

Fins to limbs: what the fossils say¹

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SUMMARY A broad phylogenetic review of fins, limbs, and girdles throughout the stem and base of the crown group is needed to get a comprehensive idea of transformations unique to the assembly of the tetrapod limb ground plan. In the lower part of the tetrapod stem, character state changes at the pectoral level dominate; comparable pelvic level data are limited. In more crownward taxa, pelvic level changes dominate and repeatedly precede similar changes at pectoral level. Concerted change at both levels appears to be the exception rather than the rule. These patterns of change are explored by using alternative treatments of data in phylogenetic analyses. Results

highlight a large data gap in the stem group preceding the first appearance of limbs with digits. It is also noted that the record of morphological diversity among stem tetrapods is somewhat worse than that of basal crown group tetrapods. The pre-limbed evolution of stem tetrapod paired fins is marked by a gradual reduction in axial segment numbers (mesomeres); pectoral fins of the sister group to limbed tetrapods include only three. This reduction in segment number is accompanied by increased regional specialization, and these changes are discussed with reference to the phylogenetic distribution of characteristics of the stylopod, zeugopod, and autopod.

INTRODUCTION

Without a phylogeny, fossils are mute (a point somewhat skirted in the article title). Even within a phylogeny, fossils are of limited use relative to extant taxa. However, if used to discover stem group conditions, then fossils represent a unique data set (Budd 2001). Stem groups include taxa external to a living radiation (crown group) but which are nevertheless more closely related to that group than they are to any other living clade (Patterson 1993). Thus, stem taxa provide the only direct morphological information on primitive fish-like conditions unique to the tetrapod lineage; there are no living finned tetrapods. Perhaps more importantly, stem groups also deliver evidence about the accumulation of derived features more usually considered unique to the crown group. These features are almost always those that have long been considered essential components of a particular ground plan or *Bauplan* (Woodger 1945; Hall 1998), such as that of the pentadactylous tetrapod limb. And, given that any *Bauplan* represents no more than a hypothesis of character states at a particular phylogenetic node, the discovery and description of stem taxa is a fundamental part of research into how both *Baupläne* and characters evolve.

Basal stem group taxa are rare and barely recognizable as such, because they share few synapomorphies with the crown group in question. Debates about phylogenetic hy-

potheses concerning these basal nodes are often intense, and conflicts arise over differing taxon and character sets, scores, and coding methods (see Coates et al. 2000; Laurin et al. 2000). Furthermore, arguments may arise about whether basal stem taxa should be included under group names long used for crown clades exclusively (e.g., possible objections to the description of *Triceratops* as a stem group bird). Rather than become mired in debates about key characters and traditional name usage, we favor a phylogenetically based approach to taxonomy (for review of current debate over phylogenetic nomenclature, see Bryant and Cantino 2002). Here, the name Tetrapoda (Goodrich 1930) is applied to the “total group,” meaning the most exclusive monophyletic clade encompassing crown and stem groups (Patterson 1993; cf. Coates 1996 and Jeffery 2001, on total group Tetrapoda). In this respect we follow the trend to use monophyletic group names in a way that emphasizes biodiversity (Greene 2001). Recognition of certain finned sarcopterygians as early tetrapods can only broaden our understanding of the fin–limb transition.

Our aim is to review fins and limbs from the base of the tetrapod total group upward and to document how the evolution of tetrapod appendages relates to the divergence of amniote and lissamphibian lineages. A variety of analytical treatments is applied to the morphological data in an attempt to obtain a more detailed picture of the transitional sequence.

Finally, unlike previous reviews, endoskeletal girdle data are also included, because pelves and scapulocoracoids, like paired fins and limbs, are products of the lateral plate mesoderm (Burke 2000; McGonnell 2001; see references within for somitic sources of amniote scapulae). Links between limbs, fins, and girdles are thus both morphofunctional and developmental. We do not, however, address changes to the dermal skeleton (fin rays in particular) in equivalent detail: for a current review of this aspect of the fin–limb story, see Jeffery 2001.

CHARACTER DISTRIBUTION AND EARLY TETRAPOD PHYLOGENY

Tetrapod stem lineage from fins to limbs

Molecular and morphological evidence suggests that the base of the tetrapod crown group extends back no further than the lowermost Carboniferous or Upper Devonian, around 360 Mya (Hedges 2001; Ruta and Coates in press). By this time, most skeletal changes marking conventional ideas about the fish tetrapod division had been largely completed. In addition to the fin–limb transition, these changes include enlargement of pelvic and pectoral girdles, origin of a sacrum, consolidation of vertebrae and ribs, origin of a neck, changes in cranial proportions, changes to sensory systems, gill arch reduction, opercular series loss, mid-line fin loss, and scale reduction and loss. Importantly, there is compelling evidence

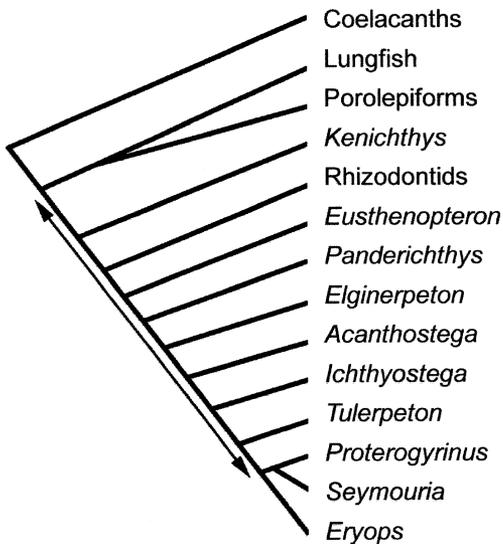


Fig. 1. A simplified phylogeny of sarcopterygians including stem group tetrapods (numerous taxa omitted) and the base of the tetrapod crown group. Branching sequence adapted from Cloutier and Ahlberg (1996), Ahlberg and Johanson (1998), Johanson and Ahlberg (2001), and Ruta and Coates (in press). Double headed arrow denotes extent of tetrapod stem group.

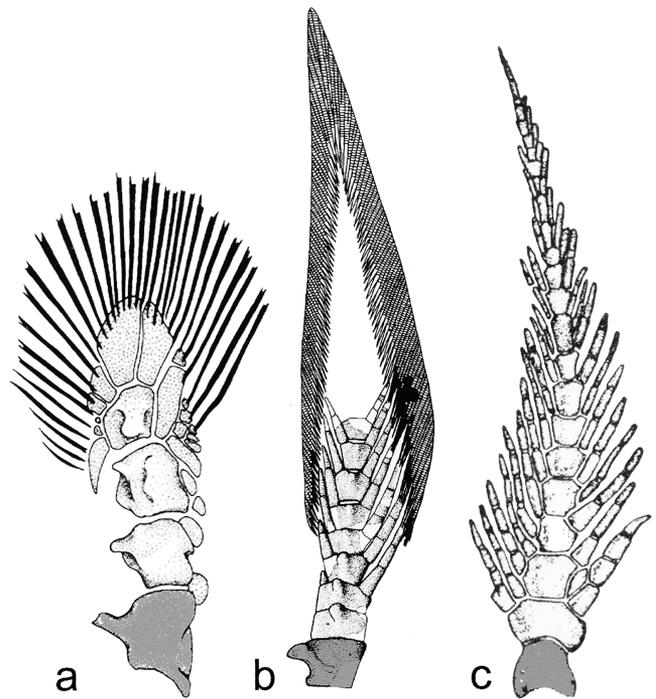


Fig. 2. Fin patterns in outgroup sarcopterygians relative to the Tetrapoda. (a) *Latimeria* (coelacanth) pectoral fin. After Forey (1998). (b) Porolepiform pectoral fin. After Ahlberg (1989). (c) Lungfish pectoral fin. After Jarvik (1980). All fins with leading edge (anterior/preaxial) to right of page.

that these transformations were initiated and largely completed in animals that were mostly, and primitively, aquatic (Coates 1996; Clack 2000).

