

Ever Since Owen: Changing Perspectives on the Early Evolution of Tetrapods

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Abstract

The traditional notion of a gap between fishes and amphibians has been closed by a wealth of fish-like fossil tetrapods, many discovered since the mid 1980s. This review summarizes these discoveries and explores their significance relative to changing ideas about early tetrapod phylogeny, biogeography, and ecology. Research emphasis can now shift to broader-based questions, including the whole of the early tetrapod radiation, from the divergence from other lobed-finned fishes to the origins of modern amphibians and amniotes. The fish-to-tetrapod morphological transition occurred within the Upper Devonian; the divergence of modern tetrapod groups is an Early Carboniferous event. Modern tetrapods emerged in the aftermath of one of the five major extinction episodes in the fossil record, but the earlier Devonian tetrapod radiation is not well understood. Tetrapod limbs, paired fins, and comparative developmental data are reviewed; again, research emphasis needs to change to explore the origins of tetrapod diversity.

INTRODUCTION

Archegosaurus (Goldfuss 1847) was the original missing link. Seized by evolutionists after Richard Owen (1859, in Desmond 1982) declared that this “old Carboniferous reptile” conducted the march of development from fish to primitive amphibian, the treatment of *Archegosaurus* foreshadowed portrayals of *Ichthyostega*, *Acanthostega*, *Tiktaalik*, and others besides: each depicted at pond- or swamp-side with tail trailing (significantly) in the water (Milner et al. 1986). Evolutionary trees of tetrapod ancestry have long since branched and filled to accommodate earlier and more thoroughly transitional forms (Clack 2002), but the vignette of beached missing links has persisted. Unfortunately, this paleo-cliché reduces the exploration of tetrapod origins to the discovery of substitute candidates for this brief episode in vertebrate history. However, questions about the origin of tetrapods now concern a much wider range of paleobiological issues. The origin of tetrapods includes the whole of the tetrapod stem (see sidebar, Defining a Tetrapod), with many groups of fish-like (i.e., finned) taxa only recently being incorporated into this wider framework (Ahlgberg & Johanson 1998, Coates et al. 2002, Jeffery 2002, Johanson et al. 2003). It is now possible to ask how the origins of the tetrapod total and crown groups relate to morphological changes and the emergence of a conventional tetrapod body plan. The fin-to-limb transition is an exceptionally rich area of integrative research and debate (e.g., Zákány et al. 1997, Coates et al. 2002, Davis et al. 2004a,b, Friedman et al. 2007). The origin of tetrapods and the water-to-land transition are not synonymous, but both events are associated with global climatic, atmospheric, and tectonic changes, as well as with serial extinctions at the end of the Devonian (Algeo et al. 2001, Berner et al. 2007, Blieck et al. 2007, Clack 2007). Taxon and character sets are now large enough to be mined for large-scale evolutionary trends (Ruta et al. 2006, Wagner et al. 2006). This review gathers reports and articles on this topic published in the past few years—some of which have gained exceptionally widespread attention—and places them in context and suggests agendas for future research.

THE POSITION OF TETRAPODS WITHIN VERTEBRATE PHYLOGENY

The first question about tetrapod origin concerns the identity of the closest relatives of land vertebrates. This issue emerged within the nineteenth century (Desmond 1982) as discoveries of lungfishes confounded diagnoses of living tetrapods as a natural group, and after fossil “rhhipidistian” fishes were recognized as belonging within the same group as limb-bearing tetrapods. Widespread acceptance of evolutionary theory redirected systematic research to discover the particular rhhipidistian ancestors of tetrapods. By the early twentieth century, phylogenetic

DEFINING A TETRAPOD

Questions associated with tetrapod origins depend on how a tetrapod is defined. Essentialist, character-based definitions create problems because much of the research program concerning tetrapod origins aims to provide a sequence of intermediates showing the assembly of the anatomical characters in question. Moreover, there is a built-in presupposition that any defining character has evolved only once. In this review, we adopt phylogenetic definitions of groups. Total-group tetrapods include all those taxa more closely related to living tetrapods than to their nearest living sister group (lungfishes), whereas crown-group tetrapods consist of the last common ancestor of all living tetrapods plus all the fossil and living descendants of that ancestor. Stem-group tetrapods form a paraphyletic assemblage equivalent to the total group minus the crown group.

hypotheses had multiplied considerably, and ranged from polyphyletic origins of limbed vertebrates from several rhipidistian groups (Jarvik 1980; Säve-Söderbergh 1932, and references therein) to a monophyletic origin from “osteolepiforms” (Watson 1920; also reviewed by Panchen & Smithson 1987). Rare objections to this rhipidistian hegemony (e.g., Kesteven 1950) were sidelined. With tetrapod ancestry anchored to specific fossils, such as the osteolepiform *Eusthenopteron*, research focused on the adaptive circumstances surrounding the invasion of dry land.

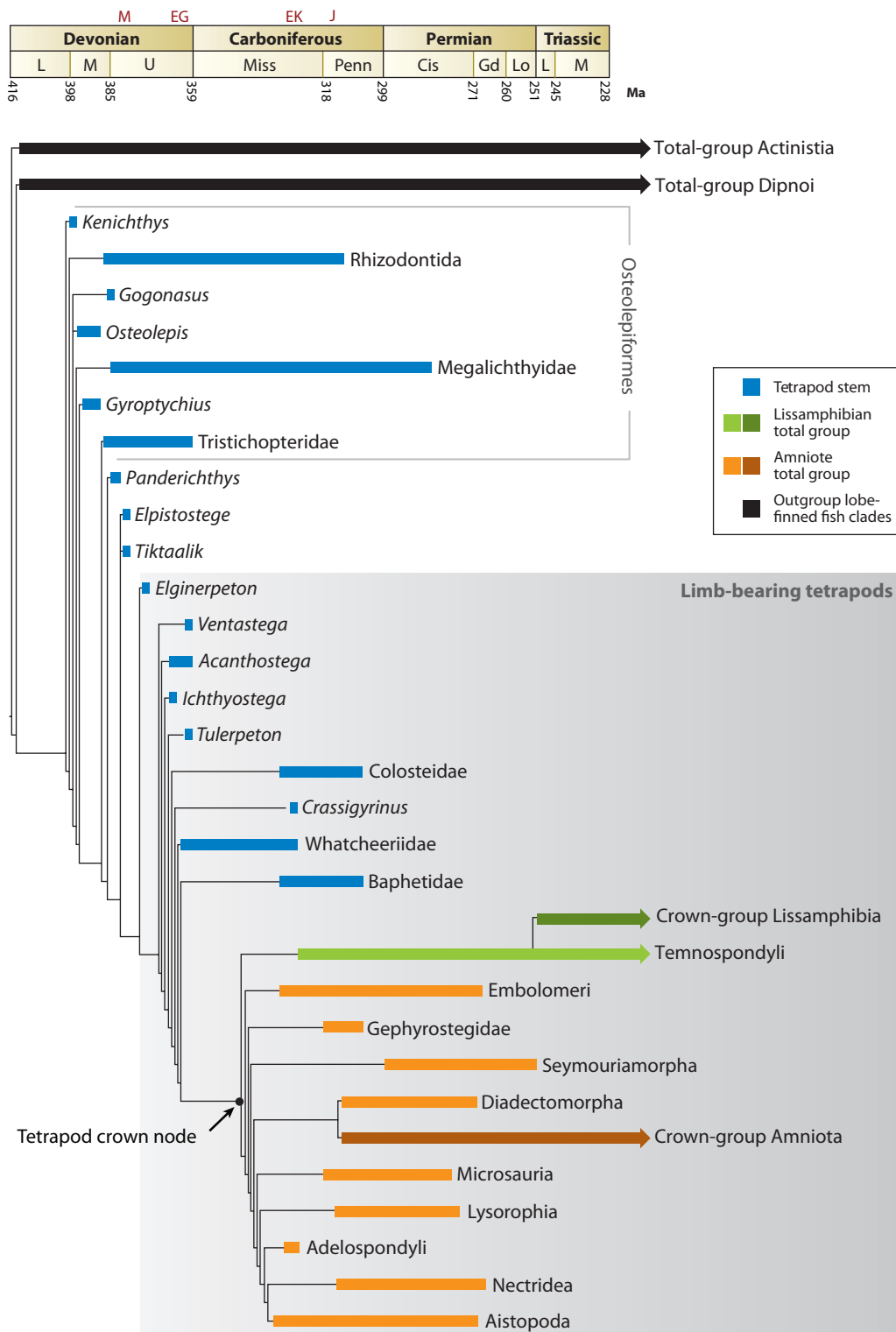
However, by the late 1970s, this passive acceptance of osteolepiforms as the closest fish relatives of terrestrial vertebrates provoked a reexamination of the status quo. A withering critique of research on tetrapod origins (Rosen et al. 1981) concluded that most characters claimed to link *Eusthenopteron* to tetrapods were either primitive or spurious. Emphasis was placed on the choana, a palatal nostril framed by a diagnostic bone arrangement, present in *Eusthenopteron* and tetrapods. Lungfishes also possess a palatal nostril, homologized by several nineteenth-century anatomists with the tetrapod choana (Desmond 1982), but dismissed by most twentieth-century paleontologists as convergent. However, newly prepared material of a Late Devonian lungfish (*Griphognathus*) revealed a bone-surrounded palatal nostril that Rosen et al. (1981) offered as evidence that a true choana was, in fact, present in primitive lungfishes.

