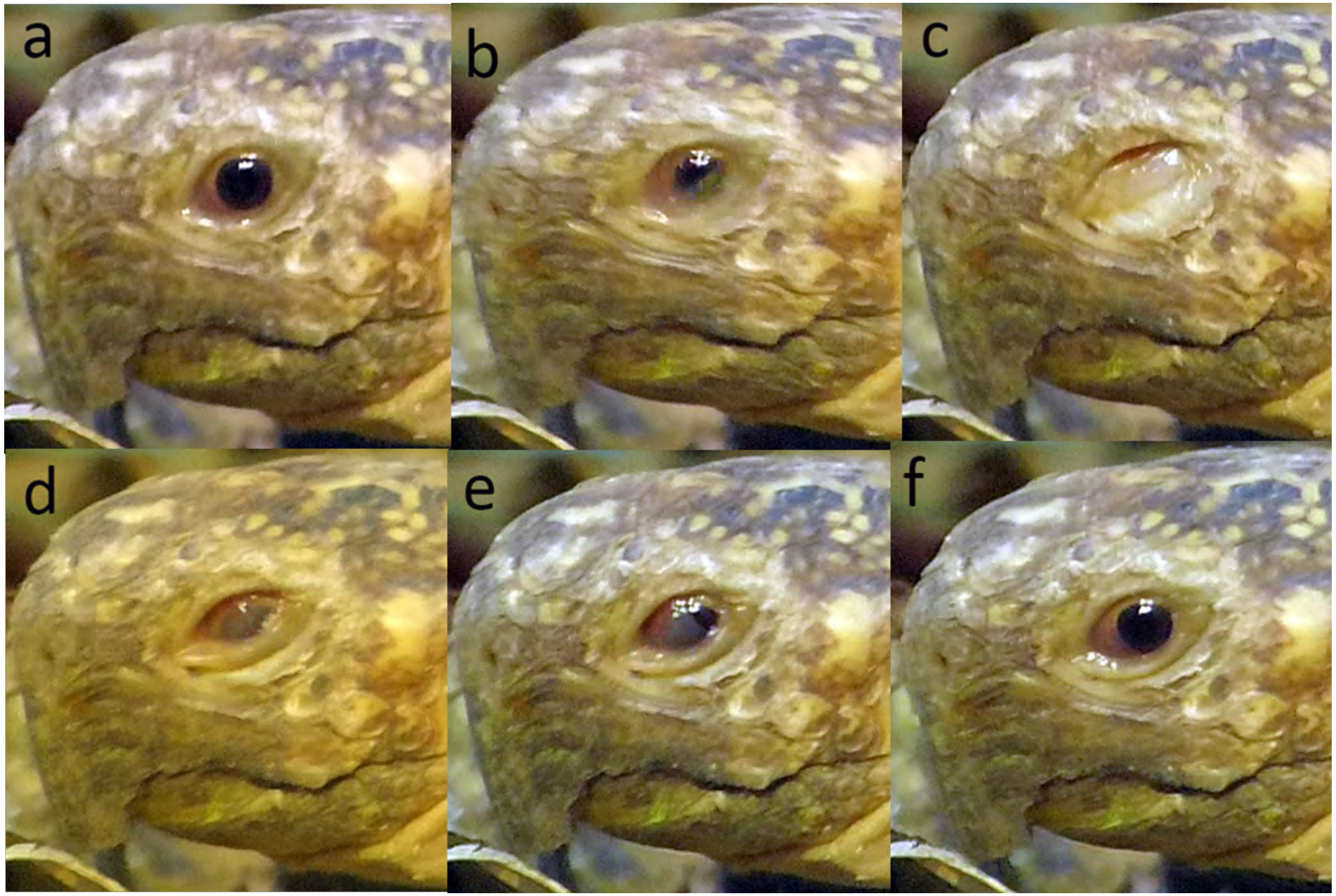
Globe retraction, elevation of lower lid and horizontal movement of 'inner canthus nictitating membrane'



Blink on head turn. a) Pre-blink. b) Retraction of globe, elevation of lower lid, appearance of white nictitating membrane at inner canthus. c) Maximal blink with full retraction of globe. d) Lower lid starting to fall revealing nictitating membrane covering the eye. e) Lower lid down, globe unretracted, nictitating membrane halfway across the eye. f) Post-blink

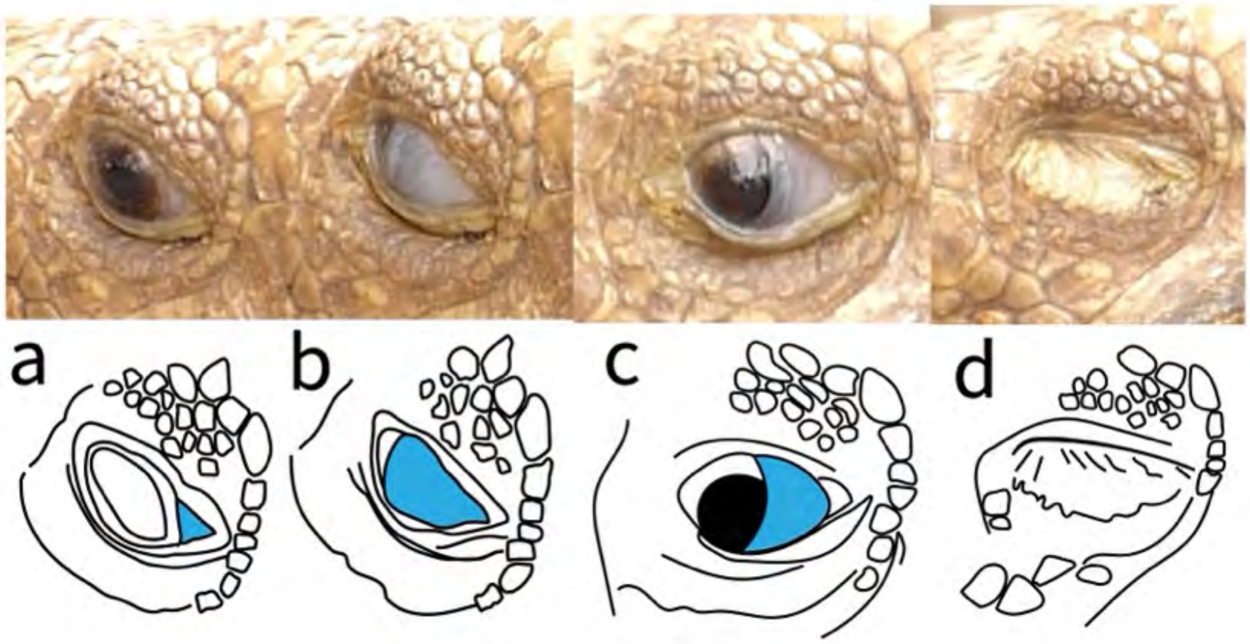
Indian star tortoise (*Geochelone elegans*)

Globe retraction, elevation of lower lid and horizontal movement of nictitating membrane



a) Pre-blink. b) Lower lid elevates to halfway across the pupil. c) Full elevation of lower lid which has a horizontal crease across it. d) Lower lid begins to descend revealing semi-translucent nictitating membrane across the eye. e) Edge of nictitating membrane halfway across the pupil. f) Post blink.

a)



Nictitating membrane blink on head turn, right eye: a) Pre-blink showing the resting nictitating membrane (blue) in the medial canthus. b) The nictitating membrane has almost covered the eye and with no elevation of the lower lid. c) The head has turned and the nictitating membrane has started to retreat. d) The upper lid has fully risen and the globe has retracted causing the lid to sink into the orbit.

Sea turtle

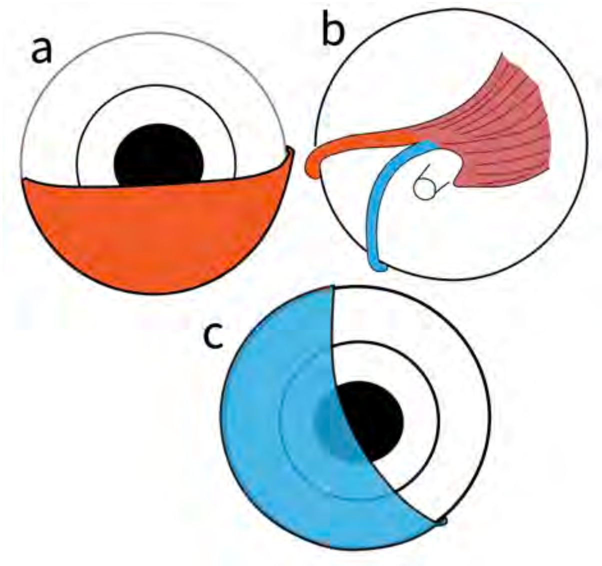
Loggerhead sea turtle (*Caretta caretta*)

Globe retraction, elevation of lower lid and horizontal movement of nictitating membrane

Nictitating membrane (blue) and lower lid (orange), left eye, redrawn from Wyneken (Wyneken, 2012)
The nictitans has multiple folds in the bulbar surface of the membrane probably to increase the production of mucus in order to protect the cornea from the hypertonic salty secretions of the harderian gland (Brudenall, Schwab, & Fritsches, 2008).

Legler (Legler, 1993) reports that Harderian glands and ducts are absent in all Australian chelids and in all chelonian taxa which lack or have vestigial nictitating membranes. Lachrymal glands occur in all chelonians. They secrete highly concentrated tears in marine turtles and some estuarine turtles. Turtles lack a nasolachrymal duct from the conjunctival cavity to the nasal passageways. Nictitating membranes are absent in the cryptodiran families Kinosternidae, Dermatemyidae and Carettochelydidae, and are absent or rudimentary in many pleurodires of both families. The membrane is absent or vestigial in all Australian chelids,

Mechanism by which the nictitating membrane and lower lid are moved in turtles



Connections of the quadratus muscle in the left eye of a turtle: a) Lower lid (orange) on the front of the eye. b) Quadratus muscle on the back of the eye with a tendon to the lower lid (orange); and another tendon to the nictitating membrane (blue). c) Nictitating membrane (blue) on the front of the eye. Adapted from Walls (Walls, 1943). *The lower lid is pulled up from the lateral side of the eye. The nictitating membrane is pulled across from the medial side of the eye by its tendon in the fornix below the eye. As the tendons arise from the same muscle, the lid and membrane have to move together. Simultaneous retraction of the globe increases the degree to which the lid and membrane cover the globe.*

It seems that this configuration does not entirely hold for all turtles as the Leopard tortoise (*Stigmochelys pardalis*) (above) was able to cover the eye with the nictitating membrane before elevating the lower lid.

Werneberg found that the pyramidalis muscle was integrated with the retractor bulbi muscle in one specimen of *Emydura subglobosa* (Werneburg, 2011). Presumably movement of the nictitating membrane would always be accompanied by globe retraction in such individuals. The quadratus and retractor bulbi muscles are supplied by the VIth cranial nerve (Gans, 1970).
Harderian gland is *p*resent. There is no lachrymal duct (Gans, 1970).

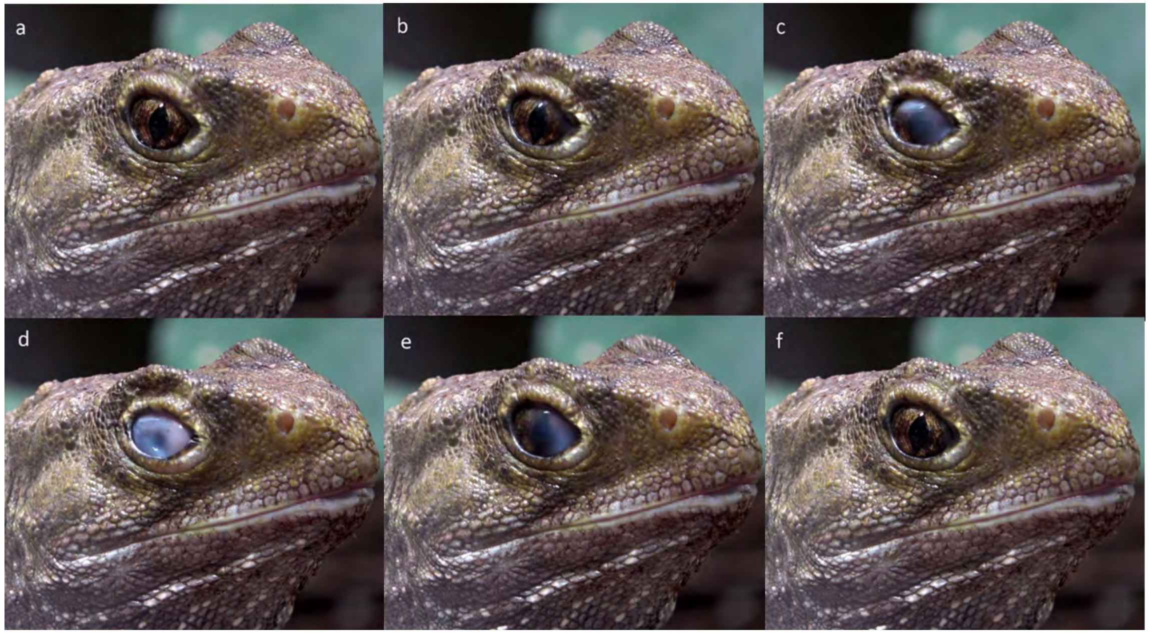
Order: Rhyncocephalia

Rhyncos (Gk: beak or snout; kephale: head). These appeared in the late Triassic (240mya) earlier than Squamata lizards. Only one species survives. Unlike Squamates, their teeth are fused to the jawbone and they have a third eye. They also live much longer (>100 years)

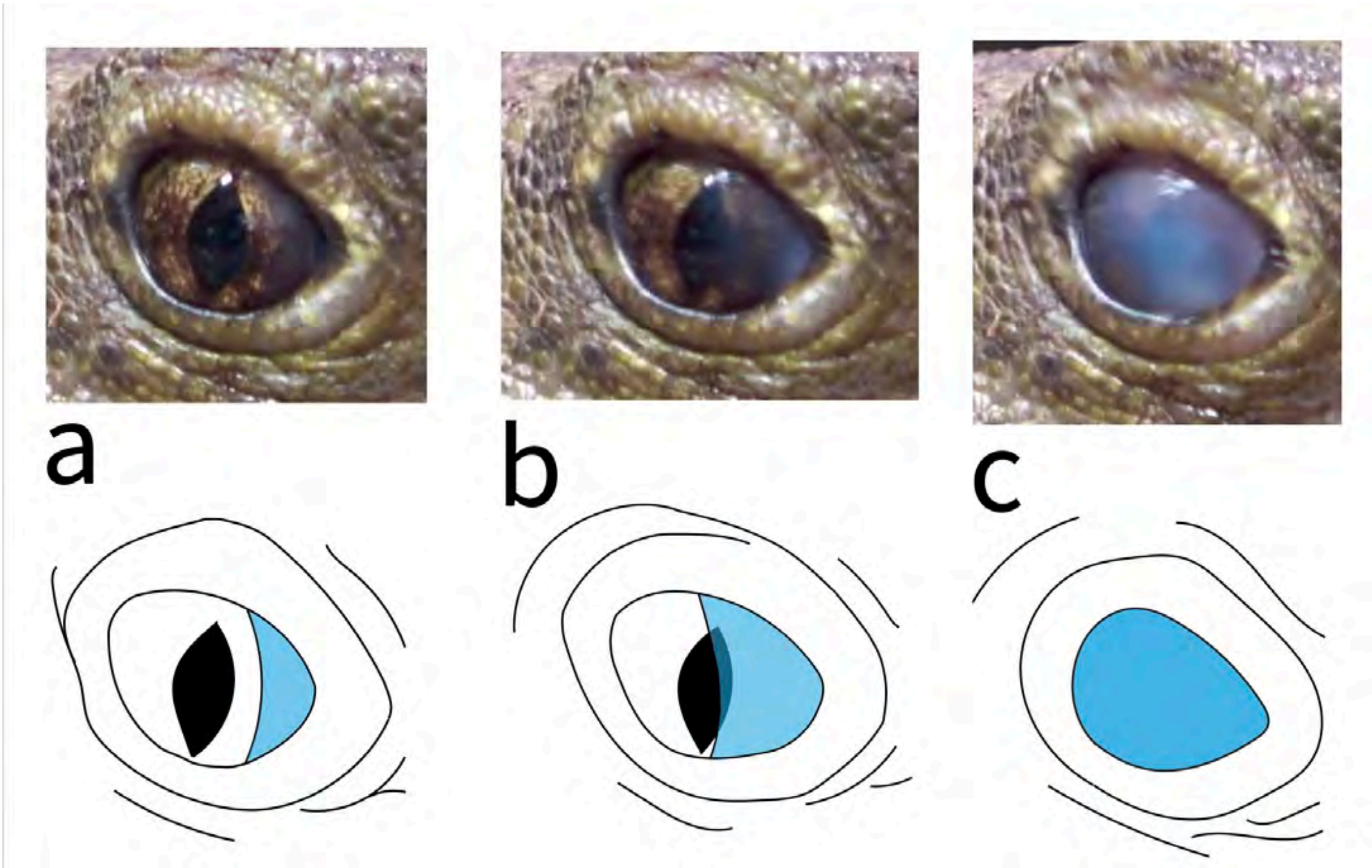
Family: Sphenodontidae

Tuatara (*Sphenodon punctatus*)

Globe retraction with inner canthus nictitating membrane blink

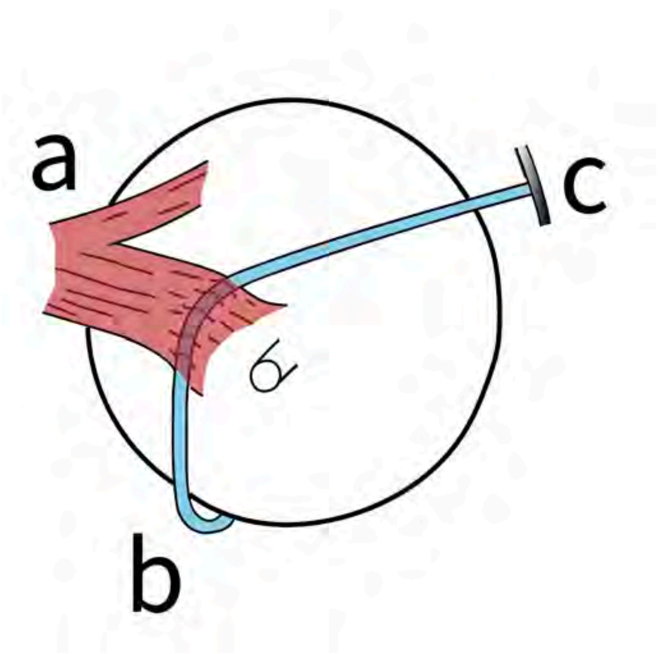


Note the vertically elongated pupil. a) Pre-blink. b) Slight retraction of the globe. c) Nictitating membrane appears from the inner canthus. d) Opaque nictitating membrane covers the eye. d) Globe unretracts and nictitating membrane starts to recede. e) Post-blink.



Nictitating membrane blink in the right eye: a) Pre-blink, showing a vertically elongated pupil and resting nictitating membrane (blue). b) The nictitating membrane reaches the pupil. The lower lid has not moved. c) The nictitating membrane has covered the eye. There is no movement of the eyelids.

Mechanism by which the nictitating membrane is drawn across the eye in the tuatara



The back of the tuatara eye: (a) The retractor bulbi muscle; (b) The tendon of the nictitating membrane, running through the retractor bulbi muscle and inserting onto the dorsal wall of the orbit (c). Adapted from Walls (Walls, 1943). *The nictitating membrane is pulled across the eye when the retractor bulbi muscle contracts. The lower lid moves independently, by the action of the orbicularis oculi muscle.*

The retractor bulbi muscle (which evolved from the lateral rectus muscle) is supplied by the VIth cranial nerve.

Order: Squamata

Lizards

Lizards belong to the Lepidosauria, one of the branches of diapsid (have two-windowed skulls) reptiles (the other being Archosauria: crocodiles and birds). Lepidosauria have two clades: Squamata and Rhyncocephalia. The order squamata (scaled reptiles) includes snakes and lizards and has over 10,000 species. Classifications based on morphology alone have been modified as nuclear (Pyron, 2013) and DNA (Zhan, et al., 2024) based genomic information has become available. According to Zhan, squamata originated in the Late Triassic (206.05 Mya), with the diversification of various superfamilies occurring during the Cretaceous period. The lineage of crown group squamates (those which have extant species) can be traced back to the period immediately after the Triassic-Jurassic extinction event 201Mya. The lizards in this study had round-shaped pupils. In lizards, retraction of the globe, elevation of the lower eyelid and movement of the nictitating membrane are said to occur relatively independently of each other (Walls, 1943). Several types of blink were observed (see table below).

Order	Family	Species	Common name	Source	Nictitating membrane blink	Globe retraction	Lower lid blink	Segmented lower eyelid	Upper lid blink
Rhyncocephalia	Sphenodontidae	Sphenodon punctatus	Tuatara	Video	Y				
Squamata	Agamidae	Ctenophorus nuchalis	Central netted dragon	Video			Y -pushes UL up		
Squamata	Agamidae	Intellagama lesueurii	Eastern water dragon	Video	Y	Y			
Squamata	Agamidae	Lophosaurus boydii	Boyd's forest dragon	Video	Y	Y			Slight
Squamata	Agamidae	Pogona vitticeps	Inland bearded dragon	Video	Y		Y		
Squamata	Chamaeleonidae	Chamaeleo chamaeleon	Common chameleon	Video	Y	Y			
Squamata	Eublepharidae	Eublepharis macularius	Leopard gecko	Video			Y		Y
Squamata	Helodermatidae	Heloderma suspectum	Gila monster	Video			Y		
Squamata	Iguanidae	Brachylophus vitiensis	Fiji crested iguana	Video		Y			
Squamata	Iguanidae	Cyclura cornuat	Rhinoceros iguana	Video			Y	Y	
Squamata	Iguanidae	Iguana iguana	Green iguana	Video	Y	Y	Y	Y	
Squamata	Scincidae	Corucia zebrata	Solomon's Island skink	Video	Y	Y	Y		
Squamata	Scincidae	Egernia cunninghami	Cunningham's skink	Video			Y		
Squamata	Scincidae	Liopholos striata	Desert night skink	Video			Y		
Squamata	Scincidae	Tiliqua rugosa	Shingleback skink	Video		Y	Y		
Squamata	Scincidae	Tiliqua scincoides scincoides	Eastern blue tongue lizard	Video		Y			
Squamata	Scincidae	Egernia rugosa	Yakka skink	Video	Y	Y	Y		
Squamata	Shinisauridae	Shinisaurua crocodilurus	Chinese crocodile lizard	Video	Y			Y	Y
Squamata	Teiidae	Kentropyx pelviceps	Forest whiptail	Internet	Y	Y			
Squamata	Varanidae	Varanus giganteus	Perentie	Video			Y	Y	
Squamata	Varanidae	Varanus komodoensis	Komodo dragon	Video	Y	Y	Y	Y	
Squamata	Varanidae	Varanus mertensi	Merten's water monitor	Video	Y	Y	Y		
Squamata	Varanidae	Varanus varius	Lace monitor	Video	Y	Y	Y	Y	

Family Varanidae

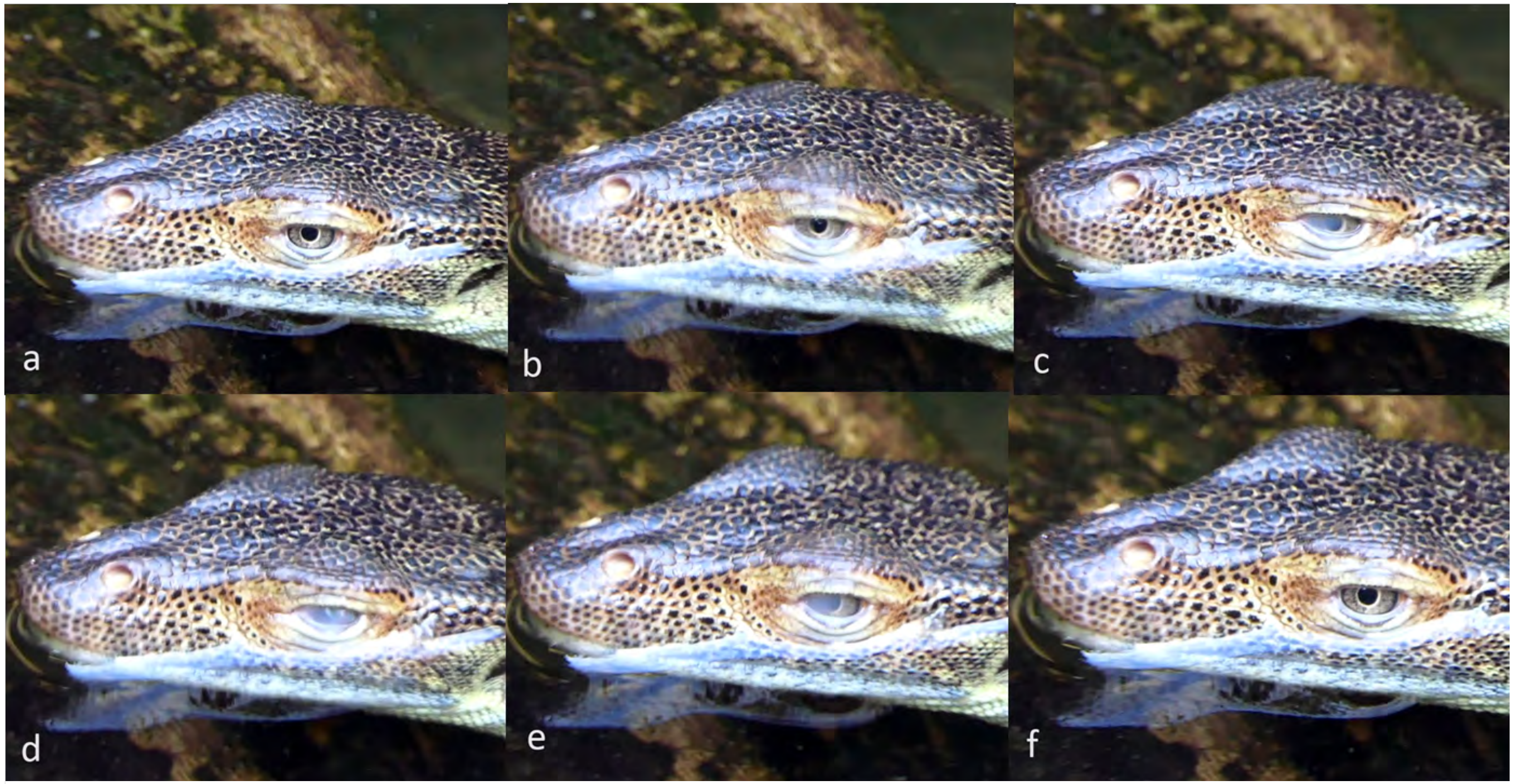
Nile monitor lizard (*Varanus niloticus*)

Lower lid elevation with sleep

Sleeping. Lower lid elevated

Merten's water monitor (*Varanus mertensi*)

Globe retraction with nictitating membrane blink



Semi-submerged in water. a) Pre-blink. Note overhanging upper lid (shading the eye from the sun). b) Slight narrowing of palpebral fissure as eye retracts. d) Semi-translucent nictitating membrane appears from inner canthus. d) and e) Eye covered by nictitating membrane. f) Post-blink

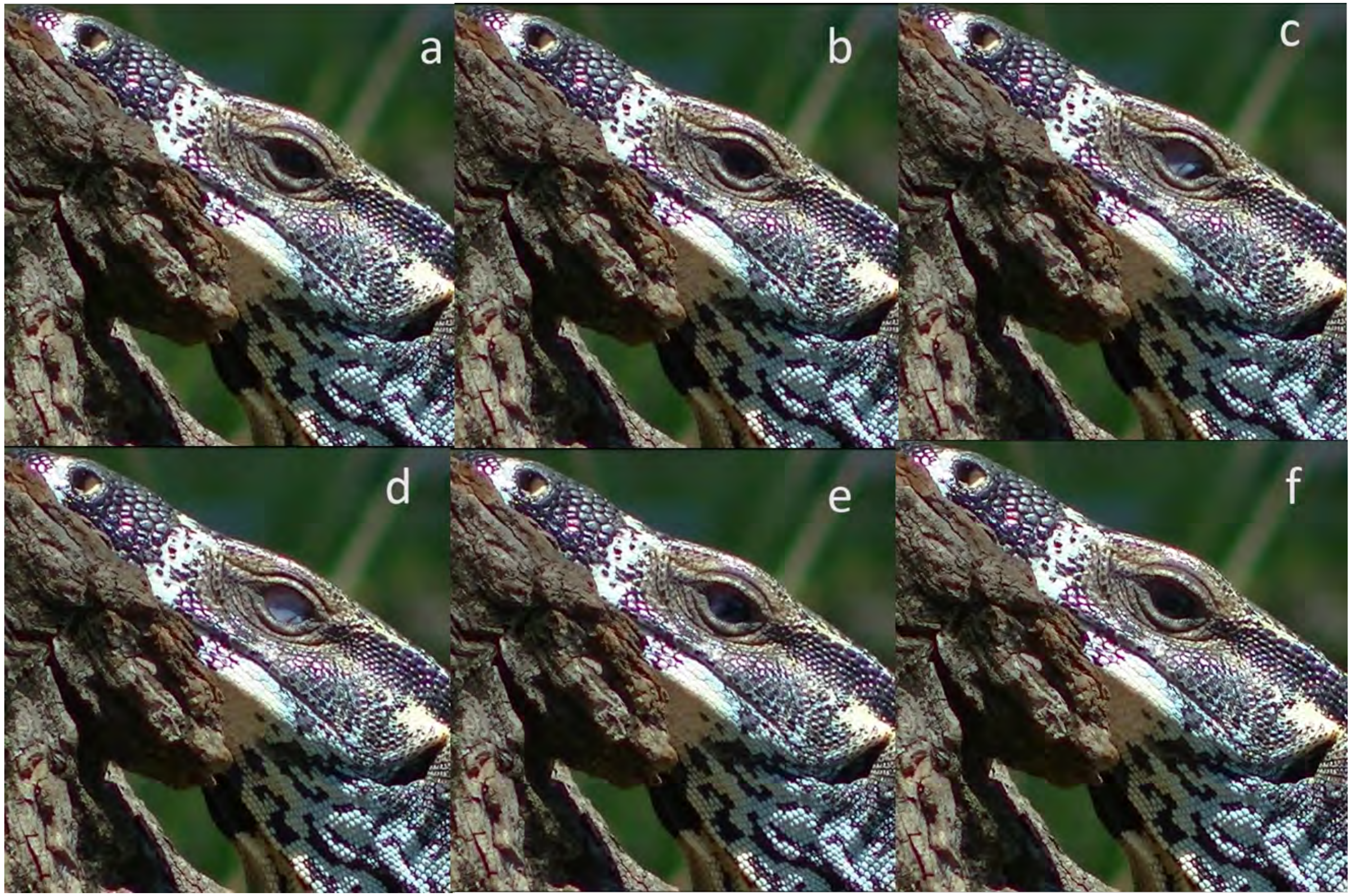
Crocodile monitor (*Varanus salvadorii*)

Globe retraction with nictitating membrane blink

a) Pre-blink. b) Globe retracts drawing upper lid beneath the brow. Opaque nictitating membrane covers eye. c) Globe un-retracts. d) Post- blink

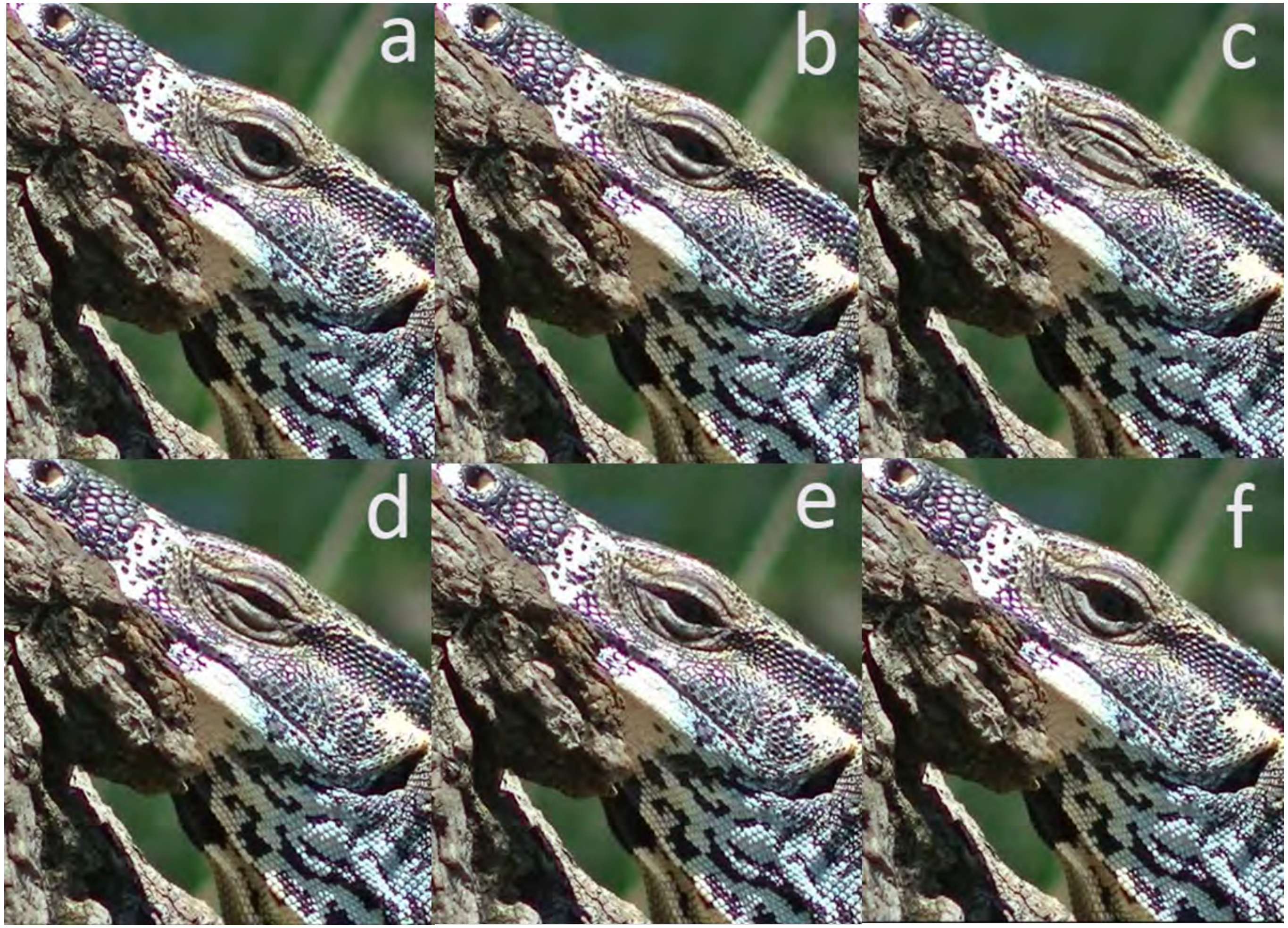
Lace monitor (*Varanus varius*)

Blink a: nictitating membrane blink



a) Pre-blink. b) No narrowing of palpebral fissure. c) Nictitating membrane emerges from inner canthus. d) Maximal blink. e) Nictitating membrane starts to withdraw into inner canthus. f) Post-blink

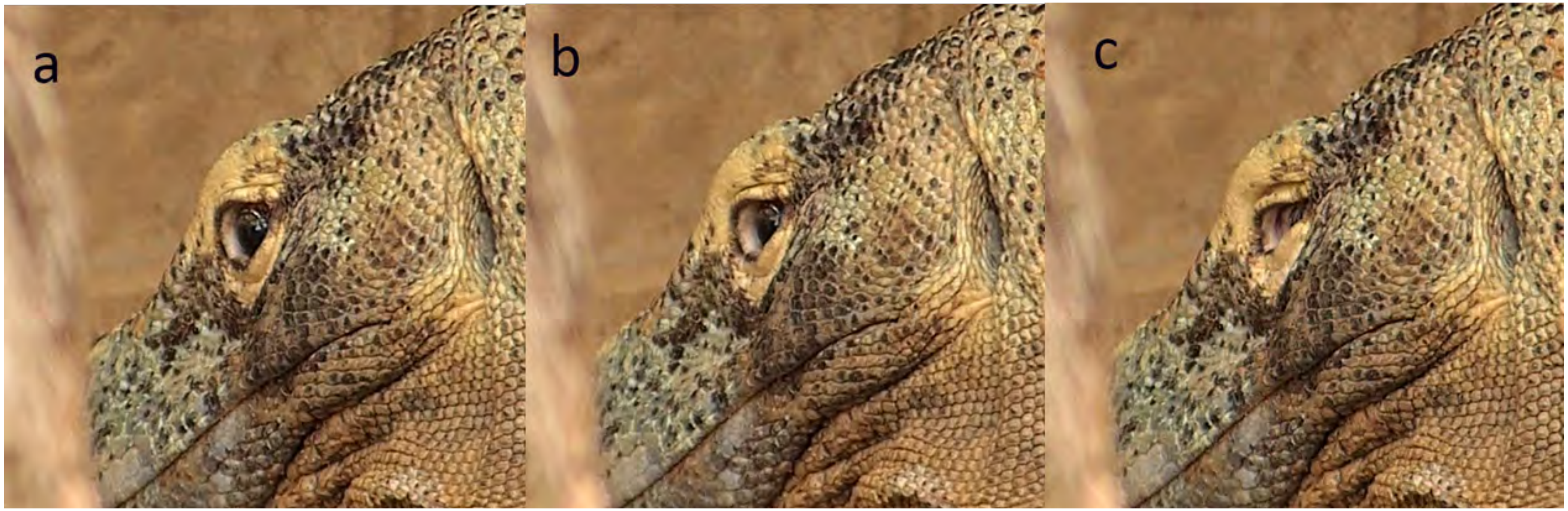
Blink b: Lower lid blink



a) Pre-blink. b) Lower lid starts to rise. c) Full blink. d) and e) Lower lid starts to fall. f) Post-blink

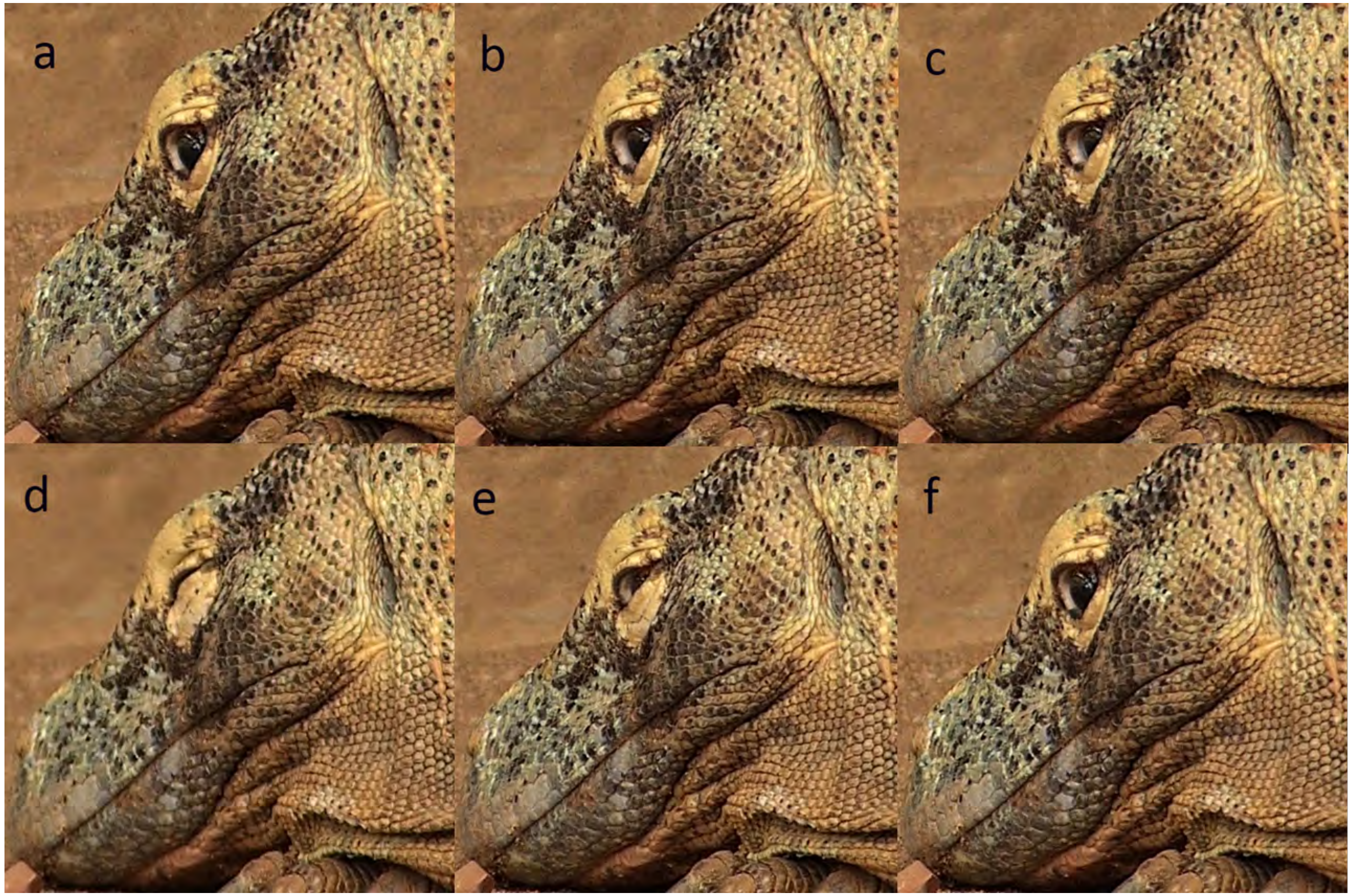
Komodo dragon (*Varanus komodoensis*)

Blink a: Globe retraction with no blink



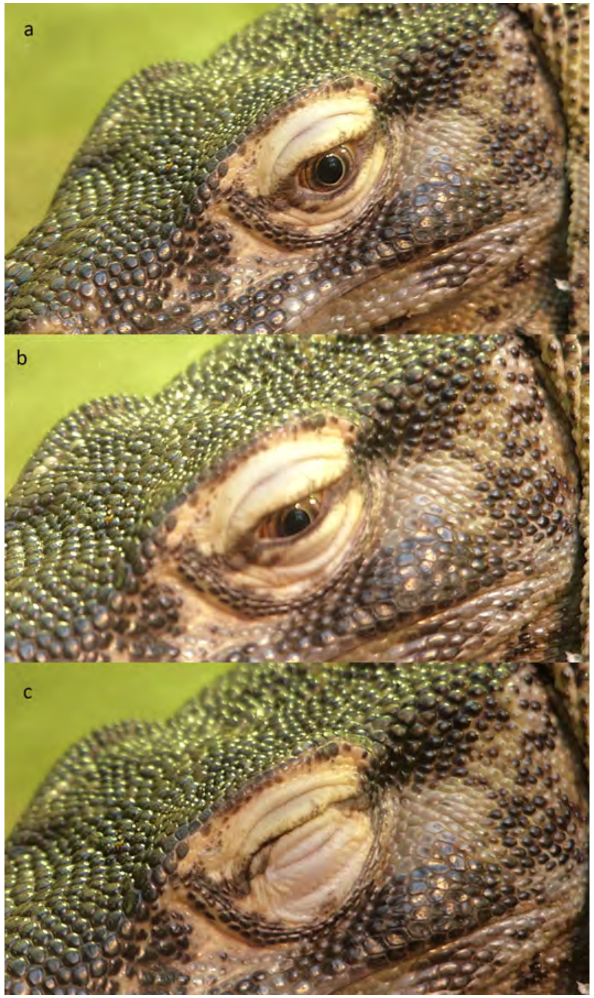
a) Pre-retraction. b) Palpebral fissure narrows as globe retracts, c) Maximal retraction.

