REPTILIAN EYES AND ORBITAL STRUCTURES

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ABSTRACT

The anatomy of the reptilian eye is similar across species, generally, but the eyes of various taxa differ in details. The eyeball is formed of layers and has three chambers. Pupil shape differs among reptilian taxa with behavior. The retina's photosensitive cells (rods and cones or all-cones) transmit signals to the optic nerve, which is an extension of the brain. Retinal sensitivity is increased by foveae in lizards and tuataras, while turtles and snakes have *areas*. The lens is soft and is shaped for accommodation by the ciliary muscles (lizards, turtles and crocodilians) or movement (snakes). All reptiles have eyelids, however some lizards have partially fused lids, while other lizards and all snakes have fused clear lids, the spectacle. Ocular glands lubricate the cornea in all species. Movements of the eyes are critical to preventing photoreceptor fatigue and loss of image recognition.

INTRODUCTION TO THE REPTILIAN EYE

Reptilian eyes are anatomically similar to those of other vertebrates in that the eyeball (= globe) is formed of layers, filled with fluid, and has a lens that focuses light on a retina. The eye is structured as a series of chambers. The *anterior chamber* is the fluid-filled space inside the eye between the iris and the cornea's innermost surface; the *posterior chamber* is a small space directly posterior to the iris, anterior to the lens, and bordered by the *ciliary body* or ciliary muscles. The anterior and posterior chambers are filled with *aqueous humour*. The *vitreous chamber* is filled with a viscous liquid, the *vitreous humour,* which fills the chamber between the lens and the retina.[11]

The eyeball sits within its bony orbit. Each reptile has two orbits that are separated from one another by a cartilaginous *interorbital septum* in lizards, crocodilians, tuataras, and turtles, or by bones and cartilages (frontal, parietal, and parasphenoid bones) in snakes.[11,19,23] The orbital bones and the septum are lined with a *periorbital membrane*, which joins with the orbital membranes, and fuses with the proximal internal parts of the upper and lower eyelids. In snakes, the conjunctiva lines the orbit as well.[19]

Ocular Adnexa Ocular adnexa include the eyelids and their parts, conjunctiva, orbital glands, and extrinsic eye muscles. The extrinsic eye muscles are addressed separately at the end of this document.

Eyelids. All reptiles have external eyelids. In most lizards, all turtles, tuataras and crocodilians, both upper and lower eyelids are present. The borders of the upper and lower lids are often rich in secretory goblet cells.[24] Most lizards have upper and lower eyelids, but most lack nictitating membranes. The lower lid of lizards contains a cartilaginous support, the *tarsus*. Lids are modified in a number of species so that they are partially fused, as in chameleons, leaving a circular opening the diameter of the cornea, or fused and clear as in many geckos and snakes.[19] In snakes, the eyelids fuse during development and form the *spectacle*. Some gecko species and some skink species have a secondarily derived spectacle. Some skinks, lacertid, and iguanine lizards have a transparent lower eyelid formed by clear scales.[13,19] In general, the upper lid has mostly smooth muscle and is less mobile than the lower lid, which has striated muscle. In crocodilians, the upper lid contains a bony plate; the lower lid lacks bone or cartilage,[5,18] but moves up to close the eye.[13,19]

The eyelids cover a poorly cornified *nictitating membrane* (= *nictitans*) along the nasal surface of the eye. The nictitans, an extension of the conjunctiva, is cartilage-supported in non-burrowing lizards and crocodilians.[5,11,19] Nictitating membranes are highly developed in crocodilians and turtles but absent in snakes and many lizards.[10,19] The nictitating membrane may be pigmented. It is usually largest toward the medial (nasal) part of the eye[26] and may have folds. Depending upon the species, it may cover all or part of the eye. The *pyramidalis* muscle draws the nictitans across the eye.[19] The nictitans acts to mechanically protect and cleanse the cornea and moisten its surface. The “lid-less” lizards, with a clear spectacle covering the cornea, lack a nictitans. Chameleons have partially fused upper and lower lids and lack a nictitans.[19]

