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The axial skeleton of *Tiktaalik roseae*

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The axial columns of the earliest limbed vertebrates show distinct patterns of regionalization as compared to early tetrapodomorphs. Included among their novel features are sacral ribs, which provide linkage between the vertebral column and pelvis, contributing to body support and propulsion by the hindlimb. Data on the axial skeletons of the closest relatives of limbed vertebrates are sparce, with key features of specimens potentially covered by matrix. Therefore, it is unclear in what sequence and under what functional context specializations in the axial skeletons of tetrapods arose. Here, we describe the axial skeleton of the elpistostegalian *Tiktaalik roseae* and show that transformations to the axial column for head mobility, body support, and pelvic fin buttressing evolved in finned vertebrates prior to the origin of limbs. No atlas–axis complex is observed; however, an independent basioccipital–exoccipital complex suggests increased mobility at the occipital vertebral junction. While the construction of vertebrae in *Tiktaalik* is similar to early tetrapodomorphs, its ribs possess a specialized sacral domain. Sacral ribs are expanded and ventrally curved, indicating likely attachment to the expanded iliac blade of the pelvis by ligamentous connection. Thus, the origin of novel rib types preceded major alterations to trunk vertebrae, and linkage between pelvic fins and axial column preceded the origin of limbs. These data reveal an unexpected combination of post-cranial skeletal characters, informing hypotheses of body posture and movement in the closest relatives of limbed vertebrates.

axial patterning | evolutionary novelty | swimming | walking | water-to-land transition

Significance

The origin of terrestrial vertebrates is marked by changes to the entire post-cranial skeleton. To date, information on the vertebrae and ribs of the closest relatives to limbed vertebrates has been limited, making it difficult to reconstruct how the axial skeleton was evolving. This paper describes the axial column of *Tiktaalik roseae*, a close relative of limbed vertebrates. The holotype specimen was µCT (micro-computed tomography) scanned, which revealed its vertebrae and posterior ribs. These data show how specialization for head mobility, body support, and pelvic fin buttressing arose in stem tetrapods, allowing for a three-dimensional reconstruction of *Tiktaalik* and shedding light on the antecedents to the terrestrial walking behaviors.

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The earliest limbed vertebrates are characterized by a regionalized axial skeleton with cervical, thoracic, sacral, and caudal domains in the vertebral column and ribs (1–4). This organization corresponds to locomotor specializations that provide support for load-bearing hind limbs and increased mobility of the head (5–7). *Acanthostega* and *Ichthyostega* have specialized ribs that provide mechanical linkage between the vertebral column and pelvic girdle, connecting to the ilium by either ligament or direct articulation (1, 2, 4). These sacral ribs are absent in early tetrapodomorphs (8–10). For example, the tristichopterid *Eusthenopteron* has ribs that are short and generally similar across their cranio-caudal distribution and they do not approach the pelvis, which is small as compared to the pectoral girdle (8). Moreover, unlike *Acanthostega* and *Ichthyostega*, *Eusthenopteron* possessed to a bony linkage between the shoulder girdle and cranium that would have limited head motility (1, 2, 4, 8).

Little is known about the axial regionalization of elpistostegalian fishes (sensu Daeschler et al., 11), a paraphyletic grade within tetrapodomorpha that comprises the closest relatives of limbed vertebrates. In *Panderichthys*, the four most rostral vertebrae are non-rib bearing (12), and four vertebrae are described from the trunk as having broad short ribs, similar in length to the combined height of the neural arch and spine (13, 14). The vertebrae of *Elpistostege* are known from a series of approximately 16 that show no heterogeneity in their length or shape; ribs were not found in association with these vertebrae, and their position along the axial column is unclear (15). Since the original discovery in 2004, the axial skeleton of *Tiktaalik* has been largely obscured by matrix. While the rostral ribs are known to be broad and laterally expanded as compared to early tetrapodomorph conditions, the vertebral column has not been observed (11). However, the pelvis and pelvic fin of *Tiktaalik* are nearly the size of the pectoral appendage (16), differentiating its overall proportions from less crownward taxa such as *Panderichthys* (13, 17). The size and depth of the acetabulum, the general robusticity of the pubis, and the broadly expanded iliac blades of *Tiktaalik* are features that have not been described in other finned tetrapodomorphs (16).

Here, we present high-resolution micro-computed tomography (µCT) scans of the type specimen of *Tiktaalik roseae*, NUFV (Nunavut Fossil Vertebrate Collection) 108, that expose the vertebral skeleton and posterior ribs (Fig. 1 and Movies S1 and S2). These data, and the reconstruction that they allow, reveal unexpected intermediate conditions and

apomorphies at the origin of limbed vertebrates and provide insight into the functional context in which they arose.

Results

Occipital–Vertebral Junction. In NUFV 108, the head appears to have settled rostrally during preservation, separating from the vertebrae and ribs (*SI Appendix,* Fig. S1 and *Supplementary Text*). The basioccipital–exoccipital complex is preserved apart from the rest of the skull, lying medial to the pectoral girdles with the left and right halves separated from one another (Figs. 1 and 2 *A–D*). Examination of a second specimen, NUFV 110, confirms that the basioccipital–exoccipital complex is not sutured to the rest of the skull (Fig. 2 *E–I*). An independent basioccipital–exoccipital complex in *Tiktaalik* differs from the general pattern of tetrapodomorphs, where the complex is fused both across the midline and to anterior cranial elements (19, 20). However, in the tristichopterid *Mandageria fairfaxi*, the basioccipital–exoccipital complex is also separated from more anterior elements; the basioccipitals were likely cartilaginous, and the exoccipitals were bilaterally fused (21). In *M. fairfaxi* this feature is inferred to allow for increased notochordal flexion at the occipital-vertebral junction (21). Separation of skeletal elements at the back of the skull in *Tiktaalik*, thus, provides further evidence for increased mobility at the head-trunk boundary, which was previously hypothesized based on the absence of an operculum and reduced and mobile extrascapular series (11).

