Article

Elpistostege and the origin of the vertebrate hand

Richard Cloutier[1,2 ✉], Alice M. Clement[2], Michael S. Y. Lee[2,3], Roxanne Noël[1], Isabelle Béchard[1], Vincent Roy[1] & John A. Long[2]

The evolution of fishes to tetrapods (four-limbed vertebrates) was one of the most important transformations in vertebrate evolution. Hypotheses of tetrapod origins rely heavily on the anatomy of a few tetrapod-like fish fossils from the Middle and Late Devonian period (393–359 million years ago)[1]. These taxa—known as elpistostegalians—include *Panderichthys*[2], *Elpistostege*[3,4] and *Tiktaalik*[1,5], none of which has yet revealed the complete skeletal anatomy of the pectoral fin. Here we report a 1.57-metre-long articulated specimen of *Elpistostege watsoni* from the Upper Devonian period of Canada, which represents—to our knowledge—the most complete elpistostegalian yet found. High-energy computed tomography reveals that the skeleton of the pectoral fin has four proximodistal rows of radials (two of which include branched carpals) as well as two distal rows that are organized as digits and putative digits. Despite this skeletal pattern (which represents the most tetrapod-like arrangement of bones found in a pectoral fin to date), the fin retains lepidotrichia (fin rays) distal to the radials. We suggest that the vertebrate hand arose primarily from a skeletal pattern buried within the fairly typical aquatic pectoral fin of elpistostegalians. *Elpistostege* is potentially the sister taxon of all other tetrapods, and its appendages further blur the line between fish and land vertebrates.

The first tetrapods known from skeletal remains date back to the Late Devonian period (about 374 million years ago)[6,7], while trackway fossils showing digitate impressions of limbs suggest an earlier origin for this clade[8]. Over the past decade, fossils that provide information on the fish-to-tetrapod transition have been used to better understand anatomical transformations associated with locomotion[5,9–12], breathing[13], hearing[14] and feeding[11,15], with regard to the change in habitat from water to land. Until now, the terrestrialization of vertebrates has primarily been a matter of comparing six relatively well-known Devonian taxa among stem-group tetrapods[16]: a true piscine sarcopterygian, *Eusthenopteron foordi*; a piscine elpistostegalian, *Panderichthys rhombolepis*; a near-tetrapod elpistostegalian, *Tiktaalik roseae*; and three true basal tetrapods, *Acanthostega gunnari*, *Ventastega curonica* and *Ichthyostega* sp. Here we adopt an apomorphy-based definition of tetrapods as 'all organisms derived from the first sarcopterygian to have possessed digits homologous with those in *Homo sapiens*'[17,18].

However, these inferences regarding terrestrialization rely critically on the handful of specimens that have been referred to elpistostegalians, none of which has been completely described. The postcranial anatomy of *Panderichthys* is primarily restricted to the morphology of the pectoral fins and girdle[2,19,20], the vertebrae[2,21], the scale patterning[22] and very little on the pelvic fin and girdle morphology[9]. Although more than 60 specimens[1,10] of *Tiktaalik* have been found, most of the anatomy of this species has been described from a fairly complete individual for which the skull[1,15], pectoral and pelvic fins and girdles[5,10,23], scales[22] and the trunk region[1] anterior to the pelvic region are preserved.

Elpistostege watsoni was first described from a partial posterior skull roof (accession code: British Museum of Natural History (BMNH) P.50063) from the Escuminac Formation of Miguasha (Quebec) as a 'stegocephalian' amphibian[4]. A second incomplete anterior half of a skull (accession code: Musée d'Histoire Naturelle de Miguasha (MHNM) 06-538) was later described as an elpistostegalian fish[3]. Until now, the postcranial anatomy of *E. watsoni* has been known only from a small patch of articulated scales and vertebral elements (MHNM 06-537)[3]. The specimen of *E. watsoni* that we describe here (MHNM 06-2067) was discovered in 2010 from laminated bed 12 in the lower part of the Escuminac Formation. It is a complete individual that is preserved flattened dorsoventrally, although the caudal region is preserved in lateral view (Fig. 1a, b). The dorsal side of the skull, trunk and the pelvic fins, as well as the ventral side of the pectoral fins, have been mechanically prepared. Ventral anatomical data are derived from computed tomography scan images (Fig. 2b, c, 3c). Compaction of other fossil fishes found in similar laminated lithofacies of the Escuminac Formation varies between 50 and 83%[24]. As the skull and visceral skeleton will be described elsewhere (R.C. et al., manuscript in preparation), we provide only a few images to support the character coding used in our phylogenetic analysis (Extended Data Figs. 1b, 3).

To our knowledge, *Elpistostege* is now the sole elpistostegalian for which we have complete knowledge of body shape and proportions. *Elpistostege* has a short head, an elongated and slender trunk and relatively short caudal region and small anal fin. The skull (Fig. 1, Extended Data Fig. 1a, b) accounts for only 14.4% of the total length; this proportion

[1]Université du Québec à Rimouski, Rimouski, Quebec, Canada. [2]College of Science and Engineering, Flinders University, Adelaide, South Australia, Australia. [3]Earth Sciences Section, South Australian Museum, Adelaide, South Australia, Australia. ✉e-mail: richard_cloutier@uqar.ca
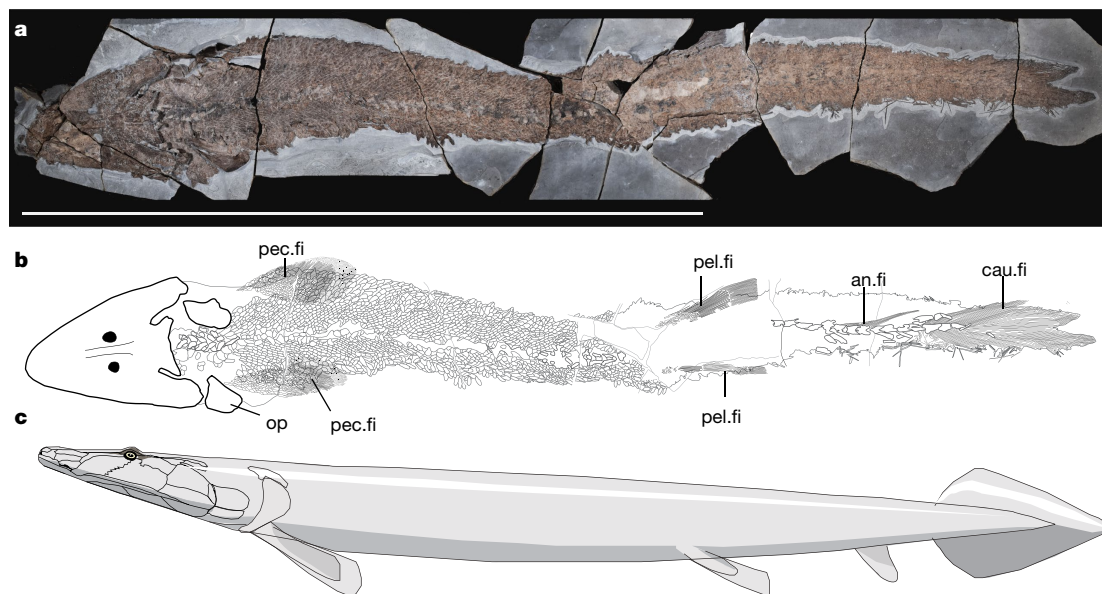
Fig. 1 | Complete specimen of *E. watsoni* MHNM 06-2067. a, Complete specimen in dorsal view. Scale bar, 1 m. **b**, Camera lucida drawing of the postcranial anatomy of the specimen; pectoral fins have been illustrated in their position, although they are only visible ventrally. **c**, Reconstruction. an.fi, anal fin; cau.fi, caudal fin; op, opercular; pec.fi, pectoral fin; pel.fi, pelvic fin.

varies between 14.4 and 26.9% of the total length for tetrapodomorphs—including the Devonian tetrapods *Acanthostega* and *Ichthyostega* (Supplementary Information)—with an average proportion of 21.38% (s.d. = 3.12). The distance between the paired fins of *Elpistostege* (41.16% of the total length) is among the greatest of the tetrapodomorphs, in which this distance varies between 26.72% and 49.62% of total length; the average tetrapodomorph condition is around 38.21% (s.d. = 6.08). *Elpistostege* is most similar to *Tiktaalik* (43% of total length) among the advanced tetrapodomorphs (Supplementary Information); in general, *Elpistostege* body proportions are closer to those of *Tiktaalik* than to those of *Panderichthys* and the Devonian tetrapods.

