Pelvic girdle and fin of *Tiktaalik roseae*

Neil H. Shubin[a,1], Edward B. Daeschler[b], and Farish A. Jenkins, Jr.[c,2]

[a]Department of Organismal Biology and Anatomy, The University of Chicago, Chicago, IL 60637; [b]Academy of Natural Sciences of Drexel University, Philadelphia, PA 19103; and [c]Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138

This contribution is part of the special series of Inaugural Articles by members of the National Academy of Sciences elected in 2011.

Contributed by Neil H. Shubin, December 3, 2013 (sent for review November 12, 2013)

A major challenge in understanding the origin of terrestrial vertebrates has been knowledge of the pelvis and hind appendage of their closest fish relatives. The pelvic girdle and appendage of tetrapods is dramatically larger and more robust than that of fish and contains a number of structures that provide greater musculoskeletal support for posture and locomotion. The discovery of pelvic material of the finned elpistostegalian, *Tiktaalik roseae*, bridges some of these differences. Multiple isolated pelves have been recovered, each of which has been prepared in three dimensions. Likewise, a complete pelvis and partial pelvic fin have been recovered in association with the type specimen. The pelves of *Tiktaalik* are paired and have broad iliac processes, flat and elongate pubes, and acetabulae that form a deep socket rimmed by a robust lip of bone. The pelvis is greatly enlarged relative to other finned tetrapodomorphs. Despite the enlargement and robusticity of the pelvis of *Tiktaalik*, it retains primitive features such as the lack of both an attachment for the sacral rib and an ischium. The pelvic fin of *Tiktaalik* (NUFV 108) is represented by fin rays and three endochondral elements: other elements are not preserved. The mosaic of primitive and derived features in *Tiktaalik* reveals that the enhancement of the pelvic appendage of tetrapods and, indeed, a trend toward hind limb-based propulsion have antecedents in the fins of their closest relatives.

At first glance, the origin of tetrapods (limbed vertebrates) from finned precursors seems an almost insurmountable transition between life in water and life on land. If the basis of comparison were living taxa alone, then the anatomical and behavioral differences among finned and limbed vertebrates could appear vast: for example, fin structure and function differ dramatically from those of limbs. Fossil evidence, in particular vertebrates from the middle and late part of the Devonian period (393–359 Mya), offers intermediate conditions that bridge this gap (1). The fossils that provide the most informative anatomical intermediates are from the tetrapodomorph lineage (also known as stem tetrapods) and have been recovered from a variety of nonmarine and marginal marine deposits from around the globe (2–4). The creatures closest to the node containing the most basal limbed vertebrates—elpistostegalids, such as *Panderichthys*, *Tiktaalik*, and *Elpistostege*—are most enlightening in understanding the primitive conditions from which tetrapods arose. Although most work has focused on revealing homologies and function of the pectoral appendage of these forms (4–7), relatively little is known of the pelvic appendage beyond limited material of *Panderichthys* (8). Consequently, analyses of the pelvic fin have been given only sporadic attention over the past decades (4, 8–11) largely because they are often poorly preserved or not preserved at all. In most cases, it is thought that this poor preservation of the pelvic appendage is due to its putative small size and fragility (10).

Pelves, and in some cases pelvic appendages, of taxa that span the fin-to-limb transition are known from *Gooloogongia* (Rhizodontida) (12), *Eusthenopteron* (Osteolepida) (10, 13), *Panderichthys* (Elpistostegalia) (7, 8), and *Acanthostega* and *Ichthyostega* (Tetrapoda) (14–17). Comparisons of these forms reveal large differences between the pelvic appendages of finned tetrapodomorphs and tetrapods (Fig. 1). Most noticeable is that, in finned taxa, the entire pelvic appendage is significantly smaller than the pectoral. In particular, the pelvic girdle of finned tetrapodomorphs is diminutive relative to the pectoral: the pelvis represents a small fraction of the length of the body (the maximum length of pelvis-to-body length is 1:20 in *Eusthenopteron* per ref. 10). In addition, there are major differences in the morphology of the pelvic girdles of finned and limbed taxa. The girdles of *Eusthenopteron* and *Gooloogongia* have posteriorly facing acetabulae and lack sacral ribs and ischial bones, among other features (10, 12). Unfortunately, the pelvic girdle of *Panderichthys* is not preserved in sufficient detail to understand the distribution of these morphological features in elpistostegalids (8). However, the best comparisons available from these data strongly supported the hypothesis that the closest finned relatives of tetrapods were "front wheel drive animals," possessing enlarged pectoral fins, robust pectoral girdles, and relatively small pelvic appendages that were incapable of providing extensive degrees of body support and propulsion.

