

# Cover illustration

## Janus on the mudflats

An amphibious fish, *Periophthalmus argentilineatus* is a mudskipper that spends most of its time on the mudflats of the tropical mangrove swamps of Africa, Asia, and Polynesia. It uses its stiff fins like walking sticks to perambulate with surprising speed and agility in the intertidal zone, seeking insects and small aquatic organisms. These remarkable fish actually spend nearly all of their time out of water on an exposed mudflat. A member of the goby family, this species can reach up to 12 cm at maturity and, although epipelagic, occurs exclusively on mudflats and mangrove swamps.

Its eyes can be raised and lowered, much like a genuine periscope. This remarkable task is accomplished by the use of a hammock-like structure composed of the inferior oblique and inferior rectus muscles. These muscles are stiffened in concert to elevate the globes. Conversely, when these retractile eyes are drawn closer to the body for protection, they are covered by puckered folds of skin.

When out of water, the eyes of mudskippers are able to focus in air because of powerful and rapid accommodation using a round piscine lens. The iris has a functional sphincter, but insufficient, if any, dilator musculature. Consequently, pupillary activity is limited, but constriction can occur, as seen on the cover. The sphincter is important because it probably has a role in accommodation. The lens is strongly retracted in accommodation and is piscine-like, which means the lens is accommodated for distance. The lens is quite rounded and serves to provide emmetropia for the fish during aquatic forays. When the eye is unaccommodated and used for near vision, the lens protrudes substantially through the pupil. The cornea is steeply curved, much more like that of a terrestrial vertebrate than a fish. The retina is populated almost exclusively by cones, at least in the inferior half. The cone rich retina gradually changes to more numerous rods in the superior half of the retina, but the cones still represent 80% of the photoreceptors. In the extreme superior periphery, there is a strip of pure rods. Although the visual acuity has not been measured, the predominantly cone

retina has been found to contain 225 000 photoreceptors and 90 000 ganglion cells per mm<sup>2</sup>. This is a substantially greater number than is found in many predatory fish. This retina will also allow diurnal feeding as the fish will not be dazzled by the excess light of the mudflat. With such a retina, though, the fish is limited at night and will then tend to seek its shallow burrow in sand. The retinal pigment epithelium is thick and pigment rich, presumably to protect its photoreceptors from the constant light exposure as this fish has no true lids. If the fish looks down below its body, as it might in water, a flap of skin forms a pseudolid, but the fish never truly blinks. These mudskippers wet their corneas by retracting the globe beneath these pseudolids, bringing their globes level with the horizontal axis of the body.



Fin prints of *Periophthalmus*.

Ocular motility in *Periophthalmus* is enviable as the fish has stalked eyes and still has the ability to move the eyes in all directions as if on a turret. Even though the eyes are stalked, the direction of gaze can be directly inferior because of this turreted ability. Eye position can vary from frontally placed that permits perhaps 10–15° stereopsis to completely back to back to apposition creating two 180° fields on each side of the fish as well as above and below the fish. This helps overcome the lack of head motility that most terrestrial vertebrates enjoy by using their necks. Although the innervation of the six extraocular muscles of each eye has not been studied, the inferior oblique and inferior rectus muscles are probably innervated by the third nerve and probably have similar actions.

In humans, only extorsion is shared by these two muscles, but in this mudskipper, globe elevation must also be a function.

The mudskipper uses its modified pectoral fins to allow “walking” to chase crustacea and insects. These fins act as levers and are provided with special anterior and posterior muscles. Tracks of the fish “fin prints” can be seen in the figure on this page.

Mudskippers consist of four genera, *Periophthalmus*, *Periophthalmodon*, *Boleophthalmus*, and *Scartelaos*, and each fish will occupy several burrow systems within a 2–3 m<sup>2</sup> area as a home range. This carnivorous fish will forage and return to its burrow with captured prey often including various species of crustacea, polychaetes, insects and flies, depending on whether the tide is spring, neap, or in flood. They conduct most of their lives and daily routines on land including hunting, courtship, and territorial defence. They excavate their burrows, which may be up to 60 cm deep, quite a challenge for an animal that is no more than 12 cm itself. They retreat to them for eating and for protection from predators. The burrows are also a nursery for developing eggs.

These nimble fish scurry across the mudflats to secure their prey, but they risk predation, and must have both good camouflage and the safety of a local burrow.

Janus, a mythological Roman solar deity, may have been a mudskipper, or surely the masthead for the species. Janus was a doorkeeper of heaven and the patron of the beginning and end of events. Similar to mudskippers, Janus had two faces, one for the rising sun and one for the setting sun. Mudskippers do it a bit differently. Like Janus, this remarkable fish greets an ebb tide with eyes elevated and breathing air by using its skin as an accessory respiratory organ as it prowls the mudflats, but with the flood tide it lowers its eyes and settles into its burrow to respire in water using gills just like any other fish. And you thought that extraocular muscles were only for ocular motility.

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Photograph by the author.



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