Here we describe the pectoral fin anatomy of *Elpistostege* and compare it with what is known of the anatomy of pectoral appendages in other tetrapodomorphs, especially other elpistostegalians and early tetrapods. Our descriptions reveal important tetrapod-like traits in the *Elpistostege* pectoral fin and provide the basis of a phylogenetically informed understanding of the evolution of pectoral appendages that spans the fish-to-tetrapod transition.

Description of the pectoral girdle

The pectoral girdle of *Elpistostege* consists of supracleithra, anocleithra, cleithra, well-developed scapulocoracoids, broad clavicles and an interclavicle (Fig. 2, Extended Data Fig. 1c). The clavicles, scapulocoracoids and interclavicle were elucidated from the computed tomography scans. The pectoral girdle is mostly articulated in situ on the left side of the body (Fig. 1a); it resembles that of *Tiktaalik*[10], and in both taxa this girdle is disconnected from the skull (as previously noted for *Tiktaalik*[5,10])—but not owing to a reduction in size of the dermal component. The ornamented supracleithra of *Elpistostege* (Extended Data Fig. 1c) are smaller than those in *Tiktaalik*. The elongate anocleithrum of *Elpistostege* (Fig. 2b, Extended Data Fig. 1c) features a well-developed anterior process, as seen in *Tiktaalik*, *Panderichthys*[19] and *Eusthenopteron*. It is overlapped ventrally by the cleithrum and dorsally by the supracleithrum. The exposed area of the anocleithrum is ornamented. The overlapped area is broader than in stem-tetrapodomorph fishes such as *Gogonasus*[25]. The cleithra (Fig. 2) are subtriangular in shape, are broad dorsally and have strongly inclined convex dorsal margins, but narrow ventrally to an apex as in *Tiktaalik*. The scapulocoracoid

(Fig. 2b-d) covers the entire ventral surface of the cleithrum and has a large supracoracoid foramen, similar to that of *Tiktaalik*[10]. The shape of the clavicle in *Elpistostege* (Fig. 2b-d) is intermediate between the rectangular clavicle of *Tiktaalik*[10] and the more triangular type of some Devonian tetrapods (such as *Acanthostega*[23] and *Ventastega*[26,27]). The clavicles do not contact each other.

The kite-shaped ornamented interclavicle (Fig. 2b-d) has posterior margins that are slightly overlapped by the clavicles. A small, mainly unornamented interclavicle has previously been reported only in a few basal actinopterygians[28] and osteolepiform sarcopterygians[25,29]. A broad interclavicle with large areas of clavicular overlap is known in *Tiktaalik*[10] and early limbed tetrapods such as *Ventastega*[30], *Acanthostega*[29] and *Tulerpeton*[31]. The kite-shaped interclavicle in *Elpistostege* (Fig. 2b-d) is similar to those of *Ventastega* and *Acanthostega*, but lacks the posterior stalk seen in *Ichthyostega* and more-derived tetrapods[32]. In contrast to early tetrapods, the sculpturing of the outer surface of the interclavicle of *Elpistostege* is composed of tubercles and pits (rather than radiating ridges), similar to most of its dermal bones.

Description of the pectoral fin

The well-preserved pectoral fins of specimen MHNM 06-2067 (Fig. 3, Extended Data Fig. 1d, e) are positioned under the body with their distal part dipping into the laminated sediment. The marginal fin webs of both pectoral fins have been only slightly damaged in vivo (Extended Data Fig. 1e). Regenerated lepidotrichia are much smaller and thinner than undamaged lepidotrichia, and show no sign of bifurcation. This condition is similar to regenerated lepidotrichia in *Polypterus*[33]. The pectoral fins of *Elpistostege* are large—approximately the same length as the pelvic fins but with three times the planar area. The proximal 50–60% of the pectoral and pelvic lepidotrichia are unsegmented, whereas the distal lepidotrichia are segmented; the distal quarter is bifurcated (Fig. 3a, b, Extended Data Fig. 1e). It has previously been reported that the pectoral[5] and pelvic[23] lepidotrichia of *Tiktaalik* are unsegmented. However, the preserved distal ends of the *Tiktaalik* lepidotrichia are large and flat, suggesting that distal segments of the lepidotrichia were present in life but not preserved.

All endochondral elements of the pectoral fins were reconstructed from the computed tomography scan of the left fin (Fig. 3); the
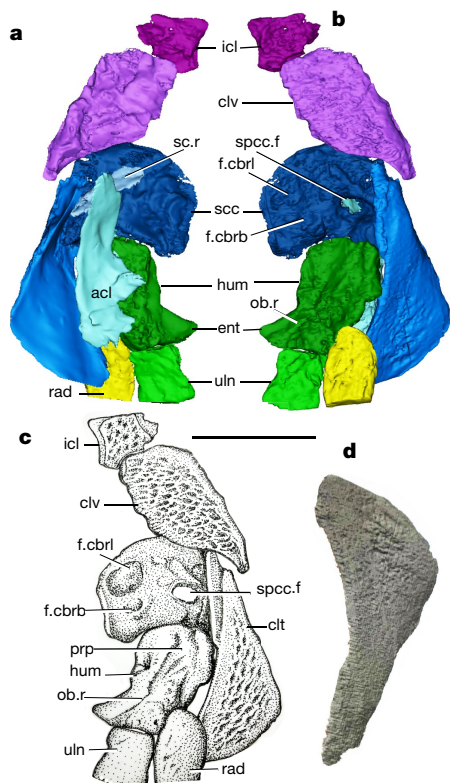
Fig. 2 | Pectoral girdle and fin of *E. watsoni* MHNM 06-2067. a, b, Computed tomography segmented images of pectoral girdle bones in dorsal (**a**) and ventral (**b**) view. **c,** Sketch interpretation. **d,** Computed tomogram of left cleithrum in lateral view. acl, anocleithrum; clt, cleithrum; clv, clavicle; ent, entepicondyle; f.cbrb, fossa for muscle coracobrachialis brevis; f.cbrl, fossa for muscle coracobrachialis longus; hum, humerus; icl, interclavicle; ob.r, oblique ridge on humerus; prp, prepectoral area; rad, radius; scc, scapulocoracoid; spcc.f, supracoracoid fossa; sc.r, scapular ridge; uln, ulna. Scale bar, 5 cm.

exoskeleton of the right fin was mechanically prepared before scanning, which impeded the contrast and resolution (Fig. 3a). In computed tomography scan imagery, the compression of the distal end of the endoskeleton results in the merging of boundaries among radials (Fig. 3c, d). We show both that compressed imagery and a restoration (Figs. 3c,d, 4a) based on moving the compressed elements slightly apart from each other, as would have been the case in life (Extended Data Fig. 4).