Previously undescribed material of the stem tetrapod, *Tiktaalik roseae*, can inform these issues. The type specimen (NUFV108), recovered in 2004 and described in 2006 (5, 6), has since been revealed to contain a partial pelvic appendage, including the right side of the pelvic girdle and an incomplete pelvic fin consisting of endochondral bones and lepidotrichia (Figs. 2 and 3). This specimen allows direct comparison of the relative size of the pelvic girdle and appendage with the rest of the body because the type consists of a relatively articulated skeleton from head to pelvis. In addition, work at the same site in Nunavut Territory during 2006, 2008, and 2013 has revealed additional isolated pelves of four other individuals. Together, these specimens offer the possibility

Significance

The earliest tetrapods have robust limbs, particularly hind limbs that are enlarged and supported by a number of modifications to the pelvic girdle. In contrast, the closest relatives of tetrapods maintain small and weakly ossified pelvic appendages as compared with the pectorals. This observation has led to the "front wheel drive" hypothesis that held that the closest relatives of tetrapods emphasized pectoral support and locomotion whereas significant pelvic support and locomotion was a tetrapod innovation. The discovery of pelvic girdle and fin material of the tetrapodomorph *Tiktaalik roseae* reveals a transitional stage in the origin of the pelvic girdle and appendage: although retaining primitive skeletal architecture, these elements are enhanced in size and robusticity much like tetrapods.

Author contributions: N.H.S., E.B.D., and F.A.J. designed research; N.H.S., E.B.D., and F.A.J. performed research; N.H.S., E.B.D., and F.A.J. analyzed data; and N.H.S. and E.B.D. wrote the paper.

The authors declare no conflict of interest.

Freely available online through the PNAS open access option.

See QnAs, 10.1073/pnas.1321499110.

[1]To whom correspondence should be addressed. E-mail: nshubin@uchicago.edu.

[2]Deceased November 11, 2012.

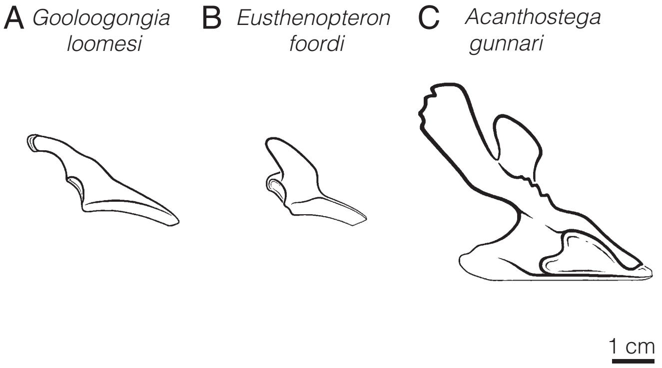

Fig. 1. Right pelves of *Gooloogongia* (*A*), *Eusthenopteron* (*B*), and *Acanthostega* (*C*) in lateral view. *Gooloogongia* is preserved as a natural cast in one orientation. Figures were modified from refs. 10, 12, and 14. Cranial is to the right.

to test the front wheel drive hypothesis and provide insights into the sequence in the acquisition of tetrapod pelvic appendage structure and locomotor function.

Results

The pelvis of *Tiktaalik roseae* is represented by five specimens, each preserved uncrushed. There is a twofold difference in size between the largest and smallest pelves, in keeping with the size variation of the *Tiktaalik* specimens recovered from the site (6). Comparison of the relative size of the pelvic and pectoral girdles is possible in NUFV 108: the craniocaudal length of the pelvis from the tip of the pubic process to the blade of the iliac process is 65 mm, in comparison with the length of the entire pectoral girdle (both endochondral and dermal) from the dorsal tip of the cleithrum to the cranial surface of the scapulocoracoid of 70 mm. The ratio of these measurements is tetrapod-like: the pelvic and pectoral girdles of *Acanthostega* are also subequal in size. In contrast to this proportion, the pelvic girdles of finned tetrapodomorphs further down the tree, *Eusthenopteron* and *Gooloogongia,* are dramatically smaller than the corresponding pectorals (Fig. 4).

The pelvis of *Tiktaalik* is unipartite, consisting of an elongate pubic process contiguous with the iliac blade (Fig. 3). This configuration is similar overall to that of finned tetrapodomorphs, such as *Eusthenopteron* and *Gooloogongia* (10, 12). Limbed forms such as *Acanthostega* and *Ichthyostega*, on the other hand, have a tripartite girdle, consisting of ilia, pubes, and ischia (14–16), which projects caudally.

The pubic process of *Tiktaalik* is an elongate and flattened beam that extends to a medial and cranial margin consisting of unfinished bone. This surface, much like that of *Eusthenopteron* (10), is deeply grooved, and its margins do not reflect breakage; therefore, the cranial margin of the pubis was likely to have been finished with a cartilaginous cap. We interpret this surface to mean that, like *Eusthenopteron*, the left and right halves of the girdle are not fused by ossified tissue at the midline and differ from the fused bony girdles seen in basal tetrapods (e.g., *Acanthostega* and *Ichthyostega*) and lungfish (11, 14, 15). The cranial and caudal margins of the pubic process are expanded, the former as a sharp ridge, the latter as a broadly rugose surface. These structures appear to be surfaces for the attachment of sheets of musculature.

The iliac blade forms a broad and flat planar surface that faces laterally. There is a slight constriction at the juncture of the iliac blade and pubic process, at the same level of the acetabulum. The pelvis is also most massive at the level of the acetabulum, and the iliac blade is thickest along the caudal margin, dorsal to the acetabulum.