In the broader phylogenetic context, the living sister groups of tetrapods are either lungfish (Dipnoi) or the coelacanth (Actinistia). Molecular data are equivocal (Zardoyer and Meyer 2001), but most morphology-based analyses including fossils favor a lungfish-tetrapod grouping (Forey 1998). Thus far, the full extent of the tetrapod stem group has been addressed primarily by Ahlberg and Johanson (1998) and Johanson and Ahlberg (2001). Their analyses (summarized in Fig. 1) place *Kenichthys*, a sarcopterygian fish from the Middle Devonian of China, as the most basal known total group tetrapod, although the split from lungfish ancestry is likely to be Lower Devonian, approximately 400+ Mya. However, *Kenichthys* is poorly preserved, and the appendages are unknown (Chang and Zhu 1993). Paired fin conditions at the base of the tetrapod stem are better indicated by fossil outgroups, such as the porolepiforms.

Cloutier and Ahlberg (1996) linked porolepiforms to the lungfish stem. Their paired fins are similar in many respects (Fig. 2, b and c), but, unlike the equally elongate pectoral and pelvic fins of extant lungfish, porolepiform pelvics fins are

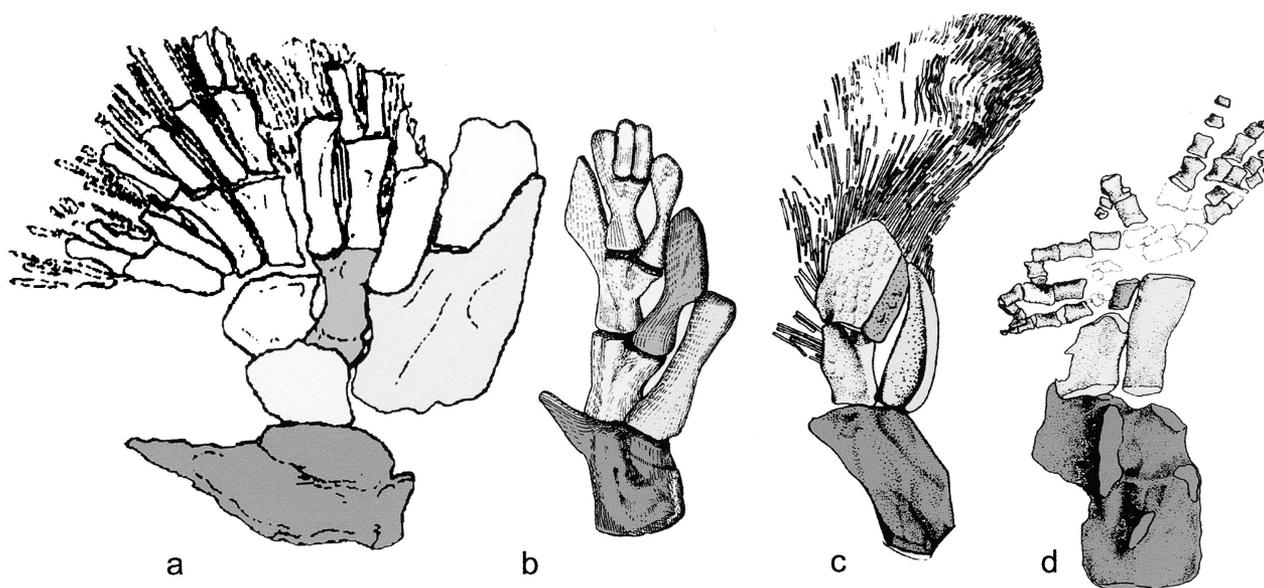


Fig. 3. Stem group tetrapod pectoral fins and a limb. (a) *Sauripterus* pectoral fin. After Daeschler and Shubin (1998). (b) *Eusthenopteron*, a tristichopterid. After Jarvik (1980). (c) *Panderichthys*. After Vorobyeva (1992). (d) *Acanthostega*. After Coates (1996). Gray shading indicates homologous structures in different limbs. Note changing proportions of intermedium (dark shaded unit in wrist or third segment/mesomere from base of figure in each example). All fins and limb with leading edge (anterior/preaxial) to right of page.

shorter, proximodistally, than the pectorals. This size difference is probably primitive (Coates 1994). Importantly, all these fins have an endoskeleton with a clear central axis, segmenting repeatedly and extending to the distal-most extremity, flanked anteriorly and posteriorly by series of secondary radials (Ahlberg 1989). A key question here concerns the extent to which porolepiform and lungfish fins represent truly primitive patterns (relative to tetrapods) rather than derived conditions in their own right. Thus far, it appears that the extreme length of these fins is derived. A shorter biserial pattern more probably represents primitive sarcopterygian conditions (Ahlberg 1989; Shubin 1995; Jeffery 2001), and in this respect coelacanth anatomy (Forey 1998) (Fig. 2a) provides a better model.

Girdle conditions in basal sarcopterygians are more easily characterized than fins. In lungfish, porolepiforms, and coelacanths, endoskeletal girdles are small. Pectoral girdles consist of a small scapulocoracoid bracket applied via buttresses to the inner surface of a large dermal bone, the cleithrum. The cleithrum itself is part of a series of dermal bones almost encircling the head–trunk boundary, at the rear of the internal gill chamber. Dorsally, the dermal pectoral girdle articulates with the rear of the dermal skull roof, and ventrally, the girdle includes broad clavicles and a slender interclavicle (for exceptions, see Forey 1998). The pelvic girdle, unlike the primitive pectoral girdle, includes no dermal bones. Each half of fin-supporting pelvis consists of an endoskeletal bar embedded in the ventral body wall musculature. No sacral attachment is present.

The Rhizodontida (Andrews and Westoll 1970), known from Devonian to Carboniferous sediments, are the most basal stem tetrapods in which paired fins are preserved in significant detail (Long 1989; Daeschler and Shubin 1998; Vorobyeva 2000; Davis et al. 2001; Jeffery 2001; Johanson and Ahlberg 2001) (Fig. 3a). Similarities with tetrapod limbs have been noted repeatedly (Jeffery 2001, and references therein), such as the 1:2 proximal to distal ratio of long bones extending from the pectoral girdle and the broad distal span of the fin, obscuring the fate of any central axis distally. Like coelacanth fins, but unlike porolepiform and lungfish examples, rhizodont fins include around five segments/mesomeres when counted proximodistally.