The ensuing controversy spurred paleontologists to frame explicitly cladistic hypotheses to refute the arguments of Rosen et al. (1981) and reinstate osteolepiforms as the closest relatives of limbed tetrapods (e.g., Panchen & Smithson 1987, Schultze 1991). Further evidence emerged from the discovery of the Early Devonian *Diabolepis* (Chang 1995, and references therein), combining lungfish specializations with generalized sarcopterygian conditions, including possession of two external nostrils. As the sister group of lungfishes (Chang 1995), *Diabolepis* indicates that lungfish palatal nostrils are convergent with the choanae of limbed vertebrates and osteolepiforms. Two decades later, another Chinese Devonian fish, the primitive osteolepiform *Kenichthys*, added a postscript to the choana debate: its posterior nostril penetrates the skull exterior close to the upper jaw rim, presenting a possible incipient condition for the choana (Zhu & Ahlberg 2004). A summary of the present consensus on sarcopterygian interrelationships is shown in **Figure 1** (for further discussion see Friedman 2007).

DEVONIAN TETRAPOD DIVERSITY

Four major Devonian groups belong to the tetrapod stem lineage: rhizodonts, osteolepidids, tristichopterids, and “elpistostegalids” plus limbed tetrapods (**Figures 1** and **2a**). Most stem tetrapods are osteolepiforms, a grade of fin-bearing groups including rhizodonts, osteolepidids, and tristichopterids, but excluding elpistostegalids. Devonian examples are known from every continent and their diversity totals approximately 40 genera. Devonian tetrapods for which limbs have been discovered or implied total approximately a dozen genera, although digit-bearing limbs are known in only three: *Acanthostega*, *Ichthyostega*, and *Tulerpeton*. Approximately seven more unnamed forms are reported from fragments (Clack 2005). Elpistostegalids are the most informative taxa for understanding anatomical changes associated with the fish-to-tetrapod transition. They are known from a handful of genera, all exclusive to the Northern Hemisphere (Daeschler et al. 2006).

Reliance upon *Eusthenopteron* in studies of tetrapod origins gives the false impression that few fin-bearing tetrapods are known. In fact, many are described in detail (e.g., Fox et al. 1995; Lebedev 1995; Long et al. 1997, 2006), but uncertainty about osteolepiform interrelationships obstructs deeper understanding of tetrapod origins. Rhizodonts and tristichopterids are widely recognized as clades (Ahlberg & Johanson 1998), but few cladistic analyses have examined this area of tetrapod phylogeny (Johanson & Ahlberg 2001, Zhu & Ahlberg 2004). These cladograms place *Kenichthys*, from the Eifelian of China, at the base of the tetrapod stem group, followed by (in increasing



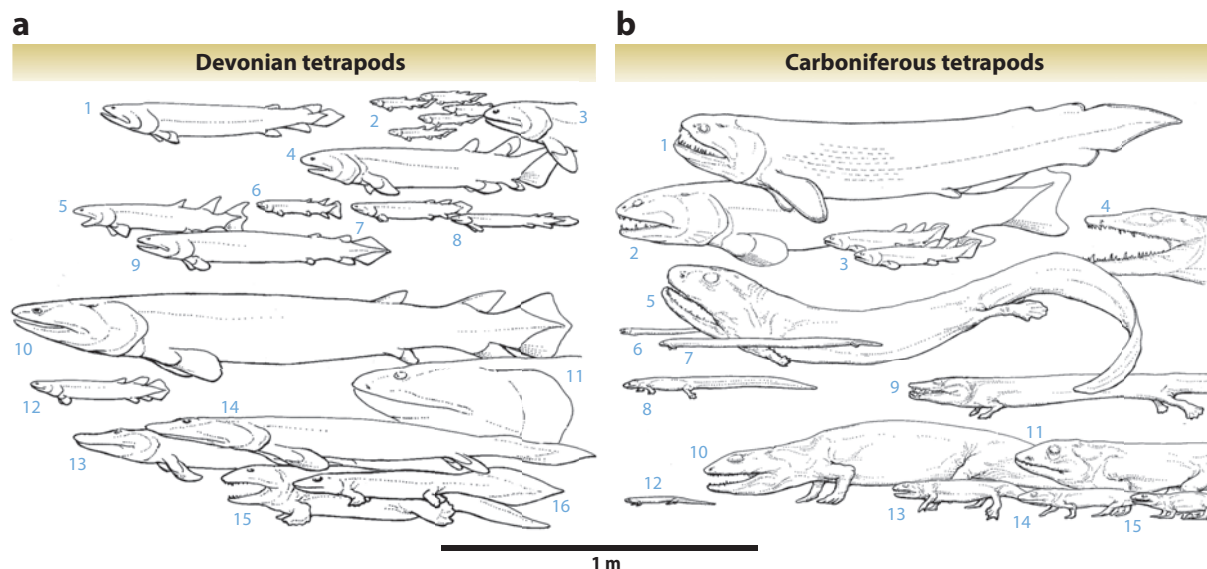


Figure 2

(a) Devonian tetrapods drawn to scale, illustrating anatomical diversity; all taxa are stem members. 1. *Gooloogongia*, a rhizodont; 2. *Osteolepis*, an osteolepidid; 3. *Kobarelepis*, an osteolepidid; 4. *Canowindra*, an osteolepidid; 5. *Eusthenopteron*, a tristichopterid; 6. *Tristichopterus*, a tristichopterid; 7. *Gyropterychius agassizi*, an osteolepidid; 8. *Gyropterychius dolichotatus*, an osteolepidid; 9. *Cabonnichthys*, a tristichopterid; 10. *Mandageria*, a tristichopterid; 11. *Eusthenodon*, a tristichopterid; 12. *Glyptopomus*, an osteolepidid; 13. *Tiktaalik*, an elpistostegid; 14. *Panderichthys*, an elpistostegid; 15. *Ichthyostega*, a limbed stem tetrapod; 16. *Acanthostega*, a limbed stem tetrapod. (b) Carboniferous tetrapods drawn to scale, illustrating anatomical diversity. Taxa shown include stem (1–5, 9, 11) and crown group (6–8, 10, 12–15) members. 1. *Strepsodus*, a rhizodont; 2. *Megalichthys*, a megalichthyid; 3. *Rhizodopsis*, a megalichthyid; 4. *Megalocephalus*, a baphetid (stem tetrapod); 5. *Crassigyrinus*, a stem tetrapod; 6. *Palaeomolgophis*, an adelospondyl (stem amniote or stem tetrapod); 7. *Brachydectes*, a lysorophid (stem amniote); 8. *Urocordylus*, a nectridean (stem amniote); 9. *Greerpeton*, a colosteid (stem tetrapod); 10. *Proterogyrinus*, an embolomere (stem amniote); 11. *Pederpes*, a whatcheeriid (stem tetrapod); 12. *Westlothiana*, a stem amniote; 13. *Silvanerpeton*, an embolomere (stem amniote); 14. *Dendrerpeton*, a temnospondyl (stem lissamphibian); 15. *Gephyrostegus*, a gephyrostegid (stem amniote).

proximity to the crown) rhizodonts, a paraphyletic assemblage of osteolepidids, tristichopterids, and the clade uniting elpistostegalids and limbed tetrapods. One solution places the osteolepidid *Gogoniasus* crownward of *Eusthenopteron* (Long et al. 2006), but this topology emerges from a limited taxon set (Friedman et al. 2007).