Vertebrae. The vertebrae of *Tiktaalik* are rhachitomous with multipartite centra that surround an unconstricted notochord that was persistent into adulthood (Fig. 3). In NUFV 108, elements of 40 vertebrae are preserved. Intercentra and neural arches are preserved, while pleurocentra are not identified. The size, shape, and spacing of intercentra and neural arches of *Tiktaalik* are similar to *Eusthenopteron* (8), suggesting a vertebral construction where pleurocentra are present and small. Therefore, pleurocentra

are likely not observed in NUFV 108 because they were unossified or have been lost among the many preserved scales due to their small size. Pleurocentra have similarly not been identified in *Panderichthys* (13) and *Elpistostege* (15), suggesting these elements are generally unossified and small in elpistostegalian fishes.

Vertebrae are not preserved in association with the four rostral most ribs of NUFV 108 (Fig. 3 *A* and *B*). It is possible that these vertebrae were ossified and lost during preservation; alternatively, they might have been cartilaginous. In *Ichthyostega*, vertebrae are also were not found with the four most rostral ribs (3). This shared gap suggests that vertebrae in the cervical domain were cartilaginous into adult stages in both *Tiktaalik* and *Ichthyostega* and that the observed pattern is not a consequence of ossified elements having been lost during preservation.

Intercentra are paired and have minor graded differences in their morphology across the series (Fig. 3*C*). Proceeding caudally, intercentra become shorter dorsoventrally, longer in the rostro-caudal direction, and bear a larger articular facet for the ribs (Fig. 3 *D–G*). Similar rostro-caudal variation is observed in the intercentra of *Eusthenopteron* (8). *Tiktaalik* is distinguished from closely related taxa in having paired intercentra along the full series. In *Eusthenopteron,* the rostral five intercentra and the intercentra above the pelvis, at approximately position 32, are bilaterally fused (8); *Acanthostega* has fused atlantal and sacral intercentra (1); and in *Ichthyostega,* most intercentra are fused, with only the anterior-most ones being paired (3).

Neural arches are inclined posteriorly and vary craniocaudally in their morphology. Frequently, they are laterally compressed in preservation. Neural arches are interpreted as being a single element, although the left and right halves separate occasionally, similar to what has been described in *Eusthenopteron* (8), *Panderichthys* (13), *Elpistostege* (15), and *Acanthostega* (1). Zygopophyses are not observed, unlike in limbed vertebrates (2, 3, 22, 23). Cranially, neural arches have a simple saddle shape (Fig. 3 *D* and *E*). The rostral 30 arches show subtle variation in their geometry, with more caudal neural arches having a slightly more vertical inclination

Fig. 1. Volumetric rendering of μCT scans of *Tiktaalik roseae*. NUFV 108 in (*A*) dorsal, (*B*) ventral, and (*C*) left lateral perspectives. μCT data reveal previously hidden detail on the exoccipital–basioccipital complex, vertebrae, ribs, and pelvic fin. The head, which was mechanically prepared and scanned separately (18), is positioned here slightly anterior to its preserved position to more clearly show the pectoral girdle. The preserved position of the head is depicted in *SI Appendix,* Fig. S1. (Scale bar, 5 cm.)
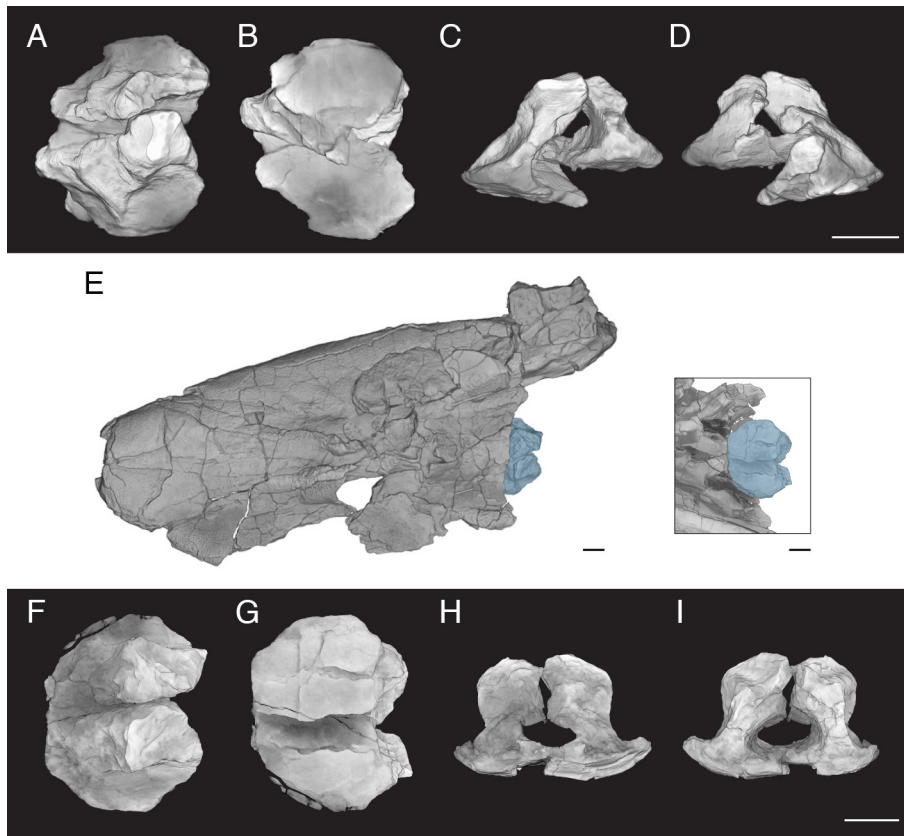
Fig. 2. Basioccipital–exoccipital complex of *Tiktaalik roseae.* The basioccipital–exoccipital complex of *Tiktaalik* is preserved in NUFV 108 and NUFV 110 as paired elements that are unfused to the rest of the braincase. In NUFV 108, the elements are preserved medial to the pectoral girdle, as depicted in Fig. 1 and *SI Appendix,* Fig. S1. The basioccipital–exoccipital elements of NUFV 108 shown in preserved positions from (*A*) dorsal, (*B*) ventral, (*C*) anterior, and (*D*) posterior perspectives. (*E*) In NUFV 110, the basioccipital–exoccipital complex is still contacting the rest of the skull. The basioccipital–exoccipital complex of NUFV 110 is shown from (*F*) dorsal, (*G*) ventral, (*H*) anterior, and (*I*) posterior perspectives. (Scale bars, 1 cm.)

