

THE ORIGIN OF THE TETRAPODS

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ABSTRACT. The search for the origins of the tetrapods, both in the sense of ancestry and the general biological context of the transition between fish and amphibian, has long been a central concern of vertebrate paleobiology. Recent discoveries have done much to improve our information about the interrelationships of lobe-finned fishes and tetrapods and to redefine the patterns of morphological change in key structures such as the skull, stapes, limb, and gills. The osteolepiform fishes remain the most likely ancestors. The first tetrapods were polydactylous and retained partial gills. The age of the first tetrapods is steadily being pushed back, and their geographical range widened. The transition probably occurred in a coastal wetland environment, no later than the end of the Middle Devonian and (depending on an inconclusive trackway) even earlier. Many unresolved questions remain, especially concerning the evolutionary mechanisms that underly the transition.

INTRODUCTION

The twin problems of the origin of tetrapod vertebrates—unraveling the ancestral lineages on both sides of the transition and understanding the ecological conditions that drove and controlled the process—have constituted one of the most intriguing of all subjects in vertebrate evolution.

The origin of tetrapods is not only one of the longest standing (and still not fully resolved) fields in vertebrate evolution, it has always commanded considerable popular interest. Some of this probably comes from a natural interest on the part of humans in their own forebears. The discovery of living lungfishes in the nineteenth century sparked interest because of their apparent intermediate position between other kinds of fishes and amphibians. (As is well known, the South American lungfish *Lepidosiren* was actually first described as a degenerate amphibian.) The discovery of the Australian lungfish provided a direct link between a living form (a “living fossil” to use Darwin’s term) and well-known Triassic fossils. The lungfishes therefore accorded well with Darwinian theory, just as did *Archaeopteryx*. The discovery of the living coelacanth *Latimeria* in 1938 continues to spark public interest (Thomson, 1991a).

It also happened that fossil lobe-finned fishes were prominent among the faunas collected widely in the nineteenth century from the Old Red Sandstone of Europe (principally Britain and Russia) and its equivalents in America (the Catskill and Escuminac formations). With the progressive discovery of fossil remains of Crossopterygii, the “Rhipidistia” replaced Dipnoi in discussions of the tetrapod ancestor/sister group/relative (one has to bear in mind the relevant terminology of the day).

The subject also got a great boost in the early part of this century with discussion of the geological/ecological significance of redbed deposits, within which many lobe-fin fish fossils were found. Were they indica-

tors of very dry tropical conditions? Barrell's (1916) classic paper on the influence of Silurian and Devonian climates on the rise of air-breathing vertebrates set the stage for much future discussion.

Most of all, the origin of tetrapods provides the paradigmatic example of a major evolutionary shift—from water to land, from gill to lung-breathing, from swimming to walking and running. As such, it is a problem the solution of which cannot come from paleontology alone but requires the full panoply of biological approaches—morphology, physiology, biochemistry, embryology, and ecology.

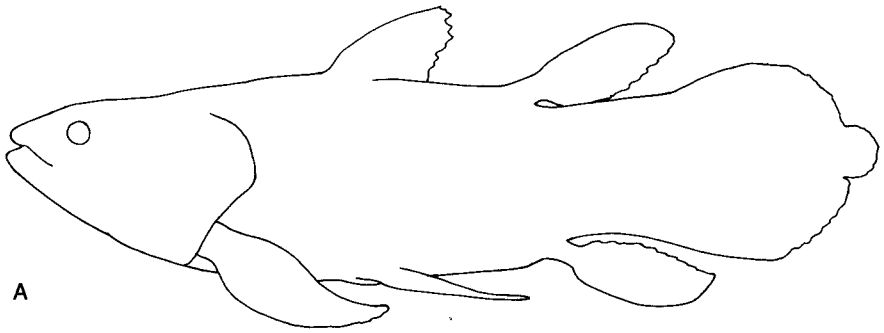
Because the subject has always been so centrally in the scientific spotlight, studies of the origin of tetrapods have been unusually theory-laden. Proponents of rival theories have contested with a ferocity that is otherwise more common to politicians, have interpreted the fossil data with more zeal than prudence, and have promoted their views with the assiduity of sellers of patent medicine. As a result the literature of the subject is difficult to read without a background understanding of the theoretical allegiances of the authors (for example, with respect to monophyletic or diphyletic origins and particularly with respect to a putative ancestral role for lungfishes). But this simply makes the subject more interesting; science being, after all, an intensely human avocation and thus subject to all the common human foibles.

