

First discovery of a primitive coelacanth fin fills a major gap in the evolution of lobed fins and limbs

Matt Friedman,^{a,*} Michael I. Coates,^{a,b} and Philip Anderson^c

^aCommittee on Evolutionary Biology, University of Chicago, 1025 E 57th St., Chicago, IL 60637, USA

^bDepartment of Organismal Biology and Anatomy, University of Chicago, 1027 E. 57th St., Chicago, IL 60637, USA

^cDepartment of Geophysical Sciences, University of Chicago, 5734 S. Ellis Ave., Chicago, IL 60637, USA

*Author for correspondence (email: mattf@uchicago.edu)

SUMMARY The fossil record provides unique clues about the primitive pattern of lobed fins, the precursors of digit-bearing limbs. Such information is vital for understanding the evolutionary transition from fish fins to tetrapod limbs, and it guides the choice of model systems for investigating the developmental changes underpinning this event. However, the evolutionary preconditions for tetrapod limbs remain unclear. This uncertainty arises from an outstanding gap in our knowledge of early lobed fins: there are no fossil data that record primitive pectoral fin conditions in coelacanths, one of the three major groups of sarcopterygian (lobe-finned) fishes. A new fossil from the Middle–Late Devonian of Wyoming preserves the first and only example of a primitive coelacanth

pectoral fin endoskeleton. The strongly asymmetrical skeleton of this fin corroborates the hypothesis that this is the primitive sarcopterygian pattern, and that this pattern persisted in the closest fish-like relatives of land vertebrates. The new material reveals the specializations of paired fins in the modern coelacanth, as well as in living lungfishes. Consequently, the context in which these might be used to investigate evolutionary and developmental relationships between vertebrate fins and limbs is changed. Our data suggest that primitive actinopterygians, rather than living sarcopterygian fishes and their derived appendages, are the most informative comparators for developmental studies seeking to understand the origin of tetrapod limbs.

INTRODUCTION

Hypotheses about the evolutionary origin of tetrapod limbs require information about primitive conditions in paired fins. Known pectoral fin endoskeletons in sarcopterygian fishes—the closest relatives of tetrapods—conform to one of three general arrangements: long and biserial, as in lungfishes; short and uniserial, as in tetrapodomorphs; short and biserial, as in the Recent coelacanth *Latimeria*. Each of these has been considered closest to the primitive condition for lobed fins (lungfish pattern: Schultze 1987; tetrapodomorph pattern: Ahlberg 1989; *Latimeria* pattern: Coates et al. 2002). Many well-preserved fin skeletons are now available for a diversity of early fossil tetrapodomorphs (Andrews and Westoll 1970a, b; Rackoff 1980; Long 1989; Jeffery 2001; Garvey et al. 2005; Long et al. 2006; Shubin et al. 2006) and lungfishes and their fossil relatives (Ahlberg 1989; Ahlberg and Trewin 1995), but corresponding material for coelacanths has remained unknown. This presents a problem, because coelacanths occupy the critical phylogenetic position of sister group to all other extant sarcopterygians (Cloutier and Ahlberg 1996; Forey 1998; Zhu and Yu 2002; Brinkmann et al. 2004; Friedman, in press). Thus far, coelacanth paired fin skeletons

are known almost exclusively from the living *Latimeria*, which has evolved independently of other sarcopterygians for at least 420 million years (Janvier 1996). During this time its fins have almost certainly accumulated a suite of specializations.

Here, we describe a coelacanth pectoral fin endoskeleton from the Devonian of Wyoming, USA. This is by far the earliest known paired fin endoskeleton for a coelacanth, and is among the oldest of all osteichthyan examples. Most importantly, this fossil fills the outstanding gap in our knowledge of primitive lobed fins. By highlighting diversity among the earliest fossil sarcopterygians and exposing the unique specializations of living forms, this ancient coelacanth changes the anatomical context for exploring the evolutionary and developmental relationships of paired fins to limbs.

MATERIALS AND METHODS

Specimen preparation and study

The only specimen of *Shoshonia* preserves the pectoral fin endoskeleton as a natural mold. Light body dental casting compound was used to produce an example in positive relief for study. This cast was dusted with a sublimate of ammonium chloride before photography in order to enhance contrast.

Cladistic analyses

The data matrix given in supplementary material was subjected to maximum parsimony analysis in the software package PAUP* (Swofford 2002). The heuristic search algorithm was used to search for the shortest networks using 30,000 random addition sequence replicates. All characters were assigned equal weights, and multi-state characters were run unordered. The shortest networks were rooted on *Acanthodes*. Bremer decay indices were calculated using TreeRot (Sorenson 1999). Character evolution was examined in MacClade (Maddison and Maddison 2000).

SYSTEMATIC PALEONTOLOGY

Osteichthyes Huxley (1880)

Sarcopterygii Romer (1955)

Actinistia Cope (1871)

Shoshonia n. g.

Diagnosis: As for the type species, by monotypy.

Etymology: After the Shoshoni tribe as well as the Shoshone National Forest, from which the specimen was collected.

Shoshonia arctopteryx n. sp.

Figs. 1 and 2

Diagnosis: Plesiomorphic coelacanth with interlocking, flange-bearing segments along the pectoral lepidotrichia differing from *Miguashaia* in the number of pectoral fin-rays (approximately 42 in *Shoshonia* versus over 52 in *Miguashaia*) (Cloutier 1996).

Etymology: Referring to the specimen locality and identity (Greek *arctos*, bear; *pteryx*, fin).

Holotype: Field Museum of Natural History, Chicago (FMNH PF 15327), incomplete impression including flank scales and pectoral fin with partial endoskeleton.

Locality and age: Middle–Late Devonian (Givetian–Frasnian), Jefferson Formation, Beartooth Butte, Shoshone National Forest, Park County, Wyoming, USA. The specimen of *Shoshonia* was collected from talus, but the surrounding matrix contains large concretions of crystalline calcite that indicate that the fossil derives from the lower 14 m of the Jefferson Formation (Dorf 1934). The base of the Jefferson Formation ranges from Eifelian (early Middle Devonian) in central Idaho to Frasnian (early Late Devonian) in western Montana (Grader and Dehler 1999), and we estimate the age at Beartooth Butte to be Givetian–Frasnian. This makes *Shoshonia* a contemporary of the early coelacanths *Diplocercides* (Jessen 1966, 1973; Forey 1998), *Holopterygius* (Friedman and Coates 2006), *Gavinia* (Long 1999), and *Miguashaia* (Cloutier 1996; Forey 1998; Forey et al. 2000).

