

# Cover illustration

## He cries crocodile tears . . .

The saurian triumph which occurred during the Mesozoic era probably ended with a cosmic bomb slamming into the Yucatan 65 million years ago annihilating the dinosaurs. Somewhere in the dark ooze that remained after that catastrophic explosion, some opportunistic creatures were able to survive by capturing live prey, be they fish or terrestrial animals, feeding exclusively on carrion, or even going for long periods without eating anything whatsoever. These grisly veterans are old—very old, as they can trace their lineage to at least the Middle Triassic epoch about 240 million years ago, and they were not about to let a comet interfere with their longevity. From those tough and resistant predecessors come our modern day crocodylians, with surprisingly few, and mostly conservative, morphological changes in their skeletal structure.

The American alligator (*Alligator mississippiensis*) is one of the 23 species of crocodylians. Living in the southeastern United States in swamps and bayous with a maximum length of 5-6 metres and weighing as much as two Sumo wrestlers (between 800–1000 lb (364–455 kg)), this species is important to the biodiversity and ecology of the area, but may also offer us an unintended glimpse into our evolutionary past by looking through their eyes.

The crocodylians, represented here by the American alligator (including an albino shown in the upper left portion of the cover), have several amphibious adaptations which are interesting and shed light on ocular evolution. The eyes are set above the principal dorsal surface axis of the body so that only the eyes and nostrils remain out of the water for camouflage, leaving a shadowy outline of the rest of the body. The eye is large, often reaching 20 mm in diameter in the alligator and larger in other crocodylians. The cornea is flatter than ours and this might be expected as an aquatic adaptation. Consequently, to compensate for the loss of the refractive power of the cornea, the lens is quite large and round or ellipsoidal much like a piscine lens. The nocturnal nature of the species and the participation of other senses for prey capture probably have put little emphasis on, or need for, accommodation. For support, cartilage lines much of the sclera, again in piscine fashion. The upper lid contains a bony or very tough cartilaginous tarsus with a cartilaginous plate in the translucent nictitans (or third eyelid). The retractor bulbi muscles are able to pull the eye beneath the horizontal plane of the skull, and with the bony plate in the upper lid, cover the eyeball with a fortress-like lid to protect



the eye from flying debris or kicking limbs during predatory attacks. The lacrimal gland is found under the dorsal orbital roof but, in addition, the crocodylians also have a series of glands lining the under-surface of the leading edge of the nictitans. These are called Harderian glands, and are seen in many birds and other reptiles. They are ancillary tear glands and may produce specialised tears. In the case of the crocodylians, the Harderian glands produce oily tears that presumably protect what was evolutionarily a terrestrial eye that returned to water and had to readapt to the chronic osmotic effects of water on the cornea. So, the proverbial crocodile tears do exist, and in two forms, at that.

The iris is thick and darkly pigmented and acts as a shade, preventing any stray light from entering the globe. The anterior layer of the iris is filled with lipophores giving a light brown or cream coloration to the iris. Sporting the vertical slit pupil of many terrestrial predators, as can be seen in the lower left portion of the cover, alligators have a surprisingly large eye similar in structure to other vertebrate tetrapods and, surprisingly, similar to birds. Alligators even have the horizontal strip of concentrated photoreceptors that resembles the infula of certain bird species, such as the flamingo, (see August 2000 *BJO* cover). This horizontal strip of concentrated photoreceptors can be seen above the optic disc in the posterior pole of the alligator eye (lower right portion of the cover). But there are some differences, and at least one difference asks startling questions. While many of the ocular structures are homologous, and even analogous to humans, the difference in retinal nutrition is perplexing. Many vertebrates have a direct retinal vascular supply such as our central retinal artery. Birds have a pecten to serve inner retinal metabolism; many fish have a falciform process for the same purpose; turtles and other reptiles have a conus papillaris, and these intraocular structures are homologous. Alligators have none of these,

although there may be an appendix-like remnant of a conus on the disc. But there is no demonstrable inner retinal nutritive support for the alligator eye. Perhaps the closest analogous structure is the choroidal gland of some fish, but the alligator does not seem to have even this seething vascular knot found in the choroid, usually in the posterior pole. Inner retinal nutrition remains a mystery especially since oxygen can diffuse only 143  $\mu\text{m}$  in tissue.

The retina has other interesting adaptations. The retinal pigment epithelium is modified in the superior half of the posterior pole to be a guanine containing non-occludable tapetum lucidum creating the eerie primeval blood red glow seen at the water's edge at night in any swamp inhabited by these predators. The tapetum allows the animal to maximise nocturnal photons by reflecting light back to the photoreceptors after these photons have passed through the retina unabsorbed. The retina contains cones but is predominantly a rod retina, as might be expected. Even the cones could be described as "rod-like" in their histological appearance, and may be an evolutionary intermediary as the cones "become" rods or are simply lost. The photograph in the lower right hand portion of the cover reveals the fundus and the tapetum.

Although we are taught that these lethargic appearing predators are closely related to other reptiles, they are not. Birds are perhaps their closest relatives, and these diapsid cousins probably split from the crocodyles during the Middle Triassic epoch as the ancestral thecodonts split into *Crocodylia* and *Aves*. This conclusion is supported by homologous neurological design as well as genomics (Janke A, *et al*, *Mol Biol Evol* 1997;14:1266–72), but may be deduced from other evidence as well.

The eye should not be overlooked as a site for biological data to understand phylogenetic relationships. Recently, investigators, discovered that the photopigments of *A mississippiensis* are more closely related to chickens, and presumably other birds, than to reptiles or mammals (Smith WC, *et al*, *Exp Eye Res* 1995;61:569–78).

The eye proves to be a window to the evolutionary soul.

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