Early tetrapod evolution

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Tetrapods include the only fully terrestrial vertebrates, but they also include many amphibious, aquatic and flying groups. They occupy the highest levels of the food chain on land and in aquatic environments. Tetrapod evolution has generated great interest, but the earliest phases of their history are poorly understood. Recent studies have questioned long-accepted hypotheses about the origin of the pentadactyl limb, the phylogeny of tetrapods and the environment in which the first tetrapods lived.

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A few decades ago, Devonian stegocephalians (Boxes 1 and 2) were known from only two taxa from East Greenland: *Ichthyostega* and *Acanthostega*[1]. The closest known relatives of these two taxa and of more recent stegocephalians were the panderichthyids, a clade of sarcopterygians that shares many derived features with stegocephalians, but that retains paired fins. However, recent studies of fragmentary remains, previously interpreted as 'osteolepiforms'[2], revealed that many of these taxa (*Metaxygnathus*, *Obruchevichthys*, *Elginerpeton* and *Ventastega*) are more closely related to tetrapods than to panderichthyids[3,4]. No limb extremity (autopod; Box 2) is preserved in any of these taxa, but the fact that panderichthyids are our closest relatives known to have possessed paired fins prompted some authors to call these taxa 'tetrapods'[3]. However, the position of these taxa does not enable us to determine whether or not these taxa possessed digits; both hypotheses are equally parsimonious (Fig. 1). An additional genus (*Hynerpeton*) claimed to be an early tetrapod, represented by recently discovered fragmentary remains, seems to be more closely related to extant tetrapods than to *Acanthostega* (a taxon known to have had digits)[5]; if this interpretation is correct, the parsimony criterion suggests that this taxon had digits (Fig. 1).

When is a vertebrate with four feet not a tetrapod?

A controversy in tetrapod taxonomy was recently triggered by the use of phylogenetic definitions of taxon names. This is part of a larger controversy between practitioners of Linnean taxonomy (who advocate using taxa diagnosed by characters) and practitioners of phylogenetic taxonomy (who use the phylogeny to define taxon names). For example, the name 'Tetrapoda' has usually been defined as the taxon that includes all vertebrates that bear digits (including those that have lost them, such as snakes). However, an alternative phylogenetic definition of Tetrapoda is 'the most recent common ancestor of extant lissamphibians and amniotes and all of its descendants'[6] (Box 1). These two concepts of Tetrapoda do not coincide (Fig. 2), because the phylogenetic definition of Tetrapoda actually excludes some digit-bearing vertebrates. A taxon that includes all vertebrates possessing digits is therefore needed, thus the old taxon name Stegocephali was given a phylogenetic definition to fill this taxonomic gap (Boxes 1 and 2; Fig. 1). Here, we use the phylogenetic definitions of the relevant taxon names, as defined by Laurin or Gauthier and colleagues (Box 1; Figs 1 and 2).

Paleontological data on the origin of digits

Paleontological data do not solve the problem of homology (or lack thereof) between the radials of early sarcopterygian fins and the digits of the autopod. Until recently, the fins most readily compared with a tetrapod limb were those of *Eusthenopteron*, which consist of a humerus (we discuss only the pectoral limb, but a similar argument could be made for the hind limb), radius, ulna, ulnare, intermedium (the homology of the last two elements is not well established) and a

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Box 1. Phylogenetic definitions

In all cases, the first published definition for each taxon name is used. This is not required by the zoological code of nomenclature, but we feel that it is advisable because one of the main goals of the principle of phylogenetic definitions is to provide a criterion of synonymy and priority that is more compatible with evolution than the type-based criterion used in linnean systematics[34].

Amniota: the last common ancestor of mammals and reptiles, and all its descendants[27].

Amphibia: extant lissamphibians and all extinct tetrapods that are more closely related to them than they are to amniotes[6].

Anthracosauria: amniotes and all other extinct tetrapods that are more closely related to amniotes than to amphibians[27].

Lissamphibia: the last common ancestor of Gymnophiones, Caudata, and Anura, and all its descendants[25].

Stegocephali: all choanates that are more closely related to Temnospondyli than to *Panderichthys*[25].

Tetrapoda: the last common ancestor of amniotes and lissamphibians, and all its descendants[6].

