The Greatest Step in Vertebrate History: A Paleobiological Review of the Fish-Tetrapod Transition*

John A. Long[1],[†]
Malcolm S. Gordon[2]
[1]Museum Victoria, Melbourne, Victoria 3001, Australia;
[2]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California 90095

ABSTRACT

Recent discoveries of previously unknown fossil forms have dramatically transformed understanding of many aspects of the fish-tetrapod transition. Newer paleobiological approaches have also contributed to changed views of which animals were involved and when, where, and how the transition occurred. This review summarizes major advances made and reevaluates alternative interpretations of important parts of the evidence. We begin with general issues and concepts, including limitations of the Paleozoic fossil record. We summarize important features of paleoclimates, paleoenvironments, paleobiogeography, and taphonomy. We then review the history of Devonian tetrapods and their closest stem group ancestors within the sarcopterygian fishes. It is now widely accepted that the first tetrapods arose from advanced tetrapodomorph stock (the elpistostegalids) in the Late Devonian, probably in Euramerica. However, truly terrestrial forms did not emerge until much later, in geographically far-flung regions, in the Lower Carboniferous. The complete transition occurred over about 25 million years; definitive emergences onto land took place during the most recent 5 million years. The sequence of character acquisition during the transition can be seen as a five-step process involving: (1) higher osteichthyan (tetrapodomorph) diversification in the Middle Devonian (beginning about 380 million years ago [mya]), (2) the emergence of "prototetrapods" (e.g., *Elginerpeton*) in the Frasnian stage (about 372 mya), (3) the appearance of aquatic tetrapods (e.g., *Acanthostega*) sometime in the early to mid-Famennian (about 360 mya), (4) the appearance of "eutetrapods" (e.g., *Tulerpeton*) at the very end of the Devonian period (about 358 mya), and (5) the first truly terrestrial tetrapods (e.g., *Pederpes*) in the Lower Carboniferous (about 340 mya). We discuss each of these steps with respect to inferred functional utility of acquired character sets. Dissociated heterochrony is seen as the most likely process for the evolutionarily rapid morphological transformations required. Developmental biological processes, including paedomorphosis, played important roles. We conclude with a discussion of phylogenetic interpretations of the evidence.

Introduction

The fish-tetrapod transition was one of the greatest events in vertebrate evolution. For many years, the hard fossil evidence showing the stages in this event was scarce. Recent discoveries are beginning to fill in major gaps in the record. Tetrapods (vertebrates having paired arms and legs with digits) first appeared in the Late Devonian about 360 million years ago (mya), but these appear to have been primarily aquatic animals (Clack 2002*c*). The first truly terrestrial form known is now recognized as *Pederpes finneyae* from the basal Carboniferous of Scotland (Clack 2002*b*).

Over the past 25 years, new discoveries have increased the number of known Devonian fossil tetrapod taxa from two (1932–1977) to 10 (1977–2003), plus three elpistostegalid fishes (Fig. 1). Elpistostegalids are now accepted as the sister group to tetrapods. This article summarizes Devonian tetrapod evolution. It discusses the major steps that occurred in the transition from fully aquatic fishes to land-living tetrapods. The paleontological data are primary, but they must be considered in context with information about paleoclimates, paleoenvironments, paleobiogeography, and taphonomy. They also have important implications with respect to implied functional morphology, physiology, behavior, and ecology. This discussion partly parallels the detailed considerations of this subject area given by Janvier (1996) and Clack (2002*c*), but it also extends, updates, and complements those accounts in many ways.

The improved knowledge of the actual events of the distant past makes clear that studies of the approximately 100 living species of amphibious fishes are at best indirectly relevant to understanding tetrapod origins. The possible analogic relevance of these fishes, all phylogenetically unrelated to the putative
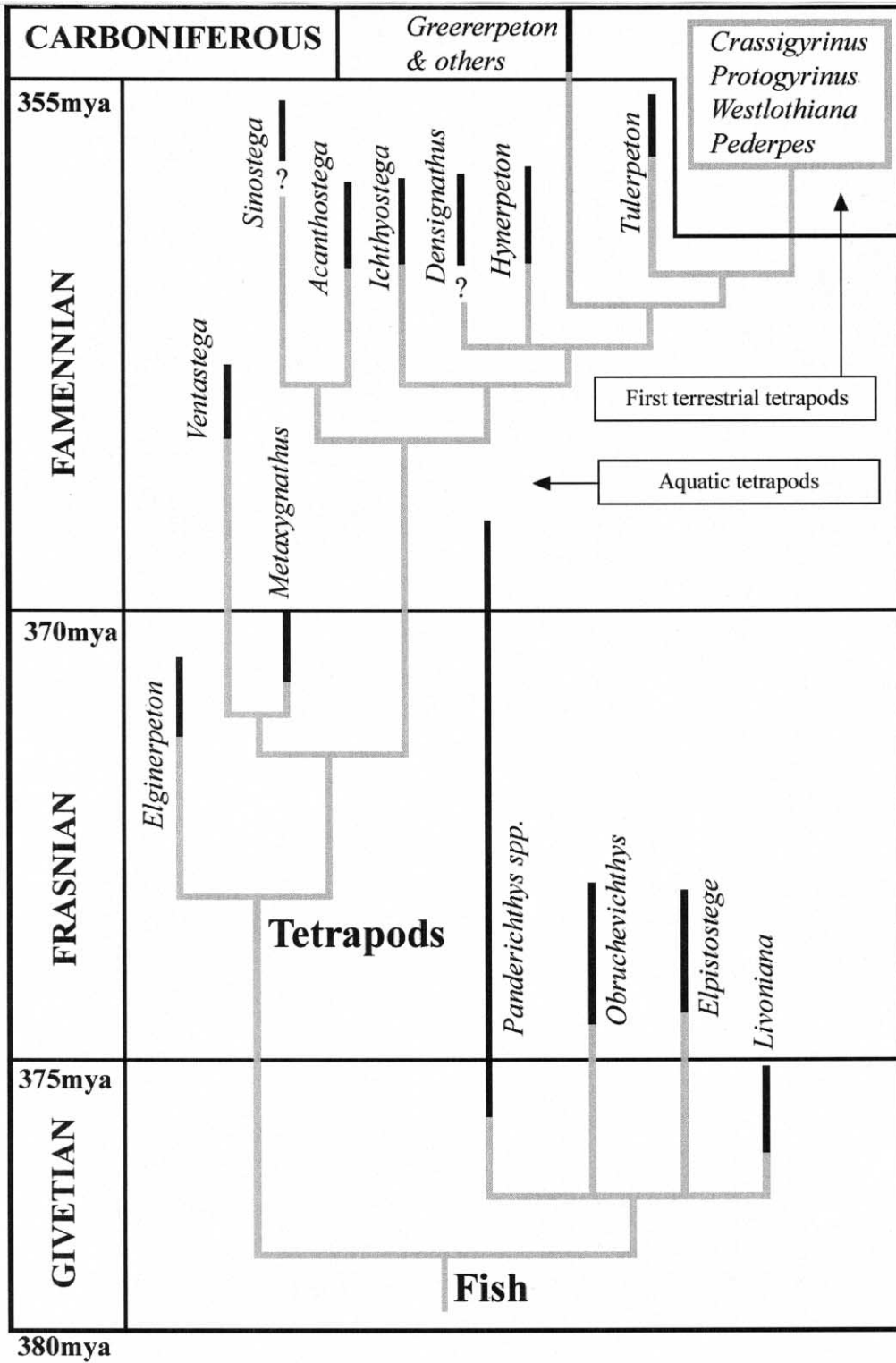
Figure 1. Interrelationships and stratigraphical appearances of the earliest tetrapods and their sister taxon, the elpistostegalid fishes (cladogram after Lebedev and Coates 1995).

Table 1: Overview of evidence and inferences from the fossil record relevant to the major functional changes involved in the evolutionary transition from fishes to terrestrial tetrapods

Functional Changes[a]	Sarcopterygian Fishes	Prototetrapods	Aquatic Tetrapods	True Tetrapods	Terrestrial Tetrapods
A	Water/fins	Water/limbs	Water/limbs, digits	Water and land/ limbs, digits	Land/limbs, digits
B	Swimming	Swimming; paddling	Swimming; paddling; walking	Swimming; paddling; walking	Paddling; walking
C	Gills (1); lungs (2)	Gills (1); lungs (2)	Gills; lungs; skin	Gills; lungs; skin	Lungs; skin
D	Gills; bp(?)	Gills; bp(?)	Gills; bp(?)	Gills; bp(?); lungs	bp(?); lungs; skin
E	Lateral line/aquatic	Lateral line/aquatic	Lateral line/aquatic	Lateral line/aquatic; aerial	Hearing(?)/aerial
F	Suction feeding(?)	Suction feeding(?)	Suction feeding(?)	Suction feeding(?); biting	Biting
G	Larvae	Larvae(?)	Larvae(?)	Larvae(?)	Metamorphosis

Note. See text for definitions and details; (?) = speculative but possible by analogy with living forms.

[a] Functional changes: A = mechanical support/environment/structures; B = probable biomechanics of locomotion; C = respiratory structures (1 = primary, 2 = secondary); D = water balance/osmoregulation: organs (bp = buccopharyngeal membranes); E = sensory systems: cutaneous mechanoreceptors/ visual environments; F = probable prey-capture and feeding mechanisms; G = probable mode of reproduction.

tetrapodomorph Devonian fishes, has been a source of interest in the living forms on the part of many neontologists for many years (Gordon and Olson 1995; Graham 1997; Gordon 1999). The living fishes remain of intrinsic evolutionary, biochemical, physiological, functional morphological, behavioral, and ecological interest in their own right. However, as Graham and Lee (2004) note elsewhere in this issue, they are probably evolutionary dead ends.

General Considerations

There are six central questions one must ask relating to the evolutionary development of the tetrapods. (1) Which groups of sarcopterygian fishes were actually basal to the tetrapods? (2) What sequences of morphological and functional changes actually occurred during the transitions from fishes to tetrapods? (3) When did these transitions occur? (4) Where did they occur? (5) What were the factors that drove or facilitated these transitions? (6) How did these transitions occur?

Answers to these questions must be viewed as, at best, working hypotheses. The reasons apply broadly to the fossil record in general (Donovan and Paul 1998; Erwin and Wing 2000; Kidwell and Holland 2002), but they are intensified by the specific conditions associated with tetrapod origins. The actual events occurred a long time ago (380–355 million years). The fossil record of the organisms that may have been involved remains small, and most of the fossils are fragmentary. The known fossils derive from geographically widely scattered regions, although most of the significant taxa come from the Euramerican Province of Young (1981). Details of precise biostratigraphic position for some of the Late Devonian occurrences (which forms preceded or were contemporary with other forms) are not well defined. Finally, the specific phylogenetic relationships within putative early lineages also remain open to debate.