relative to the notochord. By position 32, the neural arch pattern shifts abruptly where neural arches extend further dorsally and have a dorsal foramen. Neural arch 31 is broken dorsally, and so it is unclear whether the transition in neural arch morphology occurs at position 31 or 32. A change in rib morphology is also observed at this same position along the rostro-caudal axis, described below. Further caudally, four vertebrae are preserved. One of these is substantially more robust than all others (Fig. 3 *F* and *G* Movie S1), similar to neural arches preserved in the caudal domain of *Acanthostega* (1).

Ribs. NUFV 108 was physically prepared in 2004 and 2005 to expose rostral ribs (11). μCT imaging reveals additional ribs preserved beyond those previously identified, making for a total of 56 associated with the specimen, including an uninterrupted series of 32 on the left side. Across the series, ribs have a curved articular head that would have contacted the pleurapophyses of the intercentra. Ribs bear a flange posteriorly on their proximal portion that varies in its mediolateral span across the series, and the ribs lack imbricating uncinate processes (Fig. 3 *A* and *B*). The rostral-most ribs extend straight to a tapered, narrow tip. More caudally, at approximately rib number 5, the ribs become longer and have a gentle ventral curvature. At approximately rib number 20, the ribs shorten in their mediolateral span and have a broader base, gaining a more triangular shape. Ribs 31 and 32 are markedly distinct in their morphology from others in the series. Rib 31 is broad in dorsal perspective and has unfinished distal surface that is rounded, while rib 32 shows substantial ventral curvature as compared more cranial ribs (Fig. 3 *A* and *B*). An

isolated post-sacral rib is preserved to the left of the other axial elements (Fig. 1 *A* and *B* and Movie S2). Its morphology, narrow, slightly recurved, and posteriorly directed, is similar to the post-sacral ribs of *Acanthostega* (1) and *Ichthyostega* (2). No evidence of sternal structures is found.

Reconstruction of the Sacral Region. Data presented here on the vertebrae and ribs of NUFV 108 allow for reassessment of the position and orientation of the pelvis of *Tiktaalik*. The morphology of the pelvic girdle of *Tiktaalik* was described previously on the basis of five specimens (16); however, its precise position along the axial column has remained unknown. Four of the girdles are isolated specimens. The fifth belongs to NUFV 108, collected in a small block contiguous with that which held the pelvic fin. In NUFV 108, the pelvic fin was transported during preservation, both rotated and splayed caudally relative to the axial skeleton, discussed below (*SI Appendix,* Fig. S2 and *Supplementary Text*). Lacking indicators of body position from the preserved positions of the pelvis and pelvic fin, features in the axial skeleton were used to infer their positioning.

In early tetrapods, abrupt transitions in the morphology of the vertebrae and ribs denote the trunk-to-tail transition and position of the pelvic girdle. In *Eusthenopteron*, intercentra fuse bilaterally and haemal arches enclose the haemal canal between vertebrae 30 and 32, ribs are not present caudal to vertebra 30, and the pelvis is positioned ventral to vertebra 31 (1, 8). In *Acanthostega,* vertebra 31 differs from those immediately rostral in having fused intercentra and bearing a distinctive and elongate rib with a ventral expansion that would have allowed for connection to the girdle (1).
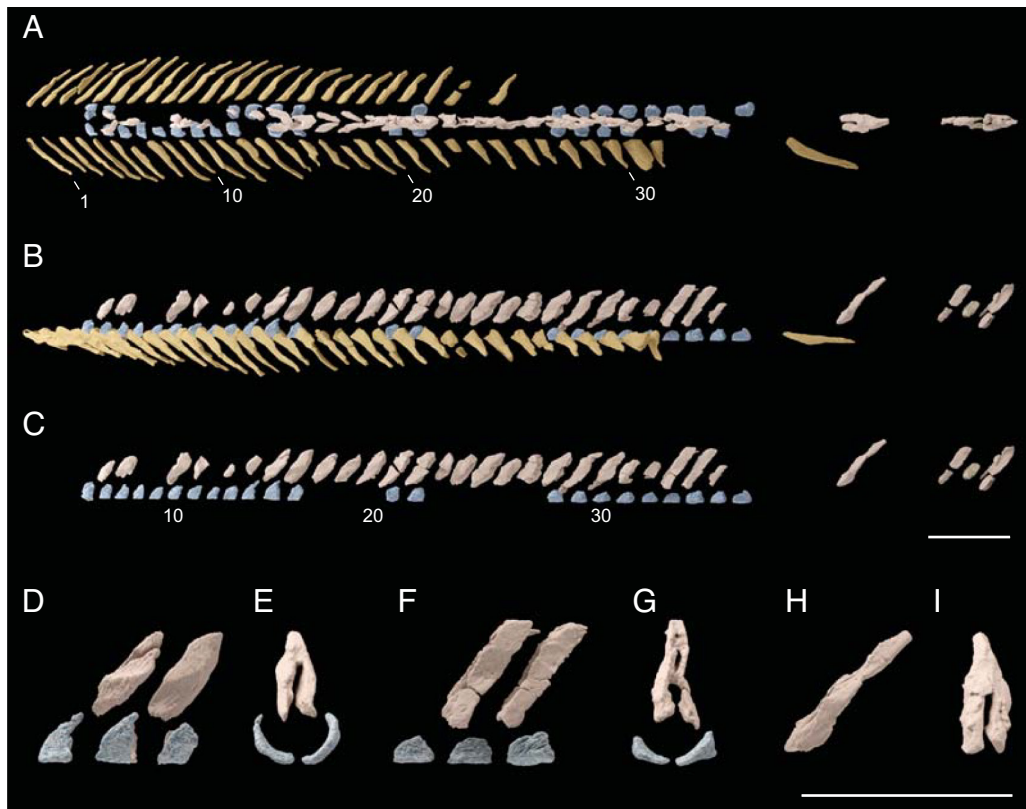
Fig. 3. Vertebrae and ribs of *Tiktaalik roseae*. Vertebrae and ribs in (*A*) dorsal and (*B*) lateral perspective. (*C*) Intercentra and neural arches in lateral perspective. (*D* and *E*) Intercentra and neural arches beginning at position 14 in left lateral and anterior perspective (*F* and *G*) Intercentra and neural arches beginning at position 32 in left lateral and anterior perspective. (*H* and *I*) Neural arch from the caudal region in left lateral and anterior perspective. Ribs are depicted in yellow, neural arches in tan, and intercentra in blue. (Scale bars, 5 cm.)