Box 2. Glossary

Amniotes: a clade that includes mammals and reptiles (birds are reptiles in modern classifications, thus they are amniotes), and their extinct relatives; all amniotes produce an egg that possesses new extra-embryonic membranes, one of which forms the amnios, a pouch in which the embryo develops.
Autopod: the third segment of the paired limb (in the proximo-distal direction), which includes the hands and feet, from the wrist or ankle to the tip of the fingers or toes.
Carpus: the part of the autopod that corresponds to the wrist.
Ceratobranchial: a bony or cartilaginous element of the branchial skeleton; in primitively aquatic vertebrates it supports the gills.
Digit: a structure composed of a series of aligned phalanges and associated tissues; when each digit can move independently of the others, it is also called a finger or a toe, but digits might be incorporated into a paddle in aquatic tetrapods (in marine turtles, whales and ichthyosaurs, etc.).
Exaptation: characteristic of a taxon that is advantageous and functional in its present environment, but that initially performed a different function, often in another environment.
Lepidotrichia: dermal fin rays consist of modified scales; they stiffen the fins of most actinopterygians and many primitively aquatic sarcopterygians.
Lissamphibians: a clade that includes all extant amphibians (frogs, toads, salamanders, newts and apodans), but none of the currently known Paleozoic amphibians.
Metacarpal: a bony element of the hand located between the carpus (wrist) and the phalanges (digits).
Osteolepiforms: a paraphyletic group of aquatic animals (all of which have paired fins) that includes more or less distant extinct relatives of tetrapods.
Radial: the endoskeletal element (bony or cartilaginous) supporting a fin.
Stegocephalians: a clade that includes all vertebrates that possess digits, and a few extinct, closely related forms that might retain paired fins; they are represented by tetrapods in the extant fauna, but they also include several other extinct groups.
Zeugopod: the second segment of the paired limb (in the proximo-distal direction), which includes the radius and the ulna in the forelimb, the tibia and fibula in the hindlimb, and the associated structures composed of soft tissues (muscles, nerves and blood vessels, etc.).

few other (generally four) smaller radial elements (Fig. 3a). The radius, ulnare and intermedium, along with the smaller elements, form a series of approximately seven rays. However, only four rays articulate proximally with an element that could be homologous with a carpal (the ulnare or elements distal to it). The fact that digits articulate on the carpus suggests that only these four radials (Fig. 3a) could be homologous with parts of digits (two are in the position of metacarpals, and two others could correspond to proximal phalanges or the precursors of all phalanges). If the homology of the elements, identified as the ulnare and the intermedium in *Eusthenopteron*, is correct, only the four elements distal to them could be homologous to metacarpals or to phalanges. Alternatively, the shape and the relationships of the seven most distal elements suggest a general homology to the whole autopodium (that is, including basi-, meta- and acropodials), before the autopod skeleton became individualized as discrete bones[1]. Other possibilities are that the four distal elements are homologous with distal carpals or that they have no homologues in the autopod. If either of these hypotheses is correct, there is no homologue of digits in *Eusthenopteron*. However, the distal portion of a recently found rhizodontid fin bears two more similarities with an autopod[7] (Fig. 3b): the rays are segmented, similar to the metacarpals and phalanges of digits, and most of them (six out of eight) articulate proximally

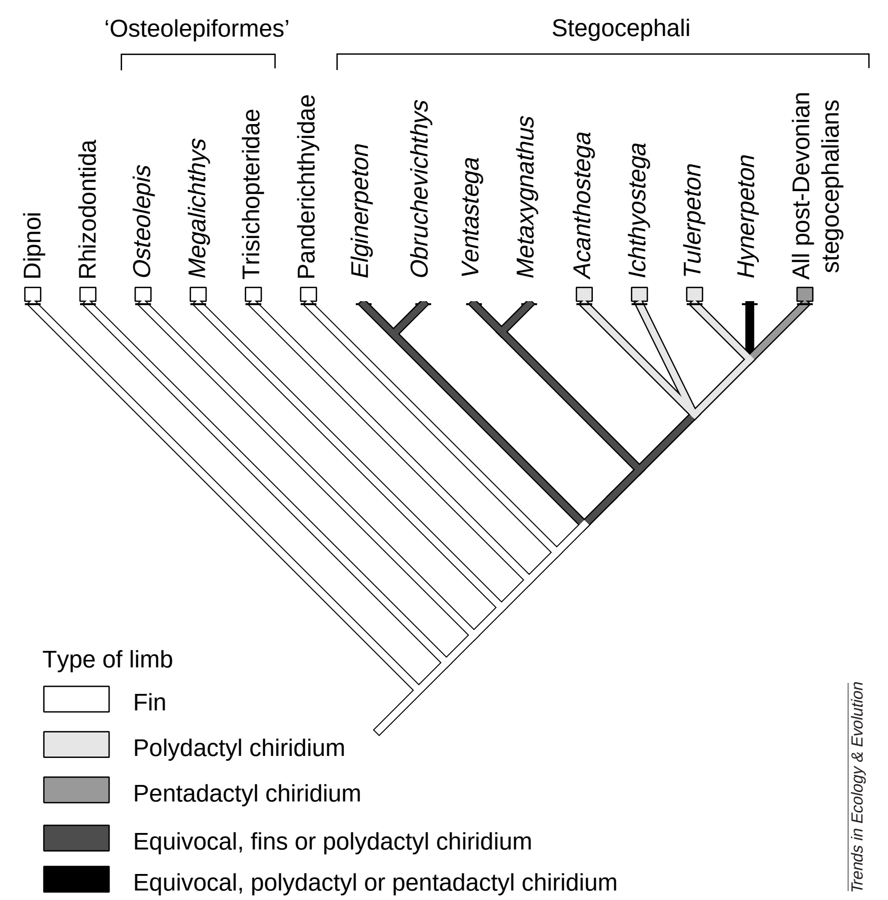

Fig. 1. Phylogeny of Devonian and Lower Carboniferous stegocephalians. The type of limb present in many poorly known Devonian stegocephalians is uncertain, as shown by the ambiguous optimization of the character 'type of limb' (the absence of data for a given taxon is indicated by the absence of a square data box below its name). Phylogeny is mostly based on the work by Ahlberg[3], but the position of *Tulerpeton*, and uncertainties about the position of *Ichthyostega* and *Acanthostega* reflect findings by Laurin[18].