The acetabulum is a deeply concave socket that consists of a smooth surface internally. The socket is relatively round in shape and much deeper than the corresponding joint surface in *Gooloogongia* or *Eusthenopteron*. A semicircular embayment of unfinished bone is continuous with the cranial margin of the acetabulum and may have housed cartilage or bone that participated in the joint. In *Tiktaalik*, the acetabulum is situated caudally on the pelvis, like other finned tetrapodomorphs. The acetabulum of *Tiktaalik* would have faced more laterally than that of fish but less than tetrapods. Consequently, *Tiktaalik* presents a mosaic of primitive and derived conditions: like fish, it has an acetabulum that sits at the caudal margin of the pelvis, but it is more tetrapod-like in the degree to which the acetabulum faces laterally.

The pelvic fin of *Tiktaalik* is represented by lepidotrichia and three elongate and rod-like endochondral bones (Fig. 2). All other endochondral bones are not preserved. The first of these endochondral elements resembles the intermedium in the pectoral appendage of the same individual, both in its size and in the morphology of the concavities and crests on the ventral surface. The other two endochondral bones are subequal in length and preserved in parallel to one another. It is unclear whether these would be the terminal series of endochondral radials, as they are unfinished distally.

The lepidotrichia are unjointed and highly asymmetrical across the fin, being robust and elongate on the leading edge and shorter and more narrow on the trailing edge (Fig. 2). The pelvic lepidotrichia are as equally robust and elongate as the corresponding elements of the pectoral appendage (maximum width of pectoral and pelvic lepidotrichia is 1.8 mm). Judging from the preserved length of the rays, the pelvic appendage was at least as long proximodistally as the pectoral appendage.

Discussion

The most dramatic difference between *Tiktaalik roseae* and other finned tetrapodomorphs is the relative size of the pelvic girdle, its general robusticity, and the inferred size of the pelvic fin (Figs. 4–6). The pelvic girdle is roughly the same rostrocaudal length as the cleithrum/scapulocoracoid block, a condition that is dramatically different from *Eusthenopteron* (10, 13), but similar to tetrapods such as *Acanthostega* and *Ichthyostega* (14–16). Although this ratio likely reflects changes to both shoulder and pelvis, the pelvis is expanded relative to body size as well, being 1/12th of estimated body length in *Tiktaalik* versus 1/20th in *Eusthenopteron* (10). Moreover, the lepidotrichia of the pelvic fin of *Tiktaalik* suggest an appendage that is at least as elongate as the pectoral. *Tiktaalik* reveals that features contributing to the trend toward pelvic-propelled locomotion in the tetrapodomorph stem began emerging in finned taxa before being enhanced in more derived digited forms. Indeed, this trend has deep roots or parallel trajectories: diverse lungfish, both fossil and extant, have pectoral and pelvic girdles that are subequal in size (17).

Antecedents of canonical tetrapod pelvic characteristics are seen in *Tiktaalik*. Although *Tiktaalik* lacks a sacral rib connecting the pelvic girdle with the vertebral column, the iliac blade is relatively more massive and dorsally expanded than in fish; indeed, it rises minimally to the level of the vertebral column (Fig. 6). This observation suggests that the origin of the vertebral articulation with the pelvis involved several steps. The first stage in the evolution of this fundamental tetrapod character was the expansion of the girdle, particularly the ilium. In more derived forms, the rib elongates to articulate with the already-expanded ilium.

