

The cranial endoskeleton of *Tiktaalik roseae*

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Among the morphological changes that occurred during the ‘fish-to-tetrapod’ transition was a marked reorganization of the cranial endoskeleton. Details of this transition, including the sequence of character acquisition, have not been evident from the fossil record. Here we describe the braincase, palatoquadrate and branchial skeleton of *Tiktaalik roseae*, the Late Devonian sarcopterygian fish most closely related to tetrapods. Although retaining a primitive configuration in many respects, the cranial endoskeleton of *T. roseae* shares derived features with tetrapods such as a large basal articulation and a flat, horizontally oriented entopterygoid. Other features in *T. roseae*, like the short, straight hyomandibula, show morphology intermediate between the condition observed in more primitive fish and that observed in tetrapods. The combination of characters in *T. roseae* helps to resolve the relative timing of modifications in the cranial endoskeleton. The sequence of modifications suggests changes in head mobility and intracranial kinesis that have ramifications for the origin of vertebrate terrestriality.

The vertebrate transition to land was accompanied by changes in a variety of functional systems including feeding, respiration, support and locomotion. The relative timing of morphological changes associated with these shifts is revealed exclusively through the study of fossil taxa. In recent years, our understanding of vertebrate terrestrialization has been greatly expanded by the description of intermediate forms such as *Panderichthys rhombolepis* from the late Givetian to early Frasnian of Latvia^{1,2}, *Elpistostege watsoni* from the early Frasnian of Quebec^{3,4}, and most recently *Tiktaalik roseae* from the early–middle Frasnian of Nunavut^{5,6}. These and other taxa have revealed that some of the innovations traditionally associated with terrestriality first appeared in aquatic elpistostegalians. Examples of such features include body-supporting forelimbs and pectoral girdle; a neck supporting a head capable of independent motion; and raised, dorsally positioned eyes on a flattened skull. Recent phylogenetic analyses^{5,7,8,9} distribute these features along the tetrapod stem and, as a result, the origin of tetrapods in the Late Devonian (375–363 million years (Myr) ago) is now recognized as a stepwise process of character acquisition, rather than an abrupt shift. Despite this progress, a morphological gap has persisted between the cranial endoskeleton of tetrapodomorph fish (finned tetrapodomorphs) and that of tetrapods (limbed tetrapodomorphs). As a consequence of this apparent morphological disparity, numerous synapomorphies have been used to distinguish the tetrapod cranial endoskeleton. Examples include reorganization of the basicranium via the reorientation of the vestibular fontanelle and loss of the lateral commissure, basicranial fenestra and intracranial joint; reduction and transverse reorientation of the hyomandibula; and changes in the shape and articulations of the palate. Owing to the lack of data from intermediate taxa, the prevailing perception has been that the transition of the cranial endoskeleton to the tetrapod condition was a rapid event^{10,11}.

T. roseae, with a phylogenetic position between *P. rhombolepis* and *Acanthostega gunnari*^{5,8,9}, provides an opportunity to fill this gap in our understanding. Multiple specimens of *T. roseae* were prepared to reveal the cranial endoskeleton in exceptional three-dimensional

detail. These new data offer insight into the evolution of the cranial endoskeleton during the vertebrate transition into shallow water and amphibious lifestyles.

Description

The braincase of *T. roseae*, like that of other tetrapodomorph fish, is comprised of ethmosphenoidal and otic-occipital components with unfused but complex contact surfaces between them (Figs 1–3; see Supplementary Information for additional photographs). The ethmosphenoid of *T. roseae* possesses ossified nasal capsules and a parasphenoid that extends rostrally to a position between the vomers. The parasphenoid is perforated by a buccohypophyseal foramen (Fig. 3). A large, laterally projecting basiptyergoid process carries, at its distal end, a dorsorostrally facing, concave surface for articulation with the palatoquadrate (Figs 2 and 3). In addition, the ethmosphenoid, like that of other finned tetrapodomorphs, has two other articulations with the palate: one is on the postnasal wall and the other is caudodorsal to the basiptyergoid process (Fig. 2). *A. gunnari* has only an enlarged basiptyergoid process as a point of articulation¹².