Overview of the Transitions

A concise overview of current knowledge of fish-tetrapod transitions may assist in following a complex narrative (Table 1). Five major groups of animals were involved: sarcopterygian fishes, prototetrapods, aquatic tetrapods, true tetrapods (eutetrapods), and terrestrial tetrapods. The evolutionary changes that occurred in these organisms involved a wide array of changes in both morphology and function. The fossils provide only minimal circumstantial evidence relating to aspects of biochemistry and severely limited, but significant, direct evidence relating to morphology, functional morphology, physiology, behavior, and ecology. Useful inferences concerning functional changes that occurred can be made with respect to at least seven important areas: mechanical support, biomechanics of locomotion, respiration, water balance and osmoregulation, sensory systems, prey capture and feeding, and reproduction. The bulk of this article presents detailed discussions of both the five groups of animals and the seven areas of functional change. The information presented provides state-of-the-art answers to five of the six central questions about the evolutionary development of the tetrapods. It also provides some circumstantial evidence relating to the sixth question.

The least well-answered question is number 5: What were the factors that drove or facilitated the transitions? Specific answers to this question may never be possible, but an envelope of possible answers is definable. There necessarily must have

been two broad categories of factors: what may be termed "evolutionary pushes" and "evolutionary pulls."

Evolutionary pushes were presumably less than optimal abiotic and biotic factors and conditions in the aquatic environments occupied by the basal sarcopterygians. These factors and conditions must also have persisted for evolutionarily significant periods of time—periods sufficient to permit selection for successor animals that both better resisted the suboptimal circumstances and had the ability to evade those circumstances to increasing extents.

Once the pushes had initiated the processes of evolutionary change, it seems probable that the newly evolved forms began to enter and to exploit a wider range of environments and habitats in shallow water and littoral situations. The evolutionary pulls then came into play: niches and habitats empty of vertebrates, with abiotic conditions and food resources favorable to continuing selection for animals capable of emerging from the water and, eventually, becoming fully terrestrial.

Sayer and Davenport (1991) discussed these issues with respect to the living amphibious fishes and why they leave the water. Conditions during the later Devonian were substantially different in many ways from those existing today, but the general circumstances seem largely parallel. Environmental hypoxia, aquatic predators and competitors, waterborne diseases, and parasites all could have been Devonian pushes. Higher environmental oxygen partial pressures, absence of vertebrate predators and competitors, lack of diseases and parasites, and abundant unexploited plant and invertebrate food supplies could have been Devonian pulls.

Paleoclimates, Paleoenvironments, Paleobiogeography, Global Events, and Taphonomy

When Late Devonian tetrapods first appeared, the global mean temperature was around 20°C, significantly warmer than today. Most of the known tetrapod occurrences during that period are situated within the arid tropical zones identified by Scotese et al. (1999). Contemporaneous with some of the major events in tetrapod evolution that occurred during the Famennian stage the earth underwent a series of mass extinction episodes collectively called the "Kellwasser events" (363.5–365 mya). Two hypotheses have been put forward to account for these extinctions, either global cooling or oceanic anoxia, and perhaps both. Up to 90% of the known phytoplankton in the world oceans died out, and reefs shrank in area by a factor of 5,000. Such massive biotic events must also have affected local ecologies at the time of tetrapod evolution. If global cooling were the culprit, then this would have had a profound affect on the terrestrial biota as well as on shallow marine ecosystems.

Late Devonian tetrapod fossils from East Greenland have come from two geological units within the Celsius Bjerg Group: the lowermost unit is the Aina Dal Formation, comprising 80 m of red coarse- to medium-grained sandstones, containing *Ichthyostega* remains. Above this unit is the Wimans Bjerg Formation, comprising nearly 200 m of unfossiliferous gray siltstones. The thick Britta Dal Formation is next, with 550 m of red and gray siltstones and some red sandstones, containing both *Ichthyostega* and *Acanthostega* (Clack 1988a, 1988b; Olsen and Larsen 1993). This unit has been interpreted as dominantly fluviatile and floodplain sediments (Nicholson and Friend 1976). The taphonomy of these sites strongly suggests that *Ichthyostega* and *Acanthostega* inhabited the sedimentary basins in which they were buried and dwelled within large freshwater river systems.

Many of the other known Devonian tetrapods also come from similar "red bed" fluviatile deposits (e.g., *Elginerpeton*, *Ventastega*, *Metaxygnathus*, *Hynerpeton*, *Densignathus*). Taphonomically, these forms are all represented by isolated fragments or occasional whole bones but without definite association. They are all interpreted by their describers as autochthonous within the depositional basins in which they are preserved. A reasonable generalization is that they most likely inhabited large freshwater river and lake systems, environments similar to those inhabited by the East Greenland forms. The Baltic sites also may be regarded as deltaic to shallow marine (Ahlberg 1998).

The geological and taphonomic evidence therefore leads to a consensus view that all known Devonian tetrapods were inhabitants of freshwater ecosystems in high latitude tropical to arid climate zones. We note, however, that this inference is not universally accepted. Schultze (1999, p. 388) states: "The tetrapods entered the terrestrial realm through the intertidal and supratidal zones." Schultze's statement is partly based on his different interpretations of parts of the stratigraphic, lithologic, and taphonomic evidence and on his interpretation of some anatomical convergences between Devonian elpistostegalid fishes and living mudskipper fishes (Schultze 1999, pp. 379–380). To date, Schultze has not specified which of the multiple, available intertidal habitats the early tetrapods might have preferred. Graham and Lee (2004) further discuss this possibility.

The age of the East Greenland sites has been placed as mid–late Famennian, with tetrapods occurring in the Lower Series as well as the Upper Series. The thick nature of the succession means that only relative biostratigraphic criteria (on the basis of the established sequence of placoderm fishes) can be used here for correlations to other Euramerican basins. Thus the occurrence of the placoderms *Phyllolepis* and *Remigolepis* with the earliest stratigraphic occurrence of tetrapods places the first appearance of *Ichthyostega* and *Acanthostega* at some time between 358 and 360 mya.

Only one Devonian tetrapod, *Tulerpeton curtum*, has been found in a definite marine deposit, but closer examination of the taphonomy indicates that it may not necessarily have been a marine-dwelling creature. Apart from the holotype of *T. curtum*, fossil bones from the Andreyevka site in Russia are well preserved, unworn, and mostly disarticulated. The environment

has been interpreted as a quiet shallow basin, with warm marine to brackish water, containing a high percentage of dissolved carbonates and clay particles (Lebedev and Clack 1993). Lebedev and Coates (1995) state that the transportation of bones into the basin appears to have been minimal. They suggested that the missing parts of the carcass resulted from postmortem disruption by bacterial action and decay gases rather than by scavenging.

There is, however, at least one other possible interpretation. A common taphonomic occurrence for ichthyosaurs is that the carcasses float, and then the skull or limbs are the first parts of the skeleton to fall off the floating decomposing carcass (Wade 1984; Martill 1986, 1993). It seems therefore possible that the remains of *Tulerpeton* were washed into the basin as a floating carcass and that the limbs simply dropped off the floating carcass. A similar taphonomic scenario can be invoked in the Late Devonian Gogo Formation of Western Australia, where fish fossils are preserved either as complete individuals or as parts that have fallen off decomposing floating carcasses (Long 1991). Thus there is no definitive evidence, either geological or taphonomic, to indicate that *Tulerpeton* in life was necessarily a marine-dwelling amphibian.

The putative ancestors of the earliest tetrapods are the elpistostegalid fishes (Epistostegalia = Panderichthyida). These forms occur in good marine deposits as articulated complete fishes (e.g., *Panderichthys rhombolepis*, from the Lode site, Latvia; Vorobyeva 1980). Vorobyeva and Kuznetsov (1992) have suggested that *Panderichthys* may have been capable of primitive land locomotion, similar to the living catfish *Clarias*. The closest prototetrapods to these fishes are the Elginerpetonidae, from the Scat Craig deposits of Scotland, which Ahlberg (1998) regarded as a river deposit.

The transition from marine to freshwater habitats in lungfishes coincided with the origin of air gulping, as evidenced by the development of cranial ribs (Long 1990). Note also that the invasion of freshwater habitats from the marine environments of the elpistostegalid fishes was coincident with the origin of the first tetrapods. The first prototetrapod, *Elginerpeton*, is late Frasnian in age and was found within the Euramerican Province, although the contemporaneous *Metaxygnathus* from Australia is seen to be the sister taxon to more advanced aquatic tetrapods. Such a widespread global distribution would attest to the fact that stem group tetrapods had radiated before the onset of the Kellwasser events.

The geographic radiation of the first aquatic tetrapods (*Ichthyostega, Acanthostega, Ventustega, Sinostega, Hynerpeton, Densignathus*) took place immediately after the Kellwasser events. This radiation therefore may be causally related to global cooling. Perhaps the cooling freed up niches not previously available, or, alternatively, perhaps preadapted partially terrestrial animals were better able to cope with cooler aquatic conditions.

A Chronology of Devonian Tetrapod Discoveries and Their Significance

The historical sequence of the discoveries of fossils of putative tetrapod progenitors and of the various early tetrapods themselves has played an important role in the development of hypotheses relating to how the transition occurred. Unsurprisingly, hypotheses have evolved as new evidence became available.

The first Late Devonian tetrapods were found in 1929 in rocks dating from the upper Famennian stage of East Greenland (on the north slope of Celsius Berg) by O. Kulling of Sweden. His specimens were recognized by Erik Stensiö as scales of a fishlike vertebrate of uncertain affinities (Jarvik 1996). Stensiö recommended that a young student, Gunnar Save-Söderbergh, go on a second Kulling expedition in 1930 to search for more vertebrate fossils. On that trip, Save-Söderbergh collected the first good skulls and other remains of Devonian tetrapods, which he named as two genera, *Ichthyostega* and *Ichthyostegopsis* (Save-Söderbergh 1932). In 1932, Erik Jarvik accompanied Save-Söderbergh on another trip to Greenland to collect more Devonian tetrapod material. Their finds included a skull of a different form, which would later be named *Acanthostega* (Jarvik 1952). Save-Söderbergh continued collecting from East Greenland over several additional years, amassing many more specimens of these early tetrapods, but nothing more was published on them until after his death in 1948. Jarvik (1952) redescribed parts of the pelvic girdle, tail, and postsacral ribs of *Acanthostega*. The genus *Ichthyostegopsis*, based on only one specimen, might be an aberrant specimen of *Ichthyostega* (Jarvik 1996). For the first three-quarters of the twentieth century, these were our only specimens of Devonian tetrapods, and only parts of their anatomy had been briefly described. Much of the work was ongoing by Jarvik and would not be published until near the end of the century (Jarvik 1996).