The specialized rhizodonts (Figure 2a: 1; Figure 2b: 1) branch furthest from the tetrapod crown node. Rhizodont pectoral fins (see below, The Origin of Tetrapod Limbs: Morphological Novelty) are characteristic, and have featured in debates about tetrapod limb origin (Davis et al. 2004a), although many limb-related similarities are probably homoplastic (Coates et al. 2002, Friedman et al. 2007). Few Devonian rhizodonts are known: *Aztecia*, *Gooloogongia*, *Sauripterus* (Johanson & Ahlberg 2001). The Frasnian *Gooloogongia* (Johanson & Ahlberg 2001) is probably the most plesiomorphic rhizodont known, but it already exhibits most of the clade-specific

Figure 1

Evolutionary tree of early tetrapods, showing total group with taxon ranges, stem and crown taxa, and the distribution of limb-bearing (quadrupedal) clades. Important fossil localities are listed above the geological column (M: Miguasha, Quebec, Canada; EG: East Greenland; EK: East Kirkton, Scotland; J: Joggins, Nova Scotia, Canada). The interrelationships of finned tetrapods are adapted from Ahlberg & Johanson (1998), whereas those of limbed tetrapods are adapted from Ruta et al. (2003).

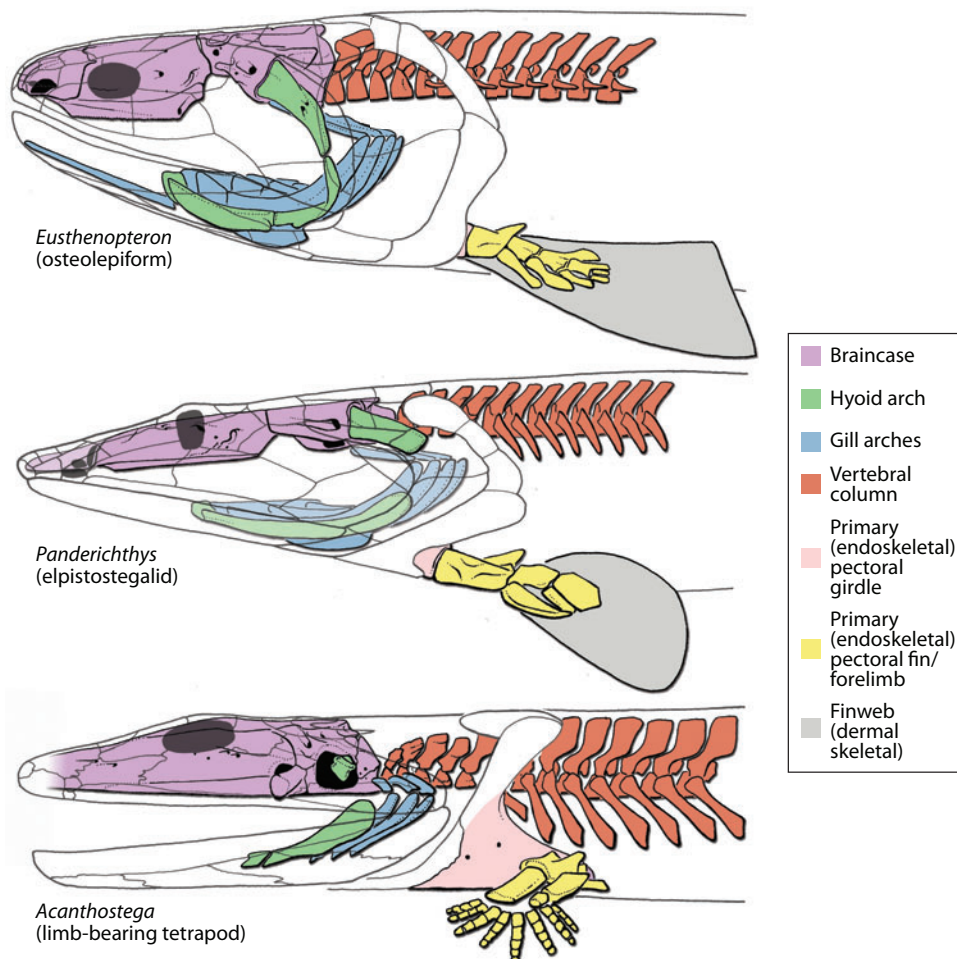


Figure 3

Eusthenopteron (top), *Panderichthys* (middle), and *Acanthostega* (bottom), shown in lateral aspect. Anatomical systems are color-coded. Light-shaded components of visceral skeleton in *Panderichthys* are inferential.

specializations. Carboniferous rhizodonts achieved colossal sizes; at an estimated length of seven meters (Jeffery 2002), *Rhizodus* was probably the largest Paleozoic osteichthyan.

Osteolepidids (Figure 2a: 2–4, 7, 8, 12; Figure 2b: 2, 3) lie crownward of rhizodonts and include many generalized stem-group tetrapods. They are probably paraphyletic and their interrelationships remain uncertain. Megalichthyids probably constitute a legitimate clade within osteolepidids. Persisting in continental settings into the Permian, megalichthyids (Figure 2b: 2, 3) were the last fin-bearing stem tetrapods.

The superficially pike-like tristichopterids are placed crownward of osteolepidids (Figure 2a: 5, 6, 9, 11). *Eusthenopteron* is the best-known genus (Figure 3), a modestly sized (80 cm) representative that features repeatedly in debates about tetrapod origins. Tristichopterids range from the Givetian to the Famennian, and trend toward increasing body size. The phylogenetically most basal and earliest form, *Tristichopterus*, was approximately 30 cm long, whereas apical members of this clade exceeded several meters in length (Figure 2a: 10, 11; Ahlberg & Johanson 1997). Like

rhizodonts, derived tristichopterids display elongated bodies and reduced median fins (**Figure 2a**: 10), suggesting convergence upon similar ecological roles (Ahlberg & Johanson 1998).

Elpistostegalids (**Figure 2a**: 13, 14) are the closest fish-like relatives of limbed tetrapods and form another paraphyletic grade. Synapomorphies with limb-bearing tetrapods include a flattened skull with dorsal orbits, a sutured dermal intracranial joint, paired frontal bones, an enlarged endoskeletal shoulder girdle, and absence of dorsal and anal fins (Ahlberg et al. 1996, Daeschler et al. 2006, Vorobyeva & Schultze 1991). Three elpistostegalids are known in detail: *Panderichthys*, *Elpistostege*, and *Tiktaalik*. Two others, *Livoniana* and *Parapanderichthys*, are known only from fragments (Ahlberg et al. 2000). The Frasnian *Tiktaalik* and *Elpistostege* appear more closely related to limbed tetrapods than do the Givetian *Panderichthys* (Daeschler et al. 2006). Notably, *Elpistostege* was presented as a limb-bearing tetrapod (Westoll 1938) long before detailed accounts of *Panderichthys* were published.

Resurgent research into tetrapod origins over the past two decades has been most apparent in the field of limb-bearing Devonian forms (**Figure 2a**: 15, 16). When Rosen et al. (1981) appeared on the scene, *Ichthyostega* (Säve-Söderbergh 1932) was the only Devonian tetrapod known to have limbs. A detailed redescription of this taxon took over 60 years to appear (Jarvik 1952, 1980, 1996). *Acanthostega* was known only from two incomplete skulls (Jarvik 1952), whereas *Metaxygnathus*, an eroded jaw from Australia, was claimed to belong to a limb-bearing tetrapod (Campbell & Bell 1977). *Tulerpeton* was the first Devonian newcomer to emerge, reported on the basis of an articulated trunk bearing hind- and forelimbs, the latter of which bore six digits (Lebedev & Coates 1995). It remains on the fringes of the tetrapod origins debate because its advanced characteristics resemble post-Devonian forms.

