

Cover illustration

The lonely eye

Although the dinosaurs are gone, extant vertebrates provide clues to the development of photoreception among the clades that probably preceded and then radiated into the dinosaurs. The ancient order *Rhynchocephalia*, which includes *Sphenodon* as its only family, with two surviving species, had its heyday between 200 million and 100 million years ago. While this order is reptilian, these creatures were not lizards, but their own order.

Approximately 100 million years ago as other members of *Rhynchocephalia* were succumbing to extinction, Gondwanaland was breaking apart and New Zealand and its islands were breaking free from Australia, thereby isolating this last member of *Rhynchocephalia*, *Sphenodon*, presumably without competition. The tuatara survives virtually unchanged, as a fossil relict and provides us with a glimpse of vertebrate evolution from perhaps as long as 200 million years ago.

In the early Jurassic (approximately 200 million years ago) tetrapods were radiating into lizards, turtles, crocodiles, dinosaurs, and eventually birds and mammals. *Sphenodon* was in an order of early reptiles and provides us with a window into those beginnings.

The tuatara has a third eye, as do some other reptiles. But this adaptation has been lost in the radiation into later orders such as crocodiles, birds, and mammals, although remnants of this organ can be found in most of these. The third eye, then, represents evolution's earlier approach to photoreception.

In the tuatara, as in the other reptiles with the organ, the third eye is a dorsal midline structure just ventral to a parietal plug which is homologous to, and resembles, a cornea. Immediately ventral to the parietal plug is a lens that is surprising similar, at least on a histological basis, to those of the lateral eyes. The vitreous cavity analogue is ventral to the lens and dorsal to a pigment epithelial layer. Ventral to the pigment epithelial cells are the primitive ciliated photoreceptors which are everted (our photoreceptors are inverted with the photopigment on the distal end of the retinal cells). Ganglion cell layers are distal to the photoreceptors, much more like the retina of an octopus rather than that of a vertebrate (see essay *BJO* July 2003). These structures can be seen

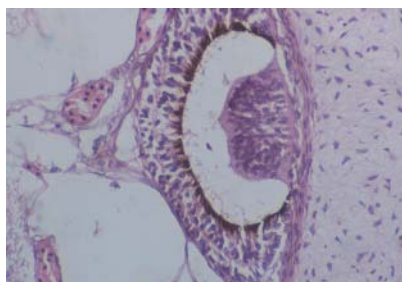


Figure 1 Developing eye of *Sphenodon*. Note early lens formation and retinal pigment epithelium in front of photoreceptors as described in text.

in the figure above (Ung CY-J, Molteno ACB, An enigmatic eye: the histology of the tuatara pineal complex. *Clin Exp Ophthalmol* 2004;32:614–18). The retina is upside down with the retinal pigment epithelium interposed between any incoming light and the photoreceptors! *Sphenodon*, and other reptiles, have everted photoreceptors with outer segments containing stacks of discs very similar to those of the lateral eyes (Eakin RM, *The Third Eye*. UC Press, 1973).

Why should the photoreceptors be everted in the third eye but not in the lateral eyes? As explained by Eakin in *The Third Eye*, it all relates to embryology. In vertebrates, all eyes begin as evaginations of the diencephalon to create optic vesicles, and the lateral eyes proceed to invaginate forming optic cups. But the third eye never invaginates and is lined with the ciliated epithelium that becomes the photoreceptors with the ciliated portion of the cells extending inward towards the centre of the vesicle or cyst. The most distal (and most dorsal) portion of the evagination of the third eye condenses to become a lens leaving the cyst lined with everted cells. The portion of the developing third eye that condenses into a lens, then, is homologous to a portion of the retina in the lateral eye. Furthermore, the ciliated cells that line this cyst in the third eye differentiate into pigment epithelium and everted photoreceptors. It is as if some stimulus is missing, and a complete "normal" vertebrate eye never forms.

If the development of the third eye seems mysterious, the function is even more obscure. Most observers believe

the organ to be a solar dosimeter useful for photoperiod recognition for circadian and seasonal rhythms, but there may be more to this murky organ than first meets the eye. The parietal eye in reptiles, including *Sphenodon*, is not laterally symmetrical which, in and of itself, is unusual in the world of bilateral symmetrical organisms such as vertebrates. Development of the reptilian third eye is actually believed to be as a pair of diencephalic evaginations with the more rostral and left sided portion becoming the parietal eye and the more caudal and right sided portion becoming the pineal sac. In animals that have lost the parietal eye, including mammals, the pineal sac is retained and condensed into the form of the pineal gland. In reptiles, the pineal synthesises melatonin and probably other hormones. In humans, the pineal synthesises melatonin and many other neuroendocrine regulatory compounds. Melatonin influences vertebrate thermoregulation and, importantly, the circadian rhythm by acting as a somnifacient.

The third eye did not spring de novo in the early reptiles or even the early tetrapods as there is a homologous photosensitive organ in frogs, and even some fishes suggesting that this central dorsal third eye is much older than reptiles and probably belongs to our watery beginnings as chordates. The lamprey, a cyclostome, is a primitive fish that has the asymmetrical pineal complex mentioned above suggesting that the structure is probably older than the Devonian period leading perhaps as far back as the protochordates. But, since the pineal complex seems to be in decline even among the reptiles and in subsequent radiations, it may be going the way of the appendix and, hence, is a very lonely eye indeed.

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