A few decades ago, Devonian stegocephalians (Boxes 1 and 2) were known from only two taxa from East Greenland: *Ichthyostega* and *Acanthostega*. 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', revealed that many of these taxa (*Metaxygnathus*, *Obruchevichthys*, *Elginerpeton* and *Ventastega*) are more closely related to tetrapods than to panderichthyids. 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'. 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). 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' (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).

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), radius, ulna, ulnare, intermedium (the homology of the last two elements is not well established) and a...
few other (generally four) smaller radial elements (Fig. 3a). The radius, ulnae 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 carpals (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 bases, meta- and acro-physees), before the autopod skeleton became individualized as discrete bones. 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 rhipidistian fin bears two more similarities with an autopod (Fig. 3b): the rays are segmented, similar to the metacarpals and phalanges of digits, and most of them (six out of eight) articulate proximally

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 Linnaean systematic.

- **Amniota**: the last common ancestor of mammals and reptiles, and all its descendants.
- **Amphibia**: extant taspids and all extinct taspids that are more closely related to amniotes than to amphibians.
- **Anthracosauria**: amniotes and all other extinct synapsids that are more closely related to amniotes than to amphibians.
- **Lissamphibia**: the last common ancestor of Gymnophiones, Caudata, and Anura, and all its descendants.
- **Stegocephali**: all choanates that are more closely related to Temnospondyli than to gymnophiones, caudata, and anura, and all its descendants.
- **Tetrapoda**: the last common ancestor of amniotes and taspids, and all its descendants.

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 amnio, a pouch in which the embryo develops.
- **Autopod**: the third segment of the paired limb (in the proximodistal direction), which includes the hand 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.
- **Carophalangeal**: a bone or cartilaginous element of the branchial skeleton; in primitive 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**: characteristics of a taxon that is advantageous and functional in its present environment, but that initially performed a different function, often in another environment.
- **Lepidoptichia**: dermal fin rays consist of modified scales; they stiffen the fins of most actinopterygians and many primitive aquatic sarcopterygians.
- **Lissamphibia**: a clade that includes all extant amphibians (frogs, toads, salamanders, newts and caudata), but none of the currently known Paleozoic amphibians.
- **Metacarpal**: a bony element of the hand located between the carpus (wrist) and the phalanges (fingers).
- **Osteolepiforme**: a paraphyletic group of aquatic animals (all of which have paired fins) that includes more or less distant relatives of taspids.
- **Radial**: the endoskeletal element bony or cartilaginous supporting a fin.
- **Stegoschophallus**: a clade that includes all vertebrates that possess digits, and a few extinct, closely related forms that might represent paired fins; they are represented by taspids in the extant fauna, but they also include several other extinct groups.
- **Zeugopod**: the second segment of the paired limb (in the proximodistal 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.).

---

**PERSPECTIVES**

![Phylogeny of Devonian and Lower Carboniferous stegocephalians](image)

---

**TREE vol. 15, no. 3 March 2000**

119
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. 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*) are expressed during limb development. 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. *HoxD* clusters 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. This second expression phase corresponds closely to the bent pattern of prechondrogenic condensations of the digital arch (Figs 5d and e). This bend of *HoxD* expression is absent in zebrafish fin bud development. This pattern suggests that the extremity of the autopod (the digits) is located at the postero-distal 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 (Figs 5e and f). 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 is not definitively ruled out. 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 sarcopterygian *Sauripterus* has putative phalanges and lepidotrichia, which are continuous with each other (Fig. 3b), 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 (*Takifugu rubripes*), another teleost, does not possess a *HoxD* gene.
cluster, whereas it does possess rather normal fins; 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 HoxD11-13 in the zebrafish is simply an autopomorphy. If so, it cannot be used to recognize the region of the tetrapod limb that corresponds to the proximal 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 actinopterygian fin is thought to correspond to the metapterygial axis of the tribasal fin to correspond to the metapterygial axis of the tetrapod limb that corresponds to the metapterygial axis of the fin in zebrafish. The major appendicular axis of the tetrapod limb that corresponds to the metapterygial axis is nearly complete autopods are polydactyl (and 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\(^{11,12}\). The fact that these three oldest known autopods are polydactyl (and the fact that they belong to the three most basal and earliest post-Devonian stegocephalians) 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\(^{14,15}\). 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\(^ {16} \). However, the recent discovery of grooved ceratobranchials, which might have supported afferent branchial arteries\(^ {17} \), and of a post-brachial 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 adaptation to the terrestrial environment.

The first autopod: how many digits?

Recent palaeontological 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\(^ {11,12}\). The fact that these three oldest known autopods are polydactyl (and the fact that they belong to the three most basal and earliest post-Devonian stegocephalians) 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\(^ {14,15}\). 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\(^ {16} \). However, the recent discovery of grooved ceratobranchials, which might have supported afferent branchial arteries\(^ {17} \), and of a post-brachial 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 adaptation to the terrestrial environment.
PERSPECTIVES

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 amphibians23, 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 environments24. 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 relatives26, whereas others considered only amniotes and their extinct presumed relatives27. Finally, some analyses sampled only Devonian and Early Carboniferous taxa, whose affinities with extant tetrapods (lissamphibians and amniotes) are currently controversial28. 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 given29. Therefore, the first rigorous tests of the traditional phylogeny were performed only a few years ago30,31.

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 differed 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 reptile32 (= amniote). This discovery was thought to extend the fossil record of amniotes from the mid-Upper Carboniferous (Viséan) 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 anthracosaur33 (Box 1). However, the affinities of this taxon are still debated and a recent study has even suggested that it might be a stem-tetrapod34 (Fig. 2b).
Another enigmatic Lower Carboniferous taxon (Eocriodus) exhibits a mixture of derived states shared with baphetids and a clade composed of embolomeres and related taxa. It was placed in Bapheti- dae, even though this is only one of two equally parsimonious solutions (the two solutions are compatible with the pos- itive correlation between baphetids, temno- spondyls and other stegocephalians that are unresolved in a strict consensus of the relationships between baphetids, temnospondyls (two groups previously marked by E.2 in Fig. 2a). The relationships between baphetids, temno- spondyls and other stegocephalians are unresolved in a strict consensus of the two most parsimonious trees, and this might result from the strange mix of char- acter states found in Eocriodus.

Another recent discovery is an early Carboniferous stegocephalian (Casineria) with the oldest known pentadactyl hand. The strong ossification of the skeleton, and the right angle between the proximal and distal humeral heads suggest a relatively terrestrial lifestyle. A phylogenetic analy- sis suggests that this animal is an anther- cosaur, however, the claim that this analy- sis shows Casineria to be an amniote 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 requir- ing a single extra step (over 100), raises doubts about these interpretations.

Prospects
More detailed anatomical studies and more phylogenetic analyses will be re- quired to evaluate the evolutionary signifi- cance of all the newly discovered Upper Devonian and Lower Carboniferous stego- cephalians. The inclusion of lissamphib- ians in more phylogenetic analyses will be especially important.

Many paleontologists marvel at the discovery of new, early potential relatives of amniotes but the fact that many recent phylogenetic analyses indicate that lepospondyls and temnospondyls (two groups previously thought to be related to lissamphibians) do not form a clad (unless amniotes are also included) has not generated enough interest. This is one of the most surpris- ing new discoveries, and finding which of these two groups (lepospondyls or temnospondyls) is actually related to lissamphibians will be necessary to im- prove our understanding of early tetra- pod phylogeny.

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