The revolution in understanding the morphological transformation from fin-bearing to limb-bearing tetrapods began with renewed expeditions to East Greenland that recovered complete specimens of *Acanthostega* (Clack 2002). This material revealed an animal less than a meter in length with a series of characters betraying its aquatic habit: a well-developed gill skeleton [Coates & Clack 1991; a gill skeleton has subsequently been reported in *Ichthyostega* (Clack et al. 2003)], paddle-like limbs bearing eight digits each (Coates 1996), and a tail with fin rays and radials (Coates 1996). These finds challenged the established notion that limbs evolved for terrestrial locomotion, and instead placed their origin squarely within an aquatic environment.

Acanthostega also yielded a series of jaw characters unique to limbed tetrapods. The resultant rash of new taxa based on isolated mandibles and mandible fragments has expanded the nominal diversity of Devonian forms and provided useful stratigraphic and geographic markers [*Elginerpeton* (Ahlberg 1991); *Ventastega* (Ahlberg et al. 1994); *Obruchevichthys*, *Densignathus* (Clack 2002); *Sinostega* (Zhu et al. 2002); unnamed Belgian “ichthyostegid” (Clement et al. 2004)]. However, although these fragmentary taxa are conventionally described as tetrapods (in the sense of limb-bearing vertebrates rather than the total-group definition applied here), digit-bearing limbs have not been recovered for any of them. *Ventastega* (Ahlberg et al. 1994, 2008) and *Elginerpeton* (Ahlberg 1991, 1998) each have a suite of attributed nonmandibular material. However, uncertainty surrounds the identity of some of the *Elginerpeton* material, most notably the putative humerus (Ahlberg 2004, Coates et al. 2004).

CARBONIFEROUS TETRAPOD DIVERSITY

Irrespective of finned or limbed conditions, tetrapod diversity in the earliest part of the Early Carboniferous is poor (**Figure 1**); it is unclear whether this reflects impoverished faunas or simply a lack of available facies. This period, often referred to as Romer’s gap, occupies much of the Tournaisian, about 360 to 350 mya. Limbed tetrapods from the upper part of the Tournaisian

(about 350 to 345 mya) are known only from the nearly complete skeleton of a whatcheeriid, *Pederpes*, from Scotland (Clack & Finney 2005), and fragments, mostly postcranial, from the slightly older locality at Horton Bluff, Nova Scotia (Clack 2002). *Pederpes* approached a meter in length (**Figure 2b**: 11), and, like other whatcheeriids, had a robust skull and a well-ossified postcranial skeleton with stout limbs bearing at least five digits, probably the earliest examples suited for terrestrial walking (Clack & Finney 2005). Further remains of similarly sized and larger whatcheeriids include *Ossinodus* from the mid-Viséan of Australia (Warren 2007) and *Whatcheeria* from a cache of spectacularly well-preserved skeletons from the upper Viséan of Iowa, United States (Bolt & Lombard 2000).

Unlike the limited record of Tournaisian tetrapods, the diversity of Viséan tetrapods is spectacular and Scottish sites deliver remarkable evidence of the diversification of crownward taxa. From Gilmerton (mid-Viséan) comes the holotype of the large (nearly two meters in length), grotesque, and Moray eel-like stem tetrapod, *Crassigyrinus* (Clack 2001) (**Figure 2b**: 5). The deep-sided skull resembles those of watcheeriids, but the axial skeleton is meager and the appendicular skeleton highly reduced. Gilmerton has delivered two further large tetrapods, a baphetid and a colosteid (Clack 2002). Both examples are the earliest occurrences of their respective clades. Baphetid skulls are large (250 mm+ in length) and many are superficially crocodile-like (**Figure 2b**: 4), although with anteriorly extended orbits; their postcranial anatomy is mostly unknown. Colosteids are one of the more widely represented and well-preserved groups of early, limb-bearing stem tetrapods. More than a meter in length and with flattened skulls and postcrania, colosteids (**Figure 2b**: 9) resemble long-trunked giant salamanders (Godfrey 1989) and, correspondingly, are interpreted as mostly aquatic.

Unlike these bulky Gilmerton tetrapods, from Cheese Bay (also mid-Viséan) originates the gracile, small (hip to shoulder length: 80 mm) but headless specimen of *Casineria* (Paton et al. 1999). This extraordinary fossil echoes the signal from *Tulerpeton*, displaying postcranial skeletal anatomy far advanced beyond those of its known contemporaries, and in this instance exhibiting characteristics of taxa close to the amniote crown.

Lethiscus (Anderson et al. 2003) from the mid-Viséan Wardie Shales of Scotland reveals a further new aspect of tetrapod diversity: secondary limb-loss. *Lethiscus* is the earliest of the aïstopods: snake-like with 80+ vertebrae; no trace of limbs and girdles; and, like *Casineria*, of small size (skull length: 60 mm).

Adelospondyls (Andrews & Carroll 1991) represent a further clade of small (total length: 300 mm), secondarily limbless tetrapods (**Figure 2b**: 6) that, unlike aïstopods, retained their pectoral girdle and were probably largely aquatic. Known from several sites of similar age to Cheese Bay and Gilmerton and extending through to the Serpukhovian, adelospondyls are among the most abundant tetrapods in the early to mid-Carboniferous beds of Scotland (Milner et al. 1986).

Aïstopods and adelospondyls are two subgroups of a much larger grade or clade, the lepospondyls. Often compared with small lizards and snakes, lepospondyls are characterized by possession of spool-shaped centra. Miniaturization probably underlies many of the apparent specializations manifest in this group. Other lepospondyl clades include the microsaur, nectrideans (**Figure 2b**: 8), lysorophids (**Figure 2b**: 7), and acherontiscids. The challenge of summarizing lepospondyls within the confines of a short article underscores their remarkable morphological diversity (Anderson 2001, Clack 2002, Ruta et al. 2003). Temporal ranges of all member clades are confined to the Carboniferous and Permian (Milner 1993) (**Figure 1**).

Temnospondyls constitute a second, temporally long-ranging tetrapod group that appear first within the Early Carboniferous. But, unlike lepospondyls, temnospondyls persist well into the Mesozoic (Milner 1993). Temnospondyl adult size ranges vary from a few centimeters to an estimated seven meters or more. Approximately salamander-like (although evolving into a vast

range of body shapes and sizes, presumably with attendant variation in life habits), temnospondyls exhibit usually broad and flat skulls with wide openings in the palate; the axial skeleton bears short ribs (except in large forms) and forelimbs have four digits (**Figure 2b**: 14). Temnospondyls have long been associated with amphibian ancestry and include the already mentioned *Archegosaurus* (Clack 2002, Milner 1993).

Anthracosaurs are a third group commonly encountered in descriptions of early tetrapod diversity; once again, these have uncertain monophyletic status. Anthracosaurs also appear first in the Early Carboniferous. They radiate throughout the remainder of the Paleozoic, and range from small- and medium-sized terrestrial forms (**Figure 2b**: 10, 13) to large predatory aquatic genera (embolomeres, another group compared to modern crocodiles) that infested Late Carboniferous coal swamps (Clack 2002, Holmes 1984). Putative anthracosaur synapomorphies have frequently emerged as no more than persistent symplesiomorphies. Although long associated with the amniote stem, this link appears to be increasingly tenuous.

The late Viséan locality of East Kirkton, Scotland, is probably the most renowned site for Early Carboniferous tetrapods. This fossil biota is diverse (Clarkson et al. 1994) and opens a unique window on the earliest known terrestrial vertebrate community (Ruta & Clack 2006). East Kirkton tetrapods include a baphetid (Clack 2001), anthracosaurs (Clack 1994, Ruta & Clack 2006, Smithson 1994), and the superficially lizard-like *Westlothiana* (Smithson et al. 1994) (**Figure 2b**: 12). East Kirkton lepospondyls include an undescribed microsauro (J. Clack, work in progress) and an aistopod (Milner 1994). Temnospondyls are present, including small and large examples (Milner & Sequeira 1994). It is noteworthy that, like *Lethiscus* and *Casineria*, these early terrestrial tetrapods are generally small (approximately 300 mm in total length).