Exposures of the Jefferson Formation at Beartooth Butte have been considered unfossiliferous (Dorf 1934), but renewed collecting in these beds have also yielded the fragmentary jaw of a tetrapodomorph sarcopterygian in addition to *Shoshonia*.

Remarks: Many primitive members of clades have been ‘assembled’ from isolated remains attributed to a single taxon (e.g., the Triassic ‘bird’ *Protoavis*), but the validity of these composite taxa is rarely tested. This can pose problems, because chimeric taxa can result in spurious reconstructions of character distribution and, in turn, faulty inferences of character polarity and evolution. For these reasons, we tentatively assign FMNH PF 15327 to its own genus rather than attribute it to an existing early coelacanth genus (e.g., *Miguashaia*) to ensure that future studies test its phylogenetic position without a priori assumptions that it belongs to a putative clade (i.e., genus).

RESULTS AND DISCUSSION

Description and comparison with other early sarcopterygians

The most conspicuous feature of *Shoshonia* is its broad, fan-shaped pectoral fin supported by a central lobe (Fig. 1). The fin bears approximately 42 lepidotrichia with moderately elongated basal segments, each of which tapers to a narrow point proximally (Fig. 1, B and C). More distal segments of the lepidotrichia have anterior flanges, resulting in a distinctive imbricating pattern (Fig. 2, A and B). This derived ‘interlocking’ arrangement is shared uniquely with the early coelacanths *Diplocercides* (Jessen 1973), *Gavinia* (Long 1999), and *Miguashaia* (Cloutier 1996), but is lost in post-Devonian taxa (Forey 1998). Lepidotrichia are asymmetrically deployed about the lobate pectoral fin of *Shoshonia* (Fig. 1, B and C); anterior rays are longer and extend further proximally along the fin than those on the posterior margin. This conforms to the pattern found in actinopterygians and many sarcopterygians, including some fossil coelacanths (Forey 1998), but differs from the near-symmetrical finweb common to the living coelacanth *Latimeria* (Millot and Anthony 1958; Forey 1998) and lungfishes and their closest extinct relatives (Ahlberg 1989).

Uniquely among fossil coelacanths, the pectoral fin endoskeleton is sufficiently well preserved in *Shoshonia* to allow meaningful interpretations of pattern (Fig. 1, B and C). A very incomplete example is known in the derived Mesozoic genus *Laugia* (Stensiö 1932; Forey 1998), but this provides few useful details, whereas paired fin endoskeletons of other extinct coelacanths appear to have been unossified (Forey 1998). The pectoral fin lobe of *Shoshonia* encloses a primary endoskeletal support consisting of a series of articulated mesomeres. Such a support is present in all other sarcopterygian-paired fins, and in extant examples forms a prominent central axis. In *Shoshonia* this structure is off-center, located closer to the posterior (trailing) edge than to the anterior; most visible endoskeleton lies anterior to the mesomeres. By convention, we refer to this endoskeletal support as the metapterygial axis,

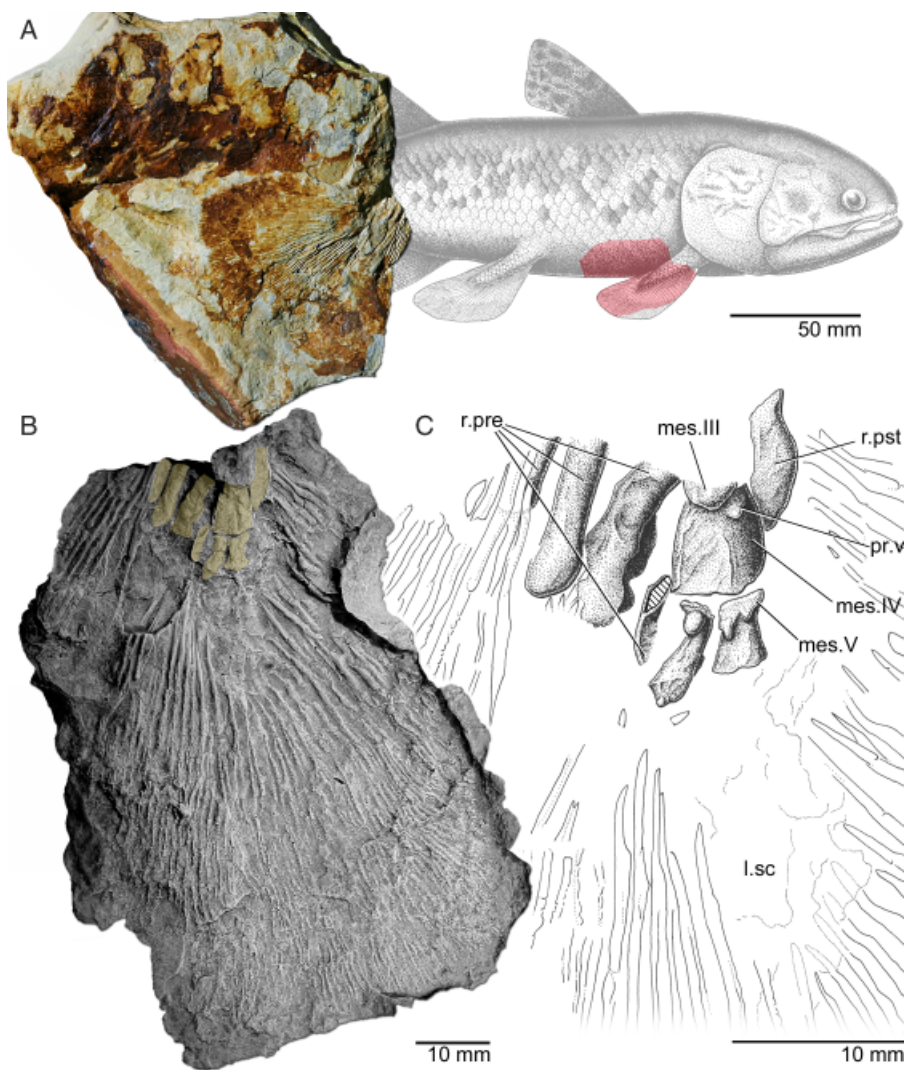


Fig. 1. *Shoshonia arctopteryx* gen. et sp. nov., an early coelacanth that preserves the oldest and most primitive paired fin skeleton known for that group. (A) Holotype (FMNH PF 15327) showing right flank scales and pectoral fin. Regions of the fish preserved in this specimen are indicated by red area highlighted in hypothetical reconstruction. (B) Positive cast of the pectoral fin, including endoskeletal and dermal components. Fin endoskeleton has been false-color tinted for clarity. (C) Interpretive drawing of the pectoral fin endoskeleton. Abbreviations: l.sc, scales covering central lobe of pectoral fin; mes.III, mesomere three; mes.IV, mesomere four; mes.V, mesomere five; pr.v, ventral process of the mesomere; r.dst, distal radial; r.pst, postaxial radial; r.pre, preaxial radial.

but reject the implications of the developmental process often associated with the term ‘axis’ (Cohn et al. 2002; Grandel 2003). We also note that it is often only possible to recognize morphologically comparable ‘axes’ to approximately the level of the third mesomere. Sarcopterygian-paired fins (including limbs) are structurally diverse beyond this point (Fig. 4), and it is unclear which portions of the distal endoskeleton are strictly comparable between groups. In fact, much of the story of pectoral appendage evolution in sarcopterygians is one of contrasting patterns of distal elaboration, ranging from the proximodistally elongate mesomere chains of lungfishes to the anteroposteriorly broad digit arrays of tetrapods (Figure 4, Table 1).