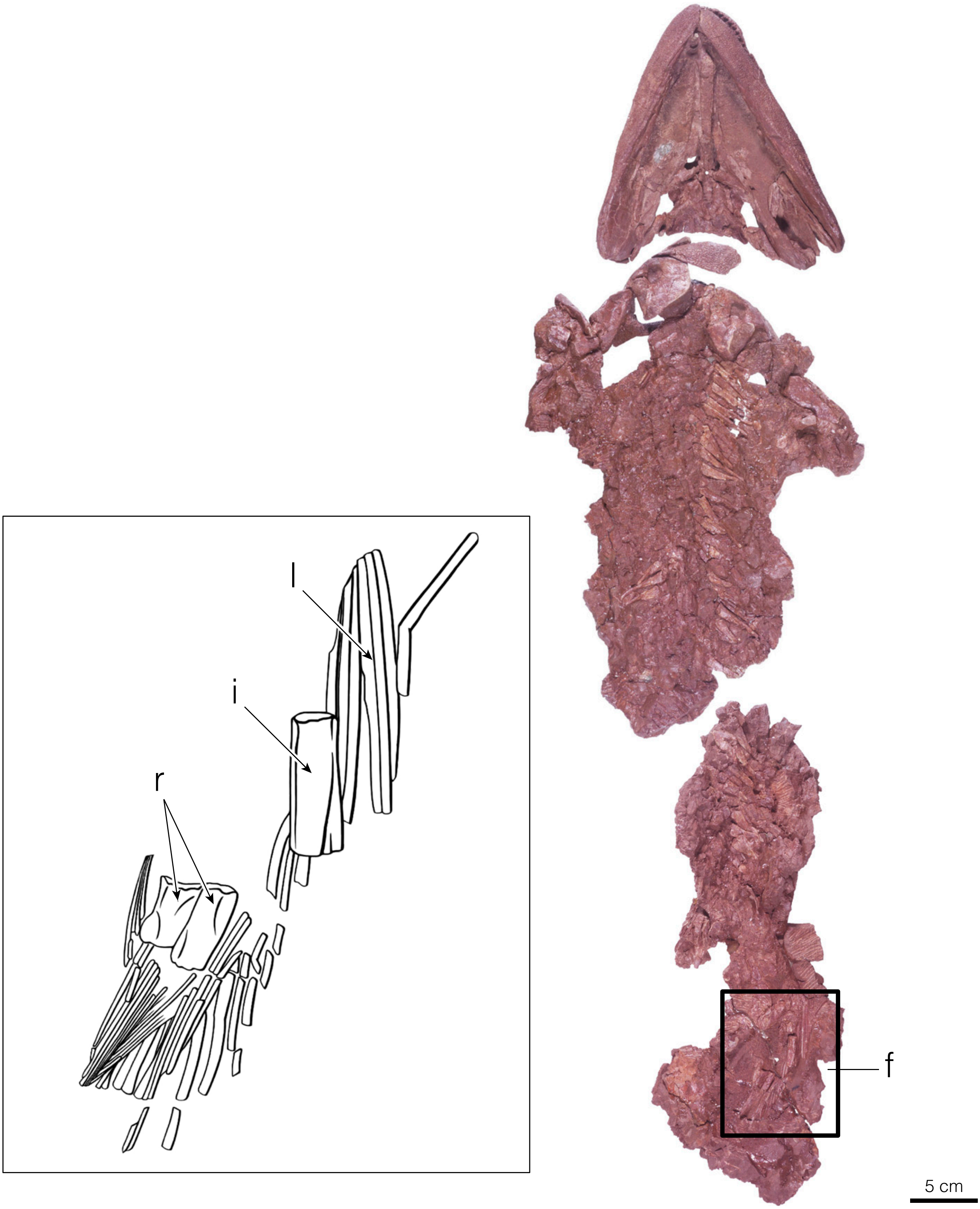

Fig. 2. Type specimen (NUFV108): ventral surface of cranial block (figured in ref. 6) aligned in preserved position with ventral view of the block containing the pelvic fin. (*Inset*) Line diagram of lepidotrichia and preserved portions of endochondral bones of pelvic fin. f, fin; i, intermedium?; l, lepidotrichia; r, radials.

