COVER ILLUSTRATION

More than black and white

Evolution has discovered interesting shapes and colours to fill the potential niches of the earth, and rays are one of the most creative examples. *Taeniura lymma*, the blue spotted fantail ray, is a member of the *Dasyatidae* family of stingrays. Although it harbours a potential sting for the unwary, this shy ray will only use it in defence. It lives in the shallow waters of tropical reefs throughout much of the world, including the western Pacific, and represents a taxon that has much to teach us about evolution and especially about vision.

Rays have a truly aquatic, piscine eye (*BJO* cover, October 2004), although there are differences in ocular morphology since the elasmobranchs (sharks, skates, and rays) diverged from the bony fish (teleosts) long ago. In contrast to teleosts, which have fixed pupils, rays, and most other elasmobranchs, with the exception of deep sea species, have highly mobile pupils. *T. lymma* displays a conventional round pupil in scotopic conditions but a rather oddly shaped pupil under photopic conditions, as can be seen on this month's cover. There is a flap, known as the operculum pupillare, protruding from the dorsal pupillary border that covers almost the entire pupillary aperture. As the operculum extends in response to strong illumination, it creates a crescent-shaped pupil, eventually leading to two small slit-like openings rostrally and caudally. As well as dramatically limiting the influx of light, multiple pupils may create a rangefinder effect as the images from the two pupils will come to focus on the retina from only one point in the surround, a manifestation of the Scheiner's disc principle (*BJO* cover, November 2000). Pupillary shape in this taxon is extremely varied, ranging from multiple pupillary apertures in some skates and rays to vertical or diagonal slit-shaped pupils in sharks.

Accommodation is not accomplished by lens deformation, as in birds and mammals, but rather with a protractor lentis muscle that pulls the lens away from the retina. This is in contradistinction to the retractor lentis muscle of teleosts, and represents a basic functional difference between these eyes: teleosts accommodate for distance vision, whereas elasmobranchs accommodate for near vision.

Pupil of the long snout shovelnose ray

Although the crystalline lens is basically spherical, some rays have asymmetrical lenses to focus the image properly on a "ramped" retina, which is a conceptual and morphological oddity. A ramped retina means that the posterior segment of the eye is not curved in a semicircle like that of half an orange, but rather like that of half a pear, almost as if the dorsal portion of the asymmetric eye is stretched upward. This means that portions of the dorsal retina are further from the lens than portions of the ventral retina, which has a more circular curvature. The dorsal retina will image the inferior field and is, in essence, myopic for the inferior field by being further away from the nodal point of the lens. Although not unique to elasmobranchs, the ramped retina will allow for simultaneous focus of distance and near—a multifocal retina.

Rays probably do not have good acuity compared to humans, although many have a horizontal visual streak with a concentration of ganglion cells that provides improved spatial vision. Visual acuity measurements have not been performed, and would probably be difficult to determine behaviourally.

The phylogeny of elasmobranchs has vanished in the murky, muddy waters of the Ordovician (about 500 million years ago) or Silurian (about 430 million years ago) eras. Nevertheless, cartilaginous fish, which include all elasmobranchs, are thought to have diverged from teleosts very early. The extinct, last common ancestor of teleosts and elasmobranchs is, therefore, important to our understanding of the evolution of vertebrate vision, as it was probably the first creature to develop, as a distinct type of retinal photoreceptor, what we regard as classic rods.

Indeed, the elasmobranchs are probably the oldest extant taxon with rods as part of their visual system. Vertebrate visual pigment opsin protein genes radiated into at least five distinct spectral classes in the jawless lampreys more than 500 million years ago. One of those opsins developed into the rod opsin found in most vertebrates, but not in lampreys, which underwent a distinct gene duplication event (*BJO* cover, December 2005). Since both teleosts and elasmobranchs have the opsin genes found in the remaining vertebrate classes, their last common ancestor was probably the locus of this transformation. The first appearance of rods in elasmobranchs, or at least in their common ancestor, was probably an adaptation by these early predatory fish to catch more photons of light and enhance visual sensitivity in order to explore the deeper, muddy waters of the forming seas. Much of this is deductive reasoning, but is a logical conclusion to the available data. Modern elasmobranchs probably retain more characteristics of this last common ancestor (such as cartilage), hence are closer phylogenetically. And yet, we know that many of the rays, particularly those inhabiting shallow reef or coastal waters, such as *T. lymma*, have three spectrally different cones as well as the rod pigment (Hart *et al*, *J Exp Biol* 2004;207:4587–94). It is quite likely, then, that trichromacy, scotopic and photopic vision, as we know it in fish, reptiles, and some mammals, was already evolving in the Ordovician period 500 million years ago.

So, although elasmobranchs were previously considered not to have colour vision or even cone photoreceptors, it would appear that some may even have trichromacy and, furthermore, are an important step in the evolution of scotopic vision in vertebrates.

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