Snakes lack movable eyelids and nictitating membranes. The cornea is covered by a transparent spectacle (= *brille*), which is derived from both upper and lower eyelids.[11,19] The spectacle does not move. It is shed when the skin is shed.[11]

*Orbital Glands***.** Orbital glands are lubricatory; their secretions often drain secondarily into the mouth and may contribute to oral lubrication, or even digestion.[19] Lizards generally have three orbital glands, which may be compact or have extended portions. Most lizards have well-developed *lachrymal glands*, located posterior, dorsal and ventral to the eye. They are absent in chameleons, calotes, some geckos, and Australian snake-lizards. *Harderian glands* are located ventral or anterior to each eyeball and drain via a duct onto the inner surface of the nictitating membrane.[19] The *Harderian ducts* drain the anterior ventral eye from the lower lid and extend to empty into the palate. A small mucous gland (= *conjunctival gland*) opens onto the outer surface of the nictitating membrane, when present.[11,19]

Snakes have well-developed Harderian glands, located dorsally and nasally that lubricate the spaces between the spectacle and the cornea. They lack lachrymal glands. The nasohardarian duct drains this fluid from the *subspectacular space* into the *Jacobson’s organ* in the palate of the oral cavity.[10] Tuataras, too, have only the Harderian gland, however it lubricates the cornea and the conjunctiva.[19]

In turtles, lachrymal and Harderian glands are well developed. They vary greatly in size with taxon. Dorsally positioned lachrymal glands are very large in marine turtles but small in freshwater and tortoise species.[19,26] The Harderian gland is present dorsally and nasally in all turtles. There are no reported *nasolachrymal ducts* in turtles,[10] however some species have the bony opening for such a duct in the floor of the orbit.

Crocodilians have three kinds of glands associated with the eye: lachrymal, Harderian, and *conjunctival* glands.[10,18] The elongated lachrymal gland is small relative to the size of the eyeball and located dorsally within the orbit. The Harderian gland is large, triangular and located anterior and medial to the eye. It secretes lubricating fluid via two ducts that drain between the nictitating membrane and the eye. The conjunctival gland is located at the junction of the conjunctiva and the eyeball within the lower lid.[18,19] It is presumed to be a lubricating gland.

EYE DEVELOPMENT

In all vertebrates, the eye develops as a composite of structures. Eye development is relevant to health because the developing eyes form early and direct or influence the fates of other facial features as they develop. Additionally, development of the *extrinsic eye muscles* is key to balance or neurologic development.[19] The eye forms as an outgrowth of the *forebrain* so the optic nerve actually is a nerve tract and not a nerve, *per se*. The *optic cup* forms the *iris* and *retina*. *Ectoderm* gives rise to the eyelids, *cornea*, and *lens.* A specialized form of ectodermal mesenchyme, the *neural crest*, forms the *sclera*, *cornea*, and *choroid*.[11] The sclera is continuous with the *dura mater*.[19] The retinal vasculature, when present, originated independently in snakes versus that of lizards and turtles.[10] In snakes, the vascular "*conus*" is a new organ of mesodermal origin while the conus organs of lizards and turtles are derived from *neuroectoderm*.[19]

LAYERS OF THE EYEBALL

The eyeball's outer layer is the *sclera* (a fibrous outer capsule to which extrinsic eye muscles attach) gives the eye stability.[11,19,21] It is usually white but can be strikingly pigmented. For example, the sclera of the Cayman blue iguana (*Cyclura lewisi*) is red.[19] The inner wall of the eyeball is supported by hyaline cartilage, or sometimes by calcified cartilage, in turtles, lizards, and crocodilians, but not in snake eyes. A ring of small bony plates, the *scleral ossicles,* (Figure 1) supports the outer (nasal) portion of the eye in lizards, turtles, and tuataras.[11,18,19,26] The ring of scleral ossicles is located where scleral and corneal tissues join.[10] Snakes and crocodilians lack scleral ossicles.[10,18,19,21]

