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ARTICLES

The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb

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Wrists, ankles and digits distinguish tetrapod limbs from fins, but direct evidence on the origin of these features has been unavailable. Here we describe the pectoral appendage of a member of the sister group of tetrapods, *Tiktaalik roseae*, which is morphologically and functionally transitional between a fin and a limb. The expanded array of distal endochondral bones and synovial joints in the fin of *Tiktaalik* is similar to the distal limb pattern of basal tetrapods. The fin of *Tiktaalik* was capable of a range of postures, including a limb-like substrate-supported stance in which the shoulder and elbow were flexed and the distal skeleton extended. The origin of limbs probably involved the elaboration and proliferation of features already present in the fins of fish such as *Tiktaalik*.

A landmark event in vertebrate history is the transformation of fish fins into tetrapod limbs. Insights into this transition illuminate the biological mechanisms that generate major shifts in developmental genetics[1–6], skeletal structure[7,8] and biomechanics[9–11]. Limb skeletons differ from those of fins mainly by the presence of bones that comprise mobile wrists, ankles and digits. In addition, limbs lack the extensive array of lepidotrichia, which are dermal rods that form much of the surface area of fins.

An impediment to understanding the fin–limb transition has been the nature of available evidence from the sister group of tetrapods. The closest living relatives of tetrapods—lungfishes and coelacanths—either lack homologous elements to distal limb bones or are so specialized that comparisons with tetrapods are uncertain. Sarcopterygian taxa with possibly intermediate morphologies are restricted to fossil forms from the Palaeozoic era. A Devonian rhizodontid, *Sauripterus*, is known to possess digit-like radials, but phylogenetic analyses indicate that this group is not the closest relative of tetrapods[12–14]. The current hypothesis is that the sister group of tetrapods are elpistostegids[15,16], sarcopterygians known from Quebec and Latvia[17–20]. Unfortunately, the distal region of the best-known pectoral fin of the elpistostegid *Panderichthys* is covered by lepidotrichia and the complete distal endoskeleton is unknown[11]. A strict interpretation of this taxon has led to proposals that the distinctive features of tetrapod limbs are novelties, with few antecedents in fish fins[1–6,8]. If this scenario is true, then the origin of tetrapods involved major changes in skeletal patterning and appendage function. Palaeontological data thus have a uniquely important role in interpreting the origin of limbs.

The discovery of *Tiktaalik roseae*[21] brings new data to bear on these issues. The material is remarkable for its phylogenetic position, three dimensional preservation and abundance. As a member of the sister group of limbed vertebrates, *Tiktaalik* can reveal the primitive pattern from which limbs were derived. Articulated pectoral fins have been prepared from three different specimens, two of which preserve the anatomical relations of endochondral bones, lepidotrichia and scales (Figs 1 and 2; see also Supplementary Information). There is little variation in articular design or appendage proportions despite a twofold difference in size between the smallest (Nunavut Fossil Vertebrate Collection (NUFV) 108) and largest (NUFV 109) fins. Left and right fins of NUFV 109 were disarticulated and individual bones prepared free to expose the joint surfaces and articular relationships (Supplementary Information). Multiple specimens record details of bony anatomy and articular geometry for major elements of the appendage, providing a high degree of confidence in the fin reconstruction and the interpretation of joint function (Fig. 2).

In overall structure, the pectoral girdle and fin of *Tiktaalik* are distinguished from those of other tetrapodomorph fish in having an expanded endoskeleton and a relatively reduced dermal exoskeleton (Figs 1–3; see also Supplementary Information). The lepidotrichia are solid rods that remain unjointed for most of their length and invest the endochondral bones dorsally and ventrally (Fig. 1; see also Supplementary Information). The lepidotrichial sheath is heterogeneous; lepidotrichia that cover anterior endochondral bones are more robust and originate more proximally than those on the posterior side (Fig. 1a). Along the fringe of the fin distal to the last endochondral radials these rods are extensively jointed. The fin is relatively stouter and anteroposteriorly narrower than the fins of other tetrapodomorph fishes (Fig. 4).

Comparative anatomy of the pectoral girdle

The shoulder of *Tiktaalik* is highly derived with a suite of features only known in tetrapods and *Panderichthys*. The endochondral components (scapula and coracoid) of the pectoral girdle are enlarged and the dermal series (cleithrum, clavicle, anocleithrum and supracleithrum) is relatively reduced (Figs 3 and 5a, b). Scapular height is increased relative to that of tristichopterids via a broad process that extends dorsal to the glenoid to lie flush against the medial aspect of the cleithrum, as in rhizodontids (Figs 3 and 5b). The glenoid is oriented posteroventrolaterally and partially exposed in lateral view, which is intermediate between the posterior orientation of the glenoid in *Eusthenopteron*[9] and the lateral orientation of *Acanthostega*[22] and other basal tetrapods[23] (Figs 3 and 5a). In addition, the glenoid lies adjacent to the ventral surface of the coracoid, and accordingly the fin projects from the body near the level of the belly, as in *Panderichthys*[24] (Figs 3 and 5a, b). The coracoid

