COVER ILLUSTRATION

A notch in time

Native to the Indo-Pacific coral reefs, the alluring Korean angelfish (*Pomacanthus semicirculatus*) captivates us with its colourful designs and surprises us with its natural history. As the juvenile angelfish (seen on the cover) matures, its coloration will change to that of an adult so different in coloration that it was considered a different species before its natural history was understood. Angelfish prey on benthic invertebrates and perhaps some sponges, but both hunting its prey and avoidance of its own predators requires good vision. As a result, these rather intelligent reef fish have very interesting visual systems.

These generally predatorial fish require binocularity especially in their sometimes monotonous, three dimensional blue world. Most fish, including the angelfish, have their eyes positioned on the sides of their heads, making stereopsis difficult. Through subtle adaptations and countless generations, these successful fish have solved this problem in a most peculiar manner.

The fish eye probably originated approximately 450 million years ago just before the Devonian period, but truly came into its own during the Devonian. The vertebrate eye probably had its humble beginnings in the Cambrian (about 550–490 million years ago) in a creature known as *Pikaia gracilens* as, more or less, an eyespot. In the subsequent 20–50 million years, this protochordate fish gradually gave rise to the vertebrate eye in a primitive fish first seen during the Ordovician period. The successful piscine model has had numerous refinements replete with creative and sometimes bizarre solutions to the challenges of survival but the globe probably had its origins in the simple eyespots of *Pikaia*.

The Korean angelfish has an excellent eye and it serves as a model for the fish eye in general. The cornea is flat and since it has virtually the same index of refraction as water, most fish do not use it for refraction. The lenses in this fish, and most others are almost completely round, as can be seen in the photograph at the top of the cover. These spherical lenses protrude through the pupil nearly to touch the cornea, and are responsible for almost all of the refraction in the piscine eye. The camera-style eye is lined with a retina similar to ours with a falciform process that extends into the vitreous from the optic nerve (fig 1). The falciform process extends inferiorly and anteriorly nearly to touch the lens, along what would be the equivalent of the fetal fissure in humans. This falciform process is essential for retinal nutrition and as an origination site for the muscles of accommodation.

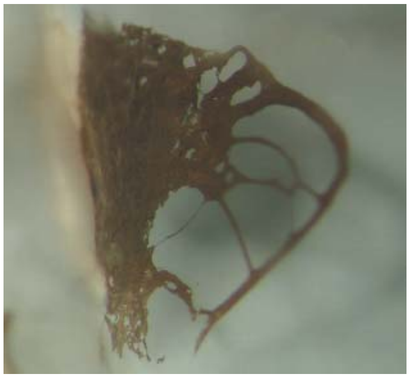

Figure 1 The falciform process.

Lenticular accommodation in teleost fish is not accomplished by lens deformation as it is in most terrestrial vertebrates. Rather, accommodation is accomplished by contraction of the retractor lentis which may be one or two separate muscles. In almost all fish, this muscle originates either at the distal end of the falciform process or at the ventral pars plana analogue and inserts into the periphery of the lens capsule. In some teleost fish, when the muscle contracts, the lens is retracted towards the retina with both an axial and nasal component. The muscle can be found in most fish extending from the falciform process to the inferior pole of the lens. On the opposite superior pole the lens is suspended from the pars plana, and it is this combination that allows the lens to be retracted posteriorly for accommodation.

The cover images of the Korean angelfish reveal other interesting adaptations allowing for binocularity. The image at the bottom shows a pyriform-shaped pupil with the narrower portion of the pupil directed rostrally. A close look at the photograph will reveal an edge of the lens visible within that pupil. The space anterior to the edge of the lens has no focusing element and is called the aphakic space. The image at the top illustrates how the fish uses this aphakic space to help it achieve stereopsis.

A most interesting retinal adaptation explains this aphakic space. Since fish began as torpedo-shaped animals with their eyes on either side of their head, those that would be predators had to achieve binocularity within those design limitations. These predatorial fish evolved a very temporal fovea near the ora, much like the kingfisher (May 2004 cover, *BJO*). When the Korean angelfish finds a prey species, it will rotate the eyes into the most forward position possible. The image will traverse the anterior notch in the pupil, through the lens, and strike the temporal foveae in both eyes, allowing binocularity. The edge of a circular pupil would interfere with that transmission. So, while it appears that the lens and the aphakic space will create a focused and adjacent unfocused image, respectively, on the retina in the usual anterior-posterior model we consider for an eye, the space actually allows for the fish to achieve binocularity.

The fish eye will grow throughout life, and a larger fish will have a larger eye even among the same species. If the retina and temporal fovea is not to be ''grown'' out of position by the enlarging globe, the retina must continue to grow. Indeed, that is exactly what happens. There are retinal stem cells at the periphery of the retina that continually make new photoreceptors in a programmed fashion to match the growth of the eye, thus allowing the fovea to remain in the same place topographically.

Retinal stem cells and a pupillary notch in fish illustrate evolution's alternative solutions to pre-existing design limitations.

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Photographs by the author.

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