The humerus (Fig. 2b, c; 3c–e, Extended Data Fig. 2a–f) has a distinct L-shape with a weakly rounded proximal caput humeri similar to that in *Tiktaalik*, but differs from the latter in its broader head shape and right-angled entepicondyle (Fig. 5b). The entepicondyle is shorter than in *Eusthenopteron*[34] and *Panderichthys*[19,20], and ends near the posterodorsal angle of the ulna. The ventral surface of the humerus has a prominent oblique ridge that starts near the scapulocoracoid articulation and finishes at the end of the entepicondyle, as in *Tiktaalik*. The ridge is slightly shorter than in *Panderichthys*. The rectangular ulna has a weak depression on the ventral side, as in *Tiktaalik* and *Panderichthys*. By contrast, *Eusthenopteron* has a pronounced depression on the ventral side of the ulna[34] and this depression is absent in *Acanthostega* and *Ichthyostega*[35]. The ulna of *Elpistostege* is much shorter than that of *Panderichthys*. The elongated radius attaches more proximally on the humerus than in *Tiktaalik*, similar to the condition in *Panderichthys* and *Ichthyostega*[12].

The distal end of the radius shows a distinct irregular mass in the computed tomography images, which we interpret as a radiale (Fig. 3d) that has partially merged with the radius through compression.

The ulnare is a large trapezoidal bone with an almost-straight distal edge, although its distal region is incomplete owing to breakage of the rock. Five radials articulate distally with the ulnare. The intermedium is a narrow rod, shorter than that in *Eusthenopteron*, *Gogonasus* and *Tinirau*. It is followed distally by a small rectangular element that is also present in both *Tiktaalik*[5] and *Panderichthys*[19]. Both of these elements are highly reduced in basal tetrapods[1,23,24].

Nineteen radials are preserved and are organized into six preaxial–postaxial rows; the first of these rows articulates with the intermedium, and the last five articulate with the ulnare (Fig. 3, Extended Data Fig. 2g, h). We identify the main branching proximal radial that articulates with the ulnare as the A4 element that is seen in many other tetrapodomorph fishes; the narrow A5 element articulates distally with a robust A4. This is a similar pattern to that in *Tiktaalik*[5] (Fig. 4) and in more-generalized forms such as *Gogonasus*[36], except that the ulnare and A4 do not bear a large postaxial process in elpistostegalians. Small proximal radials are found on both sides of the A4, forming a curved distal joint in both *Elpistostege* and *Tiktaalik*. We note that although some radials have also been found in *Panderichthys*[19] (Fig. 4) and *Eusthenopteron*[34], they are not serially aligned to one another. In *Tiktaalik*, only two proximodistal rows of radials are preserved (a third row is potentially present on the basis of the articular facets of A5), whereas in *Elpistostege* four proximodistal rows of radials are preserved in the central portion of the appendage. We interpret the most-proximal two rows of radials in *Elpistostege* as carpals in addition to the row that includes the radiale, intermedium and ulnare, similar to numerous Carboniferous tetrapods that bear three rows of elements (the proximal, central and distal carpals)[32]; by contrast, in *Tulerpeton* only two carpal rows precede the digits (Fig. 4). The two most-distal rows of radials display a one-to-one relationship and are interpreted as digits (that is, phalanges). Thus, *Elpistostege* has two identifiable digits that are composed of two non-branching endoskeletal elements that articulate one-to-one proximodistally, and—potentially—three more digits that are each composed of a single preserved element.

The exoskeleton of the pectoral fins (Fig. 3a–c) includes approximately 90 long, segmented and bifurcated lepidotrichia and 4–5-mm rhombic scales (which are smaller than the body scales). The scales of the leading edge of the fin are larger, thicker and more robust than the remaining scales of the fin. In addition, these leading-edge scales are elongated and rod-shaped. Lepidotrichia represent approximately half the area of the fin, which resembles the condition in *Panderichthys*.

