QnAs with Neil Shubin

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From the rust-brown sediments of long-dried streams that once rumbled through the rugged terrain of Canada's Ellesmere Island, a team of paleontologists unearthed in 2004 fossils of a 375 million-year-old species of fish that may have nearly crossed an evolutionary Rubicon. Named *Tiktaalik roseae*, the now-extinct animal has come to represent an intermediate link between fish and amphibians, its features likely enabling a leap from water to land. Led by National Academy of Sciences member Neil Shubin, a paleontologist at the University of Chicago, the team described the fossils—dated to the late Devonian period—in a pair of 2006 *Nature* reports, noting how the fish's pectoral, or forward, fins showed signs of budding limbs, including a primitive shoulder, wrist, and digits. Together, the long-snouted skull, limb-like pectoral fins, and scale-covered body tell a story of a fish that paved the way for the first four-limbed vertebrates that ventured onto land. But the hind parts of *Tiktaalik* have since remained a puzzle. Nearly a decade after the initial discovery, Shubin and his colleagues describe *Tiktaalik*'s pelvic appendage, presenting a long-awaited sequel to their saga of evolution in his PNAS Inaugural Article (1).

PNAS: Your discovery of *Tiktaalik*'s pelvic appendage addresses a longstanding conundrum in the evolution of locomotion in the animal kingdom: the contrast between movement using fins in the front of the body and movement using appendages in the front and back. Can you explain the evolutionary significance of the distinction between these forms of locomotion?

Shubin: Limbed vertebrates, or terapods, have four appendages, two in the front and two in the back. The hind appendages are fairly robust and supported by the pelvis. The tetrapod pelvis has a number of modifications to help support the body under a gravitational load: it is the size of a shoulder and attached by a rib to the vertebral column. If you look at the closest finned relatives of the tetrapods, they had large pectoral appendages but tiny pelvic appendages. That gave rise to the hypothesis that a major evolutionary change associated with the origin of tetrapods was an emphasis on the pelvic appendage, which meant that creatures with a "front wheel drive," such as fish moving in water with their fins, gave rise to creatures with a "four wheel drive," such as animals that walk on land using limbs.

PNAS: Your 2006 description of *Tiktaalik* furnished a view of the animal's front end. Why did it take so long to disinter and describe the pelvic appendage?

Shubin: We had collected two blocks of specimens in 2004, one of which contained the front end of the *Tiktaalik* reference specimen described in the 2006 papers. We did not look at the second block right away, mainly because it didn't seem to contain much bone and because we had collected it for the sake of completeness. It took us a number of years to prepare, study, and draw conclusions about this pelvic structure, found in the second block, partly because the material is delicate and the block was fragmented. We have since found five pelvic bones from different individuals, one of which is associated with a partial hind fin from the 2006 reference specimen. When we returned to the site last summer, we found another pelvis, and we have now put all of this together in the Inaugural Article.

PNAS: What does the pelvic appendage reveal?

Shubin: The big surprise is the sheer size of *Tiktaalik*'s pelvic girdle and hind fin relative to its pectoral girdle; in that respect, it is very much like a tetrapod, suggesting that hind fin-driven locomotion probably began before the tetrapods. That notion is further supported by our 2011 PNAS report of an African lungfish, a living cousin of *Tiktaalik*, that uses its hind fin to "walk" under water.

PNAS: And these strands of evidence reinforce the view that *Tiktaalik* straddled the evolutionary fence.

Shubin: The new evidence indeed shows that *Tiktaalik* had a mix of fish-like and tetrapod-like characteristics, suggesting that hind fin-driven locomotion probably began in fish but didn't fully develop until after the tetrapods came onto the scene.

PNAS: What are the particular features of the pelvic appendage that support that idea?

Shubin: Look closely at *Tiktaalik*'s hip joint and you will notice it has a deep socket, similar to the corresponding human socket, which allows us to move our legs in many directions. The socket suggests that *Tiktaalik*'s

Neil Shubin regards the socket in the hip joint of *Tiktaalik*'s pelvic appendage. Image courtesy of John Westlund, University of Chicago.

This is a QnAs with a recently elected member of the National Academy of Sciences to accompany the member's Inaugural Article on page 893.

pelvic appendage was able to support a load, so the animal may have walked under water with its hind fins. Hind limb walking gives an animal—especially a creature with heavy, air-filled lungs in the front of the body—incredible ability to maneuver in complex aquatic environments, such as swamps, streams, and estuaries. Unlike swimming in a still pool, navigating these waters often requires moving on the floor or on pieces of flotsam. Those kinds of movements call for fine control of locomotion, which is greatly enabled by hind fins.

PNAS: Your discovery raises several unanswered questions about *Tiktaalik*. What other secrets might those Devonian streambeds hold?

Shubin: Now that we know that the size and robustness of the pelvic appendage are primitive to tetrapods and arose in fish, the exciting question is how the architecture—in particular, the hip joint—changed as fish evolved into tetrapods. The sequence of the structural changes in the pelvic girdle is another important mystery. Also mysterious is the timing of onset of the attachment of the pelvic girdle to the vertebral column: Did that occur in finned or limbed creatures? Answers to these questions can only come from the fossils yet to be discovered.

1 Shubin NH, Daeschler EB, Jenkins FA, Jr (2014) Pelvic girdle and fin of *Tiktaalik roseae*. *Proc Natl Acad Sci USA* 111:893–899.