The otic-occipital region of the *T. roseae* braincase shares with other tetrapodomorph fish a basicranial fenestra, a lateral commissure, a groove for the jugular vein that leads to a canal through the lateral commissure, and a ventrally directed vestibular fontanelle (Figs 1–3). Several features of the otic-occipital are shared exclusively with that of *P. rhombolepis*, particularly a caudolaterally projecting lateral commissure and a broad basioccipital that gives this part of the braincase a bulbous rather than rectangular appearance in ventral view¹⁰. The lobate prootic process of *T. roseae* extends rostrally to insert into a recess on the ventral surface of the postorbital (Figs 2 and 3). The prootic process of *A. gunnari* similarly articulates with a recessed facet of the tabular¹³. Although *T. roseae* is the only finned tetrapodomorph known to possess this process, its occurrence in certain taxa, including *P. rhombolepis*, is presently impossible to determine because the palate obscures this region in the available material. *Eusthenopteron foordi* does exhibit ‘anterolateral bars’ at

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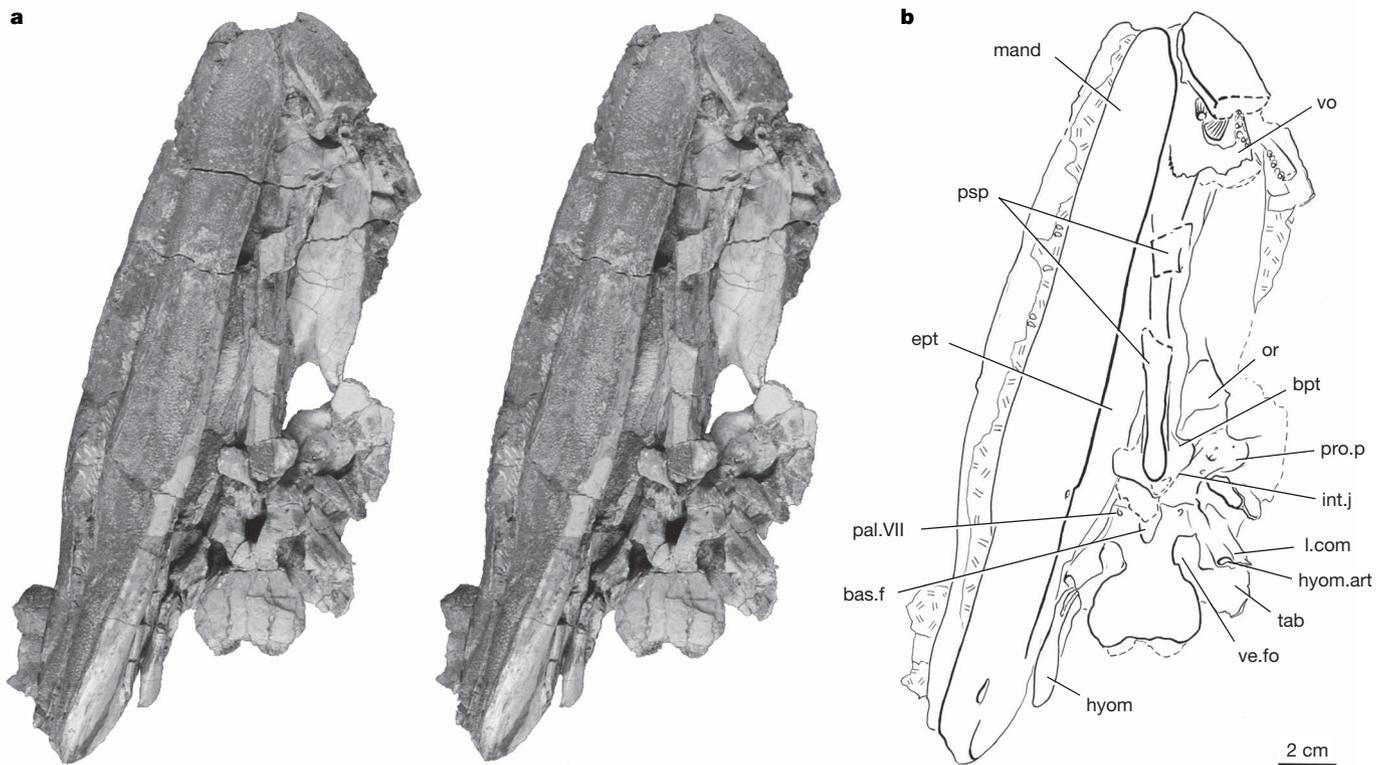