The origin of the vertebrate hand

Several definitions of digits exist in the literature (see Supplementary Information for discussion) but here we adopt a definition modified from refs. [37,38]: parallel, segmented, non-branching endoskeletal elements that are relatively uniform in size and shape (distal radials or phalanges), and that articulate one-to-one proximodistally, at the distal end of vertebrate paired appendages. It is clear that radials located distal to the ulnare and radius arose more than once in stem tetrapods, but potentially only once as a series of small, evenly sized elements. The relatively uniform size and shape of the well-organized rows of small elements in elpistostegalians and early tetrapods is very distinct from the condition in rhizodonts, which possess larger robust radials of varying size[39]. The presence of several parallel elongated radials that are subequal in size and all of which articulate directly with the ulnare and intermedium is a condition found only in *Elpistostege* and *Tiktaalik*. The condition in *Acanthostega* is unknown because its carpals were most probably cartilaginous, whereas in *Tulerpeton* the carpals articulate with the radiale, intermedium and ulnare as well as directly on the ulna (a unique condition among all known vertebrates)[31]. The origin of tetrapod limbs is marked by an elaboration of distal endochondral elements plus the loss of lepidotrichia; the presence of both digit-like distal endochondral elements and lepidotrichia in *Elpistostege*
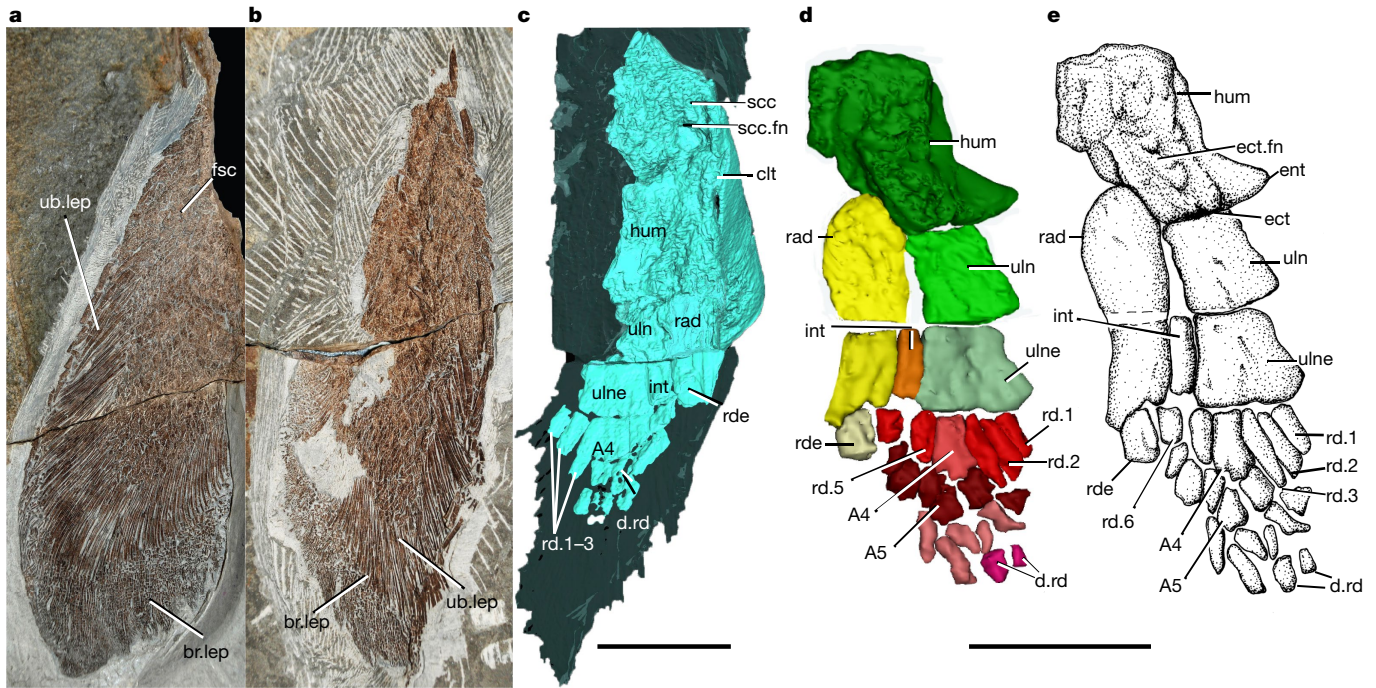
Fig. 3 | Pectoral fin of *E. watsoni* MHNM 06-2067. a, Right pectoral fin in ventral view. **b**, Left pectoral fin in ventral view. **c**, Early computed tomography interpretation of left pectoral fin endoskeleton (produced using Aviso) showing the main landmark features against a silhouette of the fin outline. Scale bar, 5 cm (applies to **a**–**c**). **d**, A later restoration of the left pectoral fin endoskeleton, produced using Mimic. **e**, Attempted reconstruction of left pectoral fin endoskeleton by estimating possible original shapes of some of the compressed radial elements. Scale bar below **d**, **e** (applies to both panels), 5 cm. A4, main element in pectoral endoskeleton distal to ulnare (the preaxial–postaxial radial row 4); A5, main element in pectoral endoskeleton distal to A4; br.lep, bifurcated lepidotrichia; d.rd, distal radials (digits); ect, ectepicondyle; ect.fn, ectepicondyle foramen; fsc, pectoral fin scales; int, intermedium; rd.1–6, preaxial–postaxial radial rows 1–6; rde, radiale; scc.fn, scapulocoracoid foramen; ub.lep., unbifurcated lepidotrichia; ulne, ulnare.
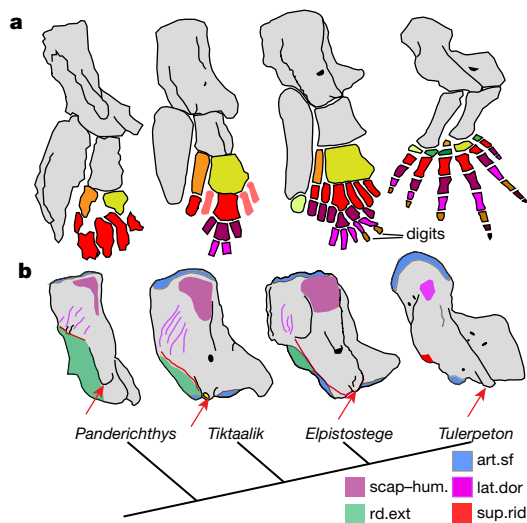
Fig. 4 | Comparative anatomy of pectoral limb endoskeleton and humerus of stem-tetrapod fish and early tetrapods. a, **b**, Comparison of the anatomy of the pectoral limb endoskeleton (**a**) and humerus (**b**) of stem-tetrapod fish (*Panderichthys*, *Tiktaalik* and *Elpistostege*) and an early tetrapod (*Tulerpeton*). Proximodistal rows of radials or digits are shown colour-coded according to the scheme in Fig. 4. Red arrows in **b** indicate the ectepicondyle. *Panderichthys* data are from ref. [13]; *Tiktaalik* data are from ref. [4]; *Acanthostega* data are from ref. [26]; *Tulerpeton* data are from ref. [31]. Images in **b** are modified from ref. [50]. art. sf, articulation surfaces; lat.dor, attachment ridges for latissimus dorsi muscles; sup.rid, supinator ridge; rd.ext, attachment area for radial extensors; scap–hum., attachment area for scapula and humeral muscles.
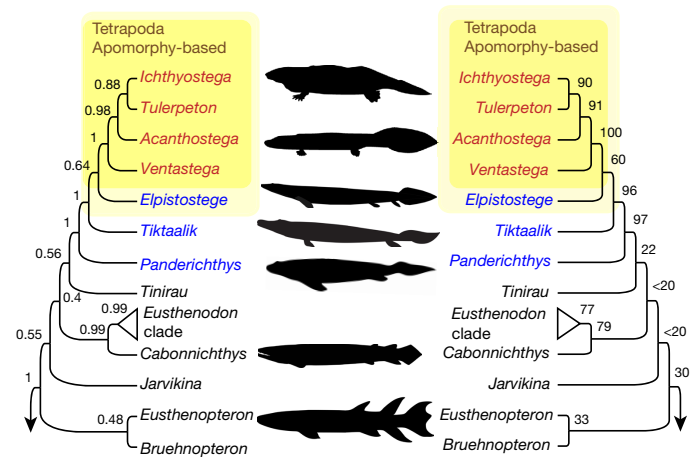

Fig. 5 | Phylogenetic analyses of elpistostegalian relationships, based on undated Bayesian and parsimony approaches. Bayesian analysis (left) was performed using MrBayes[49], and the parsimony approach (right) used PAUP*[48]. For the Bayesian approach, numbers denote the posterior probability; for the parsimony approach, numbers indicate the bootstrap percentage. Both methods place *Elpistostege* as a sister group to the remaining tetrapods. Core tetrapods are shown in red, and the elpistostegalian-grade taxa are shown in blue. Extended Data Figure 4 shows detailed trees, and the Supplementary Information provides the character list, matrix and analysis scripts. *Panderichthys* silhouette is by Nobu Tamura (vectorized by T. Michael Keesey), CC BY 3.0 (https://creativecommons.org/licenses/by/3.0/); all other silhouettes were constructed by the authors.

demonstrates that the basic architecture of the vertebrate hand evolved while the pectoral appendage was a 'typical' functioning aquatic fin. Homology between digits and the distal radials of fins has previously been asserted by palaeontologists from topologies observed in fossil fish fins[19].

Recent work by developmental biologists has shown that the *HOXA13* and *HOXD13* genes have a fundamental role in the patterning of radials in fishes, as well as in the limb autopodium (carpals and digits) in tetrapods[39]. 'Early' and 'late' phases of HOXA and HOXD transcription have a role in specifying the proximal and distal segments, respectively, during the development of paired appendages. The early phase of HOXA and HOXD genes is expressed in the stylopod and zeugopod in *Polyodon*, *Lepisosteus* and tetrapods, and the late phase of HOX genes has been recognized in the autopod of *Lepisosteus*, *Neoceratodus* and tetrapods[39–41]. In addition, although lepidotrichia and digits are not homologous in terms of morphology, the cells and regulatory processes that are involved in the patterning of distal elements beneath both the apical ectodermal fold and ridge share a deep homology that may be common to jawed vertebrates[42]. These developmental findings suggest a deep homology between digits and the distal fin region (including radials).

Elpistostege exhibits a pectoral autopodium that is intermediate between those of fishes and tetrapods in simultaneously having carpals and aligned radial elements that can be considered primitive tetrapod digits, but which are capped distally by lepidotrichia. Although digits and carpals have previously been thought to be a de novo specialization that is unique to typical tetrapods[43], the emergence of carpals and digits within the fin of elpistostegalians (with dermal fin rays) is not unexpected, as the discovery of the tetrapod humerus–ulna–radius pattern was first identified in *Eusthenopteron* over a century ago[44]. It is possible that the potential ability of the pectoral fin to bear weight while in shallow water or on land, as has been proposed for *Tiktaalik*[5], fostered the increasing evolutionary innovation of the distal-fin endoskeleton in elpistostegalians. Expanding the number of preaxial–postaxial radial rows increases the width of the 'hand' and offers greater support for lifting the body, and increasing the number of proximodistal rows of carpals and phalanges results in more planes of flexion through the 'wrist' area within the pectoral appendage. Recent research on laboratory-reared *Polypterus* has demonstrated that exposing fish to higher levels of terrestrialization can drive phenotypic plasticity in the pectoral girdle, resulting in the development of more-robust phenotypes[45]. The pectoral fin of *Elpistostege* is largely digitate, and requires only the loss of lepidotrichia to enable freer movement of the radial elements to resemble the fully digitate condition that is seen in typical tetrapods.