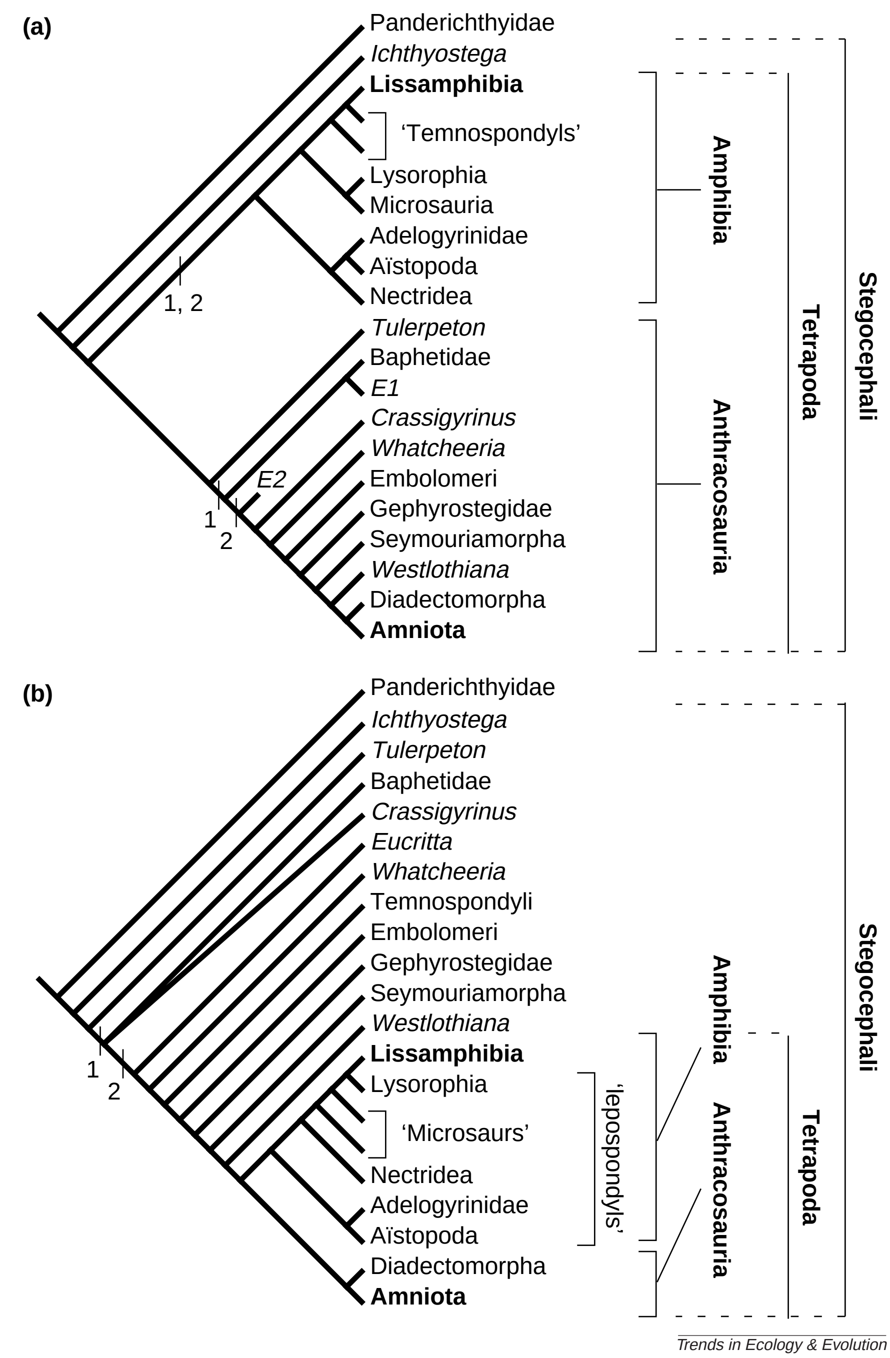

Fig. 2. Phylogenies of stegocephalians. (a) The traditional phylogeny[26–28]; and (b) the recent alternative based on the first computer-assisted phylogenetic analyses that included all the relevant taxa. The problematic taxa *Eucritta* and *Whatcheeria*, which had not been included in the original analyses on which the trees are based[18,25], have been added where they might fit, but their placement is admittedly tentative. Two possible positions of *Eucritta* (*E1* and *E2*) are indicated in (a), but only one is shown in (b) (where the name of this genus is not abbreviated). In both phylogenies, phylogenetic definitions of taxon names are used, and the appearance of digits is a synapomorphy of all included taxa except Panderichthyidae. The (1) and (2) indicate the earliest and latest possible appearances of pentadactyly on both phylogenies.

with a carpal (the ulnare and the intermedium). It is tempting to see these eight rays as homologous with the digits (Fig. 3c) of early stegocephalians (eight is also the maximum number of digits found in stegocephalians). Unfortunately, several sarcopterygians whose paired fins bear unsegmented rays, such as *Osteolepis* and *Eusthenopteron*, are thought to be more closely related to stegocephalians than to rhizodontids[2]. Therefore, the most parsimonious explanation is that these similarities are convergent. Unfortunately, the data currently available do not enable us to draw firm conclusions about the homology of the distal endoskeletal elements of the fins of early sarcopterygians.