Many tetrapod sites are known throughout the remainder of the Carboniferous. Significant examples include Greer in West Virginia (mid-Carboniferous) and the numerous classic faunas from coal swamps and deltaic fans of the Pennsylvanian of Illinois (Mazon Creek), Ohio (Linton), Nova Scotia (Joggins), Ireland (Jarrow), England (Trawden, Newsham), and Slovakia (Nyraný) (Clack 2002, Milner et al. 1986). Unlike East Kirkton, all of these faunas have a distinctly semiaquatic signature. The Joggins locality deserves particular mention because of its historical and biotic significance. Dating from the mid-Bashkirian (Ryan et al. 1991), the Joggins fauna includes one of the most primitive known temnospondyls, *Dendrerpeton*, as well as the earliest widely agreed-on crown group amniote, *Hylonomus* (Clack 2002), a marker used repeatedly in molecular estimates of vertebrate evolutionary history.

TREE SHAPES, NODE DATES, AND THE ORIGIN OF CROWN-GROUP TETRAPODS

Phylogenies of early limbed tetrapods obtained from analyses of large taxon and character sets first appeared in the mid-1990s (Carroll 1995, Laurin & Reisz 1997). Subsequent analyses (e.g., Laurin & Reisz 1999, Vallin & Laurin 2004) have indicated that the majority of Carboniferous tetrapods are members of the stem group. In these trees, the earliest crown-group tetrapods are the morphologically diverse lepospondyls, and these branch from the amphibian stem. In contrast, the amniote stem is represented solely by diadectomorphs: bulky, stout-limbed tetrapods that first appear in the Moscovian. More recent analyses have presented a somewhat different phylogenetic structure (Ruta & Coates 2007, Ruta et al. 2003) in which most Carboniferous limbed tetrapods are included within the crown. The amphibian stem is populated by temnospondyls, whereas the lepospondyls branch from the amniote stem, along with the anthracosaurs (as shown in **Figure 1**). This branching pattern conforms more closely to previous ideas about the affinities of early tetrapods to amphibian and amniote lineages (cf. Milner et al. 1986).

Importantly, under either phylogenetic regime, the aistopod lepospondyl *Lethiscus* is the earliest crown-group tetrapod, dating the amphibian-amniote divergence to a minimum of around 335 mya. The equivalent fossil marker for the divergence of lungfishes and tetrapods (*Diabolepis*) lies close the base of the Devonian, suggesting that the temporal span of the tetrapod stem group exceeds 50 million years (but note that this time range lacks hard boundaries).

It is also significant that both sets of phylogenies exclude all known Devonian limbed tetrapods from the tetrapod crown; post-Devonian limbed tetrapods are monophyletic relative to earlier members of the clade. *Acanthostega*, *Ichthyostega*, elpistostegalids, and fragments of putative near-relatives have not yet turned up in post-Devonian deposits. The suggestion that *Tulerpeton* might represent a basal “reptiliomorph” (stem amniote) (Lebedev & Coates 1995) has not survived subsequent analyses (Ruta & Coates 2007, Vallin & Laurin 2004). However, an isolated humerus from the early Carboniferous of Horton Bluff seems to link the humeri of *Tulerpeton* and early anthracosaurs (Ruta & Clack 2006), whereas another study (Ruta & Bolt 2006) groups *Tulerpeton* with Carboniferous whatcheeriiids.

Irrespective of these tenuous connections across the Devonian-Carboniferous boundary, the topology of tetrapod phylogeny shows post-Devonian limbed tetrapods as products of a phylogenetic bottleneck (sensu Jablonski 2002), yielding a second radiation into semiaquatic ecospace. Subsequently, by the mid-Viséan, groups of limbed tetrapods had established divergent character complexes and, by extension, different life habits. These and many other distinguishing features persist, in certain respects remarkably unchanged, into the later evolutionary history of the amphibian and amniote stem groups.

Evolutionary radiations are often marked by rapid diversification of new morphotypes (Wagner 2001), and tetrapods provide an increasingly well-defined example in which the origin of a new body-plan is associated with invasion of new habitat, as well as origin of a crown-group radiation. Given this context, the pattern of tetrapod phylogeny might allow for comparison between contrasting models for reducing rates of morphological change (Valentine 1980): either intrinsic constraint (i.e., developmental or genetic) or ecological restriction (i.e., filling of general ecospace). In fact, limbed tetrapods displayed a dramatic decrease in amounts of evolutionary change between the Devonian and the Early Carboniferous (Ruta et al. 2006). The initial peak of morphological evolution could easily represent relaxation of both kinds of constraint: reduced ecological restrictions and reduced intrinsic developmental and/or genetic constraints. Decreased rates of morphological evolution in the Early Carboniferous present a marked contrast, and these are associated with an apparent repeated radiation into marginal terrestrial habitats. If ecology alone were responsible for rates of morphological change, then Early Carboniferous rates ought to mimic Devonian rates. It follows that the very marked drop in rate change could be a result of increased intrinsic constraint. However, this assumes a simple model of empty or cleared ecospace, whereas, at present, we have very limited knowledge of the Early Carboniferous ecosystems that stem tetrapods occupied.

TRANSFORMATIONS: THE EMERGENCE OF A NEW BODY-PLAN

Most anatomical changes associated with the origin of limbed tetrapods occurred in groups encompassing the upper reaches of the tetrapod stem (**Figure 1**). **Figure 2** illustrates large-scale changes to body proportions and external features, such as fins and opercular flaps. **Figure 3** details the forequarters of three genera that have come to epitomize the fish-to-tetrapod morphological transition: *Eusthenopteron*, *Panderichthys*, and *Acanthostega*.

Within the skull, the braincase (neurocranium)—primitively separated into anterior and posterior divisions—unites, and proportions change so that the anterior portion is much longer than the

rear portion. The auditory capsules increase in size relative to the posterior division of the braincase, and the notochord is withdrawn from a tunnel beneath the braincase rear. These changes are reflected in transformation of the overall skull morphology, including snout enlargement and shifts in orbit position and orientation.

The gill skeleton (viscerocranium) is reduced, but ossified arches with deep grooves persist in the earliest limbed tetrapods. The hyoid arch is transformed as the palate (not shown) becomes attached securely to the braincase. The lower division of the hyoid arch, the ceratohyal, remains large and probably retained primitive functions associated with jaw, gill arch, and oropharyngeal volume change. The upper division, the hyomandibula, is reduced and reoriented as a primitive stapes. Instead of articulating wholly with the ossified sidewall of the auditory capsule, the proximal end of the nascent stapes sits mostly within an unossified window. No longer associated clearly with jaw suspension, the hyomandibula/stapes might have had an incipient role in sound conduction and/or spiracular pouch function (Clack 2002, 2007).

Postcranially, the persistently notochordal vertebral column gains expanded centra and upright neural spines, while ribs enlarge, acquire broad heads, and extend laterally. Separation of the pectoral girdle from the skull creates a neck allowing lateral movement of the head (relative to the trunk). The endoskeletal scapulocoracoid is enlarged, buttressed, and reorients to face laterally. Dermal bones of the pectoral girdle are reduced dorsally and laterally, but enlarged and expanded ventrally. Not illustrated but of clear functional significance, the pelvis enlarges and acquires direct attachment, by means of one or more sacral ribs, to the vertebral column. Associated with this, the hip socket (acetabulum) and surrounding buttresses are reoriented, as in the scapulocoracoid, to face laterally.

Finally, scale coverage of the body and fins is reduced dramatically in limbed tetrapods relative to elpistostegals (and other finned stem-taxa; **Figure 4f**). In early limbed tetrapods, ossified scales are present only as gastral plates, scales on the ventral surface of the trunk [*Ichthyostega* presents a notable exception, with reported cycloid scales on the tail (Jarvik 1952)].

THE ORIGIN OF TETRAPOD LIMBS: MORPHOLOGICAL NOVELTY

The fin-to-limb transition concerns separate events at pectoral and pelvic levels, and there is evidence that several changes occurred first at pelvic level (Coates et al. 2002). The following summary focuses on forelimbs because the data set is slightly more detailed. Key events concern fin ray loss, digit acquisition, and remodeling of the humerus. The resultant tripartite organization as stylopod (humerus), zeugopod (radius and ulna), and autopod (wrist and digits) presumably reflects the phylogenetic emergence of developmental autonomy within the outgrowing limb, in which the zeugopod initially resembles a carry-over from the primitive (fin) condition (**Figure 4a–g**).