Blink b: Lower lid blink with retraction of the eyeball

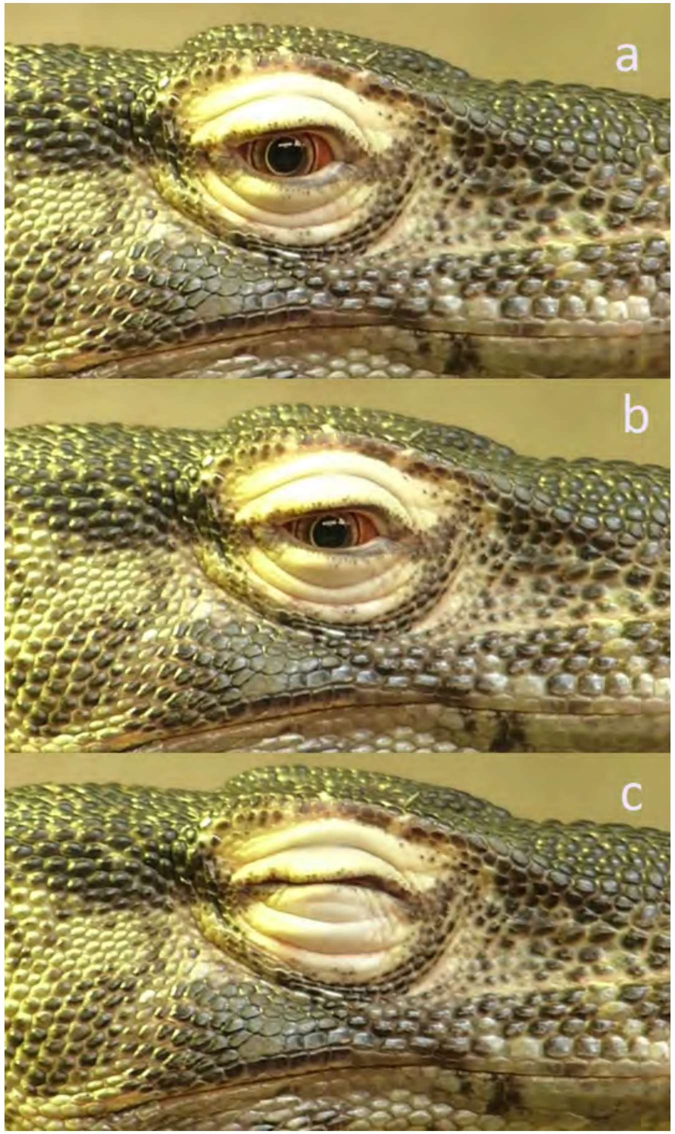


a) Pre-blink. b) and c) Palpebral fissure narrows as globe retracts. d) Lower lid elevates. e) Globe unretracts and lower lid falls. f) Post-blink.

Blink c: Lower lid pushes up against upper lid in sleep

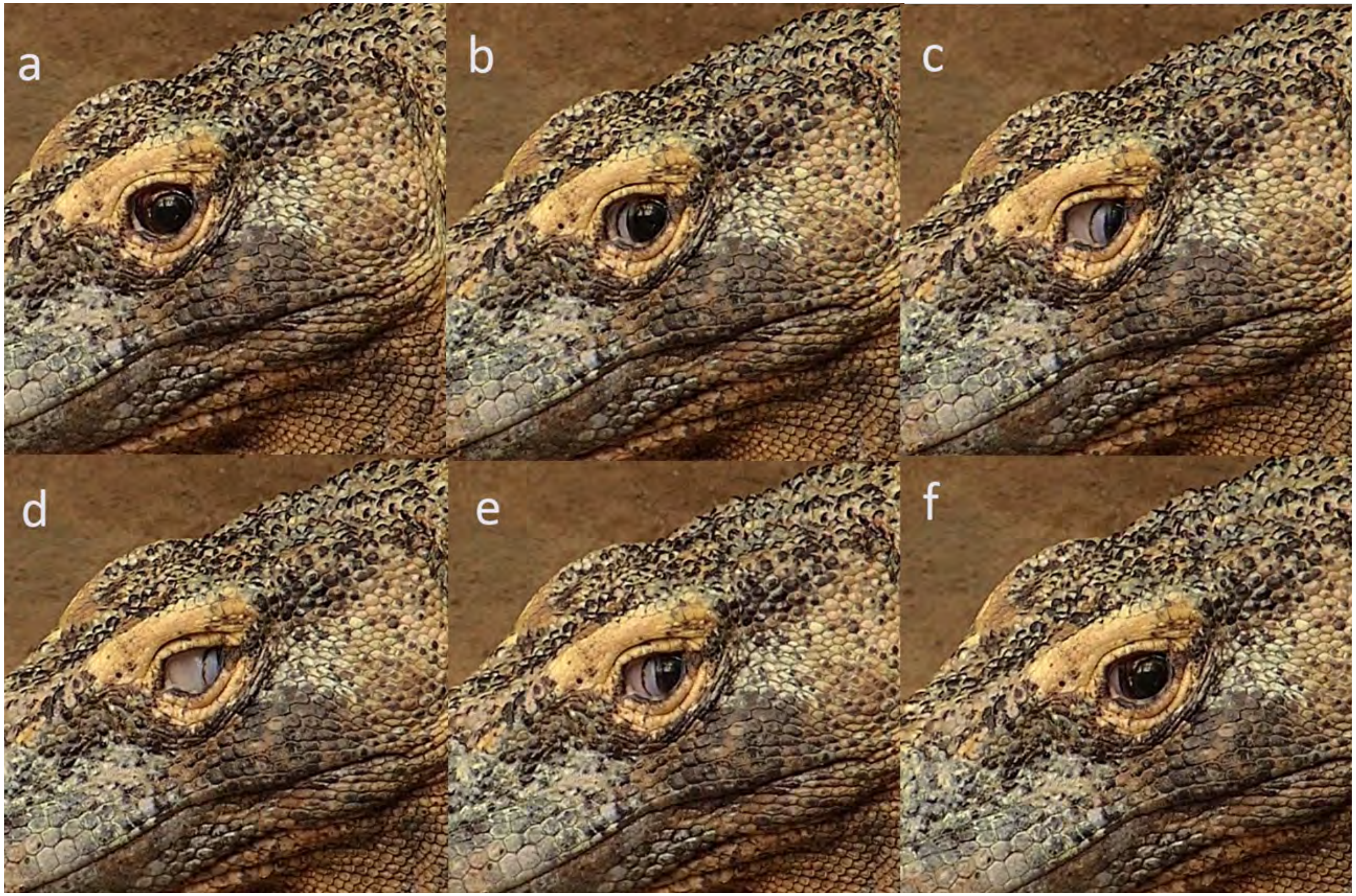


a) Pre-blink. b) Lower lid elevates. c) Full blink. Lower lid pushes up against upper lid. This was sustained – it fell asleep.

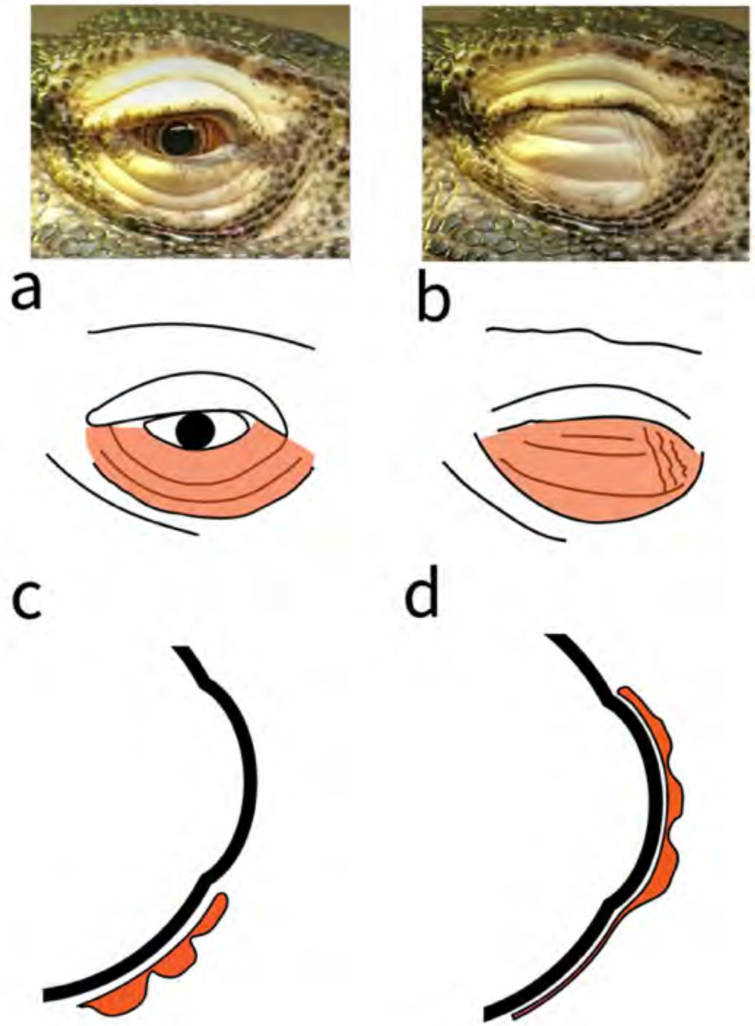


Juvenile. a) Pre-blink. b) Lower lid elevates. c) Full blink. This was also sustained – it fell asleep.

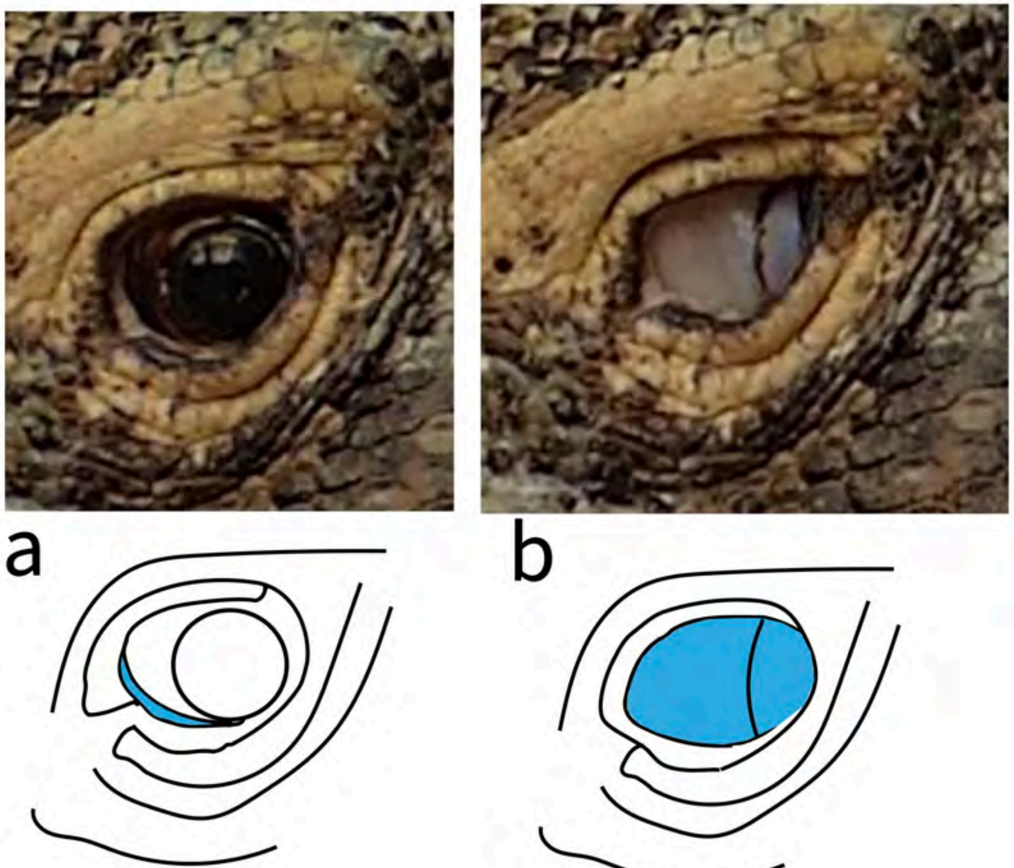
Blink d: Globe retraction with nictitating membrane blink



a) Pre-blink. b) Slight globe retraction. Nictitating membrane emerges from inner canthus. Note line of pigment parallel to the edge of the membrane. c) Nictitating membrane almost covers the eye. d) Maximal blink. e) Nictitating membrane starts to withdraw. f) Post-blink.



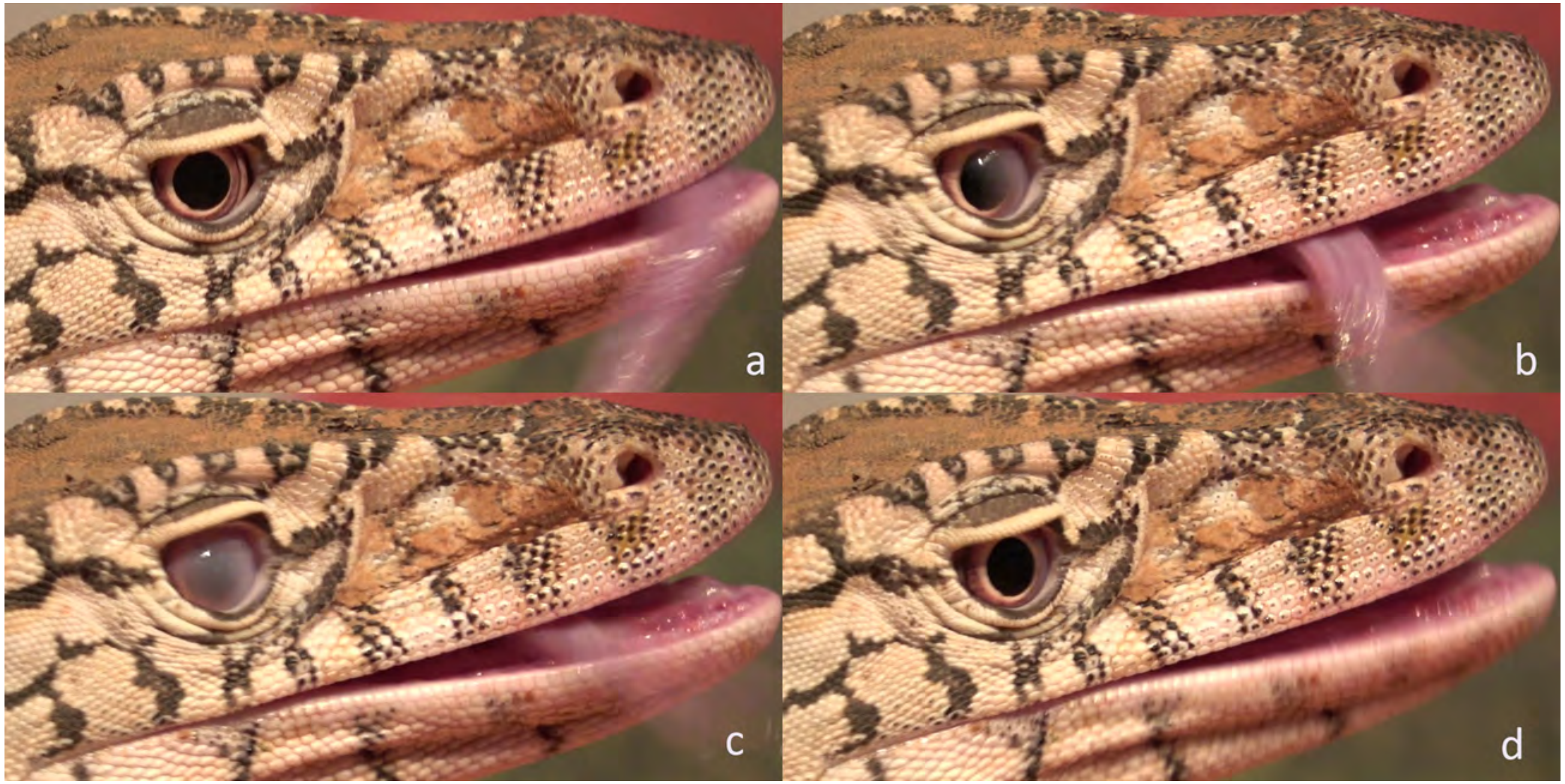
Lower lid a) Pre-blink showing three segments of the lower lid (orange) separated by creases. b) Blink involving elevation of all three segments of the lower lid with a further crease in the upmost segment covering the pupil. The upper lid has been pushed up a little. c) Sagittal plane of the eye showing the three segments of the lower eyelid. d) As for c), the lower lid covers the cornea.



Nictitating membrane blink with globe retraction in the left eye: a) Pre-blink showing the edge of the nictitating membrane (blue) in the medial canthus. b) Nictitating membrane, with a pigmented line near its edge, covering the cornea. The nictitating membrane is able to operate independently from the lower lid.

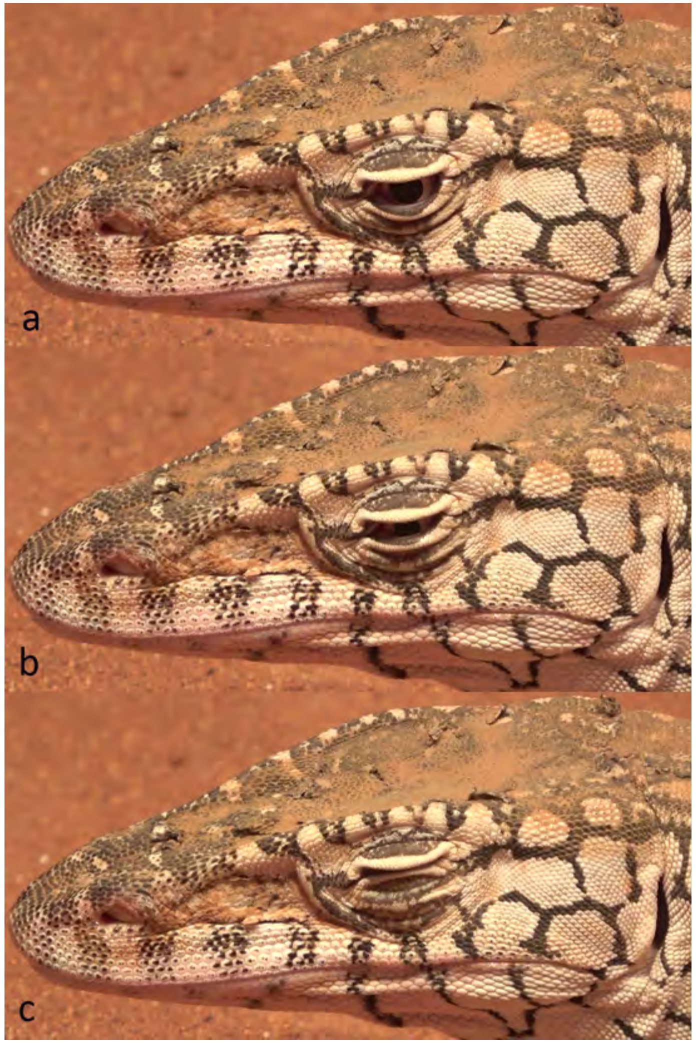
Perentie (*Varanus giganteus*)

Blink a: nictitating membrane blink on eye movement



a) Pre-blink. Note overhanging upper lid which shelters the eye from the sun. b) Eye turns forward. Upper lid is drawn back a little perhaps caused by the eye movement. Nictitating membrane appears out of inner canthus. c) Full blink with semi-transparent nictitating membrane. d) Post-blink.

Blink b: Lower lid blink with globe retraction

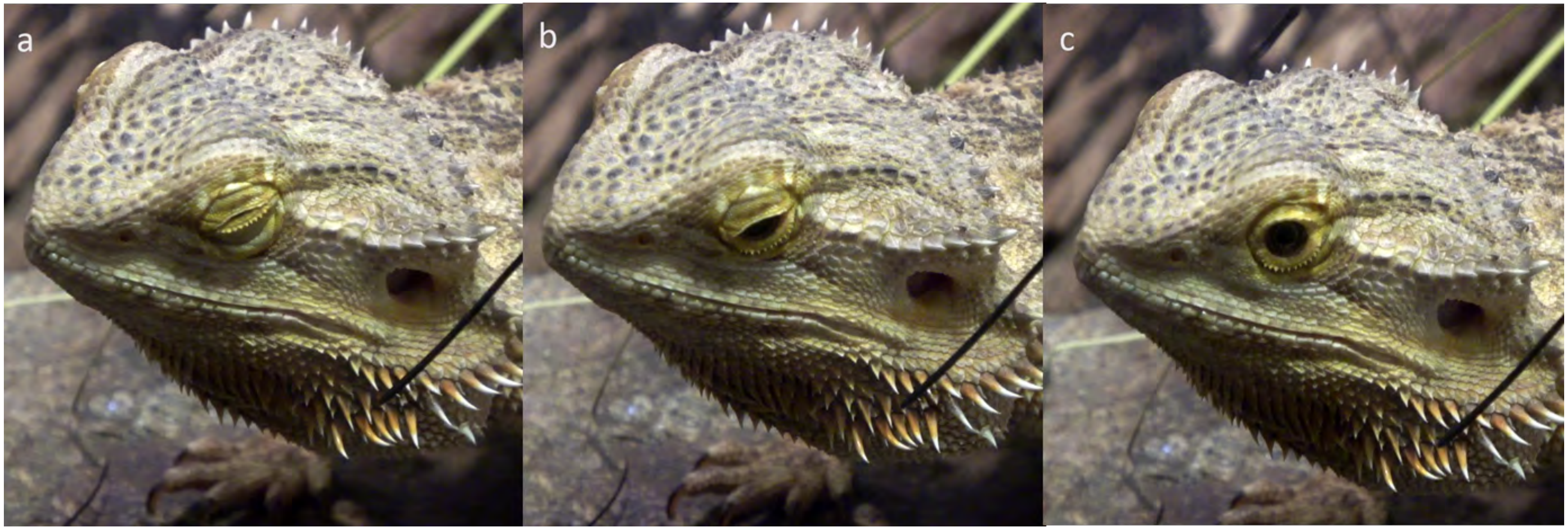


a) Pre-blink. b) Lower lid elevates a little. c) Maximal blink with globe retraction causing depression of the lower lid. No movement of the upper lid associated with globe retraction.

Family Agamidae

Inland bearded dragon *(Pogona viticeps)*

Blink a: Globe retraction with upper and lower lids meeting in sleep

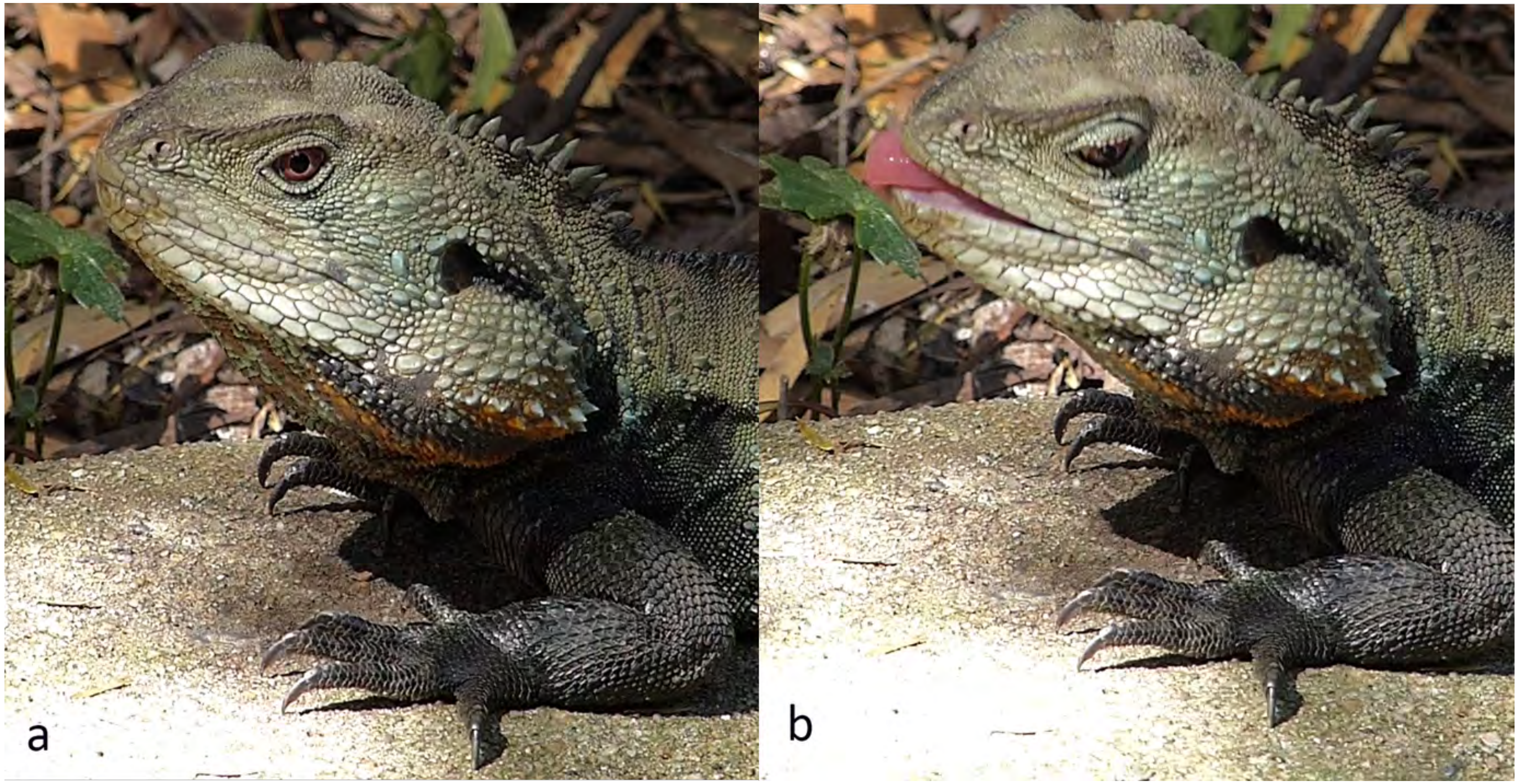


a) Asleep with eye closed. b) Lower lid falls as it wakes up. c) Eye fully open with globe un-retracted pushing upper eyelid up.

Blink b: Lower lid blink

a) pre-blink. b) Lower lid rises. c) Full blink.

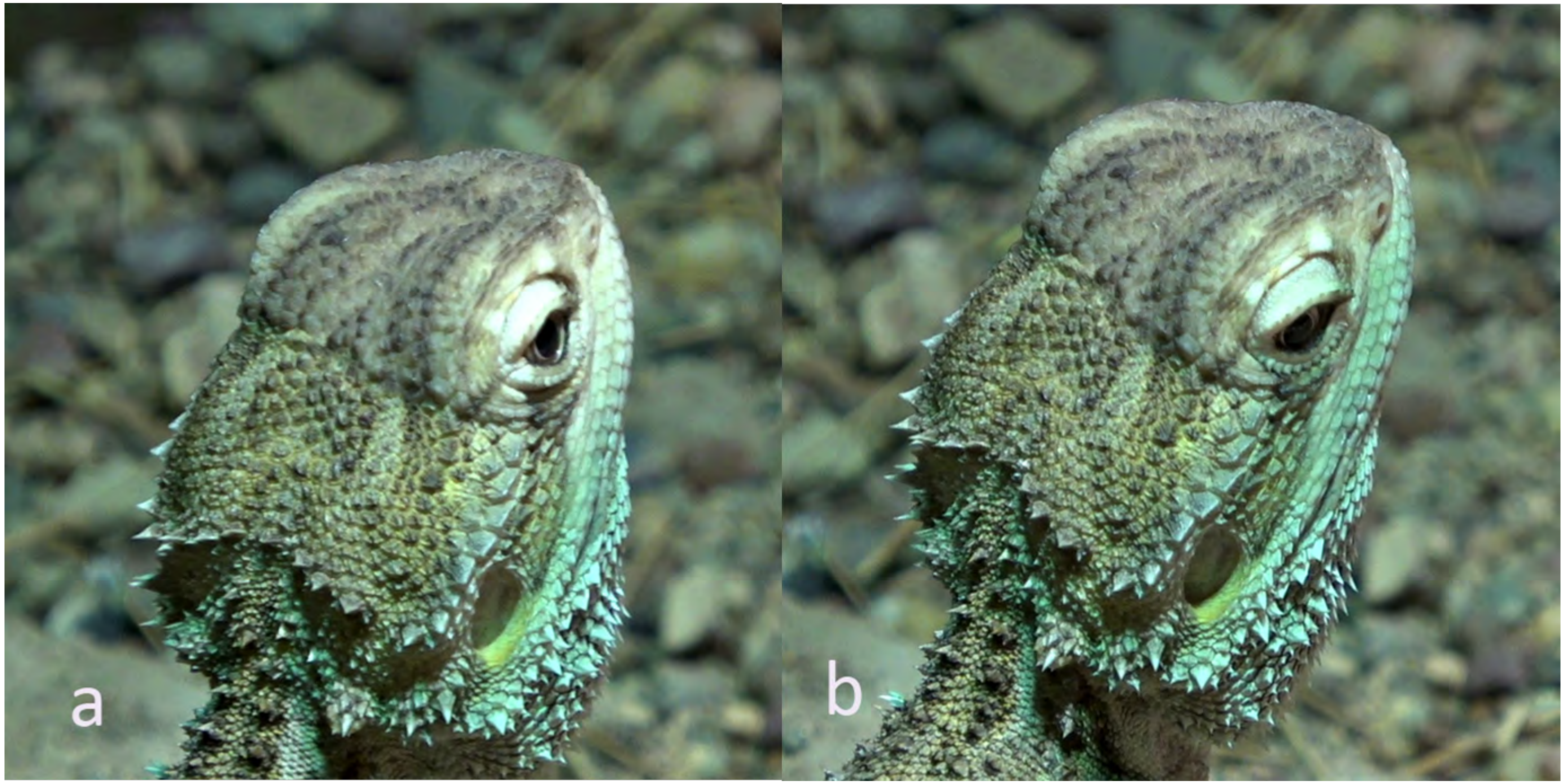
Blink c: Upper lid descends on downward gaze



a) Pre-eye movement. b) Upper lid projects outwards and downwards on downward gaze.

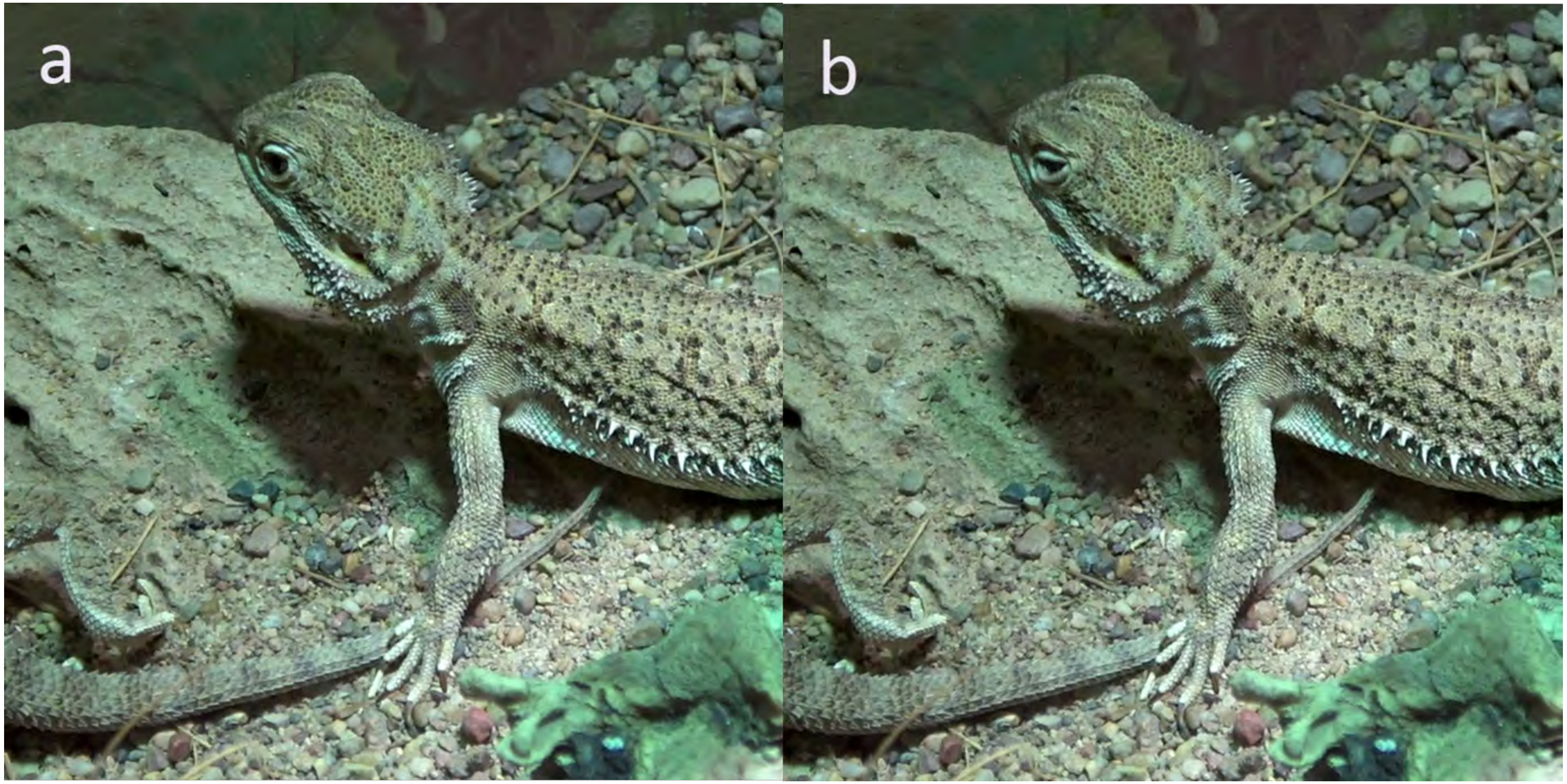
Rankin's dragon or Dwarf bearded dragon (*Pogona henrylawsonii*)

Blink a: Upper lid descends on downward gaze



a) Pre-eye movement. b) Upper lid protrudes on downward gaze.

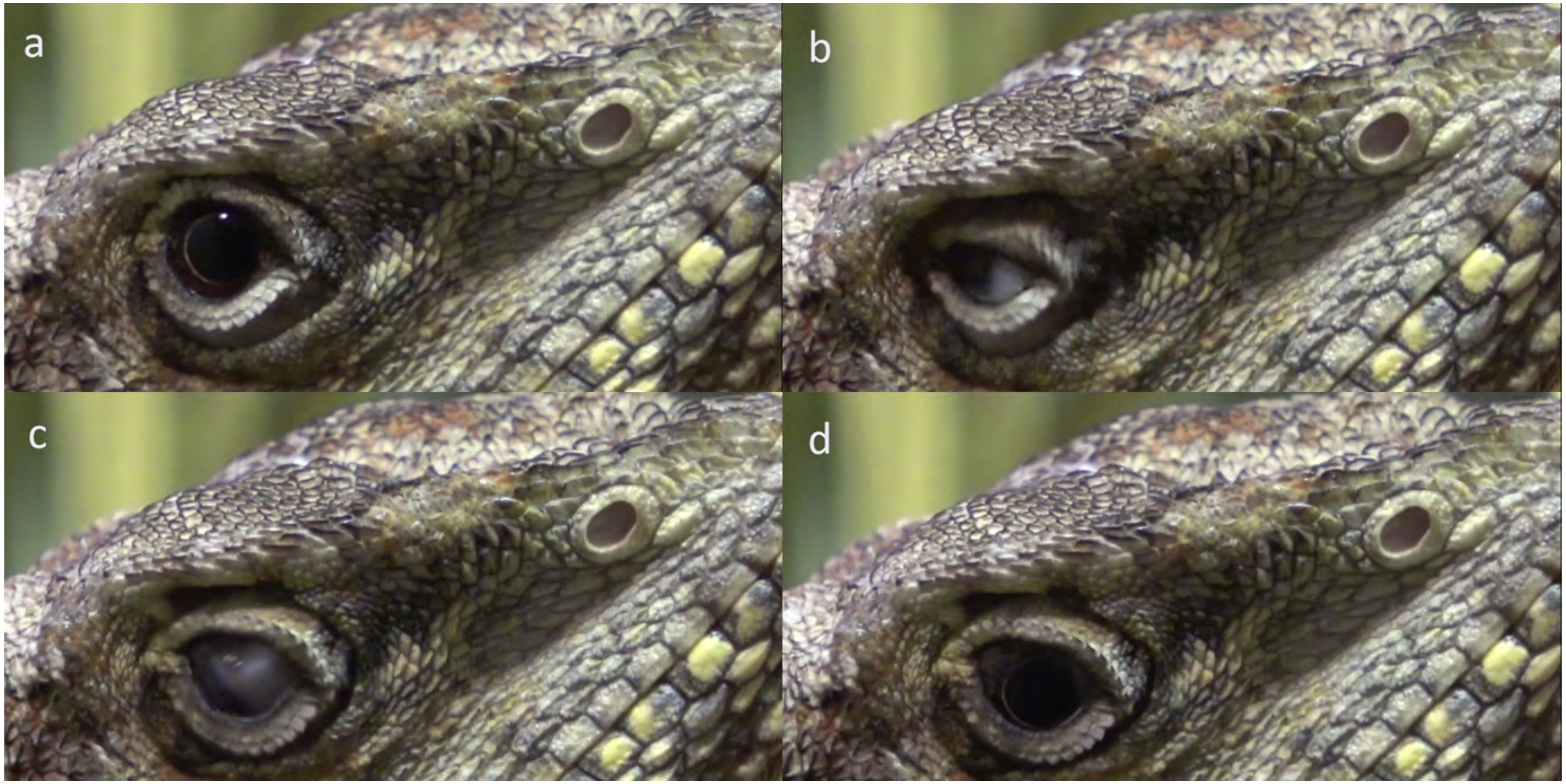
Blink b: Globe retraction with narrowing of palpebral fissure



a) Pre-blink. b) Palpebral fissure narrows as globe retracts.