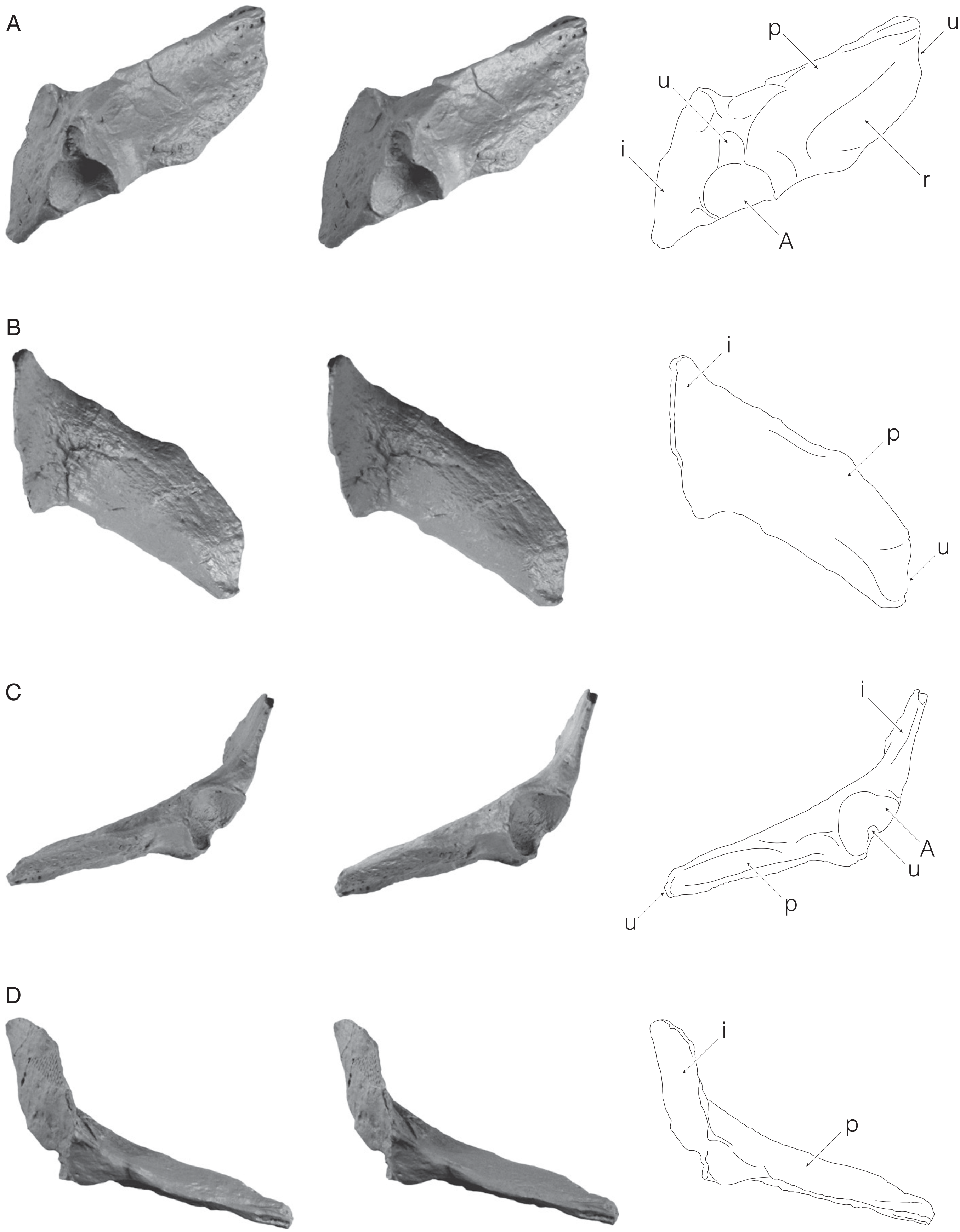

Fig. 3. *Tiktaalik roseae*, stereopairs of the right pelvis from NUFV108 in (*A*) ventral (cranial is to the *Top*), (*B*) dorsal (cranial is to the *Bottom*), (*C*) caudal (lateral is to the *Right*), and (*D*) cranial views (lateral is to the *Left*). A, acetabulum; i, ilium; p, pubis; r, ossified ridge; u, unfinished bone.

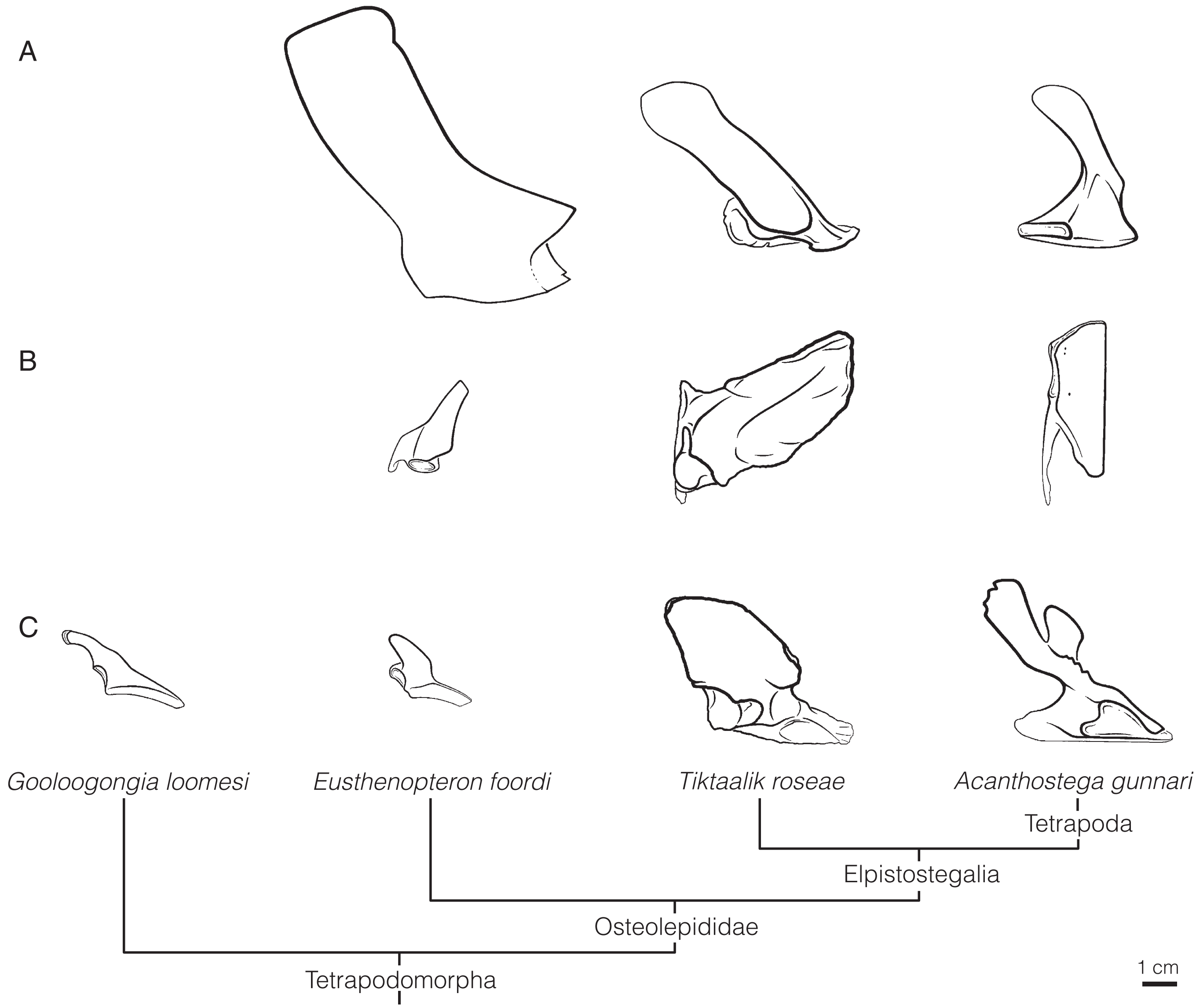

Fig. 4. Cladogram with right pectoral and pelvic girdles drawn to the same scale. (*A*) Pectoral girdles in lateral view. (*B*) Pelvic girdles in ventral view. (*C*) Pelvic girdles in lateral view. Figures were modified, and relative proportions were derived, from refs. 10, 16, and 17, and NUFV108. Cranial to the *Right* in *A* and *C*; Cranial at the *Top* in *B*.