Three mesomeres are visible in the incompletely preserved fin axis of *Shoshonia*, and each bears prominent ventral processes of the kind found in *Latimeria* (Millot and Anthony 1958; Forey 1998) and porolepiforms (Ahlberg 1989), extinct relatives of lungfishes. A fracture truncates the fin skeleton,

but the preserved arrangement of anterior radials suggests that three additional mesomeres were present proximal to this break, assuming the one-to-one ratio between mesomeres and radials common to sarcopterygian fishes. The fin endoskeleton of *Shoshonia* appears to have been unossified distally, as there is a large gap between the most distal mesomere and the proximal margin of the finweb. The proximal tips of lepidotrichia invariably embrace the distal ends of radials in osteichthyans, indicating that this region was occupied by further, unossified endoskeletal components. Sufficient space is present in this gap to have accommodated two additional mesomeres plus a set of distal radials. Taken together, this suggests that the fin of *Shoshonia* might have included as many as eight mesomeres. This is more than what are found in *Latimeria* (Millot and Anthony 1958; Forey 1998) and tetrapodomorphs (Andrews and Westoll 1970a,b; Rackoff 1980; Long 1989; Jeffery 2001; Garvey et al. 2005; Long et al. 2006; Shubin et al. 2006), which generally have four or five

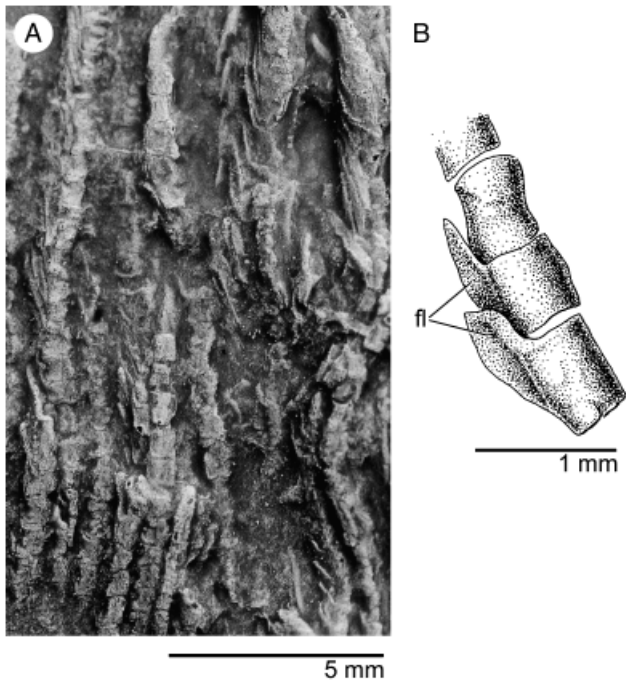


Fig. 2. Fin rays morphology of *Shoshonia arctopteryx* gen. et sp. nov, which supports its identification as a primitive coelacanth. (A) Photograph and (B) interpretive drawing of pectoral lepidotrichia, showing derived interlocking pattern between segments characteristic of early coelacanths. Abbreviation: fl, flange of lepidotrich segment.

metapterygial segments; however, it is considerably less than what is found in early dipnomorphs, which may have had as many as 24 mesomeres within their greatly elongated fin lobes (Ahlberg 1989).

The pectoral fin endoskeleton of *Shoshonia* bears both anterior (preaxial) and posterior (postaxial) radials, like those of *Latimeria* (Millot and Anthony 1958; Forey 1998) and lungfishes (Ahlberg 1989), but in contrast to those of most tetrapodomorphs (Andrews and Westoll 1970a, b; Rackoff 1980; Long et al. 2006). Reflecting finweb distribution around the pectoral lobe, the radials are arranged asymmetrically about the metapterygial axis. This strongly asymmetrical internal architecture is shared with tetrapodomorphs and *Latimeria*, but differs from the condition in lungfishes, where there is a nearly symmetrical array of pre- and postaxial radials. The single postaxial radial preserved in *Shoshonia* has a semilunate shape, like the lone postaxial radial of *Latimeria* (Millot and Anthony 1958; Forey 1998). There are no posterior lepidotrichia proximal to this ossification, indicating that it is the first postaxial radial. However, additional lepidotrichia distal to this radial suggest that the unossified portion of the fin endoskeleton of *Shoshonia* bore further postaxial radials or postaxial processes (as in tetrapodomorphs), which themselves might bear some relation to radials (Grandel 2003). A relationship between postaxial radials and postaxial processes has been proposed (Jarvik 1980a, b) and dismissed by previous authors (Ahlberg 1989), but we are impressed by the positional similarity between these structures: their spatial relationships to both the mesomeres of the metapterygial axis and the lepidotrichia of the dermal finweb are identical. Furthermore, the ‘osteolepiforms’ (Andrews and Westoll 1970a, b; Rackoff 1980; Long et al. 2006; *Gogonasus*, *Rhizodopsis* and *Eusthenopteron* in Fig. 4) that have such lepidotrich-bearing postaxial processes are nested phylogenetically between taxa that bear free postaxial radials on equivalent mesomeres (Daeschler et al. 2006; Shubin et al.