This essay, however, honors John Ostrom who is someone who has always managed to avoid the pitfalls of competitive paleontology. I would also like it to honor the late Alfred Sherwood Romer, who got me into this mess in the first place.

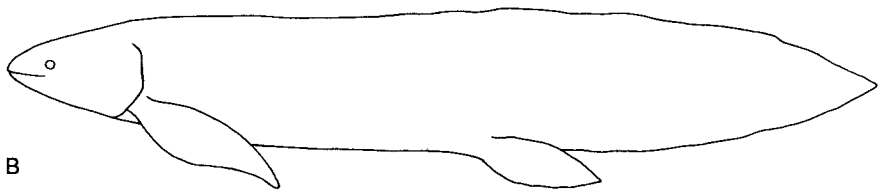
I will not attempt a complete review of every hiccup in the vast literature on tetrapod origins but will try to summarize our present state of knowledge in the following monosyllabic areas: *what* (evolved); *who* (were the organisms concerned); *when* (did the transition occur); *where* (geographically); *why* (ecologically); and *how* (by what particular evolutionary mechanisms)?

WHAT?

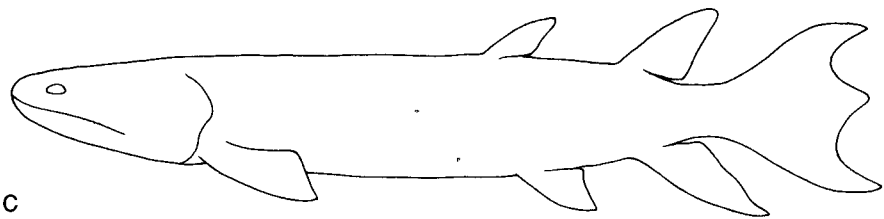
The earliest fossil tetrapods we presently know are an ill-assorted lot. From the Devonian of Greenland, in addition to the famous *Ichthyostega* (the morphology of which is known in some detail, due to Save-Soderbergh, 1932 and Jarvik, 1980; fig. 1), there are also the tantalizingly incomplete *Ichthyostegopsis*, (Save-Soderbergh, 1932) and *Acanthostega* (Jarvik, 1980; Clack, 1989; Coates and Clack, 1990, 1991). From Brazil there is an Upper Devonian trackway (Leonardi, 1983). From Russia we have *Tulerpeton* (Lebedev, 1984), consisting of an incomplete limb and girdle. From Australia there is a tantalizing trackway (Warren, Jupp, and Bolton, 1986), a later trackway (Warren and Wakefield, 1972), and a single lower jaw (*Metaxygnathus*; Campbell and Bell, 1977). These fossils are already quite diverse in morphology; for example, *Ichthyostega* is a mosaic of advanced characters (in the skull roof) and primitive ones (such as a fish-like tail). Recent collecting by Clack and her associates in Greenland



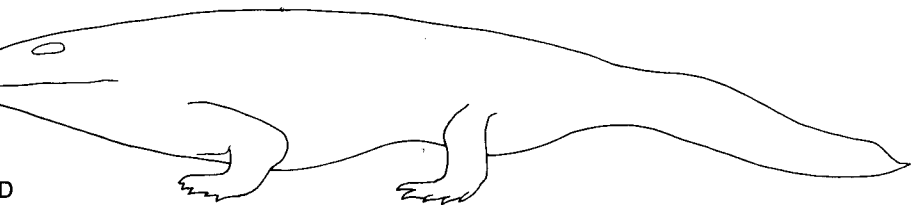
A



B



C



D

Fig. 1. Outline drawings of (A) modern *Latimeria* (coelacanth), (B) modern *Neoceratodus* (dipnoan), (C) Devonian *Eusthenopteron* (osteolepiform), (D) the Devonian tetrapod *Ichthyostega*.