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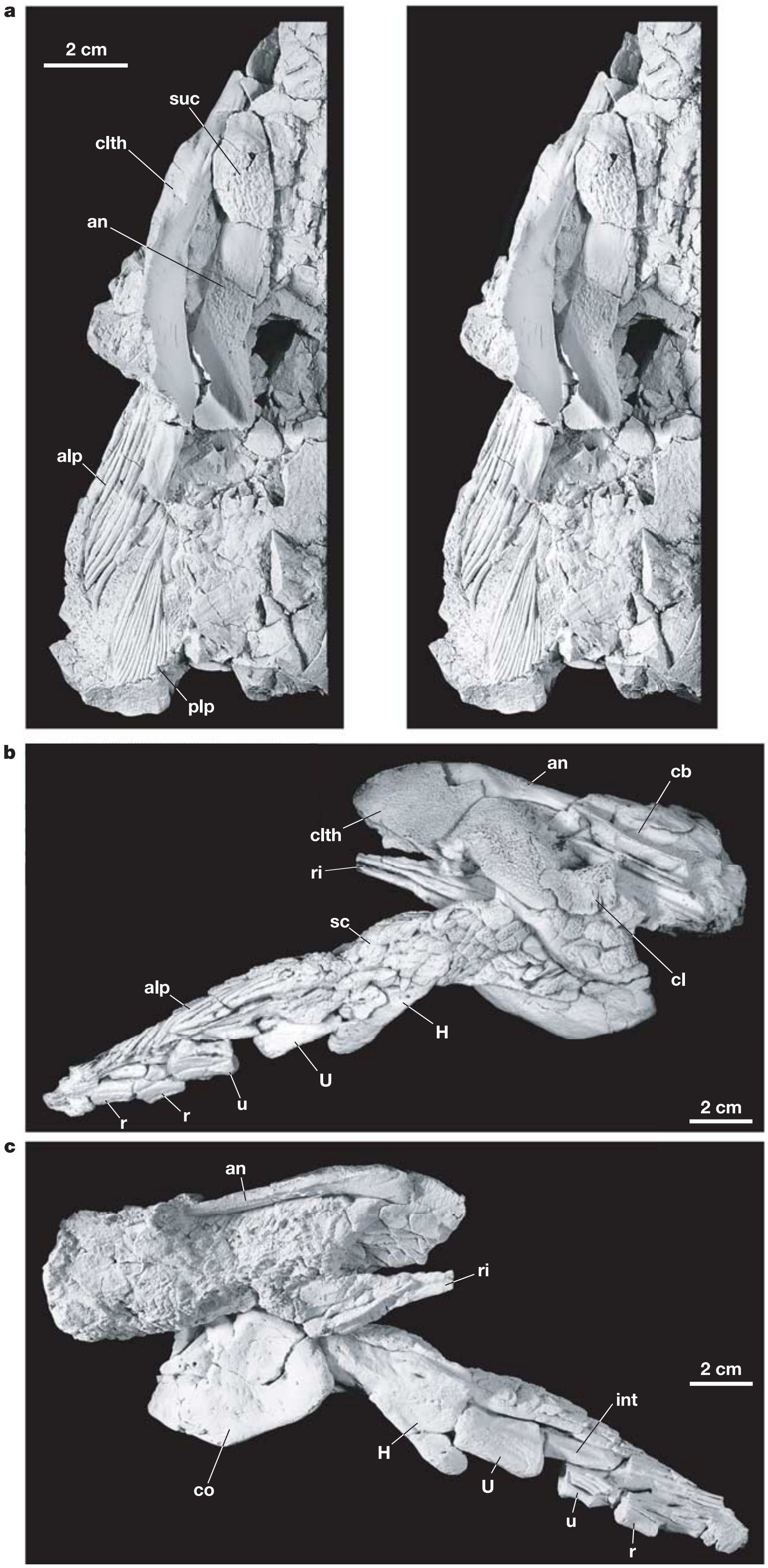

Figure 1 | **Articulated pectoral fins of *Tiktaalik roseae*.** **a**, Stereo pair of left pectoral fin of NUFV 108 in dorsal view showing disparity in size and position of anterior (alp) and posterior (plp) unjointed lepidotrichia and the relative position of dermal girdle elements. **b**, Right pectoral fin of NUFV 110 in anterior view showing preservation of anterior lepidotrichia (alp), clavicle (cl), scales (sc) and endochondral bones in articulation (H, humerus; U, ulna; u, ulnare; r, radials). The anterior lepidotrichia terminate at the elbow, thus allowing a full range of flexion at that joint. **c**, Right pectoral fin of NUFV 110 in ventral view showing positions of coracoid (co) and endochondral and dermal fin elements. an, anocleithrum; cb, ceratobranchial; clth, cleithrum; int, intermedium; ri, rib; suc, supracleithrum.

is a ventrally positioned, horizontally oriented plate that is perforated by a large foramen with a diameter of approximately one-quarter the mediolateral width of the bone (Figs 1c and 3a, b; see also Supplementary Information). A coracoid foramen of comparable size is only known in *Panderichthys*[24]. The prominent external and internal rims of the coracoid foramen are each interrupted by a sulcus (Supplementary Information). The ventromedial sulcus of the internal rim is aligned with the dorsolateral sulcus of the external rim, an arrangement that is compatible with the transmission of a neurovascular or muscular structure. We interpret the sulci as indicative of a musculotendinous bundle that extends from an origin on the dorsomedial surface of the coracoid plate to an insertion on the ventral surface of the humerus. The coracoids of *Tiktaalik* and *Panderichthys* are generally more massive and thicker than those of either *Acanthostega*[22] or *Hynerpeton*[23]. Whereas the cleithrum, anocleithrum and supracleithrum of *Tiktaalik* are reduced relative to those in other tetrapodomorph fish, the ornamentation on their exposed surfaces is a primitive retention. Notably, the dermal series is reduced to the point where the pectoral girdle has no bony connection with the skull—the extrascapular series, suboperculum and operculum are absent[21].