Frilled lizard (*Chlamydosaurus kingii*)

Globe retraction with narrowing of palpebral fissure, eye movement and nictitating membrane blink



a) Pre-blink. b) Palpebral fissure narrows as globe retracts. Nictitating membrane emerges from inner canthus (on the right). c) Globe begins to unretract, eye looks downward moving position of nictitating membrane. d) Post=blink.

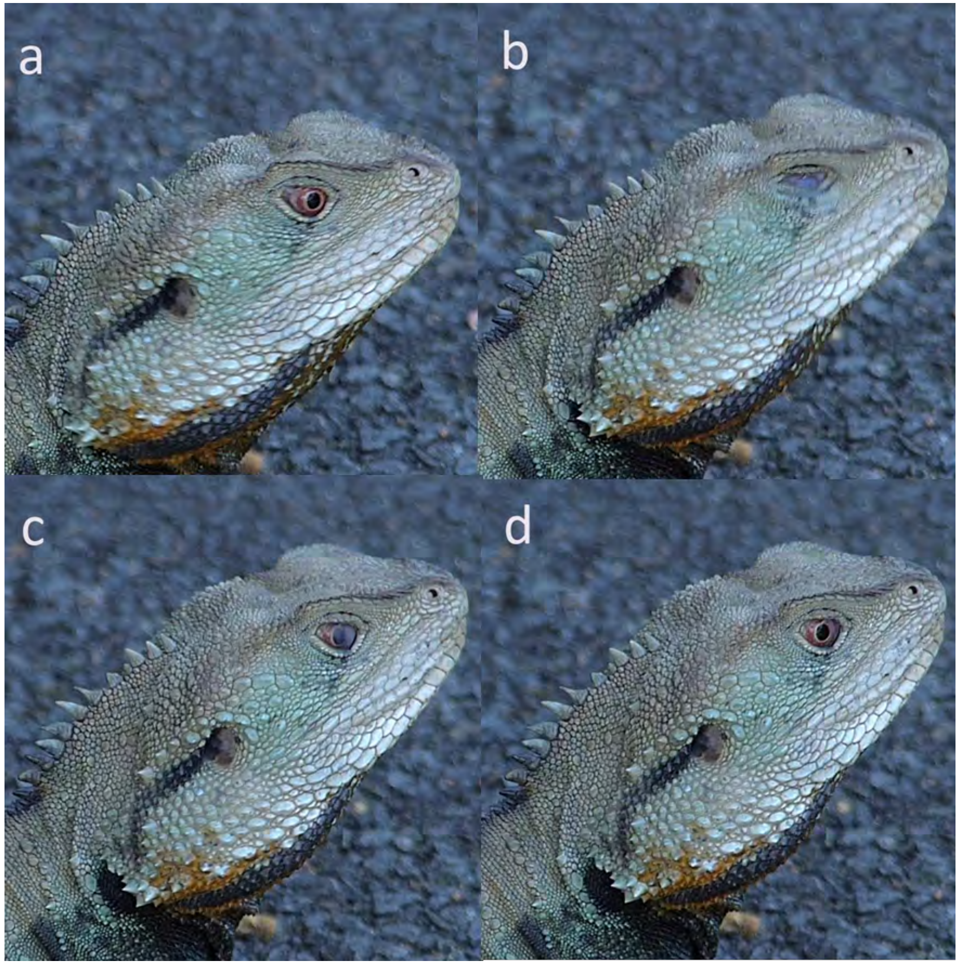
Eastern water dragon (*Intellagama lesueurii lesueurii*)

Globe retraction with narrowing of palpebral fissure and nictitating membrane blink

a) Pre-blink. b) Palpebral fissure narrows as globe retracts. Nictitating membrane arises from inner canthus. c) Maximal globe retraction. Nictitating membrane covers eye. d) Globe unretracts. e) Nictitating membrane starts to withdraw. f) Post-blink

Gippsland water dragon (*Intellagama lesueurii howittii*)

Globe retraction with narrowing of palpebral fissure and nictitating membrane blink



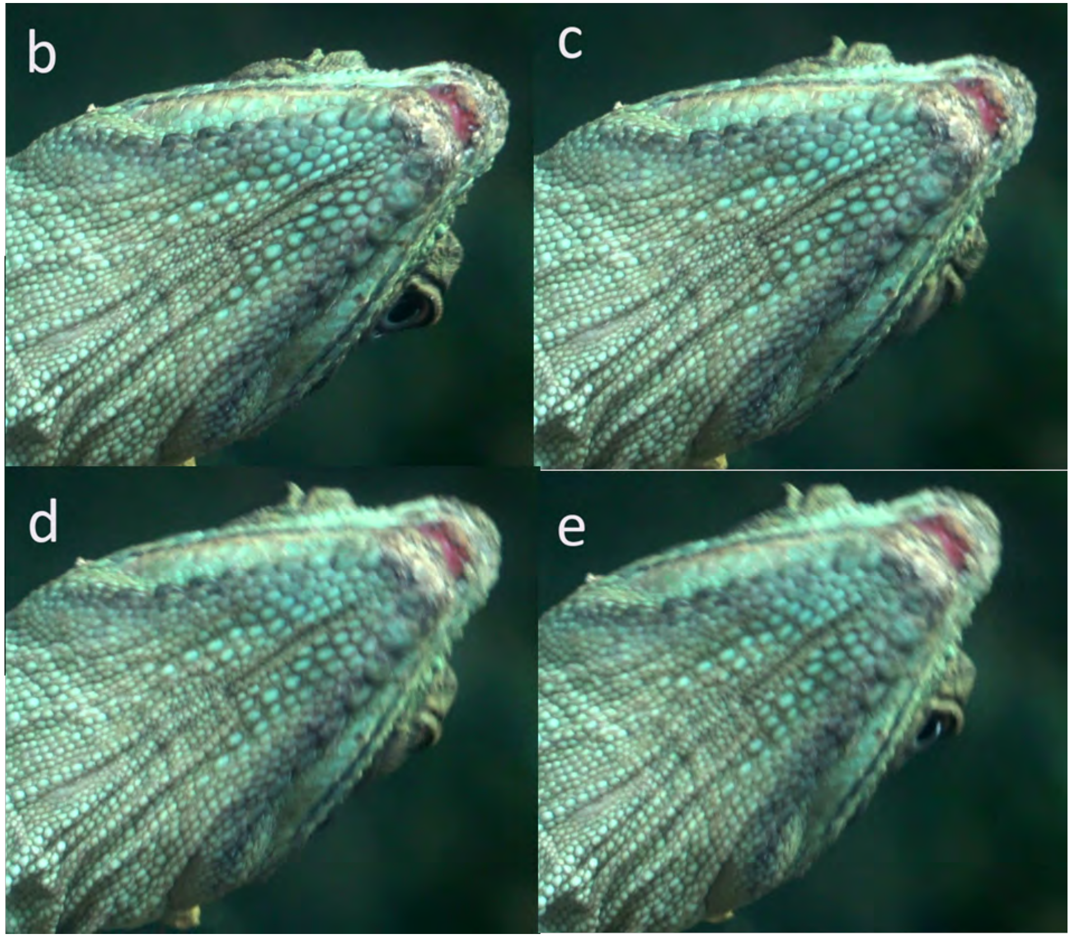
a) Pre-blink. b) Palpebral fissure narrows as globe retracts. Nictitating membrane covers eye. c) Globe unretracts. Nictitating membrane starts to withdraw into inner canthus. d) Post-blink

Philippine sailfin lizard (*Hydrosaurus pustulatus*)

Blink a: Globe retraction with narrowing of palpebral fissure and nictitating membrane blink

Note blue sclera (above).
a) Pre-blink. b) and c) Globe sinks into orbit and opaque nictitating membrane appears. d) Globe unretracts causing palpebral fissure to widen. e) Nictitating membrane starts to withdraw into inner canthus. f) Nictitating membrane still just visible towards the end of the blink.

Blink b: Globe retraction with narrowing of palpebral fissure and lower lid blink

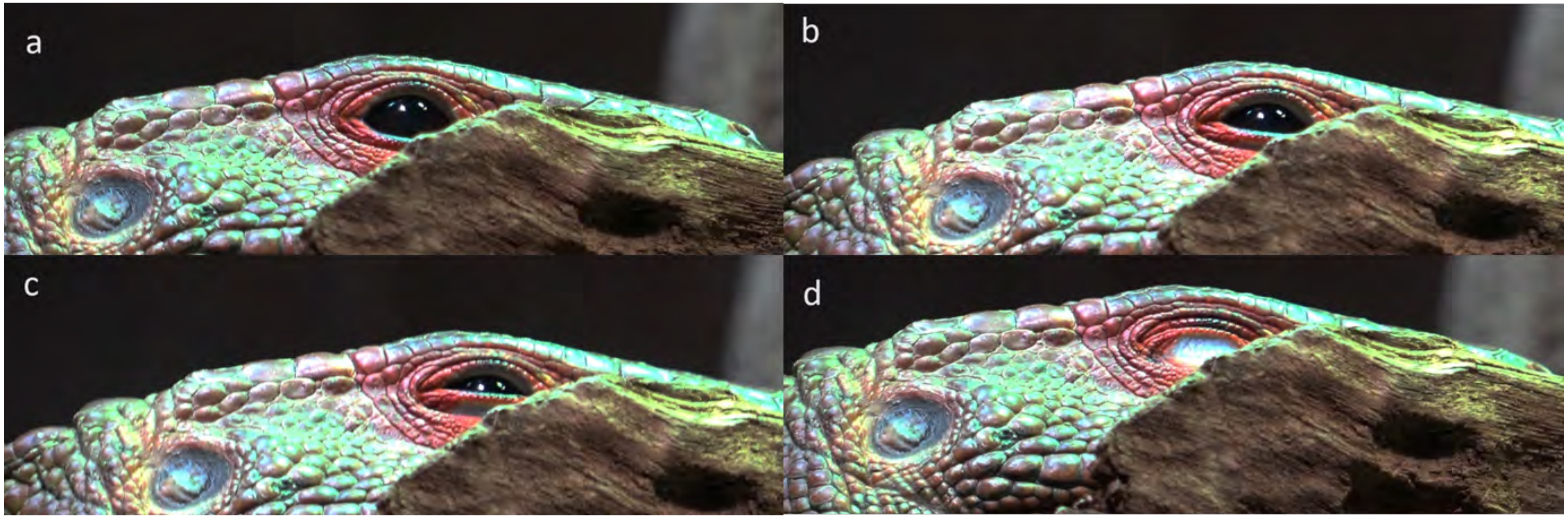


a) Side view. b) Pre-blink - left eye from below. c) Globe retracts causing upper lid to sink into orbit. Lower lid rises. d) Globe unretracts causing palpebral fissure to widen. e) Lower lid starts to fall. f) Post-blink.

Family Teiidae

Northern caiman lizard (*Dracaena guianensis*)

Globe retraction with narrowing of palpebral fissure and nictitating membrane blink

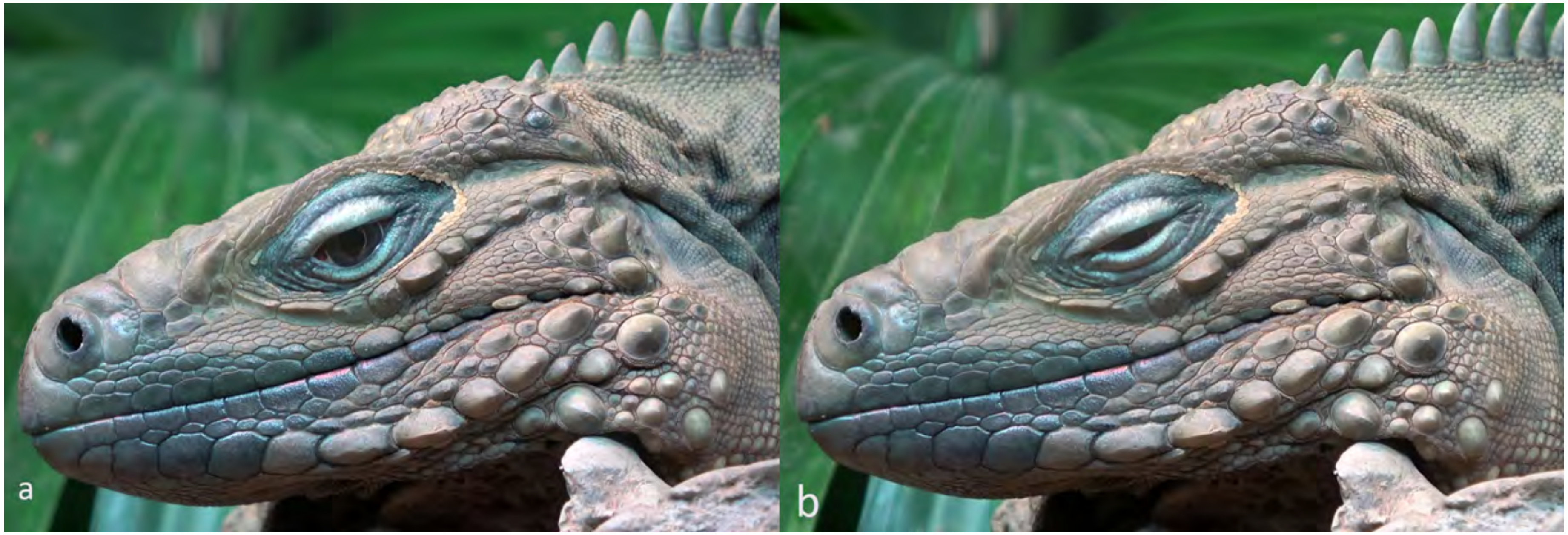


a) Pre-blink. b) and c) Palpebral fissure narrows due to globe retraction. d) Eye is covered by opaque nictitating membrane

Family Iguanidae

Grand Caiman blue iguana *(Cyclura lewisi)*

Globe retraction with narrowing of palpebral fissure



a) Pre-blink. b) Elevation of lower lid and globe has retracted.

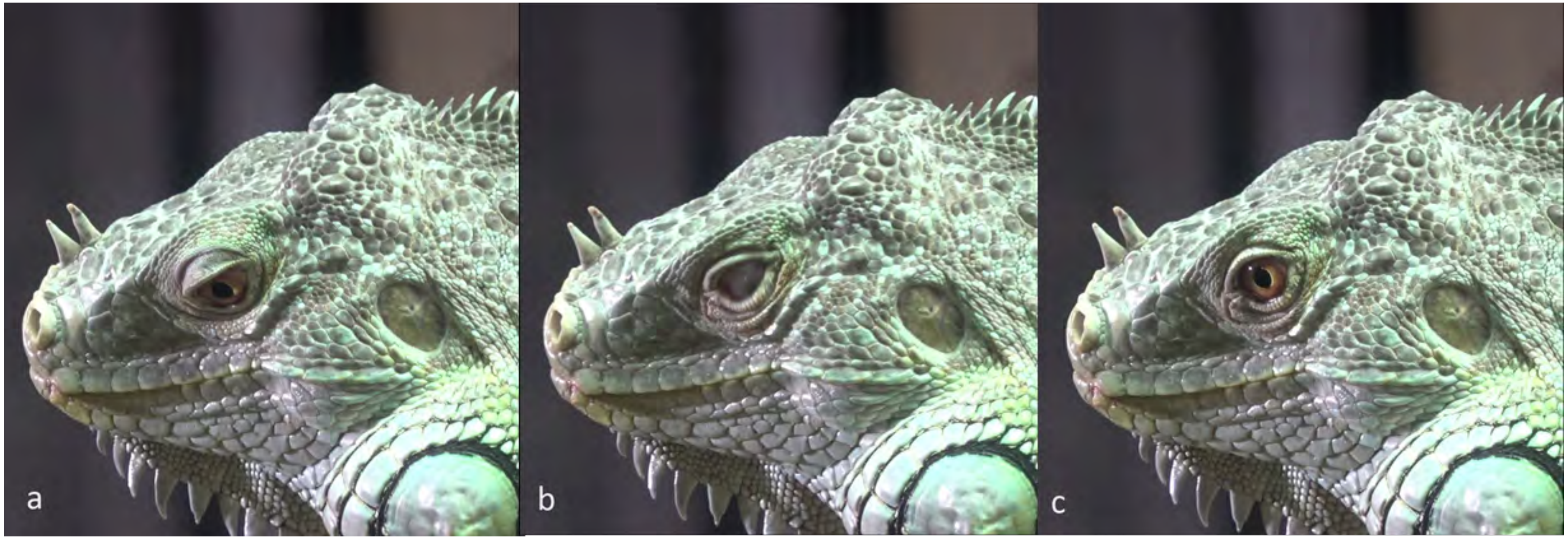
Fijian crested iguana (*Brachylophus vitiensis*)

Lower lid elevation after eye movement

Note red sclera. a) Looking forward. b) Looking to the side. c) Lower lid has elevated.

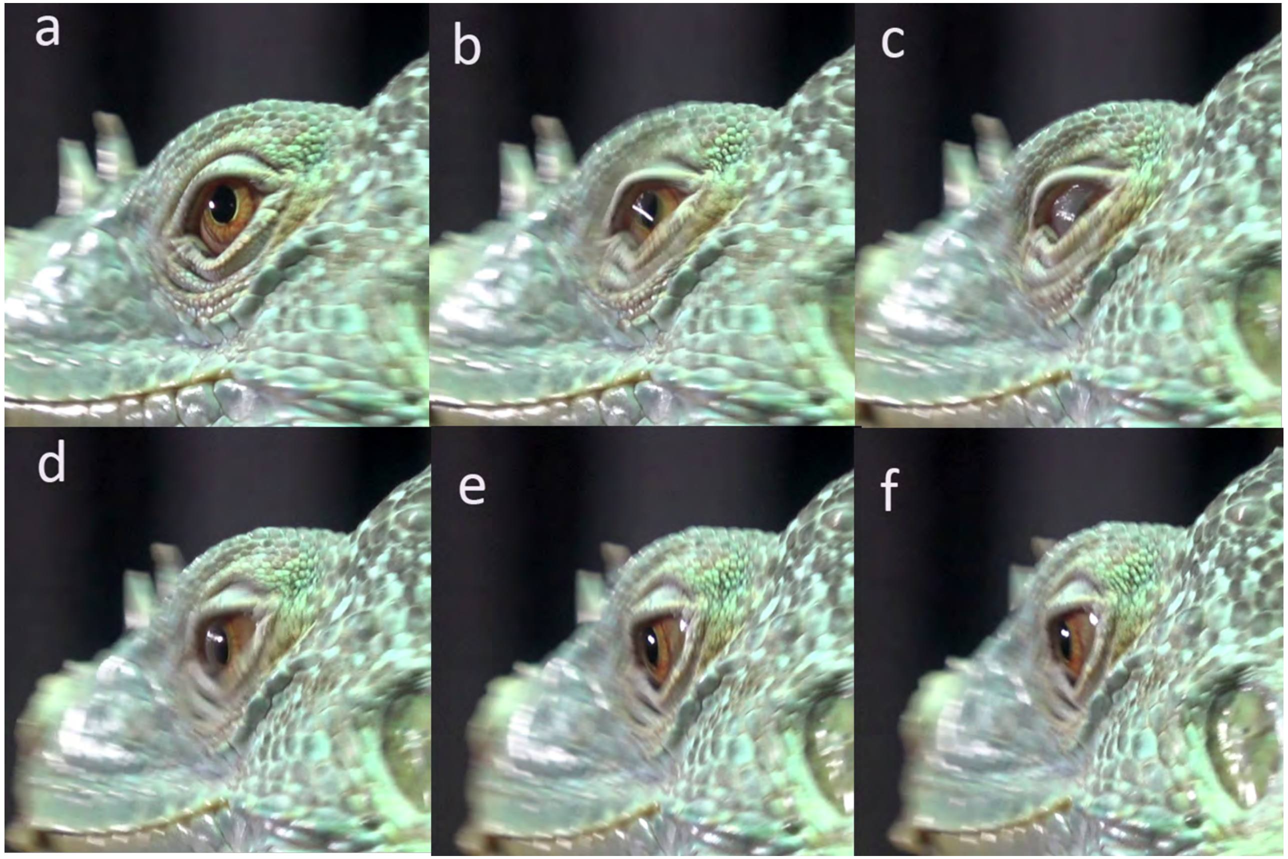
Green iguana (*Iguana iguana*)

Blink a: Upper lid descends on downward gaze then palpebral fissure narrows on globe retraction and nictitating membrane crosses



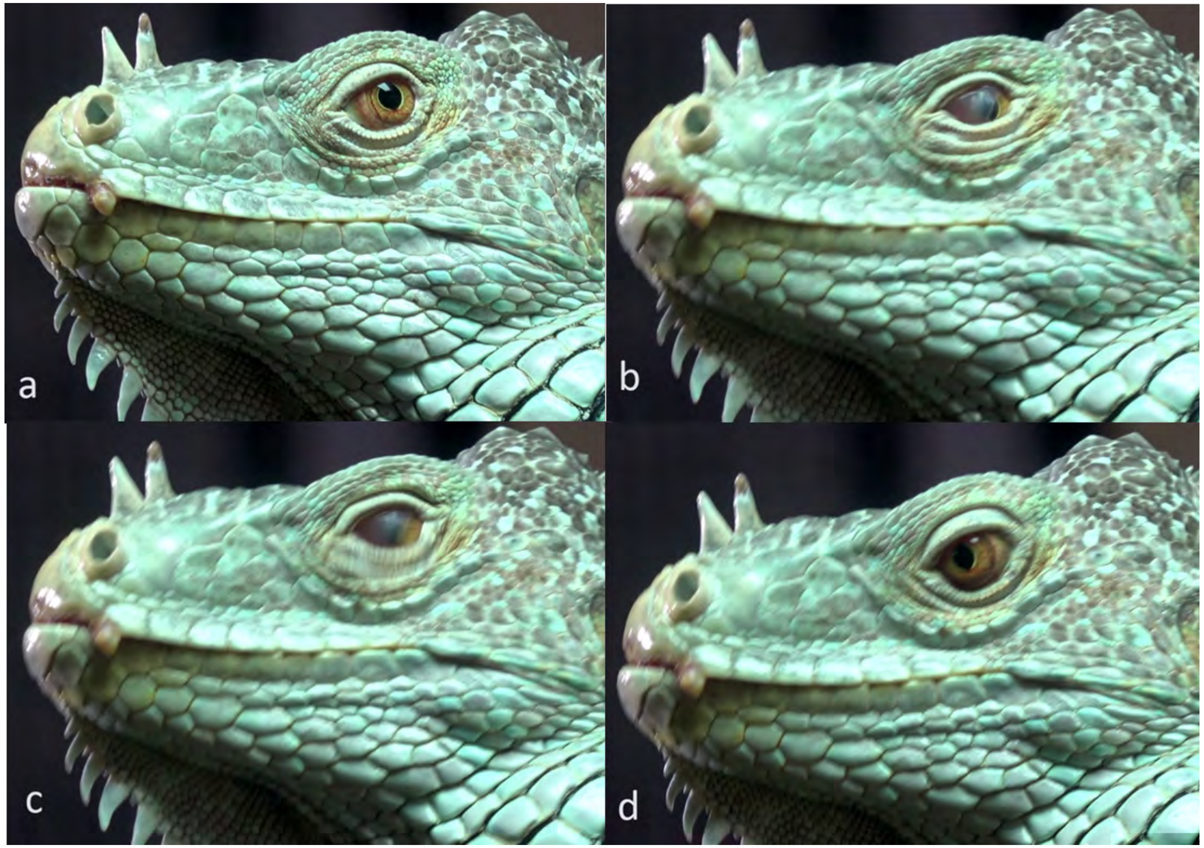
a) Pre-blink. Looking down. Upper lid lowered. b) Globe retraction. Nictitating membrane visible. Upper lid elevated. c) Post-blink.

Blink b: Globe retraction with narrowing of palpebral fissure, nictitating membrane blink and eye movement



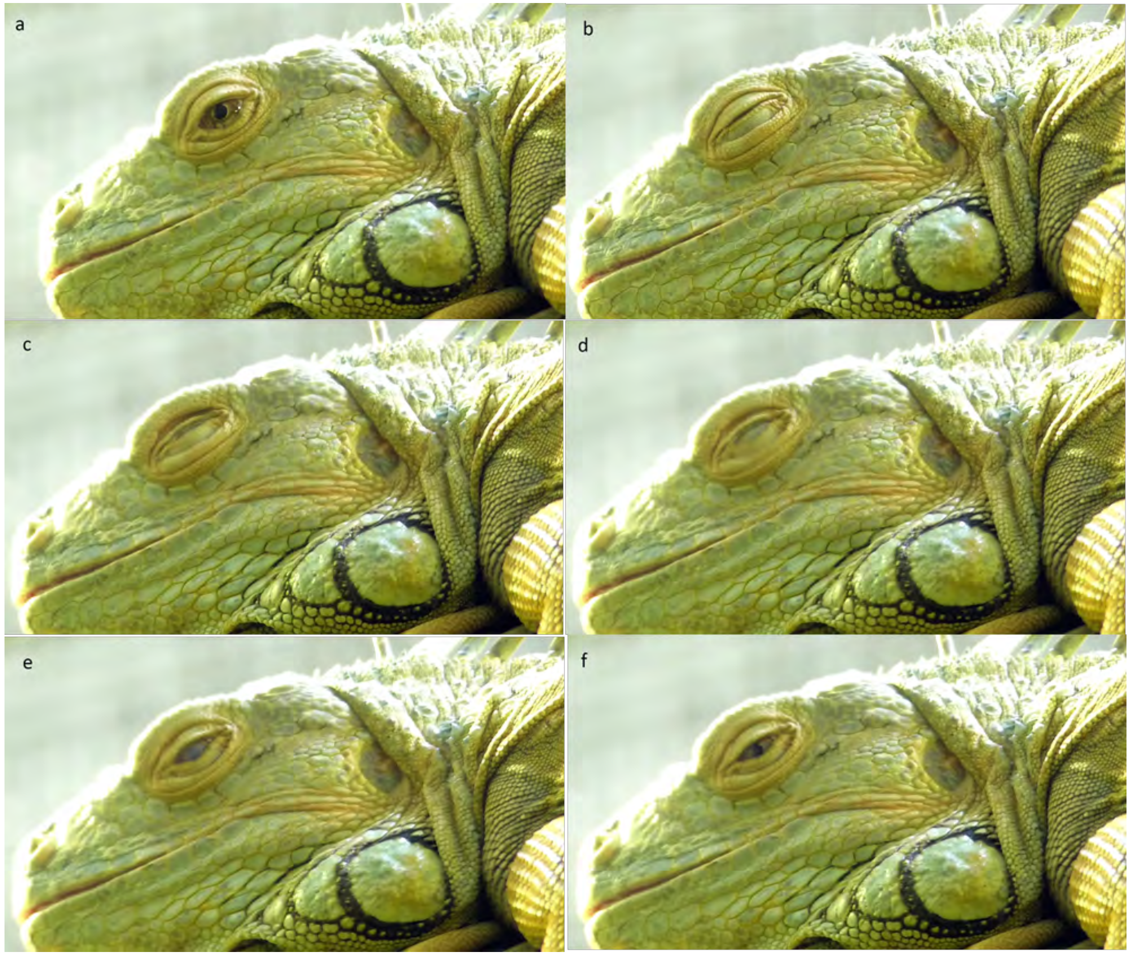
a) Pre-blink. b) Globe retraction. c) Nictitating membrane visible. d) Eye movement. Nictitating membrane moving back towards inner canthus. e) and f) Post-blink. Head turning.

Blink c: Globe retraction with narrowing of palpebral fissure, nictitating membrane blink and eye movement

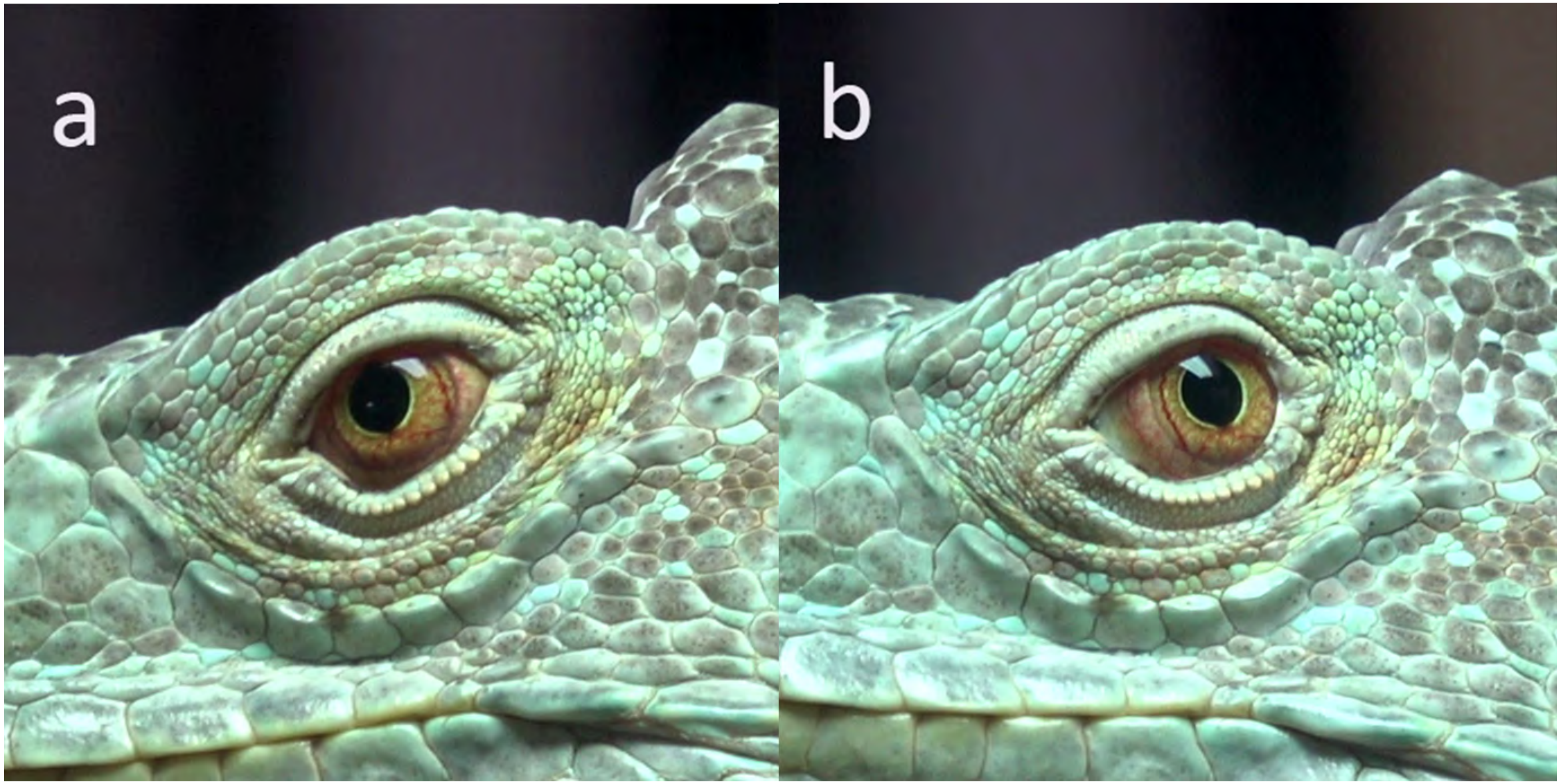


a) Pre-blink. b) Globe retraction. Nictitating membrane moving out from inner canthus. c) Nictitating membrane covers the eye. d) Post-blink. Eye has turned.

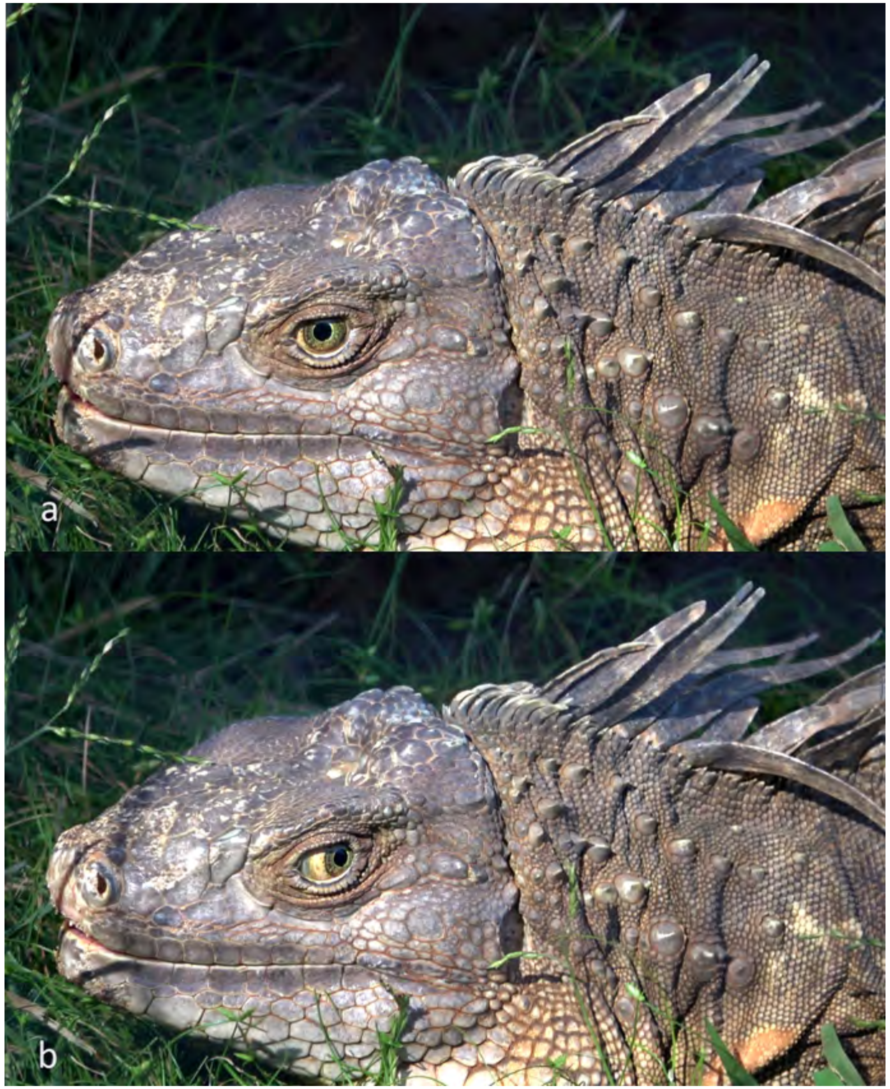
Lower lid and nictitating membrane blink with globe retraction



Drowsy. a) Pre-blink. b) Eye closed. c) Lower lid pushes up against upper lid. Globe retraction. d) and e) Lower lid descends revealing opaque nictitating membrane. f) Eye partially opens. Nictitating membrane no longer visible.



a) Looking forwards. b) Looking back. Note eyelash-like projections on the lids.



Horizontal eye movement

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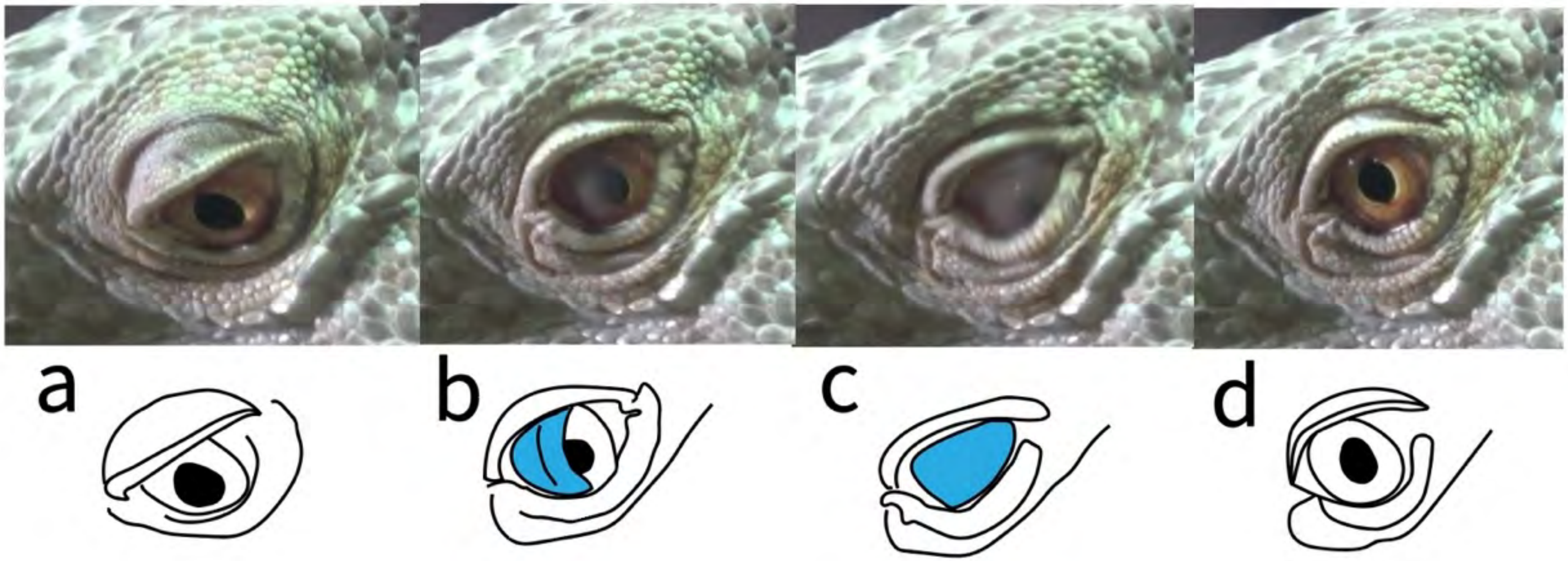


Nictitating membrane blink on eye movement in the left eye with globe retraction. a) Pre-blink showing partial descent of the upper lid with downward gaze (as occurs with humans). b) The eye and upper lid rise. and the nictitating membrane partially cover the pupil. c) The nictitating membrane covers the eye. The palpebral fissure has narrowed as the globe retracts. d) Post- blink

Family Scincidae

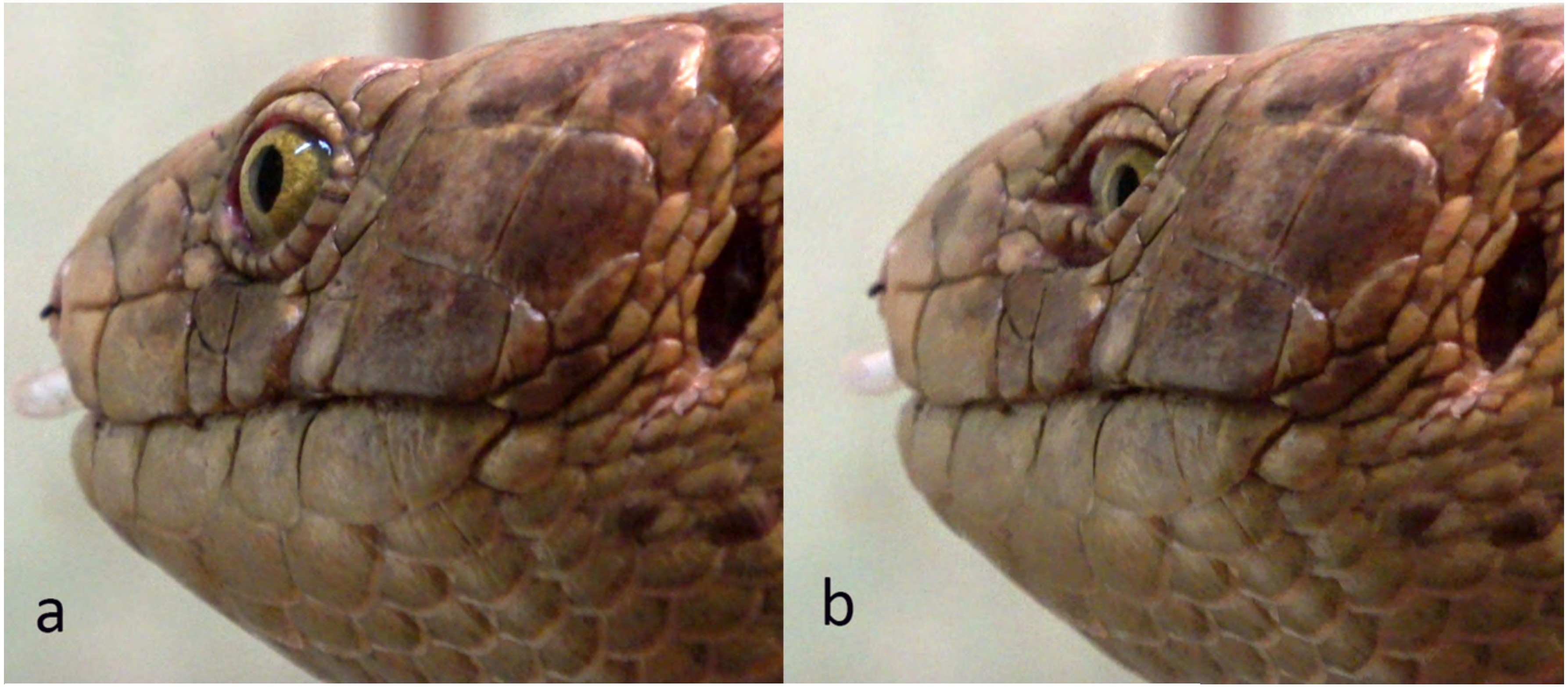
Shingleback lizard (*Tiliqua rugosa)*

Lower lid and nictitating membrane blink

Brief nictitating membrane and lower lid blink.