Rhizodontid pectoral girdles (Fig. 4a) include a scapulocoracoid that is larger than those of porolepiforms and with a broader surface for attachment to the cleithrum (Jeffery 2001). However, dermal and endochondral parts of the pectoral girdle are usually found separated, and the dermal bone series is well developed. Rhizodont pelvic fins are known only from external morphology. Like most bony fish pelvises, they are smaller than the pectorals and positioned toward the rear of the body. The pelvic girdle is now known to be bar-like, with an unossified symphysis and an acetabulum flanked by pubic and iliac processes (Johanson and Ahlberg 2001).

In comparison with rhizodontids, *Eusthenopteron* is by far the best known fish-like stem tetrapod (see Jarvik 1980, and references therein). A member of the Tristichopteridae (thus far an exclusively Devonian clade of osteolepiform fishes), Cloutier and Ahlberg (1996) and subsequent authors

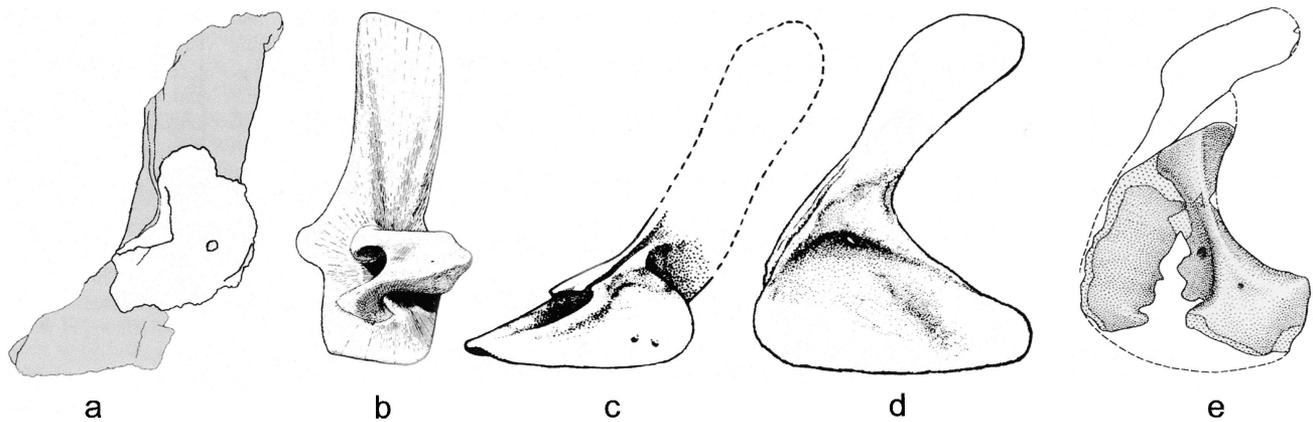


Fig. 4. Tetrapod pectoral girdles in mesial view. (a) *Strepsodus*, a rhizodontid. After Jeffery (2001). (b) *Eusthenopteron*, a tristichopterid. After Jarvik (1980). (c) *Panderichthys*. After Vorobyeva (1992). (d) *Acanthostega*. Adapted from Coates (1996). (e) *Tulerpeton*. After Lebedev and Coates (1995).

have each concluded that *Eusthenopteron* branches from a higher node on the tetrapod stem than rhizodontids. However, the pectoral fin skeleton (Fig. 3b) shows only a subset of the features common to rhizodontids and tetrapods. Like basal sarcopterygian fins (Fig. 2), a proximodistal skeletal axis is clear throughout, and, like lungfishes and porolepiforms, the anteroposterior span is broadest within the proximal half of the total fin rather than distally. Relative to rhizodontids, the endoskeleton includes slightly fewer segments proximodistally (4+), and like tetrapods, no radials (long bones) articulate with the distal end of the radius, or along the posterior, trailing edge, of the main axis.

The pelvic fin pattern is substantially similar to the pectoral, although mesomeric levels of the large, ossified, postaxial processes for major muscle insertions are out of step by one mesomere with those of the pectoral fin. This segmental shift in pattern has prompted speculation that the pelvic girdle originated as the most proximal fin segment and that at an unspecified point in phylogeny, this became embedded in the hypaxial musculature (cf. Rackoff 1980; Rosen et al. 1981, and references therein).

The endoskeletal pectoral girdle of *Eusthenopteron* is small and tripodal (Fig. 4b). The “feet” attached to the mesial surface of the cleithrum enclose a triradiate canal space. The pelvic girdle is small and bar-like, with an unossified symphysis much as in rhizodonts.

Panderichthys is the most crownward stem tetrapod with paired fins. The pectoral endoskeleton (Fig. 3c) (Vorobyeva 1992, 2000) is divided into only three segments proximodistally. Each of these is morphologically distinct, and, unlike *Eusthenopteron* and basal sarcopterygian fins, there is no clear proximodistal iterative pattern. The humerus is uniquely (for a fin) like those of early limbs. Dorsoventrally compressed, it has separate extensor and flexor surfaces instead of the cylindrical shaft present in rhizodonts and tristichopterids. A large

plate-like ulnare lies distal to the ulna. Like those of rhizodontids, the ulnare is anteroposteriorly broad, but unlike rhizodontid examples, no radials articulate distal to this plate, which appears to fit closely to the neighboring slender intermedium.

Nothing has been described of the pelvic fin endoskeleton; in reconstructions it appears smaller than the pectoral (Vorobyeva 2000). Fin rays (lepidotrichia) are well developed at pectoral and pelvic levels.

The pectoral girdle (Fig. 4c) (Vorobyeva and Schultze 1991; Vorobyeva 1992) differs significantly from that of *Eusthenopteron*. The scapulocoracoid is massive and attached to the cleithrum across a single broad surface (i.e., not tripodal as in *Eusthenopteron*). In mesial view, the more ventral position of the endoskeletal girdle obstructs any view of the cleithrum below the scapulocoracoid. The major canals perforating the scapulocoracoid are separated from the inner surface the cleithrum by cartilage bone. The largest portion of the endoskeletal girdle is the ventral coracoid region, and this is expanded posteriorly and medially. The dorsal scapular region is incomplete but does not appear to have been extensive. The pelvic girdle is currently undescribed.

Acanthostega is the most basal digitated tetrapod known in any detail. Its forelimb skeleton (Fig. 3d) shares with all stem tetrapods (rhizodonts upward) the conserved 1:2 ratio of humerus to radius and ulna and a radius that exceeds ulnar length. Like *Eusthenopteron* and more derived stem tetrapods, no radials articulate with the distal end of the radius; like *Panderichthys*, the humerus is dorsoventrally flattened, the intermedium terminates level with the radius, and the complete endoskeletal pattern can be divided, proximodistally, into (only) three segments: the stylopodium, zeugopodium, and autopodium.

Key novelties of the *Acanthostega* limbs include the presence of digits and the complete absence of dermal fin rays.