Both *Ichthyostega* and *Acanthostega* were recognized as tetrapods with well-developed limbs and digits, but they still retained many primitive fishlike characteristics, such as fin rays on the tail and deeply excavated lateral line canal grooves (Jarvik 1952). The location of these finds in East Greenland, in strata then considered to be largely fluvial, pointed at the Northern Hemisphere landmass of Euramerica as the most likely center of origin for the first tetrapods.

Since Jarvik's (1942) monograph on the snout of porolepiform and osteolepiform fishes, he has championed the view that tetrapods had a diphyletic origin, with Osteolepiformes giving rise to the mainstream of primitive labyrinthodonts (and the line leading to the reptiles), while Porolepiformes were regarded as the ancestors of the Urodeles. This view has been strongly criticized by many other workers, all of whom support the concept of tetrapod monophyly (Gaffney 1979; Rosen et al. 1981; Panchen and Smithson 1987). In view of the recent flood of new fossil evidence showing the nature of the

elpistostegalid-ichthyostegalid transition, most paleontologists no longer accept the diphyletic view.

Warren and Wakefield (1972) published an account of the first Devonian tetrapod trackway in the Southern Hemisphere. The sections of trackway came from the Late Devonian (Famennian) outcrops on the Genoa River in eastern Victoria, Australia, demonstrating the existence of early tetrapods in Gondwana at approximately the same time as the East Greenland species (although the precise stratigraphic age of the Genoa River Beds was not then known). These trackways showed the presence of six-digit prints, questioning the pentadactyl pattern previously accepted for all tetrapod hands and feet (and then not known for *Acanthostega* and *Ichthyostega*).

Further support for an alternative biogeographic model, a Gondwana origin for tetrapods, came shortly afterward when Campbell and Bell (1977) described the lower jaw of the amphibian *Metaxygnathus* from the Cloughnan Shale of New South Wales. This was the first record of a Devonian tetrapod jaw from Australia. The age was initially thought to be lower Famennian but was later referred by Young (1999) to an older late Frasnian age.

Jarvik (1980) presented the first major review of the anatomy of *Ichthyostega* in his book. Leonardi (1983) described what was thought to be a six-digit Late Devonian tetrapod footprint from Brazil, which he named *Notopus*.

Lebedev (1984) first described *Tulerpeton*, from the Late Devonian (late Famennian) Andreyevka site in Russia. This form had six fingers on the hand, as shown by skeletal remains, and was suggested as living in a shallow marine environment. Shortly after, Schultze and Arsenault (1985) redescribed the "prototetrapod" *Elpistostege* (Westoll 1938) as an advanced sarcopterygian fish in the family Elpistostegalidae and demonstrated its close similarity to early tetrapods. In the same article, they dismissed the Australian form *Metaxygnathus* as an amphibian jaw, suggesting it was piscine. A subsequent study of the Genoa River jaw by Clack (1988a) confirmed that it was indeed a true tetrapod.

In 1987, a joint expedition comprising members from Cambridge University (including Jennifer Clack and Per Ahlberg) and the Danish Geological Survey revisited sites in East Greenland where, in 1968–1970, P. Friend had collected tetrapod remains. They made many significant discoveries, which over the course of the next 15 years shed much new light on the anatomy and functional morphology of the first primitive tetrapods.

Clack (1988a) also described some new material of the skull of *Acanthostega* from East Greenland on the basis of the new expedition and postulated that a large, ornamented interclavicle is a good synapomorphy for all tetrapods. Later that year, Clack (1988b) published a preliminary account of other new discoveries of East Greenland tetrapods from the expedition. The first of several articles highlighting new anatomical discoveries in the East Greenland material was by Clack (1989), who described the earliest tetrapod stapes in *Acanthostega*. It indicated that the temporal notch of *Acanthostega* supported a spiracular opening, not a tympanum. Clack also stated that the stapes apparently controlled palatal and spiracular movements for aquatic respiration.

Long (1990) proposed that heterochrony was the most likely mechanism for the origin of tetrapods from advanced osteolepiform stock because the juveniles of such fishes (on the basis of *Eusthenopteron*; Schultze 1984) shared more features in common than did the adults with basal tetrapods like *Crassigyrinus*. This article also again supported a possible Gondwana origin for the first tetrapods.

Throughout the 1990s, work on early tetrapods reported several new records of both Devonian tetrapods and new elpistostegalid fishes, turning the biogeographical hypothesis for the place of origin of the first tetrapods from Gondwana back to Euramerica. It is not established that these two possibilities are necessarily mutually exclusive.

Coates and Clack (1990) reported the presence of polydactylous digits in *Ichthyostega* and *Acanthostega*, and Coates and Clack (1991) revealed that *Acanthostega* breathed through fish-like gills.

Rogers (1990) described possible tetrapod tracks in the Devonian of northeastern Scotland. These occur with wide arthropod tracks and other burrows.

Ahlberg (1991b) described some "near tetrapod" remains from Scat Craig beds in Scotland of late Frasnian age. These isolated bones included the tibia, humerus, and a lower jaw fragment and were significant in being much older than any previous tetrapod finds.

Lebedev and Clack (1993) described isolated tetrapod bones from Andreyevka, USSR (late Famennian). Such articles highlighted the fact that tetrapods were both widespread and diverse by the end of the Devonian period and suggested that some may have inhabited wholly marine environments.

Ahlberg et al. (1994) described a new Late Devonian tetrapod, *Ventastega curonica*, from the Upper Famennian Ketleri Formation of Latvia. It was concluded to be of a similar grade of organization as the East Greenland forms.

Clack (1994b) gave preliminary descriptions of the snout, palate, and ventral parts of the braincase of *Acanthostega gunnari* from East Greenland. Clack (1994a) then described the earliest known tetrapod braincase, and building on her earlier work (Clack 1989) on the stapes, proposed that the stapes of *Acanthostega* was not a mobile element but attached to part of the braincase with a foot plate. The stapes in *Acanthostega* incorporated both proximal heads of the ancestral sarcopterygian hyomandibular.

Daeschler et al. (1994) published the first description of a Devonian tetrapod from North America, *Hynerpeton bassetti*, on the basis of a left cleithrum and scapulocoracoid.

Gordon and Olson (1995) critically evaluated the fossil evidence and biological constraints of the terrestrial invasions of

animals and plants. With respect to the invasion of land by tetrapods, they concluded that "there are few logically justified constraints for limiting hypotheses concerning the specific properties of the earliest stages of the evolution of terrestrial vertebrates" (Gordon and Olson 1995, p. 264), suggesting that the origins of tetrapods could have taken place more than once.

Ahlberg (1995) described additional new material from Scat Craig and named this early tetrapod *Elginerpeton pancheni*. It is the earliest known tetrapod. The isolated premaxilla and fragmentary lower jaws with slender features enabled a preliminary reconstruction of the head. It has broad exposure of the Meckelian cavity on the lower jaw.

Lebedev and Coates (1995) redescribed *Tulerpeton curtum*, clearly restoring the anatomy of six-fingered hands and six-toed feet. The hand is elongated and showed aquatic adaptations for swimming rather than land walking. The hind limb has a strong, stout femur, and the foot also has a broad, splayed shape, both interpreted as primarily adaptations for swimming.

Stössel (1995) described a tetrapod trackway from the Devonian of southwest Ireland. Pressure solution had distorted and obscured the details of the individual tracks.

Coates and Clack (1995) published the first complete skeletal reconstructions of *Ichthyostega* and *Acanthostega*. Clack and Coates (1995) argued for the first time that *Acanthostega* was a primitive aquatic tetrapod, not adapted for life on land. Furthermore, they concluded that "acquisition of tetrapod-like characters may exhibit mosaic evolution comparable to that evident during the transition from mammal-like reptiles to mammals" (p. 370). Some parts of the stem tetrapod skeleton were clearly more advanced than similar areas in elpistostegalid fishes but not necessarily an advance toward terrestrial locomotion. They pointed out the inadequacy of using digits as the prime skeletal character to define tetrapods and suggested that the pelvic plate may be of greater importance in defining the group.

Ahlberg et al. (1996) showed that evolution of the braincase occurred rapidly in the transition between *Panderichthys* and the earliest tetrapods, resulting in a tetrapod-like skull but still retaining a sarcopterygian-type hinged braincase.

Jarvik (1996) published a monograph on *Ichthyostega* that gave a new reconstruction of the skull and described the skeletal anatomy in detail. He suggested that vascularization of the ribs could have indicated that *Ichthyostega* used skin breathing and thus was partially terrestrial in its lifestyle.

Coates (1996) described the postcranial anatomy of *A. gunnari* in detail and formulated a strong hypothesis of basal tetrapod interrelationships on the basis of analysis of 76 morphological (skeletal) characters within 16 taxa of primitive tetrapods and two sarcopterygian fishes.

Clack (1997) reviewed all the known Devonian tetrapods and trackways and concluded that on face value there was little evidence for the existence of any terrestrial locomotion but that they were all probably fully aquatic animals.

Clack (1998a) described the braincase of *Acanthostega* in detail and made comments about the early evolution of tetrapod audition.

Ahlberg (1998) described the postcranial elements of *Elginerpeton* in detail and hypothesized about its possible aquatic lifestyle.

Daeschler and Shubin (1998) published a note showing the "eight-fingered" precursor to the "hand" of tetrapods in the preaxial radials of the rhizodontiform fish *Sauripterus*. Ahlberg and Clack (1998) presented a major review of lower jaws of all known basal tetrapods and described the lower jaw of *Acanthostega* in detail for the first time.

Daeschler (2000) described early tetrapod jaws from the Late Devonian of Pennsylvania. Two genera were recognized: *Densignathus rowei*, identified from a well-preserved jaw, and *Hynerpeton bassetti*, identified from a partial jaw. Ahlberg et al. (2000) described another new Devonian elpistostegalid fish from Latvia, *Livoniana multidentata*, a sister taxon to *Elpistostege*.

Clack (2002c) gave a detailed overview of the problem of early tetrapod evolution in her book and later (Clack 2002b) published an article on *Pederpes finneyae*, a Lower Carboniferous primitive tetrapod, the first known form that was a true land walker.

