Biological Sciences review

Mudskippers

Blinking fishes out of water

Kevin Moffat explores why the mudskipper has become a model organism for studying the transitioning of animals on to land

What is a mudskipper?

You do not expect to see a fish run away from water, but mudskippers are no ordinary fish. A team for the BBC's *Asia* series spent 2 months studying mudskippers. While watching these enigmatic occupants of the Indonesian mudflats, they observed a range of behaviours. This included skipping on mud of course, but also skipping on water, walking, jumping, making burrows, scaling rocks and even climbing trees.

There are over 40 species of mudskipper, ranging in length from 4 cm to over 30 cm. They live an amphibious lifestyle, spending most of their time out of water. They are found in estuaries of the tropics and subtropics, across Africa, Asia, Australia and some Pacific islands (see Figure 1).

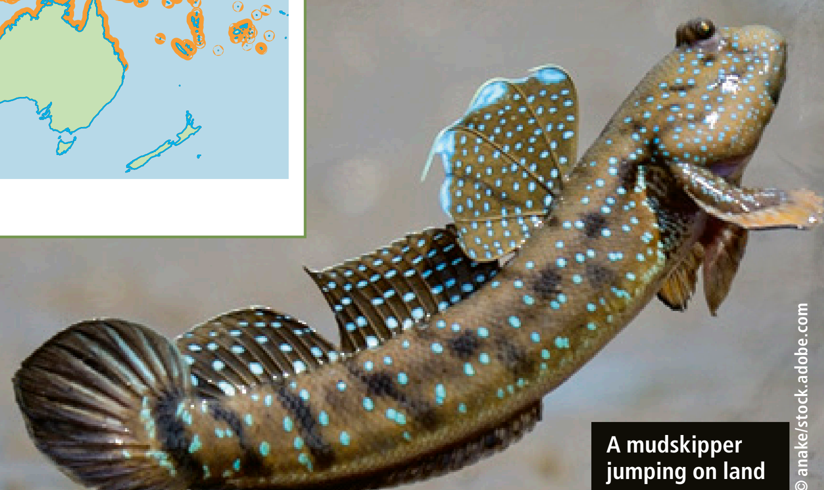
Figure 1 Mudskipper distribution (in orange)

Adaptations

Several adaptations allow mudskippers to inhabit their muddy niches:

- Prominent pectoral fins allow walking, skipping and burrowing.
- Protruding eyes enable land-based vision.
- A hydrodynamic tongue allows feeding by sucking up prey.

Their murky burrows fill with water at each tide and quickly become hypoxic (low O_2). Rolling in mud keeps mudskippers' skin, mouth compartment and gills constantly wet. With the advancing tide they typically 'run' away from the water to their burrows – gulping air bubbles as they skip. These bubbles allow gas exchange both in their gills and in their mouths – buccal breathing. This allows absorption of oxygen through the epithelia of their mouths and throat, and is enabled by dense **vascularisation**. Other adaptations deal with ammonia waste and high CO_2 levels, but it is their eyes that have commanded recent attention.



A mudskipper jumping on land

Eye evolution

Vertebrate eyes are considered to be evolutionarily expensive. Energy consumption for both developing and maintaining a visual system is 15–20% of the total energy cost to an organism. There is clearly a strong selective advantage to maintaining good vision both in water and on land. But how do animals deal with moving between these two environments?

You will appreciate the problem if you open your eyes underwater. Because of the density of water compared with air, our corneas refract light poorly and consequently our lens focuses the light behind the retina, giving a blurred image (see Figure 2). Just like humans, the visual adaptations seen in mudskippers for aerial vision lead to poor underwater vision.

The fossil record shows selection for larger eyes over evolutionary time. Larger eyes, larger pupils and therefore increased long-distance vision in air has thus evolved. The large eyes of mudskippers protrude from the top of their head. This enables excellent panoramic vision, which is good for hunting, predator avoidance and mate finding.

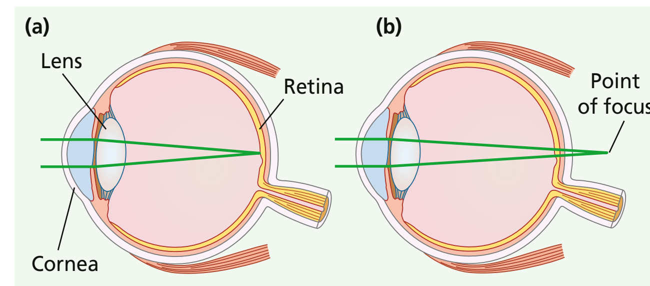


Figure 2 The human eye. (a) In air, the cornea contributes to light refraction. (b) In water, poor corneal refraction means the lens cannot focus on the retina. Green lines show the path of light

Blinking

Land-based animals must keep their eyes wet, clean and protected. This is achieved by blinking, through moving either the eyelid or a membrane across the eye. A lubrication film spread over the eye does more than just remove dust and irritants. In our own eyes, the fluid from the tear gland contains enzymes that kill bacteria, effectively protecting our eyes from infections.

Unlike mammals, mudskippers have no tear glands and no eyelids. They blink by sucking their eyes down into water-filled sockets. Evolutionary selection in this lineage has resulted in the repurposing of eye muscles and sockets for the lubrication essential for effective air vision. Mudskippers and terrestrial animals therefore demonstrate convergent evolution of blinking behaviours. This is consistent with the hypothesis that blinking is a required adaptation for animals to transition to the land.

Evolution of mudskippers

DNA analysis of extant (living) organisms, including lungfish and mudskippers, reveals shared mutations in genes required for terrestrial vision (see p. 14). Study of the adaptations of mudskippers demonstrates some fascinating examples of convergent evolution shared with lungfish, including an amphibious lifestyle, eye position, blinking, buccal breathing and modified pectoral fins. This highlights how similar environments and selective pressures can lead to similar adaptations in unrelated species.

Recent data suggest that at least two **clades** of mudskipper transitioned onto land independently. Their behaviours and molecular changes are similar. From this analysis, we now have a better understanding of the adaptations that have arisen to facilitate the 'conquering' of the land by animals.

Perhaps we now know why mudskippers run away from the water of the incoming tide – they need to keep air pockets in their burrows, to maintain available oxygen as they hide.

TERMS EXPLAINED

Clade A grouping of organisms containing the common ancestor and all its descendants.

Vascularisation The formation and growth of blood vessels in tissues.

RESOURCES

Filming mudskippers for the BBC:
https://tinyurl.com/BBC-mudskippers

Blinking in mudskippers:
https://tinyurl.com/blinking-mudskippers

Article on the evolution of terrestrial vision:
https://tinyurl.com/terrestrial-vision

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