Although the size and general robusticity of the pelvis is derived relative to other finned forms, aspects of the general architecture of the girdle are plesiomorphic. The pelvis of *Tiktaalik* is similar to that of finned tetrapodomorphs such as *Eusthenopteron* in the configuration of pubic process and iliac blade and in lacking an ischium and articulations for sacral ribs (Fig. 4). The pelvis of *Tiktaalik* is also primitive in that the acetabulum lies on the caudalmost portion of the girdle, much like in *Eusthenopteron* or *Gooloogongia*. In addition, the left and right sides remain separate bony elements as in *Eusthenopteron* (10) although the extent to which they may have been fused by cartilage remains unknown.

Plesiomorphic features of *Tiktaalik* can be interpreted as highlighting a functional difference with limbed forms: the pelvic fin was not capable of bearing stresses and strains as significant as those of *Acanthostega* and *Ichthyostega*, nor was the musculature as well-developed for appendage retraction. Fusion of left and right halves of the pelvis and the attachment of a sacral rib to the ilium are tetrapod features that enhance the load-bearing capacity of the pelvis and pelvic appendage. Moreover, the expansion of an ischium caudally provides a surface for retractors that would aid the limb in powered propulsion. There are significant differences in the acetabulum as well: although the acetabulae are derived in being robust in both *Tiktaalik* and tetrapods, there is a greater restriction of motion in the latter. The acetabulum of *Tiktaalik* is a deep spherical socket whereas that of basal tetrapods is dorsoventrally compressed (14, 18). This observation implies that a wider degree of rotation was possible in *Tiktaalik*, compared with tetrapods that had a proximal femur stabilized by the bony structure of the hip. Moreover, the hip joint of *Tiktaalik* would have allowed a greater range of appendicular motion than would the shoulder, which has an elongate glenoid with an anterior saddle-shaped facet (5). The emphasis in *Tiktaalik*, as implied from joint structure, is on stability at the shoulder and mobility at the hip.

Extant aquatic vertebrates reveal a surprising diversity of locomotor strategies, particularly in walking behaviors. Supported by the neutral buoyancy offered by water and thereby lacking constraints imposed by a gravitational load, finned vertebrates reveal a diversity of bounding, alternating, and axial gaits that could not necessarily be predicted by morphology alone, or even

