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Evolution: Blinking through deep time

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Terrestrial vertebrates blink, but most aquatic vertebrates do not. How and why did blinking evolve? A recent study looks at this through the eyes of a mudskipper, fish that stay on land for long periods and blink.

As comfortable as we are as landlubbers, it's hard for us to appreciate the manifold changes that coming up on to land forced upon our ancestors around 375 million years ago. Some of these changes are evident in our bones, such as rib cages. Our need for these early in our life on land is not entirely clear, but one idea is that they helped keep our internal organs from being squashed while pushing the initially stubbily-limbed bodies of tetrapods over ground[1] — unnecessary in the neutral buoyancy of water. Others are evident in glands, such as salivary glands to lubricate food, as well as eye glands including the lacrimal (tears) and meibomian (oil to help prevent evaporation of tears) glands[2]. On land, objects that were near neutrally buoyant in water are a thousand times denser than the surrounding medium — not only are the internal organs pressed down, but so too are airborne particles, now raining down to foul all surfaces they meet. Those who wear eyeglasses live the consequent need for perpetual wiping.

Imagine the awkwardness of life in the absence of blinking — having to, say, spit on our shirt cuffs before using them to wipe the dust off our eyes. Incidentally, that's what our spineless, land-based cousins have to do. Praying mantises, for instance, dab their femoral brush with oral mucus before they start eye-grooming with their raptorial forelegs[3,4]. Similarly, the jumping spider *Portia*, a one-centimeter-long animal with the acuity of a cheetah[5], turns their paired mouthparts (pedipalps) into windshield wiper blades. While it's clear that blinking in terrestrial vertebrates has to respond to the rain of small visual occlusions on to their eyes, it's not the only function of the blink. Blinks also protect the eye and wet the cornea to aid the diffusion of oxygen into this unvascularized tissue. But when and how did blinking arise over evolutionary time? For example, the protective function of the blink is something that some chondrichthyan and teleost fishes accomplish through a form of eye retraction. It seems impossible to answer this question given the lack of fossilizable correlates of blinking. A creative approach was taken by Brett Aiello and colleagues[6] recently in a study of blinking in the mudskipper, a teleost which can spend the better part of a day out of water. Besides giving insights into blinking's origins, the authors show us what aspects of this behavior are constant despite very different starting points 425 million years ago when tetrapods and teleosts last shared a common ancestor.

First, using a clever set of experiments Aiello and colleagues[6] showed quantitative evidence that the mudskipper's blink fulfills the same functional roles as tetrapod blinking: protection, wetting and debris clearance. But while the mudskipper blink achieves the same ends, it is performed in an entirely different way from that of

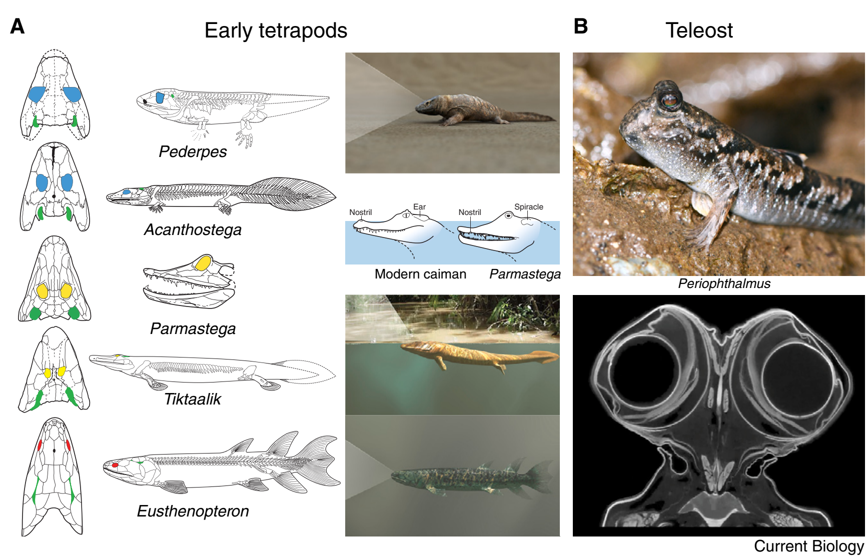

Figure 1. Eyes high on the skull in early tetrapods and for mudskippers.
(A) Some early tetrapods (from *Eusthenopteron* at ≈385 Mya to *Pederpes* at ≈348 Mya) showing progressive dorsalization of orbits, modified from[10]. (Image of caiman and *Parmastega* from[11], courtesy of Per Ahlberg.) Red orbits are finned tetrapods, yellow orbits are transitional tetrapods, and blue orbits are limbed tetrapods. Green indicates the spiracle, a breathing port (eustachian tube in humans). (B) Top: *Periophthalmus argentilineatus* (image courtesy of Christa Rohrbach). Note propping up with pectoral fins, perhaps the only avenue left for these limbless animals to get a better vantage point for their enhanced visual system, aided in this case by a bump on the substrate. Bottom: A cross-section of the mudskipper *Periophthalmus barbarus* (image from[6]). A person of a certain age could be excused for seeing a family resemblance between this image and an Earth-stranded extraterrestrial from an early '80s movie.