In *Ichthyostega*, the individual morphologies of vertebrae are undescribed in the sacral domain; however, a sacral rib at position 28 marks the position of the pelvis (2, 24). Thus, in *Tiktaalik* abrupt change in vertebral and rib morphology at positions 31 and 32 indicate the likely position of the pelvis along the rostrocaudal axis (Fig. 4).

The orientation of the pelvis was reconstructed by analyzing several features, including the size and shape of the pubis, the height of the pectoral girdle, body width along the trunk, orientation of the acetabulum, as well as comparisons to closely related taxa (*SI Appendix, Supplementary Text*). In *Tiktaalik*, the dorsal extent of the ilium is hypothesized to have approached ribs 31 and 32 (Fig. 5 and Movie S3). This result is recovered under several alternative hypotheses of pelvic orientation (*SI Appendix*, Fig. S3 and *Supplementary Text*). There is no articular facet on the internal surface of the ilium to indicate direct articulation with sacral ribs (16). However, based on the marked regionalization of the ribs, the expanded unfinished distal surface of rib 31, and predicted proximity of ribs 31 and 32 and the pelvic girdle, a ligamentous connection is inferred. *Acanthostega* likewise exhibits no distinct articular facet or marked perimeter for the attachment of the sacral rib on the ilium and is similarly inferred to have possessed a ligamentous connection (1). Positioning of the pelvis of *Tiktaalik* entails a more posteroventral-facing acetabulum than previously proposed (16), more similar to the orientation of the pelvic fins of *Eusthenopteron* (8) than the laterally positioned limbs of Devonian limbed vertebrates (1, 2, 24).

Pelvic Fin. In NUFV 108, the pelvic fin is preserved displaced from its original position: It has been rotated mediolaterally and dorsally with endoskeletal elements splayed caudally

(*SI Appendix*, Fig. S2 and *Supplementary Text*). Mechanical preparation of NUFV 108 in 2005 to 2006 exposed parts of the pelvic fin (16). µCT data reveal previously hidden details, including the full extent of the pelvic fin web and additional fin endoskeletal elements (Figs. 1 and 6*A*). Pelvic fin rays are unbranching and unsegmented. Similar to the pectoral fins of tetrapodomorphs, the pelvic fin rays are more robust on the leading edge and more gracile on the posterior side (26). Hemitrichia have accentuated asymmetry (Fig. 6*B*). Dorsal hemitrichia are larger in the cross-section than ventral hemitrichia, as in the pectoral fin of *Tiktaalik* (26). Two additional pelvic fin endoskeletal elements are identified (Fig. 6 *A* and *C*). One, inferred to be a tibia, has a robust proximal articular surface, and its distal margin appears broken, making it unclear whether a more distal element might have articulated with it. The other element is small with a posteriorly oriented ventral curving process, a feature not observed in other tetrapodomorph pelvic fins (8–10, 17, 27).

Discussion

Tiktaalik exhibits a unique constellation of primitive and derived characters in the axial skeleton that suggest it had a locomotor capacity intermediate to other known elpistostegalian fishes and limbed vertebrates. These data, and the reconstruction they imply (Fig. 7), inform the evolution of axial regionalization and the origin of quadrupedal locomotion in early tetrapods.