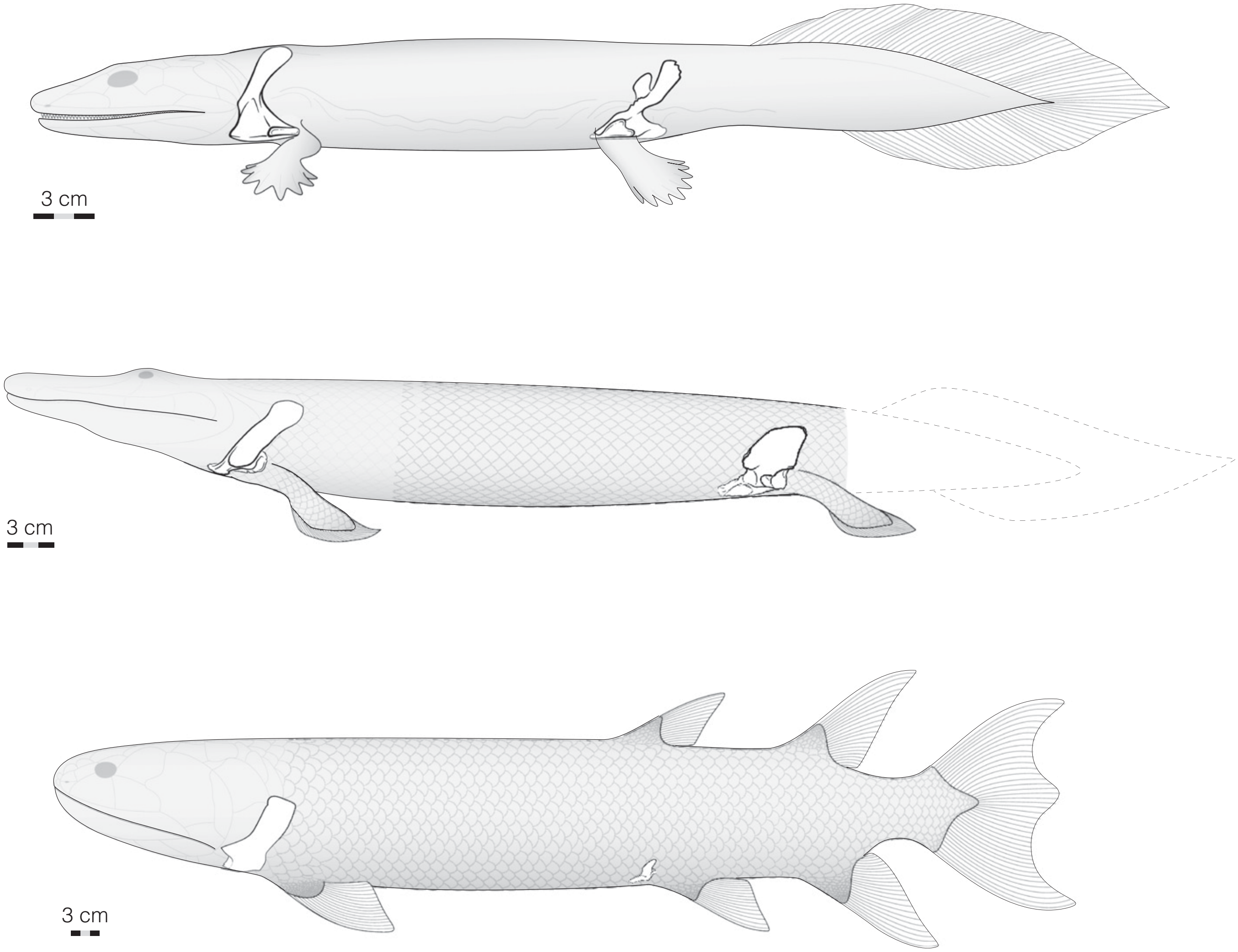

Fig. 5. *Acanthostega* (*Top*), *Tiktaalik* (*Middle*), and *Eusthenopteron* (*Bottom*) reconstructions with pectoral and pelvic girdles (proportions were derived from refs. 10, 16, and 17 and NUFV108).

be possible in a terrestrial environment (e.g., ref. 19). Indeed, walking gaits of a variety of types are known in a plethora of finned forms (20–22). Given the range of walking behaviors possible in an aquatic medium, and the expanded size, mobility, and robusticity of the pelvic girdle, hip joint, and fin of *Tiktaalik roseae*, paddling, station holding, and walking may have all been in the functional repertoire of the appendage.

The recently discovered material allows an updated reconstruction of the skeleton of *Tiktaalik roseae* (Fig. 6). With robust pelvic and pectoral fins and girdles, a flattened head, loss of the extrascapular and opercular bones, and expanded ribs, among other characteristics, *Tiktaalik* was likely a denizen of a continuum of channel, shallow water, and mudflat habitats where appendage-based support, locomotion, and head mobility would have been advantageous.

Materials and Methods

The material was recovered during paleontological excavations near Bird Fiord on southern Ellesmere Island in 2004, 2006, 2008, and 2013. All of the material was recovered from a single locality (NV2K17; N77°09.895′ W86°16.157′) and has been temporarily housed at the Academy of Natural Sciences of Drexel University until the entire collection is returned to Canada, per agreement with the

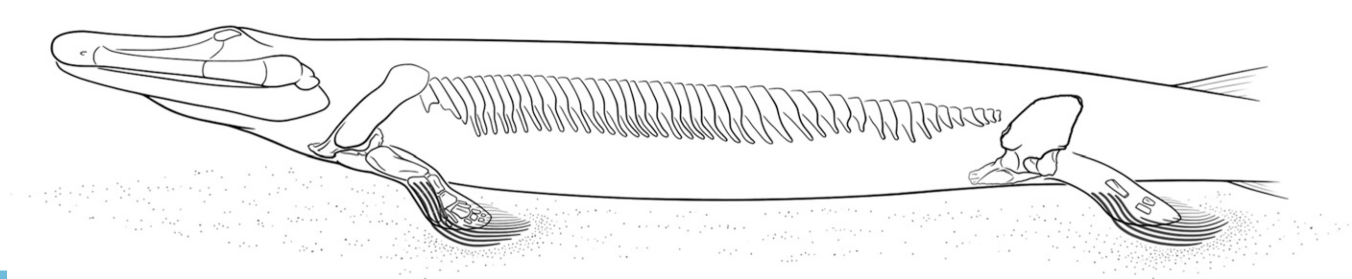

Fig. 6. Reconstruction of the skeleton of *Tiktaalik roseae*, updated from ref. 6.

Territory of Nunavut. At that time, the material will be curated in the Nunavut Fossil Vertebrate Collection (NUFV) at the Canadian Museum of Nature.

The geological context of the *Tiktaalik roseae* discovery was described in ref. 6. NUFV108, the holotype, was recovered in three blocks, one of which contained the material described in 2006. The other blocks were recently prepared mechanically and revealed the associated pelvis and pelvic fin material.