Molecular data on the origin of digits

Molecular developmental biology can provide valuable data about the evolutionary history of the endoskeletal serial elements of limbs. The differentiation of the segments is determined by a combination of the expressions of several *Hox* genes that are also involved in the identity of the posterior segments of the body. Only genes located at the 5′ end of the four tetrapod clusters (*HoxA* to *HoxD*, gene numbers 9 to 13) are expressed during limb development[8]. By contrast to tetrapods, the zebrafish (*Danio rerio*), a teleost, possesses seven clusters, with *HoxA* to *HoxC* clusters being duplicated compared with the mouse (*Mus musculus*), but *HoxD* is not duplicated[9]. *HoxD*11-13 genes are expressed in a biphasic sequence in amniotes: the first expression is restricted posteriorly, whereas the second expression forms an arch on the full width of the distal mesenchyme[10] (Fig. 4a). This second expression phase corresponds closely to the bent pattern of prechondrogenic condensations of the digital arch (Figs 5d and e)[11]. This bend of *HoxD* expression is absent in zebrafish fin bud development[12] (Fig. 4b). This pattern suggests that the extremity of the autopod (the digits) is located at the posterodistal extremity of the limb. However, the *HoxA*-11 gene does not show this bend: it is expressed in a distal position in the zebrafish (Fig. 4d), whereas it is expressed in a band at the transition between the zeugopod and the autopod in the mouse[12] (Fig. 4c). This second pattern suggests that the autopod is at the distal extremity of the limb.

Comparison of both expression patterns suggests that the digits are at the posterior extremity of the limb (Fig. 5e), but the hypothesis that digits are at the distal extremity (Fig. 5f) cannot be ruled out definitively. A limb with both phalanges and lepidotrichia would enable us to choose between these two hypotheses. If the proximo-distal axis of the limb is straight (Fig. 5f), the lepidotrichia should be distal to the phalanges; whereas if the limb is bent, lepidotrichia should be mostly anterior to the phalanges (Fig. 5e). The sarcopterigyan *Sauripterus* has putative phalanges and lepidotrichia that are continuous with each other (Fig. 3b)[7], suggesting that the proximo-distal axis is not bent. However, the homology of the distal endoskeletal elements of *Sauripterus* to phalanges is uncertain.

Several other observations complicate interpretations of the zebrafish developmental data. The fugu (*Fugu rubripes*), another teleost, does not possess a *HoxD*

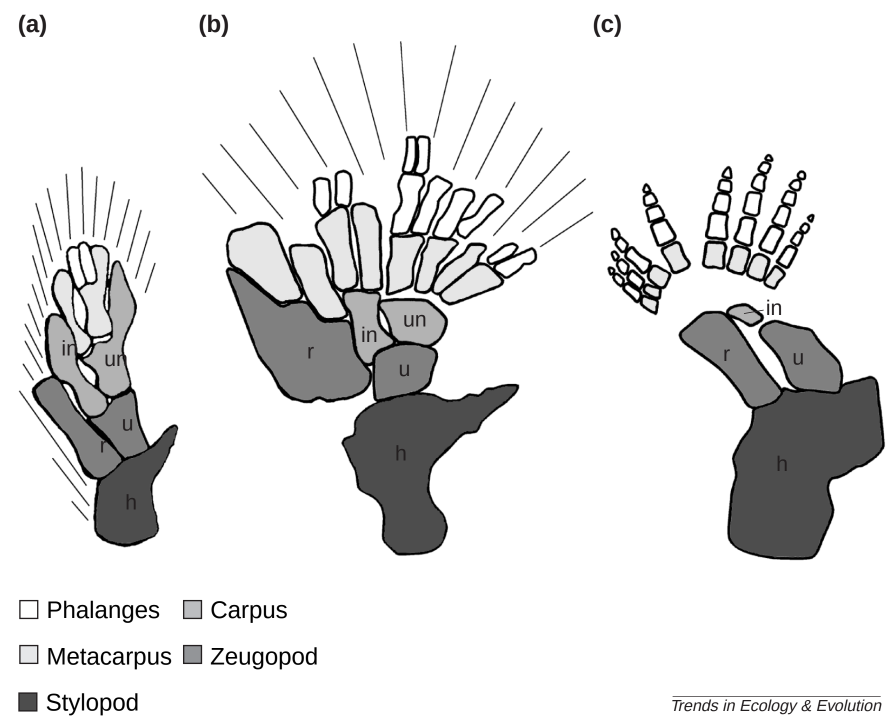

Fig. 3. Sarcopterygian limbs: (a) the forelimb of *Eusthenopteron*; (b) the forelimb of a recently discovered rhizodontid, probably showing convergent similarities with the tetrapod limb; and (c) the forelimb of *Acanthostega*. In all three limbs, the shading indicates the maximal potentially homologous regions using only the topological argument; the elements identified as homologous to metacarpals and phalanges in (a) and (b) might be homologous with distal carpals or have no homologues in stegocephalians. Anterior is to the left. Abbreviations: h, humerus; in, intermedium; r, radius; u, ulna; un, ulnare. *Reproduced, with permission, from Refs 7, 16 and 35.*