Comparative anatomy of the pectoral fin

The endochondral bones of the pectoral fin of *Tiktaalik* combine features of *Eusthenopteron* and *Acanthostega*, and in some aspects are intermediate. A robust ventral ridge, similar to that in *Eusthenopteron*[9], extends diagonally across the long axis of the humerus, from the anterior margin of the humeral head to the distal tip of the entepicondyle (Figs 2 and 5c). The leading margin of the humerus is a narrow, strap-shaped surface comparable to those in *Acanthostega*[22] and ANSP 21350 (ref. 25). On the dorsal surface, the ectepicondyle is a prominent, distally directed process that extends to the level of the ulnar and radial facets (Fig. 2), much as in basal tetrapods but in contrast to *Eusthenopteron*. The radius is elongate, tapered distally and slightly cambered ventrally (Fig. 2). Unlike the radii of tetrapods and other tetrapodomorphs, with the exception of *Panderichthys*[11], the leading margin of the radius forms a sharp crest, whereas the posterior edge is sub-cylindrical. The ulna retains a primitive cuboidal shape and lacks the olecranon process of tetrapods. The ulnare resembles that in tetrapods and *Sauripterus*[14] in the absence of a postaxial process and in the presence of multiple articular facets for distal radials (Figs 2, 4 and 6d). Unlike *Sauripterus*, these facets are evidence of synovial joints that promote inter-osseous movement. In *Tiktaalik*, the ulnare articulates with four proximal radials, whereas the intermedium articulates with only one (Figs 2 and 6d). An important functional aspect of the articulations is that the five radials share a common axis of flexion/extension that runs anteroposteriorly across the fin. The third radial in the proximal series is enlarged and supports three intermediate radials at joints that are also aligned anteroposteriorly. The central radial of this triplet is, itself, enlarged and articulates with two distal radials. Accordingly, the ulnare and enlarged proximal and intermediate radials establish a central axis to the fin, a feature common to basal sarcopterygians[7,26] but unknown in tetrapodomorphs.

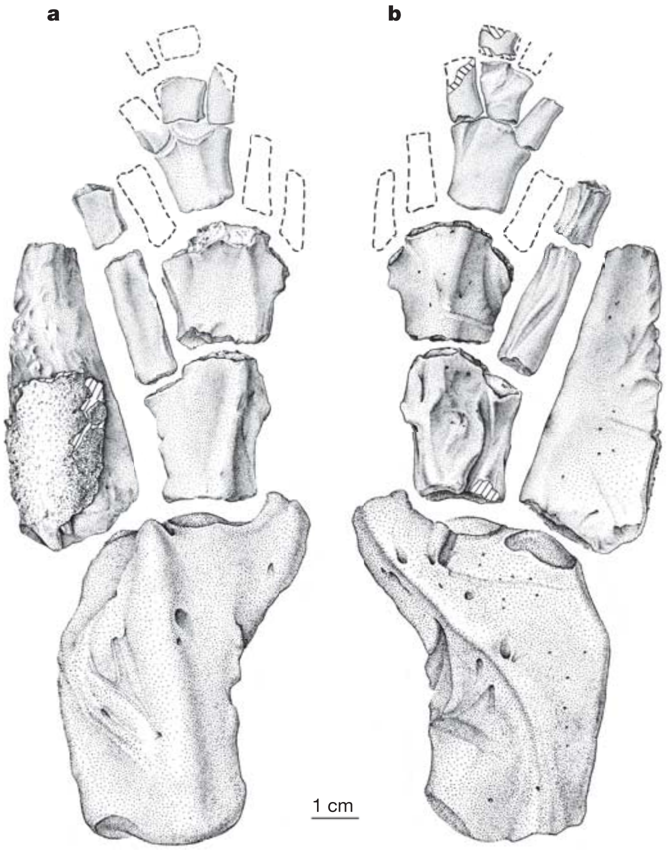

Figure 2 | **Reconstruction of the right pectoral fin of *Tiktaalik*. a**, Dorsal view; **b**, ventral view. Elements with stipple shading were preserved in articulation in NUFV 109 and prepared in the round. Elements with a dashed outline are reconstructed based on their presence in the articulated distal fin of NUFV 110. It is not known how many radials lie distal to the first, second and fourth in the proximal series. Note the dorsal expansion of the distal articular facets on the ulnare and third distal radial/mesomere. The dorsal expansion of these facets would have facilitated extension of the distal fin.

Functional anatomy

An assessment of joint excursions and fin postures and functions in *Tiktaalik* is made possible by the preservation, in multiple specimens, of complete bony articular surfaces of all the major joints of the shoulder and fin (Fig. 6). The excursions possible at each joint may be inferred from the articular geometry, in particular the curvatures of apposing cartilage-covered surfaces. Although this soft tissue is not preserved, the curvature is unlikely to have been less than that preserved as the bony supporting surface of the joint, and could possibly have been greater.

Most of the glenohumeral joint is composed of a large hemispheroidal humeral head articulating with an ovoid, concave glenoid (Fig. 6a). Typically, this kind of joint geometry permits three degrees of freedom: rotation (supination/pronation), flexion/extension (elevation/depression) and protraction/retraction. In the case of *Tiktaalik*, however, some restriction of humeral mobility is engendered by cranial extensions of the articular surfaces of the glenoid and humeral head (Figs 3d and 6a; see also Supplementary Information). These accessory facets—a shallowly concave, elongate humeral facet and a convex glenoid facet—are brought into contact as the humerus is pronated, flexed and protracted. Pronation, flexion and protraction are movements that could have been effected by the large musculotendinous apparatus passing posterolaterally through the coracoid foramen and inserting on the ventral surface of the humerus. The simultaneous apposition of the reversed concavoconvex geometries of the anterior and posterior parts of the articulation represents a close-packed, or most stable, joint position. Additional stability would be contributed through the action of the trans-coracoid musculature. With the anterior facets of the glenohumeral joint in full contact, however, protraction and supination are inhibited, and flexor forces simply compress and stabilize the humerus against the anterior portion of the glenohumeral joint.