The vertebrae of *Tiktaalik* adhere closely to plesiomorphic tetrapodomorph conditions. In NUFV 108, most of the preserved vertebrae are from the trunk, and they are similar to the trunk
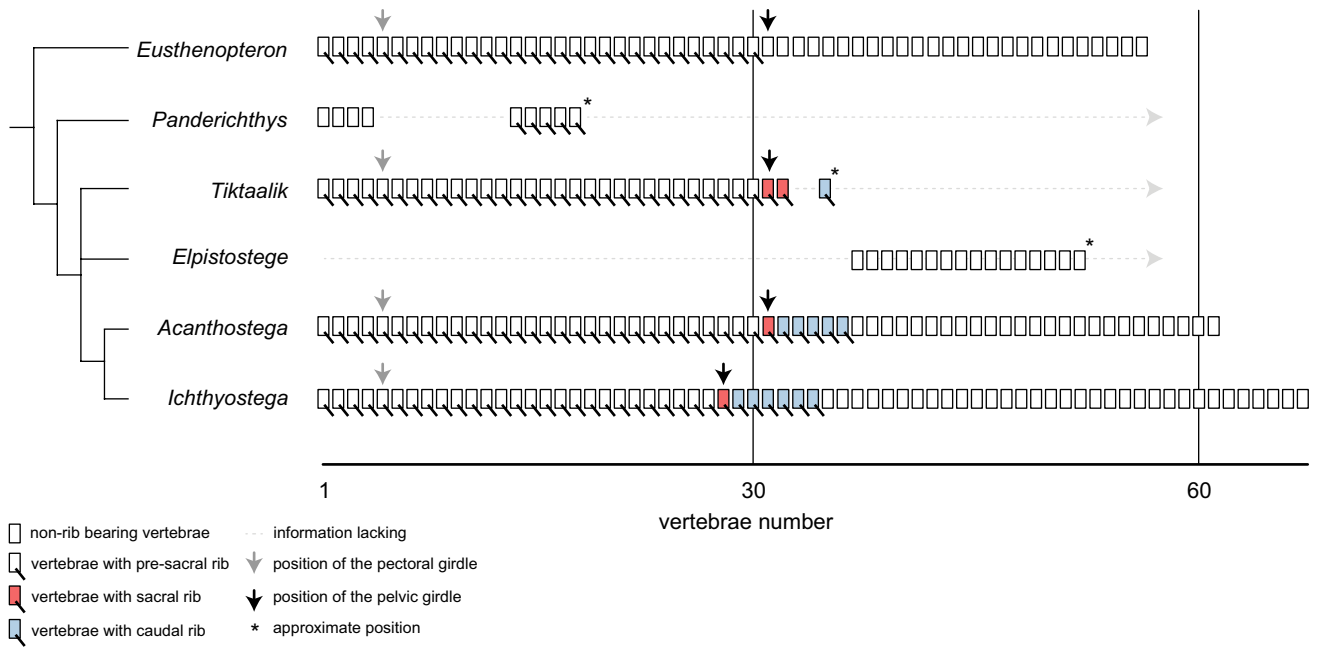
Fig. 4. Pelvic positioning in Devonian tetrapodomorphs. Data for *Tiktaalik* are based on NUFV 108. While only rib 31 shows an unfinished distal surface, rib 32 is also denoted as a sacral rib because of its ventral curvature and distinctness from caudal ribs. Data for other taxa are from the literature: *Eusthenopteron* (1, 8), *Panderichthys* (12–14), *Elpistostege* (15), *Acanthostega* (1), and *Ichthyostega* (2, 24). For *Panderichthys*, a series of four rib-bearing vertebrae are assigned to the trunk according to rib morphology, and their position is approximated. For *Elpistostege* a series of 16 vertebrae is assigned to be caudal vertebrae because they are not observed with ribs, although they might belong to the trunk with their ribs lost during preservation. Pelvic girdle position is based either on the vertebra dorsal to it (i.e., *Eusthenopteron*) or by regionalization of the vertebrae and ribs that indicate sacral connection (i.e., *Tiktaalik*, *Acanthostega*, *Ichthyostega*). Coding for pectoral girdle positioning follows Coates (1). The phylogeny is from ref. 25 and is the strict consensus tree of their maximum parsimony analysis.

vertebrae of *Eusthenopteron* both in degree of differentiation across the trunk and in overall construction, except for slight differences in intercentral fusion and in the ossification of pleurocentra (8). The number of trunk vertebrae in *Tiktaalik* is similar to other tetrapodomorphs; *Eusthenopteron*, *Acanthostega*, and *Ichthyostega* are each characterized by approximately 30 vertebrae rostral to the trunk-to-tail transition and pelvic position (1, 2, 8). While data on the vertebral counts of *Elpistostege* are not yet available, its trunk is predicted to be longer than *Tiktaalik* according to the more caudal positioning of its pelvic fins (29) (*SI Appendix*, Fig. S5).

In contrast to the vertebral column, the ribs of *Tiktaalik* show numerous derived features that are previously known only from
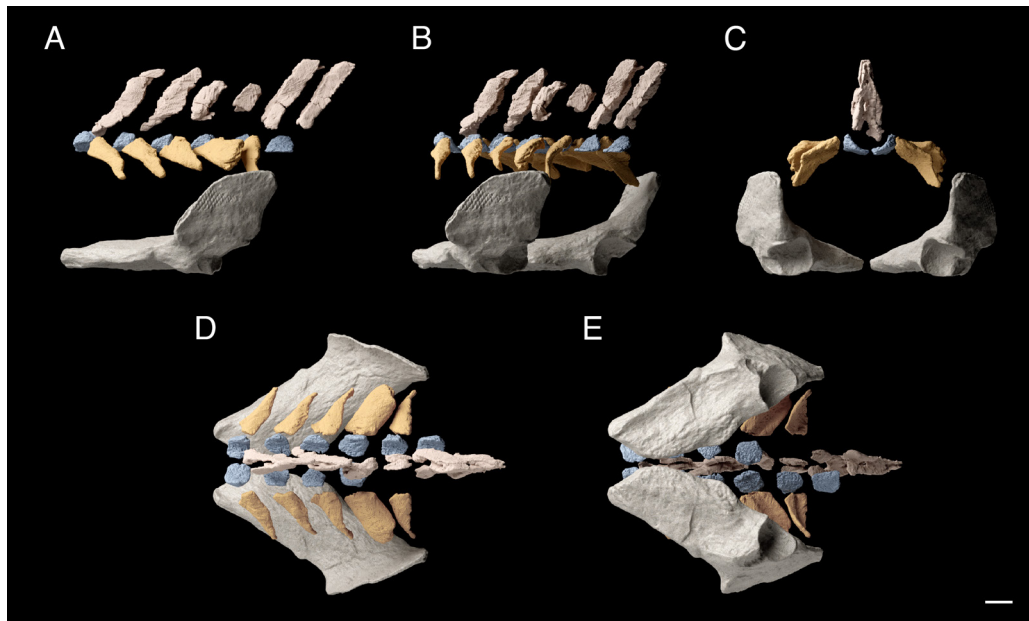