Figure 1 | Nunavut Fossil Vertebrate Collection (NUFV) 110, skull of *Tiktaalik roseae* in ventral view. **a**, Stereo pair with the left mandible and palatoquadrate removed to expose the braincase. **b**, Interpretive drawing of NUFV 110. Note the right hyomandibula in articulation with the lateral commissure of the braincase. bas.f, basicranial fenestra; bpt, basiptyergoid

process; ept, entopterygoid; hyom, hyomandibula; hyom.art, articulation with hyomandibula; int.j, intracranial joint; l.com, lateral commissure; mand, mandible; or, orbit; pal.VII, foramen for palatine branch of cranial nerve VII; pro.p, prootic process; psp, parasphenoid; tab, tabular; ve.fo, vestibular fontanelle; vo, vomer.

the rostrolateral corners of the otic-occipital that may represent poorly ossified prootic processes¹³.

Comparable to the conditions reported in *P. rhombolepis*¹⁴ and *A. gunnari*¹², the entopterygoid of *T. roseae* is horizontal and shallow (Fig. 2). This stands in stark contrast to the sinuous, dorsally reaching

element of basal tetrapodomorphs like *E. foordi*. Accordingly, like that of *A. gunnari*¹², the basal articulation of *T. roseae* lies in the same plane as the rest of the entopterygoid. As in other tetrapodomorph fish, the entopterygoids are separated by the braincase along their entire length (Fig. 1) and a denticulated field covers much of the