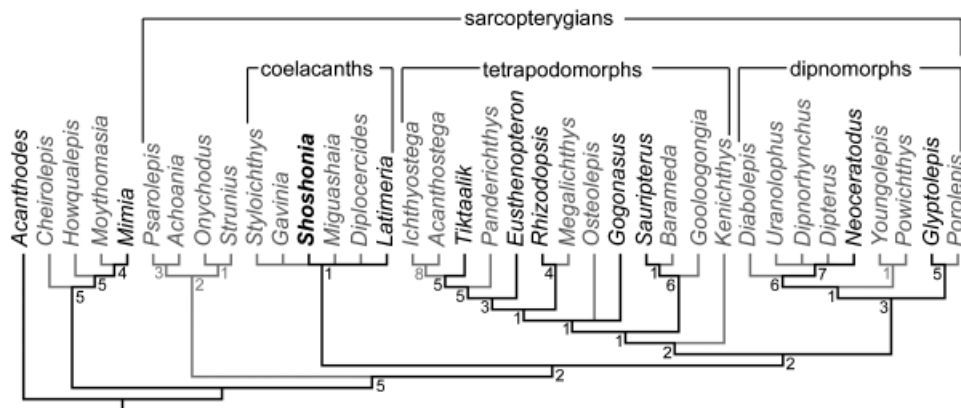


Fig. 3. Phylogenetic placement of *Shoshonia arctopteryx* gen. et sp. nov. Strict consensus topology arising from parsimony analysis of a matrix comprising 37 taxa coded 216 morphological characters ($N = 162$; $L = 510$; $CI = 0.478$ [CI excluding uninformative characters = 0.476]; $RI = 0.735$; $RCI = 0.352$) using the heuristic search algorithm in PAUP* (Swofford 2002). See supplementary material for further details, including complete character optimizations. Numbers below nodes are Bremer decay indices calculated using TreeRot (Sorenson 1999) in conjunction with PAUP* (Swofford 2002). *Shoshonia* is placed as a coelacanth in all the shortest trees. Branches and taxa in black are those shown in Fig. 4. *Gogonasus*, which has been recently interpreted as the sister group to the clade comprising ‘elpistostegalids’ plus limbed tetrapods (Long et al. 2006), is placed in a more orthodox position here, below *Eusthenopteron* and megalichthyids. This result is discussed further in supplementary material.

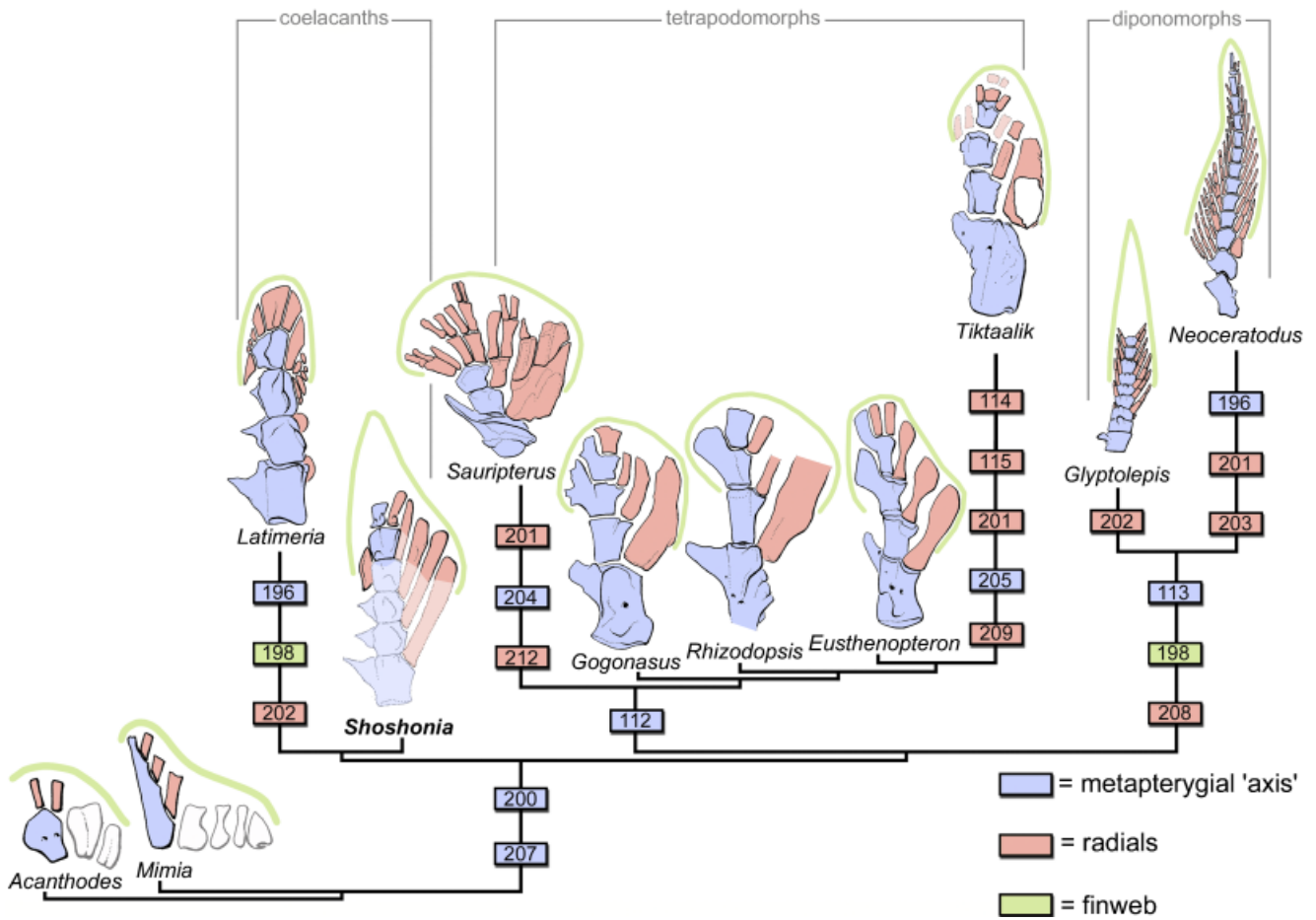


Fig. 4. The evolution of pectoral appendages in early sarcopterygian fishes. Simplified cladogram adapted from that in Fig. 3 showing the distribution of major changes in pectoral appendage pattern in sarcopterygian fishes. This diagram encompasses the early diversity of pectoral appendages within crown-clade Sarcopterygii, and also illustrates selected patterns in proximal outgroups. Many previous depictions of sarcopterygian fin evolution (Coates et al. 2002; Long et al. 2006; Shubin et al. 2006) have been confined to the dipnomorph/tetrapodomorph clade, giving the misleading impression that the conditions found in dipnomorphs might be generalized. Bars representing character changes are color coded to indicate the aspects of morphology to which they refer, while the lengths of branches are scaled to the number of unambiguous character changes occurring along them. A key for these character changes is provided in supplementary material. Few changes separate *Shoshonia* and ‘osteolepiform’-grade tetrapodomorphs such as *Gogonasmus*, *Rhizodopsis*, and *Eusthenopteron* from the base of Sarcopterygii as well as actinopterygian and acanthodian outgroups, but *Latimeria* and dipnomorphs are highly apomorphic, with many of their specializations arising in parallel. Fin skeletons adapted from: *Acanthodes*: Coates (1994); *Mimia*: Gardiner (1984); *Latimeria*: Millot and Anthony (1958); *Sauripterus*: Davis et al. (2004a); *Gogonasmus*: Long et al. (2006); *Eusthenopteron*: Andrews and Westoll (1970a); *Tiktaalik*: Shubin et al. (2006); *Glyptolepis*: Ahlberg (1989); *Neoceratodus*: Rosen et al. (1981). *Rhizodopsis* original, based on specimens P.7551 and P.7557 housed at the Natural History Museum, London.