cluster, whereas it does possess rather normal fins[9]; this proves that the *HoxD* expression can be completely lost even if fins are present, and that other genes (not yet studied) could compensate for this. This raises the possibility that the lack of secondary bent expression of *HoxD*11-13 in the zebrafish is simply an autapomorphic regression. If so, it cannot be used to recognize the region of the tetrapod limb that corresponds to the distal end of the zebrafish fin. Moreover, even the position and orientation of the proximo-distal axis of the fin in zebrafish is uncertain. The major appendicular axis of the actinopterigyan fin is thought to correspond to the metapterygial axis of the tribasal fin[11,13] (Fig. 5c). Yet, according to the developmental data, this axis is closely parallel to the proximal radials (Figs 5a and b). Unfortunately, the absence of a metapterigyium in the zebrafish hampers direct comparisons with other vertebrates. Recent developmental studies also raise doubts about the homology between the elements and the main axis of the zebrafish fin and of the tetrapod limb[14]. Resolution of many of these problems must await data on gene expression in actinopterigyans with a metapterigyium or, better still, in chondrichtyans and lungfishes.

The first autopod: how many digits?

Recent paleontological discoveries have shown that contrary to long-held views, the first autopod was not pentadactyl (i.e. it did not have five digits) but polydactyl (i.e. it had more than five digits). Three nearly complete autopods are known from the Devonian (the hand in *Acanthostega* and *Tulerpeton*, and the foot in *Ichthyostega*); they have eight (*Acanthostega*), seven (*Ichthyostega*) and six (*Tulerpeton*) digits[15,16]. The fact that these three oldest known autopods are polydactyl (and the fact that they belong to the three most basal taxa bearing digits) indicates that polydactyly is the primitive condition for the autopod (Fig. 1). Previous interpretations of the polydactylous *Tulerpeton* as an anthracosaur (a relative of amniotes) implied that pentadactyly appeared twice (Fig. 2a) from a polydactyl condition (once in amphibians and once in anthracosaurs[17]).

The initial placement of *Tulerpeton* among anthracosaurs was presumably based partly on similarities between attributed cranial remains and the much better known skull of embolomeres. However, only a part of these cranial remains were found in the same block as the holotype – the others are from the same locality, but can be attributed to *Tulerpeton* only by assuming that there is a single stegocephalian in that locality. Furthermore, some of the cranial similarities between these remains and embolomeres are also found in *Crassigyrinus*; thus, they might be primitive. A recent phylogenetic analysis suggests that *Tulerpeton* is a stem-tetrapod and that it is excluded from the smallest clade that includes all pentadactyl taxa[18]. Therefore, pentadactyly probably appeared only once (Fig. 2b). Unfortunately, we cannot specify exactly where in the evolutionary tree pentadactyly appeared, because the postcranial anatomy of the most basal and earliest post-Devonian stegocephalians (*Crassigyrinus*, *Whatcheeria* and baphetids) is poorly known. Our knowledge of the anatomy of these taxa has recently progressed significantly, including a description of the first undoubted postcranial remains of baphetids[19,20]. We know that these taxa had digits, but we do not know how many. Parsimony suggests that they had at least five digits in the hands and feet.

Gills and the initial function of digits

Digits have usually been interpreted as an adaptation to the terrestrial environment[21]. However, the recent discovery of grooved ceratobranchials, which might have supported afferent branchial arteries[22], and of a post-branchial lamina on the cleithrum of the Devonian stegocephalian *Acanthostega*, raises the possibility that this taxon retained internal gills and was primitively aquatic. This suggests that digits appeared in an aquatic environment, in which case they would only be an exaptation to the terrestrial environment.

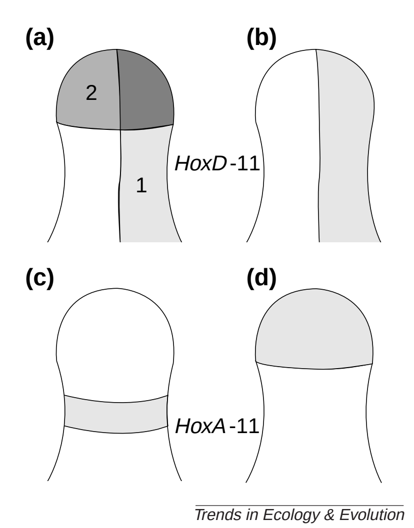

Fig. 4. Schematic comparison of *HoxD*-11 (a, b) and *HoxA*-11 (c, d) expression between a mouse forelimb bud (12.5 days) (a, c) and a zebrafish pectoral fin bud (60 hours) (b, d). 1: zone of primary expression; 2, zone of secondary expression. The anterior edge of the buds is on the left. *Modified, with permission, from Ref. 12.*