The middle layers of the eye are collectively the *uvea* and include the *choroid, tapetum lucidum, ciliary body* and *iris*.[11] The choroid is a vascular nutritive layer. The *tapetum lucidum* (reflective material) is in the choroid[11,18] and primarily occurs in animals that live in low light conditions. The *ciliary body* is in the anterior portion of the uvea and is just behind the iris. It produces the fluid of the *anterior chamber* and is responsible for *accommodation* by changing the shape of the *lens*.[11,19] The *iris* and the *pupil* are the eye's aperture control, which controls the amount of available light reaching the lens and retina[7,11,15,19] and aids in accommodation in at least some turtles.[6] The pupil size in the iris is controlled by striated muscle in reptiles. This contrasts with smooth muscles controlling the iris in most vertebrates.[10,13,19]

The inner layer of the eye is the *retina*, which itself is organized into layers. The photosensitive cells (*rods* and *cones*) are inner-most. Light passes through a layer of *ganglion* and *Amacrin*e cells, then a layer of interneurons, and then reaches the photosensitive cells. The *optic nerve* transmits the retinal signals to the brain. It exits the eye at the optic disk.[11,19,21,24]

The Retina The photosensitive cells are overlaid by a layer of interneurons (horizontal and bipolar cells) and a layer of ganglion cells and Amacrine cells; the latter layer is adjacent to the vitreous chamber. The photosensitive cells of reptiles are of two characteristic types, rods and cones. Rods detect light at low levels but not color. Cones are active in bright light.[11,19,21,24] Cone photoreceptors occur in populations with different wavelength response characteristics. They minimally must have two different photopigments and the neural machinery to process the difference in responses to provide for color vision.[19] In general, the ratio of rods to cones is related to the behavior of the animals, so that day active animals have a higher proportion of cones and nocturnal animals have a higher proportion of rods. Reptiles blur this trend in dominant photoreceptors, but not in the function of their photoreceptors. Due to the many ecological shifts reptiles have undergone in their evolutionary history, many linages shifted between diurnal and nocturnal life, and some shifted back. As a consequence some species have photoreceptors that express atypical forms or atypical photo-pigments.[3,6,12] Diurnal lizards and at least some diurnal snakes such as garter snakes (*Thamnophis sirtalis)* have all-cone or nearly all-cone retinae.[12,19] Some nocturnal lizards, such as Tokay geckos (*Gecko gecko*) have retinae formed of only rods. However, crepuscular lizards and tuataras have all-cone retinae, yet the cones have secondarily developed rod-like function.[12,14,19] Nocturnal lizards and snakes usually have rods and cones.[3,19,21] However, the rods may be secondarily derived from cones.[3,19,21,24] Turtles and crocodilians have retinas formed of both rods and cones.[13,19,24]

Most, if not all, diurnal reptiles appear to see color. The numbers of cone photopigments and their spectral sensitivity provide presumptive evidence for the ability to detect colors.[11,24] However, detection (a physiological response) and perception (the behavioral evidence that detected colors can be discriminated) may differ so that animals with more than one photopigment may not have color vision. The peak sensitivity to colors varies with species, and sometimes with age. Physiological measures of the retina's sensitivity to colored lights gives indication of how many photopigments are present and the ranges of colors (wavelengths) they can detect.[19] However, whether the animals perceive the colors requires behavioral assays (for example.[27] Many studies purporting to demonstrate color vision do not definitively do so because they fail to test for perception or control for light intensity differences among the wavelengths (colors) tested.

Oil droplets may be found in the ends of cones.[8,19-22] They represent a common mechanism by which retinal sensitivity is modified.[22] They function as filters and can increase the ability of an animal to discriminate objects or edges and detect colors.[6,8,22,27] There is some evidence that oil droplets may protect the cones from UV damage.[19] Oil droplets are found in turtles and diurnal lizards, but are not reported in crocodilians or snakes.[22,24]

Foveae are pits of concentrated cones that provide for detailed vision (increased acuity). Foveae with steep walls tend to increase acuity by causing slight expansion of the image. Lizards have one fovea or two foveae per eye; they are shallow in some species (e.g., iguanas and geckos) and deep in others, such as chameleons. Tuataras have a deep-wall fovea in each eye. Turtles, crocodilians and snakes lack foveae.[19]