2006). This suggests to us that an interpretation of postaxial processes and postaxial radials as derived, ontogenetically, from a homologous precursor is simpler than the one that posits the loss of postaxial radials and the subsequent de novo development of postaxial processes.

The pectoral fin endoskeleton of *Shoshonia* differs conspicuously from that of *Latimeria*, and in many ways appears more primitive, although both can be viewed as variations on the asymmetrical biserial arrangement. This primitiveness is most pronounced in the geometry of the radials. In *Latimeria*, the superficial appearance is of a more nearly symmetrical fin skeleton, in part because the two most proximal radials are

extremely short and bear no lepidotrichia, whereas the third radial is composed of a mosaic of small cartilages. In contrast, the fin skeleton of *Shoshonia* is more obviously asymmetrical across the anteroposterior axis. The radials are long and unjointed, proximal radials are longest, and each radial bears lepidotrichia. This resembles the condition in primitive tetrapodomorph sarcopterygians like *Eusthenopteron* (Andrews and Westoll 1970a), *Rhizodopsis* (Andrews and Westoll 1970b), and *Gogonasmus* (Long et al. 2006), as well as primitive actinopterygians like *Moythomasia* (Jessen 1972) and *Mimia* (Gardiner 1984) (Fig. 4). In particular details, such as the number of mesomeres and the corresponding pre- and post-

Table 1. Key to morphological changes depicted in Fig. 4

Taxon	Character change(s)
Sarcopterygii	200.* Metapterygial segmentation: absent (0) → present (1). This change is optimized to the sarcopterygian stem group below the divergence of the extended 'onychodont' clade comprising <i>Onychodus</i> , <i>Strunius</i> , <i>Achoania</i> , and <i>Psarolepis</i>
	207.* Entepicondyle (posterior process from most proximal mesomere): absent (0) → present (1). This change is optimized to the sarcopterygian stem group crownward of <i>Onychodus</i> , which lacks an entepicondyle (Andrews et al. 2006)
<i>Latimeria</i>	196. Pectoral fin (A: 6): unrotated (0) → rotated (1). Although the state for this character cannot be assessed for <i>Shossonia</i> , the pectoral fin appears unrotated in <i>Miguashaia</i> . If <i>Shossonia</i> is placed below or as sister to <i>Miguashaia</i> , then pectoral fin rotation would have evolved on the branch leading to <i>Latimeria</i> in Fig. 3. Regardless of the condition in <i>Shossonia</i> , the cladistic solution presented here indicates that fin rotation is homoplastic between lungfishes and coelacanth
	198. Pectoral fin web: asymmetrical (0) → symmetrical (1)
	202. Pectoral radials: all bear fin rays or lepidotrichia (0) → some 'naked' (1)
Tetrapodomorpha	112.* Deltoid and supinator processes (F: 114): absent (0) → present (1)
<i>Sauripterus</i>	201. Pectoral radials: do not bifurcate (0) → bifurcate (1)
	204.* Ball-shaped caput humeri (JA: 15): absent (0) → present (1)
	212. Distal fin or limb domain expanded across A-P axis (C: 1): no (0) → yes (1)
<i>Tiktaalik</i> and higher tetrapodomorphs	114. Pectoral fin radials (F: 116): unjointed (0) → jointed (1)
	115. Pectoral fin radials (F: 117): 'preaxial' radials only (0) → 'preaxial' plus 'postaxial' radials (1)
	201. Pectoral radials: do not bifurcate (0) → bifurcate (1)
	205.* Body of humerus (AJ: 89): cylindrical (0) → flattened with rectangular cross-section (1)
	209. Radius of equal length or shorter than humerus (C: 17): no (0) → yes (1)
Dipnomorpha	113.* Metapterygial 'axis' of pectoral fin skeleton (jointed 'axes' only) (F: 115): short (0) → long (1)
	198. Pectoral fin web: asymmetrical (0) → symmetrical (1)
	208.* Humeral radials (A: 8): present (0) → absent (1)
<i>Glyptolepis</i>	202. Pectoral radials: all bear fin rays or lepidotrichia (0) → some 'naked' (1)
<i>Neoceratodus</i>	196. Pectoral fin (A: 6): unrotated (0) → rotated (1)
	201. Pectoral radials: do not bifurcate (0) → bifurcate (1)
	203.* Postaxial radials: restricted distal to ulna (0) → first present on ulna (1)

The characters considered here concern gross aspects of pectoral appendage morphology and pattern, with an emphasis on aspects of the endoskeleton (characters 112–115, 196, 198, 200–205, 207–212). All changes given refer only to unambiguous optimizations (i.e., those reconstructed identically under ACCTRAN and DELTRAN conventions). Characters with a consistency index of 1 in the complete cladistic solution (Figs. 3, S1–S4) are marked with an asterisk (*); all other changes are homoplastic. Some apomorphies listed here do not appear in Figs. S1–S4 because the position of some changes is unclear due to missing data entries in taxa not included in the 'pruned' cladogram considered here and in Fig. 4. For example, it is unclear if deltoid and supinator processes (character 112) arose along the internode between the base of Tetrapodomorpha and *Kenichthys* or between *Kenichthys* and more crownward tetrapodomorphs. As such, this change is not mapped on Fig. S4 owing to uncertain conditions in *Kenichthys*. However, deltoid and supinator processes must have arisen somewhere between the divergence of Tetrapodomorpha from Dipnomorpha and the divergence between rhizodonts from all more crownward tetrapodomorphs, as indicated here and in Fig. 4. Sources of characters are indicated with the following abbreviations: A, Ahlberg (1989); AJ, Ahlberg and Johanson (1998); C, Coates et al. (2002); F, Friedman (in press); JA, Johanson and Ahlberg (2001). Many characters from Friedman (in press) were adapted or modified from Zhu and Yu (2002). All fins in dorsal view except for *Rhizodopsis* and *Sauripterus*; anterior (leading) edge of all fins is to the right.

axial radials, the pectoral fin endoskeleton of *Shoshonia* differs from those of other early sarcopterygians: it increases the diversity of specific pectoral fin patterns known in that group. However, apart from these meristic differences, we draw attention to an important similarity shared with the paired appendages of many other sarcopterygians and more distal outgroups: a highly asymmetrical internal and external fin pattern, which reflects a recurrent—and we argue primitive—motif.