Soloman Islands skink *(Corucia zebrata)*

Globe retraction with no blink



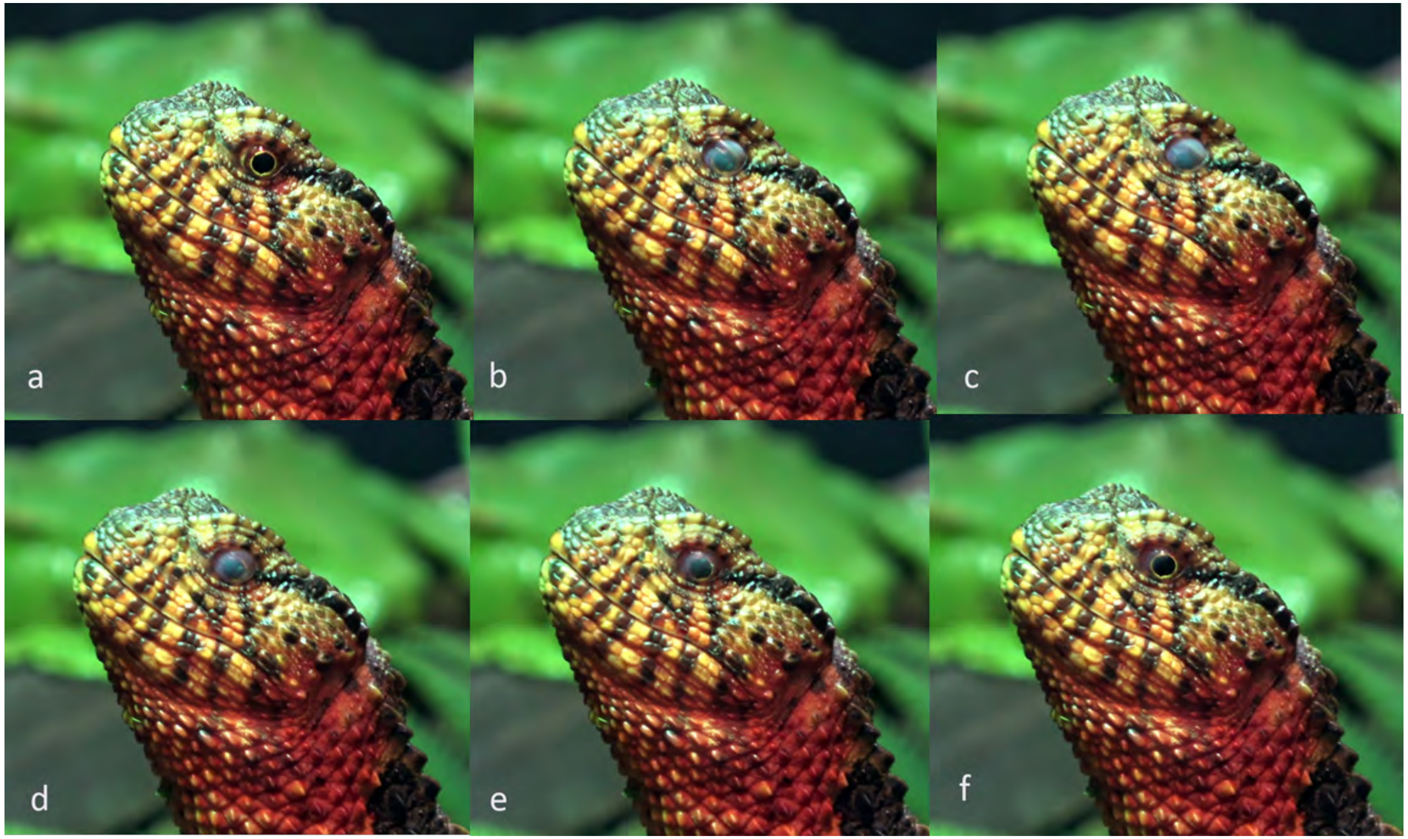
a) Pre-retraction. b) Maximal retraction.

Soloman Island skink (Corucia zebrata). Note oval pupils. a) Pre-retraction. b) and c) Palpebral fissure narrows as globe retracts. d) and e) Globe unretracts. f) Post-retraction.

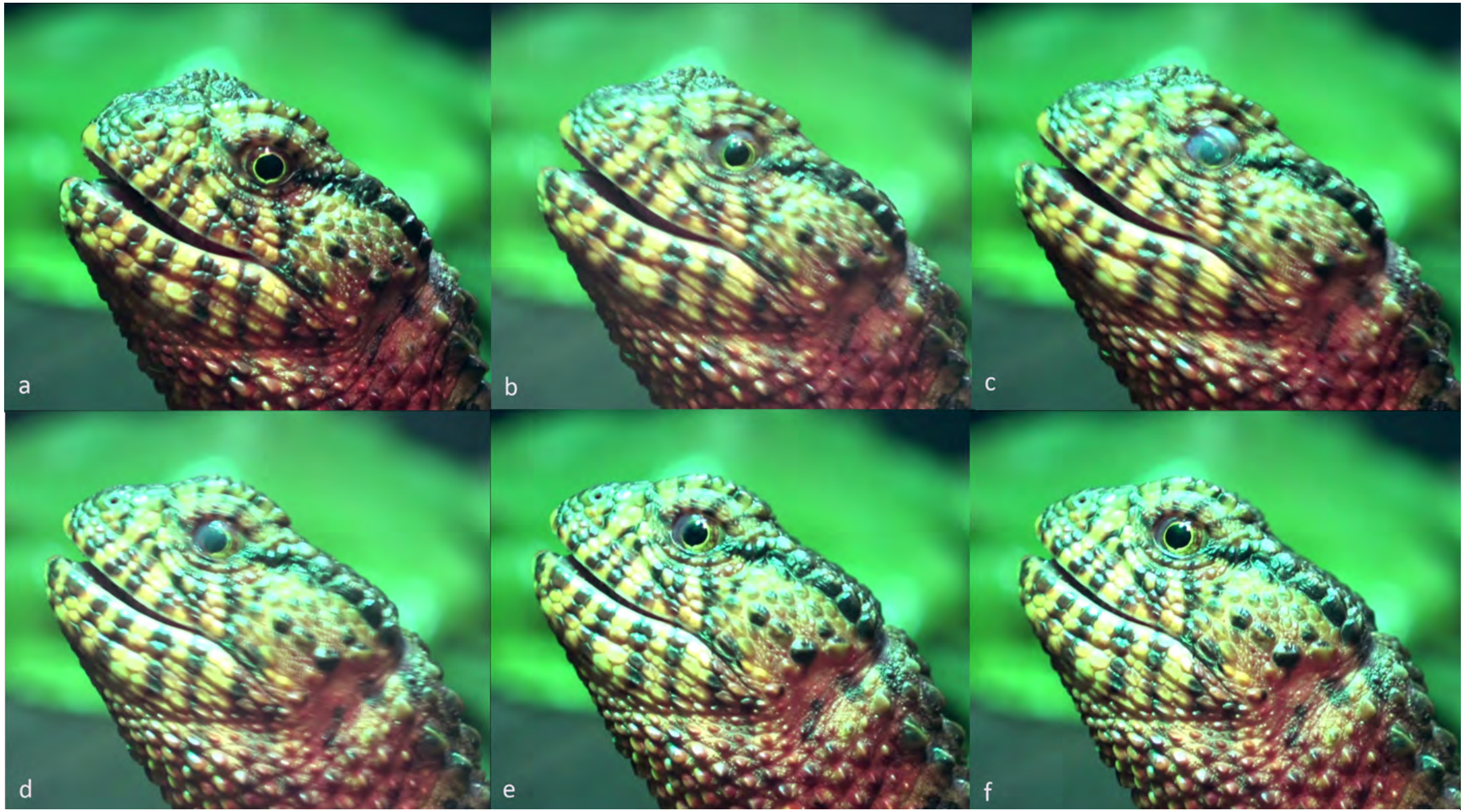
Family Shinisauridae

Chinese crocodile lizard (*Shinisaurus crocodilurus*)

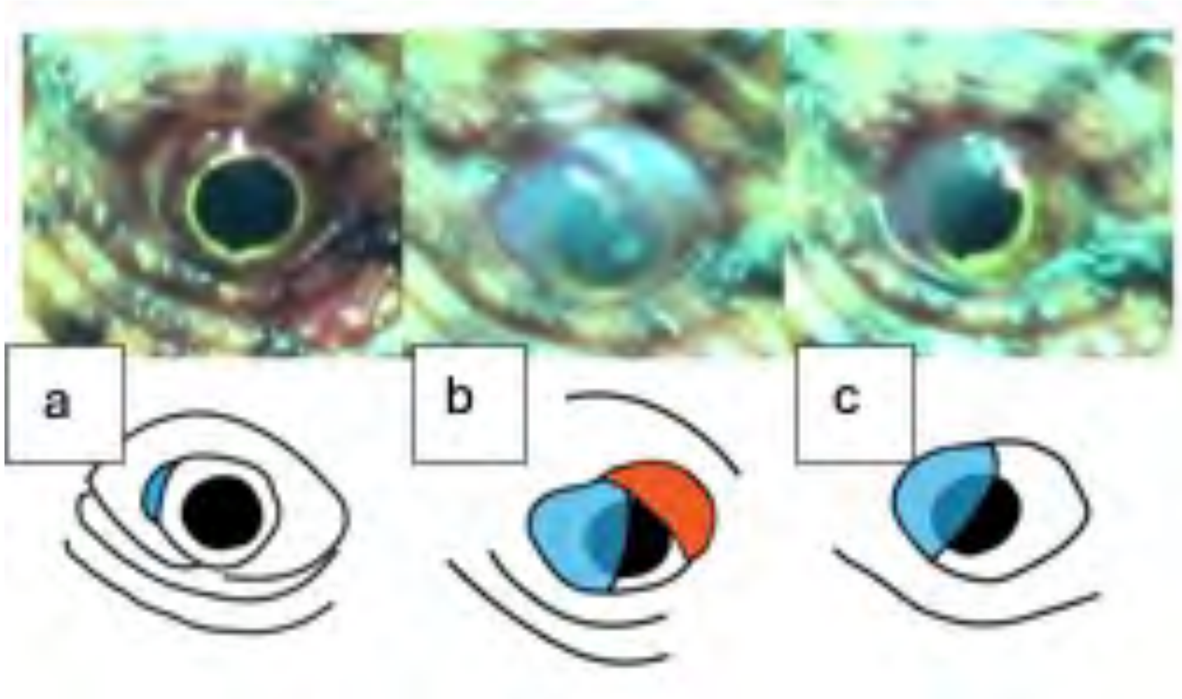
Upper lid and inner canthus nictitating membrane blink



a) Pre-blink. b) and c) Upper lid descends. Semi-translucent nictitating membrane covers the eye. d) Upper lid rises. e) Nictitating membrane starts to recede. f) Post-blink.



Chinese crocodile lizard (Shinisaurus crocodilurus). a) Pre-blink. b) Nictitating membrane appears from inner canthus. c) Upper lid descends. Semi-translucent nictitating membrane covers the eye. d) Upper lid rises. e) Nictitating membrane starts to recede. f) Post-blink.



Upper lid and nictitating membrane blink in the left eye: a) Pre-blink showing a sliver of nictitating membrane (blue) in the medial canthus. b) The upper lid (orange) descends and the nictitating membrane partially covers the pupil. c) The upper lid has returned to its resting position and the nictitating membrane is starting to return to its resting position.

Family: Gekkonidae

Giant gecko (Hemidactylus giganteus)

No blinks: eye lies behind a spectacle (transparent scale)

Note vertically elongated pupil.

Family Eublepharidae

Leopard gecko (*Eublepharis macularus*)

Eyes closed in sleep

Note this gecko has eyelids instead of spectacles.

Family: Elapidae

King cobra (*Ophiophagus hannah*)

No blink. Spectacles

Circular pupil. Note change of position of eye.

Family Colubridae

Brown tree snake (*Boiga irregularis*)

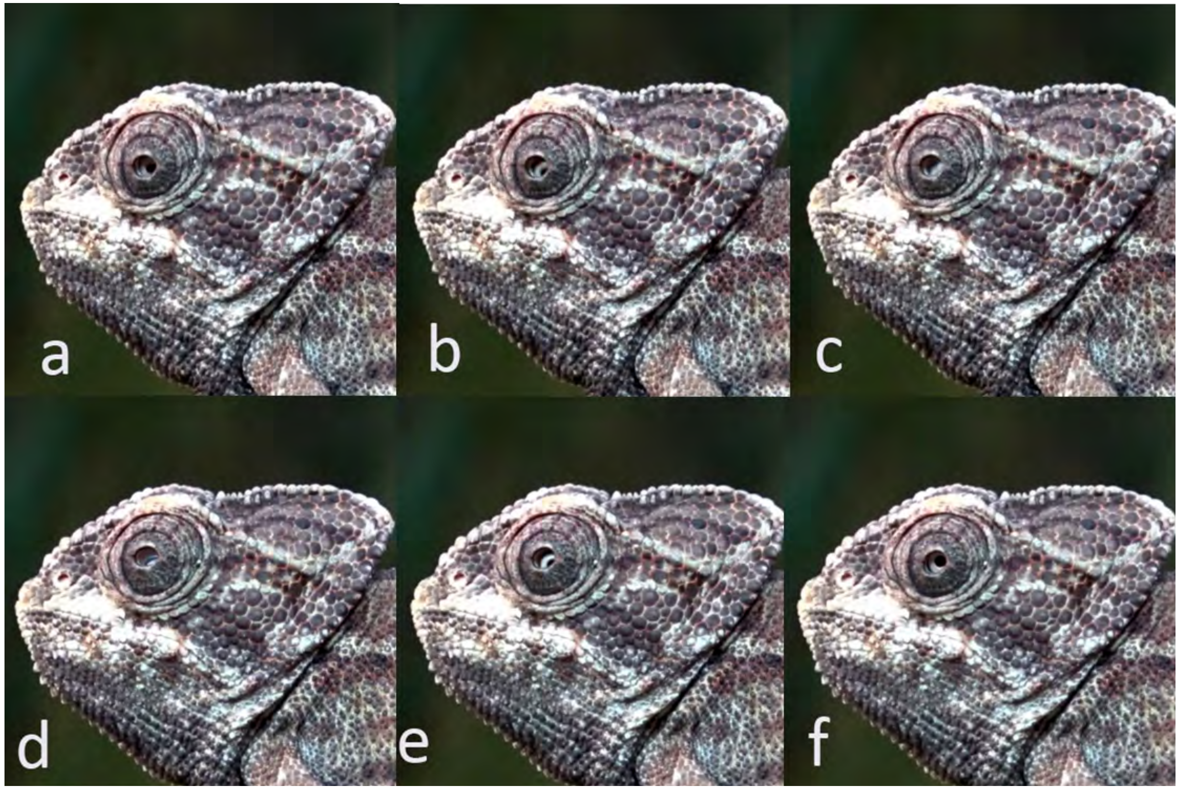
No blink. Spectacles

a) Head half rotated. Cup-shaped pupil. b) Head flat on ground. Pupil has dilated and eye has turned upwards.

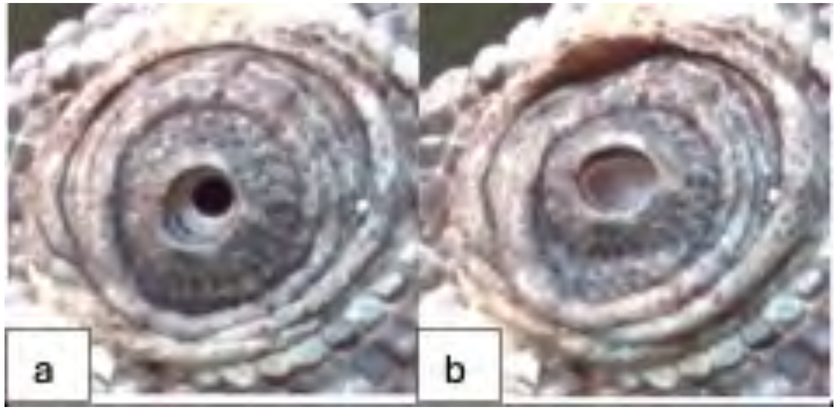
Family Chamaeleonidae

Common chameleon (*Chamaeleo chamaeleon*)

No blink. Fused eyelids with aperture



The eyelids are fused forming turrets with an aperture of fixed diameter through which the eye peers. In a), b) and c) the eyelids are stationary, but the eye can be seen moving behind them. In d), e) and f) the same thing is seen with the eyelids in a different position. The eyes and eyelids are able to move independently of each other.



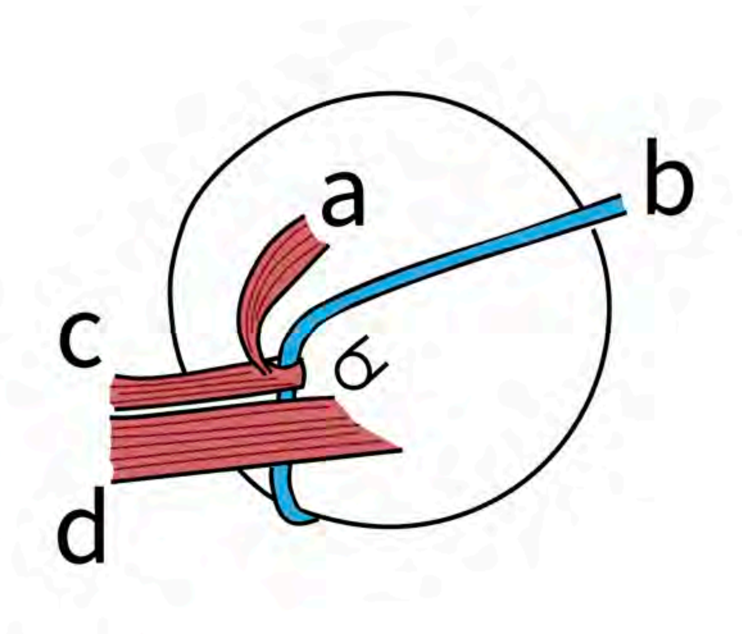
Globe retraction and eye movement: a) Pre-blink. Pupil visible. b) The eyeball has moved and only white sclera is now visible. The upper part of the upper lid has sunken into the orbit.

Veiled chameleon (*Chamaeleo calyptratus*)

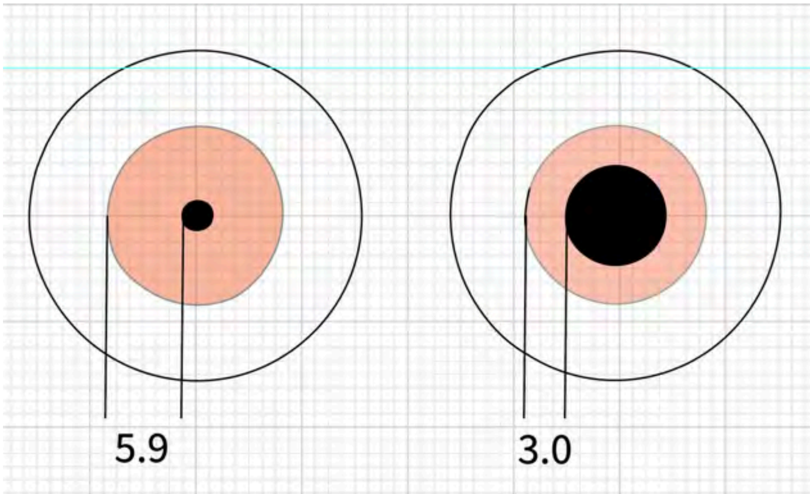
No blink. Fused eyelids with aperture

Eyelid movements

Mechanism by which the nictitating membrane is drawn across the eye in lizards



The back of the lizard eye: a) Retractor of the quadratus muscle b) Nictitating membrane tendon c) Quadratus muscle; d) Retractor bulbi muscle. Adapted from Walls (Walls, 1943). *By having two muscles effectively, pulling on the nictitating membrane tendon, quadratus and its retractor, the membrane can be made to move a greater distance. The nictitating membrane is able to move independently from the upper and lower eyelids.*



This figure compares the width of the iris when it is constricted (left) and dilated (right). It shows that the dilator muscles of the iris are able to approximately halve their length to achieve maximal pupillary dilatation. Assuming it has similar contractile properties, the quadratus muscle would have to be double the width of the visible part of the eye in order to cover it with the nictitating membrane.*

The retractor of quadratus muscle, the quadratus muscle and the retractor bulbi muscle are all supplied by the VIth cranial nerve.

Comments

In most of the lizards studied, blinking with the nictitating membrane involved retraction of the globe – sometimes easy to see, otherwise only demonstrable by slight narrowing of the palpebral fissure as the eyelids sank into the orbit. Globe retraction alone was commonly observed. Globe retraction with elevation of the lower lid was also common. In the Chinese crocodile lizard, the sole member of the family Shinisauridae, an upper lid blink was observed.

In summary, in lizards the globe can retract without involving the lower eyelid. The nictitating membrane is also able to move independently from the lower lid, unlike turtles. But movement of the nictitating membrane is always accompanied by globe retraction. What is surprising is that in the Soloman Island skink and the Komodo dragon, globe retraction occurred without involvement of the nictitating membrane suggesting that there may be variations on the theme of Wall's model. The Soloman Island skink may lack a nictitating membrane but the Komodo dragon certainly does not. In lizards, some blinks primarily involve globe retraction with movement of the nictitating membrane. In other blinks, the lower eyelid elevates with or without retraction of the globe. Walls (1963) refers to a muscle akin to but not homologous with orbicularis oculi in mammals, which elevates the lower eyelid.

Innervation of the muscles involved in blinking:
Retractor bulbi: Abducens nerve (VIth cranial nerve)
Bursalis: Abducens nerve
Bursalis retractor: --
Levator of the lower eyelid: --
The nictitating membrane blinks clean and lubricate the cornea with secretions from the Harderian and lacrimal glands. Lower lid blinks with globe retraction protect the eye from injury as does globe retraction on its own.

The eyelids of chameleons are fused, covered in scales, with only a small opening to let light into the eye beneath. Four rectus and two oblique muscles move the eye and thereby the eyelids which are fused to the sclerae of each eye. It is of interest that the eye can move independently from the lids.

The tuatara, the only surviving member of the order Sphenodontia, has a similar nictitating membrane blink to lizards with accompanying globe retraction. The tendon to the nictitating membrane is attached to the retractor bulbi muscles (Walls, 1943).

In snakes, the eye is protected by fused eyelids which form a transparent spectacle which is shed annually during moulting. The spectacle has a blood supply.

(Quekett, 1852)

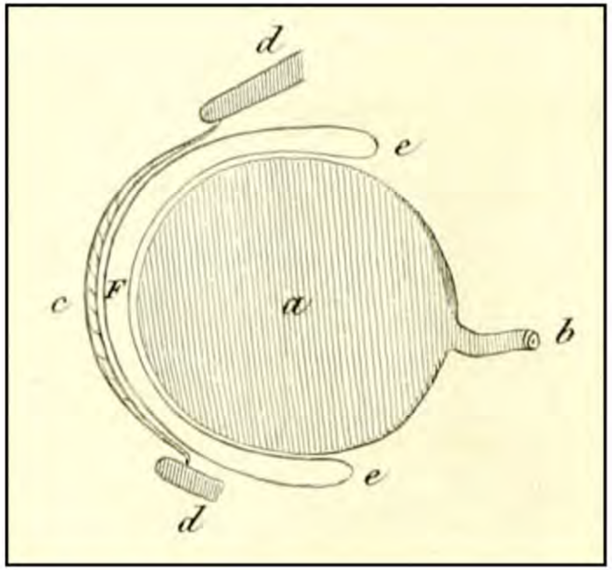


Fig. 1-1. The earliest accurate illustration of the spectacle's relationship with the eye. The spectacle (c) is separated from the eye (a) by the subspectacle space (F). Also labeled are the optic nerve (b), upper and lower periocular scales (d), and the fornix (e). Reproduced from Cloquet 1821.

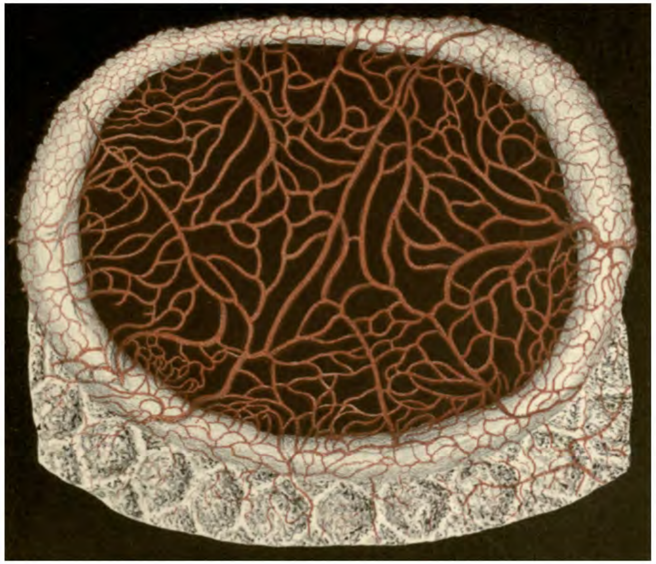


Figure 1-4. Earliest known illustration of the spectacle vasculature, drawn from the injected vasculature of a rock python (*Python molurus*). Reproduced from Quekett 1852.

Order Crocodilia

Introduction

Crocodilia (alligators, caimans, crocodiles and gharials), birds, dinosaurs (extinct) and pterosaurs (extinct) all trace their ancestry back to archosaurs (Green & alia., 2014). Crocodilians first appeared 95Ma and diverged from birds 240Ma. Compared with birds, crocodilia have changed little and there are only 22 extant species compared with 10,000 species of birds.

Present study (Mor231).

Videos were made of 14 species of Crocodilia from 3 families. Nictitating membrane blinks were seen in 14 species, 3 with visible globe retraction, 4 with no evident globe retraction) and 11 associated with globe retraction and elevation of the lower lid. In five species, there was lower lid elevation and globe retraction without visible movement of the nictitating membrane. In no case was there upper lid blinking, though in some cases the upper lid sank a little into the orbit as the globe retracted.

Table showing types of blink observed in 14 species of crocodilia

NMBl: nictitating membrane blink; Gl R: globe retraction; LLBl: lower lid blink; Y: yes.

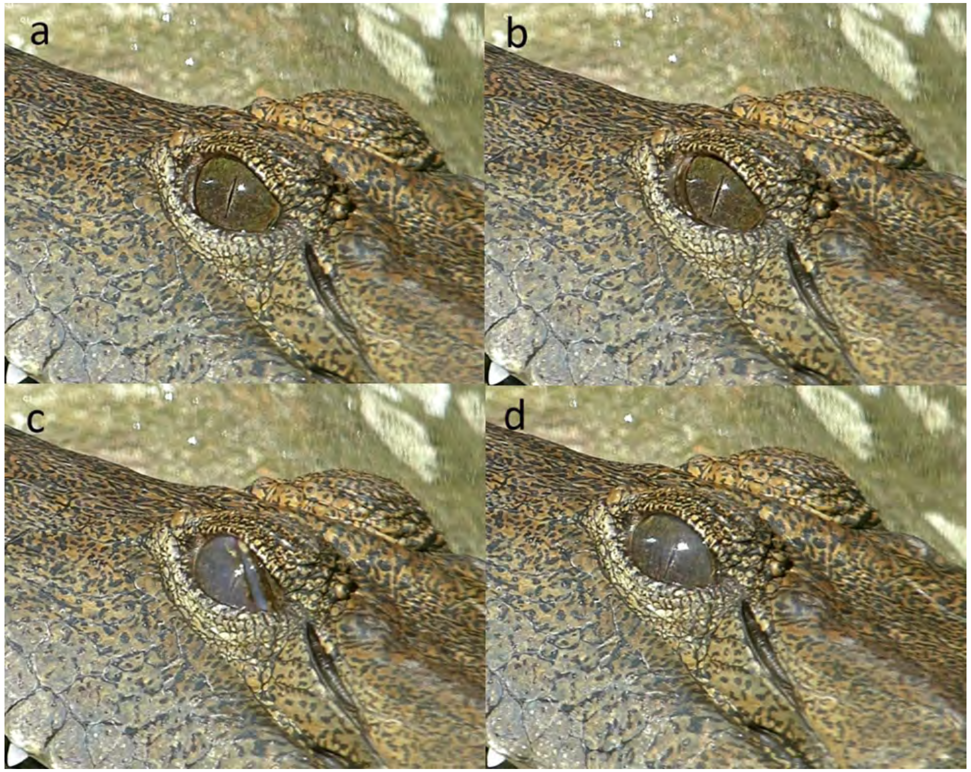
Order	Family	Species	Common Name	NMBl, Gl R	NMBl	NMBl, LLBl, Gl R	LLBl, Gl R	NMBl, LLBl
Crocodilia								
	Alligatoridae							
		Alligator mississippiensis	American alligator		Y	Y	Y	
		Caiman latirostris	Broad-snouted caiman			Y		
		Melanosuchus niger	Black caiman			Y		
		Paleosuchus palpebrosus	Cuvier's dwarf caiman			Y		
		Paleosuchus trigonatus	Schneider's dwarf caiman	Y				
	Crocodylidae							
		Crocodylus hombifer	Cuban crocodile			Y		
		Crocodylus johnstoni	Freshwater crocodile	Y		Y	Y	
		Crocodylus mindorensis	Philippine crocodile	Y				
		Crocodylus niloticus	Nile crocodile			Y		
		Crocodylus porosus	Saltwater crocodile	Y	Y	Y		
		Crocodylus siamensis	Siamese crocodile			Y		
		Mecistops cataphractus	West African slender-snouted crocodile		Y	Y	Y	
		Osteolaemus tetraspis tetraspis	West African dwarf crocodile				Y	

Order	Family	Species	Common Name	NMBI, GI R	NMBI	NMBI, LLBI, GI R	LLBI, GI R	NMBI, LLBI
Crocodilia								
	Gavialidae							
		Gavialis gangeticus	Gharial		Y			Y
		Tomistoma schlegelii	Tomistoma			Y		

Family Crocodylidae

Freshwater crocodile (*Crocodylus johnstoni*)

Blink a: Nictitating membrane blink

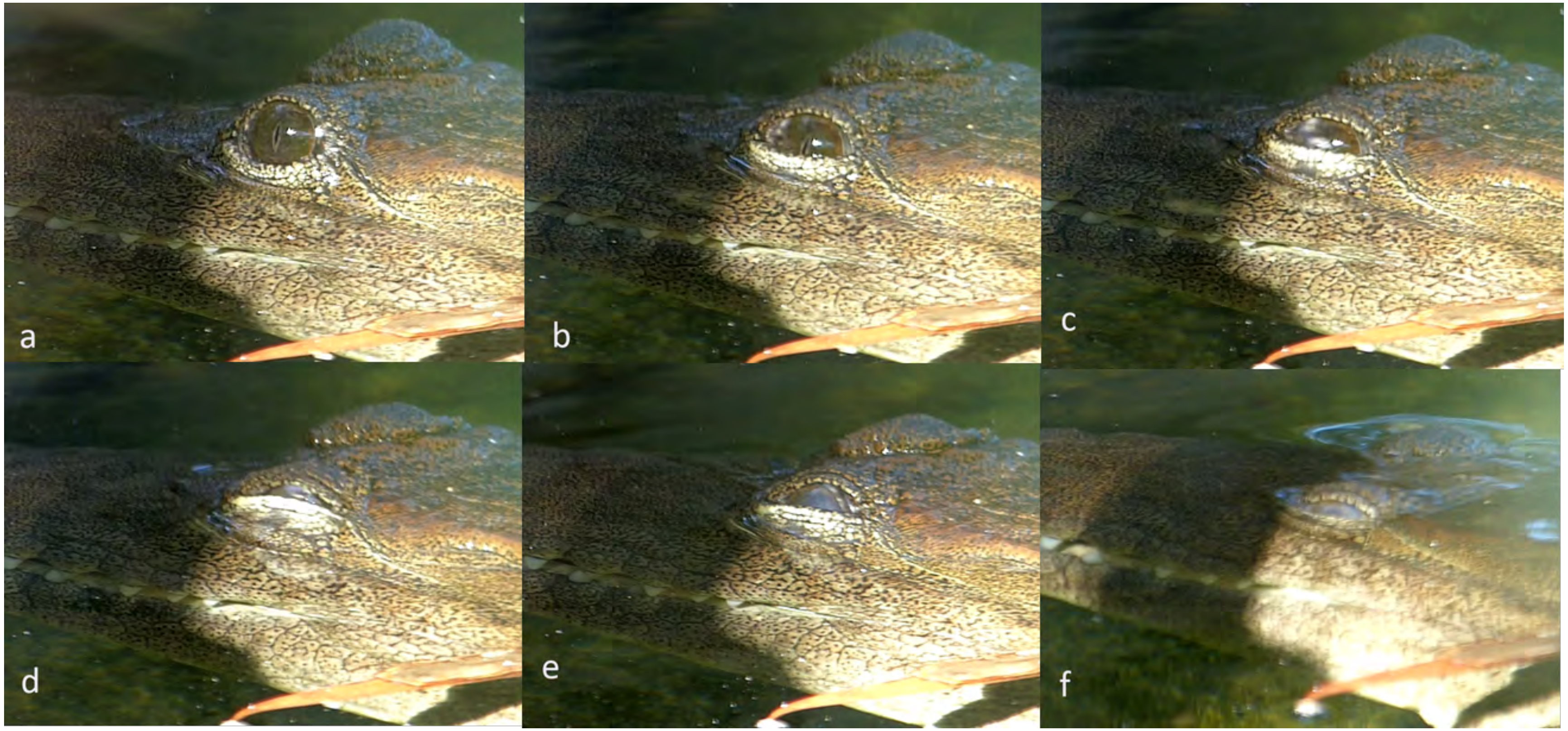


a) Pre-blink. Vertically elongated pupil. b) Nictitating membrane starts to emerge from inner canthus and lower lid. Slight narrowing of palpebral fissure as globe retracts. c) Nictitating membrane with thickened marginal rim, travels diagonally across the pupil. d) Maximal blink. Semi-transparent nictitating membrane.

Blink b: Globe retraction and elevation of lower lid

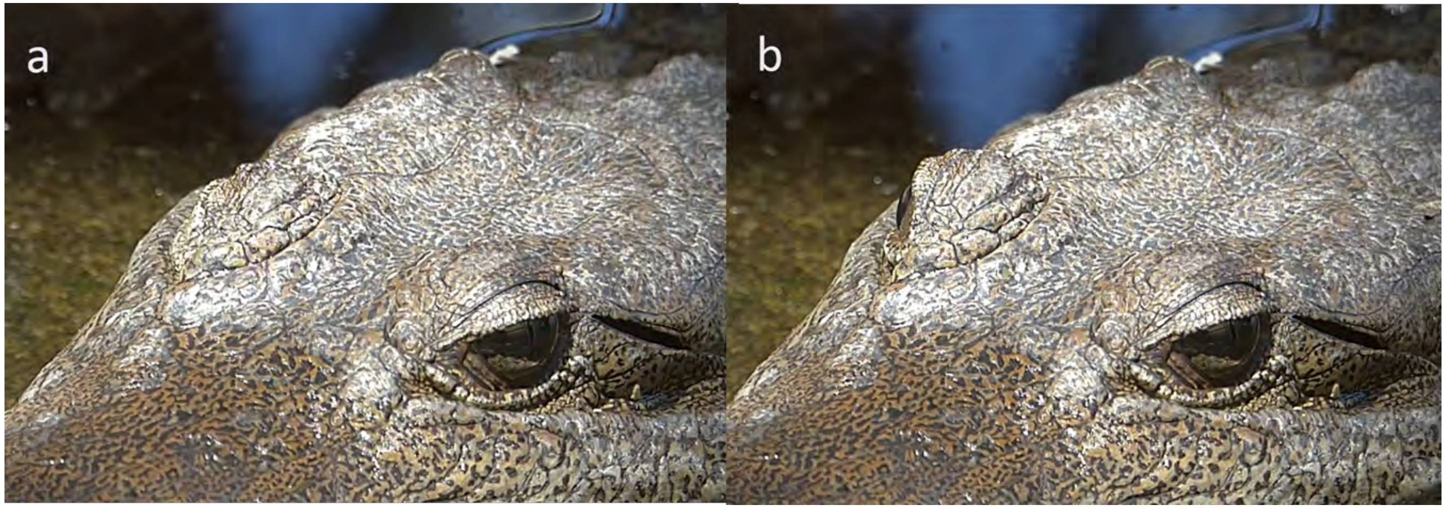
Submerging. a) Pre-submerging. b) Water covers left lower eye lid and palpebral fissure narrows as globe retracts. c) Left lower lid elevates

Blink c: Globe retraction, elevation of lower lid and nictitating membrane blink



a) Pre-submerging. b) Lower lid elevates. Upper lid sinks with globe into orbit. d) Lower lid rises further. e) Lower lid drops a little. e) Now nearly submerged. Nictitating membrane covers eye which is almost closed.

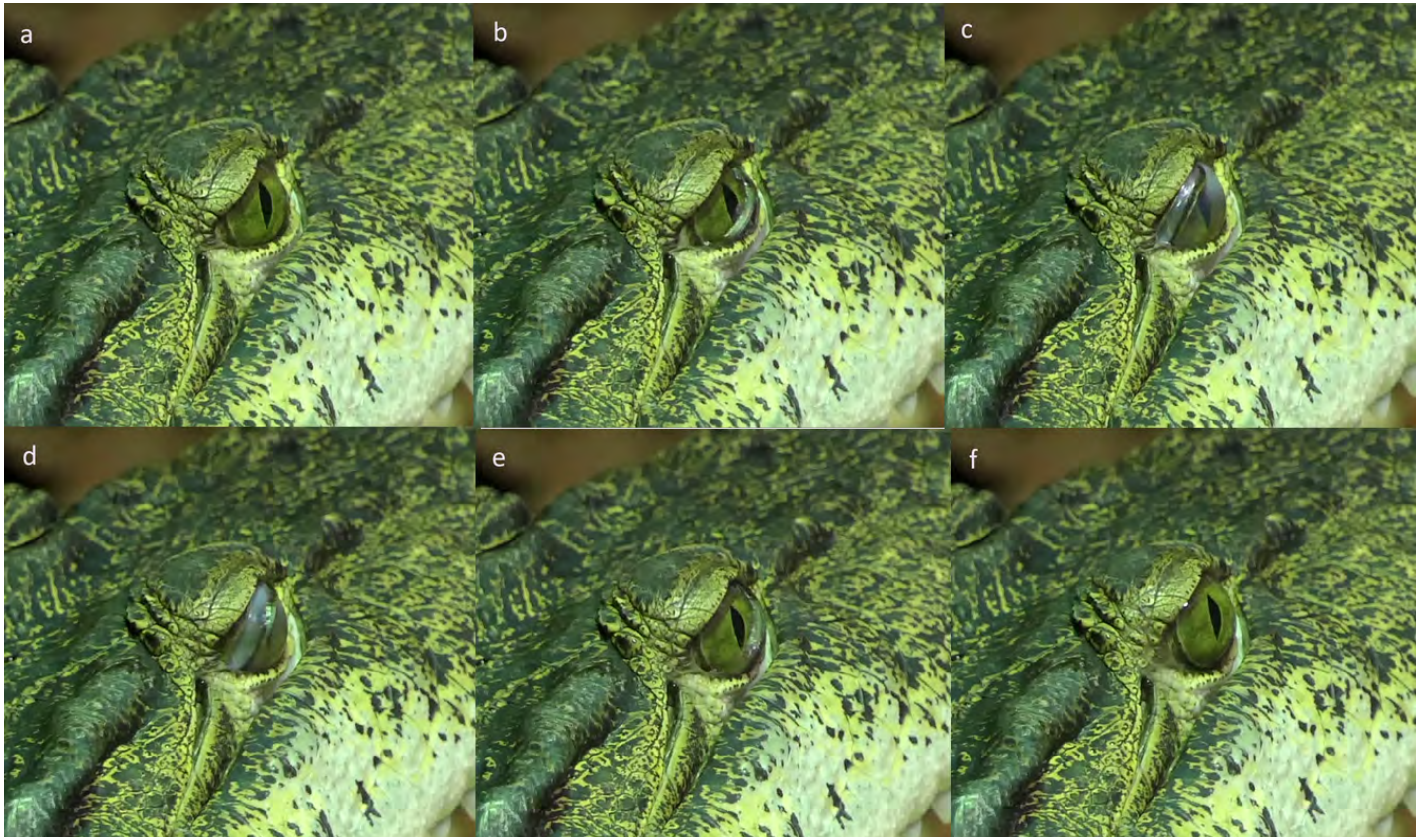
Submerging: lower lid rises and nictitating membrane crosses as the head slowly sinks into the water.



a) Right brow down as globe retracts. b) Right brow up and eye visible as globe unretracts.