Fig. 5. Reconstructed position and orientation of the pelvic girdle of *Tiktaalik roseae*. Reconstruction of the axial column and pelvis in (*A*) left lateral, (*B*) posterior-oblique, (*C*) posterior, (*D*) dorsal, and (*E*) ventral perspectives. Ribs and pelvic girdle have been mirrored to produce the reconstruction. Ribs 31 and 32 are inferred to have supported the pelvic girdle by a ligamentous connection. (Scale bar, 1 cm.)
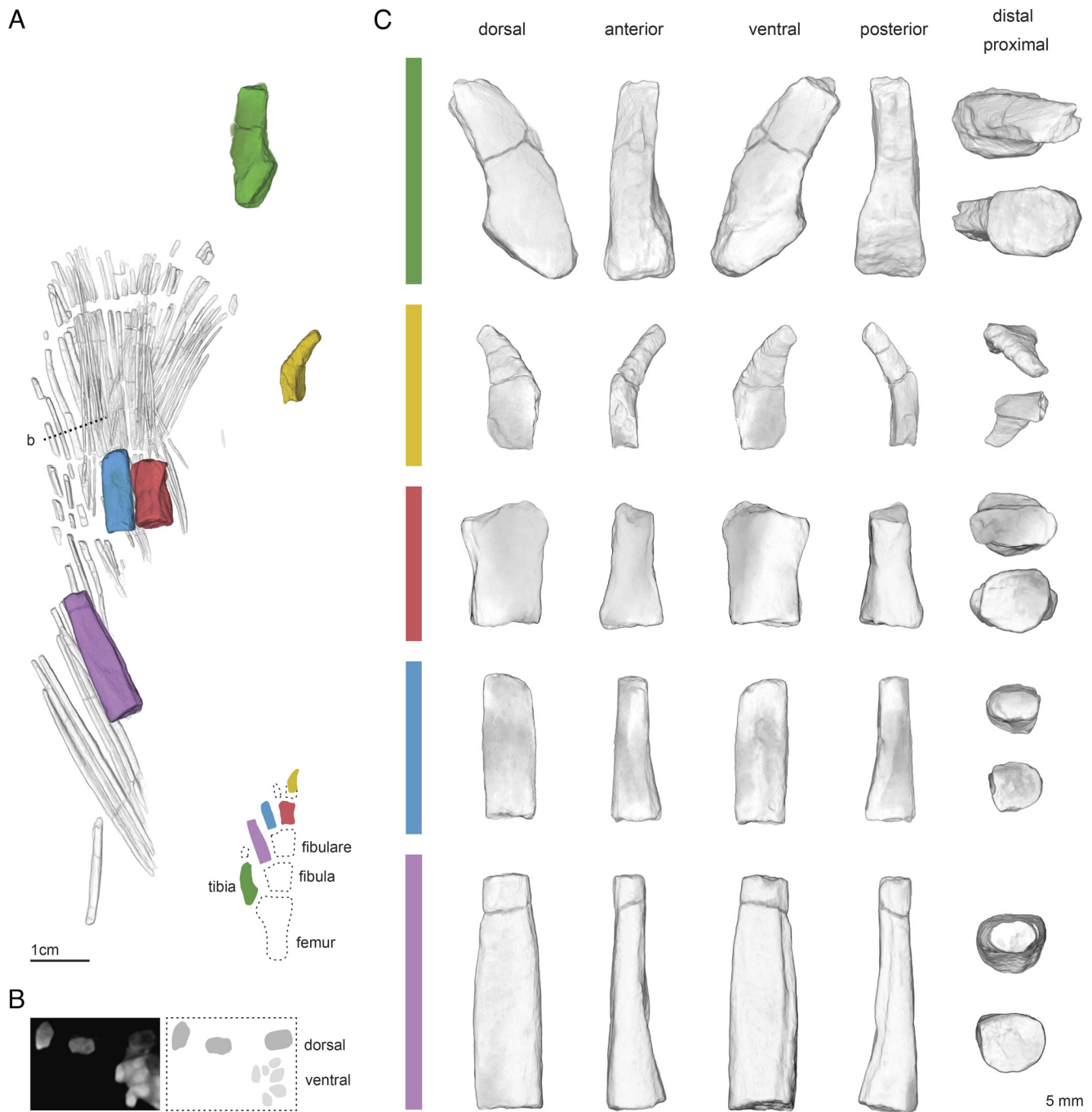
Fig. 6. Pelvic fin of *Tiktaalik roseae*. (*A*) Volumetric rendering of μCT data of the left pelvic fin of NUFV 108 and a reconstruction of the fin in ventral perspective. (*B*) Hemitrichia show dorso-ventral asymmetry. The digital cross-section, *Left*, and illustration, *Right*, were taken at the position of the dashed line labeled "b" in panel (*A*). The cross-section is oriented orthogonal to the plane of the fin web. (*C*) Endoskeletal elements of the pelvic fin in various orientations.

limbed taxa (Fig. 8). As in *Acanthostega* (1) and *Ichthyostega* (2), the ribs of *Tiktaalik* extend caudal to the trunk–tail boundary and are regionalized with a sacral module. This is a departure from the plesiomorphic tetrapodomorph pattern, seen in *Eusthenopteron*, where ribs do not extend caudal to the trunk–tail boundary and those near to the pelvis are not morphologically differentiated (8).

The rib anatomy of *Eusthenopteron*, coupled with a small ilium that does not closely approach the axial column, indicates the absence of a linkage between the axial column and pelvic fin (8, 19). In *Tiktaalik*, on the other hand, ribs 31 and 32 would have approached

