

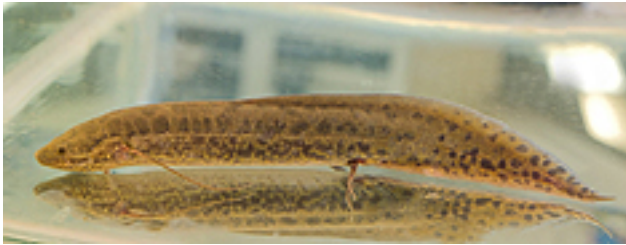
Ancient fish use thin limbs to walk and lift body, important steps for terrestriality

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<http://bcove.me/8t1slsf4>

[View video of the African lungfish using its thin pelvic limbs to lift its body off the bottom surface to propel itself forward.]

The eel-like body and scrawny "limbs" of the African lungfish would appear to make it an unlikely innovator for locomotion. But its improbable walking behavior, newly described by University of Chicago scientists (including IGERT fellow Heather King as lead author, along with IGERT project director Melina Hale and two IGERT faculty trainers, Michael Coates and Neil Shubin), redraws the evolutionary route of life on Earth from water to land.



Extensive video analysis, published in the *Proceedings of the National Academy of Sciences*, reveal that the African lungfish can use its thin pelvic limbs to not only lift its body off the bottom surface but also propel itself forward. Both abilities were previously thought to originate in early tetrapods, the limbed original land-dwellers that appeared later than the lungfish's ancestors.

The observation reshuffles the order of evolutionary events leading up to terrestriality, the adaptation to living on land. It also suggests that fossil tracks long believed to be the work of early tetrapods could have been produced instead by lobe-finned ancestors of the lungfish.

"In a number of these trackways, the animals alternate their limbs, which suggested that they must have been made by tetrapods walking on a solid substrate," said Melina Hale, PhD, associate professor of Organismal Biology and Anatomy. "We've found that aquatic animals with fundamentally different morphologies and that aren't tetrapods could potentially make very similar track patterns."

Lungfish are a popular pet in the paleontological community, treasured for their unique evolutionary heritage.

"The lungfish is in a really great and unique position in terms of how it is related to fishes and to tetrapods," said Heather King, a graduate student and lead author of the study. "Lungfish are very closely related to the animals that were able to evolve and come out of the water and onto land, but that was so long ago that almost everything except the lungfish has gone extinct."

While anecdotes and rumors circulated within the scientific community about the alleged walking behavior of these strange fish, nobody looked systematically at the biomechanics of their locomotion. An African lungfish (*Protopterus annectens*) kept in the laboratory of study co-author Michael Coates inspired King to study the species' ability to walk on its unusually thin limbs.

King and her colleagues designed a special tank in which the motions of lungfish could be videotaped from the side and below for in-depth analysis. The videos revealed that lungfish commonly use their hind, or pelvic, limbs to elevate their body off the surface and propel themselves forward. Though the forelimbs look similar to the hindlimbs, they were not involved in locomotion, the authors found.

"This is all information we can only get from a living animal," King said. "Because if you were just to look at the bones, like you would with a fossil, you might not ever know these motions could occur."



Lungfish also demonstrated both "bounding" motions, where both limbs moved at once, and "walking," marked by alternating limbs. Coupled with the ability of the lungfish to fully rotate the limb and place each subsequent footfall in front of the joint, the motion suggests that similar creatures would have been capable of producing some of the fossil tracks credited to tetrapods.

"It's tempting to attribute alternating impressions to something like the footfalls of an early tetrapod with digits, and yet here we've got good evidence that living lungfish can leave similar sequences of similar gait," said Coates, PhD, professor of Organismal Biology and Anatomy. "The fin or limb use thought to be unique to tetrapods is actually more general."

The lungfish's ability to use its thin limbs to support its body may be helped by the reduced demands of gravity underwater, the authors proposed. By filling its lungs with air, the lungfish may increase the buoyancy of its front end, enabling the scrawny hindlimbs to lift the entire body off the ground.

"If you showed me the skeleton of this creature and asked me to make a bet on whether it walks or not, I would have bet it couldn't," said co-author Neil Shubin, PhD, Robert R. Bensley Professor of Organismal Biology and Anatomy. "Their fins seem like the furthest thing from walking appendages possible. But it shows what's possible in an aquatic medium where you don't have to support yourself with gravity."

The discovery suggests that many of the developments necessary for the transition from water to land could have occurred long before early tetrapods, such as *Tiktaalik*, took their first steps on shore. Lobe-finned ancestors of the lungfishes as well as tetrapods could have evolved hindlimb propulsion and the ability to walk on the substrate at the bottom of a lake or marsh millions of years before limbs with digits and land-dwelling animals appeared.

"This shows us -- pardon the pun -- the steps that are involved in the origin of walking," Shubin said. "What we're seeing in lungfish is a very nice example of how bottom-walking in fish living in water can easily come about in a very tetrapod-like pattern."

The paper, "Behavioral evidence for the evolution of walking and bounding before terrestriality in sarcopterygian fishes," will be published in the online Early Edition of *Proceedings of National Academy of Sciences* the week of December 12, 2011. Funding for this work was provided by the National Science Foundation, including the IGERT training grant in Motor Control and Movement.