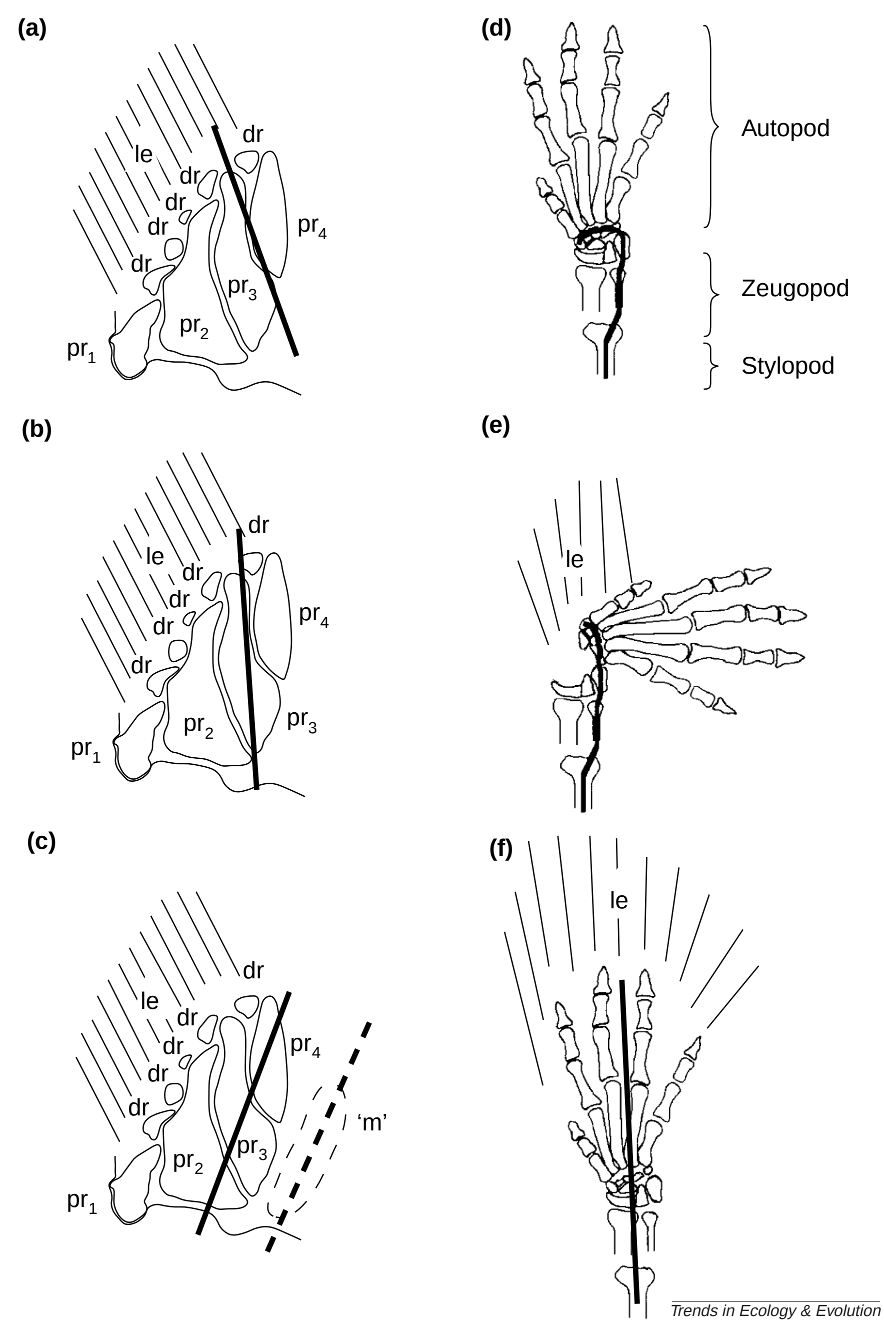

Fig. 5. Osteichthyan limbs. Bold lines show the major appendicular axis in an adult zebrafish pectoral fin [(a)–(c)] based on molecular data *[(a) and (b) modified, with permission, from Ref. 12]*, or on an inference from the putative position of the metapterygium (c) (Ref. 13). The position of the putative primitive metapterygium (absent in the zebrafish) and the orientation of the corresponding axis are represented by dashed lines based on the discussion in Coates[13]. The major appendicular axis of the adult mouse forelimb [(d)–(f)] is based on the timing of the appearance of the prechondrogenic arch and *HoxD*-11 expression (d) (Ref. 11). The putative position of lepidotrichia (present in the distant ancestors of tetrapods) at the distal part of the limb are shown according to a bent (e) or linear (f) proximo-distal axis hypothesis. Abbreviations: dr, distal radials; le, lepidotrichia; m, metapterygium; pr, proximal radials. The anterior edge of limbs or fins is to the left.

Marine amphibians?

