Cover illustration

Seeing out of the shell

The turtle shell, or carapace, is a surprising novelty in the vertebrate world, and is emblematic of the entire Order, Testudines. No other species carries its home and its armor in such a long-suffering manner making its morphology very recognisable. Yet, the animals of this ancient and special clade should be recognised as much for their ocular adaptations, which have implications for the basal radiations of reptiles.

Extant turtles evolved from the oldest known turtle of the Jurassic over 210 million years ago, but this could not have been the first turtle. The carapaces of these (mostly) vegetarians developed from fused ribs to encase the body in a bony or leathery shell that surely evolved for protection, but could not have appeared without a period of gradual change.

The turtles are likely to have descended from a stem reptilian creature that had descended from the early anurans (frogs) and before that, the slow moving tetrapod pioneers emerging from an aquatic environment as terrestrial vertebrates.

Although the order of descent from the first stem reptile is controversial, it probably radiated into several different branches during the Carboniferous (about 350 Mya), or a bit later. There is dispute about the timing and organisation of this descent. Nonetheless, current molecular evidence suggests that the last common ancestor radiated into mammal-like reptiles, the true reptiles (squamata), crocodiles, parareptiles (including Testudines), and birds. But, the turtle eye would suggest a descent pattern not currently in favour. On the basis of the retinal examination, the turtle clade would be closer to birds than to reptiles, crocodiles or mammals.

Lungfish are close relatives to the early tetrapods and probably shared many ocular characteristics with them (*BJO* July 2006). These characteristics included photoreceptor oil droplets, four visual pigments, scleral ossicles, (*BJO* February 2002) and a falciform process (*BJO* October 2004). Similarly, turtles must have shared much with that early tetrapod, because all of these unusual ocular traits from the lungfish pass through that first tetrapod into the turtles. Furthermore, these

Red eared slider. Photograph by Michael D Kern, www.thegardensofeden.org.

common traits betoken the later and close radiation into birds from the same stem organism since birds retain these classic and unusual features, as well.

Turtles share with lungfish, some amphibians, most lizards, a few mammals, and all birds, the presence of oil droplets in their photoreceptors. Other species do not share this adaptation, and this structure points to a close relationship to birds, perhaps closer than to the other species mentioned. Similarly, turtles, and most other reptiles, possess a conus projecting into the vitreous cavity from the optic nerve. This structure is homologous to the pecten in birds (*BJO* January 2006) and is found in no other families. Many fish have a analogous structure, the falciform process, suggesting that this structure derived from fish as a method for inner retinal nutrition as the retina became more complex and thicker.

Preceding or subsequent evolution from that stem organism led to a creature that would become nocturnal and arboreal and would lose almost all of these characteristics to become mammals, although whippers of those characteristics (oil droplets, scleral ossicles) can be found in monotremes, and some marsupials.

As a Class, birds have the best and most complicated visual system, at least for perception and acuity, but it is the turtle that has the most complicated retina. The Red-eared slider turtle, *Trachemys scripta elegans*, seen on the cover, has six different coloured oil droplets, and four different visual pigments (617 nm or "red;" 515 nm or "green;" 458 nm or "blue;" and 372 nm or "ultraviolet") included in a retina that has rods and both single and

double cones. Pigmented oil droplets act as long-pass filters to shift the effective sensitivity peak of the cone to a wavelength longer than the maximum of the visual pigment contained in the other segment. The droplets also narrow the spectral sensitivity function of the cone and reduce the overlap with adjacent spectral types. The oil droplets are optically dense, and essentially no light of a shorter wavelength gets through the oil droplet, thus shifting the spectral sensitivity.

The Red-eared slider has (at least) seven different cone populations and one rod. The seven different cones include double cones with (1) "red" visual pigment in the principal cone combined with an orange oil droplet and (2) "red" visual pigment in the accessory cone with no oil droplet, single cones with (3) "red" visual pigment and either a red or an (4) orange oil droplet, (5) single cones with "green" visual pigment and either orange or yellow oil droplets, single cones with (6) "blue" visual pigment combined with an oil droplet that absorbs ultraviolet, and a cone that has an (7) "ultraviolet" pigment with a colorless oil droplet (Loew *et al. Vis Neurosci* 2001;18:753). Turtles, however, share other morphologic features with birds. Both turtles and birds have double cones that are photoreceptors that are electrically and optically coupled. These paired cones probably assist both birds and turtles in motion detection and discrimination. This intricate and complicated retina has no rival in the animal kingdom outside of the class, Aves.

The visual system of turtles, then, is surprisingly similar to birds despite the marked difference in ecological niche, habitat and foraging methods of these creatures. These striking similarities are so specialised that they almost certainly came from the same stem organism, and roughly at the same time. Other radiations such as true reptiles, crocodiles, and mammals for example, simply do not have all these characteristics.

The turtle may indeed see its way out of its shell.

I R Schwab

University of California, Davis, Sacramento, CA, USA; irschwab@ucdavis.edu