has produced some interesting new results with respect to *Acanthostega*, showing that sometimes an ounce of data is worth a pound of theorizing. For example, the pentadactyl limb turns out not to be an apomorphy of tetrapods but a later derived character. *Acanthostega*, *Ichthyostega*, and *Tulerpeton* were polydactylous (fig. 2; Coates and Clack, 1990; compare Cook, 1990). (This result is less surprising if one remembers that the rhizodontid fish *Sauripterus* (fig. 3) has at least eleven rays in its fore limb: Thomson, 1968. Here is a case where too much attention has been paid to the fish species *Eusthenopteron foordi*.)

A difficult question is: What is a tetrapod, and, in particular, what was the first tetrapod? Obvious features characterizing most amphibians, at least, would be the following.

1. Absence of gills, total dependence on breathing through the lungs and skin. Carbon dioxide principally excreted through the lungs (only partially through the skin).

2. Circulatory pattern with discrete pulmonary circulation and separation of blood in the ventricle.

3. Limbs with carpals/tarsals and digits.

4. Ulna and radius more or less equal in length and both participating in the "wrist" joint.

5. Opposite flexure of the elbow and knee joints.

6. Torsion of the humerus.

7. Shoulder girdle and pelvic girdle modified for weight support and limb function.

8. True choana as an air passage-way; mucus cells in the lining to protect against desiccation; connected with the nasal organ.

9. Axial skeleton reinforced for support (weight bearing) against gravity.

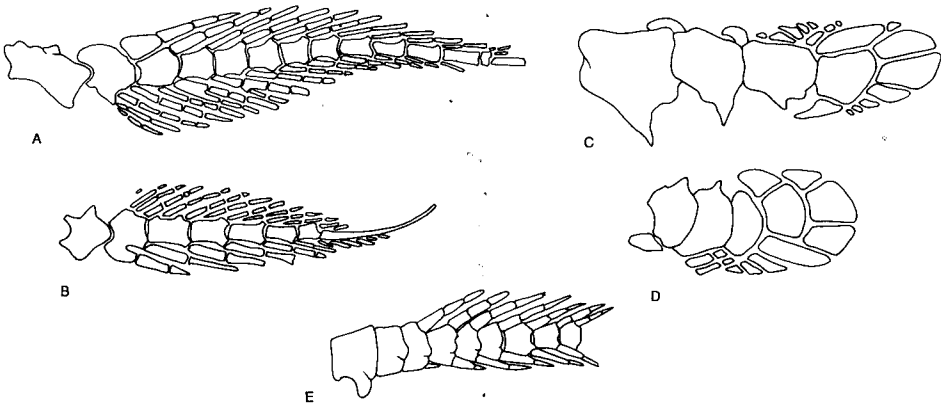


Fig. 2. Left fin skeletons of (A) *Neoceratodus* (pectoral), (B) *Neoceratodus* (pelvic), (C) *Latimeria* (pectoral), (D) *Latimeria* (pelvic), (E) the porolepiform *Glyptolepis* (pectoral), after Rosen (1981), and Ahlberg (1989).