Figure 4 shows Devonian and Carboniferous tetrapod pectoral fin and limb endoskeletons. Tetrapod fin skeletons (**Figure 4a–g**) are clearly different from limb skeletons, and, as argued by Rosen et al. (1981), they retain an essentially primitive, asymmetrically branched pattern (Friedman et al. 2007). Within a phylogeny of tetrapod fins and limbs, the longest internal branch (length proportional to total character-state change) spans the fin-to-limb divide (Coates et al. 2002). Only the Late Devonian Catskill humerus (Shubin et al. 2004) slots into this gap, and the question of whether it supported fin rays or digits remains unanswered.

All fins shown (**Figure 4a–g**) supported ossified and segmented fin rays, and, in life, the endoskeleton was encased within a scale-covered muscular lobe (only shown in **Figure 4f**). Primarily, the radius is consistently longer than the ulna. The humerus has been described as the first mesomere or segment of an axis drawn through the ulna and ulnare toward the outermost extremity of the fin. Usually labeled the metapterygial axis (Coates 2003, Grandel 2003), this easily maps

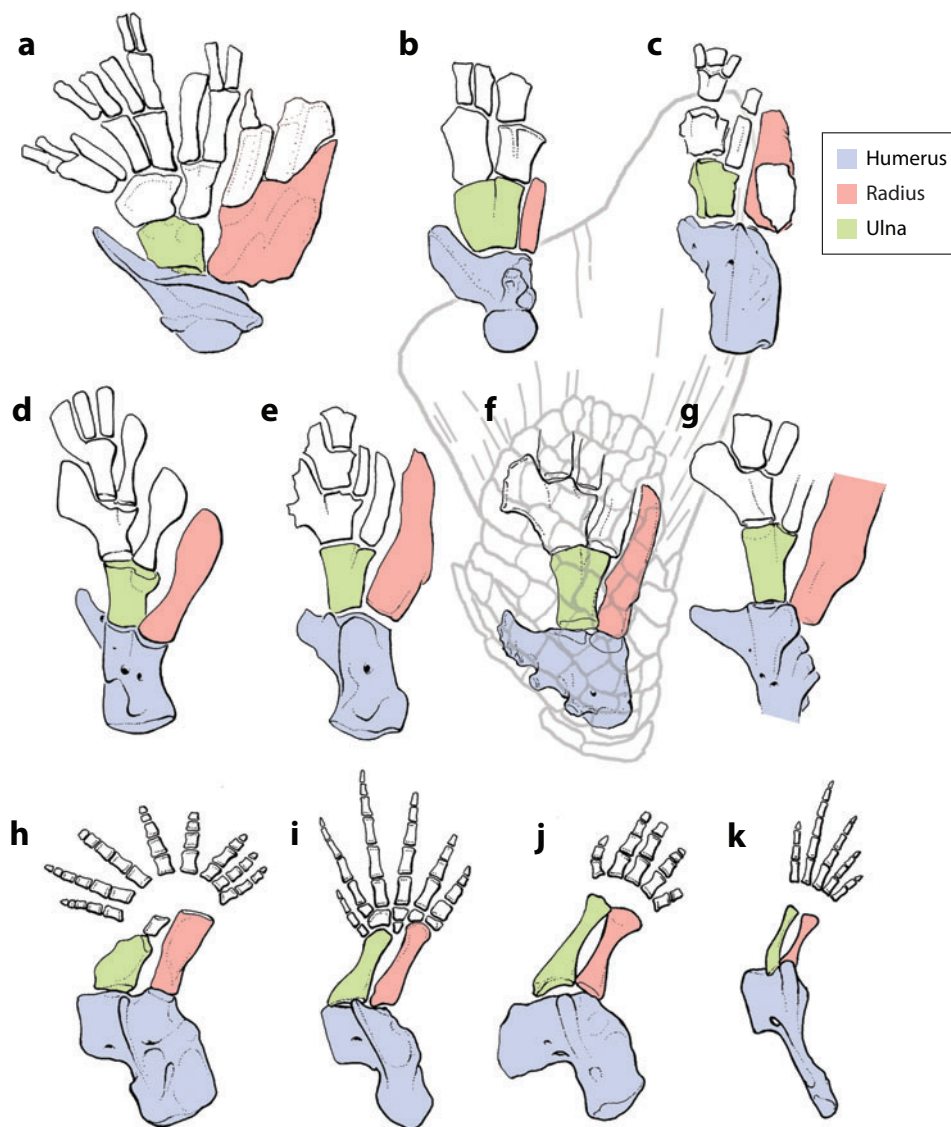


Figure 4

Fin and limb skeletons. (a) *Sauripterus*, a rhizodont, after Davis et al. (2004a). (b) *Barameda*, a rhizodont, after Long (1989) and Garvey et al. (2005). (c) *Tiktaalik*, an elpistostegolid, after Shubin et al. (2006). (d) *Eusthenopteron*, a tristichopterid, after Andrews & Westoll (1970). (e) *Gogonassus*, an osteolepidid, after Long et al. (2006). (f) *Sterropterygion*, a megalichthyid (original). (g) *Rhizodopsis*, a megalichthyid, after Friedman et al. (2007). (h) *Acanthostega*, a limb-bearing stem tetrapod, after Lebedev & Coates (1995). (i) *Tulerpeton*, a limb-bearing stem tetrapod, after Coates (1996). (j) *Greerpeton*, a limb-bearing stem tetrapod, after Coates (1996). (k) *Westlothiana*, a stem amniote, after Smithson et al. (1994). Dermal fin skeleton, comprising fin rays and scales, are shown in light gray for *Sterropterygion* (f); similarly elaborate dermal skeletons are present, but not illustrated, in all taxa in the top two rows. These features are absent from the digit-bearing taxa in the bottom row. All skeletons are shown with leading edge to right of Figure; all are in dorsal aspect except for (a) and (f) (ventral aspect).

out to the third or fourth mesomere, but the pattern is often indistinct distally (Friedman et al. 2007). None of these skeletons is outstandingly limb-like. Although the pectoral fin of *Tiktaalik* (Figure 4c) is related most closely to digit-bearing limbs (Shubin et al. 2006), unambiguously limb-like characteristics are restricted to humerus shape.

Digits can be regarded as a subgroup of radials, but they possess distinguishing characteristics, including alignment as a series across the distal end of the appendage (functionally uniting distal ends of the radius and ulna) and the absence of a distally branched pattern. Furthermore, digits are known only in appendages where fin rays and scales are absent. In primitive limb skeletons (Figure 4b–k) the humerus is L-shaped with a large, posterior flange, the entepicondyle. There is a distinct elbow joint; distal to this the limb skeleton is generally flexed (contrast Figure 4b–k with 4a–i). Several trends are apparent from the most primitive (*Acanthostega*, Figure 4b) to the most advanced (*Westlothiana*, Figure 4k) examples shown. The humerus gains a shaft; the ulna extends to equal radius length; the intermedium is moved into the wrist region (instead of flanking the radius); a complex wrist joint (including a noncylindrical intermedium) intercalates between the radius, ulna, and digits; and digit numbers diminish to stabilize at five.

THE ORIGIN OF TETRAPOD LIMBS: DEVELOPMENTAL CHANGE

Most information about vertebrate limb development has been obtained from studies of chicks and mice [reviewed recently by Tanaka & Tickle (2007)]. Fin data are largely from the teleost zebrafish (Grandel 2003), although further data are being obtained from paddlefish (nonteleost actinopterygians) (Davis et al. 2007, Metscher et al. 2005), lungfish (sarcopterygians) (Johanson et al. 2007), and elasmobranch chondrichthyans (Dahn et al. 2007, Freitas et al. 2007). Importantly, it appears that bony fishes as a whole (from tetrapods to teleosts) share most of the same genes and developmental regulatory systems, and that most of the same materials examined thus far are deployed and used similarly in paired fin buds and limb buds.