The joints of the elbow provide evidence of the independent mobility of the radius and ulna (Figs 6b and 7). As in *Acanthostega*[22], the humeral facets for the radius and ulna are separate from one another, in contrast to the confluent facets in *Eusthenopteron*[9] and other non-tetrapodomorph fishes[25]. The radial facet is smaller than and anteroventral to the ulnar facet. Neither facet faces exactly distally; both are slightly ventrally oriented, with the radial facet more so than the ulnar. On this evidence the antebrachium would have been slightly flexed in the rest position, with the radius more flexed than the ulna.

Joint geometry provides evidence of the movements possible at the elbow. In outline the convex radial facet of the humerus is a bent ellipsoid; the apposing facet on the radius is a simple, oval concavity (Fig. 6b). Given these shapes, the radius was not capable of independent rotation on the humerus without conjunct translation. The radial facet forms a curved pathway on the humerus: the anterior portion of the facet's surface is nearly in the plane of the ventral surface of the humerus, whereas the posterior part of the facet faces more distally. Accordingly, translation of the radius along this facet provides for a small degree of pronation and supination. The bulbous ulnar facet of the humerus is principally oval in outline and hemispheroidal. The humeral facet of the ulna is a shallow concavity that occupies the entirety of the subrectangular proximal end of the bone. The simple geometry of the humeroulnar joint readily accommodates flexion/extension, protraction/retraction as well as rotation.

Joints distal to the ulna are formed by low convexities proximally and shallow concavities distally, and thus permitted three degrees of freedom (flexion/extension, ab/adduction and rotation) (Fig. 6c, d). On the intermedium, ulnare and the largest of the proximal radials the distal articular surfaces extend onto the dorsal surfaces, indicating that extension was of predominant importance (Fig. 2a; see also Supplementary Information). The mobility of distal segments of the fin of *Tiktaalik* is further augmented by the transverse alignment of the joints distal to the epipodials (Figs 6 and 7). At least three transverse alignments are presently recognized: one at the joints distal to the radius, intermedium and ulnare; another at the joints distal to the next set of radials; and a third between the intermediate and distal radials. Additionally, numerous processes and rugosities, particularly on the ventral surfaces on the ulna, ulnare and distal radials, are suggestive of the presence of an extensive musculotendinous apparatus to control these fin segments (Fig. 2b). Not surprisingly, the enhanced mobility of a well-developed distal endoskeleton is accompanied by an apparent reduction in the length of the distal lepidotrichia (Supplementary Information).

Fin posture and function in *Tiktaalik*

The sister group of tetrapods[23] is now known to include fish with pectoral fins that can assume both fin-like and limb-like postures. In a quasi-planar position, with minimal flexion of the antebrachium,