Elpistostege and digitate tetrapods

The phylogenetic data matrix (comprising 202 characters coded for 43 taxa) was based on several previous publications, and included 169 characters from ref. [46], 13 characters from ref. [1] and 11 characters from ref. [47]; 5 additional characters were included to capture the newly described features of the anatomy of *Elpistostege* (Supplementary Information). We corrected or updated 275 cell codings on the basis of recent publications and personal observations of 33 taxa; in addition, we completely recoded *Elpistostege*. We performed phylogenetic analyses using parsimony in PAUP*[48] and undated Bayesian approaches in MrBayes[49] (see Supplementary Information for detailed methods). Both analyses support an arrangement in which *Elpistostege* alone is the sister taxon to tetrapods (Fig. 5, Extended Data Fig. 4)—although support is not strong. By contrast, *Tiktaalik* has previously been placed[1] as either the sister taxon to tetrapods or as sharing this position with *Elpistostege* (which was poorly known in previous phylogenetic analyses). In our analysis, the additional characters (including the presence of digits) place *Elpistostege* closer to tetrapods than to any other sarcopterygian taxa.

Figure 4 highlights trends in some key features of the pectoral appendage across the fish-to-tetrapod transition, showing the increasing number of distal radials and patterning of rows of these radials in the fin-to-limb transition. *Elpistostege* shares with tetrapods a pectoral appendage with at least two digits composed of at least two parallel, subequal unbranched radials that articulate in a one-to-one relationship. Figure 4b illustrates the position of the ectepicondyle and areas of major muscle attachment on the dorsal side of the humerus. The humerus of *Elpistostege* is also close to that of the putative tetrapod ANSP 21350[35,50] in possessing a large dorsal scapula–humeral muscle attachment area and more proximal radial articulation surface. It is closer to the humerus of tetrapods in having a more-robust and posteriorly positioned ectepicondyle and a slightly broader dorsal caput region. We note that, in having a larger ulnare ossification than other elpistostegalians, *Elpistostege* diverges from the trend in tetrapods to reduce the relative size of this element. The presence of the ossified radiale does not appear until the node below *Elpistostege*; the two large radials of *Sauripterus* most probably evolved independently.

In summary, *Elpistostege* further blurs the line between fish and tetrapods in showing a greater number of tetrapod novelties than are present in any other 'fish'. Our analyses place it crownward of *Tiktaalik*, at the node immediately below the unequivocally digitate tetrapods. If one adopts an apomorphy-based interpretation of Tetrapoda[17,18] and considers the parallel, unbranched distal radials in the *Elpistostege* fin to be true digits, then *Elpistostege* would represent the earliest and most-primitive known tetrapod. The pectoral fin anatomy of *Elpistostege* provides a window into how fish developed digit-like structures within typical fins that retained lepidotrichia, and while these fish still occupied an aquatic lifestyle. The typical hand pattern—formed by serial rows of digits in tetrapods—began its assembly within advanced sarcopterygian fish fins, possibly driven by increasing evolutionary lability as these fishes began to foray into shallow water or briefly onto land.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-020-2100-8.

1. Daeschler, E. B., Shubin, N. H. & Jenkins, F. A. Jr. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature* **440**, 757–763 (2006).
2. Vorobyeva, E. & Schultze, H.-P. in *Origins of the Higher Groups of Tetrapods. Controversy and Consensus* (eds Schultze, H.-P. & Trueb, L.) 68–109 (Cornell Univ. Press, 1991).
3. Schultze, H.-P. & Arsenault, M. The panderichthyid fish *Elpistostege*: a close relative of tetrapods? *Palaeontology* **28**, 293–309 (1985).
4. Westoll, T. S. Ancestry of the tetrapods. *Nature* **141**, 127–128 (1938).
5. Shubin, N. H., Daeschler, E. B. & Jenkins, F. A. Jr. The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. *Nature* **440**, 764–771 (2006).
6. Clément, G. & Lebedev, O. Revision of the early tetrapod *Obruchevichthys* Vorobyeva, 1977 from the Frasnian (Upper Devonian) of the north-western East European platform. *Paleontol. J.* **48**, 1082–1091 (2014).
7. Ahlberg, P. E. *Elginerpeton pancheni* and the earliest tetrapod clade. *Nature* **373**, 420–425 (1995).
8. Niedźwiedzki, G., Szrek, P., Narkiewicz, K., Narkiewicz, M. & Ahlberg, P. E. Tetrapod trackways from the early Middle Devonian period of Poland. *Nature* **463**, 43–48 (2010).
9. Boisvert, C. A. The pelvic fin and girdle of *Panderichthys* and the origin of tetrapod locomotion. *Nature* **438**, 1145–1147 (2005).
10. Shubin, N. H., Daeschler, E. B. & Jenkins, F. A. in *Great Transformations in Vertebrate Evolution* (eds Dial, K.P. et al.) 70–83 (Univ. of Chicago Press, 2015).
11. Hohn-Schulte, B., Preuschoft, H., Witzel, U. & Distler-Hoffmann, C. Biomechanics and functional preconditions for terrestrial lifestyle in basal tetrapods, with special consideration of *Tiktaalik roseae*. *Hist. Biol.* **25**, 167–181 (2013).
12. Callier, V., Clack, J. A. & Ahlberg, P. E. Contrasting developmental trajectories in the earliest known tetrapod forelimbs. *Science* **324**, 364–367 (2009).
13. Clack, J. A. Devonian climate change, breathing, and the origin of the tetrapod stem group. *Integr. Comp. Biol.* **47**, 510–523 (2007).
14. Brazeau, M. D. & Ahlberg, P. E. Tetrapod-like middle ear architecture in a Devonian fish. *Nature* **439**, 318–321 (2006).
15. Downs, J. P., Daeschler, E. B., Jenkins, F. A. Jr & Shubin, N. H. The cranial endoskeleton of *Tiktaalik roseae*. *Nature* **455**, 925–929 (2008).