Digits have the following characteristics: they consist of two or more spool-shaped bones/cartilages articulating one-to-one proximodistally, they occur as an anteroposteriorly arranged set or series radiating from the distal end of the appendage, and they bear no simple ratio of unit-to-unit correspondence with more proximal limb parts. Unlike previous definitions (cf. Coates 1994), these criteria can be used to distinguish between digits and endoskeletal radials when they occur in conjunction with dermal fin rays (lepidotrichia): compare patterns in Fig. 3, a and b.

Acanthostega is further distinguished from *Panderichthys* by the relative sizes of pectoral and pelvic appendages: the hindlimb (Fig. 5a) is either equal to or larger than the forelimb. Furthermore, the bones of the hindlimb zeugopod (second mesomere), the tibia and fibula, are significantly shorter than the femur (first mesomere), and the ankle is ossified, unlike most of the wrist. The only ossified wrist component is the short cylindrical intermedium. Both the humerus and femur bear a series of large processes indicating much greater development and elaboration of the appendicular musculature.

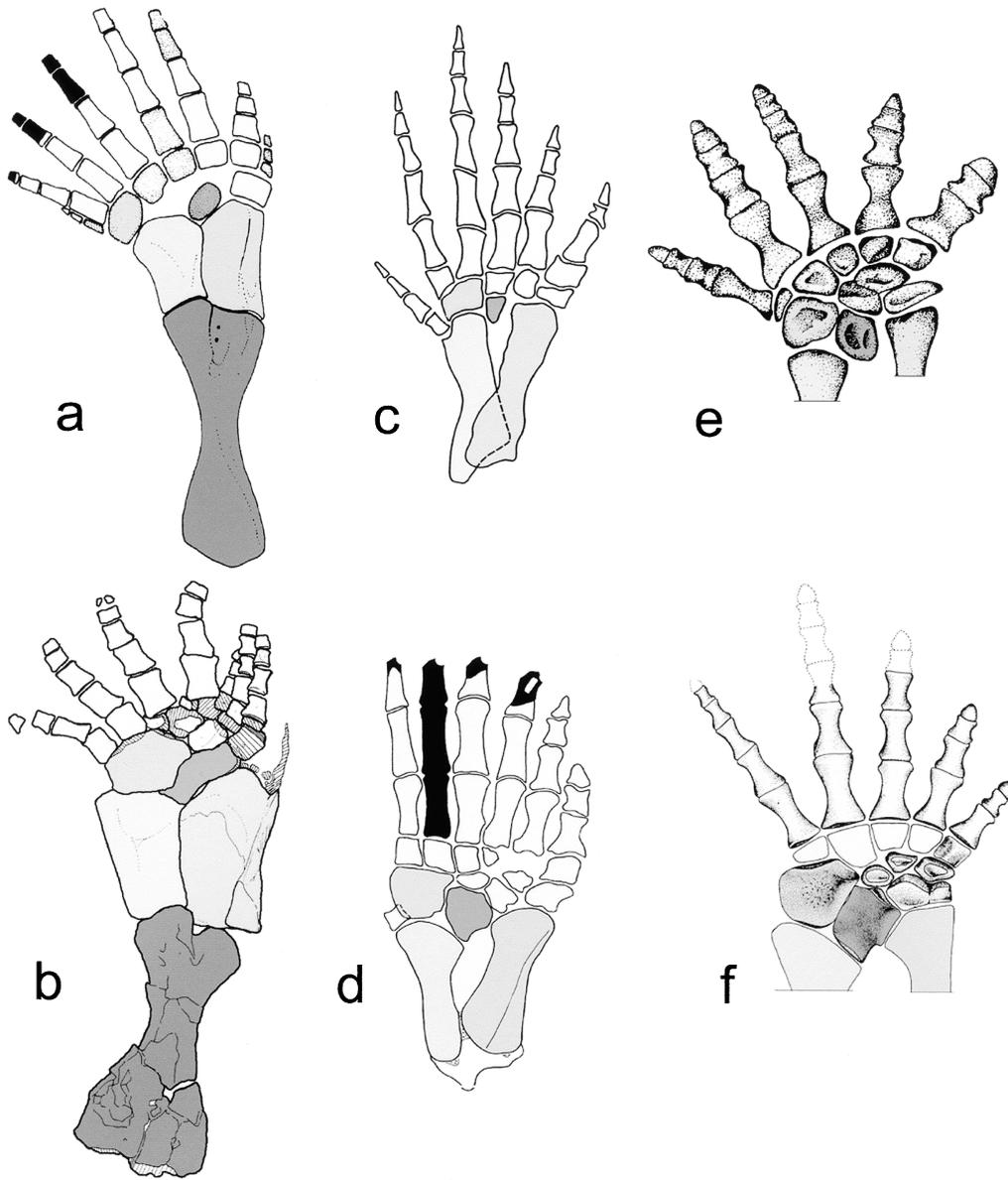


Fig. 5. Pectoral fin and limb patterns. (a) *Acanthostega* hindlimb. After Coates (1996). (b) *Ichthyostega* hindlimb. (c) *Tulerpeton* forelimb and (d) hindlimb. After Lebedev and Coates (1995). (e) *Seymouria* forelimb. After Berman et al. (2000). (f) *Proterogyrinus* hindlimb. After Holmes (1984). Gray shading indicates homologous structures in different limbs; solid black indicates restored structure. All limbs with leading edge (anterior) to right of page.

The endochondral pectoral girdle of *Acanthostega* (Fig. 4d) is in several respects similar to that of *Panderichthys*, except for the absence of large canals passing through the scapulocoracoid in an anteroposterior direction and the presence of a broad fossa on the mesial surface. The coracoid region is broader than in *Panderichthys*, but the dorsal extent of the scapular region appears similarly limited: the endochondral scapular fuses with the large dermal cleithrum. The dermal bones series of the girdle is reduced dorsally and separated from the skull rear. Pelvic differences are more dramatic. Relative to all pelvises noted thus far, the *Acanthostega* pelvis is much larger, the iliac region articulates with the axial skeleton via a sacral rib, a broad ischial plate is present, and the two pelvic halves are united along a puboischiadic symphysis.

Character acquisition across the stem-crown boundary

The phylogenetic location of the tetrapod crown radiation is the focus of intense debate. The most taxon-inclusive crown hypothesis incorporates the hexadactylous Late Devonian genus *Tulerpeton* as a basal stem amniote, thereby pegging the lissamphibian amniote divergence to a minimum date of around 360 Ma (Lebedev and Coates 1995; Coates 1996). In contrast, the least inclusive hypothesis excludes a series of taxa from the crown group, so that several putative stem amphibians and stem amniotes are repositioned as stem tetrapods (Laurin 1998; Laurin et al. 2000). The minimum age of the crown group in this alternative hypothesis is about 340 million years (Lower Carboniferous). Neither extreme is used directly in the present work. The simplified tree apex used here (Fig. 1) is abstracted from a combined reanalysis (Ruta and Coates in press), which places *Tulerpeton* plus several Lower Carboniferous taxa on the tetrapod stem, but most early limbed tetrapods remain within the crown group.