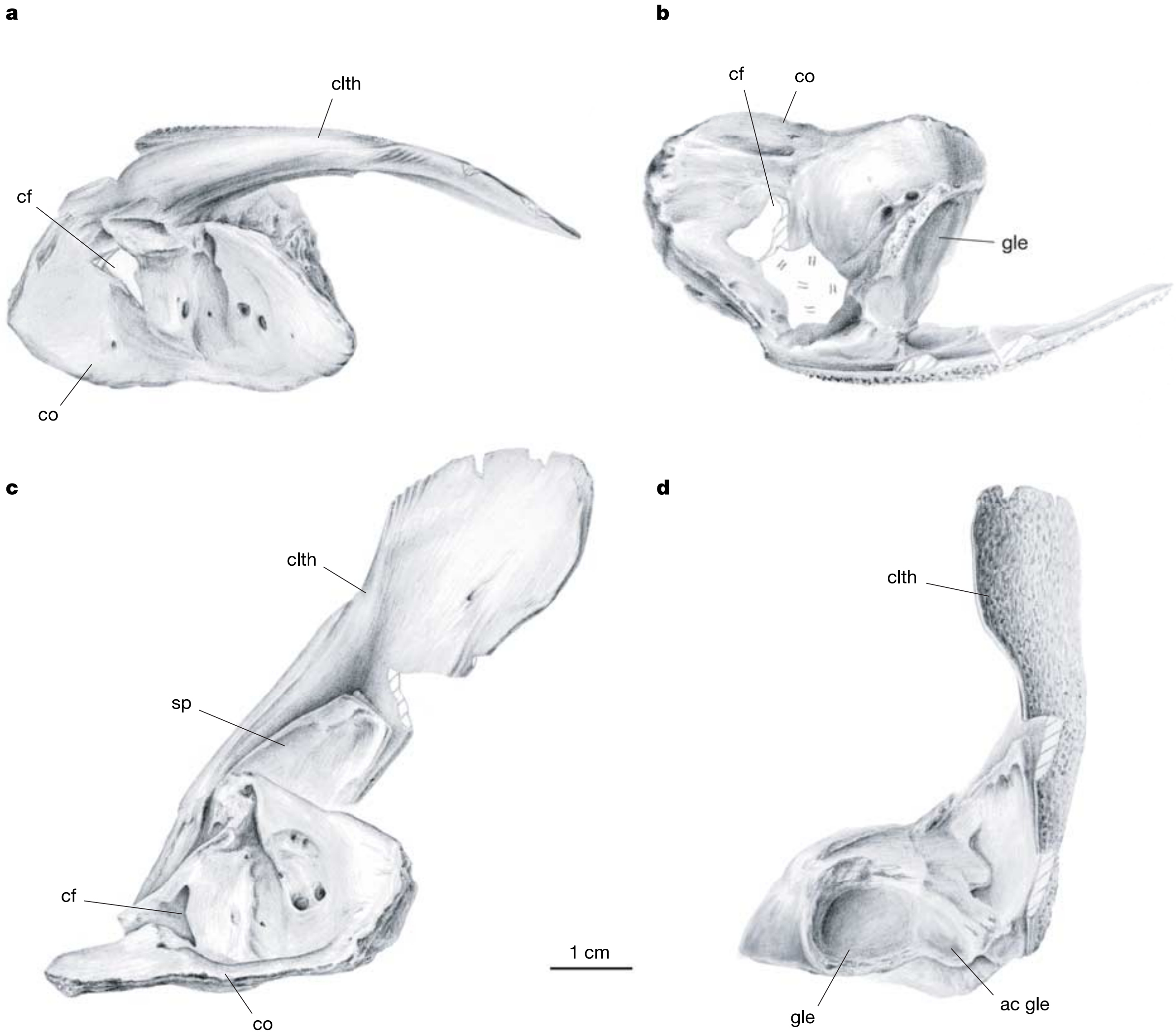

Figure 3 | **Isolated right shoulder girdle of *Tiktaalik* (NUFV 112).** **a**, Dorsal view; **b**, ventral view; **c**, medial view; **d**, posterior view. ac gle, anterior cam of glenoid facet; cf, coracoid foramen; clth, cleithrum; co, coracoid; gle, glenoid facet; sp, scapular process. The hatched area is covered by matrix.

the fin approximates a generalized posture for a sarcopterygian such as *Eusthenopteron*[9] (Fig. 7a, c). But the fin could also assume a posture appropriate for a substrate-supported, upright stance by flexing the shoulder and elbow and extending the proximal and distal inter-radial joints (Fig. 7b, d). Multiple features enable the fin to prop the body in a limb-like manner: the base of the fin is positioned near the ventral surface of the body; glenohumeral architecture and trans-coracoid musculature augment flexion and stability at the shoulder joint; a broad and deep posterior glenoid allows transmission of substantial propulsive stresses through the pectoral girdle; a robust coracoid plate provides broad areas for flexor muscle origins; elaborate ventral processes on the humerus represent extensive surface area for flexor insertions; flexion/extension, pronation/supination and rotation are possible at the elbow; and there is an expanded series of mobile proximal, intermediate and distal radials distal to the epipodials. Notably, the highly mobile yet robust distal fin segments could provide a stable but compliant extremity that could conform to complex and varied substrates.

The interpretation that the fins of *Tiktaalik* were used in supporting the body on a substrate is corroborated by the architecture of the axial skeleton. Expansion and imbrication of the ribs is a feature previously unknown in fish but seen in some early tetrapods such as *Ichthyostega*[21,27]. The mechanical reinforcement of the spine engendered by costal overlap, together with a robust and mobile fin, suggest that both the axial and appendicular systems were playing a role in supporting the weight of the animal. With a dorsoventrally compressed head and body, raised and dorsally placed eyes, and a mobile head that is independent of the shoulder girdle, *Tiktaalik* possesses a range of features consistent with locomotion on the water bottom, along the water margins, and on subaerial surfaces—an interpretation that is in accord with the shallow meandering stream deposits from which *Tiktaalik* was recovered[21].

Tiktaalik and limb origins

The pectoral fins of *Tiktaalik* reveal that development of robusticity and mobility of the distal skeleton was underway before the origin of tetrapods. The array of joints in the distal fin is functionally similar to the multiple transverse joints that characterize the carpal, metacarpophalangeal and interphalangeal joints of the tetrapod manus. The distal endoskeleton of *Tiktaalik* invites direct comparisons to the wrists and digits of limbed vertebrates. The intermedium and ulnare of *Tiktaalik* have homologues to eponymous wrist bones of tetrapods with which they share similar positions and articular relations. In both *Tiktaalik* and early tetrapods, the ulnare is block-shaped and articulates with multiple radials or digits, whereas the intermedium is a simple rod. The formation of a mobile transverse joint at the distal margin of these bones in *Tiktaalik* presages the establishment of a functional proximal carpal joint. As in the digits and phalanges in a tetrapod limb, the inter-radial joints distal to this primordial wrist are more or less transversely aligned and capable of flexion and extension. The occurrence of multiple distally facing radial rows that