Philippine crocodile (*Crocodylus mindorensis*)

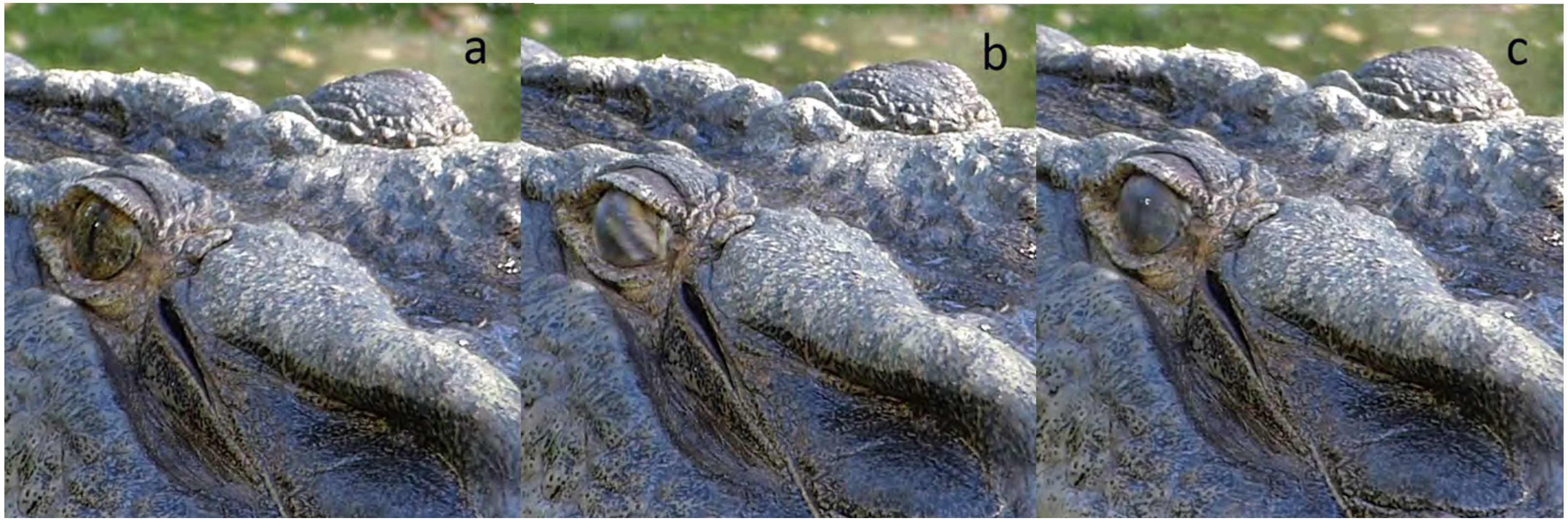
Nictitating membrane blink where the membrane appears to be arising from the lower lid



a) Pre-blink. Vertically aligned pupil. Note heavy brow and upper lid projecting over eyeball. b) Edge of nictitating membrane, parallel to the lower lid is seen rising from inside the lower lid. c) Semi-transparent nictitating membrane with a line of pigment in the marginal fold, covers the eye. d) and e) Nictitating membrane descends. f) Post-blink. Globe more prominent than at the start of the series showing that retraction had already begun.

Saltwater crocodile (*Crocodylus porosus*)

Blink a: Inner canthus nictitating membrane blink



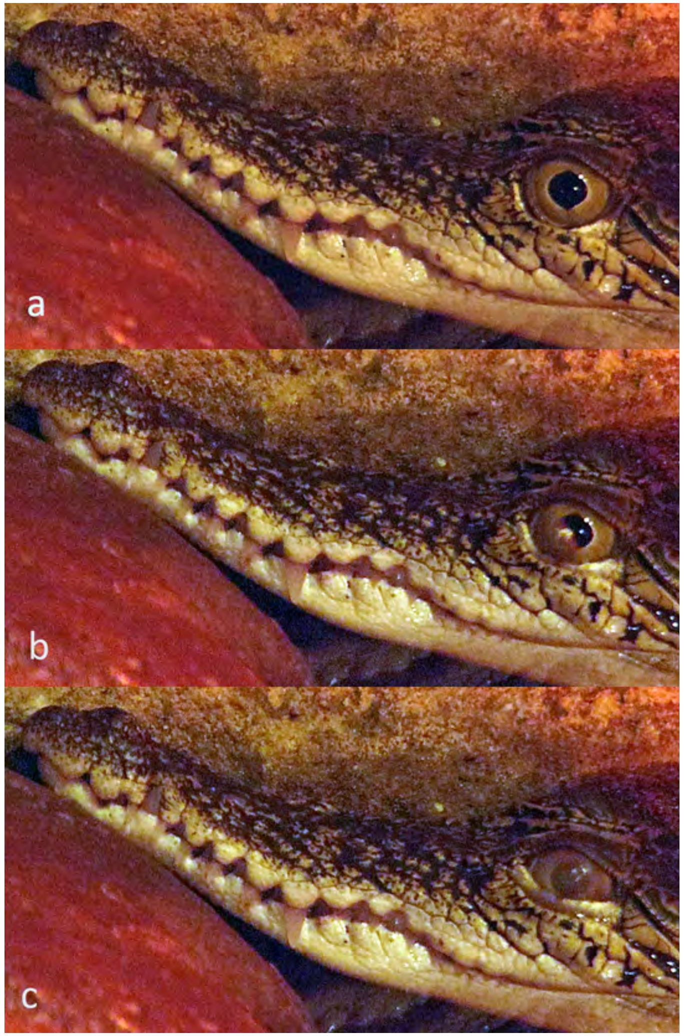
a) Pre-blink. Vertically aligned pupil. b) Nictitating membrane moves obliquely across the eye from the inner canthus. c) Maximal blink with semi-transparent nictitating membrane.

Juvenile. a) Pre-blink. b) Nictitating membrane rises obliquely from inner canthus and lower lid. c) Maximal blink. Nictitating membrane partially covers pupil. Little or no narrowing of palpebral fissure. d) Post-blink.

Blink b: Inner canthus nictitating membrane blink with narrowing of palpebral fissure due to globe retraction

In sunlight. a) Pre-blink. Vertically aligned pupil. b) Nictitating membrane moves obliquely across the eye from the inner canthus. c) Maximal blink.

Blink b: Inner canthus nictitating membrane blink with narrowing of palpebral fissure due to globe retraction

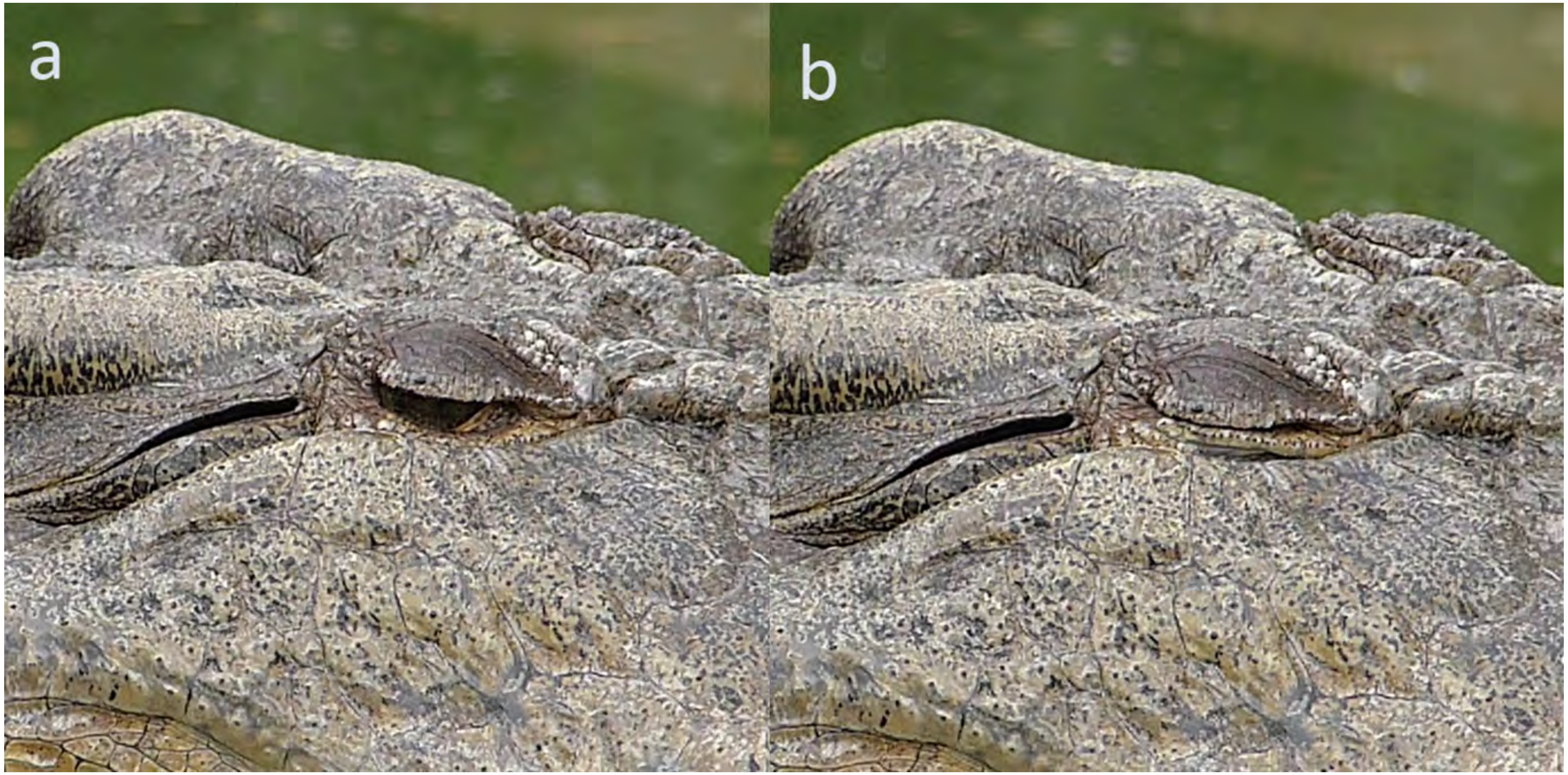


Juvenile. a) Pre-blink. Pupil fully dilated and almost circular (has vertically elongated slit pupils in light). b) Nictitating membrane rises obliquely from inner canthus. c) Maximal blink. Eye covered by semi-translucent nictitating membrane. Narrowed palpebral fissure due to globe retraction.

Blink b: Nictitating membrane blink with narrowing of palpebral fissure due to globe retraction

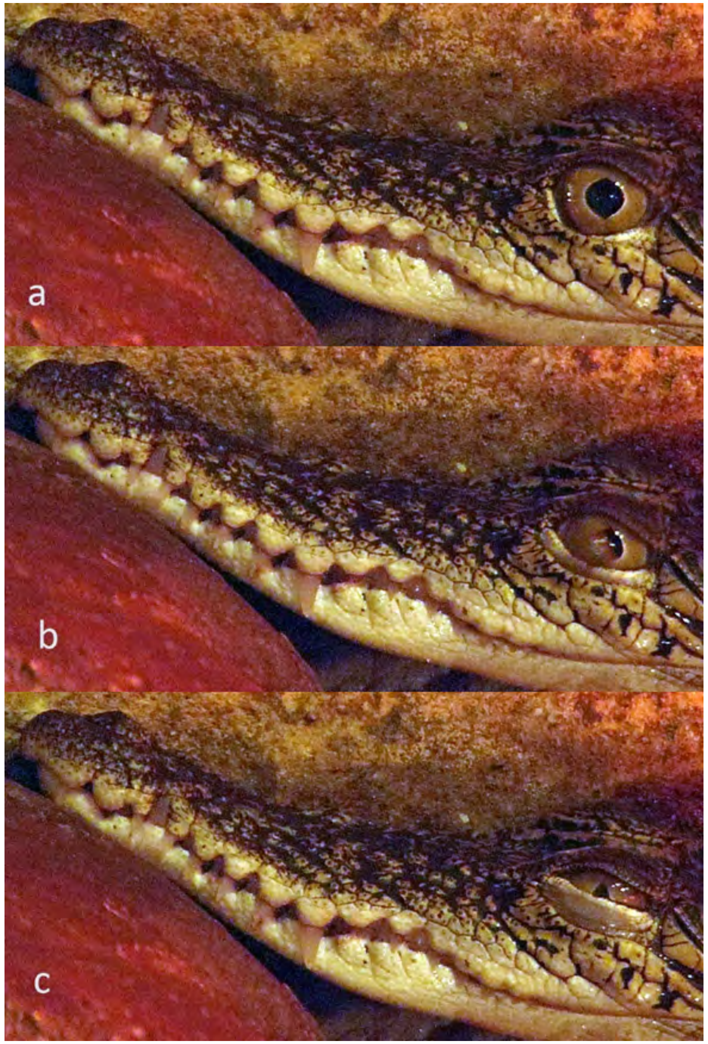
Juvenile a) Pre-blink. Vertically elongated pupils almost fully dilated. b) Palpebral fissure narrows as globe retracts. c) Nictitating membrane reaches pupil from inner canthus. d) Semi-translucent nictitating membrane covers eye. e) Maximal blink. f) Post-blink.

Blink c: Inner canthus nictitating membrane blink with elevation of lower lid



Drowsy. a) Eye almost shut. Protruding upper lid. Nictitating membrane lying obliquely across the eye at inner canthus. b) Lower lid rises.

Blink c: Nictitating membrane blink with elevation of lower lid



Juvenile a) Pre-blink. b) Palpebral fissure narrows as globe retracts. Nictitating membrane reaches pupil from inner canthus. c) Lower lid rises. Maximal blink

Frontal view showing that the position of the eyes would allow stereoscopic vision

Nile crocodile (*Crocodylus niloticus*)

Nictitating membrane blink with elevation of lower lid and globe retraction

a) Pre-blink. Vertically elongated pupil. b) Globe retracts. Nictitating membrane moves diagonally from inner canthus. Lower lid rises. c) Maximal blink. d) Globe starts to unretract.

West African slender-snouted crocodile (*Mecistops cataphractus*)

Blink a: Elevation of lower lid with sleep

Blink b: Nictitating membrane blink (with no globe retraction)

Juvenile. Nictitating membrane blink

West African dwarf crocodile (*Osteolaemus tetraspis tetraspis*)

Globe retraction with elevation of lower lid

Family Alligatoridae

American alligator (*Alligator mississippiensis*)

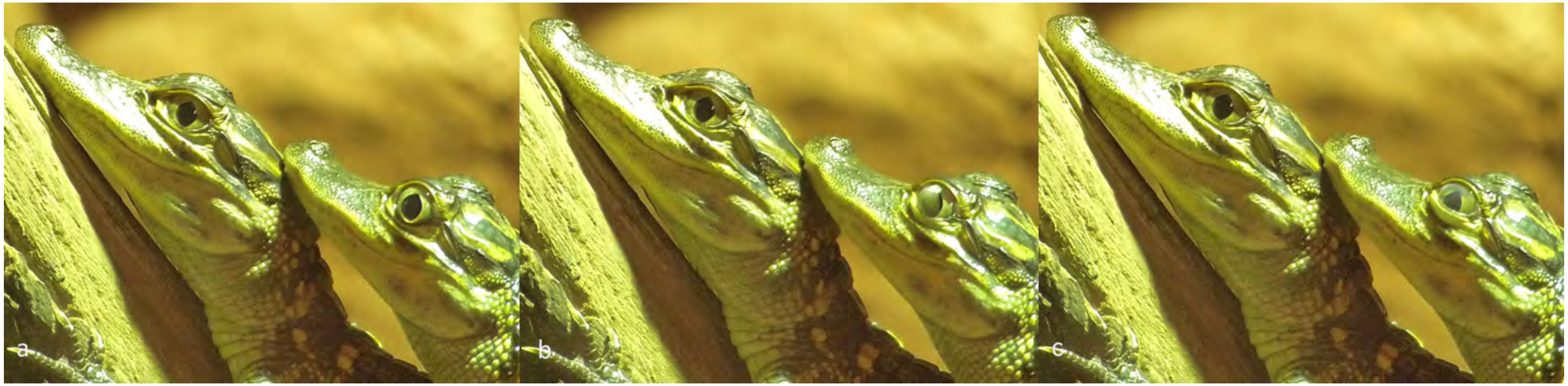
Blink a: Nictitating membrane blink

a) Pre blink. Note heavy brow and visible nictitating membrane in the inner canthus. b) Opaque nictitating membrane with thickened marginal rim rises obliquely from the inner canthus and lower lid. c) Maximal blink. Hardly any change in the size of the palpebral fissure suggesting no globe retraction.

Blink a: Nictitating membrane blink

Hatchling. a) Pre-blink. Vertically elongated pupil partially dilated. b) Nictitating membrane with vertically aligned edge moves from the inner canthus and half covers the globe. c) Maximal the eye is covered by a transparent nictitating membrane. No globe retraction.

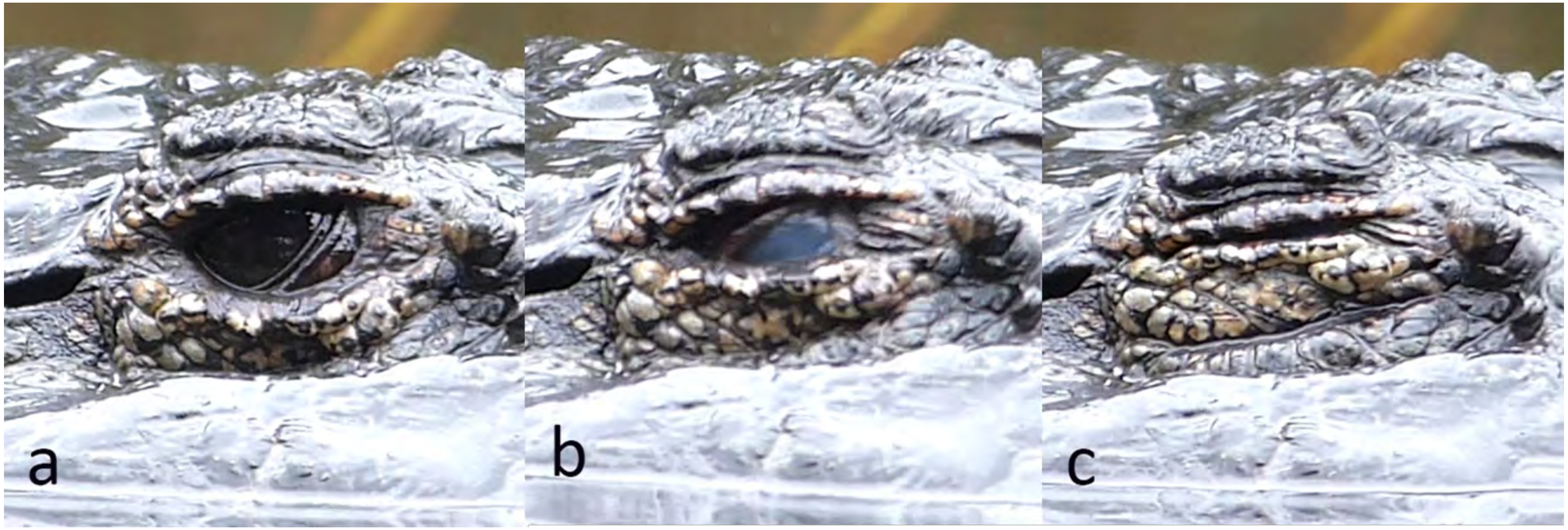
Blink b: Nictitating membrane blink with elevation of lower lid



A pair of hatchling American alligators. a) Pre-blink. Note prominence of globe in the hatchling on the right showing that the globe of the left-hand hatchling is a little retracted. b) Nictitating membrane arising from the inner canthus of the right-hand hatchling half covers the globe. c) Maximal blink. The eye is covered by a transparent nictitating membrane and the lower lid is slightly elevated. The upper lid has not moved showing that the lower lid has been elevated and there has been no globe retraction.

Hatchling. Showing that the position of the eyes would allow stereoscopic vision

Blink c: Nictitating membrane blink with elevation of lower lid and globe retraction

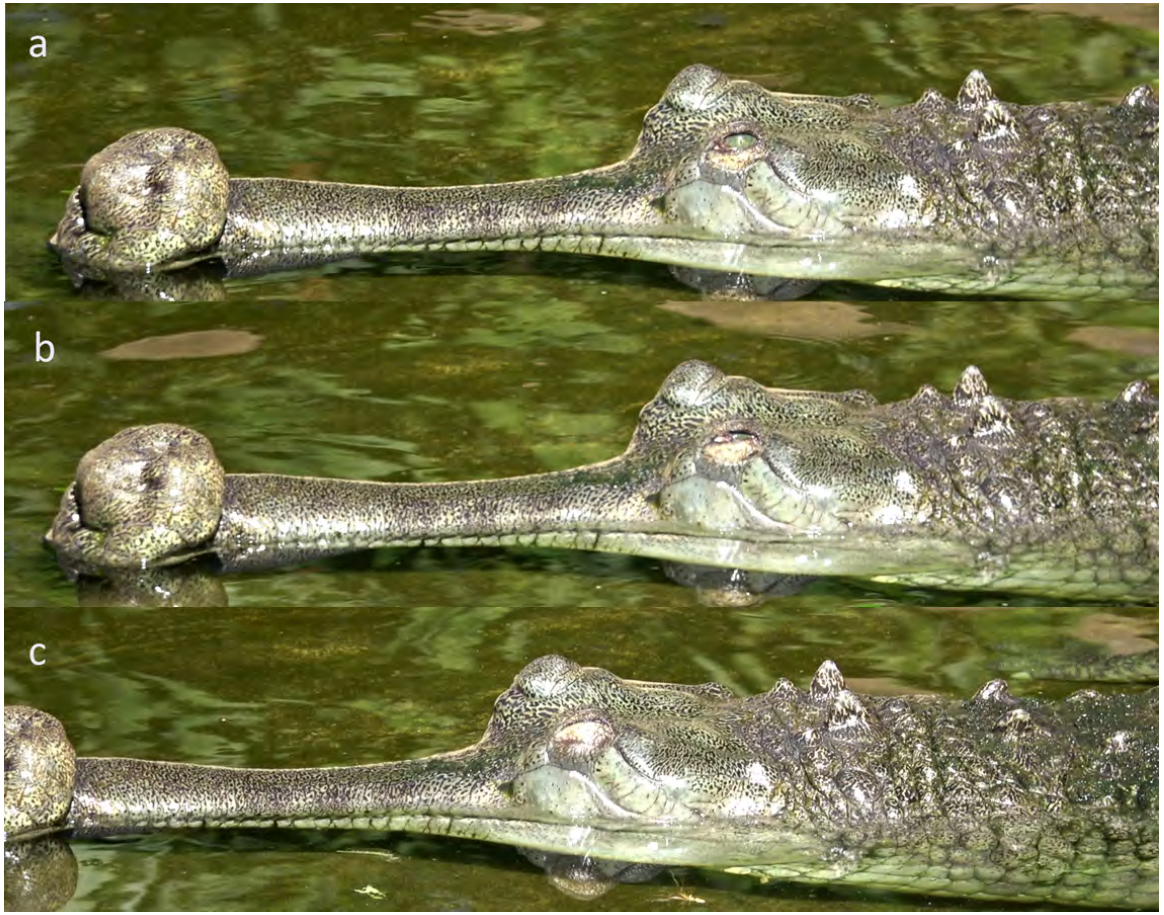


a) Pre-blink. Edge of nictitating membrane visible at inner canthus. b) Opaque nictitating membrane rises obliquely. Lower lid rises. c) Maximal blink with lids tightly opposed. Upper lid has sunk into orbit denoting globe retraction.

Family Gavialidae

Gharial (*Gavialis gangeticus*)

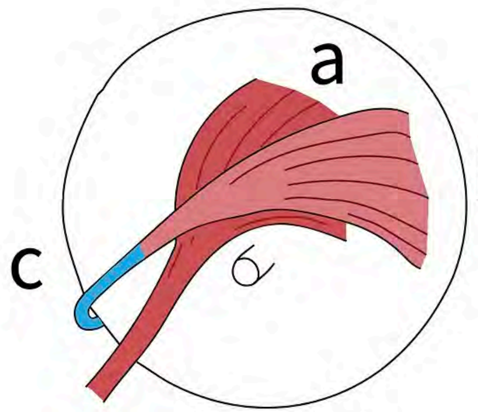
Nictitating membrane blink with elevation of lower lid



a) Pre-blink. b) Lower lid elevates. Nictitating membrane crosses eye from inner canthus. c) Full blink. Lids tightly opposed.

The mechanism of blinking in crocodilia

The muscles involved in blinking in crocodilia are shown in the figures below.



The back of an alligator eye: a) Retractor bulbi muscle. b) Quadratus muscle c) Nictitating membrane tendon. Adapted from Walls (Walls, 1943).

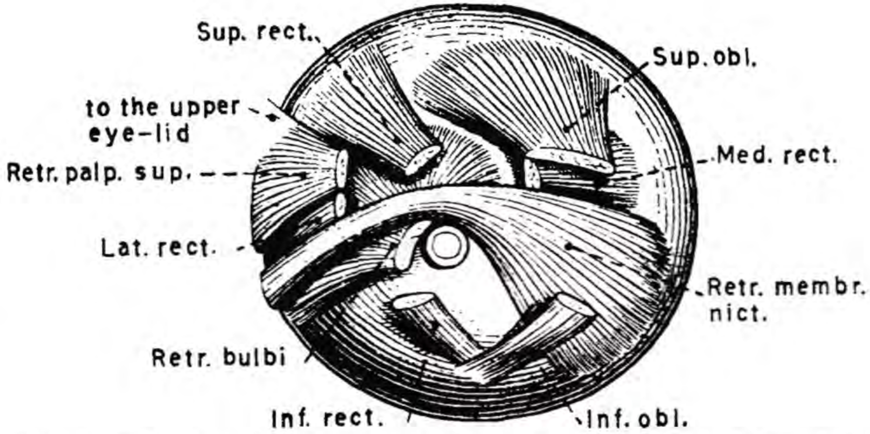


Fig. 1 The eye muscles of Alligator mississippiensis according to Nishi ('38) in Bolk-Göppert et al., vol. V. Left bulbus from the medial side.

Drawing from a dissection of the eyeball of the *Alligator mississippiensis*. The pyramidalis muscle is here labelled Retr. membr. nict. (retractor membranae nictitantis). Of note is the muscle labelled Retr. palp. sup (retractor palpebrae superioris), which is attached to the upper eyelid. There is also a depressor palpebrae inferioris (Underwood, 1970).

The lower lid and nictitating membrane are able to move independently as is globe retraction. The membrane has a cartilage (Underwood, 1970). The retractor bulbi and quadratus muscles are supplied by the VIth cranial nerve. Other muscles involved in blinking include: depressor palpebralis inferioris and levator palpebralis superioris (Underwood, 1970).

Hardner's gland discharges on the inner face of the nictitating membrane. Drainage of tear fluid is through 3-8 canaliculi on the margin of the lower lid which join the lachrymal duct.
palpebrae inferioris (Wedin 1953) (Underwood 1970).

Summary

Two main types of blink were observed. The nictitating membrane blink was often accompanied by mild globe retraction shown by slight narrowing of the palpebral fissure. The membrane rose obliquely from the inner canthus and from behind the lower lid. The lower lid blink was accompanied by movement of the nictitating membrane and marked globe retraction. In some species, a bony moveable 'brow' covered in horny scales (scutes), closed like a trapdoor on a hinge over the orbit as the eyeball retracted, providing extra protection from the flailing limbs of prey.

Eyelid blinking begins with passage of the nictitating membrane. Then the eyeball retracts and as it does so, the upper eyelid and the 'brow' to which it fixed, sink into the orbit on their hinge, initially passively but then by contraction of the branch of retractor bulbae superioris muscle which inserts into the upper lid. This would be important in the face of a large flailing prey. While retraction of the upper eyelid is the most visible movement in this type of blink, the full closure of the eye is performed by the lower eyelid which slides up over the cornea as the eyeball retracts. The lower eyelid can also rise independently from any movement of the upper eyelid. Reflex lower eyelid closure in response to submergence has been described (Garrick & Saiff, 1974). The depressor palpebrae inferioris draws the lower eyelid down at the end of a blink.

Birds (Class Aves)

Introduction

Birds have a number of features which, together, distinguish them from other animals. These include feathers; forelimbs modified into wings with fused hand bones; hollow bones with fusion of some vertebrae; a wishbone; keratinous beaks with no teeth and lungs connected to air sacs that allow one way airflow. Like mammals, they are warm blooded (maintain a constant body temperature). They lay amniotic eggs with hard shells in nests. The amnion is a layer, not present in fish, which protects the contents of the egg from drying out. They have a large forebrain relative to body size and excellent vision. They have a single occipital condyle at the base of the skull (mammals have two) and a syrinx (voice box) located at the base of the trachea not at the top (in the larynx) like mammals.

The lineage of birds separated from other reptiles during the Mesozoic. Birds closest living relatives are crocodilians with which they share a common ancestor in the archosaur lineage (250mya - Triassic). The first true birds appeared in the late Jurassic (150mya). Diversification accelerated after the end of the Cretaceous mass extinction about 60mya. Most current orders e.g. Passeriformes, Anseriformes and Falconiformes, arose and diversified rapidly in the Palaeocene (66 to 23mya). There are over 10,000 species of birds across more than 40 recognised orders.'

Present study

References and much of what follows are included in *The various ways that birds blink* (Morris & Parsons, 2023).

Order Accipitriformes

Family Accipitridae

Bald eagle (Haliaeetus leucocephalus)

Nictitating membrane blink on head turn

Nictitating membrane blink on head turn, ending in the left eye before the right. Note prominent brow.

Nictitating membrane blink.

Wallace's hawk-eagle (*Nisaetus nanus*)

Blink a: Nictitating membrane blink on head turn

Juvenile. Nictitating membrane blink.

Nictitating membrane blink on head turn.

Blink b: Lower lid and nictitating membrane blink on preening

Nictitating membrane blink on preening.

Bateleur (*Terathopius ecaudatus*)

Nictitating membrane blink on head turn

Nictitating membrane wink on head turn.

Nictitating membrane emerges from inner canthus.

Nictitating membrane blink on head turn.

Black-breasted buzzard (*Hamirostra melanosternon*)

Blink a: Nictitating membrane blink on head turn

Nictitating membrane blink on head turn.

Blink b: Lower lid elevation with preening

Lower lid elevation with preening.

Possible eye movement (note position of pupil).

Nictitating membrane blink. Note upper lid.

Brahminy kite (*Haliastur indus*)

Blink a: Nictitating membrane blink on head turn

Nictitating membrane blink.

Blink b: Nictitating membrane blink on head turn with slight fall in inner part of upper lid

Nictitating membrane blink.

Blink c: Lower lid elevation with preening

Whistling kite (*Haliastur sphenurus*)

Blink a: Nictitating membrane blink on head turn

Blink b: Nictitating membrane blink on head turn with slight lowering of inner part of upper lid

Eye movement.

Nictitating membrane blink with slight lowering of inner part of upper lid.

Nictitating membrane blink with slight lowering of inner part of upper lid of left eye only.

Black kite (*Milvus migrans*)

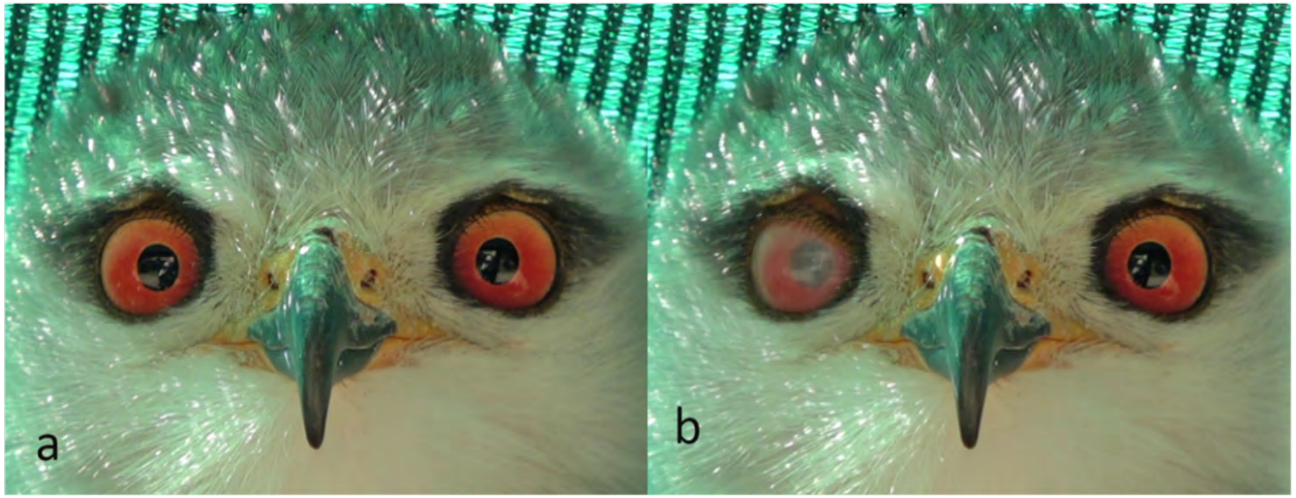
Nictitating membrane blink on head turn

Nictitating membrane blink.

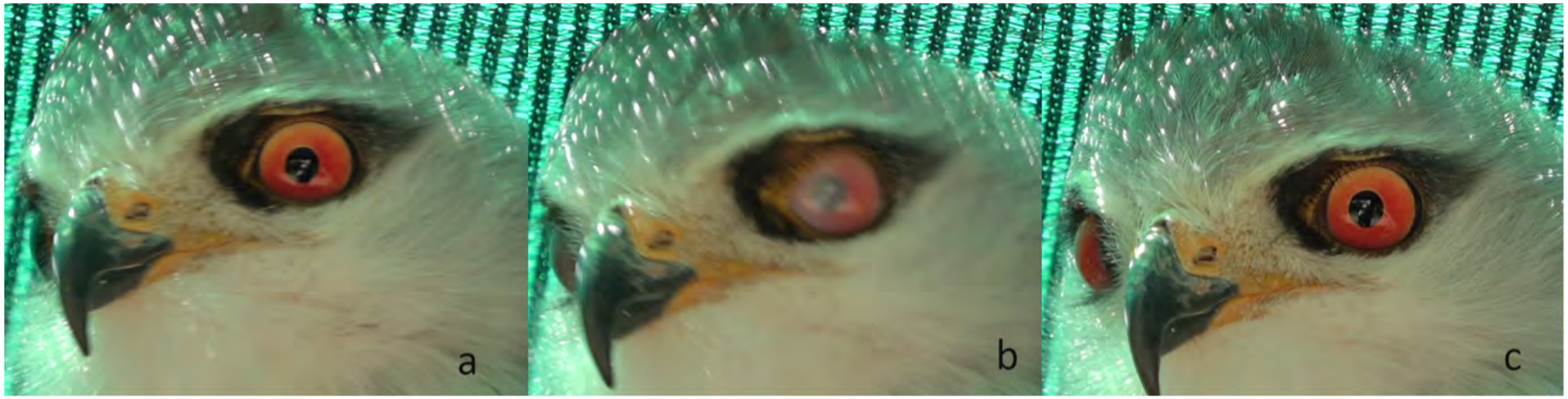
Black winged kite (*Elanus caeruleus*)

Side to side movement of the head while maintaining visual fixation - peering

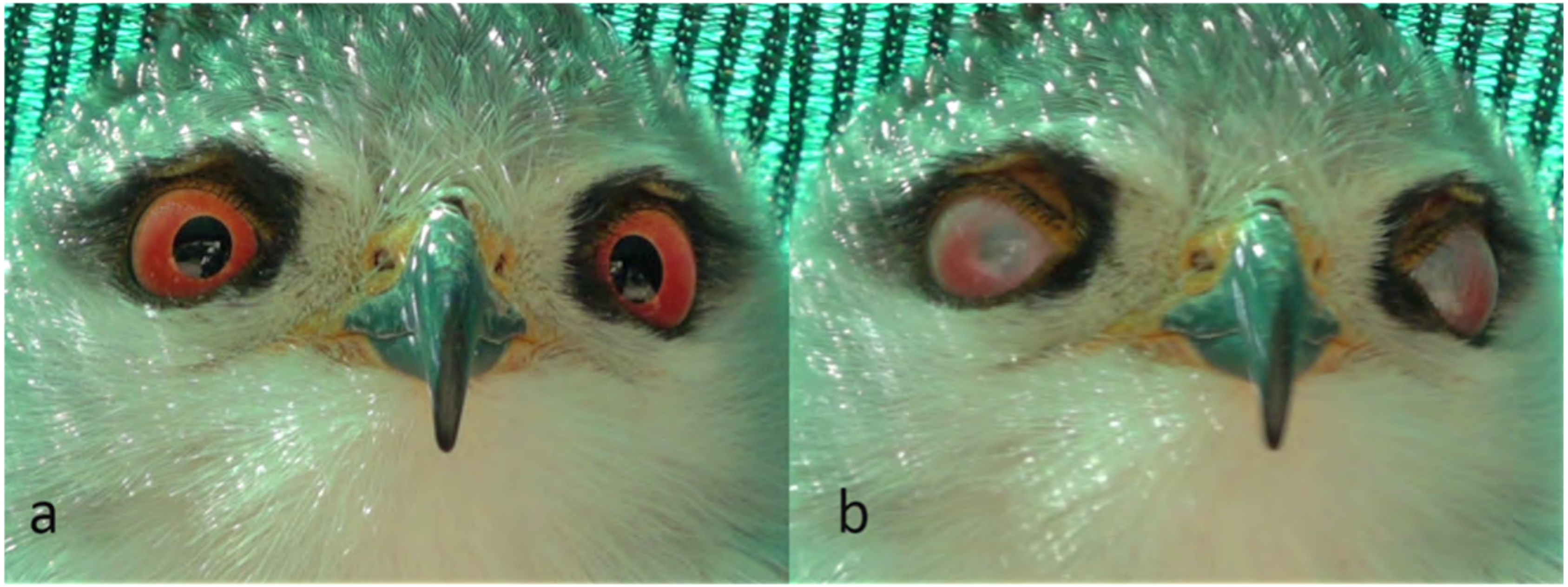
Nictitating membrane blink in right eye with minimal head movement



A second nictitating membrane blink on head movement. a) Pre-blink. b) Nictitating membrane covers both eyes. c) Nictitating membrane still over right eye but not left



Slight lowering of medial part of upper lid during nictitating membrane blink



Crowned eagle (*Stephanoaetus coronatus*)

Nictitating membrane blink on head turn

Little eagle (*Hieraaetus morphnoides*)

Nictitating membrane blink on head turn

Common buzzard (*Buteo buteo*)

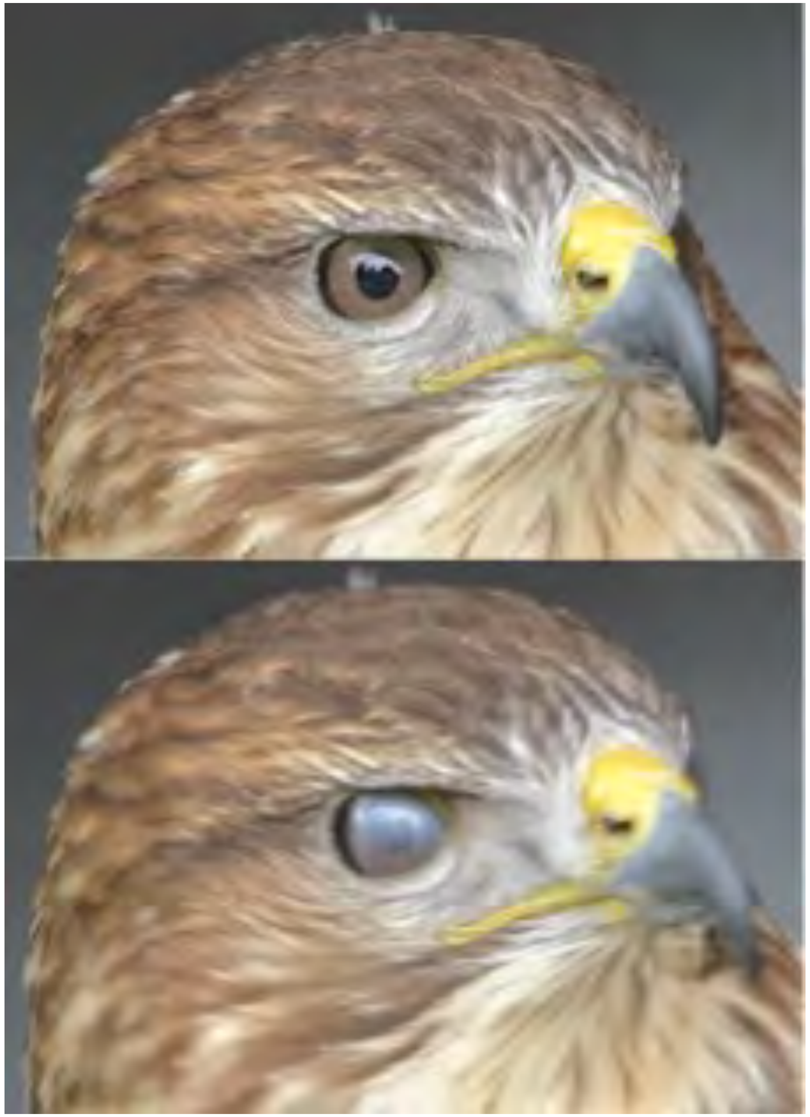
Nictitating membrane blink on head turn

a) Pre-blink. b) Nictitating membrane blink. c) Post-blink at end of head movement.

a) Pre-blink. b) Nictitating membrane blink in both eyes. c) Post-blink at end of head movement.

a) Pre-blink. b) Nictitating membrane blink in right eye only. c) Post-blink at end of head movement. Note prominent brow.