Implications for the evolution and development of lobed fins

To investigate the impact of *Shoshonia* on inferred patterns of pectoral appendage evolution in sarcopterygians, we have included this genus in a cladistic analysis using a data set modified from those in two recent studies of early osteichthyan interrelationships (Zhu and Yu 2002; Friedman, in press). All shortest trees recovered from this analysis support the interpretation of *Shoshonia* as an early coelacanth (Fig. 3). However, this result also shows how closely the pectoral endoskeleton of this genus approaches the primitive arrangement inferred for the sarcopterygian crown group (Fig. 4). A tree that maps unambiguous changes in gross fin structure places a zero-length branch between *Shoshonia* and the node subtending all living lobe-finned fishes. This implies that *Shoshonia* maintains a pectoral fin pattern close to that which was primitive for crown-group Sarcopterygii as a whole: an internally and externally asymmetrical structure bearing unsegmented, unbranching radials articulating with a short to moderately long metapterygial axis. In turn, this generalized sarcopterygian metapterygial pattern differs in only a few minor details from that found in fossil and living actinopterygians (the most notable of which is the presence of discrete mesomeres) (Jessen 1972; Gardiner 1984), and even chondrichthyans (Daniel 1922; Coates 2003; Grandel 2003). The primitive lobed fin morphology is remarkably unmodified throughout most of the tetrapod stem group (Fig. 4), supporting previous interpretations of the paired appendages of early tetrapodomorphs like *Eusthenopteron* as highly conservative structures (Rosen et al. 1981; Ahlberg 1989). In contrast, lungfishes, *Latimeria*, and the immediate relatives of limb-bearing tetrapods are placed at the tips of long branches. This implies that considerable morphological evolution separates the pectoral appendages of these taxa from a basic sarcopterygian ‘ground plan.’

Our solution indicates that many changes in pectoral appendage structure separating close relatives of tetrapods such as *Tiktaalik* and *Panderichthys* from more plesiomorphic ‘osteolepiforms’ concern aspects of radial morphology (Fig. 4). These findings are relevant, because they indicate that considerable modifications to radials—arguably the closest equivalent to digits in paired fin endoskeletons (Grandel

2003)—were established in tetrapod-like fishes that retained a finweb. To describe digits as neomorphic avoids questions about antecedents in ontogeny and phylogeny. Digits are either a particular kind or a subset of paired fin radials, or, alternatively, paired fin radials and digits are different kinds of a larger category of endoskeletal paired fin supports. This homology hypothesis rests on the usual criteria: anatomy—position and connectivity; morphology—including the asymmetry of having a dorsal (extensor) and ventral (flexor) surface, unlike mid-line fin radials; embryology—digits and paired fin radials develop within a bud rather than within a fold; gene regulation—many of the same molecular-genetic systems are involved in paired fin radial and digit development. In this context, differences between paired fin radials and digits are comparatively minor, and relate to distal position and the absence of fringing lepidotrichia, as well as the absence of an apparently straightforward proximal to distal branching pattern connecting digits to more proximal parts of the appendicular skeleton.

By clarifying the morphological pattern at the base of the evolutionary tree of lobed fins, *Shoshonia* provides a new comparative framework for developmental investigations aimed at understanding the fin-to-limb transition. Our findings further question the utility of lungfish-like appendages as models for understanding the origin of tetrapod limbs in both developmental and phylogenetic contexts (Rosen et al. 1981; Joss and Longhurst 2001; Long et al. 2006; Shubin et al. 2006), which remain common even though lungfish fins and those of their fossil relatives have been interpreted as exceptionally autapomorphic (Ahlberg 1989; Coates et al. 2002; Coates 2003). Coupled with the cladistic analysis presented here, new data from *Shoshonia* help to expose many features common to the fins of *Latimeria* and lungfishes (‘bifurcating’ and segmented radials, symmetrical finweb, pectoral fin rotation) as independently derived novelties. Despite the popular notion of lungfishes (Pearson 2006), and especially *Latimeria* (‘old fourlegs’; Smith 1956), as ‘living fossils,’ their appendages make poor approximations of primitive conditions.

Tetrapod limbs, like primitive sarcopterygian paired fins, are conspicuously asymmetrical. In contrast, lungfish paired fins show extraordinary near-symmetry combined with extreme distal outgrowth. It follows that lungfishes provide a potential model system for understanding lobed fin developmental diversity. However, given the retention of what is now corroborated as a conservative, highly polarized pectoral endoskeleton in fin-bearing stem-tetrapods, informative insights into the pre-conditions for the complex, phased regulation of tetrapod limb development (Tarchini and Duboule 2006) are more likely to be obtained from non-teleostean actinopterygians with a well developed and strongly asymmetrical metapterygium, such as *Polyodon* and *Acipenser* (Davis et al. 2004b; Mabee and Noordsy 2004; Metscher et al. 2005).

Acknowledgments

We thank R. Masek (University of Chicago) for advice in stabilizing the specimen of *Shoshonia*, and the representatives of the US Forestry Service and Bureau of Land Management for their assistance. Per Ahlberg and Martin Brazeau (Uppsala University), John Long (Museum Victoria), Martin Cohn (University of Florida), and Matthew Harris (Max Planck Institute) provided helpful discussion. We thank Peter Forey (The Natural History Museum) for providing helpful comments, while an anonymous referee furnished a useful critique of this work. This work was supported by a University of Chicago faculty research grant (M.I.C.) and a National Science Foundation Graduate Research Fellowship (award number DGE-0228235) and Environmental Protection Agency STAR Fellowship (award number FP916730) (M.F.).