Acanthostega branches from a point several nodes below the crown radiation, and, as might be expected, its octodactylous limbs (Figs. 3d and 5a) lack features associated with most tetrapod limbs. For example, the radius is unusually long, and the cylindrical intermedium, like those of sarcopterygian fins, articulates only at proximal and distal ends. The intermedium is thus unlike the ankle bones, which articulate across both proximodistal and anteroposterior axes (compare intermedia in Figs. 3d and 5f, both shaded mid-gray). This cross-articular pattern has long been used to characterize “true” tetrapod limbs (Gaffney 1979).

The hindlimb of *Ichthyostega* (Fig. 5b) (Jarvik 1980, 1996; Coates 1996) shares many features with that of its contemporary, *Acanthostega* (Fig. 5a). In both taxa the limbs are paddle-like, the tibia and fibula are broad and flat, and both have a well-ossified ankle. However, in these early ankles the skeletal pattern is simple. Distal tarsals are absent, and at least two digits articulate directly with a massive fibulare. In

Ichthyostega the toes include seven members arranged in two sets, four large posteriorly and three small anteriorly. This is a conserved pattern, preserved in at least three specimens.

Ichthyostega forelimb remains are incomplete. The humerus resembles a robust version of that in *Acanthostega*, radius and ulna are of near equal length, but the manus is unknown. Limb girdles are (also) broadly similar: the pectoral retains an extensive dermal component, and the pelvic consists of a pair of large well-ossified plates. Both genera have endoskeletal girdles in which there are no traces whatsoever of sutures indicating the limits of pubis, ishium, ilium, scapula, and coracoid.

The third Devonian limbed tetrapod, *Tulerpeton*, was the first polydactylous early tetrapod to be discovered and recognized as such (Lebedev 1984; Lebedev and Coates 1995). The hexadactylous forelimb (Fig. 5c) includes a simple ossified wrist lacking distal carpals, but the intermedium cross-articulates like those of more derived tetrapods. The hindlimb (Fig. 5d) is more conventionally limb-like and, despite the six-digit pattern, resembles those of crown group tetrapods. The tibia and fibula each have a subcylindrical shaft; the ankle includes at least 12 bones, with a distal tarsal series separating metatarsals from the fibulare and broad intermedium.

The pectoral girdle condition (Fig. 4e) repeats this trend (pelvic girdle remains are fragmentary). Dermal and cartilage bone components are not co-ossified: the cleithrum is separate from the scapulocoracoid. The cleithrum is more slender than in previous examples, and the scapulocoracoid is larger, with two further novelties: dorsally, a distinct scapular blade, and ventrally, an infraglenoid buttress.

Two examples of limbs from early crown group genera, *Proterogyrinus* (Fig. 5f) (Holmes 1984) and *Seymouria* (Fig. 5e) (Berman et al. 2000), are used to exemplify conditions approximating to the traditional idea of a pentadactylous ground plan. The hindlimb of *Proterogyrinus* bears five digits but otherwise resembles the *Tulerpeton* hindlimb. The forelimb of *Seymouria* is included because it remains one of the earliest examples with a well-ossified wrist. This includes a complete set of distal carpals, indicating that by this stage in tetrapod phylogeny, (amniote) forelimb and hindlimb patterns were broadly similar.

With regard to the girdles, in both genera the scapulocoracoid has a broader and taller scapular blade and the cleithrum is further emarginated from the posterior side. The pelvis in both display an enlarged supra-acetabular buttress, as well as persistent sutures between the pubis, ishium, and ilium.

ALTERNATIVE ANALYSES OF LIMB CHARACTERS

Thus far, characteristics of paired fins, limbs, and girdles have been mapped on to a pre-existing phylogeny. However,

these appendicular characters (also) represent an alternative and/or supplementary source of data, available for testing against the reference tree. Hypotheses such as that shown in Fig. 1 are usually based on analyses in which few characters describe alternative conditions between the paired appendages (e.g., Cloutier and Ahlberg 1996; Johanson and Ahlberg 2001). Mostly, this is because appendicular endoskeletons are rarely well preserved in Paleozoic fish. However, a strong phylogenetic signal might be expected from contrasting morphologies in taxa bracketing transitional nodes in phylogeny, such as fins and limbs in taxa close to traditional idea of the fish-tetrapod boundary. In fact, these paired appendages and girdles are peppered with distinctive morphological features. The 46 character matrix (Appendix 1) assembled here is not exhaustive, and the fact that 12 of these character statements describe features of the humerus highlights a further region of intense anatomical variation.

For the purposes of this exercise we used a small taxon set, including a hypothetical outgroup: a series of primitive states (zeros) inferred from recent and fossil nontetrapod sarcopterygians. Rhizodontids were treated en masse, because of a lack of adequate material from any one species, and coded from relevant data in recent papers (Vorobyeva 2000; Johanson and Ahlberg 2001; Davis et al. 2001; Jeffery 20001). Treating rhizodontids in this way is far from ideal, and there are recognized problems with such large terminal groups (cf. Ruta and Coates in press). Other contributory taxa not discussed thus far include *Elginerpeton*, a fragmentary putative stem tetrapod with limbs from the Upper Devonian of Scotland (Ahlberg 1998); *Greererpeton*, a colosteid limbed stem tetrapod from the Lower Carboniferous of Vir-

ginia, USA (Godfrey 1989); and *Eryops*, a stem lissamphibian from the Permian of Texas, USA (Miner 1925).

A search of these data using PAUP* 4.0b10 (Swofford 2002) with heuristic search options yielded five trees of 74 steps. An Adams consensus of these (Fig. 6) includes three polytomies, because of conflicting signals within the data set (the source of this noise is discussed later). However, the general branching pattern is in broad agreement with the phylogeny in Fig. 1, with one important exception: rhizodontids and *Eusthenopteron* have swapped positions.

These results can also be shown as a phylogram (Fig. 7), in which branch lengths are in direct proportion to the relevant number of inferred character state changes. Note that the phylogram represents only one of the five trees contributing to the consensus shown in Fig. 6.

A second analysis treated appendicular skeletons at pectoral and pelvic levels as if they represented separate terminal taxa or operational taxonomic units (OTUs). The purpose of this exercise was to test assumptions that pelvic- and pectoral-level appendages evolved in tandem. As serial homologues, it might be expected that fore- and hindlimbs were most similar in primitive taxa, paralleling the similarity of serial homologues during early ontogeny. Early phylogenetic and ontogenetic similarity could indicate, and result from, shared (co-regulated) mechanisms of growth and patterning. The null hypothesis is that limbs from the same par-

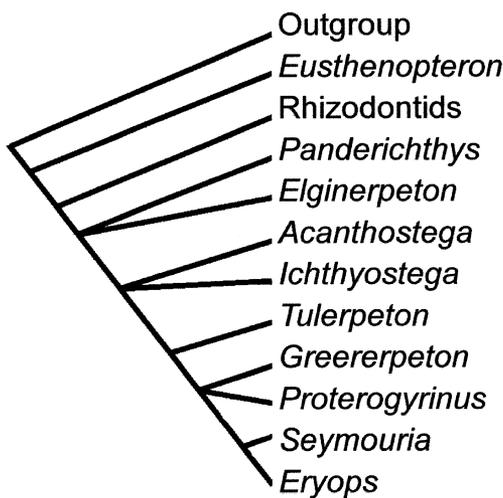


Fig. 6. Adams consensus of five shortest trees obtained from Appendix 1. 12 taxa, 46 characters, ci: 0.72, tree length: 74 steps. With *Elginerpeton* removed, analysis yields 1 tree, ci: 0.75, tree length 71 steps.