Areas are sections of the retina that are particularly sensitive due to increased number or density of photoreceptors or ganglion cells.[2,11,19] Turtles have areas (e.g., an *area centralis* or *area temporalis*) or horizontal strip areas called *visual streaks*, which are sections of the retina that are especially sensitive.[2,6,19] Crocodilians also have visual streaks. Several taxa of lizards also show visual streaks.[4,16,25] Visual streaks have been identified in several species of sea snake, and in the garter snake.[9,19] Snakes supplement vision with acute chemical sensitivity and, in some cases, infrared radiation detection. Areas and visual streaks are linked closely with the visual ecology of the animal. These areas of higher sensitivity help the animals avoid predators, find essential habitat and find food.[19]

The *optic disk* is the region in the retina where nerve fibers from the retina exit to become part of the optic nerve. Arising from the optic disk is a papillary cone (*conus papillaris*) that extends into the vitreous body.[11,19,21,24] It is often melanic and highly vascular. It is believed to function in providing supplementary nutrition to deep ocular tissues. A papillary cone is present in lizards and some snakes, but not in turtles, crocodilians or tuataras. Some snakes supply nutrition to the retina via choroidal diffusion, while others rely upon a network of blood vessels lying on top of the retina (vitreal vessels).[19]

Pupils Pupil shape differs among reptilian taxa and with behavior. The pupil acts as the aperture setting for the eye. Pupil shape reflects function. The shape of the pupil can have a profound effect on the retinal image because pupil shape influences the characteristics of light reaching the retina.[6,21,24] Turtles, diurnal lizards and colubrid snakes tend to have round pupils. Many nocturnal hunters such as crocodilians, geckos, and many snakes have slits. Snakes may have elliptical slit or round pupils. The crocodilian pupil is a vertical ellipse that can contract to a slit. Slit pupils tend to improve focus in an orientation that is perpendicular to the slit.[11,10,19] So, a vertical pupil provides the best focus along the horizontal axis relative to the animal's head. Schwab[20] points out that it is important to remember that an animal’s horizon may be different from your own. For example, geckos are often found on vertical perches (or on ceilings). Horizontal pupils, common among herbivores but rare or absent in reptiles, focus best along the vertical axis. Slit pupils with multiple pinholes, found in some geckos, allows the animals to use the pinhole images as a range finder by forming several images of an object on the same point on the retina. If an object is too close or too far, the images from the individual pinholes will not be in focus or be coincident with one another.[15,20] Additionally, slit pupils with multiple apertures can dilate to a much larger field of view than a round pupil. Such dilation is advantageous for nocturnal activity.[20]

The Cornea The cornea is clear and thin walled.[19,21,24] In many species the cornea is tall and the lens is relatively flat on the side nearest the cornea. The cornea is formed of thin layers in most tetrapods. It functions as a lens and refracts light except underwater.[6,19] In aquatic reptiles, the cornea tends to be domed with a curvature that is similar to the sclera. In crocodilians, the cornea is flatter than is expected for aquatic species and appears to do little refraction.[19] It is likely that other sensory systems (such as dome receptors that sense waves) and hearing play more important roles than vision in crocodilians. Snakes too have a relatively flat cornea.[11,21,24]

INTRINSIC MUSCLES

Pupil diameter (*pupillary reflex*) is controlled by the oculomotor nerve.[11,21] The *pupillary sphincter* is formed from striated muscle or a combination of smooth and striated muscle in reptiles, except for snakes. Snakes have a smooth muscle iris.[2] Thus, most reptilian eyes differ from the pupillary muscular system in mammalian eyes (purely smooth muscle sphincter). Striated *ciliary muscles* shape the lens directly or by pulling on the *zonular fibers*.[1,11,19] The ciliary muscles may also push on the iris and squeeze part of the lens through the pupil, slightly reshaping it to focus. Some turtles and lizards are able to move the lens nasally and medially with the *transversalis* muscle for binocular vision.[19]