Nictitating membrane blink in both eyes.



Grey goshawk (*Accipiter novaehollandiae*)

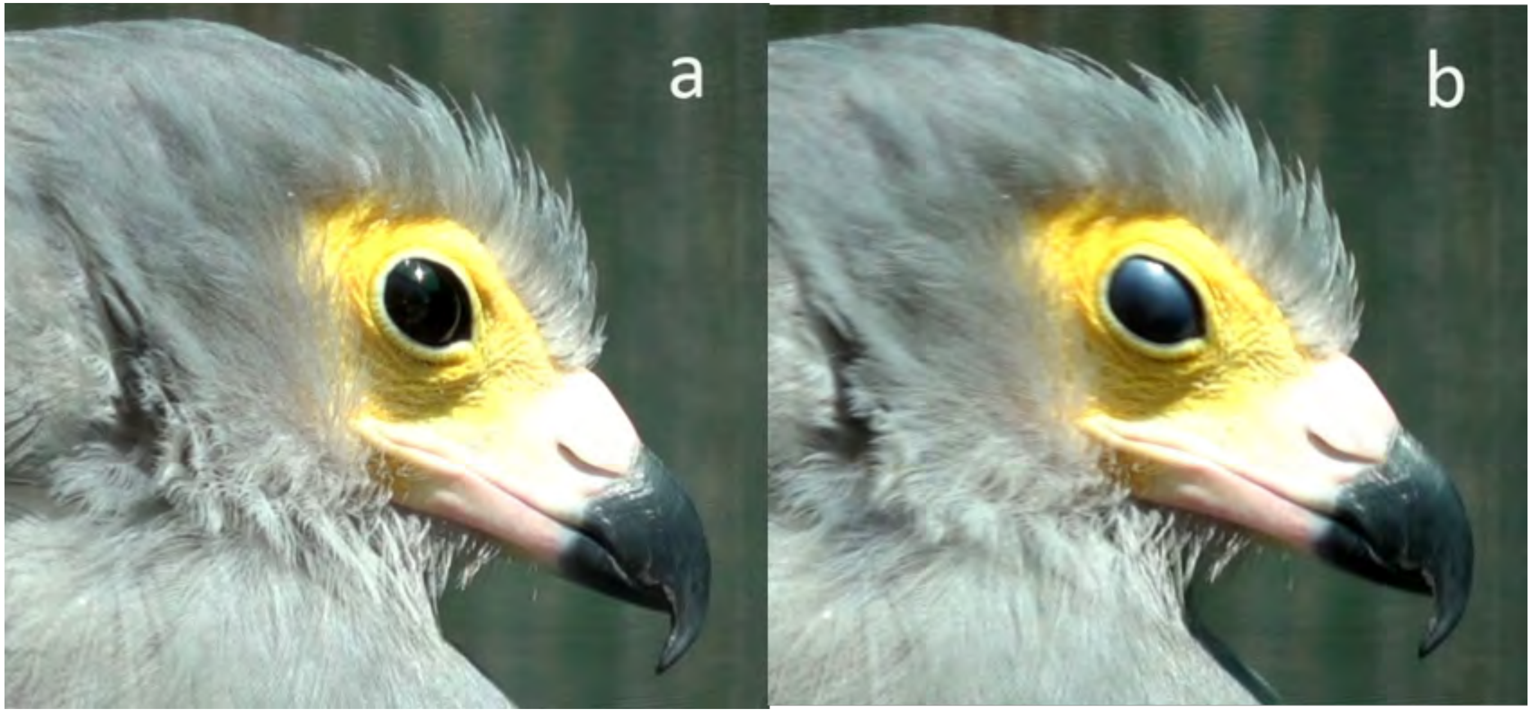
Nictitating membrane blink on head turn

African harrier-hawk (*Polyboroides typus*)

Nictitating membrane blink on head turn

a) Pre-blink. b) Nictitating membrane blink on head turn.

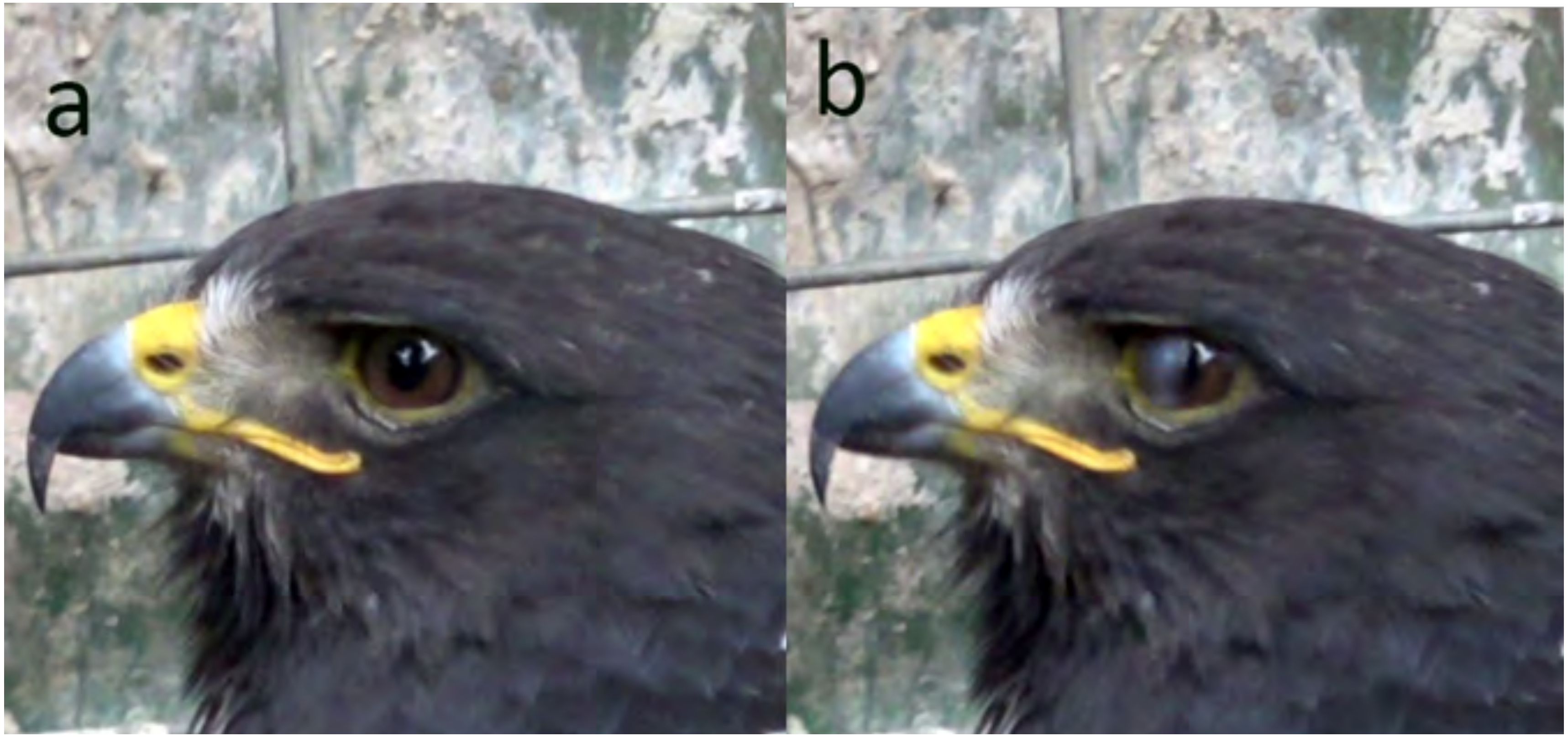
a) Pre-blink. b) Nictitating membrane covers half the eye. c) Nictitating membrane covers the eye. d) Blink ends at the end of the head turn.



a) Pre-blink. b) Nictitating membrane blink on head turn.

Jackal buzzard (*Buteo rufofuscus*)

Nictitating membrane blink on head turn



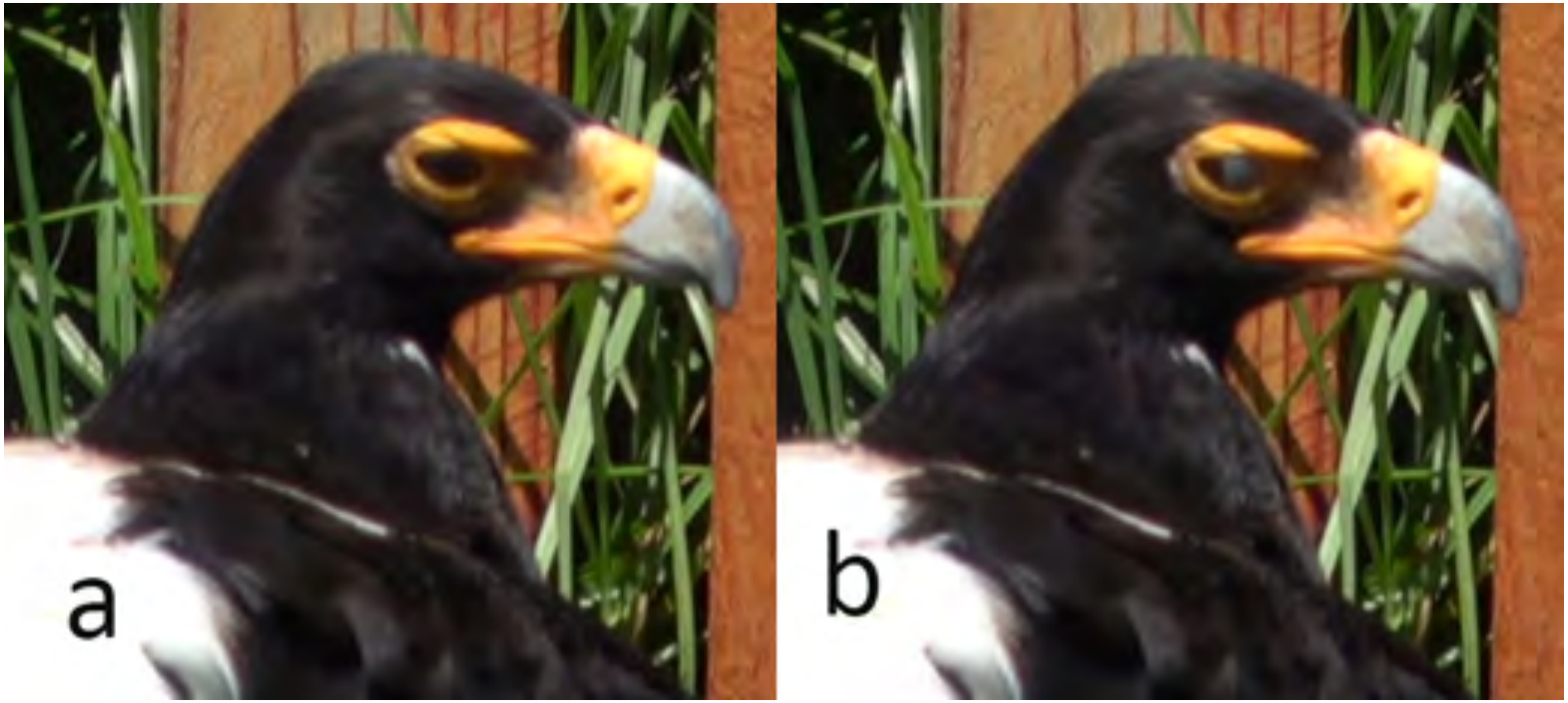
a) Pre-blink. b) Nictitating membrane halfway across the pupil.

Nictitating membrane blink on head turn.

No blink on head turn.

Black eagle (*Ictinaetus malaiensis*)

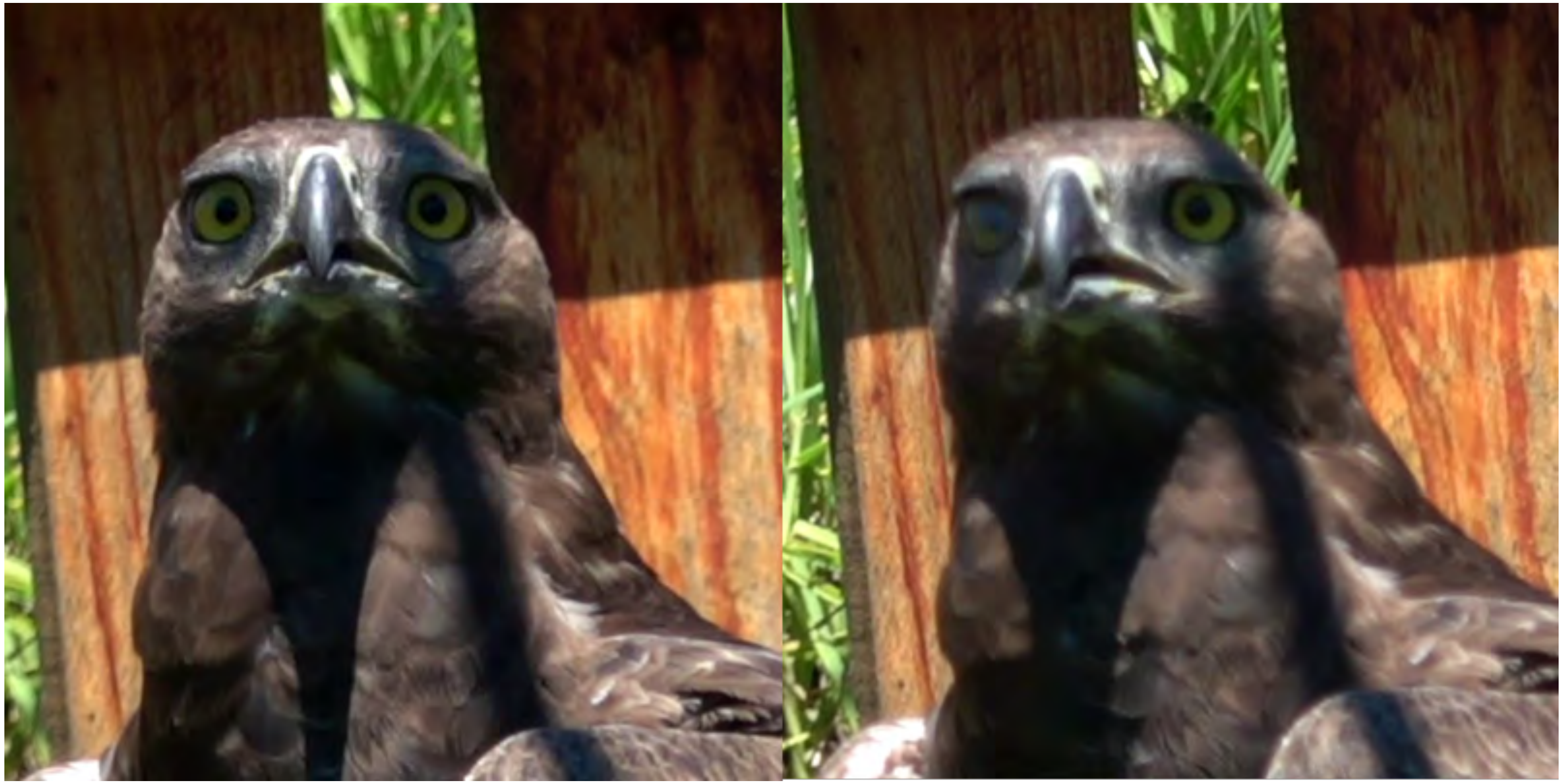
Nictitating membrane blink on head turn



a) Pre-blink. b) Nictitating membrane halfway across the pupil.

Martial eagle (*Polemaetus bellicosus*)

Nictitating membrane blink on head turn



Only the right eye blinks on head turn

White-bellied sea eagle (*Haliaeetus leucogaster*)

Nictitating membrane blink on head turn

Juvenile

Forest buzzard (*Buteo trizonatus*)

Nictitating membrane blink on head turn

a) Pre-blink. b) Nictitating membrane blink. c) Post-blink at end of head movement. Note prominent brow.

Harris's hawk (*Parabuteo unicinctus*)

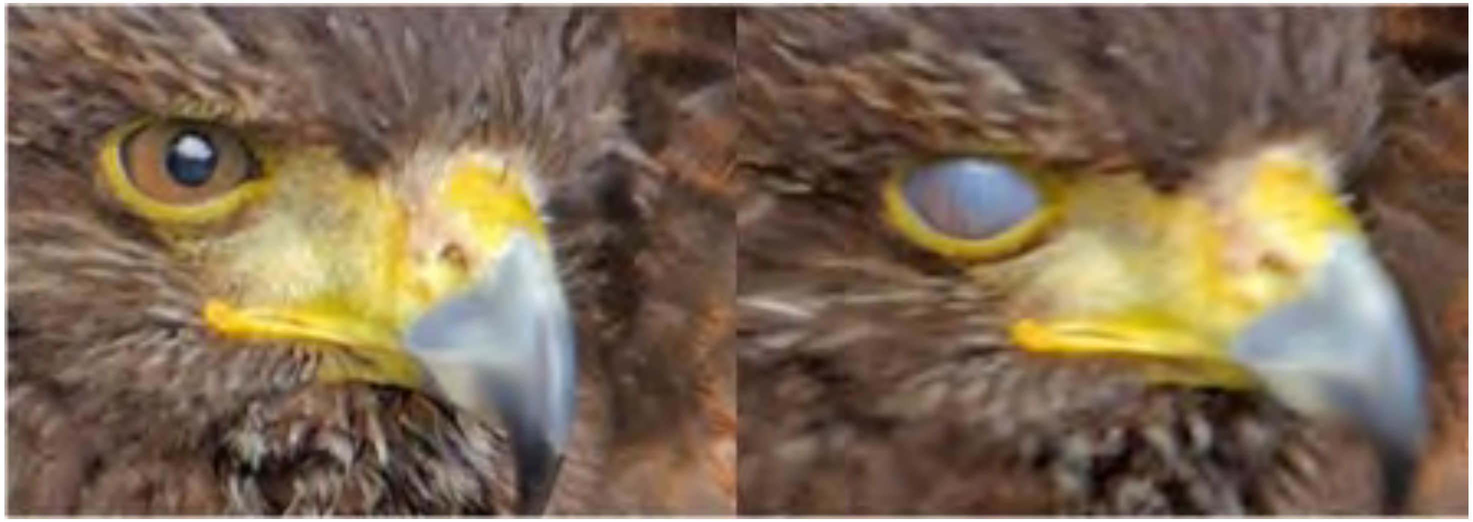
Blink a: Nictitating membrane blink on head turn

a) Pre-blink. b) Nictitating membrane blink on slight head turn.

Not all head movements are accompanied by blinking.

Blink b: Lower lid and nictitating membrane blink on preening

Nictitating membrane and lower lid blink while preening neck feathers with talons.



Pale chanting goshawk (*Melierax canorus*)

Nictitating membrane blink on head turn

Pacific baza (*Aviceda subcristata*)

Nictitating membrane blink on head turn

No eyelid blink on pecking.

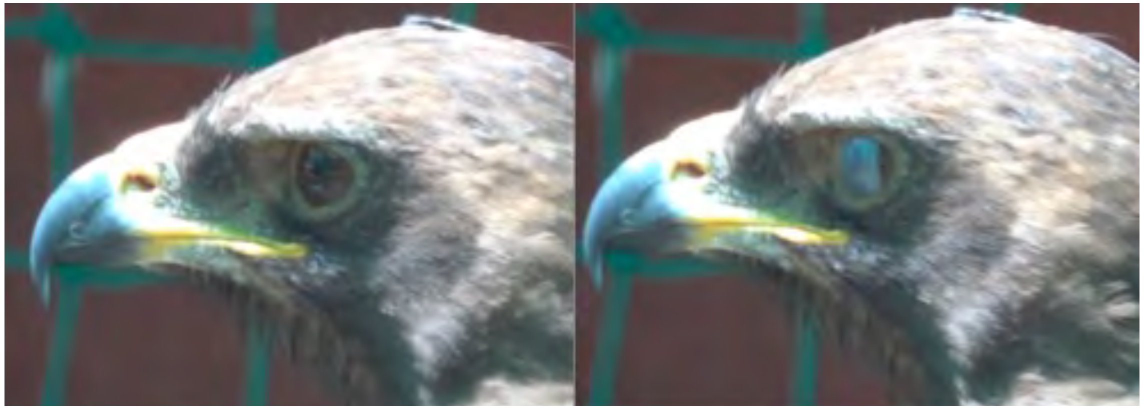
Tawny eagle (*Aquila rapax*)

Nictitating membrane blink on head turn

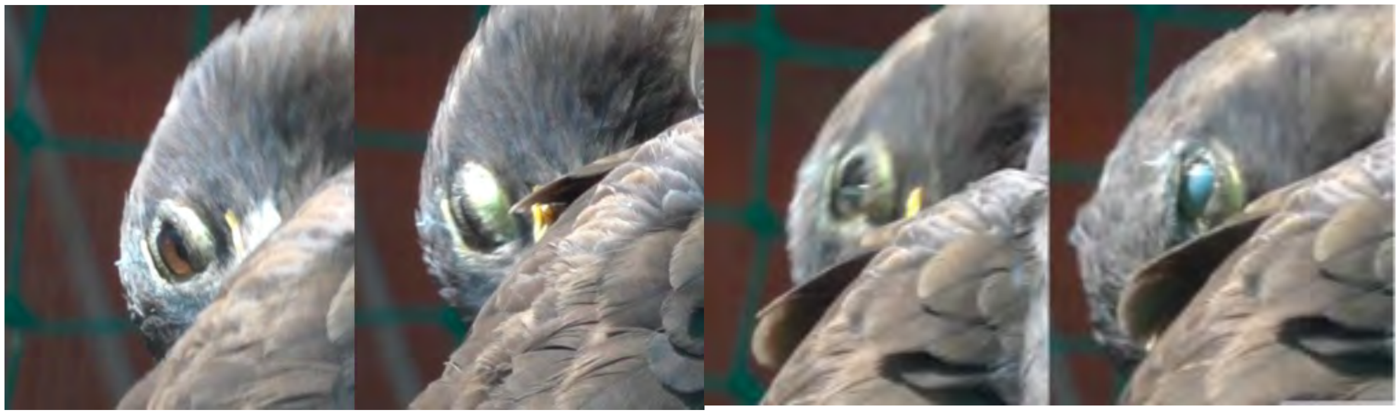
Nictitating membrane blink. a) Membrane starts to emerge. b) Membrane covers cornea.

Wahlberg's eagle (*Hieraaetus wahlbergi*)

Blink a: Nictitating membrane blink on head turn

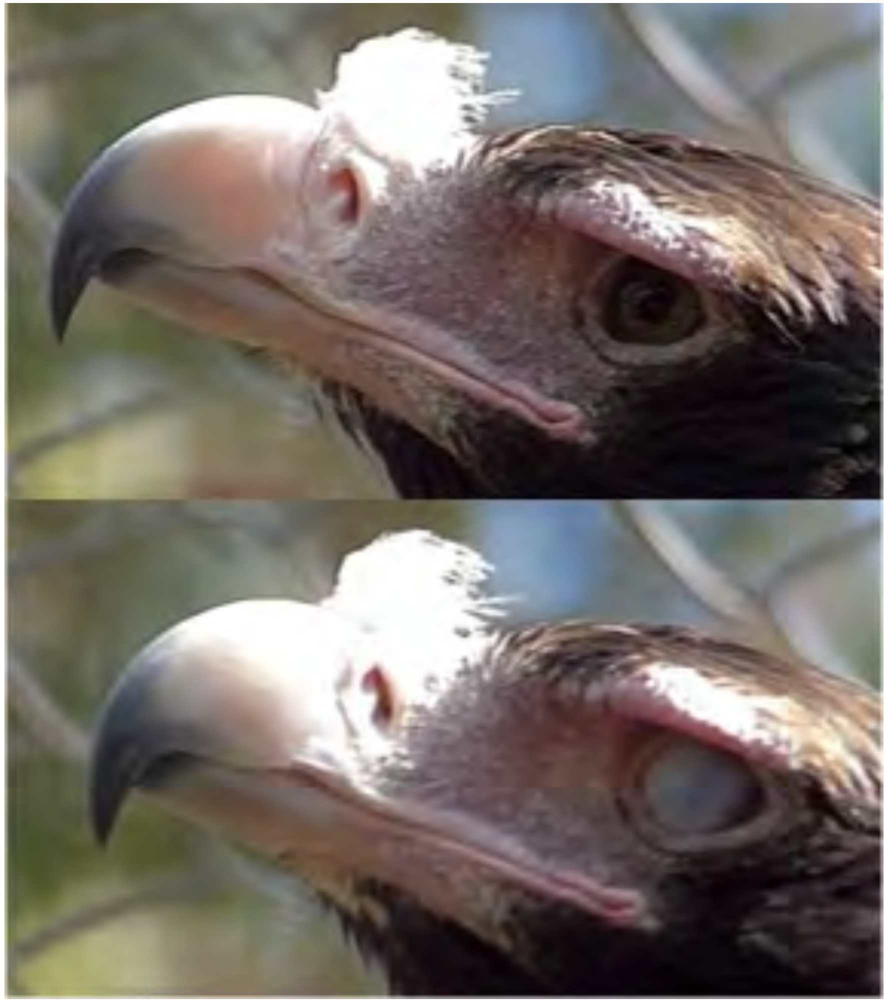


Blink b: Lower lid and nictitating membrane blink on preening



Wedge-tailed eagle (*Aquila audax*)

Nictitating membrane blink on head turn



Note prominent brow

White-backed vulture (*Gyps africanus*)

Nictitating membrane blink

Note prominent brow.

White-headed vulture (*Trigonoceps occipitalis*)

Nictitating membrane blink on head turn

Nictitating membrane blink.

Palm-nut vulture (*Gypohierax angolensis*)

Nictitating membrane blink on head turn

Griffon vulture (*Gyps fulvus*)

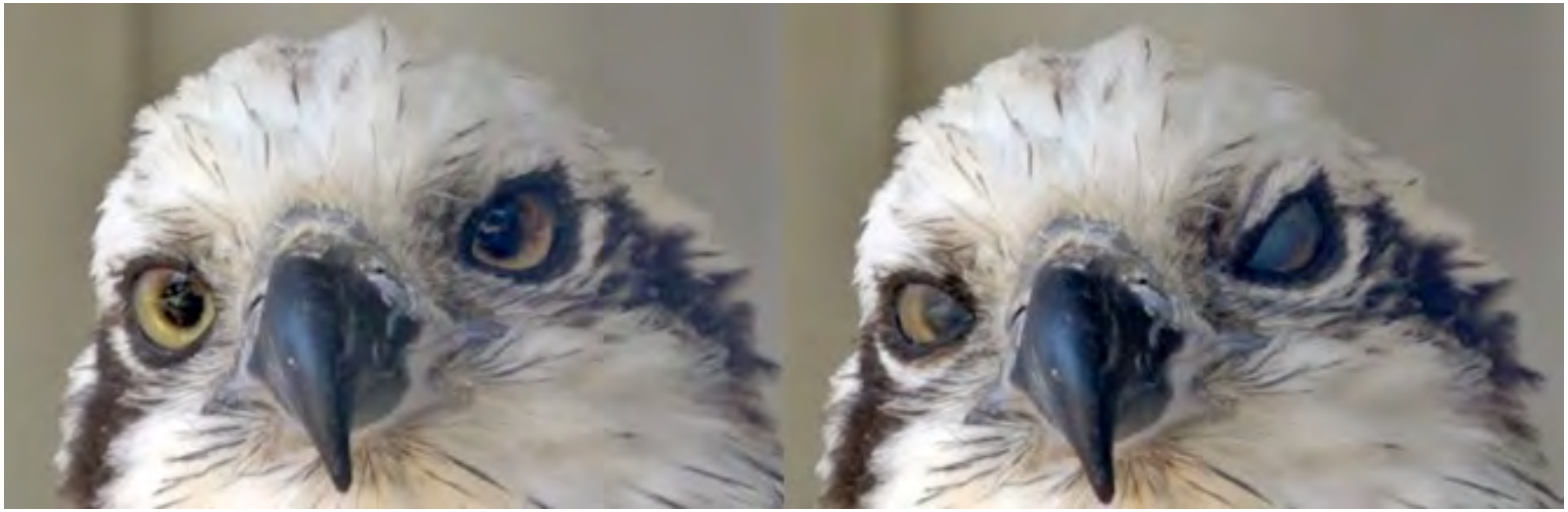
Blink type: Nictitating membrane blink on head turn

Family Pandionidae

Western osprey (*Pandion haliaetus*)

Blink a: Lower lid and nictitating membrane blink with drowsiness

Lower lid starts off elevated in the left eye. Then the nictitating membranes come across both eyes. Then both lower lids rise.



Nictitating membrane blink.

Blink b: Nictitating membrane blink with drowsiness with slight depression of inner part of upper lid

Note vascularity of membrane

Family Sagittariidae

Secretary bird (*Sagittarius serpentarius*)

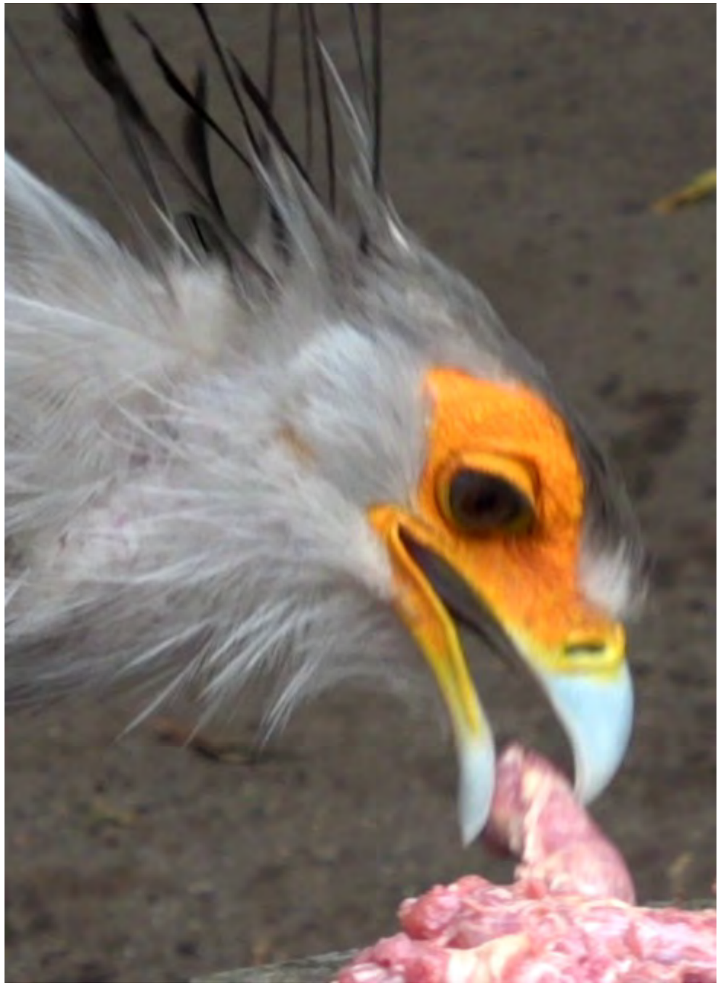
Blink a: Nictitating membrane blink on head turn

a) Pre-blink. b) Nictitating membrane blink

Blink b: Upper lid lowers on downward eye movement

a) Looking to the side. b) Looking down – upper lid moves down with globe.

'Eye lashes'



No lid blink on feeding

Family Cathartidae

Andean condor (*Vultur gryphus*)

Nictitating membrane blink on slight head turn

Nictitating membrane blink on head turn

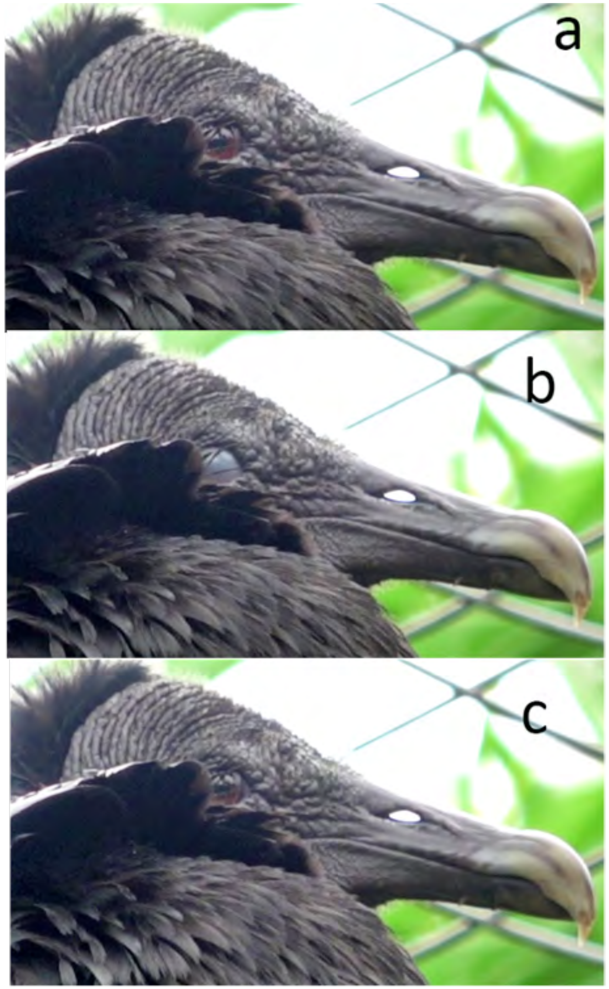
a) Pre-blink. Note red iris. b) Head remains still. Almost completely transparent nictitating membrane covers left eye.

Nictitating membrane blink.

Nictitating membrane blink.

Black vulture (*Coragyps atratus*)

Nictitating membrane blink



Nictitating membrane blink with head still.

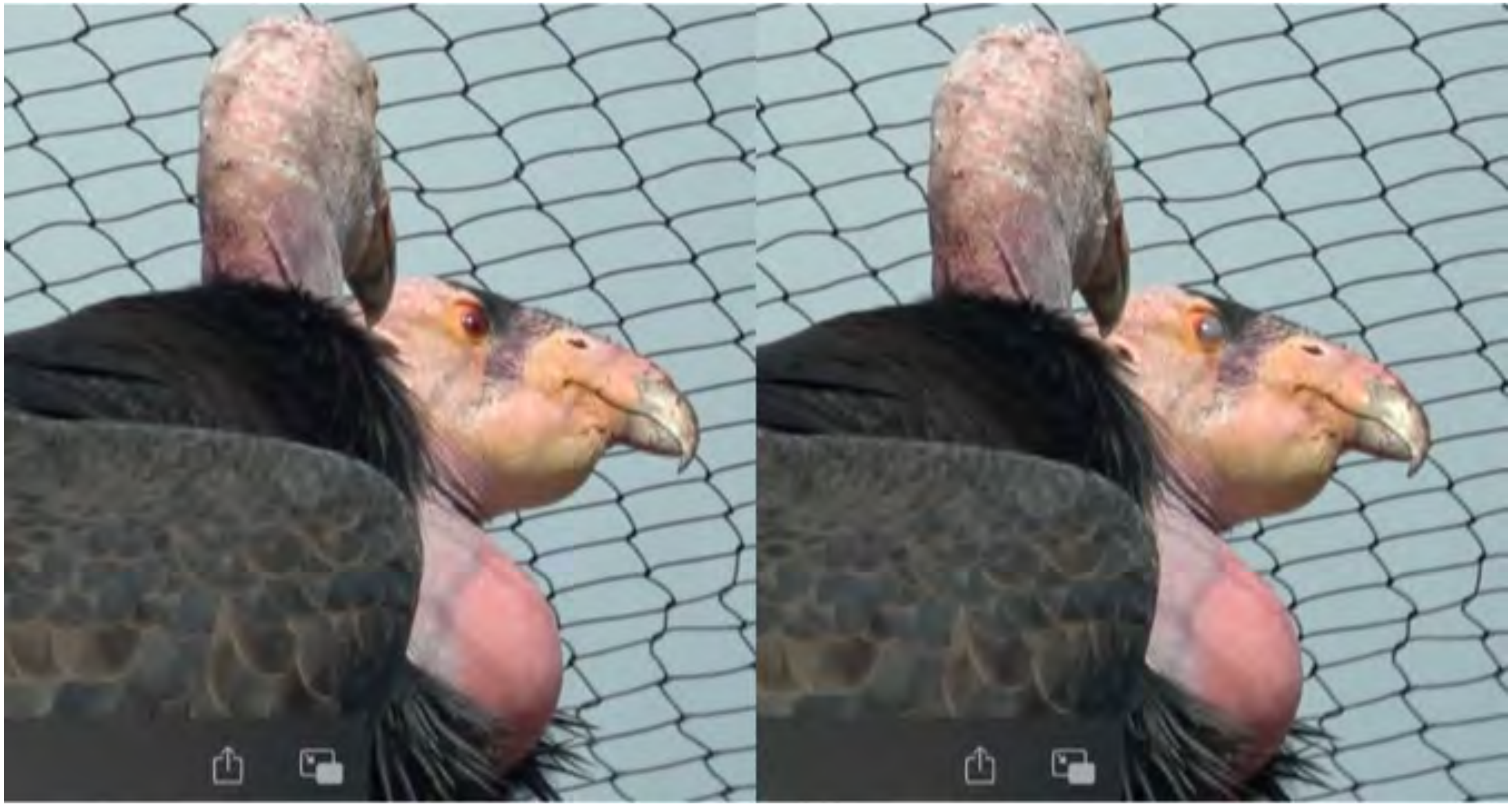
Turkey vulture (*Cathartes aura*)

Nictitating membrane blink on head turn

Nictitating membrane blink.