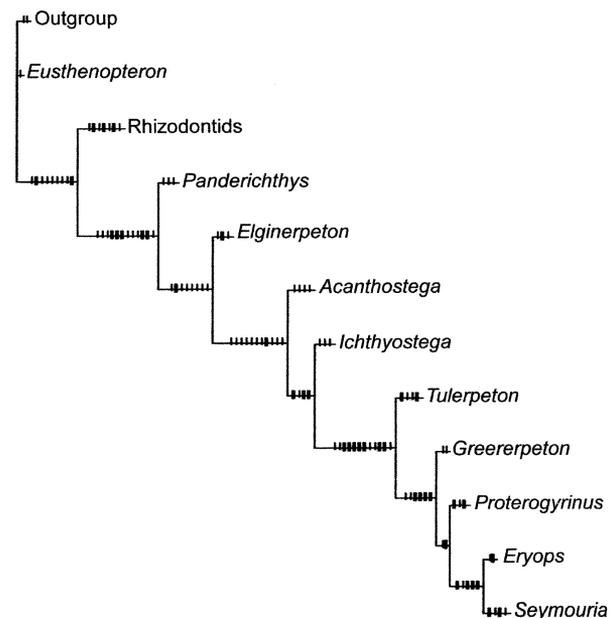


Fig. 7. Phylogram: branch lengths proportionate to number of character state changes. Unambiguous state changes shown by bold cross-bar, ambiguous changes by narrow cross bar (Almost all Possible option used in MacClade, Madison and Madison 2000). Note that this should not be interpreted as an ancestor-descendent sequence (likewise for Fig. 8).

ent taxon should cluster together or branch from the same node in any resultant tree(s) and that the branching sequences of these appendage OTUs should be congruent with results obtained from conventional data sets.

Characters for this analysis needed to be applicable to both fore- and hindlimbs to prevent the clustering of pectoral- or pelvic-level appendages, each united by mutually exclusive synapomorphies. This factor excludes a lot of morphological information specific to pectoral or pelvic skeletons, and the list of appropriate characters used in the present work includes a total of only 12 (Appendix 2). Likewise, only those taxa in which characters could be scored for pectoral and pelvic appendages were included. Lungfish pectoral and pelvic skeletons were imposed as a monophyletic outgroup. Significantly, a search (PAUP; search options as before) delivered a single tree (Fig. 8) in which hindlimbs repeatedly cluster with the forelimbs of more derived taxa.

DISCUSSION

The review section of this article shows that character state changes associated with the fin–limb transition are distributed throughout tetrapod stem and basal parts of the crown groups. However, the tripartite organization of tetrapod limbs into stylopod, zeugopod, and autopod has not been addressed thus far, even though this might be a defining characteristic of the “archetypal limb” (Wagner and Chiu 2001). In practice, morphological descriptions of tetrapod limbs rarely use these terms because of their imprecision. The areas they represent are almost always described by clusters of characters. When applied to primitive examples, the boundaries of stylopod, zeugopod, and autopod areas are unclear, and these terms are increasingly associated with developmental theory, such as the phased pattern of *Hox* expression (Nelson et al. 1996; Sordino and Duboule 1996; Shubin et al. 1997; Zakany et al. 1997; Wagner and Chiu 2001).

In an attempt to apply these terms in a more theory-neutral manner, if defined on the basis of pattern alone (i.e., as a monobasal connection between fin and girdle), then stylopod presence is a synapomorphy of all sarcopterygian paired appendages. A zeugopod, literally meaning “paired foot,” appears to have an identical monophyletic distribution. All living sarcopterygians have a second mesomere consisting of paired elements, even if only during early ontogeny, as in lungfish fins (Rosen et al. 1981; Vorobyeva 1992, and references therein). Primitive tetrapod zeugopods are specialized in two respects: the stylopod–zeugopod boundary includes well-formed articular surfaces and the radius (preaxial radial) is longer than the ulna (axial radial) (see all examples in Fig. 3; compare with those in Fig. 2). However, the distal extent of the zeugopod in nondigitated sarcopterygian paired fins is unclear: are the extremities of coelacanth and lungfish

fins also zeugopodial (Fig. 2)? Alternatively, is there a missing term here for these (distal) fin regions?

The autopod as defined by Wagner and Chiu (2001, p. 233) consists of (proximally) a mesopod with “nodular” elements, meaning proximal wrist/ankle bones/cartilages, and (distally) an acropod with an anterior-posterior series of “small long bones,” meaning digits and metacarpals/metatarsals. This definition is congruent with Gaffney’s (1979) characterization of true tetrapod limbs as having wrist/ankle bones that articulate across both proximodistal and antero-posterior axes. Under these definitions, the *Acanthostega* hindlimb has a complete autopod, but the forelimb, although acropodial, lacks a mesopod, because the only preserved wrist bone, the intermedium, is a (small) long bone, like all of those shown in Fig. 3. We suggest that although the *Acanthostega* forelimb might not be a true limb under Gaffney’s (1979) definition, the broad array of digits is a sufficient marker for an autopod and that presence of a characterizable mesopod is a derived condition, intercalated between the primitive autopod (exclusively acropodial) and the zeugopod at a later point in phylogeny.

Differences between the distal patterns of *Eusthenopteron* (Fig. 3b) and *Panderichthys* (Fig. 3c) pectoral fins might provide further insight into preconditions for autopod evolution. Digit-like radials are absent in *Panderichthys*, but the presence of an ulnare plate is accompanied by a marked anterior shift in the boundary between ulnare and intermedium. Dimensions of the intermedium in the *Acanthostega* (Fig. 3d) forelimb and, notably, the position of the fibulare:intermedium boundary in the ossified ankle of *Ichthyostega* (Fig. 5b, darker shaded unit in wrist/ankle of all illustrated limbs = intermedium) indicate that this asymmetry might be a further conserved feature established before the origin of digits. It is also noteworthy that this increased proximodistal regionalization of stem tetrapod paired fins evolves in tandem with the general trend of appendicular truncation in terms of segment or mesomere number.

Rhizodontid fin and tetrapod limb similarities were re-emphasized by the result of the fin and limb character analysis, in which *Eusthenopteron* is displaced to an unconventionally lower node (Fig. 6). This is not the forum for a detailed discussion of sarcopterygian phylogeny, and comments on the cause of this shift have to be restricted. Most authors would interpret the appearance of rhizodontids as the sister group of *Panderichthys* and higher tetrapods as a spurious product of convergent fin/limb characters. Future analyses of tetrapod stem topology can test this assumption by including the current appendicular character set. Synapomorphies responsible for the derived rhizodontid position include the attachment mode between dermal and endoskeletal pectoral girdle units and the anteroposterior span of the distal fin/limb region. Further, convergent similarities include presence of narrow canals in the scapulocoracoid (absence of large fossae/canals) and conditions of the humeral

flexor surface. Conjectural homologies with primitive tetrapod limbs are spread throughout the appendicular skeleton; the unconventional branching sequence of the cladogram is not, therefore, solely dependent on the span of digit-like radials.