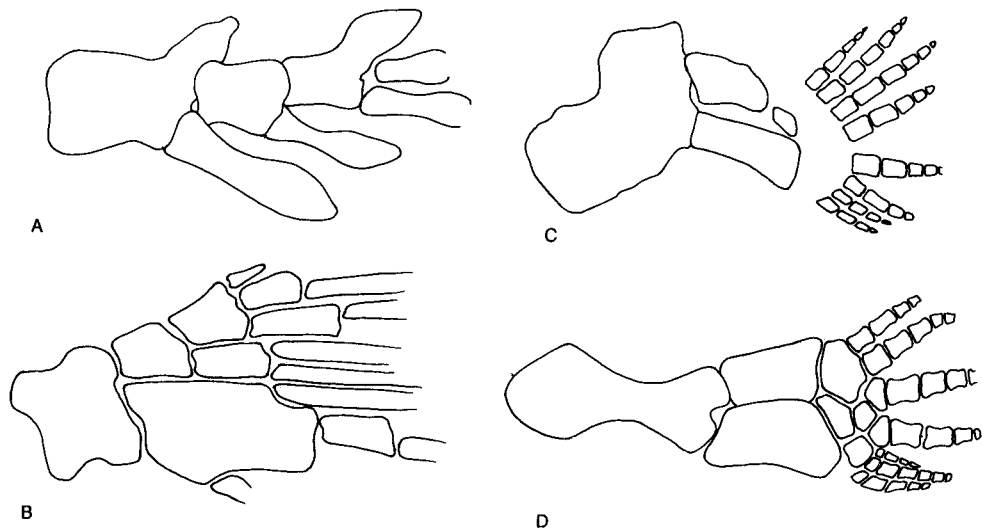


Fig. 3. Fin skeletons of (A) *Eusthenopteron* (osteolepiform pectoral), (B) *Sauripterus* (osteolepiform, pectoral), (C) *Acanthostega* (tetrapod, pectoral), (D) *Ichthyostega* (tetrapod, pelvic). After Andrews and Westoll (1970), Thomson (1972), and Coates and Clack (1990).

10. True post-mandibular depressor mandibulae muscle system and retroarticular process.

11. A middle ear (including stapes, tympanic cavity, and possibly ear drum) connected to a fenestra ovalis.

12. The principal nitrogenous waste product is urea, although ammonia is still excreted through the skin.

13. Skull with frontals and nasals.

14. A relatively large egg, a fully aquatic larva with external gills, and therefore a more or less pronounced "metamorphosis" between larva and adult.

One approach would be to rely on the highly specific individual characters as used in a cladistic analysis. Then we would assemble a list that included some of the preceding list, but also others, such as:

15. Exclusion of dentary from the adductor fossa.

16. Sutural contact between presplenial and anterior coronoid.

17. External naris positioned very low down, right at the margin of the mouth.

These lists are somewhat misleading, for paradoxically opposite reasons. First, characters may change in isolation, leading to a mosaic condition. Second, many morphological characters do not exist alone. It would be more informative to isolate complexes of characters that must have been changed together. The previous list would then boil down to the following groups: (A) gill, jaw, and ear; (B) axial skeleton and limbs;

(C) respiratory system, circulatory system, nasal apparatus, skin, and even excretory system; (D) reproduction and life cycle.

The real difficulty in trying to define the *first* tetrapod as opposed to a *generalized* tetrapod is that not all these characters could logically be expected to be present in all the very earliest tetrapods. What characters appeared first and in what order? How many characters would have had to change before we would consider that the line between fish and tetrapod was crossed (Thomson, 1991b)?

At the same time, of course, in considering the mutual definitions of fishes and tetrapods, a lot depends upon the group of fishes projected as the possible tetrapod ancestor. Some of the characters listed above were already present in some lobe-fin lineages and therefore cannot characterize tetrapods.

As an example of the difficulty of characterizing the transitional fish-tetrapods, we can take the mandible from Australia (*Metaxygnathus*). This specimen was assigned to the tetrapods by Campbell and Bell (1977) on the basis of interpretations of the musculature and the assumption that the gill apparatus had been lost. In view of the evidence from *Acanthostega*, this assumption is no longer justified. However, Clack (1989a) lists two tetrapod characters that *Metaxygnathus* has—numbers 15 and 16 on the previous list. (In fact, the description by Campbell and Bell is not completely clear on point 15.) Interestingly, *Ichthyostega*, obviously a mosaic form, lacks these two characters, retaining the osteolepiform condition. In other respects the jaw is highly plesiomorphic for lobe-finned fishes. To what extent can we extrapolate from the presence of two “tetrapod” characters to conclude, for example, that *Metaxygnathus* would have had tetrapod limbs? Is this simply the jaw of an advanced “mosaic” fish?