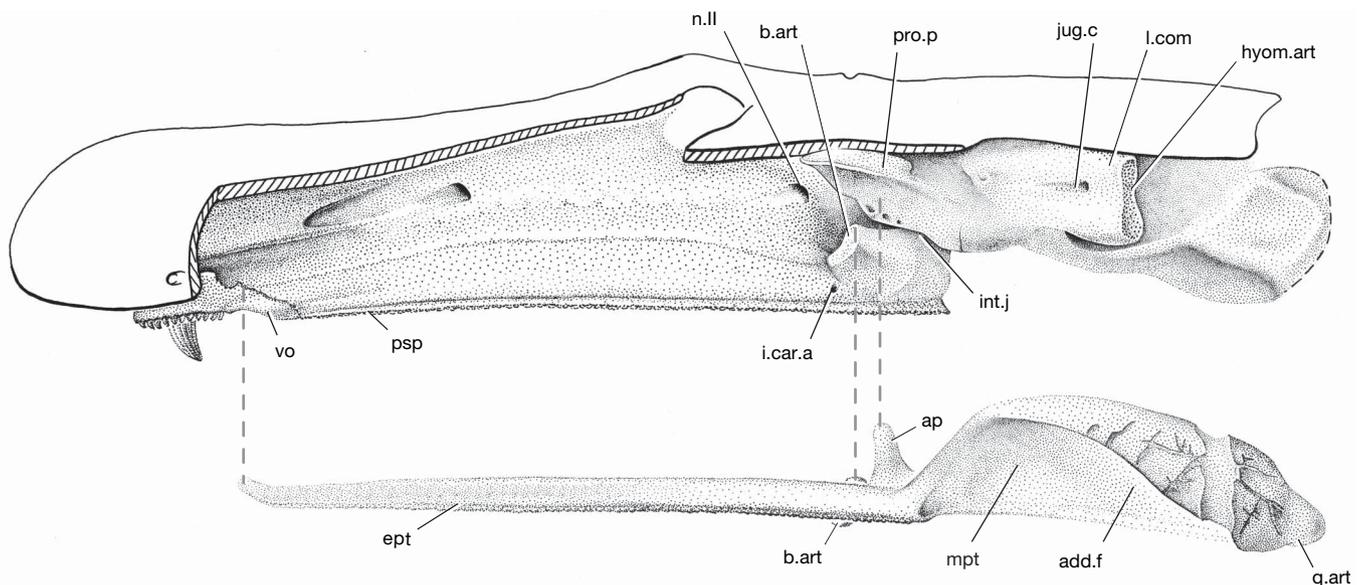


Figure 2 | Reconstruction of the braincase and palatoquadrate of *Tiktaalik roseae* in lateral view. Hashed lines indicate the three articulation sites between braincase and palatoquadrate. add.f, adductor fossa; ap, ascending process; b.art, basal articulation; ept, entopterygoid; hyom.art, articulation

with hyomandibula; i.car.a, internal carotid artery; int.j, intracranial joint; jug.c, jugular canal; l.com, lateral commissure; mpt, metapterygoid; n.II, foramen for cranial nerve II; pro.p, prootic process; psp, parasphenoid; q.art, articulation surface of quadrate; vo, vomer.

elements' buccal surfaces. Caudal to the denticulated field, the entopterygoid increases in depth and narrows to a vertically oriented bar at its caudal juncture with the metapterygoid. The metapterygoid is flat, vertical and tall and therefore compares more closely with that of other elpistostegalians^{12,14} than with the shallow, wide metapterygoid of basal tetrapodomorphs¹⁵. Caudal to the basal articulation, a dorsomedially projecting, cylindrical ascending process (columella cranii of ref. 12) terminates against the ethmosphenoid in a position medial to the prootic process (Fig. 2; see Supplementary Information for photographs). The same process in *A. gunnari* is interpreted to meet neither the skull roof nor the braincase¹².

The ossified portion of the hyomandibula of *T. roseae* is short and straight, unlike the boomerang-shaped element of basal finned tetrapodomorphs^{15–21,23} (Figs 4 and 5; see Supplementary Information for photographs). The extent to which the hyomandibula continued distally in cartilage cannot be determined. Rather than being steeply inclined like that of *E. foordi*, it is oriented horizontally like that of *P. rhombolepis*¹⁴. A longitudinal sulcus on the medial surface adjacent to the ventral margin (Fig. 4b) represents the passage for the hyomandibular nerve as in other tetrapodomorph fish^{15–23}. Unlike the condition in these taxa, the groove does not lead to a bony fenestra. The hyomandibula of *T. roseae* articulates with the braincase along the distal edge of the lateral commissure. In contrast to the condition in other finned tetrapodomorphs^{15–21}, however, the hyomandibula

articulates with the lateral commissure along a single, strap-shaped surface rather than at separate dorsal and ventral facets (Fig. 4c). As has been proposed for *P. rhombolepis*¹⁴, the hyomandibula of *T. roseae* does not articulate with the palatoquadrate, and cartilaginous elements may have connected the hyomandibula to the ventral hyoid elements. *T. roseae* lacks an ossified operculum and, accordingly, the hyomandibula exhibits no opercular articulation.

Ventral elements of the branchial skeleton are known for *T. roseae*, including two basibranchials; the urohyal; right and left hypohyals and ceratohyals; hypobranchials for the first three arches; and ceratobranchials for four arches (Fig. 6; see Supplementary Information for photograph). As in *Gogoniasus andrewsae*²⁰, *Medoevia lata*²³, *Mandageria fairfaxi*²⁴ and *E. foordi*¹⁵, the larger, more rostral of the two basibranchials bears articulations for the hypohyals, the hypobranchials of the first two arches, and the second basibranchial. The octagonal shape (in dorsal and ventral views) of basibranchial 1 in *T. roseae* is similar to the octagonal shape of the first basibranchial in *G. andrewsae*²⁰ and *M. lata*²³, and is quite unlike the longer, more rectangular element of the tristichopterids *M. fairfaxi*²⁴ and *E. foordi*¹⁵. Two of three *T. roseae* specimens exhibit dental plate fragments attached to the dorsal surface of this element. Whether basibranchial 1 of *T. roseae* carries one, two, or more dental plate(s) is impossible to determine from the preserved fragments. Basibranchial 2 is an arched (concave ventral) element that appears to carry the articulations for the third arch hypobranchials on its caudolateral margins. The ventral concavity of the second basibranchial and a depression on the ventral face of the first (the ventral basibranchial fossa) accommodate the urohyal, which bears a deep midsagittal crest on its ventral aspect. A site lacking perichondral bone on the medial margin of hypobranchial 3 probably represents the articulation with the fourth branchial arch, a condition observed in dipnomorphs and other finned tetrapodomorphs²⁴. *T. roseae* has deeply grooved ceratobranchials like those of *G. andrewsae*²⁰, *E. foordi*¹⁵ and *A. gunnari*²⁵. Typical of gilled osteichthyans, the groove of the ceratobranchial houses the afferent branchial artery²⁵.