the pelvic girdle, with ribs lying medial to the large, plate-like ilium. Although there is no evidence of a bony articulation, the nature of the expansion of both ribs and ilium and the unfinished distal margin of rib 31 suggest that a ligamentous connection was likely. Such a connection, also proposed to be present in early limbed forms, including *Acanthostega* (1), likely allowed for a degree of structural support and for a restricted range of motion between the elements. A ligamentous linkage between the girdle and axial column would have provided a less robust connection than direct bony articulation hypothesized for *Ichthyostega* (4) and observed more clearly in more crownward forms, like *Whatcheeria* (30). However, mobility of the
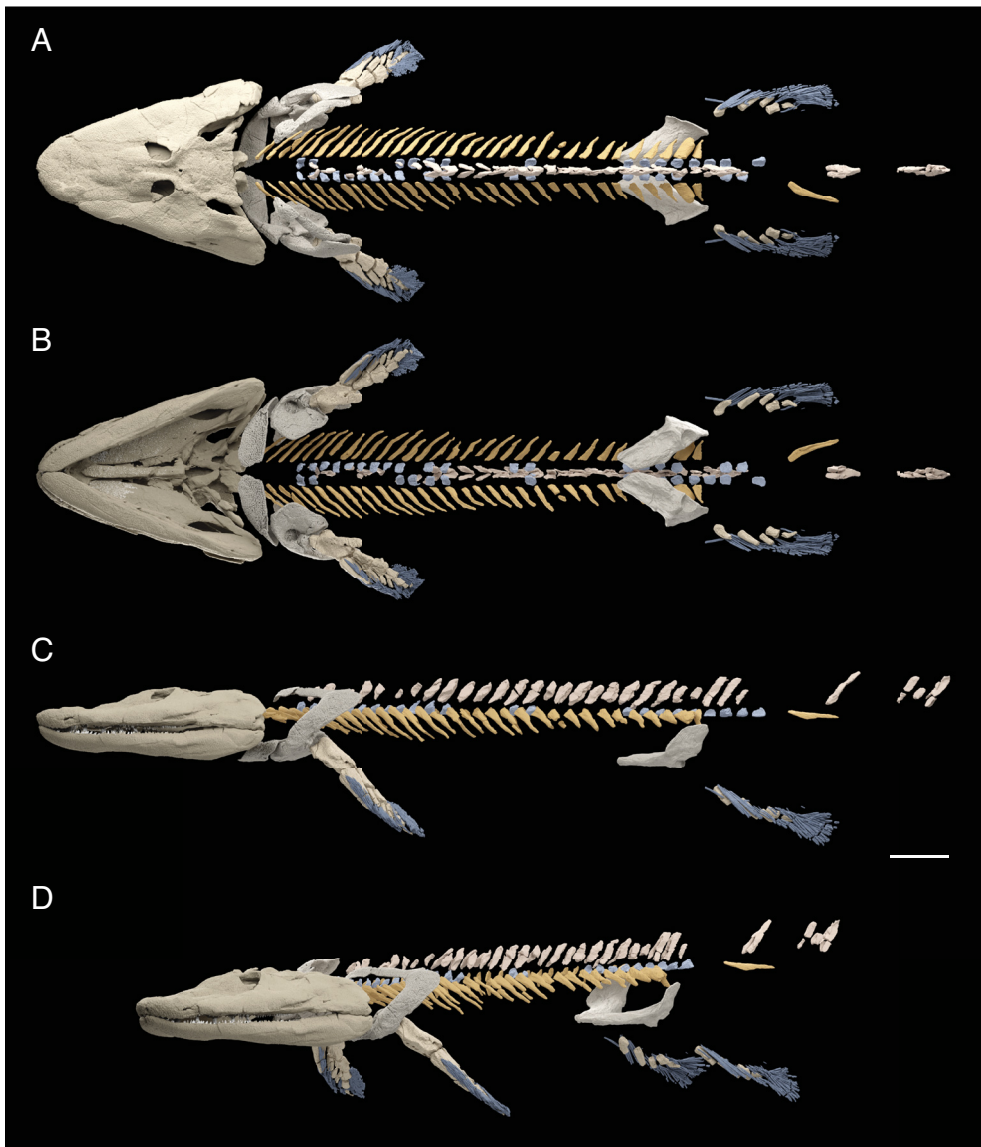
Fig. 7. Reconstruction of *Tiktaalik roseae*. Reconstruction in (*A*) dorsal, (*B*) ventral, (*C*) left lateral, and (*D*) oblique views. Cranial materials are repositioned according to ref. 18 to account for settling during preservation. Select elements that are preserved from only one side of NUFV 108 (i.e., pre-sacral ribs, pelvic girdle, and pelvic fin) are reflected for symmetry. The pectoral fin is from NUFV 110 (26) scaled to the length of the right humerus of NUFV 108. Additional skeletal elements are known for *Tiktaalik*, including branchial skeleton (11) and interclavicle (28), but have not been rendered here. A model showing only the materials of NUFV 108 (i.e., without duplications of certain features and with its original pectoral fin materials) is depicted in *SI Appendix*, Fig. S4. (Scale bar, 5 cm.)

pelvic girdle could have allowed for slight changes in the orientation of the acetabulum during locomotor behaviors. The post-cranial skeleton of *Tiktaalik*, therefore, reveals that sacro-iliac specializations arose in the ribs and pelvis prior to modifications to the vertebral column. Subsequent modifications to the axial column observed in limbed vertebrates include expansion of the dorsal extent of neural arches, either squared as in *Acanthostega* or rounded as in *Ichthyostega*, and the origin of zygapophyses (1, 2).

The presence of sacral ribs, robust pelvis, deep acetabulum, and large pelvic fin in *Tiktaalik* indicates that the rear appendage was generating greater forces in locomotion than is predicted of other elpistostegalian fishes, such as *Panderichthys*. In addition, these features suggest that *Tiktaalik* was capable of more axial support for the trunk when the pelvic fins were loaded against the substrate than less crownward elpistostegalians. Despite these apomorphic features, *Tiktaalik* retains numerous plesiomorphic characteristics in its pelvic anatomy, such a posteriorly facing acetabulum, left

and right pubes unfused along the midline, and lack of an ischium, which imply that the pelvic fin was not able to retract as extensively as limbed forms such as *Acanthostega* and *Ichthyostega* (16). The posterior orientation of the acetabulum of *Tiktaalik* and concomitant inability to use retraction for limb propulsion suggests that the pelvic fin was unable to play a significant role in terrestrial walking.

