Cover illustration

Look before you leap

The African butterfly fish, *Pantodon buchholzi*, is the sole member of the family *Pantodontidae* and is found only in west Africa. This fish has been described as a fresh water flying fish because it leaps out of the water as an escape behaviour. It has a bizarre appearance for a fish, with distinctive dorsal and anal fins that act almost like vertical stabilisers. Its lateral or pectoral fins are especially wide, like butterfly wings, as can be seen on the cover of this month's *BJO*. Although it is a strong leaper and may jump to a height well beyond its body length, it does not "fly" in the same manner as the pelagic species of the genera *Cypselurus* or *Exocoelus*.

Ecologically, it occupies a highly specialised visual niche just below the water's surface. *Pantodon* is an obligate surface feeder and will prey upon insects and other creatures which it sees on or above the water line but rarely, if ever, feeds in the water column. It must simultaneously see into the air and water and yet it lives just beneath the surface. To succeed in its niche, this tropical novelty has evolved a most peculiar eye with a set of intriguing adaptations that are reflected in its visual pathways.

Pantodon is a strong leaper and will actually soar out of the water to seize its prey. But, it apparently has not developed a consistent mechanism to neutralise the refraction at the water's surface as it cannot always accurately target its prey above the water's surface.

Pantodon's eyes are most unusual and have adapted for simultaneous vision in air and water. A falciform process, composed of heavily pigmented epithelial cells, extends from the optic nerve to the posterior capsule of the crystalline lens (as seen in Fig 1). This pigmented shelf divides the eye horizontally and delimits the dorsal and ventral retinas. The ventral retina subserves aerial vision and has its own separate nucleus to which it sends fibres. The dorsal retina subserves aquatic vision. Functionally, the falciform process prevents intraocular light scatter particularly from the intense aerial light that could otherwise dazzle the dorsal retina.

Study of the geometric organisation of the retina reveals that the photoreceptors in both the dorsal and ventral retinas are directed simultaneously along independent optic axes. Cones in both retinas are directed towards the pupillary aperture to exploit the Stiles-Crawford effect of the first kind. This property permits each photoreceptor to maximise the wave guide optics effect of its anatomy. Cones in the ventral retina are narrower than those in the dorsal portion of the eye suggesting improved aerial acuity compared to aquatic acuity (Saidel WM, *Phil Trans R Soc Lond B* 2000;**355**:1177). This characteristic difference in cone size reflects an evolutionary adaptation within one portion of the retina to the different physical constraints of image formation in air and water.

Figure 1 Section of the eye of *Pantodon*. Note the falciform process and thinner ventral photoreceptors. Histology by Thomas Blankenship, PhD.

Figure 2 Side view of *Pantodon*. Photograph by William Saidel, PhD.

But, the neural connections of the ventral retina are the most interesting. Saidel and Butler have traced the fibres from the ventral retina to a distinctive diencephalic nucleus called the nucleus rostrolateralis or NRL (Saidel WM, Butler AB, *Cell Tissue Res* 1997;**287**:91). As an aerial or surface target is presented to one eye, the information is conveyed to two separate areas in the brain, the optic tectum and the NRL. These two areas and their complex neurological connections make up part of a "feeding circuit" to include identification and acquisition of prey. This circuit is relatively unknown, and otherwise unrecognised in vertebrates, although it has been found in a few other unrelated teleost species. Interestingly, one of these species is *Anableps anableps*, the so called four eyed fish of central America featured on the September 2002 *BJO* cover. *Anableps* must also be able to interpret simultaneous vision above and below the water line.

Pantodon's eye and visual system have evolved to the niche it fills and are closely tied to its behaviour. The ventral retina and visual pathway are primarily designed for feeding; and the dorsal retina and its visual pathway are primarily for predator recognition and avoidance. Curiously, the dorsal, but not the ventral, visual pathway has an optomotor response (akin to the mammalian optokinetic nystagmus). The previously mentioned *Anableps* has a similar optomotor response, although seen in the ventral but not the dorsal retina.

There is still more to the story. Most teleost species, including *Pantodon*, have a lateral line, a set of sensitive hair cells similar to those in the mammalian cochlea. These cells are supreme mechanoreceptors, sensing vibrations and bioelectric currents. The wave action induced by the movements of an insect on the surface is sensed by the lateral line system of *Pantodon*. Much like pit vipers integrate infrared and visual stimuli, as discussed in the December 2002 *BJO*, the input of the lateral line is integrated with the visual input at the level of the optic tectum. So, this marvellous fish actually "sees" with its lateral line.

Pantodon, then, must look very carefully before it leaps.

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Photograph of *Pantodon buchholzi* by William Saidel, PhD.