Discussion

The transition from the cranial endoskeleton of finned tetrapodomorphs, such as *E. foordi*, to that of limbed forms, such as *A. gunnari*, entailed a number of morphological changes including a reduction and reorientation of the hyomandibula, reorganization of the basicranium and the articulations between palate and braincase, and alteration of skull architecture including flattening of the head, loss of the intracranial joint, and lengthening of the ethmosphenoid relative to the otic-occipital. *T. roseae*, the sister group of tetrapods, provides new context in which to interpret these alterations as a

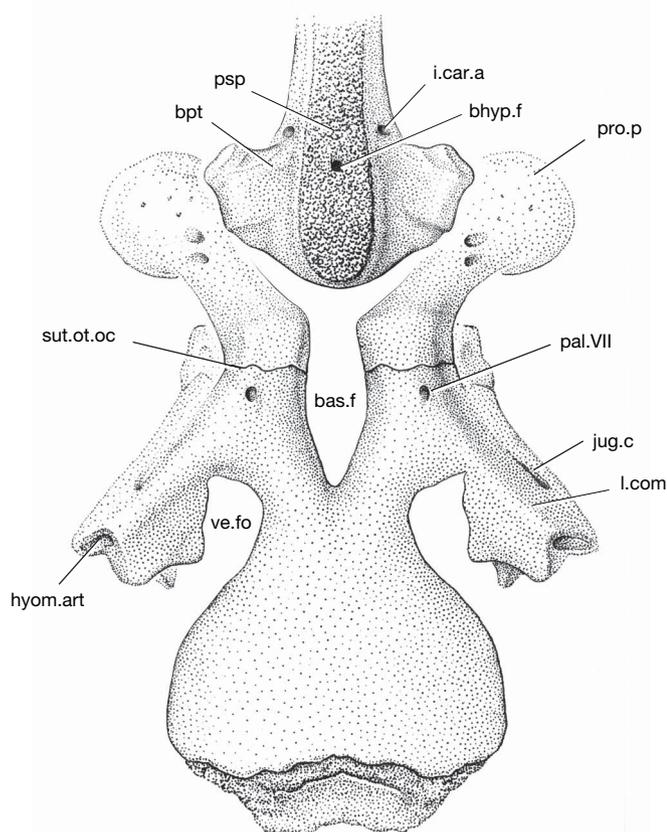


Figure 3 | Reconstruction of the otic-occipital and caudal end of the ethmosphenoid of *Tiktaalik roseae* in ventral view based primarily on NUFV 110. Note that the location and size of the buccohypophyseal foramen and jugular canal are based on NUFV 109 because these structures are not visible in NUFV 110. bas.f, basicranial fenestra; bhyp.f, buccohypophyseal foramen; bpt, basipterygoid process; hyom.art, articulation with hyomandibula; i.car.a, foramen for internal carotid artery; jug.c, jugular canal; l.com, lateral commissure; pal.VII, foramen for palatine branch of cranial nerve VII; pro.p, prootic process; psp, parasphenoid; sut.ot.oc, otic-occipital suture; ve.fo, vestibular fontanelle.