An abstract by Ahlberg et al. (2002) revealed that a CT scan of the braincase of *Ichthyostega* shows it has a specialized ear anatomy. The stapes has plates fixed at both ends that attach to the braincase.

Zhu et al. (2002) published a report on the discovery of a Devonian tetrapod jaw from Ningxia Autonomous Region, China, named *Sinostega pani*. This specimen indicated that tetrapods had achieved an almost global distribution by the end of the Devonian period. A large overview of the phylogenetic origin and interrelationships of the first tetrapods was recently published by Ruta et al. (2003).

A fragment of Devonian tetrapod jaw closely approaching *Ichthyostega* was recently reported by Clement et al. (2004) from the late Famennian of Belgium. Shubin et al. (2004) described an early humerus from the Famennian Red Hill Locality in the United States, which showed an intermediate morphology between elpistostegalid fishes and *Acanthostega*.

Anatomical Stages in the Fish-Tetrapod Transition

This section looks at the chronological order in which tetrapod characters or character complexes appear to have evolved. The order is based on their first, stratigraphically controlled occurrences in the sarcopterygian fishes. We also discuss morphofunctional concepts relevant for each step of the transition. The starting point for this series is the appearance of osteichthyan fishes at the end of the Silurian period, some 420 mya. The major stages, from a fully aquatic fish to a terrestrial tetrapod,
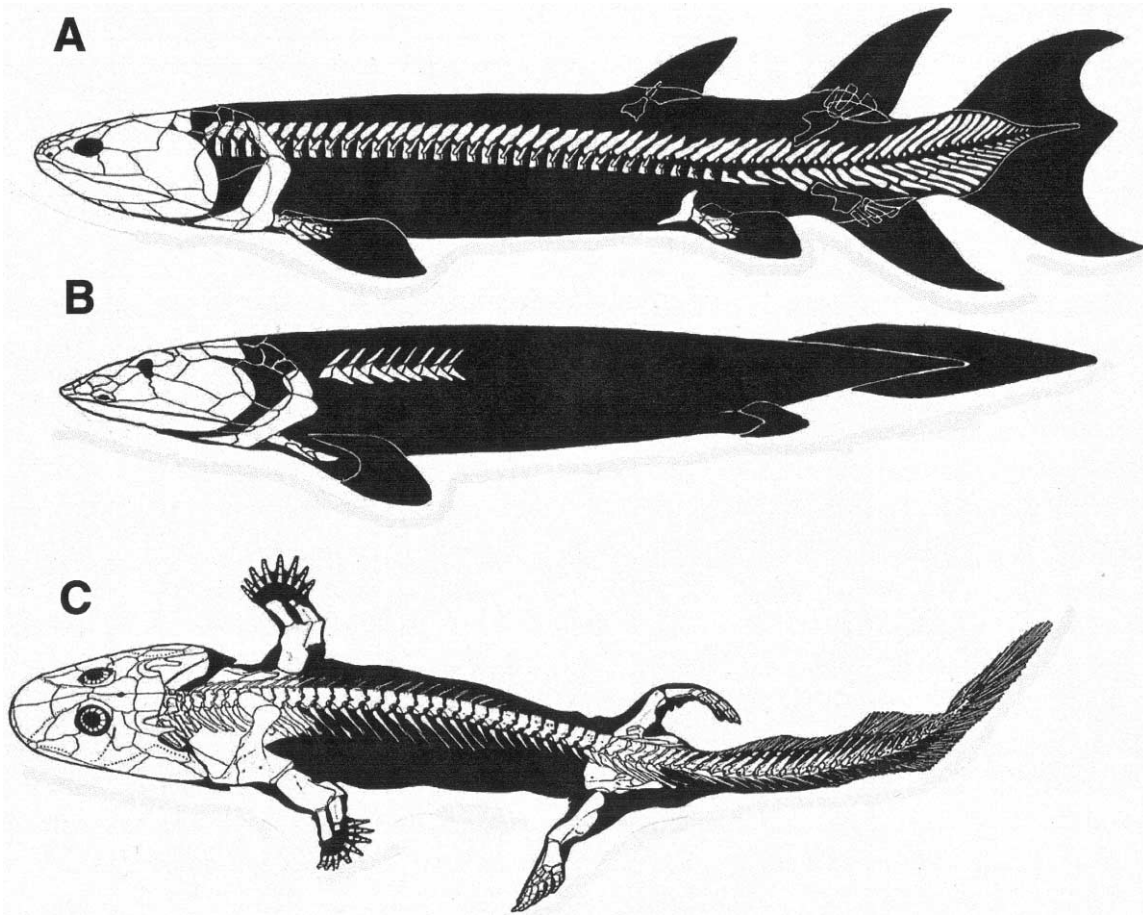
Figure 2. Skeletal comparison between advanced sarcopterygian fishes. *A*, *Eusthenopteron*; *B*, *Panderichthys*; and *C*, a primitive aquatic tetrapod (*Acanthostega*). With permission of Michael Coates.

involved several stages that divide logically into five steps (Fig. 1).

1. Osteichthyan Diversification

Basal osteichthyans of the Late Silurian fall into two major groups: actinopterygians (ray-finned fishes and their closest allies, such as lophosteiforms) and basal sarcopterygians (cosmine-covered forms whose basic skull roof and cheek patterns closely match that of later sarcopterygians). The interrelationships of osteichthyans have long been debated (e.g., Rosen et al. 1981; Panchen and Smithson 1987; Schultze 1987; Long 1989) and even in the new millennium appear to be in a state of flux. The addition of every new basal taxon seems to generate another cladogram (Zhu et al. 1999, 2001; Zhu and Schultze 2001; Zhu and Yu 2002). However, new discoveries of basal stem group gnathostomes, such as *Psarolepis* from the Lower Devonian of China, when fully described, should significantly influence the consensus on osteichthyan interrelationships, mainly because they exhibit intermediate stages both in morphology and in histology that should greatly assist in the assessment of polarity of characters used in previous analyses (J. Long, personal observation).

The diversification of osteichthyan fishes into advanced forms with basic tetrapod skeletal characteristics (the Tetrapodomorpha; Ahlberg 1991*a*) took place at the end of the Lower Devonian. The earliest osteolepiform fishes occur in the beginning of the Middle Devonian (Young and Gorter 1981; Chang and Zhu 1993). The Osteolepiformes and Elpistostegalia (also called "Panderichthyida"; Vorobyeva and Schultze 1991) are the two crown groups of rhipidistians with respect to the tetrapods (Fig. 2). Within this radiation, we see the development in osteichthyan fishes of the following tetrapod features: skull roof and cheek bone patterns that match those seen in the earliest tetrapods (Fig. 3); more robust axial skeleton; pectoral and pelvic fins with single first metamere that distally articulated with two elements (humerus, ulna, radius; femur, tibia, fibula); palatal and nasal skeletal features such as choanae that correlate with modern amphibians and indicate that incipient air breathing had developed; and some modification of
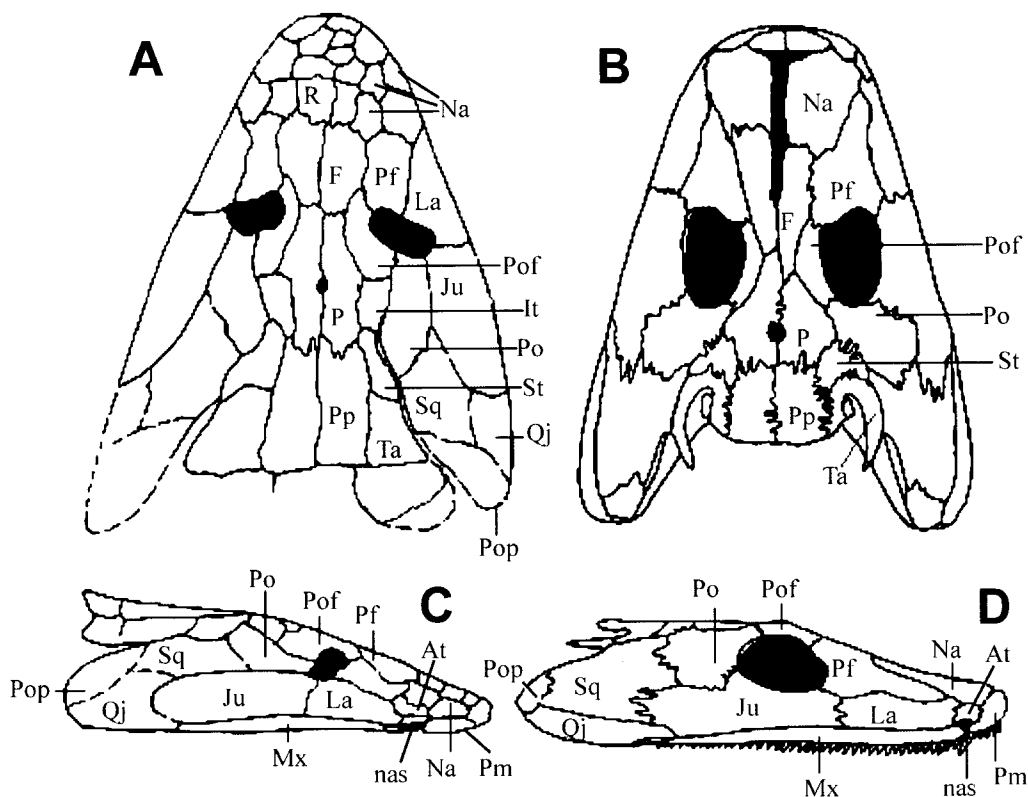
Figure 3. Comparison between the skull roof patterns of an advanced sarcopterygian fish *Panderichthys* (*A*, *C*) and a primitive tetrapod *Acanthostega* (*B*, *D*). Abbreviations: *At* = anterior tectal; *F* = frontal; *It* = intertemporal; *Ju* = jugal; *La* = lacrimal; *Mx* = maxilla; *Na* = nasal; *nas* = external naris; *P* = parietal; *Pf* = prefrontal; *Pm* = premaxilla; *Po* = postorbital; *Pof* = postorbitofrontal; *Pop* = preoperculum; *Pp* = postparietal; *Qj* = quadratojugal; *R* = rostral; *Sq* = squamosal; *Ta* = tabular. After Clack (2003) and Vorobyeva and Schultze (1991).

the hyoid arch toward stapes development (e.g., as in shorter, more dorsally oriented hyomandibular, *Gogonasus*; Fig. 4).