Digit primordia appear late in limb bud development, and some of the most widely discussed work on this aspect of limb development concerns the similarly late and distal activity of particular Hox genes and how this might affect digit patterning. Hox gene nested expression patterns in outgrowing limb buds are dynamic and phased (Zákány et al. 1997) and relate to proximodistal patterning (Wellik & Capecchi 2003, Tàrchini & Duboule 2006). A subset of Hox genes is expressed at high levels in the digit-forming region (Kmita et al. 2002), and this expression phase was thought to be absent in paired fins. Functional studies provide important clues about the significance of this episode in digit development, as well as the evolutionary assembly of this regulatory architecture (Kmita et al. 2002, Tàrchini & Duboule 2006, Zákány et al. 1997). These data contributed to the notion of the distal region of tetrapod limbs, including digits and the wrist/ankle (the autopod), as an evolutionary novelty (Wagner & Chiu 2001). However, discovery of an autopodial-like Hox gene expression pattern in the developing paired fins of osteichthyans and chondrichthyans (Davis et al. 2007, Freitas et al. 2007) suggests otherwise (consistent with patches of Hox gene expression in lungfish fins: Johanson et al. 2007). It appears increasingly likely that aspects of autopodial developmental patterning are general characteristics of paired fin buds in all gnathostomes. Just as digits can be characterized as a new and precise arrangement of fin radials, their development probably co-opted more general patterns of gene regulatory activity (Friedman et al. 2007, Grandel 2003).

Unlike digits, fin rays are unambiguously unique to fins. Fin rays are components of the dermal skeleton (rather than endoskeleton), and the dermal skeleton is a derivative of the neural crest. Trunk crest has evident skeletogenic potential, although in living tetrapods this capacity is only expressed by the cranial neural crest (McGonnell & Graham 2002). Fin rays develop within the

apical fold of an embryonic fin bud (Grandel 2003, Witten & Huysseune 2007) and this fold is an outgrowth of the apical ectodermal ridge, a major signaling center involved in limb bud development. Loss of fin rays during the evolutionary origin of limbs implies significant change in the developmental activity of the apical ectodermal ridge. Proximodistal patterning, outgrowth, and anteroposterior patterning result from complex feedback-linked signal systems between the apical ridge and other signaling centers of limb and fin buds. Moreover, experimental and clinical studies show that large-scale morphological abnormalities occur when such signals are disrupted (Tanaka & Tickle 2007).

These differences between fins and limbs have barely been considered from a comparative and evolutionary standpoint (Freitas et al. 2007): the transition from apical ectodermal ridge to apical fold, the arrest or persistence (in development) of an apical signaling center, the possible presence and influence of skeletogenic neural crest mesenchyme. Any or all of these probably interlinked factors, subject to natural variation, seem likely to have provided the material basis for morphologically significant and perhaps rapid evolutionary change.

THE ORIGIN OF TETRAPOD LIMBS: FUNCTIONAL CHANGE

As in discussions of developmental change, scenarios of functional change at the fin-to-limb transition have focused on the endoskeleton, whereas the role of scales and fin rays has been neglected. The suggestion that limbs evolved in a primitively aquatic taxon is based on conjunction of paddle-like limbs, grooved gill bars, and skeletally supported tail fin in *Acanthostega* (Coates 1996, Clack 2002). However, this now accompanies discussions of load-bearing fins in *Tiktaalik* (Shubin et al. 2006) and other stem tetrapods (Boisvert 2005). These speculations need not be mutually exclusive, because vertebrate exploitation of marginal aquatic habitats probably happened under different ecological circumstances for a variety of tetrapod groups, just as occurs today for many kinds of teleost fishes (Graham 1997).

As for speculation about the biomechanics of limb-like fins, few substantial studies have been completed. Histological analysis of the paired fin skeletons of *Eusthenopteron* (Figure 3, top; Figure 4d) indicates that this stem tetrapod, at least, was wholly aquatic (Laurin et al. 2007). Among the descriptions of walking gaits in living fishes (Pridmore 1995, Wilga & Lauder 2001, Lucifora & Vassallo 2002a) an axial-driven walking trot has been proposed as primitive for tetrapods (Pridmore 1995). Perhaps within stem tetrapods this aquatic walking trot was superseded by a pelvic-driven bipedal gait, because air-filled lungs would have supported the anterior trunk region. Such a scenario is consistent with the phylogenetic sequence of limb evolution, in which conventional limb characteristics occur first in pelvic appendages (Coates et al. 2002). Fossil trackway data might deliver further insights (Clack 2002), but assigning Devonian tracks to the earliest limbed tetrapods is especially difficult, given the paddle-like form and orientation of primitive hind limbs.

HABITATS AND PALEOBIOGEOGRAPHY

Thus far, the late Givetian to early Frasnian elpistostegals are confined to the fringe of Euramerica (Daeschler et al. 2006) (Figure 5). The Euramerican fringe also includes the Viséan midland valley of Scotland, source of the earliest crown-group tetrapods. Sandwiched between these last two groups, the earliest limbed (and less-certainly limbed) genera have been collected from a wide area, including the Frasnian-Famennian of Euramerica, North China, and easternmost Gondwana (Blieck et al. 2007). The paleoenvironments of these Late Devonian tetrapods range from proximal, near-shore marine localities to continental, freshwater lakes and rivers (Blieck et al. 2007,