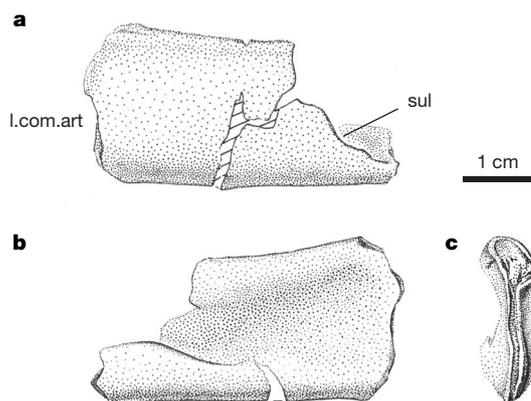


Figure 4 | NUFV 110, left hyomandibula of *Tiktaalik roseae*. a, Lateral view. b, Medial view. c, Proximal view. Note that the unfinished distal margin is not the result of breakage but rather represents the limit of ossification. l.com.art, articular surface with lateral commissure; sul, medial sulcus.

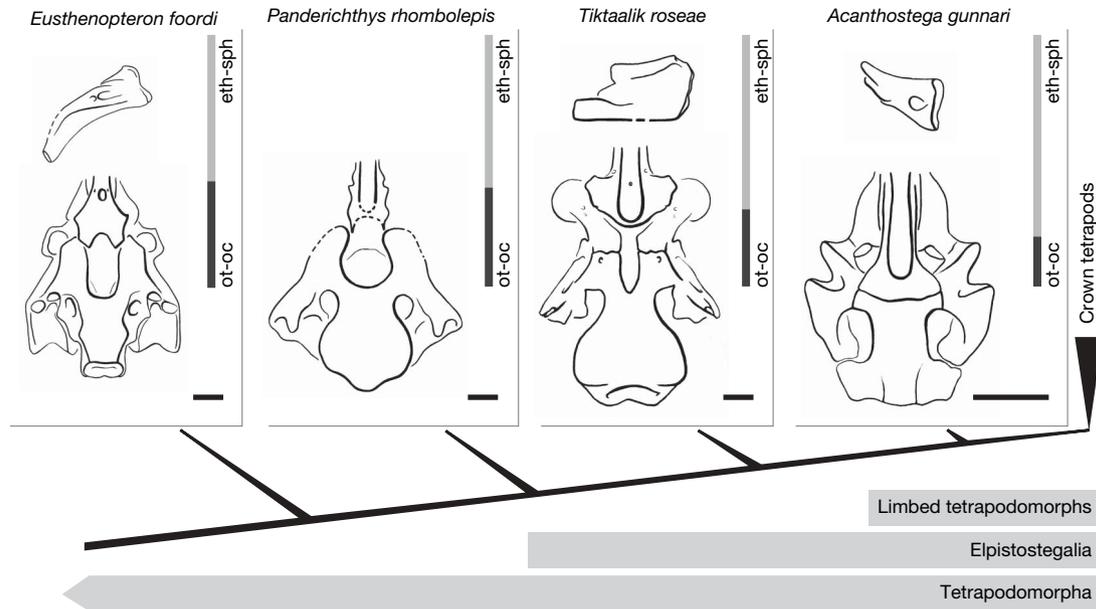


Figure 5 | Cladogram of select tetrapodomorphs. Topology according to ref. 5. Reconstructions of the caudal end of the braincase in ventral view for each of four tetrapodomorph taxa (*Eusthenopteron foordi*, *Panderichthys rhombolepis*, *Tiktaalik roseae* and *Acanthostega gunnari*); reconstructions of the left hyomandibula in medial view (left stapes in caudal view for *A. gunnari*) for taxa in which the element is well known (*E. foordi*, *T. roseae* and *A. gunnari*). The bicoloured bars represent relative length proportions of ethmosphenoid (eth-sph) and otic-occipital (ot-oc) for each of the four represented taxa (*E. foordi*, SMNH (Swedish Museum of Natural History) P.222; *P. rhombolepis*, LDM (Latvian Museum of Natural History) 60/123;