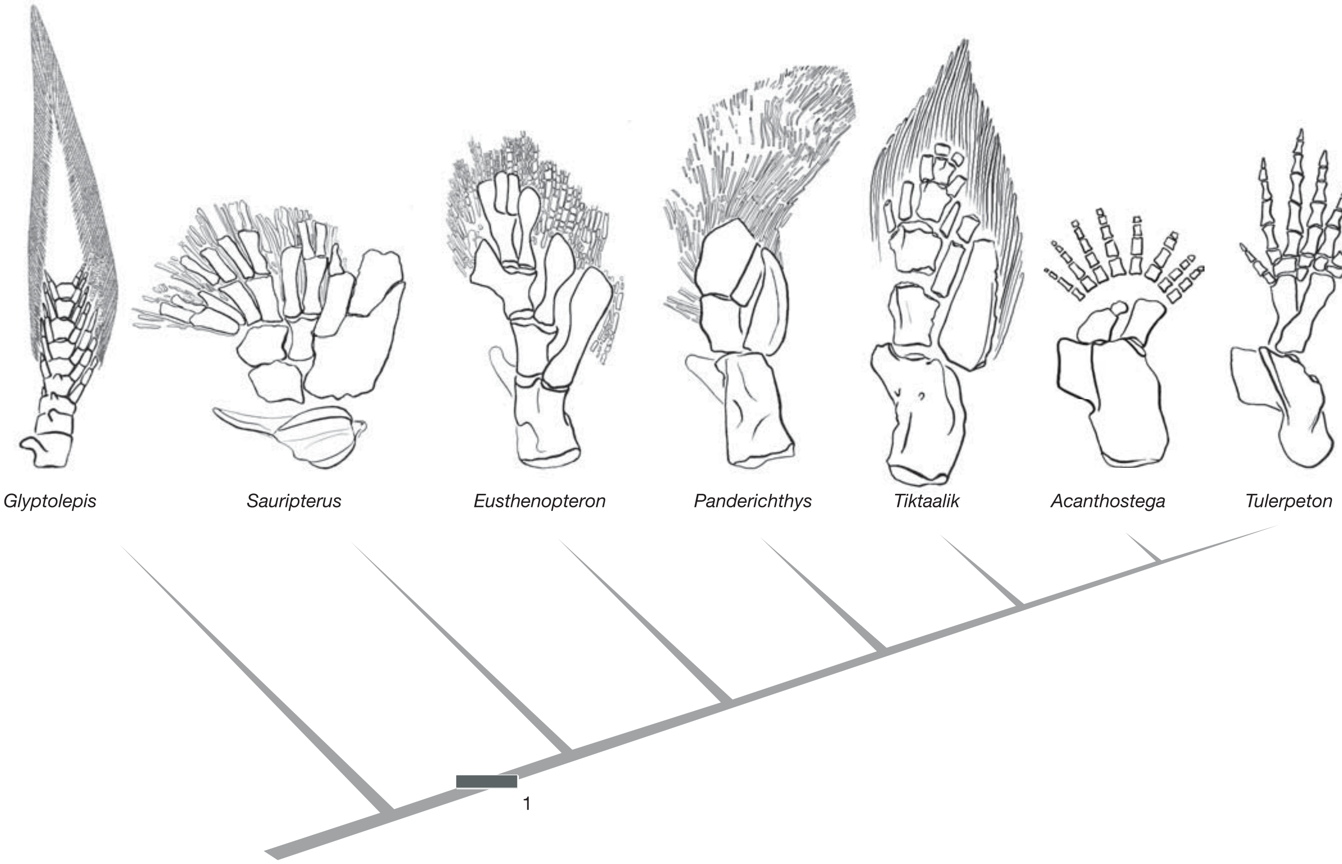

Figure 4 | Cladogram of the pectoral fins of taxa on the tetrapod stem. Unlike other tetrapodomorph fishes (1), *Tiktaalik* has reduced the unjointed lepidotrichia, expanded the radials to a proximal, intermediate and distal series, and established multiple transverse joints in the distal fin. The fin also retains a mosaic of features seen in basal taxa. The central axis of enlarged endochondral bones is a pattern found in basal sarcopterygians and accords with hypotheses that a primitive fin axis is homologous to autopodial bones of the tetrapod limb. In some features, *Tiktaalik* is similar to rhizodontids such as *Sauripterus*. These similarities, which are probably homoplastic, include the shape and number of radial articulations on the ulnare, the presence of extensive and branched endochondral radials, and the retention of unjointed lepidotrichia. Figures redrawn and modified from *Glyptolepis*[31], *Eusthenopteron*[9], *Panderichthys*[32], *Acanthostega*[22] and *Tulerpeton*[33].

are capable of flexion and extension is a likely antecedent condition to the dactyly of early tetrapods. The transformation of fins to limbs, then, probably entailed the elaboration and proliferation of structures, joints and functions already present in the fins of fish such as *Tiktaalik*.

The notion that the autopod is a developmental novelty of tetrapods may have been an artefact of relying exclusively on derived teleosts, such as zebrafish, in the analysis of limb origins[1–6]. Zebrafish lack any fin bones homologous to tetrapod limbs. Therefore, a comparison of developmental mechanisms between zebrafish and tetrapods may be too coarse to provide insight into the developmental shifts that transformed fins—such as those in *Tiktaalik*—into the limbs of tetrapods. Accordingly, studies of the genetic basis of cartilage patterning in more basal actinopterygians or sarcopterygians may ultimately be more informative of the transformations that occurred in the Devonian period[28–30].

The presence of an elaborate tetrapod-like distal endoskeleton in rhizodontids and *Tiktaalik* may reflect the great antiquity of this feature or its parallel evolution in the two groups[14]. The kinematics of the endoskeleton, however, differ between these two taxa. Unlike rhizodontids, such as *Sauripterus*[14], the distal endoskeleton of both *Tiktaalik* and tetrapods contains multiple joints capable of extensive degrees of flexion and extension.

A fin axis that extends distal to the ulnare has been unknown in any tetrapodomorph[7] until the discovery of *Tiktaalik*. As in porolepiforms and dipnoans, the axis of *Tiktaalik* lies in the centre of the fin. If the five radials of *Tiktaalik* are homologous to digital rays, then the axis of the tetrapod limb would extend from the humerus through digit three. Unfortunately, the absence of a well-defined axis in other tetrapodomorphs leaves uncertain whether a central axis is primitive for tetrapods or if it evolved separately in *Tiktaalik*. Testing these competing hypotheses awaits the discovery of other tetrapodomorph fins with axes that project into the distal fin.

The pectoral skeleton of *Tiktaalik* is transitional between fish fin and tetrapod limb. Comparison of the fin with those of related fish reveals that the manus is not a *de novo* novelty of tetrapods; rather, it was assembled in fishes over evolutionary time to meet the diverse challenges of life in the margins of Devonian aquatic ecosystems.