These characters are the basis of the argument about why osteichthyans, rather than any other piscine gnathostome group, are now widely accepted as the sister group of tetrapods. They are also the basis for why certain osteichthyans (the tetrapodomorphs), which have better development of these characters, are accepted to be the immediate sister group to tetrapods. All of these characters can be seen best developed in the order Osteolepiformes and more so within the Elpistostegalia (actually a subgroup of Osteolepiformes that have been elevated taxonomically to the same ordinal rank, Panderichthyida; Vorobyeva and Schultze 1991).

The elpistostegalid fishes (represented by *Panderichthys, Elpistostege,* and *Livoniana*) are regarded as the most apomorphic of all fishes with respect to tetrapods. Those known from well-preserved material share the following features with tetrapods: a platybasic skull with eye ridges, external nares situated on the margin of the mouth, a humerus with an anterior keel (Fig. 5), and the dorsal fin is lost. Ahlberg et al. (1996) also pointed out that *Panderichthys* has an intracranial joint, as in other sarcopterygian fishes, and they suggested that the tetrapod

braincase must have evolved more rapidly than its external skull morphology.

Functional discussion. Functional interpretations of the implications of elpistostegalids having acquired this suite of morphological traits have received little discussion. The flattening of the skull and the development of eye ridges are common features also seen in many primitive fossil amphibians and in some aquatic reptiles (e.g., crocodiles). It is best interpreted as an adaptation for aerial vision above the waterline. Danger inherent in the life of Late Devonian aquatic tetrapods such as *Acanthostega* would likely have been from large predatory tristichopterid fishes such as *Eusthenodon*. The ability to look out of the water would have been advantageous in several ways. It would have enabled the animal to see safe spots to head for on land if chased by predators in the water, and it would have been useful for searching for large arthropod prey items above the water (on land or in overhanging vegetation). Such aquatic tetrapods probably relied substantially on their water-based lateral line systems to detect impending danger from aquatic predators.

The elongation of the humerus, the development of the anterior keel for the deltoid muscles, as well as the presence of a
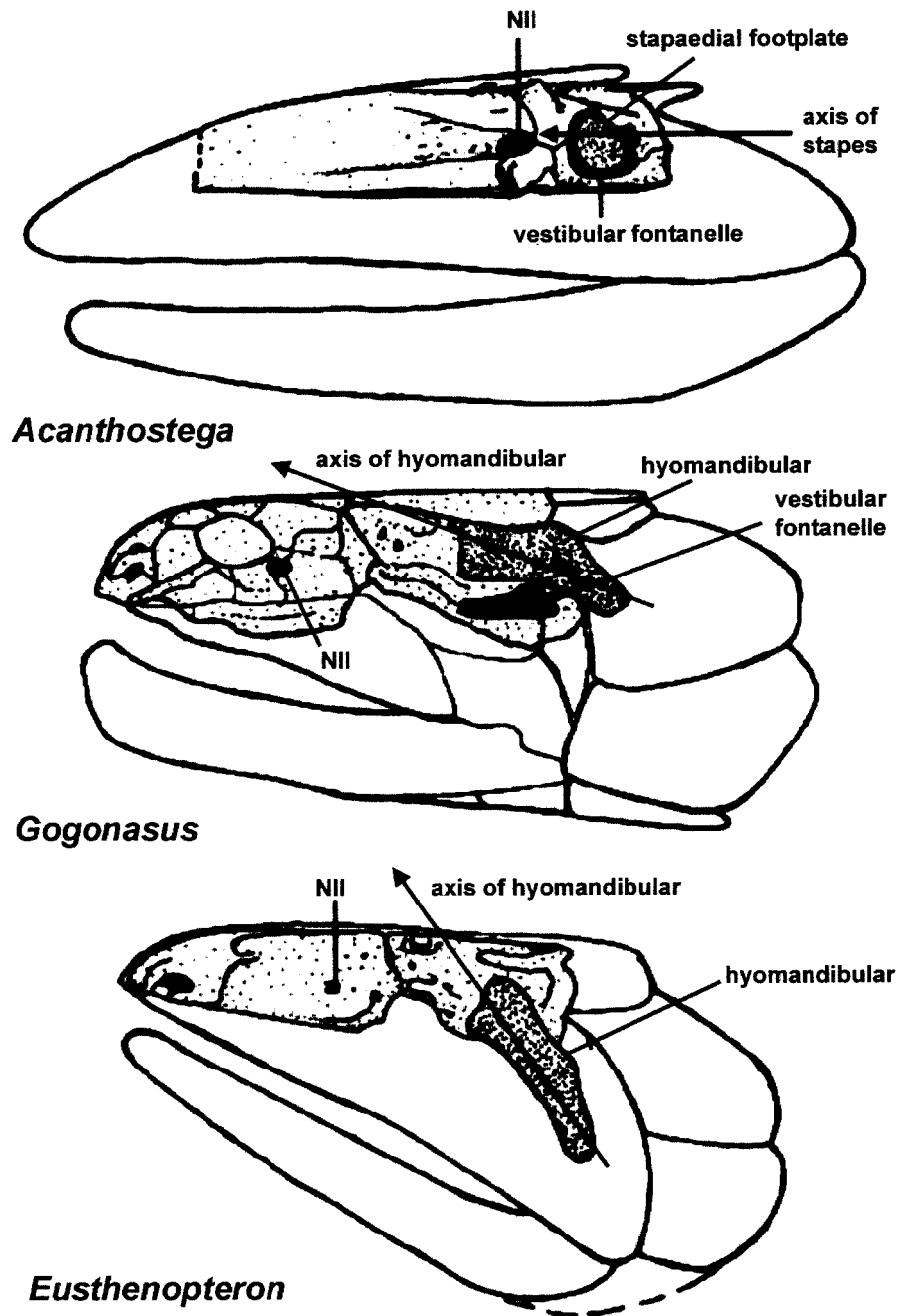
Figure 4. Comparison between the hyoid arches and braincases of sarcopterygian fishes (*Eusthenopteron*, *Gogonasus*) and a basal tetrapod (*Acanthostega*). Note the axis of the hyomandibular is closer to horizontal in *Gogonasus*, an osteolepiform fish, which also retains a large vestibular fontanelle in the braincase. *NII* = optic nerve. After Clack (1998*a*), Long (1990), and Jarvik (1980).

ventral keel or ridge (Shubin et al. 2004) provide more area and better orientation for muscle attachments to develop more powerful pectoral fins. Similarly, an isolated near tetrapod humerus from the Late Devonian of North America described by Shubin et al. (2004) shows that the beginnings of the tetrapod-style humerus, as first seen in elpistostegalids, started with the humeral shaft being flattened dorsoventrally, minimizing shoulder rotation. Such fins might have been used in sudden lunges to seize prey; to facilitate movement on land during short, out-of-water forays; or for fin walking in shallow depths.

There were no significant changes that can be discerned relating to respiration. This can be seen from external bone pat-
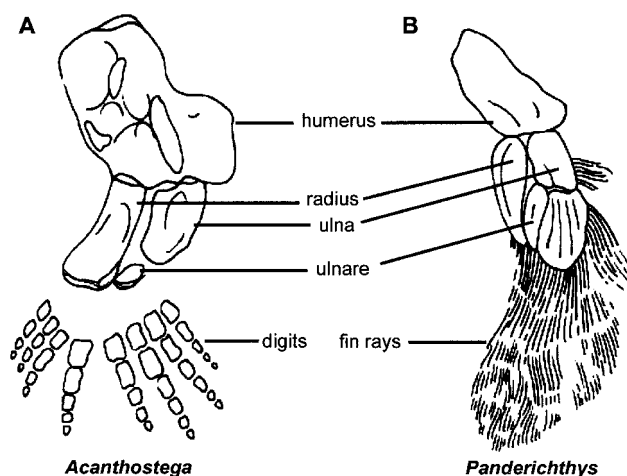
Figure 5. Comparison between forelimb structures of (*A*) a primitive tetrapod (*Acanthostega*) and (*B*) an advanced sarcopterygian fish (*Panderichthys*). After Coates (1996) and Vorobyeva and Kuznetsov (1992).

terns, nasal region anatomy, and palatal morphology in the elpistostegalid fishes compared with their osteolepiform ancestors.

Morphofunctional analyses of the complex of characters that changed during the transition from advanced osteolepiform/elpistostegalid fishes to aquatic tetrapods have focused primarily on minor changes in preexisting skull roof patterns (which were paedomorphically retained; Long 1990) and on increased strengthening of the appendicular skeleton (attributed to peramorphosis; Long 1990; Clack and Coates 1995), coupled with the loss of median fins (possibly a developmental by-product of accelerated axial skeleton growth). Other functional adaptations likely were also important. This transition, from basic osteolepiform-like ancestors to the first elpistostegalid, had occurred by the end of the Middle Devonian, as seen in *Livoniana*.

2. "Prototetrapods"

The Elginerpetonidae, represented by fragmentary remains of *Elginerpeton pancheni* (Ahlberg 1991*b*, 1995) from the late Frasnian Scat Craig site in Scotland, and the lower jaw of *Obrutchevichthys* from Russia (Ahlberg 1995) show basic tetrapod characteristics in the known parts of the cranium, especially the lower jaw, and parts of the postcranial skeleton (ilia and limb bones are at a similar level of development as in *Ichthyostega*). These taxa, although poorly known, fill in an important gap between the elpistostegalid fishes and the first well-preserved completely known Devonian tetrapods, such as *Acanthostega* and *Ichthyostega*. *Elginerpeton* retains accessory teeth on the crest of the dentary's vertical lamina, a condition seen in *Panderichthys* but not in any tetrapods. *Elginerpeton* is further considered more derived than elpistostegalid fishes in having lost

the intracranial joint (as inferred from skull roof morphology, which lacks the visible expression of the intracranial gap), in having paired fangs on the parasymphysial toothplate, in having a slender-shaped anterior coronoid, and in the loss of the precoronoid fossa (Ahlberg and Clack 1998).