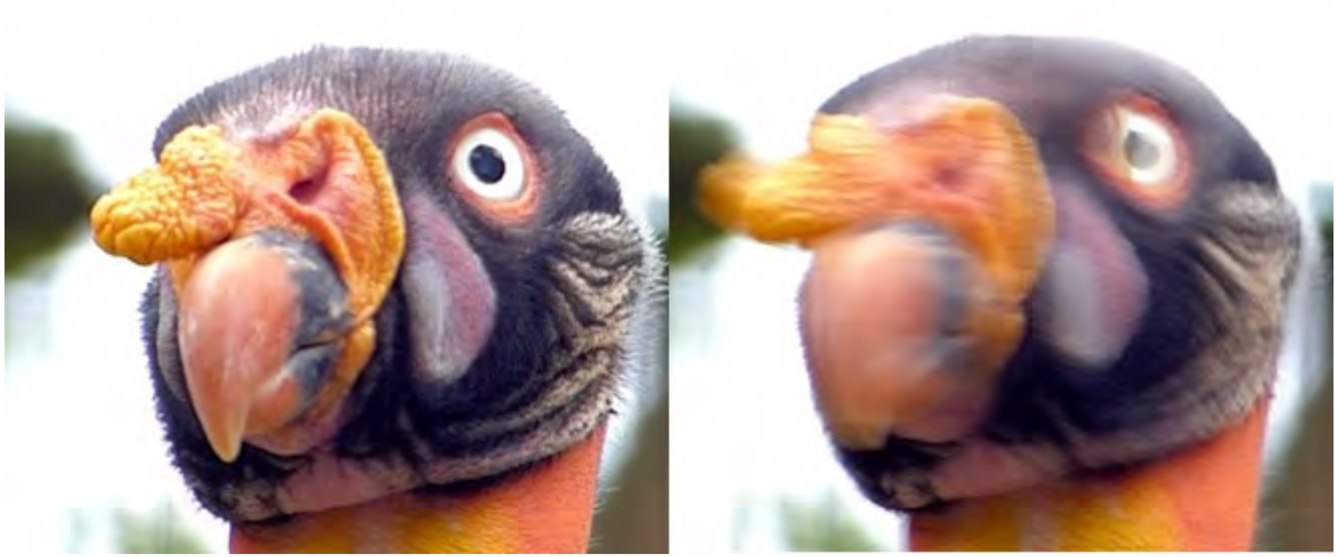
California condor (*Gymnogyps californianus*)

Nictitating membrane blink on head turn



King vulture (*Sarcoramphus papa*)

Nictitating membrane blink on head turn



It is striking that not all these raptors have evolved protective prominent brows. This is noticeable scavengers like vultures where theprey does not put up a fight.

Order Charadriiformes

Family Turnicidae

Black-breasted buttonquail (*Turnix melanogaster*)

Upper lid blink

Upper lid blink on pecking

Painted buttonquail (*Turnix varius*)

Upper lid blink

Upper lid blink.

Upper and lower lid blink with drowsiness

Chestnut-backed buttonquail (*Turnix castanotus*)

Lower lid elevated with drowsiness

Family Haematopodidae

African oyster catcher (*Haematosis moquini*)

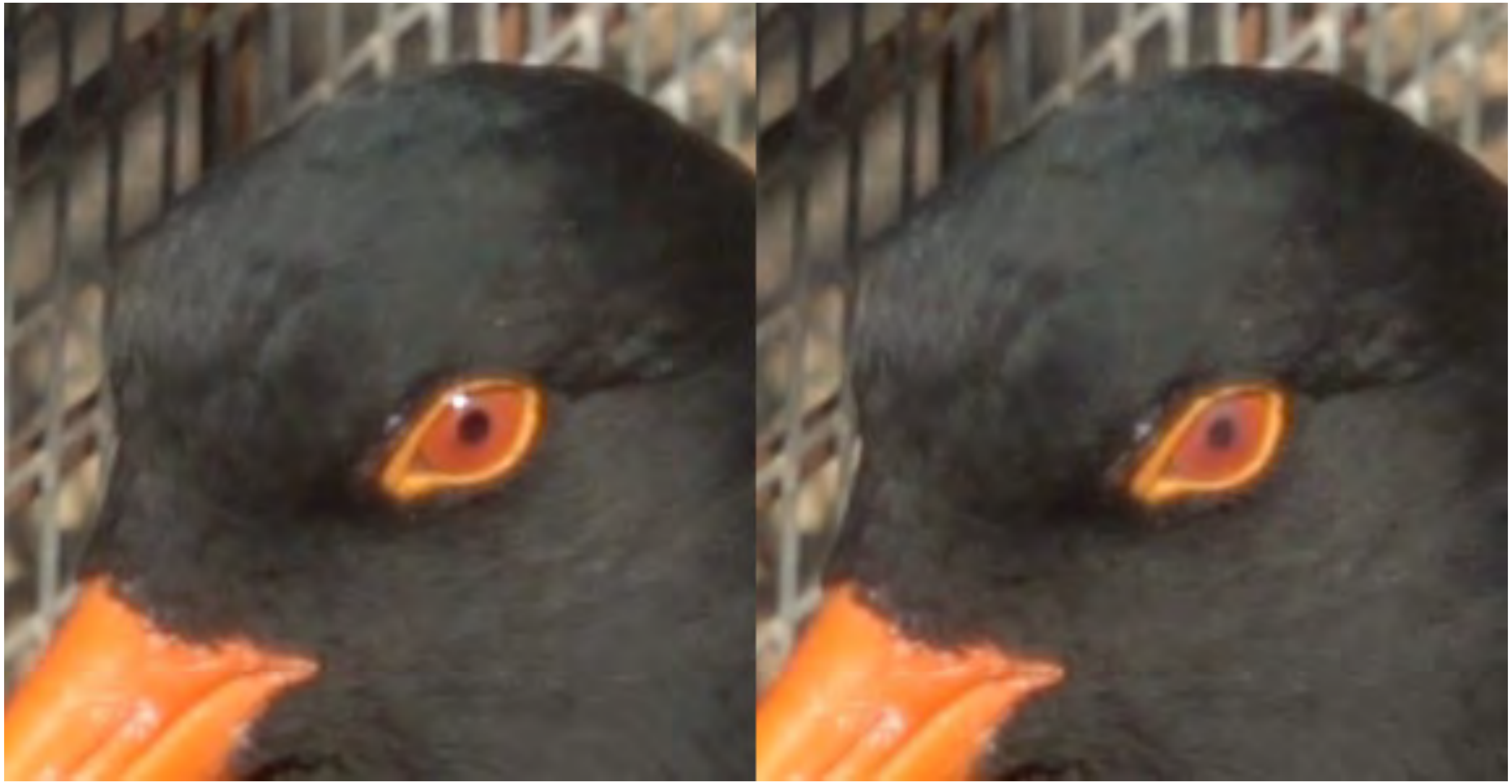
Note the red sclera and yellow eyelids. No blinks were recorded.

Eurasian oystercatcher (*Haematopus ostralegus*

Nictitating membrane blink on head movement

Pied oystercatcher (Haematopus longirostris)

Nictitating membrane blink



Lower lid elevation with drowsiness

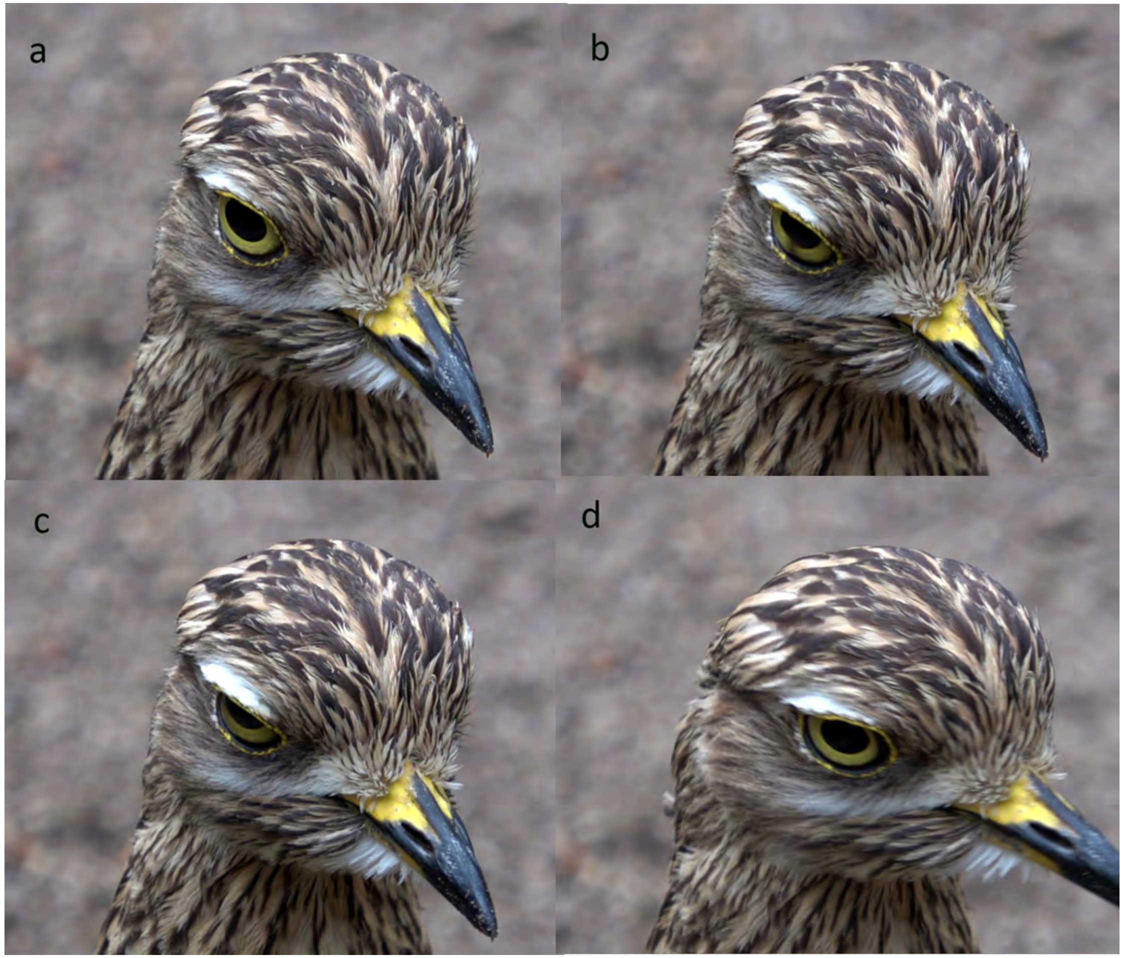
Nictitating membrane blink and elevation of lower lid.

Sooty oystercatcher (*Haematopus fuliginosus*)

Family Burhinidae

Spotted thick-knee (*Burhinus capensis*)

Mainly nictitating membrane Slight lowering of upper lid.



a) Pre-blink. b) Transparent nictitating membrane reaches halfway across the pupil. Upper lid lowers a little. c) Maximal blink. Nictitating membrane covers cornea. d) Post-blink after head movement ends.

Beach stone curlew (*Esacus magnirostris*)

Nictitating membrane blink on head turn with slight lowering of upper lid.

Nictitating membrane blink and lower lid elevation with drowsiness

Bush stone-curlew (*Burhinus grallarius*)

Nictitating membrane blink on head turn with slight lowering of upper lid and elevation of lower lid.

Note upper eyelid 'sun screen'.

Nictitating membrane blink on head turn

Lower lid elevated on preening.

Lower lid elevated on preening. Nictitating membrane visible.

Nictitating membrane blink on head turn.

Nictitating membrane blink on head turn.

Nictitating membrane and lower lid blink during saccadic oscillation

Lower lid elevation during preening

Upper lid, lower lid and nictitating membrane blink.

Upper lid, lower lid and nictitating membrane blink.

Nictitating membrane blink.

Nictitating membrane and lower lid blink.

Upper lid blink

Nictitating membrane blink.

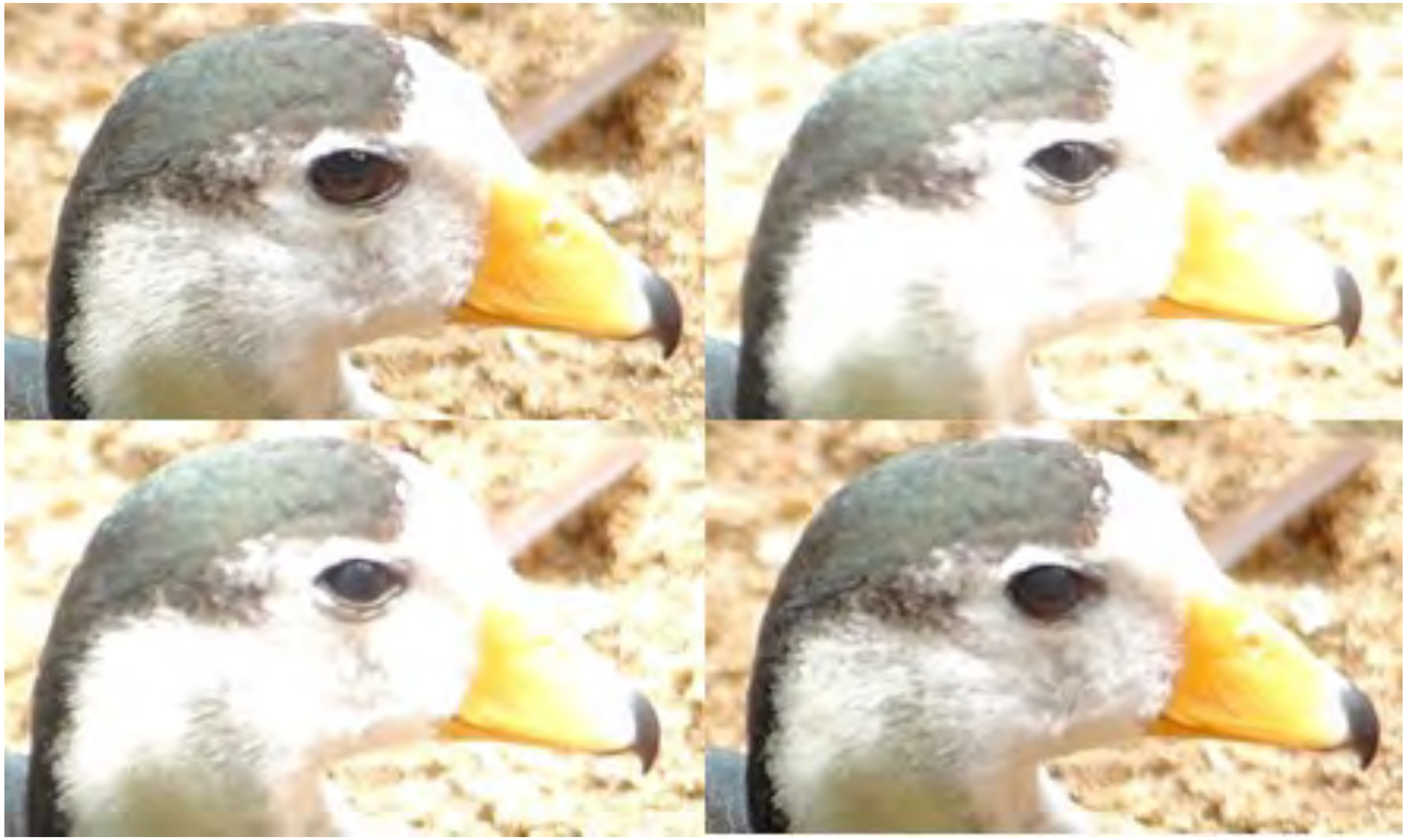
Order Anseriformes

Family Anatidae

African pygmy goose (*Nettapus auritus*)

Lower lid elevation with drowsiness

Nictitating membrane blink on head turn

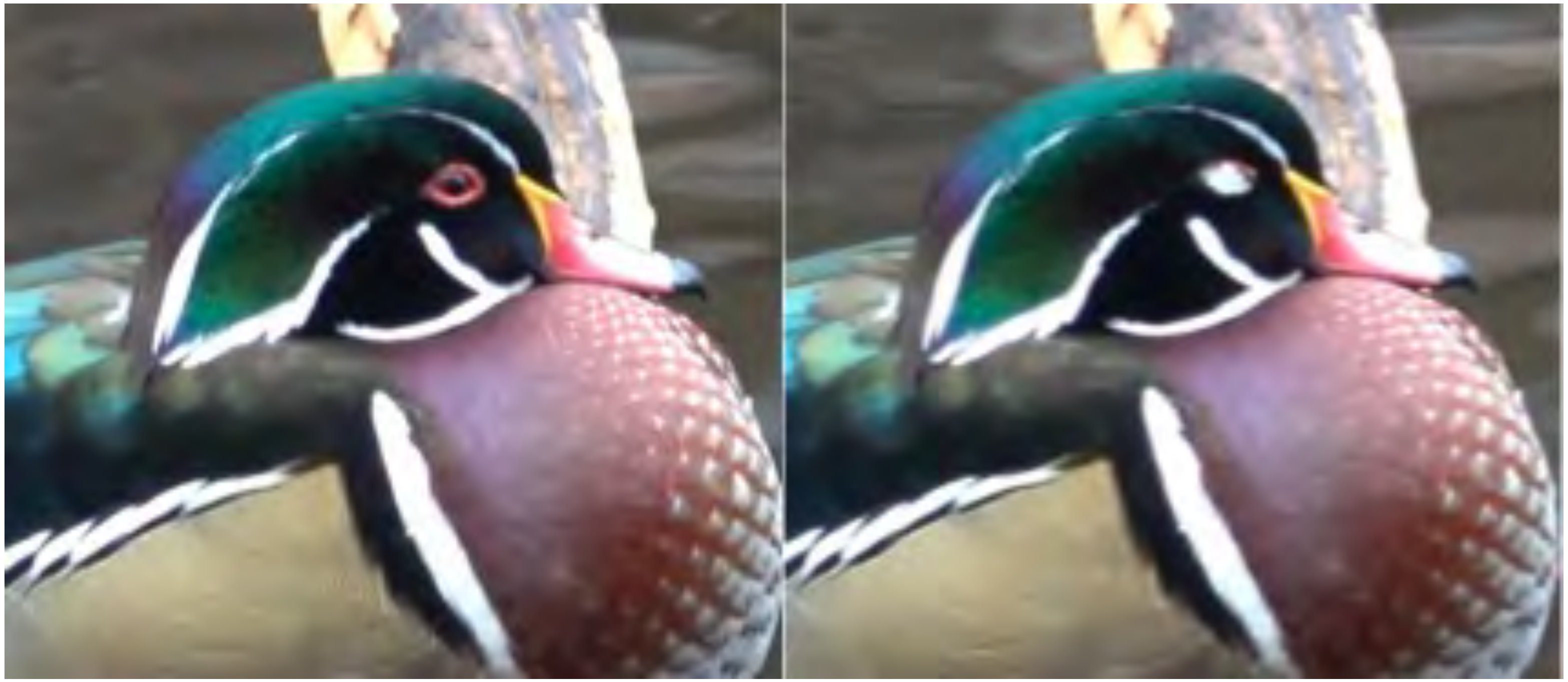


Carolina duck (*Aix sponsa*)

Blink a: Nictitating membrane blink with possible lowering of upper lid

a) Pre-blink. Note red rim around eyes. b) Nictitating membrane has reached the pupil. c) The nictitating membrane has withdrawn at the end of the head movement. The palpebral fissure has narrowed. This appears to be due to lowering of the upper lid.

Blink b: Elevation of lower lid with drowsiness



White lower lid elevates with drowsiness.

No elevation of lower lid during preening.

Blink type: Lower lid elevation with preening

Tufted duck (*Aythya fuligula*)

Nictitating membrane blink on head turn

Lower lid elevation with drowsiness

White-winged duck (*Asarcornis scutulata*)

Nictitating membrane and lower lid blink with preening

Pacific black duck (*Anas superciliosa*)

Blink a: Nictitating membrane blink then lower lid elevation with preening

Blink b: Nictitating membrane blink

Ruddy shelduck (*Tadorna ferruginea*)

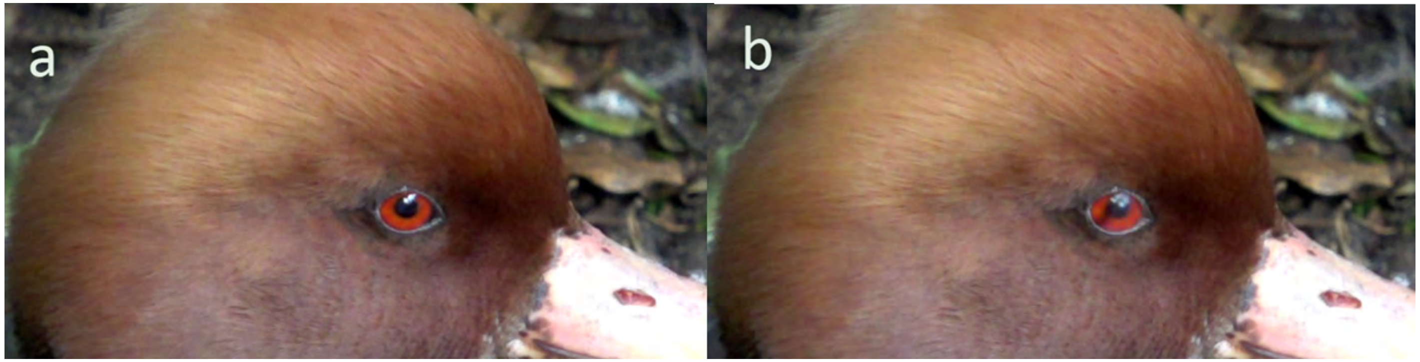
Lower lid elevation with drowsiness

Comb duck (*Sarkidiornis sylvicola*)

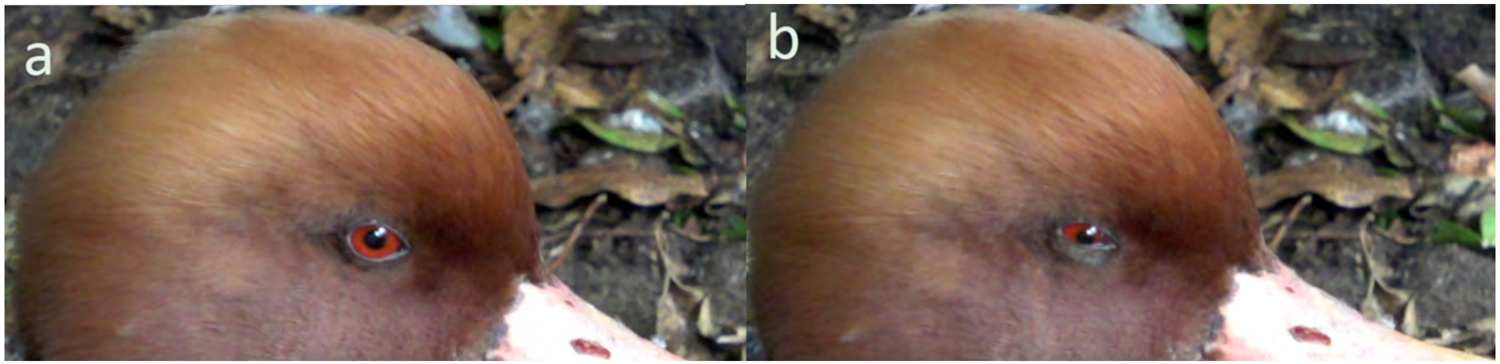
Lower lid elevation with preening

Red-crested pochard (Netta rufina)

Blink a: Nictitating membrane blink on head turn



Blink b: Elevation of lower lid with drowsiness

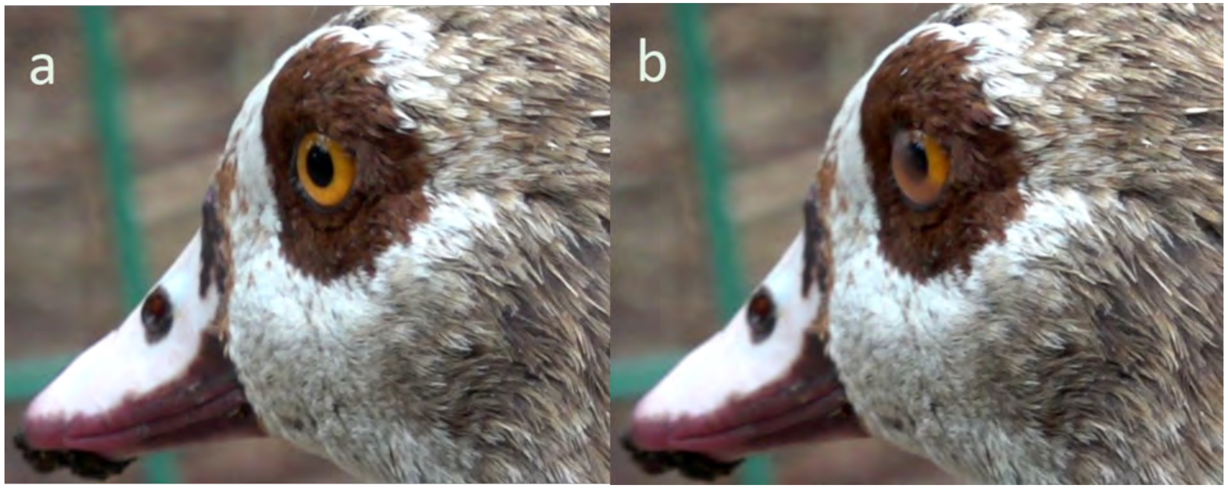


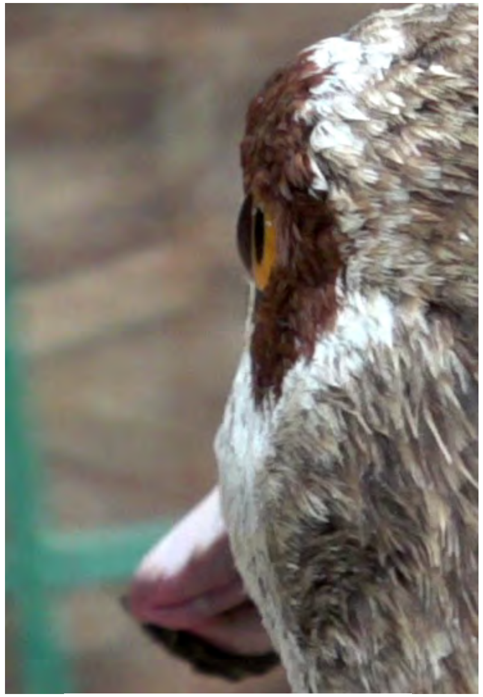
Female. Nictitating membrane blink.

No lid blink on preening.

Egyptian goose (*Alopochen aegyptiaca*)

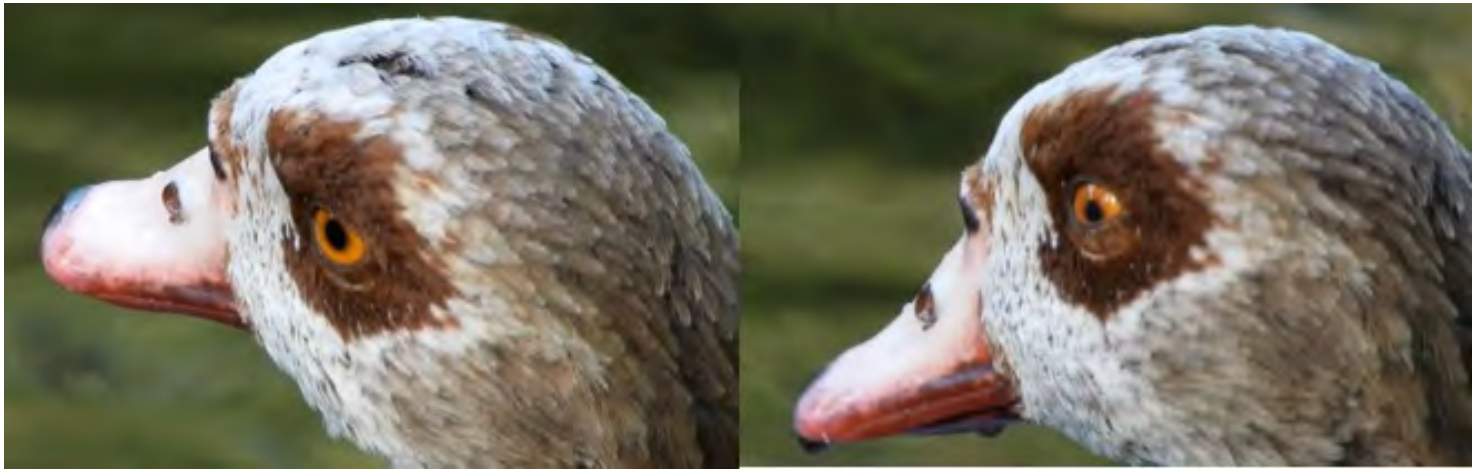
Blink a: Nictitating membrane blink on head turn





Note depth of cornea.

Blink b: Lower lid elevation with drowsiness



Nictitating membrane blink.

Blink c: Lower lid elevation with preening

Mandarin duck (*Aix galericulata*)

Blink a: Nictitating membrane blink on head turn

Female. a) Pre-blink. b) Nictitating membrane blink on head turn. c) Post-blink. End of head movement.

Blink b: Lower lid elevation with drowsiness

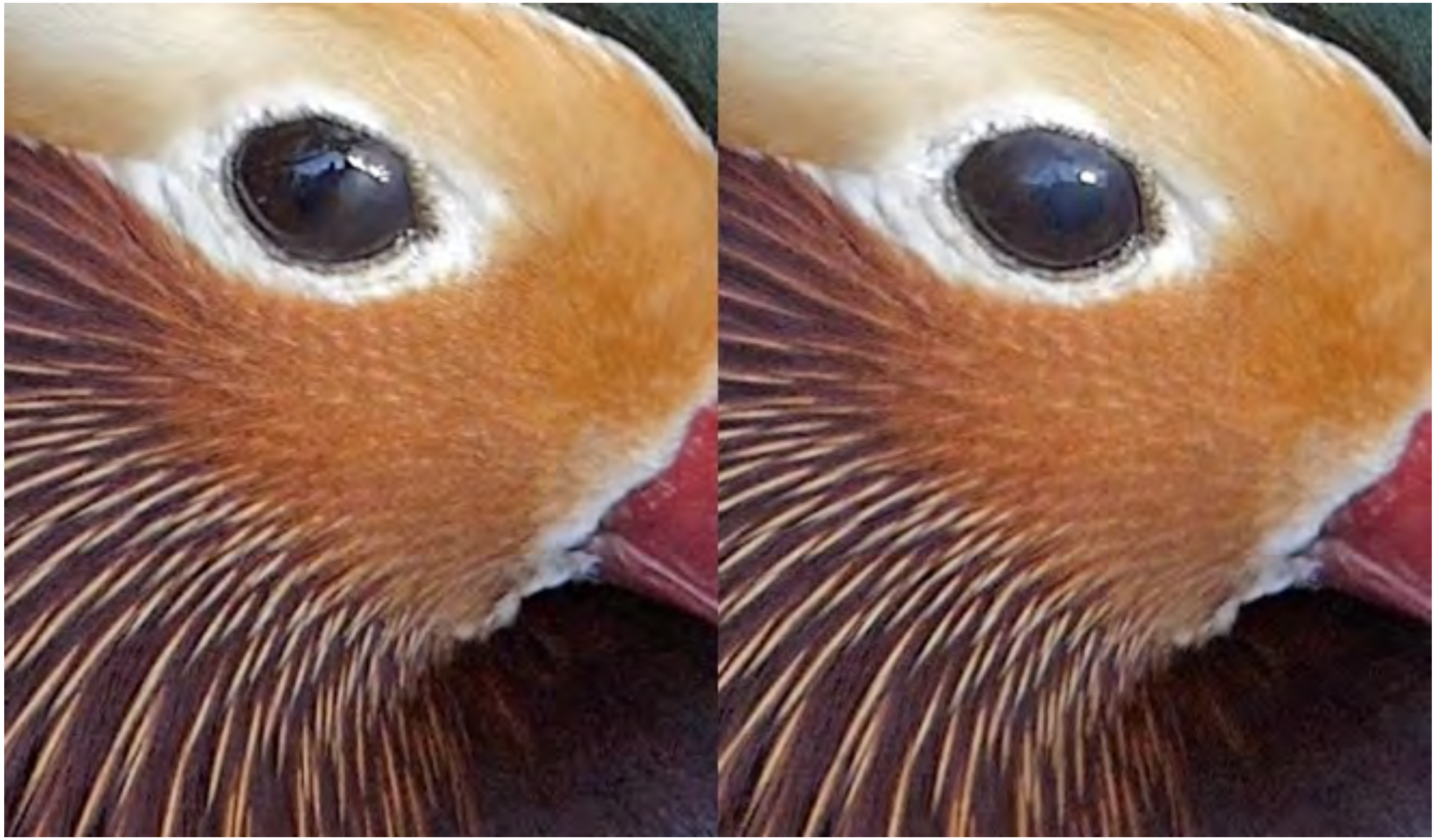
a) Drowsy. b) Nictitating membrane crosses. Lower lid rises. c) Lower lid nearly reaches upper lid. Maximal closure – nearly asleep.

Blink c: Nictitating membrane blink on eye movement

Female: Nictitating membrane blink.

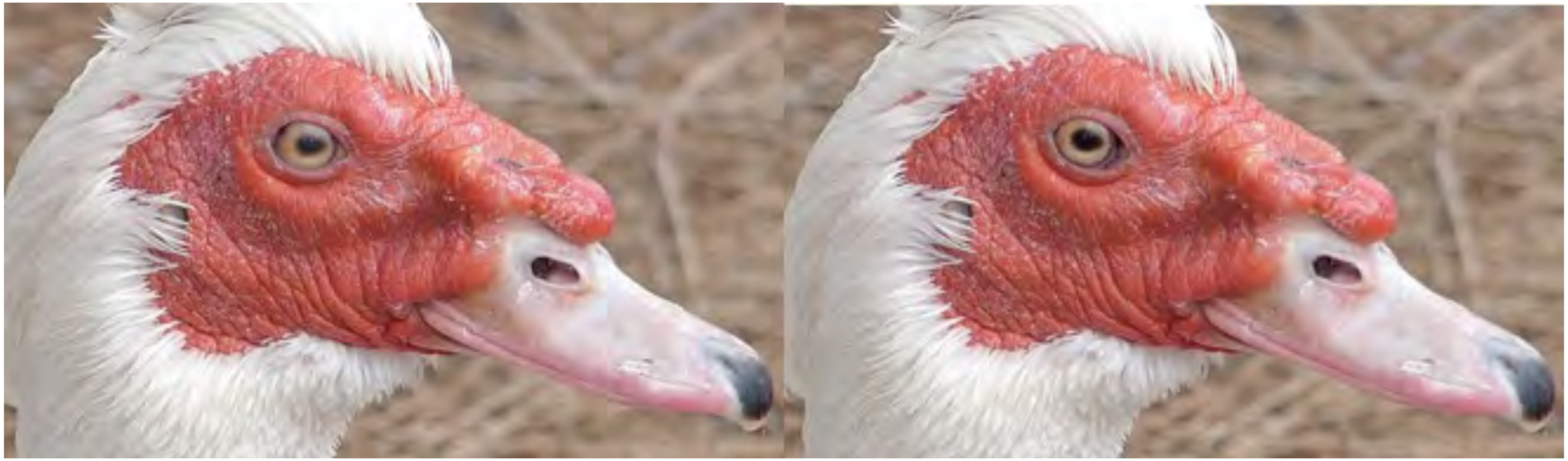
Male. Lower lid elevation with drowsiness.

Male. Nictitating membrane blink on eye movement.



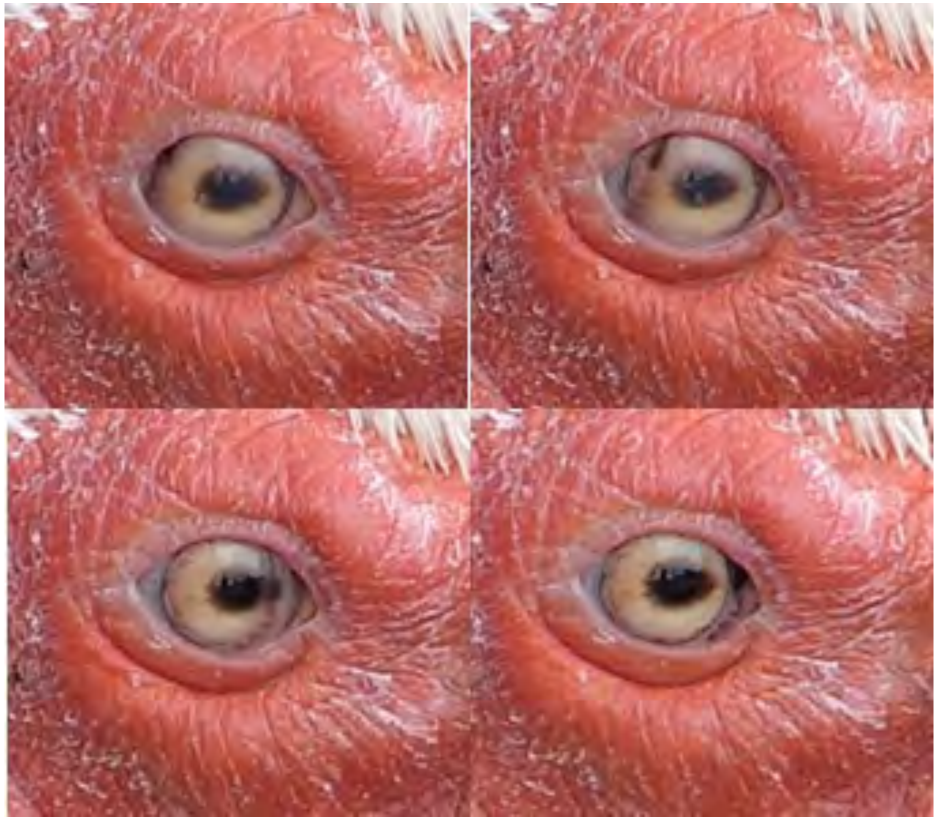
Male. Nictitating membrane blink on eye movement.

Muscovy duck (*Cairina moschata*)



Eye movements.

Blink a: Nictitating membrane blink' on eye movement



Nictitating membrane blink on eye movement.

Blink b: Lower lid elevation with sleep

Hatchling. Lower lid elevation with sleep.

Blink c: Nictitating membrane blink and lower lid elevation with drowsiness

Blink d: Nictitating membrane blink

Nictitating membrane blink.

Nictitating membrane and lower lid blink.

Nictitating membrane blink.

Nictitating membrane and lower lid blink. NB No fall in upper lid.

Nictitating membrane blink with eye movement.

Cape Barren goose (*Cereopsis novaehollandiae*)

Nictitating membrane blink on head turn

Nictitating membrane blink on head turn.

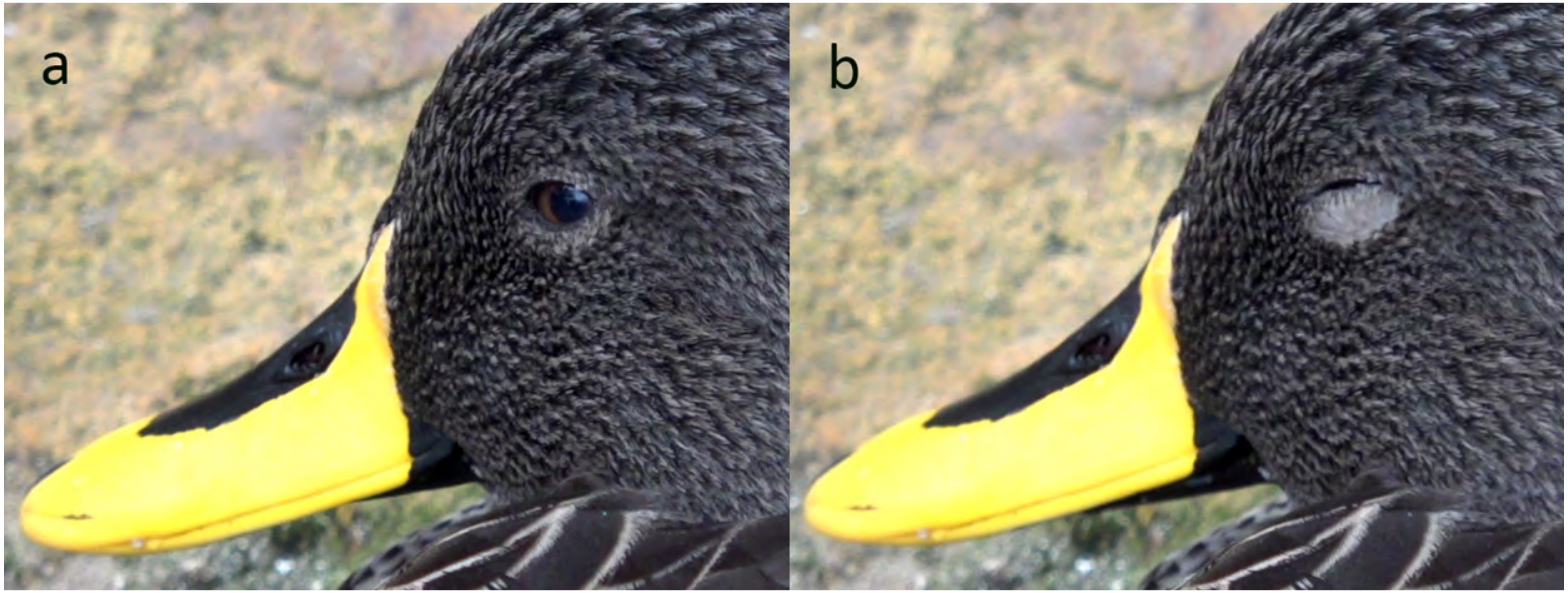
Graylag goose (*Anser anser*)

No blink on pecking

Nictitating membrane blink on head turn

Yellow-billed duck (*Anas undulata*)

Blink a: Lower lid elevation with drowsiness



a) Pre-blink. b) Lower lid rises with drowsiness.