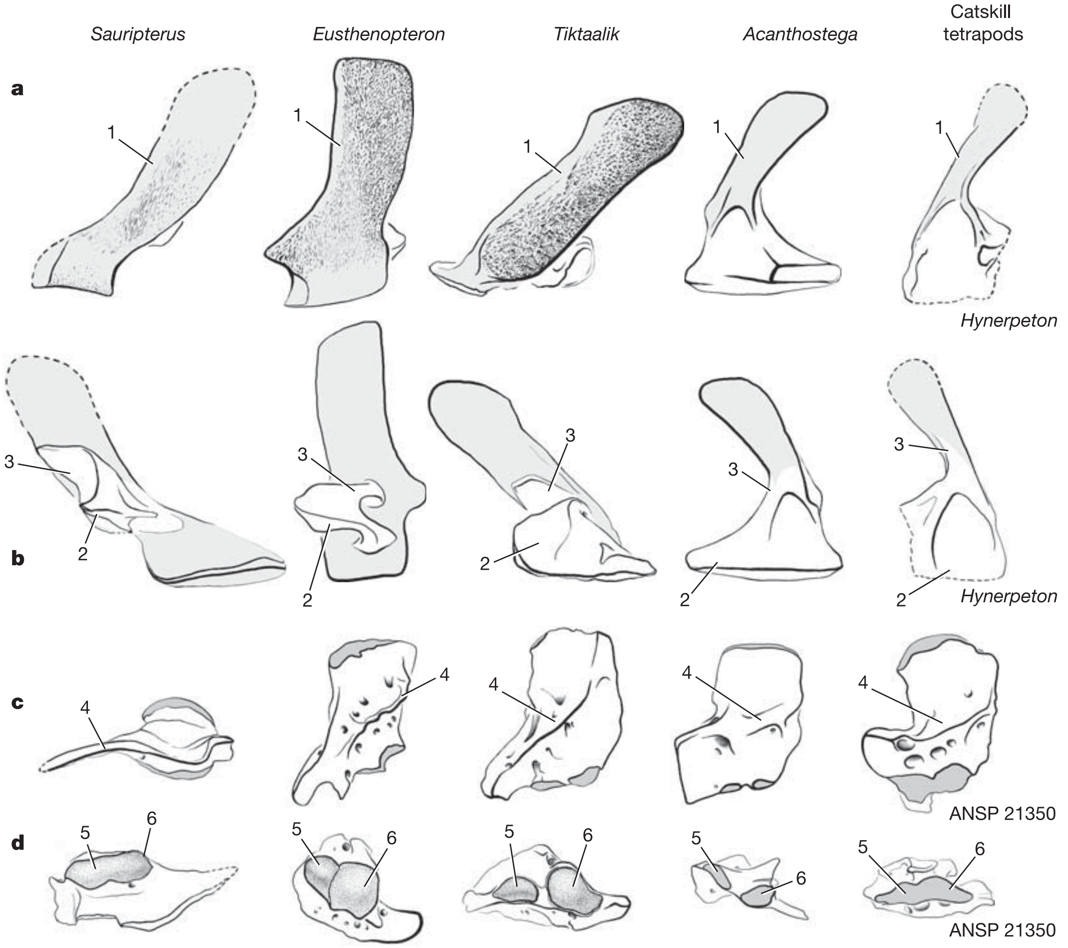

Figure 5 | **A comparison of pectoral girdles and humeri in taxa along the tetrapod stem.** **a**, **b**, Left pectoral girdles in lateral (**a**) and medial (**b**) views (dermal bone shaded). **c**, **d**, Left humeri in ventral view (**c**; articular surfaces shaded) and articular view (**d**; articular facets stippled; articular area shaded). *Tiktaalik* is intermediate between basal tetrapodomorphs and stem tetrapods in a wide range of features. **a**, As in basal taxa, the cleithrum (1) of *Tiktaalik* is heavily ornamented. *Tiktaalik* is intermediate in the degree to which the glenoid faces laterally, and hence, the appendage projects laterally. In both *Acanthostega* and *Tiktaalik* the appendage projects ventrolaterally from the body wall. **b**, *Tiktaalik* has an enlarged scapulocoracoid relative to basal tetrapodomorphs that consists of an expanded coracoid plate (2) and a dorsally projecting scapular process (3). **c**, The humerus of *Tiktaalik* retains a diagonal ventral ridge (4) orientation as in *Eusthenopteron*, but has a prominent keel on the leading edge of the bone as in *Acanthostega* and ANSP 21350 (ref. 25). **d**, The radial (5) and ulnar (6) facets of *Tiktaalik* are separated by a narrow area of cortical bone and are dorsoventrally offset from one another. *Sauripterus* redrawn and modified from ref. 14; *Eusthenopteron* redrawn and modified from ref. 9; *Acanthostega* redrawn and modified from ref. 22.

