COVER ILLUSTRATION

Bringing the eyes along

Vertebrates lumbered ashore in the Devonian period, perhaps 400 million years ago, using modified swim bladders as lungs. The creatures that crossed this Rubicon interface were probably part of the clade that includes the Dipnoan order, and some of these dipnoans are still with us. Although this order is not the oldest order of fish, it is ancient and has changed little since the Devonian period. Today, the extant dipnoans are represented by the lungfish, with three distinct genera on three of the remnants of Gondwana, including South America, Africa, and Australia. The most primitive representative of these three groups is the Australian species *Neoceratodus forsteri* (cover image), an animal has changed little over the last 100 million years, thus providing a window to primitive tetrapod vision.

Although *N forsteri* has been observed walking across land, much like a seal, it is unable to aestivate, or caulk itself in a mucous lined mud case during drought as its fellow genera in Africa and South America can. This primitive trait suggests it is closer to the last common ancestor that led to *Ichthyostega*, or the first terrestrial tetrapod. Therefore, *N forsteri* can teach us about the visual system that was first hauled ashore with the early tetrapods.

Resembling eels, these endemic Australian fish are stout, heavy bodied, powerful and aggressive omnivores. Electroreception and olfaction represent key sensory modalities to locate prey, with vision thought to have a supplemental role. Although its eyes do not provide stellar vision, there are unique ocular adaptations with implications for tetrapod descent. To feed, these fish have a sensory organ for electroreception, much like those in sharks, that permit discovery of hidden prey. Primarily, these fish feed in the muddy depths of brackish or freshwater rivers. Nevertheless, they do spend considerable time in slow moving pools, where clearer fresh water would allow better visibility and eyes would be of more use. Lungfish also regularly come to the river surface and breath air in times of increased activity, such as mating, or when the water becomes stagnant in dry periods.

Lungfish retinal whole mount. Note the red and yellow droplets and the large rods.

N forsteri's eye is small in relation to body size, illustrating the eye's relative importance to this animal. The fish and the eye grow together throughout life, and as it ages, the Australian lungfish actually adds photoreceptors to the peripheral retina, although the overall density of cones decreases. The photoreceptor diameter increases with age as well. Since all portions of the eye are growing, the focal length of the lens also increases, leading to an increase in spatial resolving power. The retina is thin, perhaps 150–190 μm , with no intraretinal vessels or vitreal vessels to nourish the inner retina.

N forsteri has eyes that are well adapted for the lower light levels of a benthic lifestyle and possess the largest vertebrate photoreceptors described to date, measuring as much as 21 μm in diameter. Remember that some birds have photoreceptors that are approximately 1 μm in diameter. The very large rods seen in *N forsteri* are similar to the astronomical "light bucket" telescopes that collect any and all stray photons, and would be useful in the low light environment of a muddy stream but would not afford much discrimination. Even the cones in this lungfish are larger, with diameters up to 14 μm . So, to maximise photon capture, this lungfish evolved very large photoreceptors and a tapetum (BJO cover, May 2005), which creates a pinkish reflex. Since vision is probably not a principal mechanism of prey detection and since these animals will eat anything, good discrimination may not be a high priority. Vision is used as an adjunct to olfaction and electroreception.

There are at least four cone types in the lungfish retina; three cone types with an oil droplet (BJO cover, May 2004) and one with a yellow myoid pigment (Bailes *et al*, *Comp Neurol* 2006; 494:381). Phylogenetically, this is the earliest known fish to have coloured oil droplets. One oil droplet is brightly coloured (red) with the two other types of droplets being colourless. All intracellular inclusions are situated in the inner segment of the cone. Most fish do not have oil droplets, although these droplets are commonly seen in amphibians, turtles, and birds. Although the rods in *N forsteri* do not have an oil droplet, other members of the dipnoan clade do, so it is suspected that once split from the other dipnoans, *N forsteri* lost the rod droplet.

In birds, oil droplets function as high pass filters, as they absorb wavelengths below a certain value to limit the spectral range transmitted to the outer segments containing the visual pigments and control the spectrum of light that initiates a response. As a result, coloured oil droplets help colour vision by increasing the amount of visible colours, suggesting colour vision is important to lungfish in addition to high sensitivity.

Photoreceptor morphology in the dipnoans is closer to that of urodele amphibians (those that retain their tails into adulthood, such as newts and salamanders) than it is to most fish. This is further evidence that the dipnoans are part of the piscine clade that eventually led to the tetrapods that first walked the earth.

So, that first tetrapod, believed to be *Ichthyostega* using its ancillary lungs, may have brought one very large rod and at least four large cones, ashore in the Devonian period. The stage was set for terrestrial development and evolution.

I R Schwab

University of California Davis, 4860 Y Street,
Suite 2400, Sacramento, CA 95817, USA;
irschwab@ucdavis

S Collin

The Vision, Touch, and Hearing Centre, the
School of Biomedical Sciences, University of
Queensland, Brisbane Australia

H Bailes

Faculty of Life Sciences, University of
Manchester, Manchester, UK

Images by Shaun Collin.