Article

16. Clack, J. A. *Gaining Ground: the Origin and Evolution of Tetrapods* (Indiana Univ. Press, 2012).
17. Lee, M. S. Y. Stability of higher taxa in phylogenetic nomenclature - some comments on Moore (1998). *Zool. Scr.* **28**, 361–366 (1999).
18. Anderson, J. S. Use of well-known names in phylogenetic nomenclature: a reply to Laurin. *Syst. Biol.* **51**, 822–827 (2002).
19. Boisvert, C. A., Mark-Kurik, E. & Ahlberg, P. E. The pectoral fin of *Panderichthys* and the origin of digits. *Nature* **456**, 636–638 (2008).
20. Boisvert, C. A. The humerus of *Panderichthys* in three dimensions and its significance in the context of the fish-tetrapod transition. *Acta Zoologica* **90**, 297–305 (2009).
21. Vorobyeva, E. I. & Tsessarskii, A. A. The evolution of vertebrae in rhipidistians. *Zhurnal Obshchei Biologii* **67**, 735–747 (1986).
22. Witzmann, F. Morphological and histological changes of dermal scales during the fish-to-tetrapod transition. *Acta Zoologica* **92**, 281–302 (2011).
23. Shubin, N. H., Daeschler, E. B. & Jenkins, F. A. Jr. Pelvic girdle and fin of *Tiktaalik roseae*. *Proc. Natl Acad. Sci. USA* **111**, 893–899 (2014).
24. Béchard, I., Arsenault, F., Cloutier, R. & Kerr, J. The Devonian placoderm fish *Bothriolepis canadensis* revisited with three-dimensional digital imagery. *Palaeontol. Electronica* **17**, 1–19 (2014).
25. Long, J. A. The structure and relationships of a new osteolepiform fish from the Late Devonian of Victoria, Australia. *Alcheringa* **9**, 1–22 (1985).
26. Coates, M. I. The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution. *Trans. R. Soc. Edinb. Earth Sci.* **87**, 363–421 (1996).
27. Ahlberg, P. E., Luksevics, E. & Lebedev, O. The first tetrapod finds from the Devonian (Upper Famennian) of Latvia. *Phil. Trans. R. Soc. Lond. B* **343**, 303–328 (1994).
28. Cloutier, R. & Arratia, G. in *Recent Advances in the Origin and Early Radiation of Vertebrates* (eds Arratia, G. et al.) 217–270 (Dr. Friedrich Pfeil, 2004).
29. Clack, J. A. New material of the early tetrapod *Acanthostega* from the Upper Devonian of East Greenland. *Palaeontology* **31**, 699–724 (1988).
30. Ahlberg, P. E., Clack, J. A., Luksevics, E., Blom, H. & Zupiņš, I. *Ventastega curonica* and the origin of tetrapod morphology. *Nature* **453**, 1199–1204 (2008).
31. Lebedev, O. A. & Coates, M. I. The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. *Zool. J. Linn. Soc.* **114**, 307–348 (1995).
32. Carroll, R. L. & Holmes, R. B. in *Fins to Limbs. Evolution, Development, and Transformation* (ed. Hall, B.K.) 185–224 (The Chicago Univ. Press, 2007).
33. Cuervo, R., Hernández-Martínez, R., Chimal-Monroy, J., Merchant-Larios, H. & Covarrubias, L. Full regeneration of the tribasal *Polypterus* fin. *Proc. Natl Acad. Sci. USA* **109**, 3838–3843 (2012).
34. Andrews, S. M. & Westoll, T. S. The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Trans. R. Soc. Edinb.* **68**, 207–329 (1970).
35. Ahlberg, P. E. in *Studies on Fossil Tetrapods* (eds Barrett, P.M. & Milner, A.R.) 17–29 (The Palaeontological Association, 2011).
36. Holland, T. Pectoral girdle and fin anatomy of *Gogonasus andrewsae* Long, 1985: implications for tetrapodomorph limb evolution. *J. Morphol.* **274**, 147–164 (2013).
37. Coates, M. I. The origin of vertebrate limbs. *Dev. Suppl.* **1**, 169–180 (1994).
38. Stewart, T. A., Bhat, R. & Newman, S. A. The evolutionary origin of digit patterning. *Evodevo* **8**, 21 (2017).
39. Johanson, Z. et al. Fish fingers: digit homologues in sarcopterygian fish fins. *J. Exp. Zool. B Mol. Dev. Evol.* **308B**, 757–768 (2007).
40. Gehrke, A. R. et al. Deep conservation of wrist and digit enhancers in fish. *Proc. Natl Acad. Sci. USA* **112**, 803–808 (2015).
41. Woltering, J. M., Noordermeer, D., Leleu, M. & Duboule, D. Conservation and divergence of regulatory strategies at *Hox* loci and the origin of tetrapod digits. *PLoS Biol.* **12**, e1001773 (2014).
42. Nakamura, T., Gehrke, A. R., Lemberg, J., Szymaszek, J. & Shubin, N. H. Digits and fin rays share common developmental histories. *Nature* **537**, 225–228 (2016).
43. Godfrey, S. J. The postcranial skeletal anatomy of the Carboniferous tetrapod *Greererpeton burkemorani* Romer, 1969. *Phil. Trans. R. Soc. Lond. B* **323**, 75–133 (1989).
44. Cope, E. D. On the phylogeny of the Vertebrata. *Proc. Am. Phil. Soc.* **30**, 278–281 (1892).
45. Standen, E. M., Du, T. Y. & Larsson, H. C. E. Developmental plasticity and the origin of tetrapods. *Nature* **513**, 54–58 (2014).
46. Zhu, M., Ahlberg, P. E., Zhao, W. J. & Jia, L. T. A Devonian tetrapod-like fish reveals substantial parallelism in stem tetrapod evolution. *Nat. Ecol. Evol.* **1**, 1470–1476 (2017).
47. Swartz, B. A marine stem-tetrapod from the Devonian of western North America. *PLoS ONE* **7**, e33683 (2012).
48. Swofford, D. L. *PAUP*. Phylogenetic Analyses Using Parsimony (*And Other Methods)* (Sinauer Associates, 2003).
49. Ronquist, F. et al. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* **61**, 539–542 (2012).
50. Shubin, N. H., Daeschler, E. B. & Coates, M. I. The early evolution of the tetrapod humerus. *Science* **304**, 90–93 (2004).

Methods

X-ray computed tomography

A preliminary computed tomography scan using Siemens SOMATOM (INRS Centre Eau Terre Environnement) was performed to precisely localize the specimen in the sediment and to access rapidly the state of preservation. The 18 blocks containing the complete specimen were scanned individually with a high-energy computed tomography scan at the University of Texas at Austin. Smaller blocks were also scanned with a micro-computed tomography scan using SkyScan 1173 (Bruker-micro-CT). Specimen MHNM 06-538 was scanned with a high-resolution micro-computed tomography scanner at the Australian National University at Canberra. Projection images were reconstructed using NRecon (version 1.6.6.0, SkyScan, Bruker-microCT). All scan data were segmented in Avizo v.7.1., Mimics v.18 and v.19 and Drishti v.2.6.3. The pectoral fin was segmented independently in Avizo v.7.1. (by I.B.), Mimics v.18 and v.19 (by A.M.C.) and Drishti v.2.6.3 (by R.N.).

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

Morphological data are deposited in MorphoBank at https://morphobank.org/index.php/Projects/ProjectOverview/project_id/3480. The complete character-by-taxon matrix, PAUP* and MrBayes scripts as well as full trees are presented in the Supplementary Information and available to download as source data files.

