COVER ILLUSTRATION

Are you calling me primitive?

Lampreys are animals without bones or jaws, and yet they are prototype vertebrates. Related to hagfishes, the lampreys are cartilaginous fish with sucker-like mouths and are 550–450 million years old. These two groups comprise the agnathans and are reminiscent of *Pikaia gracilens*, the Cambrian fossil believed to be close to the first vertebrate. Despite lampreys and hagfish lacking bone and tooth enamel or other hard parts, they are still surprisingly well preserved in the fossil record. However, as a result of a paucity of fossils, the phylogeny of these groups is controversial and incomplete. Current evolutionary evidence suggests that hagfishes preceded the lampreys, with all three extant lamprey families coming from a common ancestor. The southern lamprey, *Geotria australis*, spends the first 4–5 years of its life in freshwater streams of southern hemisphere lands including Australia, New Zealand, South Africa, and South America. During this time, its eyes are only poorly developed. Although usually thought of as parasites, lampreys actually begin life as filter feeders, feasting mainly on detritus and unicellular algae. During metamorphosis into the pelagic stage, which takes 6 months, the lamprey's eyes enlarge and develop the visual pigments necessary for managing its impending pelagic lifestyle. In the second stage of its life, the lamprey descends into the Southern Ocean, where it attaches onto the flanks of other fish. It uses its sucker mouth and rasp-like teeth, illustrated on the right of this month's cover, to attach and tear into the body tissues to feed on muscle. After approximately 2 years of this predatory life, it leaves the ocean and swims back into freshwater streams to spawn. This journey can take up to 18 months and, during this time, the lamprey does not feed. Like salmon, lampreys are anadromous and return to fresh water from the sea to spawn, lay eggs, and die. Once spawning takes place by the female, the eggs are fertilised by the male, and both die.

Although depauperate (lacking in species variety), lampreys occur in three families with one family found only in the northern hemisphere and the other two families found only in the southern hemisphere. All three extant lamprey families have probably changed little during the past 280 million years, and illustrate just how ancient the basic mechanisms of much of our visual system are likely to be.

Evolutionarily, recent molecular research suggests that the most recent common ancestor of the agnathans possessed four of the five major classes of the visual pigments found in the radiation of gnathostome vertebrates. *Geotria australis*, pictured on the left of the cover and this page, has a pure cone retina with five visual pigments, three of which are orthologous to opsins found in jawed vertebrates. These three common cone opsins have peak sensitivities in the long wavelengths (red), short wavelengths (blue), and very short wavelengths (ultraviolet). A fourth cone opsin with a peak sensitivity in the medium wavelengths (green) underwent an independent gene duplication within the jawless (lampreys and hagfishes) and jawed (all others) fish, leading to two different cone opsins) in *G australis*, and a different cone opsin in addition to a rod opsin in the jawed fishes (Collin SP *et al*, *Curr Biol* 2003;**13**:R864–5).

This molecular research has several profound implications. Importantly, rods and rhodopsin are relative latecomers to the visual party as they probably did not appear until at least the mid or late Cambrian (approximately 500 million years ago). This actually makes sense, since an opsin with a peak in the short wavelengths (blue) was probably the first visual pigment (bacteriorhodopsin) and probably appeared with very early prokaryotes.

Surprisingly, this is not the only unusual feature of the eye of *G australis*. The lens is asymmetrical with an increased anterior to posterior diameter as a result of a small posterior protrusion of lens material, much as if it were posterior lenticonus. This pyriform lens is multifocal although its function is not understood. The central visual axis and more dorsal retina are moderately to highly myopic and the more peripheral and ventral retina would be hyperopic (Collin SP *et al*, *Brain Behav Evol* 1999;**54**:96–118). Since *G australis* is preyed upon by albatrosses during the epipelagic phase, a predation that comes from above, the ventral retina may be useful for avoiding predation.

The only other family of southern lamprey is *Mordaciidae*. These animals are nocturnal and have lost the variation in visual pigment and photoreceptor type. They have a single large photoreceptor which is much more rod-like, while still retaining some cone characteristics, suggesting that this family has traded diurnal vision for nocturnal vision. As might be expected, the *Mordaciidae* species has a tapetum to maximise photon capture, helping further with their nocturnal lifestyle (Collin SP *et al*, *Brain Behav Evol* 2000;**55**:120–38).

G australis are survivors indeed, with five visual pigments in its retina, a bizarre lifestyle, and an unusual eye. Perhaps they aren't so primitive, after all.

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