T. roseae, NUFV 110; *A. gunnari*, based on the reconstruction of ref. 13). *T. roseae* shares with more basal tetrapodomorphs the presence of a buccohypophyseal foramen, ossified nasal capsules, three sites of articulation between the braincase and palate, a basicranial fenestra, a lateral commissure, a ventrally directed vestibular fontanelle, and an unfused endoskeletal intracranial joint. *T. roseae* shares with tetrapods an enlarged basal articulation and a flat, horizontally oriented palatoquadrate. The reduced hyomandibula of *T. roseae* appears intermediate between the condition observed in other finned tetrapodomorphs and that observed in tetrapods. Reconstructions are modified from refs 10, 13, 15 and 31. Scale bars equal 1 cm.

sequence of changes (Fig. 5). Changes in cranial dimensions and reduction of the hyomandibula began before the enlargement of the basiptyergoid process^{5,7,8}. These changes preceded major alterations in braincase morphology including loss of the lateral commissure and basicranial fenestra, reorientation of the vestibular fontanelle, and loss of the intracranial joint (Fig. 5). The plesiomorphies retained by *T. roseae* reinforce the suggestion that significant changes to the braincase occurred relatively late in the transition to the tetrapod condition^{10,11}. The overall sequence of modifications to the cranial endoskeleton suggests changes in head mobility and

cranial kinesis that carry important implications for feeding and respiration in Late Devonian marginal aquatic environments.

A flat and broad skull, as seen in *P. rhombolepis* and more crownward tetrapodomorphs, had structural ramifications for virtually every component of the cranial endoskeleton. In *T. roseae*, as in tetrapods, a diminution of cranial depth is associated with the flattening of the palatoquadrate and the ventral displacement and increase in the size of the basal articulation. These alterations are coincident with the trend towards lengthening the ethmosphenoid relative to the otic-occipital^{10,11}. With cranial proportions approaching those of *A. gunnari*, *T. roseae* supports the hypothesis that the general cranial dimensions of tetrapods were attained in tetrapodomorph fish (Fig. 5).

These changes in the shape of the head seem to be related to the reduction and reorientation of the hyomandibula. In the primitive condition, as in *E. foordi*, the bone is boomerang-shaped and ventrally inclined, whereas in elpistostegalians, the hyomandibula is a short, straight, horizontal element (Fig. 5). In *E. foordi*, the hyomandibula articulates with the braincase, palatoquadrate, operculum and branchial skeleton. In *P. rhombolepis*, the ossified portion of the hyomandibula does not articulate with the palatoquadrate and extends from the lateral commissure to a facet on the opercular bone¹⁴. The stapes (the homologue of the hyomandibula) of *A. gunnari* is oriented transversely, extending laterally from the fenestra vestibuli of the braincase (in part, the homologue of the vestibular fontanelle)^{13,26,27}. The hyomandibula of *T. roseae* appears intermediate in size and orientation between those of *P. rhombolepis* and *A. gunnari*. Projecting caudolaterally from its articulation with the lateral commissure, it does not articulate with the palatoquadrate and, concomitant with the lack of an opercular bone, it has no opercular articulation.

With the loss of opercular and extrascapular elements, head mobility is enhanced in *T. roseae* relative to other tetrapodomorph fish. The establishment of a neck has clear ramifications for feeding and

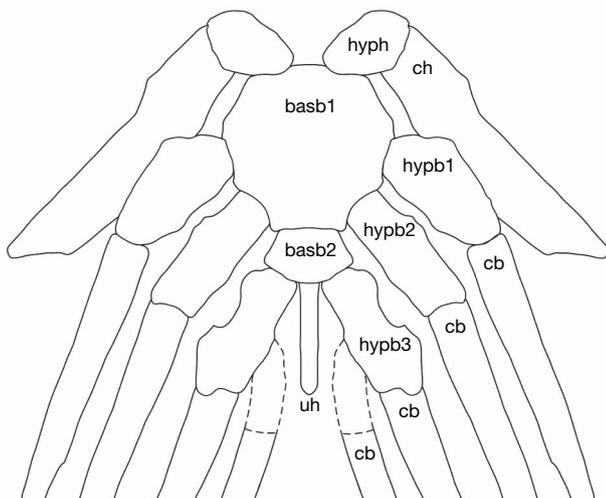


Figure 6 | Schematic diagram of ventral branchial elements of *Tiktaalik roseae* in dorsal view. basb1, basibranchial 1; basb2, basibranchial 2; cb, ceratobranchial; ch, ceratohyal; hyph, hypohyal; hypb1, hypobranchial 1; hypb2, hypobranchial 2; hypb3, hypobranchial 3; uh, urohyal.

locomotion in shallow water and marginal aquatic settings. Fish move and feed in three-dimensional space and are readily able to orient the body in order to position the mouth towards prey. A neck is advantageous in settings where the body is relatively fixed, as is the case in shallow pools of water or in marginal settings where the body is supported by appendages planted against a substrate.