The phylogram in Fig. 7 provides an approximate read-out of change or morphological difference between nodes on the tetrapod tree. Inevitably, this kind of representation can be skewed by excessive atomization (character splitting), and there is no time scale, so it provides no direct information about evolutionary rate. Nevertheless, the general pattern is noteworthy because the distribution of character state changes is more or less even throughout the stem. The major exceptions are the narrow internode branch between *Acanthostega* and *Ichthyostega* and the narrow internodes at the tree apex, surrounding the crown radiation (marked here by the branching point of *Proterogyrinus*). Primarily, this indicates an approximate measure of taxon sampling relative to morphological diversity as indicated by character distribution (for a thorough review of tree-based assessments of the fossil record, see Wagner 2000). Short internal branch lengths (internodes) indicate that the sample of diversity among basal crown group tetrapods is better than that among stem taxa separated by longer internal branches. However, the evenly spaced nodes along the stem conceal a potentially much greater gap at the locus of perhaps greatest interest. The branch between *Panderichthys* and *Acanthostega* is bisected by the node connecting with *Elginerpeton*. But, as noted above, material of *Elginerpeton* (Ahlberg 1998) is fragmentary and consists of disarticulated incomplete bones from a deposit of reworked sand, mud, and pebbles. *Elginerpeton* is included because previous analyses (Ahlberg 1998) place it at its present pivotal location. If *Elginerpeton* is excluded, the relative branch length is almost doubled, and an area of outstanding ignorance is not so much exposed as highlighted, encompassing the point(s) of fin ray loss and digit origination. It may also be significant that *Elginerpeton* exclusion results in a single, fully resolved, and shorter tree (branching sequence otherwise identical to that in Fig. 7): *Elginerpeton* is thus a prime source of “noise” in the data set.

The emerging picture of the fin–limb transition is increasingly complex, and it includes a distinct pattern of partial independence of changes at pectoral and pelvic levels. The degree of phylogenetic resolution is barely adequate, but a glimpse of what might and might not be evolving in a concerted manner (Shubin 2002) in fore and hind limbs is beginning to appear. Initially, tetrapod-like features originate in the pectoral assembly: endoskeletal girdle enlargement, humeral morphology change implying appendicular muscle increase and elaboration, and anteroposterior expansion of the distal part of the fin. These changes seem to have been initiated quite independently in the rhizodontid lineage and in the lineage leading to *Panderichthys* and crown group tetrapods. But this pectoral-level lead is not sustained. Morphofunc-

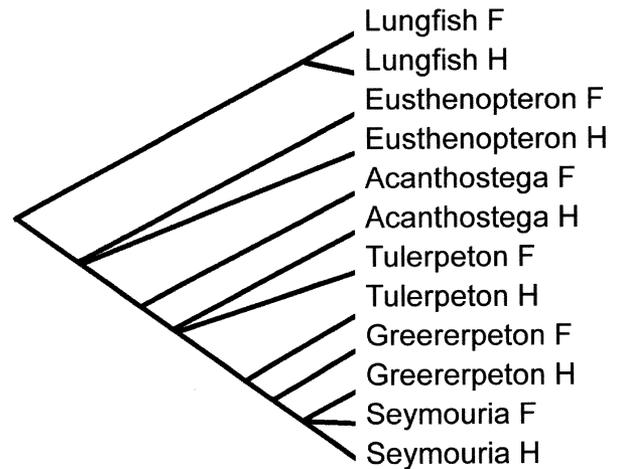


Fig. 8. Single shortest tree obtained from data set in Appendix 2. Pectoral appendages marked F, pelvic appendages marked H.

tionally, the fish–tetrapod transition is also marked by a shift in predominant appendage size and locomotor function from anterior to posterior. Again, these differences, together with fin-ray loss and the origin of digits at pectoral and pelvic levels, bracket the *Panderichthys*–*Acanthostega* internode. Coincident with this shift, and in the present context the concerted switch from fin-rays to digits represents a noteworthy exception, from *Acanthostega* onward, hindlimb evolution is in advance of forelimb change, hence the analysis with the second data set. The results (Fig. 8) support this perceived trend throughout all three included stem tetrapods. The hindlimb of *Acanthostega* branches from the same node as the forelimb of *Tulerpeton* and the hindlimb of *Tulerpeton* is the sister group of the forelimb of *Greererpeton* plus other limb OTUs, and so on. Thus far, however, this kind of analysis is frustrated by missing data: pelvic morphologies in rhizodontids and *Panderichthys* are either absent or simply undescribed, and morphological diversity is almost unknown from the data gap preceding *Acanthostega*.

At present, hindlimb size increase and repatterning is inseparable from the massive change in size and shape of the pelvic girdle. Most of the enlargement of the hindlimb can be accounted for by the considerable lengthening of the most proximal mesomere: the femur. Functionally, this lengthening is a simple way of increasing stride length (or paddle sweep); similar changes in the forelimb are not nearly so apparent (although coded as present in the data set). Other differences concern the evolution of wrist/ankle patterns, and the shift from plate-like girdles to those consisting of separate bones.

Functional explanations may be proposed for all these changes, but a central point of this review is that the inferred

sequence of pattern transformation is not simple and unidirectional. As far as we can tell, hindlimbs are not primitively similar to forelimbs. Similar characteristics emerge at both appendage levels, but not all of these do so at the same time. The diversity of forelimb and hindlimb morphologies seen in living taxa has deep phylogenetic roots (Coates 1994; Coates and Cohn 1998). These historical patterns of morphological change provide the fundamental phylogenetic context for the interpretation of the unfolding picture of the developmental genetics underpinning limb number, level, and identity (Gibson-Brown et al. 1996; Ruvinsky et al. 2000).