Functional discussion. The closure of the intracranial joint has occurred at least twice within osteichthyan evolution, first within the Dipnomorpha (if assuming it was not primitively absent on the basis of actinopterygian evidence as basal osteichthyans; Gardiner and Bartram 1977; Gardiner 1984; Basden et al. 2000) and second within the fish-tetrapod transition. The platybasic skull of elpistostegalids is not dissimilar to that of *Elginerpeton* (as restored by Ahlberg 1995). Although *Panderichthys* retained the intracranial joint, it apparently had no ability for intracranial kinesis because the sutures of the skull table were strongly interdigitated, which would have prevented any movement (Vorobyeva and Schultze 1991). In *Elginerpeton*, the loss of the intracranial joint was possibly a direct functional requirement to strengthen the long, broad platybasic skull when the animal was out of water. Similarly, the lower jaw of *Elginerpeton* is more tubular in form rather than the flat-lamina jaw shape in fishes, which structurally gave it the greater cross-sectional strength required when not supported in an aqueous environment. Such an adaptation for lifting the skull out of water and opening the mouth could alternatively be interpreted as a specialization for buccopharyngeal (perhaps palatal) breathing. Although the evidence is tenuous, this could be seen as a possible first step toward aerial respiration within the fish-tetrapod transition.

The presence of zygapophyses and an ilium with a sacral facet led Ahlberg (1998) to suggest that the postcranial skeleton of *Elginerpeton* was to some extent adapted as a weight-bearing structure. However, the hind limb probably functioned more as a paddle in water than as a walking leg. The forelimb appears to have been strengthened as a weight-bearing prop and may have been permanently flexed. Ahlberg (1998) concluded that *Elginerpeton*, although better adapted to bear its weight than elpistostegalid fishes, had nonetheless diverged from the semi-amphibious mode of life toward a more aquatic lifestyle. The timing of the transition from elpistostegalids to elginerpetonids must have taken place toward the end of the Frasnian stage, immediately before the Kellwasser extinction events, if biostratigraphic data are reliable.

3. Aquatic Tetrapods

The transition in water from fishes with fins to fishlike aquatic tetrapods with digits (e.g., *Acanthostega*, *Ichthyostega*) appears to have taken place before the start of the Famennian stage if the phylogenetic placement of the late Frasnian *Metaxygnathus* is considered (Coates 1996; Ahlberg and Clack 1998). However, as *Metaxygnathus* is based on only a single lower jaw, we will base the timing of the origin of true aquatic tetrapods on the

occurrence of *Ichthyostega* and *Acanthostega* from East Greenland; it is thus more safely seen as a lower-middle Famennian event. There are several major anatomical characters that define both these tetrapods and higher clades on the basis of the well-described anatomy of *Acanthostega*, *Ichthyostega*, and *Tulerpeton* (this list of characters is taken from Lebedev and Coates 1995 but reorganized into clusters of morphofunctionally related characters).

In the cranium, we see a fenestra ovalis in the otic capsule of the braincase; a stapes, derived from the hyomandibular of fishes; a single bilateral pair of nasal bones; and the jugal/quadratojugal contact excludes squamosal/maxilla contact (Fig. 3).

The axial skeleton shows the presence of a sacrum; ischia that form part of the pelvic symphysis; limb epipodials that are parallel; carpus/tarsus with skeletal elements articulating laterally as well as proximodistally; dactyly, a series of digits present; femur with extensive adductor blade; humeral/femoral epipodial facets separated by a strip of periosteal bone; and the tibial distal articular surface is distinctly L shaped.

The sensory system shows the bony enclosure of the infra-orbital sensory canal is interrupted by the external naris.

Functional discussion. These features, which characterize the first "tetrapods" (defined as vertebrates with four limbs having digits), may be discussed within the framework of major morphofunctional complexes that all relate to increasing the animals' potential to be able to leave the water for short periods and possibly toward increased aerial respiration (at least in *Ichthyostega*). It is possible that several of these features were specializations for aquatic locomotion that were serendipitously advantageous in the steps leading toward terrestrialization.

The changes in the dermal bones of the skull involve both the enlargement of the jugal to exclude the maxilla from contacting the squamosal and the single bilateral pair of nasal bones. Both features increase the strength of the skull, making it both stronger for exerting a more powerful bite or more functional out of the aquatic environment. The fused, solid cheek plate adds to this strength. The stapes, although not fully functional as a sound-conducting structure in air, was initially interpreted as a specialized transmitter for waterborne sound in *Ichthyostega* (Ahlberg et al. 2002; Clack et al. 2003). Clack (1994*b*) had earlier shown that the stapes in *Acanthostega* was not functional in transmitting sound to the braincase and suggested that it may have given structural support between the palate and the stapedial plate of the braincase. The fenestra ovalis in the otic capsule is derived from the vestibular fontanelle of osteichthyans (Clack 1994*b*; Basden et al. 2000). It is interesting to note that the retention of this large opening in the otic wall of the braincase has been interpreted as a paedomorphic feature for tetrapods by Clack (1994*b*, p. 393), a comment that lends further support for the directive role of heterochrony in lower tetrapod evolution.

Both characters (stapes and fenestra ovalis) are clearly linked

functionally. The cranial articulation of the piscine hyomandibular is the same as the thick, broad stapes in early tetrapods, except for the fact that the stapedial plate in *Acanthostega* is thought to represent the separated single head of the piscine double-headed hyomandibular (Clack 1994*b*, p. 394). Figure 4 shows an unusual condition where some relatively primitive osteolepiform fishes, such as *Gogonasus*, developed an almost horizontally oriented hyomandibular that approached the condition seen in basal tetrapods more closely than that found in other fishes (interpreted by Long [1990] as a modification for opening the operculum resulting from the high-vaulted shape of the head). The otic capsule of the braincase in basal tetrapods was mesial to the stapedial plate, in the perfect position to pick up sound vibrations from the stapes. Whether the sound was picked up from the palate or the otic notch is a matter of degrees of hearing efficiency. It is likely that in *Acanthostega* hearing was rudimentary and picked up from vibrations caught by opening the mouth by way of the palate. As the stapes decoupled from the palate in later tetrapods, the distal end of the stapes became braced against the otic notch at the back of the skull table and from there transmitted sound waves to the otic capsule.

Clack (1998*a*) concluded that the anatomical changes seen in the otic region of *Acanthostega* (such as the elimination of the ventral cranial fissure by suturing of the prootic to the basioccipital; the loss of the lateral commissure; the loss of hyomandibular facets and the jugular canal; the expansion of the head of the hyomandibular as the stapedial foot plate; and the associated modifications of soft tissues) all preceded the advent of tetrapod terrestriality. Other factors and forces that subsequently drove aquatic tetrapods to spend more time on land facilitated the development of terrestrial hearing. The development of a typanum within an otic notch thus came later and has arisen independently within tetrapods at least three times and possibly as many as six times (Laurin 1998).

The most profound morphological changes at this stage are seen in the axial skeleton, particularly in the limbs. The development of a sacrum and ischia forming part of the pelvic symphysis relates to strengthening the structure of the hip for supporting the body either out of water or in the shallows. Similarly, the strengthening of adductor muscle attachments by development of a prominent blade on the femur provided the hind limb with more muscular power. The presence of digits at this stage may not necessarily have been related to improving mobility on land but possibly served to increase the area and strength of the paddle. Digits may thus be seen, alternatively, as a specialized aquatic condition, which occurred in many later groups of secondarily aquatic tetrapods (e.g., polydactylous paddles of plesiosaurs and ichthyosaurs).

Further specializations in the limbs for improving maneuverability and increasing power are seen in the parallel epipodials and carpus/tarsus skeleton with skeletal elements articulating laterally as well as proximodistally. The widening of

articular surfaces of the distal face of the humerus and femur would improve the flexibility of the epipodials in the limb. The large L-shaped distal articular face on the tibia may have provided a larger surface area for attachment of the foot or, alternatively, facilitated flexure at the ankle joint.

The laterosensory system in aquatic tetrapods retained fish-like features in having broad, open canals but also showed the specialized condition of the bony enclosure of the infraorbital sensory canal being interrupted by the placement of the external naris.

Acanthostega and *Ichthyostega* are regarded as being more derived than other basal "aquatic tetrapods" in having the pectoral girdle detached from its connection to the back of the skull (Clack 2001), and the posttemporal and supracleithrum bones are lost from the pectoral girdle. Furthermore, *Ichthyostega* and higher tetrapods share latissimus dorsi process of the humerus in line with the ectepicondyle, basal articulation immobile, "dark" dentine in the teeth, and ribs with a broad laminar region having a vascular canal (Jarvik 1996).

The decoupling of the pectoral girdle from the skull and the loss of the dorsal pectoral girdle bones (supracleithrum and posttemporal) permitted a greater degree of movement for the shoulder, a necessity for improving both aquatic maneuverability and terrestrial locomotion. It also facilitated greater mobility of the neck, a feature that may have been initially driven by nonrelated feeding mechanism specializations as suggested by Johanson et al. (2003) or, alternatively, for lifting the head to aid aerial respiration by using the nostrils and choanae. The presence of dark dentine, a denser tissue in the teeth for strengthening the tusks, is a potentially useful feature if a derived form of "snapping food capture" was used (as postulated for the tristichopterid *Mandageria*; Johanson et al. 2003).

The peculiar ribs of *Ichthyostega* show a broad laminar region pierced by a canal that Jarvik (1996, p. 56) interprets as a possible specialization for subcutaneous breathing by comparison with similar structures observed in the frog *Rana*. If so, this is the first skeletal evidence for accessory subaerial respiration in a Devonian tetrapod.

4. "True Tetrapods"

Tulerpeton was considered to be a "reptiliomorph" by Lebedev and Coates (1995) and Coates (1996), but Ahlberg and Clack (1998) and Warren and Turner (2003) regard it as a stem tetrapod that is still more apomorphic than *Ichthyostega* or *Acanthostega*. This taxon represents the level of tetrapod development defined as the first "true tetrapods" by Lebedev and Coates (1995). These share a number of specialized features in the appendicular skeleton: humeral/femoral epipodial facets rejoined by an isthmus of unfinished endochondral bone; femoral adductor blade reduced distally; tibial distal articular surface ovoid; hinged wrist joint in the forelimb and knee joint in the hind limb; ankle joint rotary; scapulocoracoid separate from cleithrum; clavicle with rodlike ascending process; fibula waisted with sigmoid distal profile; tarsus with more than two centralia.

Tulerpeton has two reversals of characters used in the cladogram of Lebedev and Coates (1995), implying secondary loss of these features: the distally extended femoral adductor blade and an L-shaped distal facet on the tibia.

Functional discussion. Most of these characters relate to the appendicular skeleton, increasing muscular power and maneuverability of the joints. Lebedev and Coates (1995) point out that the extensive adductor blade on the humerus and the indistinct trochanters could indicate a less differentiated limb musculature associated with a powerful, rear-thrusting swimming stroke. The rodlike ascending process on the clavicle is a feature also seen in some osteichthyan fishes (e.g., rhizodontids [Andrews and Westoll 1970] and *Onychodus* [Long 2001]) and, alternatively, may be regarded as a primitive feature.