ACKNOWLEDGMENTS. Sadly, this paper could not be completed during the lifetime of our longtime collaborator and friend, Farish A. Jenkins, Jr. We are, indeed, grateful that Farish was able to participate in the recovery and analysis of the pelvic material. Specimens were prepared by C. Fredrick Mullison. John Westlund rendered the figures. Logistical support in the field came from the Polar Continental Shelf Project of Natural Resources of Canada. Permission to work in the field came from the Nunavut Ministry of Culture, Language, Elders and Youth, the Hamlets and Hunters and Trappers of Grise Fiord, and Resolute Bay. Assistance in the field was provided by W. Amaral, B. Atagootak, J. Conrad, R. Dahn, M. Davis, J. Downs, S. Gatesy, A. Gillis, B. Kilbourne, S. Madsen, K. Middleton, J. Miller, K. Monoyios, C. Schaff, B. Shearman, M. Shapiro, C. Sullivan, and M. Webster. We benefitted from comments by R. Blob, M. Coates, J. Lemberg, and J. Long. Financial support came from National Geographic Society Committee for Research and Exploration Grants 7223-02, 7665-04, 8040-06, and 8420-08; Dane and Louise Miller; The Brinson Foundation; the Putnam Expeditionary Fund of the Museum of Comparative Zoology of Harvard University; an anonymous donor to the Academy of Natural Sciences; the Biological Sciences Division of The University of Chicago; and the National Science Foundation (to N.H.S. and E.B.D.). This material is based upon work supported by the National Science Foundation under Grants EAR 0207721 (to E.B.D.), EAR 0544093 (to E.B.D.), EAR 0208377 (to N.H.S.), and EAR 0544565 (to N.H.S.).

1. Clack JA (2012) *Gaining Ground: The Origin and Evolution of Tetrapods* (Indiana Univ Press, Bloomington, IN), p 369.
2. Ahlberg P, Johanson Z (1998) Osteolepiforms and the ancestry of tetrapods. *Nature* 395:792–794.
3. Janvier P (1996) *Early Vertebrates* (Oxford Univ Press, Oxford).
4. Coates MI, Jeffery JE, Rut M (2002) Fins to limbs: What the fossils say. *Evol Dev* 4(5):390–401.
5. Shubin NH, Daeschler EB, Jenkins FA, Jr. (2006) The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. *Nature* 440(7085):764–771.
6. Daeschler EB, Shubin NH, Jenkins FA, Jr. (2006) A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature* 440(7085):757–763.
7. Boisvert CA, Mark-Kurik E, Ahlberg PE (2008) The pectoral fin of *Panderichthys* and the origin of digits. *Nature* 456(7222):636–638.
8. Boisvert CA (2005) The pelvic fin and girdle of *Panderichthys* and the origin of tetrapod locomotion. *Nature* 438(7071):1145–1147.
9. Gregory WK, Raven HC (1941) Studies on the origin and early evolution of paired fins and limbs. Part 4. A new theory of the origin of the pelvis of tetrapods. *Ann N Y Acad Sci* 42(1):329–360.
10. Andrews MS, Westoll ST (1970) The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Trans R Soc Edinb* 68(9):207–329.
11. Boisvert CA, Joss JMP, Ahlberg PE (2013) Comparative pelvic development of the axolotl (Ambystoma mexicanum) and the Australian lungfish (Neoceratodus forsteri): Conservation and innovation across the fish-tetrapod transition. *Evodevo* 4(1):3.
12. Johanson Z, Ahlberg PE (2001) Devonian rhizodontids and tristichopterids (Sarcopterygii, Tetrapodomorpha) from East Gondwana. *Trans R Soc Edinb* 92:43–74.
13. Jarvik E (1980) *Basic Structure and Evolution of the Vertebrates* (Academic, New York), Vol 1.
14. Coates MI (1996) The Devonian tetrapod *Acanthostega gunnari* Jarvik: Postcranial anatomy, basal tetrapod relationships and patterns of skeletal evolution. *Trans R Soc Edinb* 87:363–421.
15. Jarvik E (1996) The Devonian tetrapod *Ichthyostega*. *Fossil and Strata* 40:1–206.
16. Ahlberg PE, Clack JA, Blom H (2005) The axial skeleton of the Devonian tetrapod *Ichthyostega*. *Nature* 437(7055):137–140.
17. Young GC, Barwick RE, Campbell KSW (1989) *Pathways in Geology: Essays in Honour of Edwin Sherbon Hills*, ed Le Maitre RW (Blackwell Scientific, Melbourne), pp 59–75.
18. Pierce SE, Clack JA, Hutchinson JR (2012) Three-dimensional limb joint mobility in the early tetrapod *Ichthyostega*. *Nature* 486(7404):523–526.
19. King HM, Shubin NH, Coates MI, Hale ME (2011) Behavioral evidence for the evolution of walking and bounding before terrestriality in sarcopterygian fishes. *Proc Natl Acad Sci USA* 108(52):21146–21151.
20. Macesic LJ, Kajiura SM (2010) Comparative punting kinematics and pelvic fin musculature of benthic batoids. *J Morphol* 271(10):1219–1228.
21. Fricke H, Hissmann K (1991) Locomotion, fin coordination and body form of the living coelacanth *Latimeria chalumnae*. *Environ Biol Fishes* 34:329–356.
22. Pridmore PA (1995) Submerged walking in the epaulette shark *Hemiscyllium ocellatum* (Hemiscyllidae) and its implications for locomotion in rhipidistian fishes and early tetrapods. *Zoology (Jena)* 98:278–297.