Until recently, it was assumed that nearly all early amphibians and other stegocephalians lived only in freshwater bodies and on dry land (in a similar manner to extant amphibians[23], which generally cannot tolerate the marine environment). This assumption was supported partly by the freshwater paleoenvironmental interpretation of many localities in which early amphibians, other stegocephalians and their sarcopterygian relatives were found. However, many of these localities have recently been re-interpreted as estuarine, deltaic or even as coastal marine environments[24]. These recent interpretations raise the possibility that the intolerance of lissamphibians to the marine environment is a relatively recent specialization of this clade.

New phylogenies

The most widely accepted phylogeny was proposed (in a simple form) by Cope in the 1880s (Ref. 25) and, therefore, has a long history. According to this phylogeny (Fig. 2a), all known post-Devonian, and even some Devonian, stegocephalians were either related to lissamphibians or to amniotes. Strangely, most computer-assisted phylogenetic analyses of early stegocephalians were not designed to test the validity of this phylogeny. Some included only lissamphibians and their extinct presumed relatives[26], whereas others considered only amniotes and their extinct presumed relatives[27]. Finally, some analyses sampled only Devonian and Early Carboniferous taxa, whose affinities with extant tetrapods (lissamphibians and amniotes) are currently controversial[19]. Of course, many of the published phylogenies included all the relevant groups, but these were based on manual phylogenetic analyses, which are now known to give poor results (in many such cases the published tree is not the shortest one), and data matrices were usually not given[28]. Therefore, the first rigorous tests of the traditional phylogeny were performed only a few years ago[18,25,29,30].

These recent studies are based on computer-assisted phylogenetic analyses of data matrices that included between 18 and 44 taxa, and between 50 and 184 characters. Although there are slight differences between the proposed phylogenies, in general, they resemble each other. However, these studies differ so much from previous hypotheses that the scientific community will need a few more years to test them further and accept or reject them. The new phylogenies suggest that many Carboniferous taxa, and all known Devonian stegocephalians, are excluded from the Tetrapoda (Fig. 2b). Indeed, many taxa previously believed to be related to lissamphibians (such as temnospondyls) or to amniotes (such as seymouriamorphs and embolomeres) seem to be stem-tetrapods.

Enigmatic new fossils

A few years ago, an enigmatic fossil, now known as *Westlothiana*, was described as the oldest known 'reptile'[31] (= amniote). This discovery was thought to extend the fossil record of amniotes from the mid-Upper Carboniferous (Westphalian) to the mid-Early Carboniferous (Viséan). Subsequent studies demonstrated that *Westlothiana* was not an amniote, but suggested that it was probably one of the oldest known anthracosaurs[29] (Box 1). However, the affinities of this taxon are still debated and a recent study has even suggested that it might be a stem-tetrapod[25] (Fig. 2b).

Another enigmatic Lower Carboniferous taxon (*Eucritta*) exhibits a mixture of derived states shared with baphetids and a clade composed of embolomeres and related taxa[32]. It was placed in Baphetidae, even though this is only one of two equally parsimonious solutions (the two solutions are compatible with the positions marked by *E1* and *E2* in Fig. 2a). The relationships between baphetids, temnospondyls and other stegocephalians are unresolved in a strict consensus of the two most parsimonious trees, and this might result from the strange mix of character states found in *Eucritta*.

Another recent discovery is an early Carboniferous stegocephalian (*Casineria*) with the oldest known pentadactyl hand[33]. The strong ossification of the skeleton, and the right angle between the proximal and distal humeral heads suggest a relatively terrestrial lifestyle. A phylogenetic analysis suggests that this animal is an anthracosaur; however, the claim that this analysis shows *Casineria* to be an amniote[33] is debatable, because it is not supported by a strict consensus of the shortest trees. The low resolution of the phylogeny, as well as the high number of trees requiring a single extra step (over 100), raises doubts about these interpretations.

Prospects

More detailed anatomical studies and more phylogenetic analyses will be required to evaluate the evolutionary significance of all the newly discovered Upper Devonian and Lower Carboniferous stegocephalians. The inclusion of lissamphibians in more phylogenetic analyses will be especially important.

Many paleontologists marvel at the discovery of new, early potential relatives of amniotes[31,33], but the fact that many recent phylogenetic analyses[18,25,29,30,33] have indicated that lepospondyls and temnospondyls (two groups previously thought to be related to lissamphibians) do not form a clade (unless amniotes are also included) has not generated enough interest. This is one of the most surprising new discoveries, and finding which of these two groups (lepospondyls or temnospondyls) is actually related to lissamphibians will be necessary to improve our understanding of early tetrapod phylogeny.

The timing of the conquest of land by vertebrates is also worth investigating. We still ignore whether several Devonian and Carboniferous taxa were primitively or secondarily aquatic, and, in many cases, we do not even know how terrestrial or aquatic these taxa were. Future investigations using new types of data (isotopic, paleohistological, etc.) are needed to clarify these issues.