REFERENCES

- Ahlberg, P. E. 1989. Paired fin skeletons and the relationships of the fossil group Porolepiformes (Osteichthyes: Sarcopterygii). *Zool. J. Linn. Soc.* 96: 119–166.
- Ahlberg, P. E., and Johanson, Z. 1998. Osteolepiforms and the ancestry of tetrapods. *Nature* 395: 792–794.
- Ahlberg, P. E., and Trevisan, N. H. 1995. The postcranial skeleton of the Middle Devonian lungfish *Dipterus valenciennesi*. *Trans. Roy. Soc. Edinb.: Earth Sci.* 85: 159–175.
- Andrews, S. M., Long, J. A., Ahlberg, P. E., Barwick, R. E., and Campbell, K. S. W. 2006. The structure of the sarcopterygian *Onychodus jandemarri* n. sp. from Gogo, Western Australia: with a functional interpretation of the skeleton. *Trans. Roy. Soc. Edinb. Earth Sci.* 96: 197–307.
- Andrews, S. M., and Westoll, T. S. 1970a. The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Trans. Roy. Soc. Edinb.* 68: 207–329.
- Andrews, S. M., and Westoll, T. S. 1970b. The postcranial skeleton of rhipidistian fishes excluding *Eusthenopteron*. *Trans. Roy. Soc. Edinb.* 68: 391–489.
- Brinkmann, H., Vankatesh, B., Brenner, S., and Meyer, A. 2004. Nuclear protein-coding genes support lungfish and not the coelacanth as the closest living relatives of land vertebrates. *Proc. Natl. Acad. Sci. USA* 101: 4900–4905.
- Cloutier, R. 1996. The primitive actinistian *Miguashaia bureaui* Schultze. In H.-P. Schultze and R. Cloutier (eds.), *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Dr Friedrich Pfeil, München, pp. 227–247.
- Cloutier, R., and Ahlberg, P. E. 1996. Morphology, characters, and interrelationships of basal sarcopterygians. In M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson (eds.), *Interrelationships of Fishes*. Academic Press, San Diego, pp. 445–479.
- Coates, M. I. 1994. The origin of vertebrate limbs. *Development* 1994 (Suppl.): 169–180.
- Coates, M. I. 2003. The evolution of paired fins. *Theory Biosci.* 122: 266–287.
- Coates, M. I., Jeffery, J. E., and Ruta, M. 2002. Fins to limbs: what the fossils say. *Evol. Dev.* 4: 390–401.
- Cohn, M. J., Lovejoy, C. O., Wolpert, L., and Coates, M. I. 2002. Branching, segmentation and the metapterygial axis: pattern versus process in the vertebrate limb. *BioEssays* 24: 460–465.
- Cope, E. D. 1871. Contribution to the ichthyology of the Lesser Antilles. *Trans. Am. Philos. Soc.* 14: 445–483.
- Daeschler, E. B., Shubin, N. H., and Jenkins, F. A. Jr. 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature* 440: 757–763.
- Daniel, J. F. 1922. *The Elasmobranch Fishes*. University of California Press, Berkeley.
- Davis, M. C., Shubin, N. H., and Daeschler, E. B. 2004a. A new specimen of *Sauripterus taylori* (Sarcopterygii, Osteichthyes) from the Famennian Catskill Formation of North America. *J. Vert. Paleontol.* 24: 26–40.
- Davis, M. C., Shubin, N. H., and Force, A. 2004b. Pectoral fin and girdle development in the basal actinopterygians *Polyodon spathula* and *Acipenser trammontanus*. *J. Morphol.* 262: 608–628.
- Dorf, E. 1934. Stratigraphy and paleontology of a new Devonian formation at Beartooth Butte, Wyoming. *J. Geol.* 42: 720–737.
- Forey, P. L. 1998. *History of the Coelacanth Fishes*. Chapman & Hall, London.
- Forey, P. L., Ahlberg, P. E., Lukševičs, E., and Zupinš, I. 2000. A new Devonian coelacanth from the middle Devonian of Latvia. *J. Vert. Paleontol.* 20: 243–252.
- Friedman, M., and Coates, M. I. 2006. A newly recognized coelacanth highlights the early morphological diversification of the clade. *Proc. Roy. Soc. B* 273: 240–245.
- Friedman, M. *Styloichthys* as the oldest coelacanth: implications for early osteichthyan interrelationships. *J. Syst. Palaeontol.*, in press.
- Gardiner, B. G. 1984. The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bull. Br. Mus. Nat. Hist. (Geol.)* 37: 173–428.
- Garvey, J. M., Johanson, Z., and Warren, A. 2005. Redescription of the pectoral fin and vertebral column of the rhizodontid fish *Barameda decipiens* from the Lower Carboniferous of Australia. *J. Vert. Paleontol.* 25: 8–18.
- Grader, G. W., and Dehler, C. M. 1999. Devonian stratigraphy in east-central Idaho: new perspectives from the Lemhi Range and Bayhorse area. In S. S. Huges and G. D. Thackray (eds.), *Guidebook to the Geology of Eastern Idaho*. Idaho Museum of Natural History, Pocatello, pp. 31–56.
- Grandel, H. 2003. Approaches to a comparison of fin and limb structure and development. *Theory Biosci.* 122: 288–301.
- Huxley, T. H. 1880. On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proc. Zool. Soc. London* 1880: 649–662.
- Janvier, P. 1996. *Early Vertebrates*. Clarendon Press, Oxford.
- Jarvik, E. 1980a. *Basic Structure and Evolution of Vertebrates*. Vol. 1. Academic Press, London.
- Jarvik, E. 1980b. *Basic Structure and Evolution of Vertebrates*. Volume 2. Academic Press, London.
- Jeffery, J. E. 2001. Pectoral fins of rhizodontids and the evolution of pectoral appendages in the tetrapod stem-group. *Biol. J. Linn. Soc.* 74: 217–236.
- Jessen, H. 1966. Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach—Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtigung von amerikanischem und europäischem *Onychodus*-Material. *Ark. Zool.* 18: 305–389.
- Jessen, H. 1972. Schultergürtel und Pectroalflosse bei Actinopterygiern. *Fossils Strata* 1: 1–101.
- Jessen, H. 1973. Weitere fischreste aus dem Oberen Plattenkalk der Bergisch-Gladbach—Paffrather Mulde (Oberdevon, Rheinisches Schiefergebirge). *Palaeontogr. Abt. A* 143: 159–187.
- Johanson, Z., and Ahlberg, P. E. 2001. Devonian rhizodontids and trichopterids (Sarcopterygii; Tetrapodomorpha) from East Gondwana. *Trans. Roy. Soc. Edinb. Earth Sci.* 92: 43–74.
- Joss, J., and Longhurst, T. 2001. Lungfish paired fins. In P. E. Ahlberg (ed.), *Major Events in Early Vertebrate Evolution*. Taylor & Francis, London, pp. 370–376.
- Long, J. A. 1989. A new rhizodontiform fish from the Early Carboniferous of Victoria, Australia, with remarks on the phylogenetic position of the group. *J. Vert. Paleontol.* 9: 1–17.
- Long, J. A. 1999. A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia. *Rec. West. Aust. Mus. Suppl.* 57: 37–53.
- Long, J. A., Young, G. C., Holland, T., Senden, T. J., and Fitzgerald, E. M. G. 2006. An exceptional Devonian fish from Australia sheds light on tetrapod origins. *Nature* 444: 199–202.
- Mabee, P. M., and Noordsy, M. 2004. Development of the paired fins in the paddlefish, *Polyodon spathula*. *J. Morphol.* 261: 334–344.
- Maddison, W. P., and Maddison, D. R. 2000. *MacClade: Analysis of Phylogeny and Character Evolution, Version 4.0*. Sinauer Associates, Sunderland, MA.
- Metscher, B. D., Takahashi, K., Crow, K., Amemiya, C., Nonaka, D. F., and Wagner, G. P. 2005. Expression of *Hoxa-11* and *Hoxa-13* in the pectoral fin of a basal ray-finned fish, *Polyodon spathula*: implications for the origin of tetrapod limbs. *Evol. Dev.* 7: 186–195.