Blink b: Lower lid elevation with preening

Blink c: Lower lid elevation with sleep

Common eider (Somateria mollissima)

Almost impossible to see the eye of the male.

Lower lid elevation with drowsiness

Spectacled eider (*Somateria fischeri*)

Lower lid elevation with drowsiness

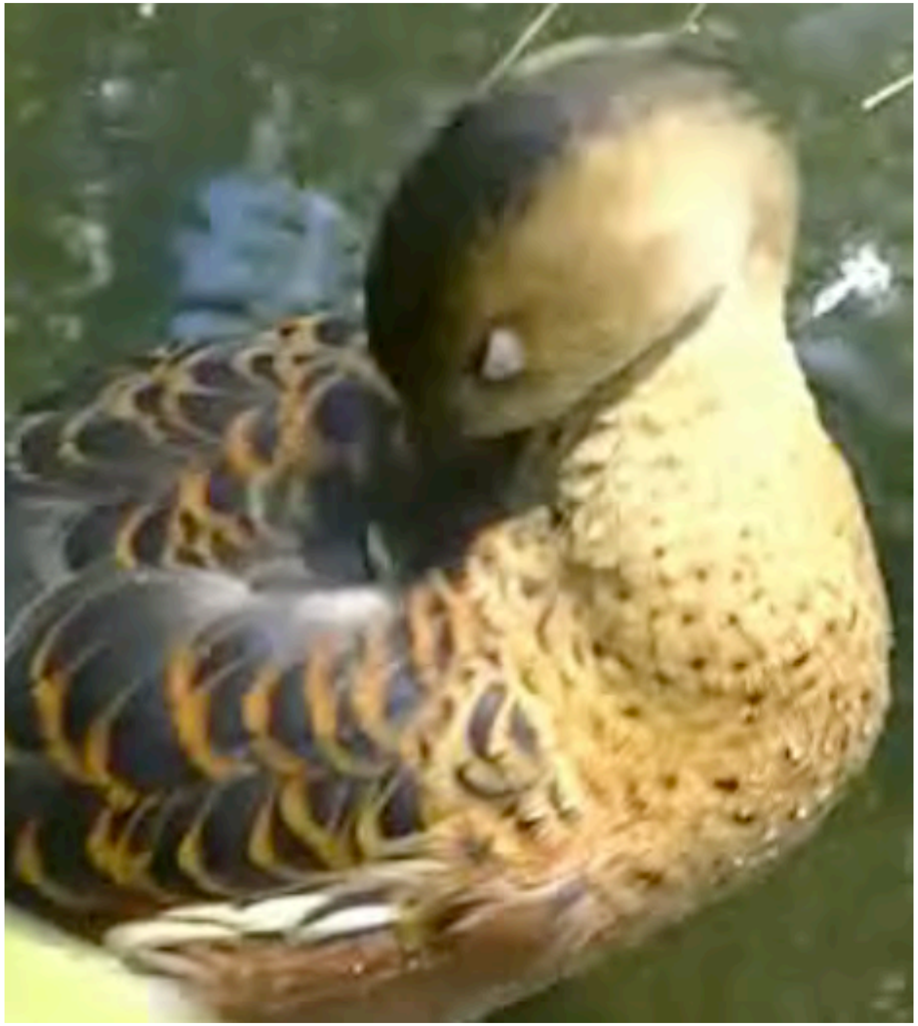
Elevation of lower lid in a drowsy male – nictitating membrane can be seen.

White-faced whistling duck (*Dendrocygna viduata*)

Turning its head to the side to look up suggests that it has limited eye movement.

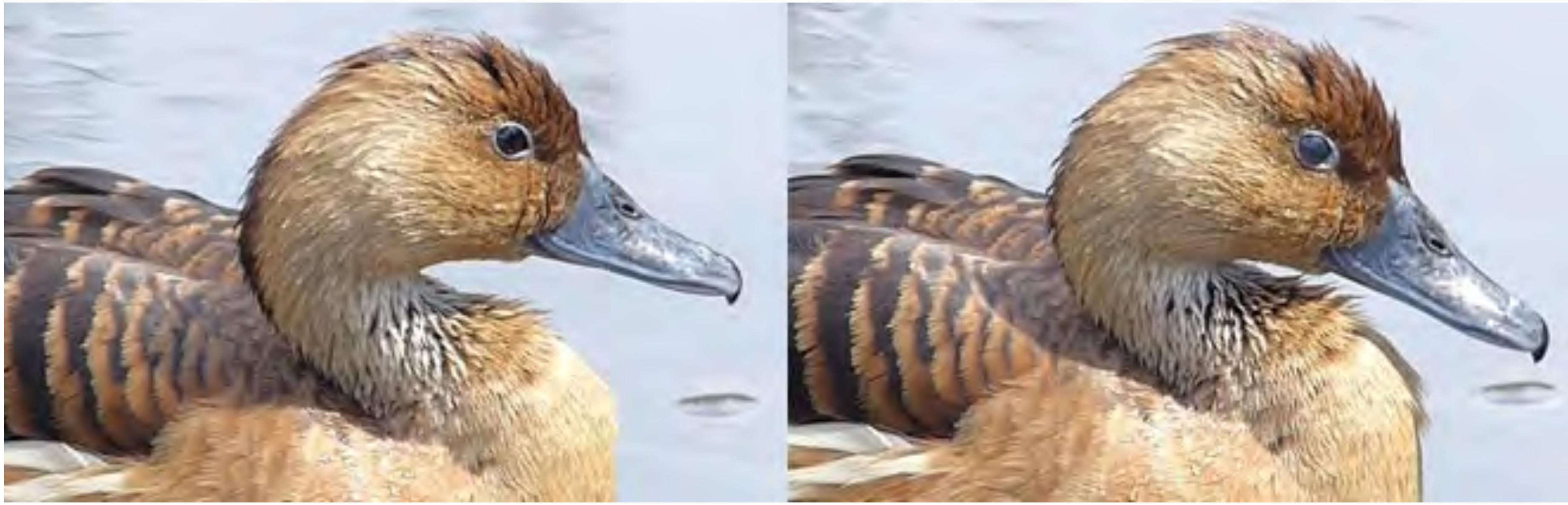
Wandering whistling duck (*Dendrocygna arcuata*)

Lower lid elevation on preening

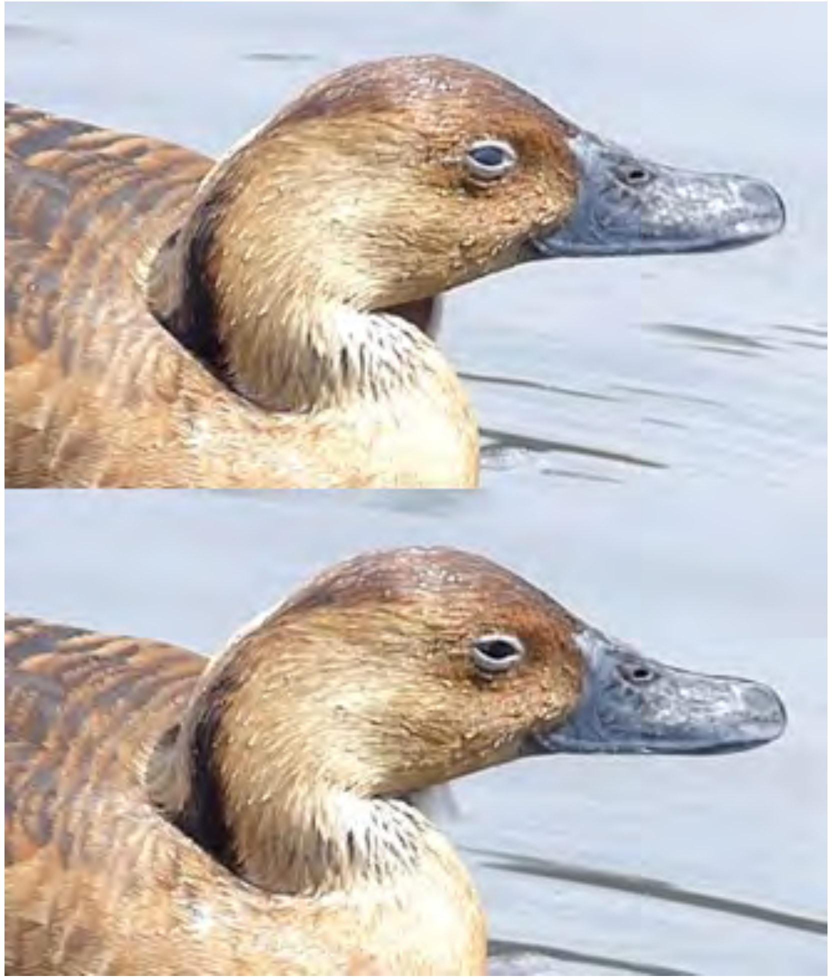


Fulvous whistling duck (*Dendrocygna bicolor*)

Blink a: Nictitating membrane blink on head turn



Blink b: Nictitating membrane blink and lower lid elevation with drowsiness



Nictitating membrane crosses at onset of lower lid elevation then resumes resting position.

Blink c: Lower lid elevation with preening

Smew (*Mergellus albellus*)

Nictitating membrane blink on head turn

Female

Blue-billed duck (*Oxyura australis*)

Blink a: Lower lid elevated with sleep

Blink b: Nictitating membrane blink

Blink c: Nictitating membrane blink and elevation of lower lid with drowsiness

Female. Lower lid elevated while sleeping.

Blink d: Nictitating membrane blink with narrowing of palpebral fissure

Juvenile

Canada goose (*Branta canadensis*)

Nictitating membrane blink on head turn

Hardhead (*Aythya australis*)

Blink a: Nictitating membrane blink then elevation of lower lid

Blink b: Nictitating membrane blink on head turn

Family Anseranatidae

Magpie goose (*Anseranas semipalmata*)

Nictitating membrane blink on head turn

Nictitating membrane blink on head turn.

Mallard (Anas platyrhynchos)

Blink a: Lower lid elevation with drowsiness

Male. Lower lid elevation with drowsiness.

Blink b: Nictitating membrane blink then lower lid elevation with drowsiness

Female

Blink c: Nictitating membrane blink on head turn

Nictitating membrane blink.

Nictitating membrane blink on eye movement.

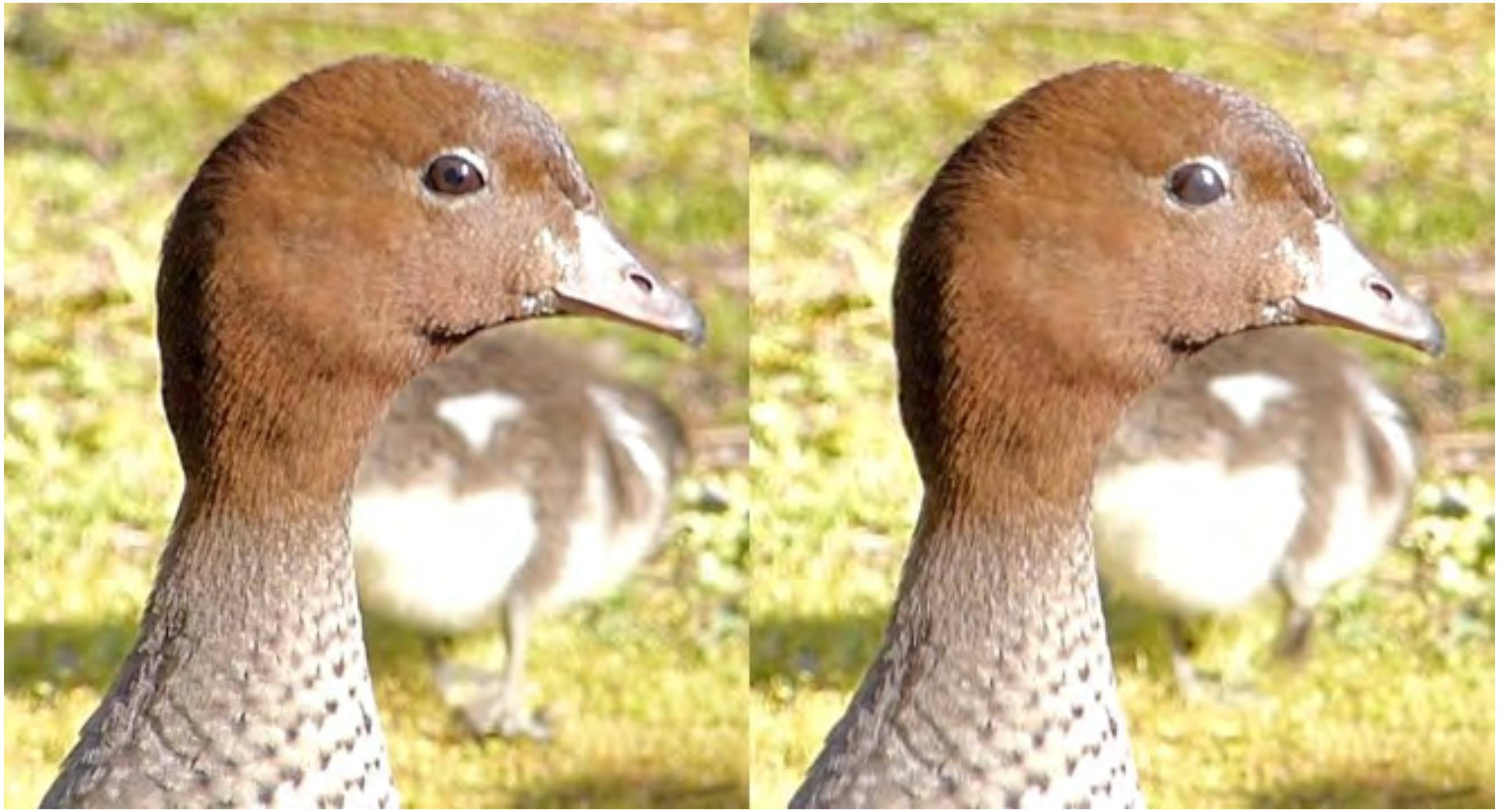
Nictitating membrane and lower lid blink.

Australian wood duck (*Chenonetta jubata*)

No blink on pecking.

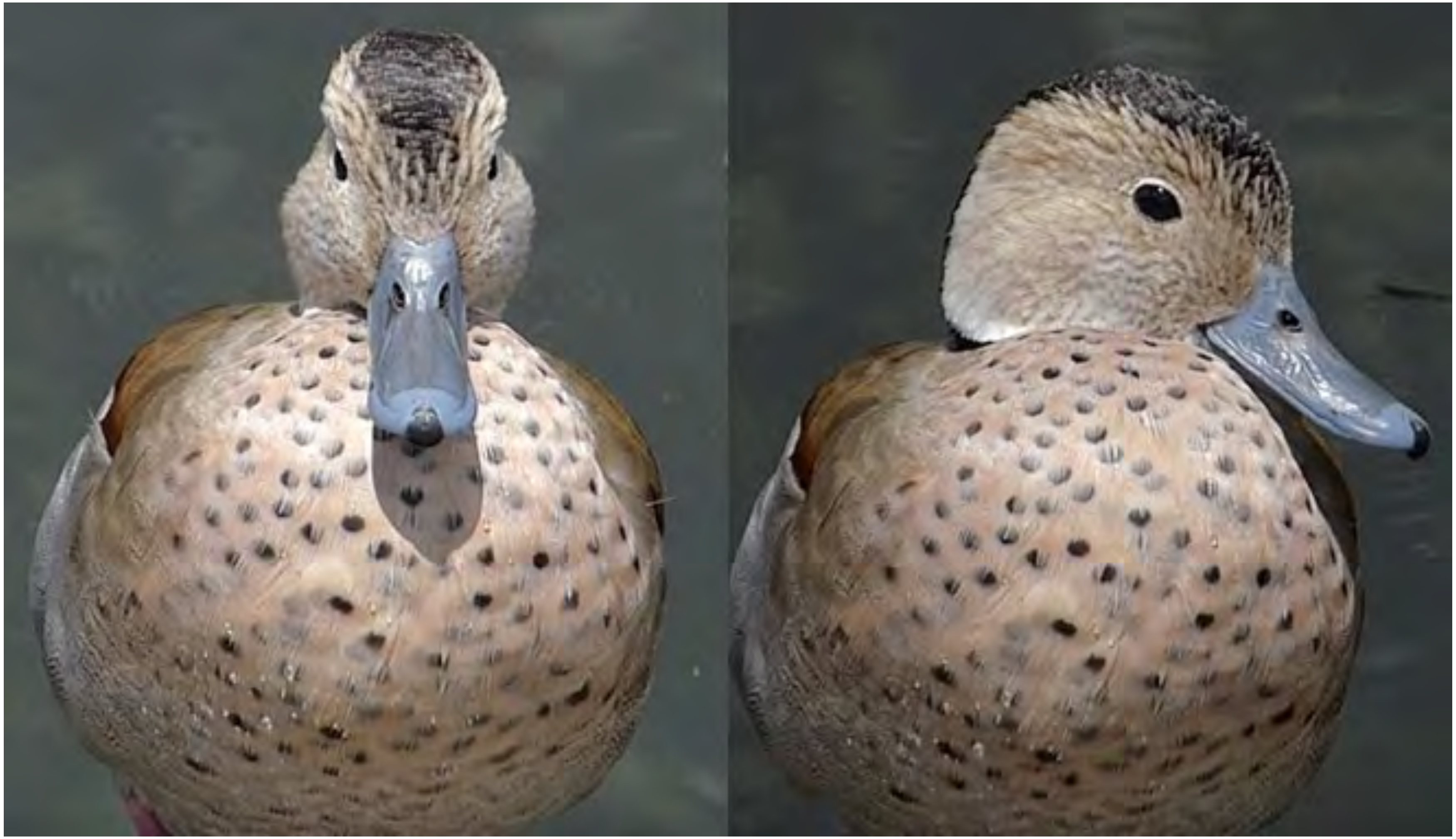
Nictitating membrane blink on head turn.

Blink a: Nictitating membrane blink on head turn



Blink b: Lower lid elevation with drowsiness in a chick

Ringed teal (*Callonetta leucophrys*)



Nictitating membrane blink

Chestnut teal (*Anas castanea*)

Blink a: Nictitating membrane blink on head turn

Blink b: Nictitating membrane blink on feeding

Blink c: Lower lid elevation with drowsiness

Hottentot teal (Spatula hottentota)

Nictitating membrane blink

Whooper swan (*Cygnus cygnus*)

Nictitating membrane blink on head turn

Black swan (*Cygnus atratus*)

Nictitating membrane blink and lower lid elevation with drowsiness

Nictitating membrane blink on head turn

Blue duck or whio (*Hymenolaimus malacorhynchos*)

Nictitating membrane blink on head turn

Nene (Branta sandvicensis)

Blink a: Nictitating membrane blink on head turn

Blink b: Lower lid elevation on preening

Blink c: Nictitating membrane blink and lower lid elevation with drowsiness

Blink d: Lower lid elevation with pecking

Radjah shelduck (*Radjah radjah*)

Eye movement.

Blink a: Nictitating membrane blink

Nictitating membrane blink with head still.

Blink b: Lower lid elevation with drowsiness

Lower lid elevated during sleep. Pupil visible through lower lid.

Nictitating membrane.

Eye movement.

Family Anhimidae

Southern screamer (*Chauna torquata*)

Blink a: Nictitating membrane blink on head turn

Order Bucerotiformes

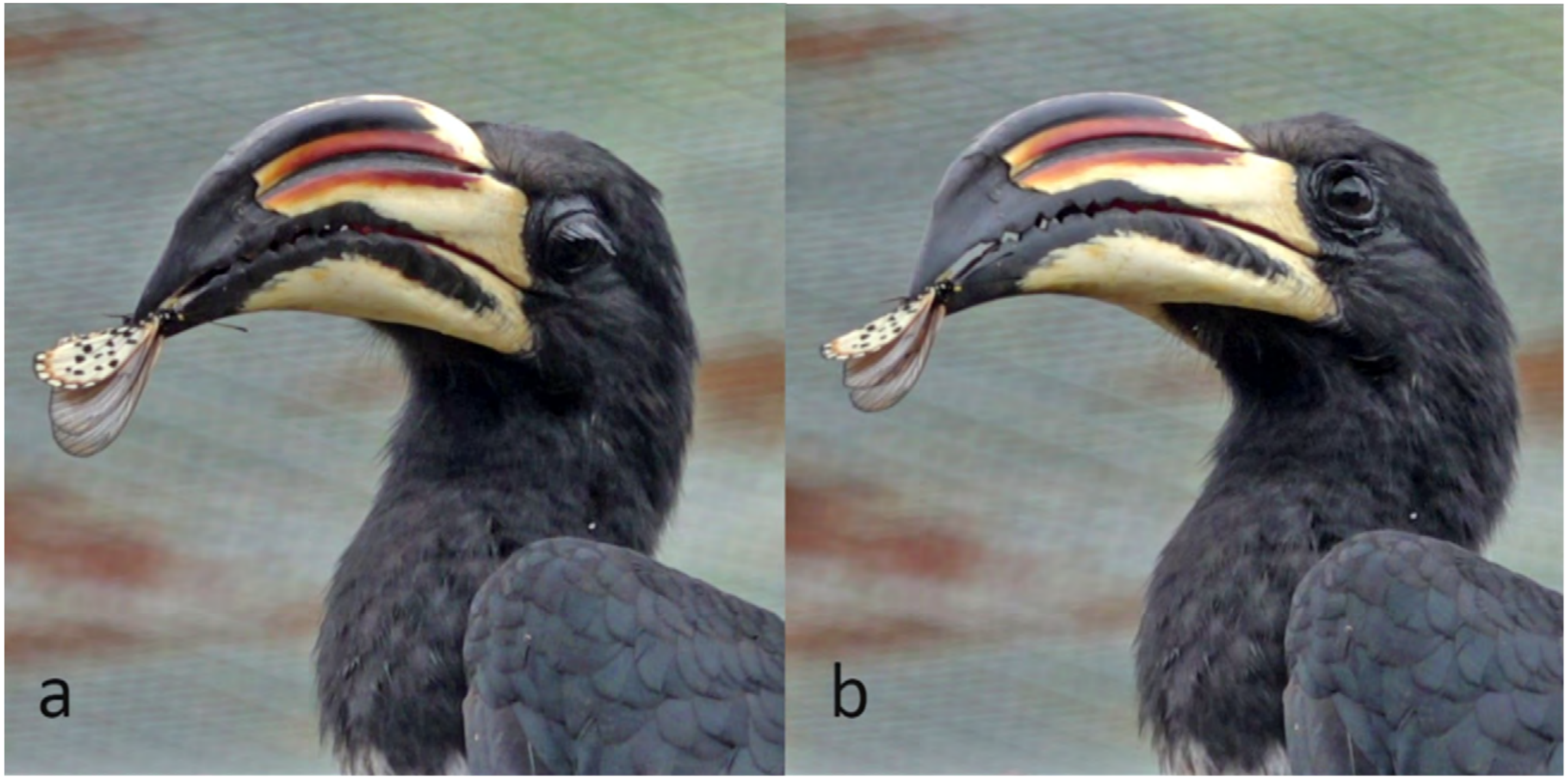
Family Bucerotidae

African grey hornbill (*Lophoceros nasutus*)

Nictitating membrane blink on eye movement

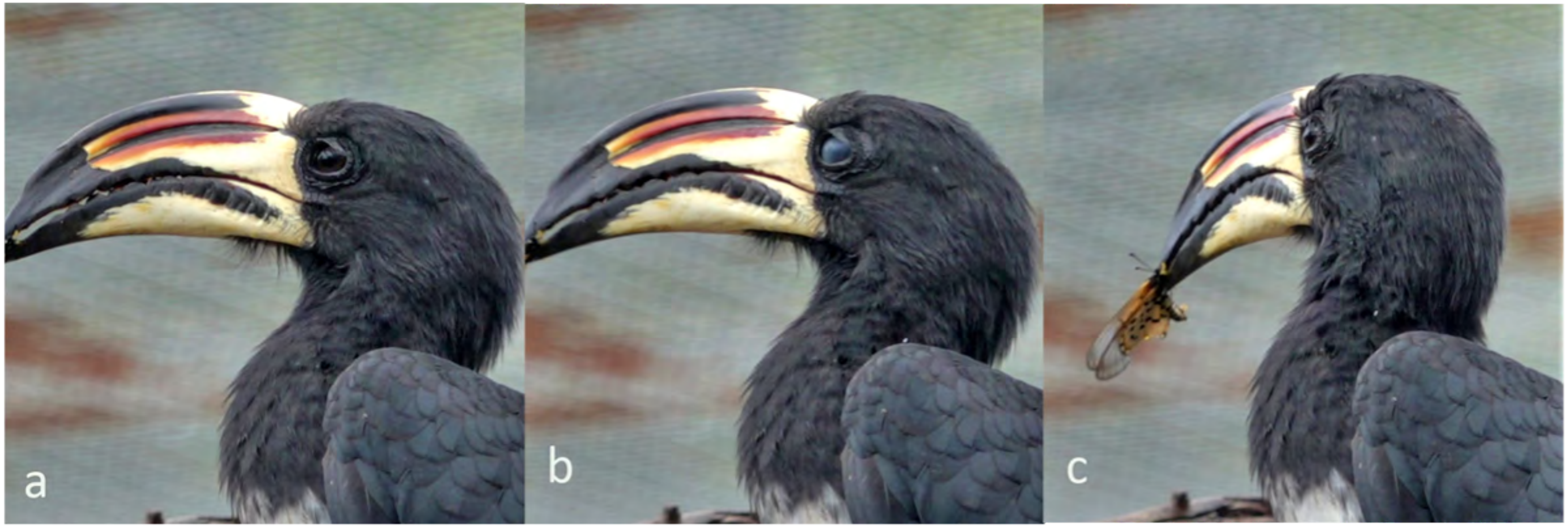
a) Pre-blink. Looking upwards. b) Nictitating membrane blink during eye movement. c) Post-blink. End of eye movement.

African pied hornbill (*Lophoceros fasciatus*)



a) Prominent upper lid and 'eye lashes' on looking down. b) These disappear on looking up.

Nictitating membrane blink on head turn



a) Pre-blink. b) Nictitating membrane blink throughout head turn. c) Post-blink. End of head turn.

Von der Decken's hornbill (*Tockus deckeni*)

Blink a: Nictitating membrane blink on head and eye movement

Blink b: Nictitating membrane blink on head turn

Nictitating membrane blink.

Great hornbill (*Buceros bicornis*)

Blink a: Nictitating membrane blink on eye movement

Nictitating membrane blink on eye movement - upward gaze.

No blink on eye movement.

Eye movements.

Nictitating membrane blink.

Blink b: Lower lid blink

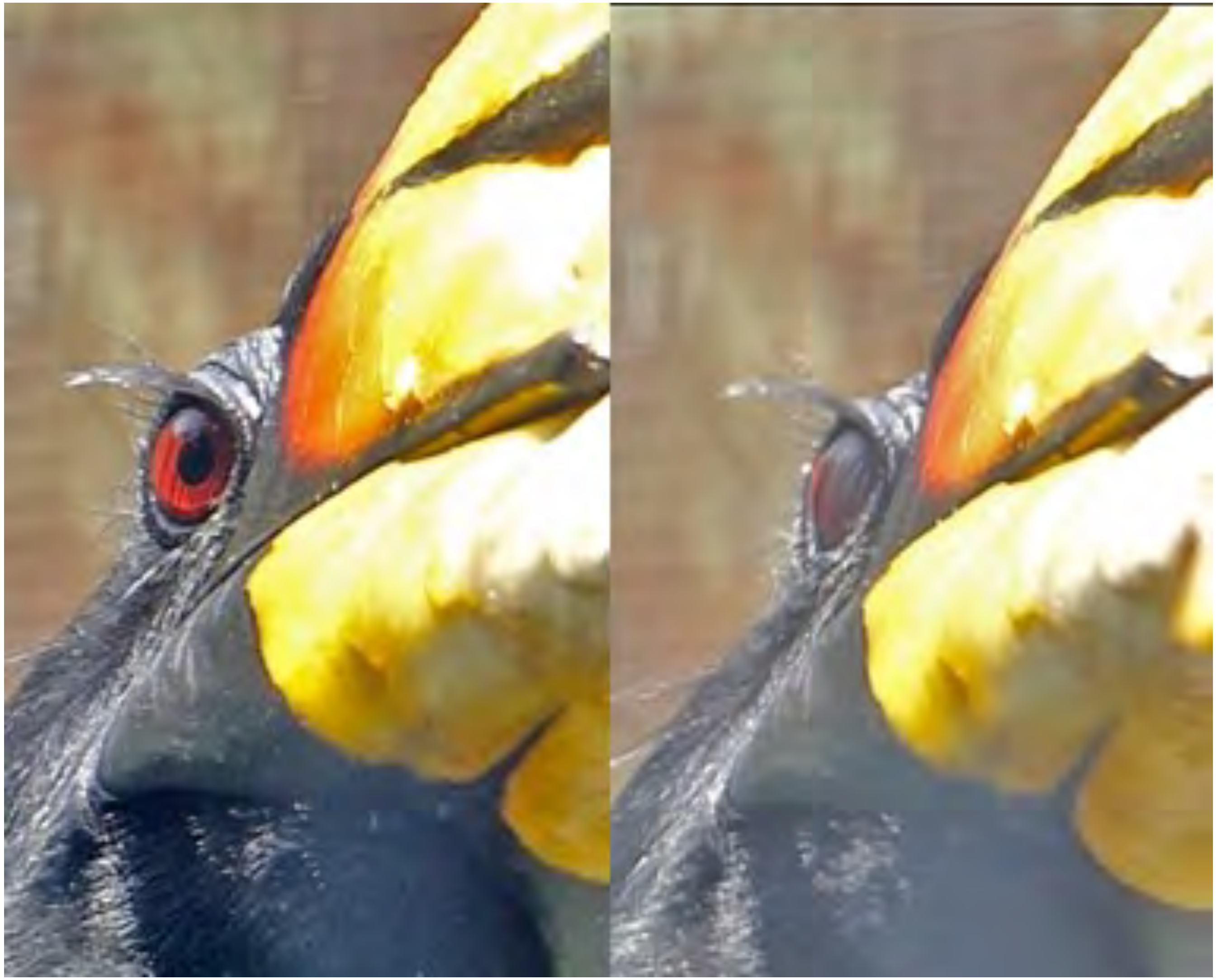
Lower lid blink and eye movements .

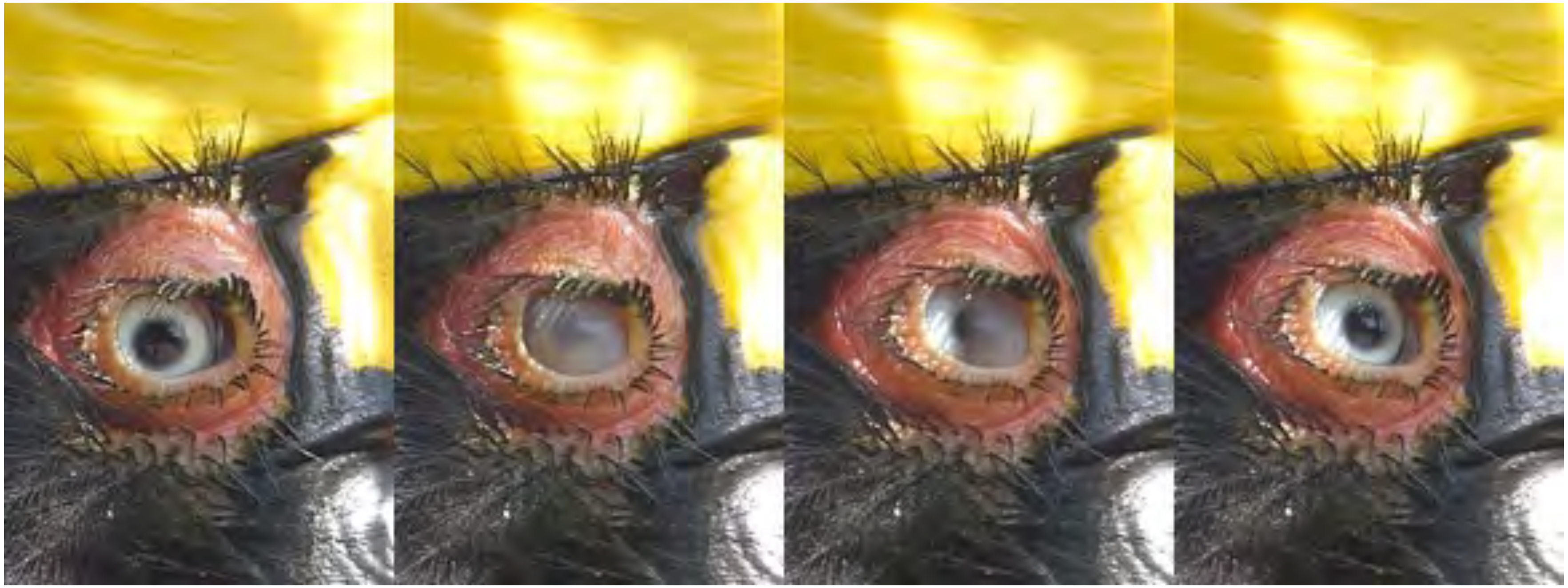
Blink c: Nictitating membrane blink on eye movements

Rhinoceros hornbill (*Buceros rhinoceros*)

Blink a: Nictitating membrane blink on eye movement

Blink b: Nictitating membrane blink on head turn





Female. Nictitating membrane blink on eye movement.

Female. Pupillary dilatation.

Eye movement.

Nictitating membrane blink on head movement. Note large bill and casque.

Nictitating membrane blink on head movement.

Nictitating membrane blink on eye movement.

Eye movements.

White-crested hornbill (*Horizocerus albocristatus*)

Blink a: Nictitating membrane blink on eye movement

Nictitating membrane blink on eye movement - downward gaze.

Downward gaze.

Blink b: Nictitating membrane blink on head turn

White-crowned hornbill (*Berenicornis comatus*)

Nictitating membrane blink on head turn

Eye movement and feather 'eye-lashes'.

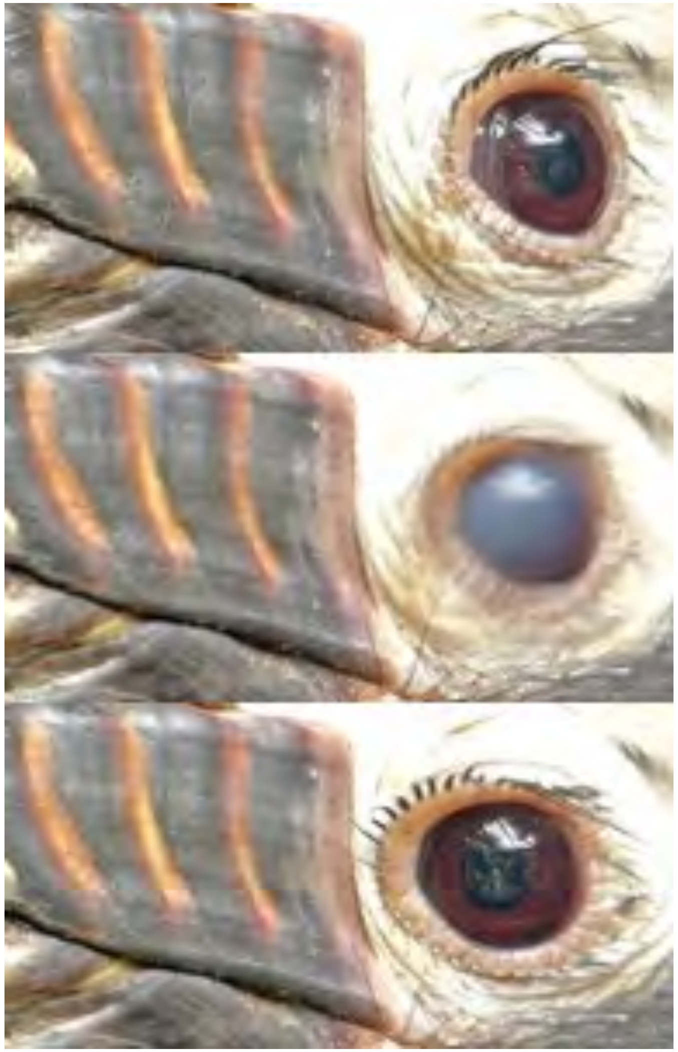
Blink b: Nictitating membrane blink on eye movement

Wreathed hornbill (*Rhyticeros undulatus*)

Blink a: Nictitating membrane blink on head turn

Eye movement – easier to see on video.

Blink b: Nictitating membrane blink on eye movement



Silvery-cheeked hornbill (*Bycanistes brevis*)

Blink a: Nictitating membrane blink on head turn

Blink b: Lower lid elevation with preening

Blink c: Nictitating membrane blink on eye movement

Blyth's (Papuan) hornbill (*Rhyticeros plicatus)*

Blink a: Nictitating membrane blink on head turn

Blink b: Nictitating membrane blink on eye movement

Female. Nictitating membrane blink on eye movement.

Female. Nictitating membrane blink on eye movement.

Rufous hornbill (*Buceros hydrocorax*)

Nictitating membrane blink on eye movement (female)

Family Bucorvidae

Southern ground hornbill (*Bucorvus leadbeateri*)

Blink a: Nictitating membrane blink on eye movement

Downward gaze

Blink b: Nictitating membrane blink on head turn

No sustained blink on preening.

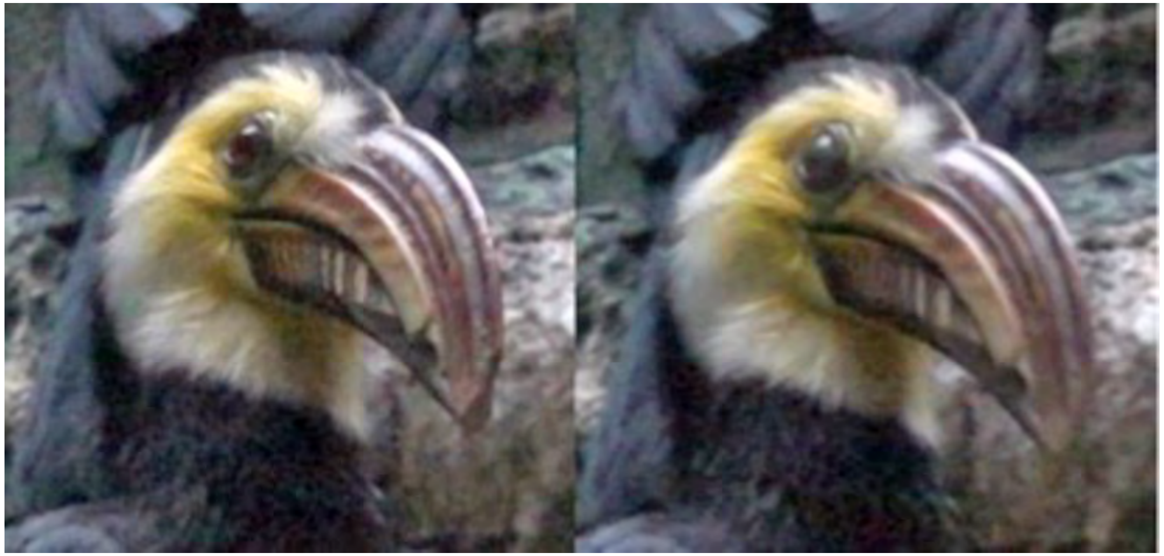
Nictitating membrane blink then downward gaze.

Nictitating membrane blink on eye movement.

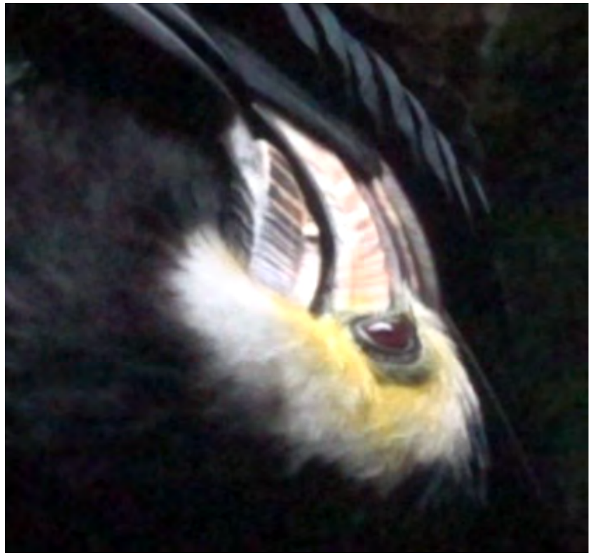
Minimal fall in inner part of upper lid with nictitating membrane blink.

Sulawesi hornbill (*Rhabdotorrhinus exarhatus*)

Nictitating membrane blink on head turn



Nictitating membrane blink on head movement.



No lid blink on preening

Family Upupidae

Eurasian hoopoe (*Upupa epops*)

Hard to see if there is a lid blink during pecking.

Species