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7. Supinator process prominent and separate from latissimus dorsi process. Absent = 0, present = 1.
8. Latissimus dorsi process as a distinct landmark: absent = 0; located anteriorly relative to ectepicondyle = 1; aligned with ectepicondyle = 2.
9. Ectepicondyle prominent above and distal to radial and ulnar condyles. Absent = 0, present = 1.
10. Ectepicondyle aligned distally with ulnar condyle = 0, between ulnar and radial condyles = 1, aligned with radial condyle = 2.
11. Ectepicondyle imperforate. Absent = 0, present = 1.
12. Entepicondyle subcylindrical in cross-section = 0, proximodistally flattened = 1, dorsoventrally flattened = 2.
13. Entepicondylar processes 3 and 4 (cf. Jarvik, 1980). Absent = 0, present = 1.
14. Entepicondyle broad and subrectangular in dorsal aspect. Absent = 0, present = 1.
15. Entepicondyle perforated by canal(s) = 0; imperforate = 1.
16. Radial condyle terminal = 0, or ventral = 1.
17. Radius of equal or shorter length than humerus. Absent = 0, present = 1.
18. Radius longer than ulna = 0, same length as ulna = 1, shorter than ulna = 2.
19. Ulna with olecranon process. Absent = 0, present = 1.
20. Ossified carpus includes elements articulating laterally as well as proximodistally. Absent = 0, present = 1.
21. Distal carpals. Absent = 0, present = 1.
22. Femur with distinct internal trochanter. Absent = 0, present = 1.
23. Femur with internal trochanter separated by distinct cleft from femoral head. Absent = 0, present = 1.
24. Femur with distinct, rugose, fourth trochanter. Absent = 0, present = 1.
25. Femur with proximal end of adductor crest terminating at midshaft level. Absent = 0, present = 1.
26. Fibula waisted. Absent = 0, present = 1.
27. Fibula with ridge near posterior edge of flexor surface. Absent = 0, present = 1.
28. Tibia with cnemial crest absent = 0, present and extending distally = 1, present, directed mesiolaterally, and subsiding distally = 2.
29. Ossified tarsus includes elements articulating laterally as well as proximodistally. Absent = 0, present = 1.
30. Distal tarsals. Absent = 0, present = 1.
31. One or more centralia present in tarsus. Absent = 0, present = 1.
32. L-shaped intermedium in either pectoral or pelvic appendages. Absent = 0, present = 1.
33. Digits absent (and leipotrichia present) = 0, more than five digits present = 1, five or fewer digits present = 2.

APPENDIX 1

Character list A

1. Distal fin or limb domain expanded across the antero-posterior axis. Absent = 0, present = 1.
2. Radius articulates distally with further radial = 0; terminates or articulates with wrist element = 1.
3. Appendicular skeleton with more than four mesomeres proximodistally = 0; no more than four mesomeres = 1.
4. Humerus dorsoventrally flattened. Absent = 0, present = 1.
5. Humerus waisted. Absent = 0, present = 1.
6. Ventral ridge (ventromedial crest) of humerus acute and pierced by three or more foramina = 0, ridge low, rounded, and pierced by two or fewer foramina = 1, ridge absent = 2.

Taxa and sources. Outgroup, from lungfish (Jarvik 1980), Latimeria (Forey 1998), and porolepiforms (Ahlberg 1989); Rhizodontida (Vorobyeva 2000; Davis et al. 2001; Johanson and Ahlberg 2001; Jeffery 2001); Eusthenopteron (Jarvik 1980); Panderichthys (Vorobyeva 1992, 2000); Acanthostega (Coates 1996); Ichthyostega (Jarvik 1980; Coates 1996); Tulerpeton (Lebedev and Coates 1995); Greererpeton (Godfrey 1989); Proterogyrinus (Holmes 1984); Elginerpeton (Ahlberg 1998); Eryops (Miner 1925); Seymouria (White 1939).

Data Matrix 1.

OUTGROUP	00000	00000	00000	00000	00000	00000	00000	00000	00000	0
Rhizodonts	10001	10000	11000	00000	0????	?????	?0001	01100	00000	0
<i>Eusthenopteron</i>	01000	00000	00000	00000	00?00	00000	00000	00000	00000	0
<i>Panderichthys</i>	11110	00000	02?00	11000	0????	?????	?0000	11010	0????	?
<i>Elginerpeton</i>	???10	2????	?2?01	1????	?????	?11??	?????	?????	1??1?	?
<i>Acanthostega</i>	11110	10110	02110	01000	01100	01110	00110	11110	11110	0
<i>Ichthyostega</i>	11110	10?10	02110	1121?	?1000	00110	101?0	11110	11110	0
<i>Tulerpeton</i>	11110	?0211	12?10	01111	01110	11111	11111	11111	1????	?
<i>Greererpeton</i>	11110	10211	12?10	01211	11111	10211	10211	11111	11111	1
<i>Proterogyrinus</i>	11110	10212	12110	01111	11011	11211	11211	11111	11111	1
<i>Eryops</i>	11111	21212	12?11	11211	11111	11?11	10211	11111	11111	1
<i>Seymouria</i>	11111	21212	12010	11211	100?0	11211	10211	11111	11111	1

34. Pelvic appendage equal to or larger than pectoral appendage. Absent = 0, present = 1.
35. Scapulocoracoid and cleithrum fused = 0, separate = 1.
36. Cleithrum visible only above scapulocoracoid level in mesial view. Absent = 0, present = 1.
37. Scapulocoracoid attachment to cleithrum tripodal = 0; broad and plate-like = 1.
38. Scapulocoracoid penetrated by only narrow canals (large supracoracoid and supraglenoid fossae/canals closed). Absent = 0, present = 1.
39. Coracoid broad, ventromedially. Absent = 0, present = 1.
40. Scapulocoracoid with scapular blade. Absent = 0, present = 1.
41. Subscapular fossa. Absent = 0, present = 1.
42. Pelvis with broad ischial plate. Absent = 0, present = 1.
43. Pelvis with elongate puboischiadic symphysis. Absent = 0, present = 1.
44. Pelvis with sacral attachment. Absent = 0, present = 1.
45. Persistent sutures between pubis, ischium and ilium. Absent = 0, present = 1.
46. Pelvis with major supra-acetabular buttress. Absent = 0, present = 1.
4. Axis identifiable beyond second mesomere = 0; axis indeterminate = 1.
5. Lepidotrichia. Present = 0, absent = 1.
6. Anterior radial much longer than axial radial in second mesomere = 0; anterior radial of similar length to axial radial in second mesomere = 1.
7. First and second mesomeres of near equal proximo-distal length = 0; first mesomere exceeds second segment length = 1.
8. Cross-articulating bones in the carpus/tarsus. Absent = 0, present = 1.
9. Distal carpals/tarsals absent = 0, present = 1.
10. Digits absent = 0; more than five digits = 1; five or fewer digits = 2.
11. Endoskeletal girdle enlarged. Absent = 0, present = 1.
12. Endoskeletal girdle with sutures. Absent = 0, present = 1.

Taxa and sources. Lungfish (Jarvik 1980); *Eusthenopteron* (Jarvik 1980); *Acanthostega* (Coates 1996); *Tulerpeton* (Lebedev and Coates 1995); *Greererpeton* (Godfrey 1989); *Seymouria* (White 1939).

Data Matrix 2.

Lungfish_F	00000 00000 00
Lungfish_H	00000 00000 00
<i>Eusthenopteron</i> _F	11100 00000 00
<i>Eusthenopteron</i> _H	11100 00000 00
<i>Acanthostega</i> _F	11111 01001 10
<i>Acanthostega</i> _H	11111 11101 10
<i>Tulerpeton</i> _F	11111 11101 10
<i>Tulerpeton</i> _H	11111 11111 1?
<i>Greererpeton</i> _F	11111 11112 10
<i>Greererpeton</i> _H	11111 11112 11
<i>Seymouria</i> _F	11111 11112 11
<i>Seymouria</i> _H	11111 11112 11

APPENDIX 2

Character list B

1. First mesomere with two well formed joint surfaces distally. Absent = 0, present = 1.
2. Girdle with concave articular surface; humerus/femur with convex proximal head. Absent = 0, present = 1.
3. Radials articulate with opposing sides of axes formed of mesomeres = 0; present only along leading edge = 1.