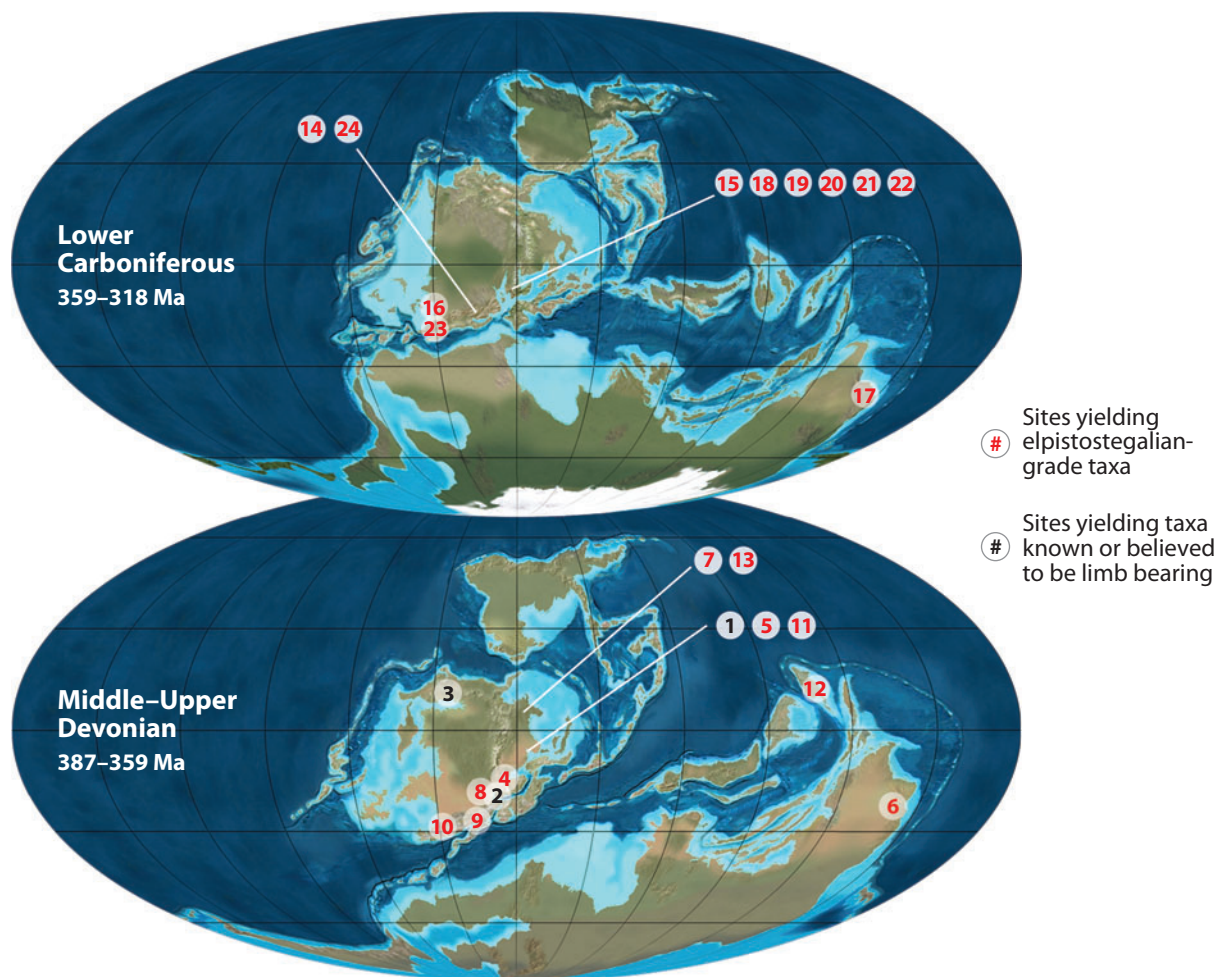


Figure 5

Devonian and Carboniferous paleogeographic maps (adapted, with permission, from originals by Ron Blakey, Northern Arizona University) marked with numbers corresponding to the following important tetrapod localities (black numerals indicate localities yielding elpistostegalian-grade taxa, whereas red numerals denote sites yielding forms either known or believed to have been limb bearing). Middle and Upper Devonian sites (taxon lists adapted from Clack 2007): 1, Gauja Formation, Latvia and Estonia (upper Givetian; *Livoniana*, *Panderichthys*); 2, Miguasha, Quebec, Canada (lower Frasnian; *Elpistostege*); 3, Fram Formation, Nunavut, Canada (lower Frasnian; *Tiktaalik*); 4, Scat Crag, Scotland (upper Frasnian, *Elginerpeton*); 5, Velna-Ala, Latvia (upper Frasnian; *Obruchevichthys*); 6, Jemalong, New South Wales, Australia (upper Frasnian-lower Famennian; *Metaxygnathus*); 7, Gornostayevka quarry, Russia (lower Famennian; *Jakubsonia*); 8, Aina Dal and Britta Dal formations, East Greenland (upper Famennian; *Acanthostega*, *Ichthyostega*, new genus); 9, Evieux Formation, Belgium (upper Famennian; *Ichthyostega*-like form); 10, Catskill Formation, Pennsylvania, USA (upper Famennian; Catskill humerus, *Densignathus*, *Hynerpeton*, whatcheerid-like form); 11, Ketleri and Pavāri, Latvia (upper Famennian; *Ventastega*); 12, Ningxia, China (upper Famennian; *Sinostega*); 13, Andreyevka-2, Russia (uppermost Famennian; *Tulerpeton*). Lower Carboniferous sites (taxon lists adapted from Clack 2002, Milner et al. 1986): 14, Horton Bluff, Nova Scotia, Canada (Tournaisian); 15, Ballagan Formation, Scotland (middle Tournaisian; *Pederpes*); 16, Delta, Iowa, USA (lower Viséan; *Whatcheeria*); 17, Duckabrook Formation, Queensland, Australia (lower Viséan; *Ossinodus*); 18, Wardie, Scotland (lower Viséan; *Lethiscus*); 19, East Kirkton, Scotland (middle Viséan; see text for taxon list); 20, Cheese Bay, Scotland (middle Viséan; *Casineria*); 21, Gilmerton Quarry, Scotland (middle Viséan; *Crassigyrinus*, *Loxomma*, colosteid); 22, Dora, Scotland (upper Viséan; *Crassigyrinus*, *Doragnathus*, *Eoherpeton*, *Proterogyrinus*, adelogyrinid); 23, Greer, West Virginia, USA (upper Viséan-lower Serpukhovian; *Greererpeton*, *Proterogyrinus*); 24, The well-known Joggins locality (Upper Carboniferous, mid-Bashkirian).

Lebedev 2004). Paleocontinental reconstruction (Averbuch et al. 2005) indicates that all 10 noted localities for what might be the earliest limbed tetrapods lie within 30° of the estimated equator, consistent with macroevolutionary ideas about cradles of diversity (Goldberg et al. 2005). However, it remains unclear whether this distribution is the result of collection bias. Marginal deposits of Late Devonian age have not been fully exploited in Africa, South America, or Antarctica.

THE END DEVONIAN EXTINCTION AND RECOVERY

The Late Devonian extinction, marked by an estimated loss of between 70% and 82% of marine species (McGhee 2001), extended from the latest Frasnian and into the Famennian. This drawn-out biotic crisis has been correlated with global cooling (Joachimski & Buggisch 2002, Streel et al. 2000), atmospheric change (Berner et al. 2007, Scott & Glasspool 2006, Algeo et al. 2001), and the radiation of terrestrial plants leading to aquatic eutrophication and anoxia on an intercontinental scale (Algeo et al. 2001). Furthermore, the Late Devonian was a period of intense tectonic activity, with incipient collisions of continental crustal blocks including Laurussia, Gondwana, Kazakhstan, and Siberia (Averbuch et al. 2005). These tectonic events closed entire oceanic domains (**Figure 5**), had a widespread influence on other marine environments, and probably contributed to global cooling (Averbuch et al. 2005, Blieck et al. 2007).

Tetrapods (the total group) originated prior to this episode of massive change, and by the end of it, most of the group seems to have perished. The greening (aquatic and terrestrial) of continents, from the late Silurian through to the Middle Devonian, was a late phase in a vast sequence of continental invasions (Labandeira 2005). But those processes that provided the structural and trophic complexity necessary for terrestrial vertebrate life might also have been those that devastated the tetrapod clade (Algeo et al. 2001).

The ~15 million year post-Devonian trough in the record of limbed tetrapods (Clack 2002, Ruta et al. 2003) is also apparent in the fossil history of terrestrial arthropods (Ward et al. 2006). Absence of both groups throughout most of the Tournaisian has been attributed (Ward et al. 2006) to an estimated trough in atmospheric oxygen levels (Berner et al. 2007), constraining both groups to aquatic habitats. Physiological arguments have some bearing on this scenario, but the sudden diversity of Viséan limbed tetrapods implies that this gap might equally reflect unevenness of the fossil record (Clack 2007). Tetrapod phylogeny clearly underwent multiple branching events and encompassed considerable morphological diversification during this interval, the results of which include aistopods, adelogyriiniids, temnospondyls, and *Westlothiana* (and we have correspondingly little idea about any hidden diversity of as yet unknown post-Devonian elpistostegals, “acanthostegids,” and ichthyostegids). If there is any signature in the tetrapod record that might be more safely attributed to early Carboniferous atmospheric conditions, then it is the reduced size of these crown tetrapods and their close relatives (**Figure 2**), compared with the larger dimensions of earlier and more basally branching clades (Clack 2007).

CONCLUSIONS AND FUTURE DIRECTIONS

Early tetrapod distribution is clumpy at any scale, from detailed features of anatomy (note the almost bimodal array paired fin and limb skeletons; **Figure 4**) up to the patchy distribution of body shapes and higher taxonomic categories. These patterns should be investigated; it seems unlikely that they result wholly from extinctions editing chunks from evenly spread morphological continuity (cf. Erwin 2007). The use of nontraditional node-based rather than character-based group definitions is disputed (Blieck et al. 2007, Clack 2007), but it permits a better perspective of early tetrapod evolution, and provides an explicit means of framing questions about group

origins and change. The “vast structural gaps” (Milner et al. 1986) separating *Ichthyostega* from osteolepiforms and Carboniferous tetrapods have effectively closed: The research program started by Owen approximately 150 years ago is largely completed. Narratives of morphological change from fish to tetrapod can be refined, but there are other issues to address. The turnover in clade composition across the Devonian–Carboniferous boundary is dramatic, and we note that it yields two groups that radiate significantly within the post-Devonian Paleozoic: limbed tetrapods and rhizodontids. If research explores only the limbed subset of the tetrapod total group, much of the evolutionary signal will be missed (as if research on mammal evolution ignored noneutherians). A detailed phylogenetic analysis of the whole of the tetrapod stem is needed. Similarly, Devonian tetrapod-containing biotas need to be subjected to the level of study applied to Carboniferous localities such as East Kirkton (Clarkson et al. 1994). Paleocological understanding of the earliest tetrapods would also be assisted by substantial biomechanical analyses of structures such as lobed fins, and vertebrae retaining a large notochordal component. Finally, developmental analyses of differences between fins and limbs, rather than searches for general, and perhaps primitive, conditions, are more likely to improve our understanding of present and past morphological diversity.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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