Clack (2002*b*) argued that the first functional wrist and ankle joints are seen in truly terrestrial forms such as *Pederpes finneyae* on the basis of the presence of asymmetrical digit bones (Fig. 6), closely approaching the form of the pentadactyl manus and pes pattern seen in all post-Devonian tetrapods.

5. Terrestrial Tetrapods

The transition from aquatic tetrapods to true terrestrial tetrapods involved primary changes in the wrists and ankle as well as structural changes in the axial skeleton facilitating both locomotion and air breathing. Coates and Clack (1995) define this group as having a closed operculum and hypaxial exhalation and costal inhalation (the latter inferred to be present in *Tulerpeton*; Lebedev and Coates 1995). *Pederpes finneyae*, described by Clack (2002*b*) from the Early Carboniferous Dumbarton Limestone of Scotland, is specialized for terrestrial locomotion in having five digits on the hind limb, asymmetrical phalanges in the pes, and the foot rotated to face anteriorly, as in modern tetrapods. The front limb is poorly preserved and only two small digits are visible, one of which is so small that it possibly represents a sixth supernumerary digit. *Ossinodus*, a stem tetrapod from the Lower Carboniferous (mid-Visean) of Queensland, Australia, sits just below the node of *Pederpes* on the cladogram of Warren and Turner (2003). It possesses two metapodials that are bilaterally and proximodistally asymmetrical, as in *Pederpes*, and a flattened, broad unwaisted tibia that is better ossified than in other stem group tetrapods such as *Acanthostega*, so it may well have had some degree of terrestrial adaptation. Observations on the small femur of *Ossinodus* suggested that its juveniles were more aquatic than the adult, which was possibly more adept at terrestrial locomotion.

Functional discussion. *Pederpes* is regarded as the first tetrapod with true terrestrial abilities, as seen in the development of wrist and ankle joints that can bend to move the animal forward while out of the water (Clack 2002*b*). All previously discussed
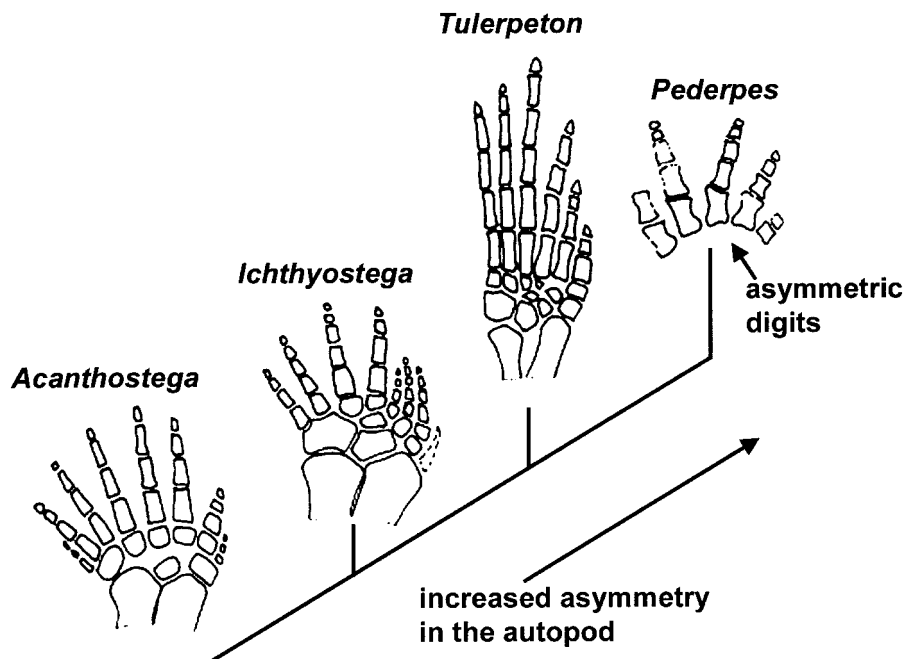
Figure 6. Evolution of the tetrapod hand, showing increased asymmetry of the digits. After Coates (1996) and Clack (2002a). Here *Pederpes* is recognized as the earliest terrestrial tetrapod after the work of Clack (2002a).

tetrapod taxa may have been fully or partially aquatic, having only incipient flexibility in the wrist or ankle, which could be useful for short forays on land or, alternatively, for powerful strokes of the limbs underwater. The symmetry of the phalanges in *Pederpes* relates to the twisting of the foot to an anteriorly facing position and the need to push off from one edge of the foot when moving forward. *Pederpes* still retained fishlike characters in the laterosensory system (partially open canals) and so did not live entirely out of water and would have almost certainly depended on water for reproduction. The later development of the hard-shelled amniote egg is perhaps the first real evidence of any tetrapod having the potential to live an entire life out of water.

By the end of the Lower Carboniferous, there are numerous examples of terrestrial tetrapods from sites in Scotland, North America, Canada (Clack 2002a), and Australia (Warren and Turner 2003). The invasion of land by the tetrapods was by that time well underway.

Evolutionary Mechanisms for Tetrapod Evolution

Long (1990) proposed a general model for the evolution of tetrapods by heterochrony, citing dissociated heterochrony as the most likely mechanism for how tetrapods evolved from fishes. This analysis used *Crassigyrinus* as a typical primitive tetrapod, a taxon now known to be a more derived genus than the Late Devonian East Greenland genera (Clack 1998b), or

Ossinodus (Warren and Turner 2003). Coates and Clack (1995) have criticized the proposal because it was based on juvenile "small" skulls of *Eusthenopteron* that have more resemblance to the basal tetrapod *Crassigyrinus* than adult *Eusthenopteron*. They rightly point out that some of these characters are missing in the elpistostegalid-*Acanthostega* transition, regarded as the most likely stepwise progression for fish-tetrapod evolution.

These points may now be revisited, both in light of new data obtained in the past 13 years and considering how the original article was intended. At the time the original article was written (Long 1990), *Eusthenopteron* was the only advanced tetrapodomorph fish with growth series data published, so this was the only taxon for which generalized growth sequence could be gauged. Another article by Cote et al. (2002) has detailed the growth in the postcranial skeleton of *Eusthenopteron*, showing that tail growth proceeded in a different direction from that in early amphibians.

McNamara (1997) has shown that the generation of digits in tetrapods is caused by the progressive delay in the transition from dermal to endoskeletal production, arising from a progressive delay in folding of the ectoderm. This folding did not occur in tetrapods (as it does in teleost fish, producing fin rays), so only endoskeleton is formed, resulting in digits. McNamara named this process "sequential heterochrony."

Individual characters criticized by Coates and Clack (1995) on the basis of the use of *Crassigyrinus* as the basal tetrapod model are here reevaluated. If the character was also found to hold true in *Acanthostega*, it was considered a valid feature for

supporting a heterochronic model for early tetrapod evolution (as shown in Fig. 7).

1. Deep postorbital bone participating in the orbital rim. This applies equally well to *Acanthostega*, as demonstrated by the Cartesian transformation of Coates and Clack (1995, Fig. 2*E*).

2. Notched squamosal. This supports the contention that *Crassigyrinus* represents a primitive amphibian-type skull insertion into the squamosal for the anterodorsal expansion of the preopercular. This character is absent from the elpistostegalid-*Acanthostega* transition so is dismissed by Coates and Clack (1995). Subsequent study of *Crassigyrinus* has demonstrated it lacked a preopercular bone (Clack 1998*b*), so this character is now redundant.

3. Posteriorly directed margin of the squamosal contributes to the opercular hinge of *Eusthenopteron*. This is present in *Acanthostega* in which Coates and Clack (1995) agreed it would contribute to the support of a soft operculum.

4. Extensive contribution of the jugal and lacrimal to the orbital rim. This (jugal only) is also found in *Acanthostega*, so it holds as being a good ontogenetic character. The character of the lacrimal contact (missing in *Acanthostega* and *Ichthyostega*, for which juvenile phases are not known) can also be

considered as a good ontogenetic character that is present in some other primitive temnospondyls in which juvenile phases are documented (e.g., *Eugyrinus*; Milner 1980) and is seen in some primitive adult taxa such as *Greererpeton* (Smithson 1982).

5. Fewer ossifications of the snout in juvenile *Eusthenopteron* compared with many in the adult. This holds for all basal tetrapods as well (Coates and Clack 1995, p. 382).

6. Shorter contact between the cheek unit and the skull table. Also seen in *Acanthostega* adults.

7. Intricate sutures, shared by all taxa excluding adult *Eusthenopteron*, so holds as a valid observation.

Long's conclusion (1990, p. 160) that "it is suggested from these studies that although the skull of early amphibians could have evolved from osteolepiform fishes through paedomorphosis, the development of the limbs with digits probably arose through peramorphosis" was upheld by Coates and Clack (1995). Yet to infer that heterochrony has played a major role in the evolution of a higher taxonomic group, any primitive taxon can be used, even living salamanders would suffice (Alberch and Alberch 1981).

Coates and Clack (1995, p. 385) stated that "however, despite increased knowledge of ever closer osteolepiform relatives (the
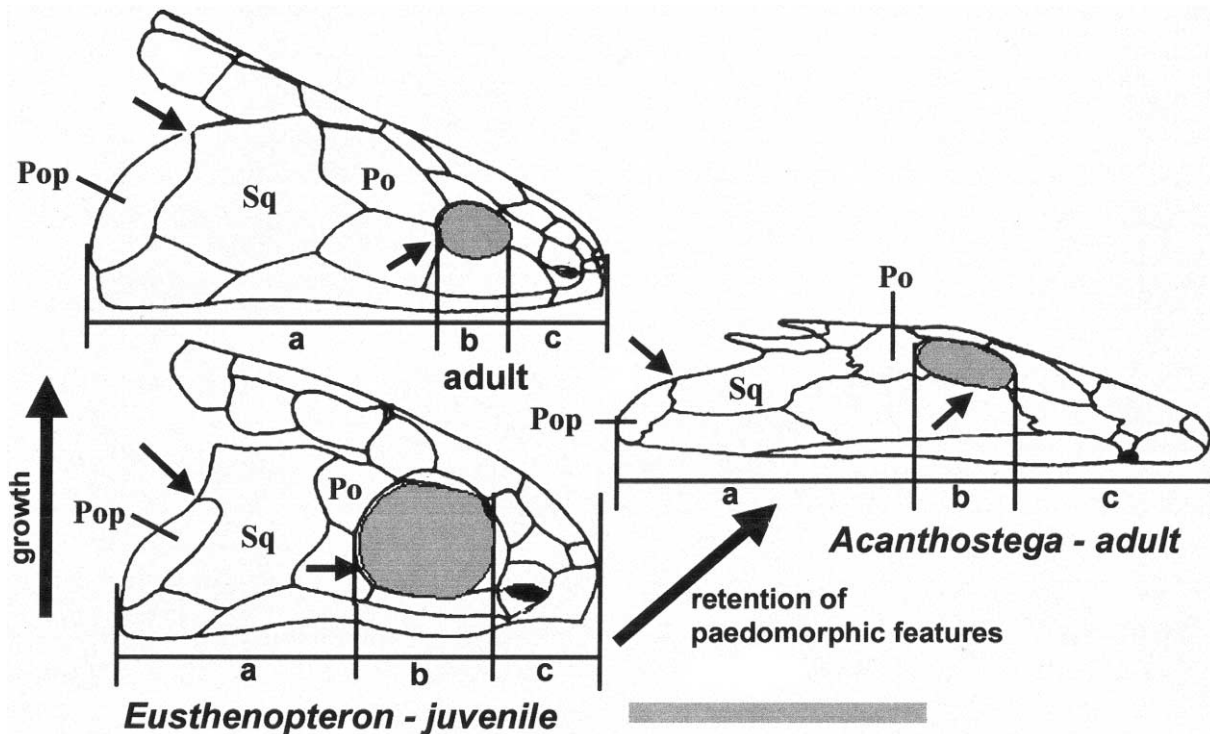