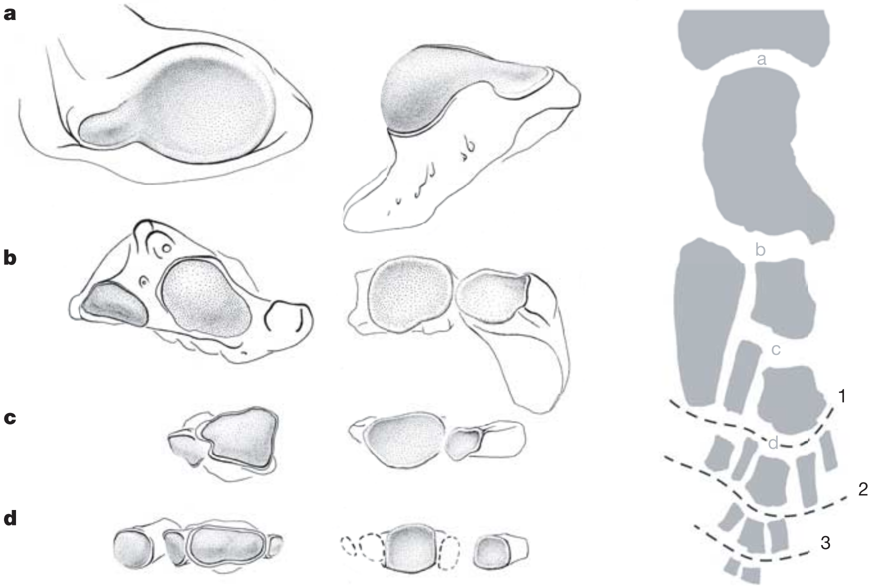

Figure 6 | Apposing joint surfaces of the left pectoral fin of NUFV 109 in articular view. a, The shoulder joint consists of a large, shallow ball and socket posteriorly and a small accessory cam anteriorly. The cam serves to limit humeral protraction and supination. **b**, At the elbow joint, both epipodial facets of the humerus face slightly ventrally, with the radial facet offset anteroventrally from that for the ulna. **c**, The joints of the ulnare and intermedium with the ulna are also offset from one another. As in the anteroventral offset of the humeroradial joint, the joint of the intermedium is similarly offset relative to the joint for the ulnare. **d**, The distal ulnare, intermedium and radius form a transverse joint plane across the appendage; the ulnare and intermedium articulate with five radials at shallow concavoconvex joints. 1, 2 and 3 indicate proximodistal succession of joints that run transversely across the fin.

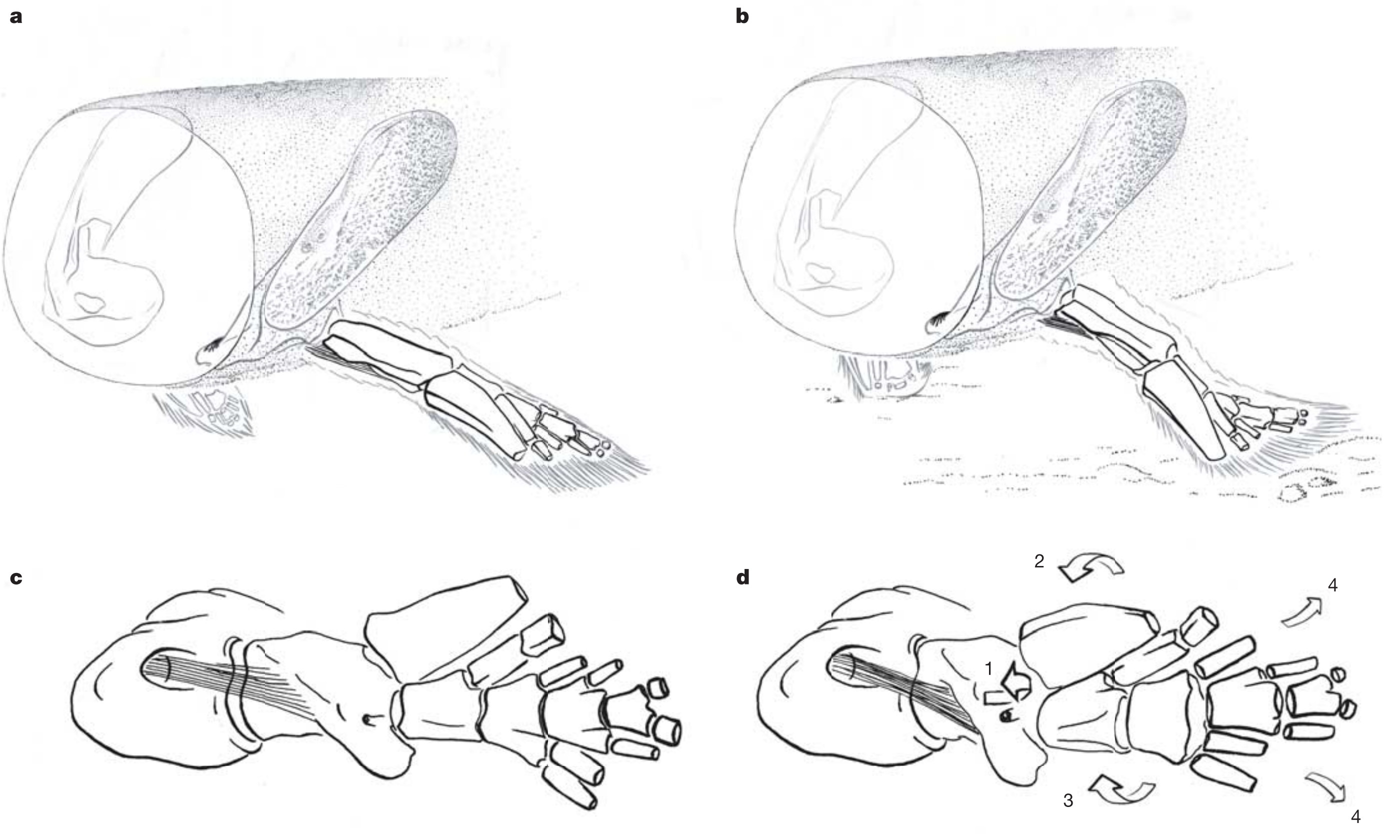

Figure 7 | Reconstruction of fin postures of *Tiktaalik*. a, **b**, Anterolateral view. **c**, **d**, Ventral view. **a**, **c**, Resting posture with the fin partially flexed at the antebrachium. In this position the radius is slightly more flexed than the ulna. **b**, **d**, Resistant contact with a firm substrate entails flexion at proximal joints and extension at distal ones. The shoulder joint is flexed by ventral muscles, including the trans-coracoid muscle. The elbow is flexed (**d**, arrow 1), with slight pronation of the radius (**d**, arrow 2) and rotation of the ulna (**d**, arrow 3). The transverse joints distal to the ulnare and intermedium are extended (**d**, arrows 4).

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