- Millot, J., and Anthony, J. 1958. *Anatomie de Latimeria chalumnae. Tome I. Squelette, Muscles, et Formations du Soutien*. Éditions du Centre National de la Recherche Scientifique, Paris.
- Pearson, H. 2006. Dam project threatens living fossil. *Nature* 442: 232–233.
- Rackoff, J. S. 1980. The origin of the tetrapod limb and the ancestry of tetrapods. In A. Panchen (ed.). *The Terrestrial Environment and the Origin of Land Vertebrates*. Academic Press, London, pp. 252–292.
- Romer, A. S. 1955. Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii? *Nature* 176: 126.
- Rosen, D. E., Forey, P. L., Gardiner, B. G., and Patterson, C. 1981. Lungfishes, tetrapods, paleontology, and plesiomorphy. *Bull. Am. Mus. Nat. Hist.* 167: 159–276.
- Schultze, H-P. 1987. Dipnoans as sarcopterygians. *J. Morphol.* 1 (Suppl.): 39–74.
- Shubin, N. H., Daeschler, E. B., and Jenkins, F. A. Jr. 2006. The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. *Nature* 440: 764–771.
- Smith, J. L. B. 1956. *Old Fourlegs: The Story of the Coelacanth*. Longman Green, London.
- Sorenson, M. D. 1999. *TreeRot, Version 2*. Boston University, Boston.
- Stensiö, E. A. 1932. Triassic fishes from East Greenland. *Meddr. Grønland.* 83: 1–305.
- Swofford, D. L. 2002. *PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4*. Sinauer Associates, Sunderland, MA.
- Tarchini, B., and Duboule, D. 2006. Control of Hoxd genes' colinearity during early limb development. *Dev. Cell* 10: 93–103.
- Zhu, M., and Yu, X. 2002. A primitive fish close to the common ancestor of tetrapods and lungfish. *Nature* 418: 767–770.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

- Part A.** Characters used in cladistic analysis.
- Part B.** Primary literature used to code characters.
- Part C.** Taxon-by-character matrix used in cladistic analysis.
- Part D.** Systematic methodology.
- Part E.** Character optimizations: complete cladogram.

Fig. S1. Unambiguous character changes plotted on one of 162 shortest cladograms ($L = 510$; $CI = 0.478$ [CI excluding uninformative characters = 0.476]; $RI = 0.735$; $RCI = 0.352$) recovered from maximum parsimony analysis of the data matrix in supplementary material C. Zero-length branches have been collapsed. Continued on Figs S2–S4.

Fig. S2. Unambiguous character changes plotted on one of 162 shortest cladograms ($L = 510$; $CI = 0.478$ [CI excluding uninformative characters = 0.476]; $RI = 0.735$; $RCI = 0.352$) recovered from maximum parsimony analysis of the data matrix in supplementary material C. Zero-length branches have been collapsed. Continued on Figs. S3–S4.

Fig. S3. Unambiguous character changes plotted on one of 162 shortest cladograms ($L = 510$; $CI = 0.478$ [CI excluding uninformative characters = 0.476]; $RI = 0.735$; $RCI = 0.352$) recovered from maximum parsimony analysis of the data matrix in supplementary material C. Zero-length branches have been collapsed. Continued on Fig. S4.

Fig. S4. Unambiguous character changes plotted on one of 162 shortest cladograms ($L = 510$; $CI = 0.478$ [CI excluding

uninformative characters = 0.476]; $RI = 0.735$; $RCI = 0.352$) recovered from maximum parsimony analysis of the data matrix in supplementary material C. Zero-length branches have been collapsed.

Part F. Extended discussion of cladistic results, with special reference to *Gogonasmus*.

Fig. S5. Comparison of plesiomorphic tetrapodomorph humeri in dorsal view. (A) The 'osteolepidid' *Gogonasmus* (adapted from Long et al. 2006); (B) the tristichopterid *Eusthenopteron* (adapted from Andrews and Westoll 1970a); (C) the 'elpistostegalid' *Tiktaalik* (adapted from Shubin et al. 2006). Arrow for each figure indicates the position of the ventral process of the humerus that is interpreted as a synapomorphy uniting *Gogonasmus* with *Tiktaalik* and *Panderichthys* by Long et al. (2006), but is here considered a character underpinning a much more extensive tetrapodomorph clade that includes *Eusthenopteron* in addition to these taxa.

Fig. S6. Comparison of plesiomorphic tetrapodomorph humeri in proximal and distal views. Areas shaded in grey are unfinished articular facets. Humeri in upper row are pictured in proximal view, while those in the lower row are depicted in distal view. (A) The 'osteolepidid' *Gogonasmus* (adapted from Long et al. 2006); (B) the tristichopterid *Eusthenopteron* (adapted from Andrews and Westoll 1970a); (C) the limb-bearing stem-tetrapod *Acanthostega* (adapted from Coates 1996). It has been proposed that the humerus of *Gogonasmus* shares a derived flattened cross-section with 'elpistostegalids' and limbed tetrapods, and that this feature unites these taxa to the exclusion of other tetrapodomorphs, including *Eusthenopteron* (Long et al. 2006). We reject this line of argumentation, because the cross-sectional shape of the humerus of *Gogonasmus* agrees more closely with the condition seen in *Eusthenopteron* than it does with that in either 'elpistostegalids' or limbed tetrapodomorphs.

Fig. S7. Comparison of the pectoral fin endoskeletons of a range of plesiomorphic tetrapodomorphs. (A) The rhizodont *Barameda* (adapted from Long 1989, with considerations drawn from Garvey et al. 2005); (B) the tristichopterid *Eusthenopteron* (adapted from Andrews and Westoll 1970a); (C) the 'osteolepidid' *Gogonasmus* (adapted from Long et al. 2006); (D) the 'elpistostegalid' *Tiktaalik* (adapted from Shubin et al. 2006). Abbreviations: int, intermedium; mes. IV, fourth mesomere; mes.V, fifth mesomere.

Part G. Supplementary references.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1525-142X.2007.00169.x> (This link will take you to the article abstract).

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.