ACCOMMODATION: LENSES AND FOCUSING MECHANISMS

Accommodation involves the lens and the cornea in terrestrial reptiles.[1,2,4,9] The cornea plays an important role in light refraction in many terrestrial reptiles. It plays a lesser role in refracting light in aquatic reptiles.[2,4,9,12] The steeper the curvature of the lens or the cornea, the greater the light gathering capacity.[2] The lens is a composite of relatively soft crystalline proteins. Reptilian lenses are often oval and are focused by deformation (= lenticular deformation). Some aquatic species have round lenses (e.g., sea turtles) that are deformable.[12] Snakes have round lenses that are moved toward or away from the retina to focus.[1,2,9,26]

EYE MOVEMENTS: EXTRINSIC EYE MUSCLES

Eye movement is essential to prevent fatigue of photoreceptors.[19] Turtles, crocodilians, and most lizards (except *Heloderma*) have mobile eyes. Snake eyes, effectively, are not mobile.[21] Reptiles have *retractor oculi* and *protractor oculi (= levator bulbi = retractor bulbi)* muscles inserting on the sclera adjacent to the optic nerve that move the eye inward and outward within the socket.[1,2,4,9] These muscles are weakly developed in crocodilians, some turtles and many lizards without hinged snouts and braincases (akinetic lizards). They are strongly developed in lizards with kinetic skulls, including chameleons, most turtles, and snakes.[21,24] Cranial nerve VI (Abducens), and possibly Cranial nerve VII (Facial), innervate(s) them. Reptiles have six extrinsic eye muscles that are responsible for rotating the eyeball within the orbit (Table 1); they insert on the sclera.[11,23] The extrinsic eye muscles are characterized by fine movement control and coordinated control with eyes with the vestibular system.[11,19,23]

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Table 1. Extrinsic eye muscles, their innervations and actions. Muscle actions are given in general terms because of species-specific differences detailed actions. The eye muscles are organized functionally as antagonists and are listed as agonist-antagonist pairs. The oblique muscles together are responsible for torsion of the eyes so that the eyes return to the correct vertical position when the head is tilted. Some innervation must cross from one side of the brainstem to the other to coordinate the movements of these pairs of eye muscles in both eyes.[19]

Muscle	Innervation	Action
medial rectus	Cranial Nerve III (*Oculomotor*)	draws gaze nasally
lateral rectus	Cranial Nerve VI (*Abducens*)	draws gaze temporally
superior rectus	Cranial Nerve III (*Oculomotor*)	draws gaze temporally and dorsally
inferior rectus	Cranial Nerve III (*Oculomotor*)	draws gaze nasally and ventrally
inferior oblique	Cranial Nerve III (*Oculomotor*)	draws gaze temporally and ventrally
superior oblique	Cranial Nerve IV (*Trochlear*)	draws gaze nasally and dorsally

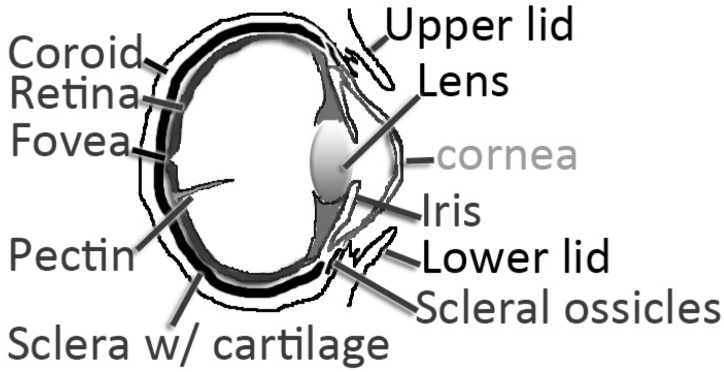

Figure 1. Diagrammatic representation of the reptilian eye in sagittal section. The major anatomical parts are labeled. The chambers and ciliary bodies are left unlabeled to reduce clutter. The parts and chambers of the eye and their relationships to other structures are discussed in the text. The snake eye deviates from this structure in the lack of moveable lids and scleral ossicles.