NEWS & VIEWS

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EVOLUTIONARY DEVELOPMENTAL BIOLOGY

Dynasty of the plastic fish

Ambitious experimental and morphological studies of a modern fish show how developmental flexibility may have helped early 'fishapods' to make the transition from finned aquatic animals to tetrapods that walk on land.

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Napoleon Bonaparte's military excursions into Egypt in 1798–99 led a young French naturalist, Étienne Geoffroy Saint-Hilaire, to cross paths with a strange fish that had paired lungs and could 'walk' on land on its stubby, lobe-like fins. In 1802, he dubbed this fish "*Polyptère bichir*"[1], today known as the Nile bichir (*Polypterus bichir*). The bichir's melange of primitive and advanced traits helped to establish Geoffroy as a leading anatomist, embryologist and early evolutionary-development researcher of repute even today[2]. Now, in a paper published on *Nature*'s website, Standen *et al.*[3] focus on *Polypterus* in their own excursion under the 'evo-devo' flag that Geoffroy helped to raise. The authors suggest that the remarkable plasticity of the skeleton of *Polypterus senegalus* (the smaller West African relative of *P. bichir*) reveals a key part of the mechanism that might have facilitated the gradual transition of limbed vertebrates from water to land.

In a bold experiment, Standen and colleagues reared a group of bichirs on land for eight months and compared them with bichirs that had developed in their normal aquatic environment (Fig. 1). They then studied how the fish from the two groups moved on land, and how the shape of the skeletal elements of their paired front fin bases differed. They found that, compared with water-raised bichirs, the land-acclimated fish took faster steps, their fins 'slipped' across the substrate less frequently, they held their fins closer to their bodies, their noses stayed more aloft and their tails undulated less, with less-variable motions overall. These were behaviours that the authors had predicted should develop to enhance walking abilities on land.

Furthermore, the bones of the neck and shoulder region in the land-reared fish had altered in shape to produce a more mobile fin base with greater independence of motion between the fin and the neck, along with improved bracing of the ventral 'collarbone' region. These environmentally induced traits probably fostered the locomotor changes observed in the land-reared fish and helped the animals to resist gravity, thereby representing a common biological phenomenon termed developmental plasticity[4,5]. Surprisingly, the land-reared fish could swim just about as well as the aquatic cohort, so there was no clear trade-off between being a good swimmer and a good walker.

Considered alone, the developmental plasticity of bichir form and function shows how impressive these amphibious fish are. But Standen and colleagues ventured further, to apply the lessons learned from bichir ontogeny to a phylogenetic context and a macroevolutionary question.

The authors infer that the plasticity of bichir development could have been harnessed during the evolutionary transformation of fins used for swimming into limbs used for walking, in the 'fishapod' ancestors of tetrapods (four-limbed vertebrates). Indeed, bichirs are close to the base of the family tree of fishes[6], and other living relatives of tetrapods have reduced or no fins (for example, lungfishes), or are adapted to strange deep-sea swimming lifestyles, never walking on land (coelacanths). Therefore, perhaps bichirs and the fishapod lineage share what Geoffroy called 'unity of type', today termed homology, with regard to their developmental plasticity in response to a land environment. Surveying the fossil record of early fishapods and tetrapods, Standen *et al.* found that the macroevolutionary changes of neck and shoulder anatomy in these gradually land-adapted animals parallel changes that they observed in 'terrestrialized' *Polypterus*, providing support for this hypothesis.

Further testing of the relevance of *Polypterus*'s plasticity to tetrapod evolution is, of course, difficult. However, the fishapod lineage has some exceptional examples of fossil preservation, and a rigorous indirect test of this hypothesis might be possible if there are sufficient sample sizes (for example, from fossil beds that reveal specimens at different developmental stages, such as the Late Devonian Miguasha site in Canada[7]) and palaeoenvironmental gradients in fish or tetrapod habitats. Even small samples could be helpful. For example, the early tetrapod *Ichthyostega* exhibited some developmental changes in its forelimb suggesting that individuals became more terrestrial as they grew, whereas the related *Acanthostega* did not show such changes[8], hinting at developmental plasticity in the former animal.

Might it be that, during the Devonian period (around 360 million to 420 million years ago), the fishapod ancestors of tetrapods were intermittently floundering about on land, gradually shifting from anatomy and behaviours that were more developmentally plastic (as in bichirs) to ones that were more canalized into the forms and functions of land-adapted tetrapods? We don't know, but Standen and colleagues suggest that the developmental plasticity could have led to fixation (reduction of plasticity). This is an example of a proposed evolutionary phenomenon called

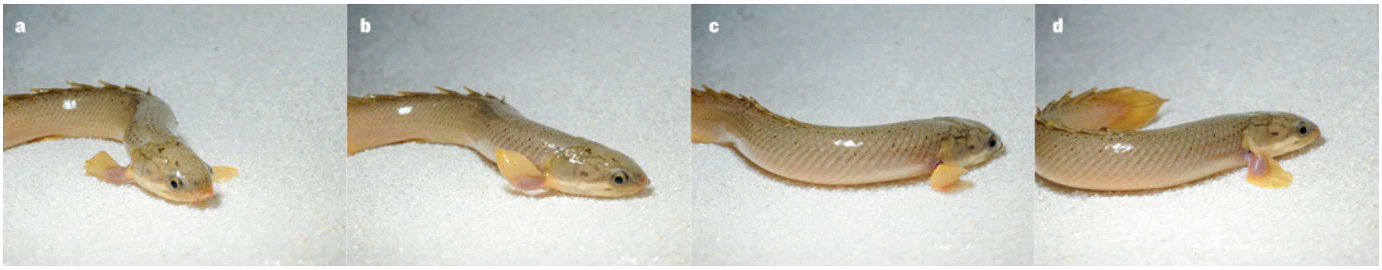

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Figure 1 | Walk this way. The typical walking sequence of *Polypterus bichir* on land. **a**, The fish plants its left fin while its right fin swings forward; **b**, **c**, the head and tail turn towards the left fin; **d**, finally, the right fin is planted on the ground as the left is raised.

genetic assimilation — a concept promoted by Conrad Hal Waddington, an intellectual descendant of Geoffroy, from the 1950s onwards[9]. There is some empirical support for this idea[10], and the findings in bichirs may eventually add to it.

The nature of the genetic and developmental mechanisms by which bichirs achieve developmental plasticity is unclear. If the plasticity is sufficiently heritable, then it might be selected for in multi-generational experiments, such that (with enough time and luck raising these unusual fish) we could directly test the hypothesis that the animals' plastic response to a terrestrial environment can become genetically assimilated. Such a study could thus become an exemplar of how genetic assimilation can contribute not only to microevolutionary change, but also to macroevolutionary events, as has been previously suggested[4].

Geoffroy would probably have applauded Standen and colleagues' study of developmental plasticity, all the more for involving his beloved bichirs. Much as Napoleon's landfall in Egypt was not a lasting success, bichirs never produced wholly terrestrial descendants, despite their malleable locomotor system. But the same type of plastic developmental mechanism that bichirs use today to make tentative, floppy incursions of the terrestrial realm might have been harnessed by our own fishapod forebears, leaving a much more revolutionary dynasty on Earth. ■

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