In the transition to land, physical parameters were altered from a relatively viscous, neutrally buoyant environment to one in which oxygen availability and the effects of gravity are radically different from water. Intracranial kinesis in fish is an adaptation for feeding and respiring in the viscous, fluid medium of water. In tetrapods, intracranial kinesis is lost. Although the head has become more mobile in *T. roseae*, intracranial kinesis is restricted relative to more primitive tetrapodomorphs. Although *T. roseae* retains the bipartite components of the braincase, loss of the dermal intracranial joint, prootic processes that articulate with the postorbitals, and the complexity of the apposing ethmosphenoidal and otic-occipital surfaces obviate the possibility of motion at their contact²⁸. In addition, the enlarged size of the basal articulation points to a palate less capable of motion relative to the braincase. Likewise, the loss of the primitive bicondylar joint between hyomandibula and lateral commissure is suggestive of a restricted range of motion. *T. roseae*, then, reveals an intermediate stage in the origin of the consolidated skull of tetrapods.

As the skull becomes a more solid structure, the role of the hyomandibula in respiration is diminished. Primitively, by forming a structural link between the branchial skeleton, operculum, palate and lower jaw, the hyomandibula helps to coordinate their motions^{28,29}. The hyomandibula in obligate gill breathers is part of an osseous system that accommodates the stresses associated with branchial and opercular pumping of a relatively viscous medium (water) across the gills. In tetrapods, this function of the hyomandibula is entirely lost, making the element available for an eventual role in hearing³⁰. *T. roseae* reveals an intermediate stage in this transition. In *T. roseae*, the reduction and reorientation of the hyomandibula and the consequent loss of its articulations with other components of the cranial endoskeleton suggest a decreasing reliance on water pumping as a mode of respiration.

With appendages able to support the weight of the body, a more consolidated skull, ribs capable of sustaining the trunk under a gravitational load, a respiratory system less reliant on water breathing, a head capable of independent motion, and cranial proportions approaching those of tetrapods, *Tiktaalik* reveals an important stage in the origin of terrestrial vertebrates^{5,6}. *T. roseae* probably inhabited the benthos, shallows, and mudflats of freshwater floodplains while supporting itself on a solid substrate. In the Late Devonian, marginal freshwater environments were an important locus of the evolutionary changes that led to the origin of amphibious lifestyles among tetrapodomorphs.

Note added in proof: Reference 9, published after acceptance of this Article, provides relevant details regarding tetrapodomorph phylogeny across the fin–limb transition.

Received 21 November 2007; accepted 23 June 2008.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements The illustrations are the work of K. Monoyios. Specimen preparation was performed by C. F. Mullison. This research was made possible by permits from the Nunavut Ministry of Culture, Languages, Elders and Youth, the Grise Fiord Hamlet and HTA, with logistical support from the Polar Continental Shelf Project and collections support from the Canadian Museum of Nature. M. Brazeau improved interpretation of *P. rhombolepis* and offered input. Assistance in the field (1999–2006) was provided by W. Amaral, B. Atagootak, J. Conrad, M. Davis, S. Gatesy, A. Gillis, B. Kilbourne, S. Madsen, K. Middleton, J. Miller, K. Monoyios, C. Schaff, M. Shapiro, R. Shearman and C. Sullivan. This research was supported by an anonymous donor, the Academy of Natural Sciences of Philadelphia, the Putnam Expeditionary Fund (Harvard University), the University of Chicago, the National Science Foundation, and the National Geographic Society Committee for Research and Exploration.

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