Extended Data Fig. 1 | Complete specimen of *E. watsoni* MHNM 06-2067, with close-up views of skull, anocleithrum and supracleithrum, and pectoral fins. a, Complete prepared specimen in dorsal view (high-resolution image). **b**, Close-up view of main skull block 8, showing spiracles and tabular horns. Photograph with ammonium chloride whitening. **c**, Close-up view of right anocleithrum and supracleithrum (scl). Photograph with ammonium chloride whitening. **d**, Ventral view of pectoral fins from blocks 8, 9 and 10.
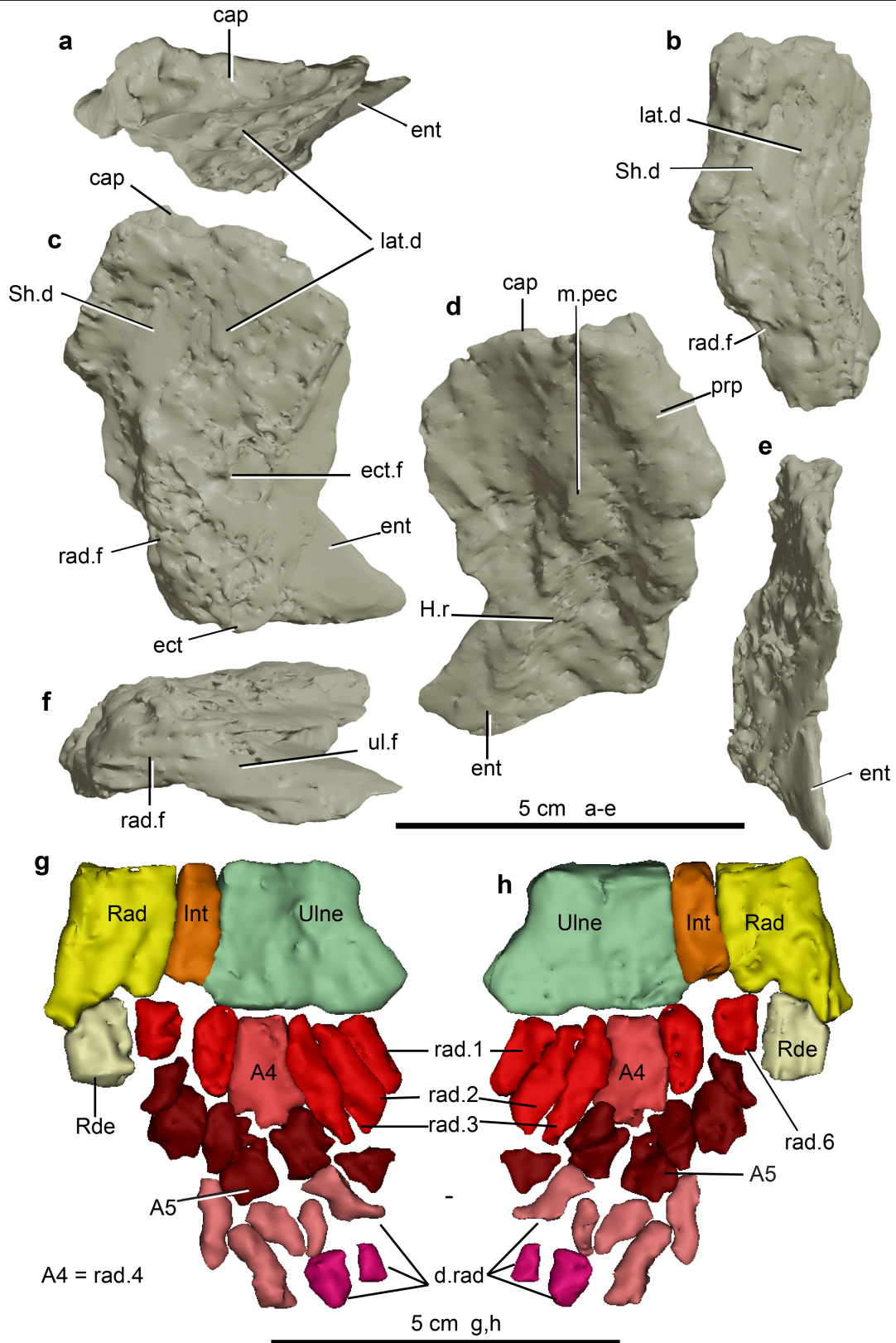
Extended Data Fig. 2 | Pectoral-fin endoskeleton of *E. watsoni* MHNM 06-2067, restored using Mimics v.18 from micro-computed tomography data. **a**–**f**, Views of the left humerus: **a**, dorsal; **b**, preaxial (anteroventral); **c**, oblique preaxial; **d**, ventral; **e**, dorsal; **f**, ventral (distal) view. **g**, **h**, Close-up view of distal pectoral-fin elements in ventral (**g**) and dorsal (**h**) views. cap, caput humeri; d.rad, distal radials; ect.f, ectepicondyle foramen; h.r, humeral ridge; lat.d, latissimus dorsi process; m.pec, pectoralis muscle; rad, radius; rad.1–6, preaxial–postaxial radial rows 1–6; rad.f, radial facet; sh.d, scapula–humeral depression; ul.f, ulnar facet.
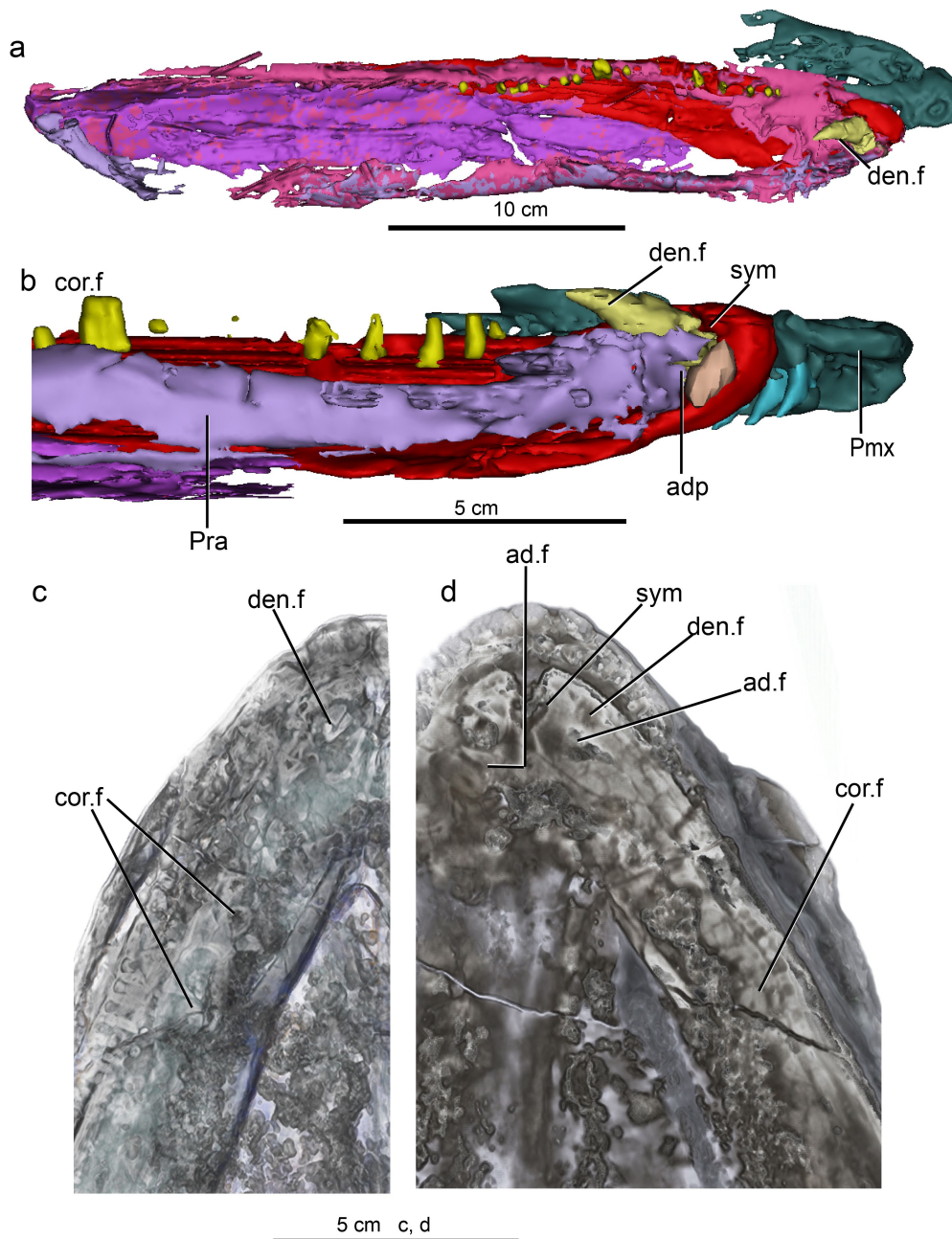
Extended Data Fig. 3 | *E. watsoni* lower jaw features restored from micro-computed tomography data. a, **b**, MHNM 06-2067 in lateral view. **a**, Whole jaw. **b**, Close-up view of anterior region, individual bones and teeth segmented using Mimics v.18. **c**, **d**, MHNM 06-538, left lower jaw in dorsal view (**c**), and right lower jaw and symphyseal area of left jaw in dorsal view (**d**), volume rendered using Drishti v.2.6. ad.f, adsymphysial fang; adp, adsymphysial plate; cor.f, coronoid fang; den.f, dentary fang; pmx, premaxilla; pra, prearticular; sym, symphysis.