The body proportions of *Tiktaalik*, with pelvis and pelvic fin subequal in size to the shoulder girdle and pectoral fin, hew closer to those of *Acanthostega* (1) and *Ichthyostega* (2, 24) than to *Eusthenopteron* (8, 19), *Panderichthyes* (13, 17), and *Elpistostege* (29) (*SI Appendix*, Fig. S5). The pelvic and sacral anatomy of *Tiktaalik* indicates that its large pelvic appendage was stabilized by the axial skeleton and capable of being used in diverse paddling, walking, and propping behaviors on aquatic substrates. Such functions were likely antecedents to the terrestrial walking behaviors possible in limbed forms.
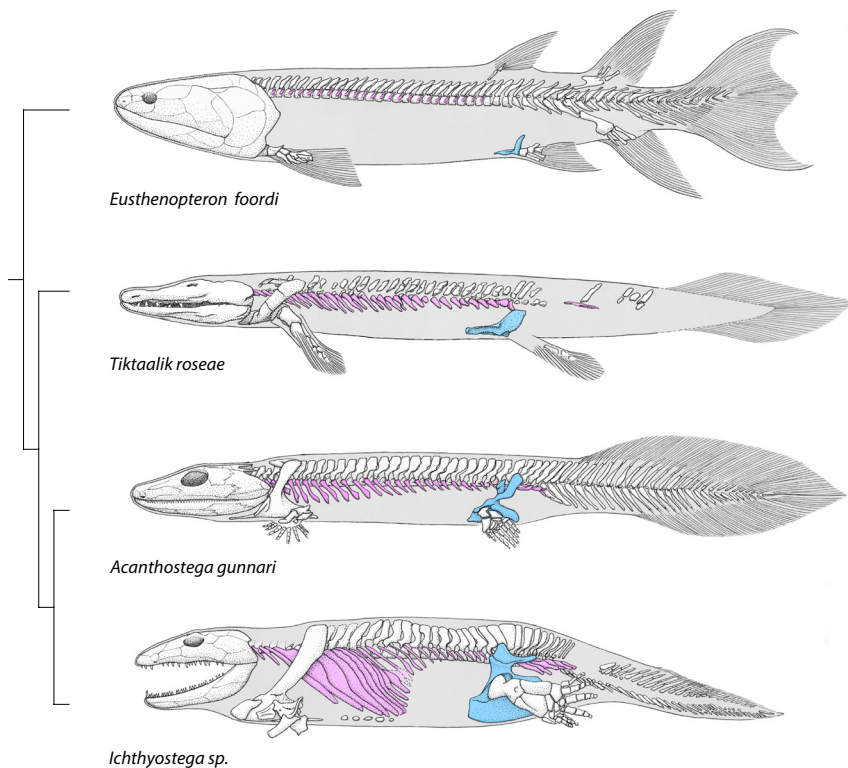
Fig. 8. Reconstructions of Devonian tetrapodomorphs. The anatomy of *Tiktaalik roseae* shows that specializations in the axial column for head mobility, body support, and pelvic fin buttressing had evolved in elpistostegalians prior to the origin of limbs. Illustration of *Tiktaalik roseae* based on NUFV 108. Illustrations of other taxa are based on previously published descriptions: *Eusthenopteron foordi* (8, 19), *Acanthostega gunnari* (1, 2), and *Ichthyostega sp.* (2, 24). Ribs are depicted in purple. Pelvic girdles are shown in blue.

Materials and Methods

Tiktaalik specimens were recovered during paleontological excavations near Bird Fiord on southern Ellesmere Island over six field seasons (2000, 2002, 2004, 2006, 2008, and 2013). All specimens were recovered from a single locality (NV2K17; N77°09.895′ W86°16.157′) within the Fram Formation (Frasnian Stage, Late Devonian) (11). The fossils are curated in the NUFV at the Canadian Museum of Nature.

Due to jacketing requirements in the field, NUFV 108 was collected in several blocks. Two large blocks contained the head and trunk. A third block, which was contiguous to the block containing the pelvic fin, contained the right pelvic girdle. At the time of collection, only a small slice of the bone was visible, and it was not until 2008, when the material was mechanically prepared, that the pelvis of NUFV 108 was revealed.

We present data μCT data for NUFV 108 that allow for a description of the vertebral column and for a redescription of the ribs of *Tiktaalik*. To better understand the functional morphology of *Tiktaalik*, we also produce a three-dimensional reconstruction that contains nearly all elements known for the taxon (*SI Appendix, Supplementary Text*). This reconstruction contains surface models generated from the μCT datasets, a surface scan of the right pelvis of NUFV 108, and surface models from previously published studies of the head of NUFV 108 (18) and pectoral fin of NUFV 110 (26).

μCT Scanning. The μCT scans of NUFV 108 were collected at The University of Chicago's PaleoCT scanning facility with a GE Phoenix v|tome|x 240 kv/180 kv scanner. The vertebrae and ribs of NUFV 108 are contained in two large blocks, which also contain the specimen's pectoral and pelvic fins (Movie S1). These blocks were too large for single multiscan. Therefore, each block was scanned twice: first oriented vertically with the rostral edge down and then rotated 180° and scanned again with the caudal edge down. Scanning parameters for these four scans are provided in *SI Appendix*, Table S1. μCT data were reconstructed with Phoenix Datos|x 2 (version 2.3.3), imported to VGStudio Max (version 2.2) for cropping, and exported as a tiff stack. For each block, the two multi-scans were manually stitched together and then manually segmented in Amira (version 20.2) (Thermo Fisher Scientific).

Surface Scanning. The right pelvis of NUFV 108 was collected in a palm-sized block contiguous with the blocks that were μCT scanned. The pelvis was previously exposed by mechanical preparation, and a three-dimensional model of the element was produced by surface scanning a cast of the element with a FARO Design ScanArm 1.0 at a resolution of 40 to 75 μm.

Images and Animations. Volumetric images of the segmented μCT data were generated using Amira (Figs. 1, 2, and 6 and *SI Appendix*, Figs. S1 and S2). All other renderings of skeletal elements are of surface models, which were generated from the segmentation label fields of Amira or directly by surface scanning. Surface models were visualized in Blender (version 3.3.1). Movies were created by exporting animations as tiff stacks from Amira or Blender and then using Adobe Premier (version 13.12) to combine and edit the images into movies.

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