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References

1 Jarvik, E. (1952) On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Meddr Grønland* 114, 1–90
2 Ahlberg, P.E. and Johanson, Z. (1998) Osteolepiforms and the ancestry of tetrapods. *Nature* 395, 792–794
3 Ahlberg, P.E. (1998) Postcranial stem tetrapod remains from the Devonian of Scat Craig, Morayshire, Scotland. *Zool. J. Linn. Soc.* 122, 99–141
4 Ahlberg, P.E. *et al.* (1994) The first tetrapod finds from the Devonian (Upper Famennian) of Latvia. *Philos. Trans. R. Soc. London Ser. B* 343, 303–328
5 Daeschler, E.B. *et al.* (1994) A Devonian tetrapod from North America. *Science* 265, 639–642
6 Gauthier, J. *et al.* (1989) Tetrapod phylogeny. In *The Hierarchy of Life* (Fernholm, B. *et al.*, eds), pp. 337–353, Elsevier
7 Daeschler, E.B. and Shubin, N. (1998) Fish with fingers? *Nature* 391, 133
8 Nelson, C.E. *et al.* (1996) Analysis of *Hox* gene expression in the chick limb bud. *Development* 122, 1449–1466
9 Amores, A. *et al.* (1998) Zebrafish hox clusters and vertebrate genome evolution. *Science* 282, 1711–1714
10 Morgan, B.A. and Tabin, C. (1994) Hox genes and growth: early and late roles in limb bud morphogenesis. *Development* 36 (Suppl.), 181–186
11 Shubin, N.H. and Alberch, P. (1986) A morphogenetic approach to the origin and basic organisation of the tetrapod limb. *Evol. Biol.* 20, 318–390
12 Sordino, P. *et al.* (1995) Hox gene expression in teleost fins and the origin of vertebrate digits. *Nature* 375, 678–681
13 Coates, M.I. (1995) Limb evolution. Fish fins or tetrapod limbs – a simple twist of fate? *Curr. Biol.* 5, 844–848
14 Hinchliffe, J.R. *et al.* Is there a tetrapod developmental bauplan underlying limb evolution: evidence from a teleost and from urodele and anuran amphibians? In *Major Events in Early Vertebrate Evolution* (Ahlberg, P.E., ed.) (in press)
15 Lebedev, O.A. (1986) The first record of a Devonian tetrapod in the USSR. *Dokl. Akad. Nauk.* 278, 220–222
16 Coates, M.I. and Clack, J.A. (1990) Polydactyly in the earliest known tetrapod limbs. *Nature* 347, 66–69
17 Coates, M.I. (1996) The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution. *Trans. R. Soc. Edinb.* 87, 363–421
18 Laurin, M. (1998) A reevaluation of the origin of pentadactyly. *Evolution* 52, 1476–1482
19 Clack, J.A. (1998) The Scottish Carboniferous tetrapod *Crassigyrinus scoticus* (Lydekker) – cranial anatomy and relationships. *Trans. R. Soc. Edinb.* 88, 127–142
20 Milner, A.C. and Lindsay, W. (1998) Postcranial remains of *Baphetes* and their bearing on the relationships of the Baphetidae (=Loxommatidae). *Zool. J. Linn. Soc.* 122, 211–235
21 Westoll, T.S. (1943) The origin of the tetrapods. *Biol. Rev.* 18, 78–98
22 Coates, M.I. and Clack, J.A. (1991) Fish-like gills and breathing in the earliest known tetrapod. *Nature* 352, 234–236
23 Carroll, R.L. (1988) *Vertebrate Paleontology and Evolution*, W.H. Freeman and Company
24 Schultze, H-P. (1999) The fossil record of the intertidal zone. In *Intertidal Fishes: Life in Two Worlds* (Horn, M.H. *et al.*, eds), pp. 373–392, Academic Press
25 Laurin, M. (1998) The importance of global parsimony and historical bias in understanding tetrapod evolution. Part I – systematics, middle ear evolution, and jaw suspension. *Ann. Sci. Nat. Zool. 13 Ser.* 19, 1–42
26 Trueb, L. and Cloutier, R. (1991) A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). In *Origins of the Higher Groups of Tetrapods – Controversy and Consensus* (Schultze, H-P. and Trueb, L., eds), pp. 223–313, Cornell University Press
27 Gauthier, J. *et al.* (1988) The early evolution of the Amniota. In *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds* (Benton, M.J., ed.), pp. 103–155, Clarendon Press
28 Ahlberg, P.E. and Milner, A.R. (1994) The origin and early diversification of tetrapods. *Nature* 368, 507–514
29 Carroll, R.L. (1995) Problems of the phylogenetic analysis of Paleozoic choanates. *Bull. Mus. Natl. Hist. Nat. Paris, 4è Sér.* 17, 389–445
30 Ahlberg, P.E. and Clack, J.A. (1998) Lower jaws, lower tetrapods – a review based on the Devonian genus *Acanthostega. Trans. R. Soc. Edinb.* 89, 11–46
31 Smithson, T.R. (1989) The earliest known reptile. *Nature* 342, 676–678
32 Clack, J.A. (1998) A new Early Carboniferous tetrapod with a mélange of crown-group characters. *Nature* 394, 66–69
33 Paton, R.L. *et al.* (1999) An amniote-like skeleton from the Early Carboniferous of Scotland. *Nature* 398, 508–513
34 de Queiroz, K. and Gauthier, J. (1990) Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Syst. Zool.* 39, 307–322
35 Jarvik, E. (1980) *Basic Structure and Evolution of Vertebrates*, Academic Press