tetrapods. The authors found that, unlike the tetrapods with their multiple types of eye glands, mudskippers do not have any glands uniquely dedicated to wetting the eyes. Instead, they found that mudskippers execute a body roll on their typically wet substrates more often when conditions cause their eyes to dry more rapidly.

Then there is the motor pattern of mudskipper blinking. While tetrapods move an eyelid while keeping the eye steady, mudskippers flip that around, like brushing teeth by holding the brush steady while shaking your head. Rather than move an eyelid over a stationary eye, they move their eye down through the stationary head using their eye's *retractor bulbi* muscle. A stretchy and moist 'dermal cup' passively wipes the eye on retraction and again on release. Finally, spontaneous blinks in the mudskipper are slower than evoked blinks, as in tetrapods. All of this, as Aiello and colleagues[6] detail, is occurring with different muscles through different cranial nerves between fish and tetrapods. In the end, the mudskipper's eye is moistened, cleared and protected. Particularly neat is how they measured the effectiveness of the blink in clearing the eye of debris. They identified that dried brine shrimp eggs have about the same diameter as sand in the mudskipper's environment, and dusted these evenly on to the eye surface, measuring the fraction cleared on blinking.

Aiello and colleagues[6] take advantage of comparisons to the mudskipper's nearest relatives, other oxudercid fishes which do not come out of the water and do not blink. In addition, during their early, purely aquatic stage of life (prior to becoming amphibious) mudskippers also skip blinking. All of this points toward terrestrialization itself as the most likely driving force for the evolution of blinking. Convergently evolved features of blinking help us understand which of its features are essential and which are optional.

Parallels to the situation of tetrapods just as they started to transition on to land 385 million years ago are instructive. There is evidence that one early tetrapod, *Acanthostega gunnari*, had the same *retractor bulbi* muscle that mudskippers use to pull down their eye in performing their blink. Aiello and colleagues suggest that the blink mechanism seen in the mudskipper was also present at the base of the terrestrial tetrapod lineage[6]. But mudskippers also show signs of two other water-to-land transition adaptations related to vision that have been established in the early tetrapods. First, during the transition the eyes of tetrapods tripled in absolute size compared to ancestral fish, helping to achieve a 100-fold increase in visual range[7]. Similarly, there is preliminary evidence of increased eye size in mudskippers compared to purely aquatic oxudercids[8]. Second, as a fish begins to surface during the transition on to land, having eyes above water first likely had many advantages: monitoring the bank to find a good spot to get out of the water, looking over the water surface for signs of the ripples of a submerged predator, among others. But this requires that eyes migrate from their usual mediolateral positions on the sides of a typical fish's head to something further up on the skull. In the early tetrapods, the eyes migrated from their fish-like position on the sides of the skull to the top of the skull (Figure 1A)[7]. Similarly, the dorsalized eyes of mudskippers[9] (Figure 1B) could suggest similar selective benefits in this group of animals as in the early tetrapods.

Overall, the demands of living in a medium a thousand times less dense than water generates an intricate series of knock-on effects across many aspects of vertebrate life. Things formerly suspended in the water column now rain down upon your eyes. Suddenly light can come from very far away before being absorbed, instead of from just a few body lengths away in water. But taking advantage of this visual richness requires constant clearing of the eye, among other important roles of blinking, as well as related changes, such as larger eyes that are raised higher on the skull — whether or not you come to it as a fish or a tetrapod. Aiello and colleagues[6] give strong reasons to believe that it's the mudskipper's penchant for staying out of the water that led to blinking, and thus imply that the same is true for tetrapods. Furthermore, blinking is a behavior with a limited set of good solutions for the aerial eye. Combining careful quantification of extant analogs of a target behavior across several taxa together with their phylogenetic relationships presents the exciting prospect that the evolutionary origin of other behaviors may be inferred in the future.

DECLARATION OF INTERESTS

The author declares no competing interests.

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