COVER ILLUSTRATION

An eye for the land

Tetrapods gained ground in the late Devonian period, over 360 million years ago (mya), a profound advance requiring major changes in anatomy and physiology. Early tetrapods remained partially aquatic and fettered to water, but other terrestrial niches would beckon requiring dissolution of those bonds.

The first lizard appeared approximately 350 mya in the early Carboniferous period but this creature did not resemble modern lizards. This stem organism would give rise to several classes including Squamata, the class that would beget modern lizards and snakes. Terrestrial freedom permitted radiation into a brighter and more defined environment, and the visual system would have to respond to this challenge.

Basiliscus galeritus, pictured on the cover, represents the lizards and the complexity of their lifestyle. This mostly carnivorous reptile must accomplish visually complex tasks as it is a diurnal predator of invertebrates and other vertebrates. It also illustrates the visual imperative placed upon lizards as they became terrestrial.

In Greek legend, the basilisk is the king of serpents. According to most versions of the legend, the basilisk was a huge lizard endowed with a crest or crown, poisonous breath and a baleful gaze that could kill. In real life, however, the real basilisk, shares only the crest with its mythical namesake. Undoubtedly, the legend arose before Europeans knew about the living animal, but there is nearly a mythical quality about the real basilisk, a quality that is almost as good as the legend. This animal can walk on water.

The physics are understood but are complicated. *B. galeritus* will "slap" the water with its foot. Each of its five toes has a fringe that is extended as the foot strikes the water, almost like a webbed foot. This increases the surface area of the footpad. As the foot enters the water, it creates a pocket of air around it adding to the thrust generated by the impact. The clever reptile closes the fringes and extracts its foot before the water can close around it and create drag (Glasheen JW, McMahon TA. *Nature* 1996;380:340–2). A robust and complicated ecological niche, such as the one filled by *B. galeritus*, would require changes to the visual system of the semiaquatic tetrapods. Although it is not clear when these changes occurred, the demands of a completely terrestrial lifestyle suggest that these

Photomicrograph of the conus papillaris of an adult gecko (courtesy of the Veterinary Ophthalmology Service, University of California, Davis, California, USA).

changes would have occurred early in the transition from water to land.

Evolutionarily, the nictitans or "third eyelid" appeared for the first time in the reptiles, presumably to protect and moisten the terrestrial cornea. An oily secretion is produced by the Harderian gland in the ventromedial orbit and is spread over the corneal surface by the nictitans.

As a semiaquatic, semiterrestrial life was realised, the amphibian cornea became smoother and steeper to assist refraction and image quality, but accommodation remained piscine (*British Journal of Ophthalmology* October 2004). Evolutionarily, though, the lens would move posteriorly in the globe to enlarge the image, and the method of accommodation would change as well.

The ciliary processes lengthened and fused to the lens capsule, permitting rapid lens deformation. Lens deformation, as an accommodative mechanism, first appeared in lizards; this mechanism is found only in mammals, birds and reptiles, the latter two doing so by squeezing the lens. At the same time, other anatomical demands were being made on the evolving globe as the retina thickened and visual processing became more complex.

All diurnal lizards, including *B. galeritus*, have a fovea centralis, and a thicker retina than most fish and amphibians. Some lizards are nocturnal, but most are diurnal and have a cone-dominated retina often with four visual pigments. Most diurnal reptiles have single and double cones with oil droplets. The retinal anatomy reveals a thick, complex retina with well-defined layering that nearly

matches the complexity of that found in birds. Evolutionarily, as the retina thickened and became more complex, visual processing also improved. These changes would demand improved retinal nutrition.

Many teleosts (bony fish) have a falciform process that projects into the vitreous cavity through the fetal fissure. The falciform process is a melanotic vascularised choroidal projection that provides nutrition to the inner retina and probably to the retractor lentis muscle, as well. Some teleosts, however, do not have this falciform process. Instead, they have developed a membrana vasculosa retinae; a dense, preretinal, vascular plexus distributed over the surface of the retina. In almost all fish, these vessels do not penetrate the retina. This vascular morphology apparently has been passed on to the anurans, as frogs exhibit this form of preretinal vascularisation as well. In the teleosts and the anurans, these vessels are derived solely from the hyaloid system. By contrast, the lizards have evolved the conus papillaris, which resembles the falciform process and is homologous to the pecten in birds. Like the falciform process, the conus papillaris and pecten are richly vascularised mesodermal protrusions into the vitreous cavity. However, the conus papillaris and the pecten also have an ectodermally derived outer layer of melanotic cells. Therefore, although the falciform process and membrana vasculosa retinae are analogous to the conus papillaris and pecten, they are not homologous with them, suggesting that the conus papillaris of lizards evolved separately from the membrana vasculosa retinae of frogs.

All of these ocular changes encouraged and empowered lizards to become the first completely terrestrial vertebrate species, only to have the basilisk walk on water.

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