Figure 7. Comparison between the juvenile and adult skulls of the sarcopterygian fish *Eusthenopteron* (scaled to same size) compared with that of a primitive tetrapod *Acanthostega* to show some of the paedomorphic features retained in the basal tetrapod skull. The proportions of cheek (*a*), orbit (*b*), and snout (*c*) relative to overall length are marked, and arrows indicate the length of the jugal-orbital margin (the bone in front of the squamosal [*Sq*]), and dorsal extent of the preopercular (*Pop*), respectively. Note also how the postorbital bone (*Po*) in *Acanthostega* retains its similar deep shape to that in the juvenile *Eusthenopteron*. From Long (1990) and Clack (2003).

elpistostegalids), we cannot yet identify the nodal location of these metamorphic events with any precision in tetrapod phylogenetic history." The point of heterochronic analysis should be emphasized as not being primarily concerned with nodes on a cladogram but interpreting how changes in ontogeny can reflect high-level evolutionary trends (McNamara 1990). Characters used in heterochronic analysis must relate to large-scale (discretely measurable) ontogenetic change, and in some cases, it has been shown that morphological regions of highest allometric variation indicate areas of phylogenetic plasticity when examined at higher taxonomic levels (as shown in antiarch placoderms; Werdelin and Long 1986). This is rare enough for Devonian rhipidistian fishes, let alone early tetrapods (the first of which in the fossil record that shows good ontogenetic growth sequences are possibly the Permian branchiosaurs from Saar-Basin). Schoch (1992, 1995, 1997, 2003) has demonstrated that heterochrony has been the dominant factor in shaping major evolutionary radiations within the Paleozoic Amphibia, and it is most likely the mechanism that has facilitated the rapid change from elpistostegalid fishes to terrestrial tetrapods.

Finally, the character of metamorphosis, a biological transformation that has defined the living Amphibia since their discovery, warrants some comment in the light of recent paleontological work. Schoch (2001) observed that metamorphosis is much less frequently observed in Paleozoic amphibians, corroborating Romer's (1958) idea that the origin of tetrapods and the event of their terrestrialization were not coincident. The absence of metamorphism in primitive tetrapods (Coates and Clack 1991, 1995; Schoch 2001) facilitates the invasion of land for fully matured aquatic tetrapods. However, the transition from water to land is accompanied by a number of ontogenetically related anatomical changes: loss of lateral line sulci; loss of branchial ossicles; large complex septomaxillary; large choanal opening and voluminous narial passage; and the adaptive features of the humerus, scapula, and ilium (Schoch 2001). Schoch also noted that certain features thought to be associated with terrestrialization of tetrapods—hypobranchial apparatus, dermal sculpturing, and degree of ossification in the skeleton—also occur in neotenic species (preserved in fossilized larvae). Metamorphosis, as seen in the Lissamphibia today, is thus regarded as a specialized combination of ontogenetically driven features that accompanied the invasion of land.

In summary, heterochrony appears to have played a major role throughout amphibian phylogeny as the driving force of emerging new morphologies (Schoch 1995, 2003), and it has been the primary evolutionary mechanism in the origin of the first tetrapods (Long 1990; Coates and Clack 1995).

Developmental Biology and the Origin of Tetrapods

Various authors have explored the relationship between observations on the fins and limbs in modern fishes and tetrapods and their developmental origins within the various scenarios of the fish-tetrapod transition (Ahlberg and Milner 1994; Coates 1994; Daeschler and Shubin 1995; Shubin et al. 1997; Coates and Cohn 1998). These works all recognize that linkages between forelimb and hind limbs are an ancient feature resulting from gene co-option during the early evolution of gnathostome fishes. Hox genes are most likely responsible for the patterns of serial homology exhibited in the similar structures of the hind limb and forelimb skeletons in fishes. Sordino et al. (1995) showed that by analysis of HoxD and HoxA complex genes during development of the zebrafish *Danio* that autopods (hand and foot patterns of bones) could be a neomorphic structure, and therefore digits would be a vertebrate speciality. The origins of evolutionary novelties, such as digits in tetrapods, thus appear to be associated with the alteration of existing genes rather than the invention of new regulatory genes (Daeschler and Shubin 1995). Coates (1994) pointed out that the reduction of the dermal skeleton is another significant event in the evolution of the tetrapod limb.

Shubin et al. (1997) showed that the presence of phase III Hox expression in tetrapod limbs (absent in teleost fins) and a uniquely tetrapod enhancer for phase III is a derived condition that defines the clade, including advanced sarcopterygian fish such as *Sauripteris* (with radials that are functional equivalents to digits) plus tetrapods. Thus similar genetic shifts were involved at this level of the fish-tetrapod transition. The axis of the fin was developmentally bent during the origin of tetrapod limbs as the branching of the axis shifted from the anterior (preaxial) to the posterior (postaxial) compartment of the limb. Shubin et al. (1997) suggested that this reversal of morphological polarity in the appendages of Devonian vertebrates correlates with the reversal of Hox gene expression seen in phase III, a proposition they claim is supported by the evidence of the elpistostegalid pectoral fin. The fins of elpistostegalids were highly reduced (in their number of skeletal elements), and this reduction is most prominent in the distal part of the fin. The paleontological evidence is clear that vertebrates spanning the fish-tetrapod transition have either digits or fin rays but never both on the same limb.

Integrating the hypothesis of dissociated heterochrony into the fish-tetrapod scenario provides the much-needed link between developmental mechanisms and observed rapid evolutionary transition (Ahlberg et al. 1996). The changing of growth rates and timing of development through the alteration of regulatory genes result in large changes in gross morphology over relatively short time periods and thus fits the observable paleontological evidence for the fish-tetrapod transition. It is hoped that with continued field exploration some of the poorly known stem group tetrapodomorphs, such as the elginerpetonids, will one day be described from more complete material (including juvenile phases) to provide further data on the anatomical transformations that took place at this crucial stage in vertebrate evolution.

Possible Phylogenetic Alternatives

The large amount of new information concerning tetrapod origins and evolution obtained in recent years has provided reasonable answers to the six general questions posed at the beginning of this essay. However, although many of the larger-scale features of the transition are clearly much better documented and understood, some basic uncertainties remain.

This review, like Clack's (2002*c*), is primarily based on the current consensus cladistic analyses of major parts of the evidence. The consensus may indeed be correct, and the conservative, possibly parsimonious, approach would be to accept that position as the first tetrapods evolving from elpistostegalid-like fishes sometime in the Frasnian stage. However, we think it remains useful to remember that other models may also yet turn out to be valid. We point out the following considerations.

1. The uncertainties of the fossil record of tetrapods genuinely persist because 80% of all Devonian tetrapods are known from only very incomplete skeletal material. The wide geographic dispersal of primitive tetrapods by the beginning of the Fammenian (Australia, Baltic) suggests there is presently no unambiguous way to determine whether there was a single "main line" of tetrapod evolution (as the cladistic analyses assume) or whether any of the problematic older fragmentary fossil forms (e.g., *Metaxygnathus*, from the late Frasnian of Australia) imply the possibility of a diphyletic origin of tetrapods.

2. The approximately 100 species of living amphibious fishes, phylogenetically irrelevant as they are, are indirectly relevant as demonstrations by analogy of the wide variety of situations in which fishlike protoamphibians might have thrived. As documented by Graham (1997), living amphibious fishes occur in freshwater, brackish, and marine environments; they occur from the Tropics to the subarctic, on open, rocky coastlines, in coastal mangrove areas, and in protected bays and estuaries. They have a wide variety of reproductive and developmental modes and they have a diversity of diets. Air breathing has evolved independently in modern fishes at least 38 and possibly as many as 67 times. It is both realistic and conservative to focus primarily on what has been found in the fossil record, but we suggest that it may also be useful to think outside that box with respect to where else we might look for additional evidence for alternative physiological pathways for an invasion of the land by fishes.

3. A similar argument by analogy relates to the diversity of the Lissamphibia (Duellman and Trueb 1986; Feder and Burggren 1992; Stebbins and Cohen 1995; online guide to all living amphibian species: http://research.amnh.org/herpetology/amphibia/index.html). Living amphibians are mostly confined to aquatic and relatively mesic terrestrial environments, but substantial numbers of forms occur in marine mangrove environments, in harsh deserts, in the subarctic and arctic (where several species tolerate long-term freezing), and at high ele-

vations. There is also surprising biochemical, physiological, behavioral, ecological, and reproductive diversity (e.g., there are many examples of direct development, eliminating the necessity for metamorphosis). It is not therefore inconceivable that the early tetrapods were also far more diverse in their physiology and behavior than we can infer from the fossil record. There is no requirement that whatever evolutionary paths were followed by early tetrapods meant that a single pattern of morphological, physiological, behavioral, and ecological adaptations necessarily was basal to all of the organisms that followed. The recent evidence, summarized above, that tetrapods appeared almost worldwide within a geologically relatively short time span following their first appearances in the geological record, when combined with the biological considerations just outlined, implies to us that ideas of tetrapod monophyly, although strongly supported by fossil evidence, may not necessarily be the most parsimonious biological interpretation.

Acknowledgments

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