a: Bayesian
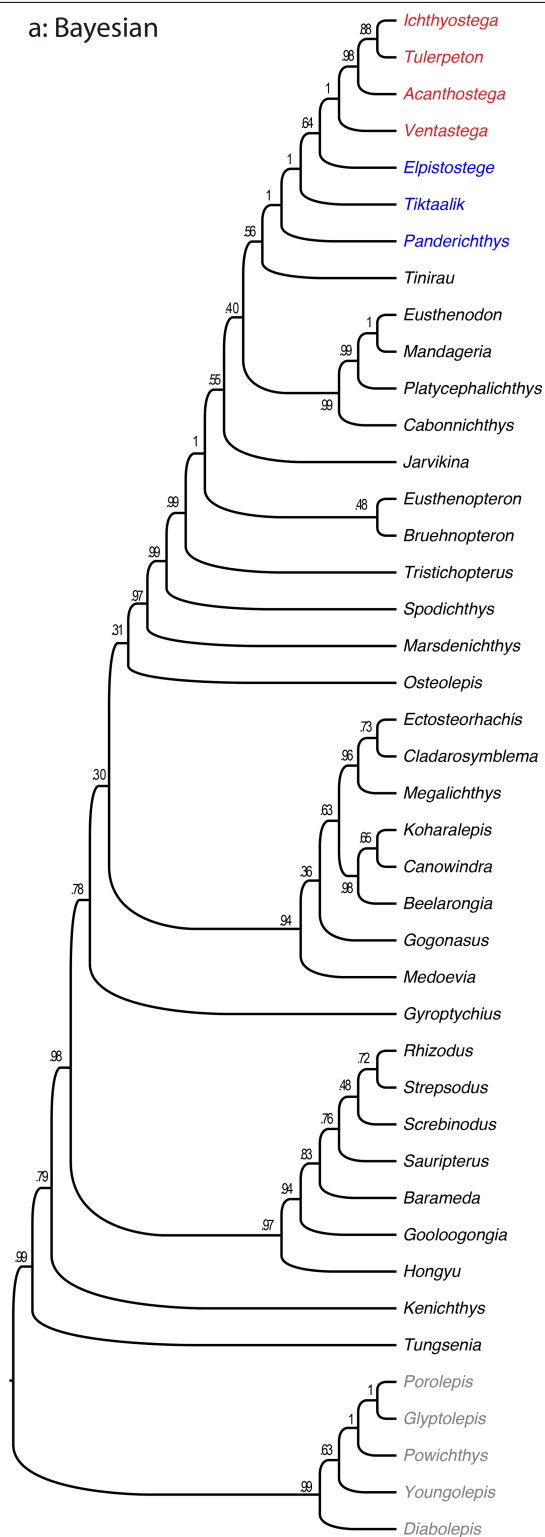
b: Parsimony
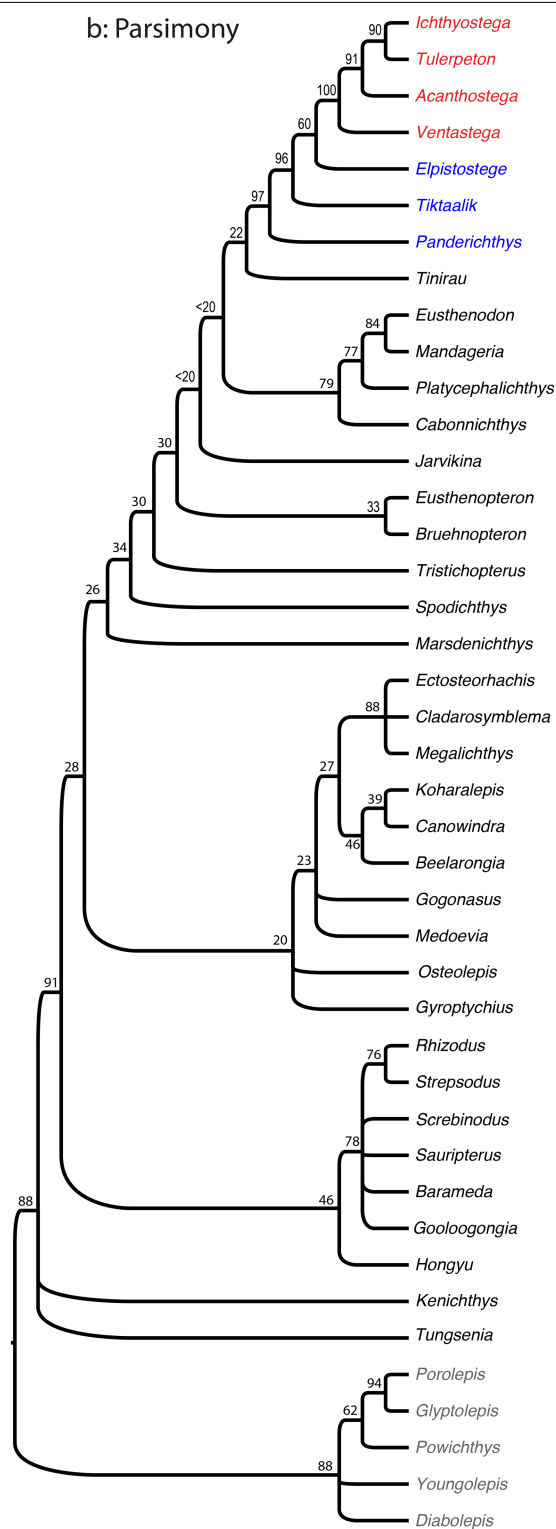
Extended Data Fig. 4 | Phylogenetic relationships of *Elpistostege* and other tetrapodomorphs. Core tetrapods shown in red, elpistostegalian-grade taxa in blue and outgroups in grey. **a**, Undated Bayesian analysis using MrBayes[49]. Majority-rule consensus of 32,000 post-burnin trees (mean log-likelihood of 1,694.88). Numbers at nodes refer to posterior probabilities.

See Supplementary Information for full details of analysis, and the executable MrBayes script. **b**, Parsimony analysis using PAUP*[48]. Strict consensus of all 216 most-parsimonious trees (445 steps). Numbers at nodes denote bootstrap percentages, based on 200 replicates. See Supplementary Information for full details of analysis and the executable PAUP* script.

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Study description	Fossil material studied was already collected and is housed in a major state museum at the Parc de Miguashua in Quebec.
Research sample	Our spoecimens are very rare so only few exits, all are discussed inour paper.
Sampling strategy	NA
Data collection	NA
Timing and spatial scale	NA
Data exclusions	NA
Reproducibility	NA
Randomization	NA
Blinding	NA

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☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Palaeontology

Specimen provenance	Escuminac Formation,
Specimen deposition	Museum at the Parc de Miguashua, Quebec, Canada
Dating methods	The specimen is date by biostratigraphic association with other Late Devonian age fossils found within the Escuminac Formation, such as microfossils (pollen, spores etc).

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