Before I began drafting this paper, I was strongly of the opinion that any organism still having internal gills would have to be considered a fish. But Coates and Clack (1991) have now released another new result from *Acanthostega*. Judging from the nature of branchial skeleton and the cleithrum, this animal had a gill chamber and reduced internal gills and was still at least a facultative gill-breather. As *Acanthostega* has already developed very tetrapod-like limbs and, according to Clack, 1989b, a stapes (and therefore presumably a middle ear), we obviously must consider it to be on the tetrapod side of the transition. It is worth noting, however, that *Acanthostega* did not preserve the full piscine internal gill arrangement. The hyomandibular was already modified to (or toward) the “stapes” configuration, and the opercular bones were apparently already lost.

This discovery points up the fact that it is difficult and perhaps impossible to predict from theory which character states would be “mosaic.” We need empirical fossil evidence; but, if *Acanthostega* really does have internal gills, then the events of the transition are beginning to become clearer. We now have confirmatory evidence that the transitional forms were basically aquatic in habitat, and we should expect that some

aquatic adaptations were retained (perhaps to varying degrees in different lineages) quite far across the tetrapod side of the transition. On the other hand, it is confirmed that the transitional organisms were capable of (and adapted for) spending major portions of time either completely out of the water or at least only partially submerged (for example, in their terrestrial type of tetrapod limbs and "tetrapod" suspensorium and middle ear).

WHO?

While we still do not have any really intermediate fossil forms between fishes and tetrapods (we are getting closer, with the description of *Panderichthys* and *Elpistostege*; see later), we are free to argue vociferously about the identity of the group of fishes that must be the tetrapod ancestor. (This is like the joke about the baseball player who, although he was terrible at bat, couldn't field either.)

Lobe-finned fishes are bony fishes with two dorsal fins. The first dorsal is wholly spiny; the second dorsal, anal, and both sets of paired fins are lobed with an internal skeleton (in the case of pectoral and pelvic fins, with 4 mesomeres) and musculature. There are bony sclerotic elements in the eye and a two-headed hyomandibular. Within the group, many characters are variously described as primitive or specialized (for example, the "micromeric" skull pattern of Dipnoi). Cosmine is common to Dipnoi and many "Rhipidistia" but not the coelacanth. Paired lungs are primitive for the whole group, but not unique, as the first Actinopterygii also had lungs.

Early classifications of the lobe-fins used the term *Crossopterygii* for the entire group. At that time, the primitive actinopterygian *Polypterus* was also included as a lobe-fin. An exchange of letters in *Nature* (Romer, 1955; Trewavas and others, 1955) finally established a parity between two groups—Dipnoi and *Crossopterygii*, as subunits of the larger group *Sarcopterygii*. The *Crossopterygii* then included the *Coelacanthini* and the so-called *Rhipidistia* (essentially all the other non-dipnoan lobe-fins then known) and was defined in part by the possession of an intracranial joint. With the discovery of the newer groups of lobe-fins, discussion of lobe-fin interrelationships has been much more interesting, leading to the view that neither of the terms *Rhipidistia* or *Crossopterygii* defines a monophyletic group, and both are therefore quite irrelevant.

Modern debate over lobe-fin relationships has been marked by two theoretical positions and related disputes over the question of which lobe-fins possessed a choana homologous to that of tetrapods. Jarvik (1942) sought to show that both principal rhipidistian subgroups (*Osteolepiformes* and *Porolepiformes*) had a true choana, absent in all other fishes. An early debate concerned his theory of diphyletic origin of tetrapods (*Urodela* from *Porolepiformes* and all the rest from *Osteolepiformes*). This theory derived in turn from previous attempts to link at least some tetrapods with lungfishes. Much time was wasted on confronting this theory (including, *mea culpa*, Thomson, 1968). Eventually the

standard "osteolepiform ancestor" view (see review of history in Schaefer, 1965) prevailed, until Rosen (1981) revived the theory of a close dipnoan-tetrapod relationship, restated in terms of sister-groups. However, their effort was weakened by adherence to the view that only living forms could be used in cladistic analysis. As the osteolepiforms have no living representatives they could scarcely be expected to fare well in such an analysis. Rosen and others (1981) also seem to have had a preoccupation with showing that the osteolepiforms had no choana while the dipnoans (whose narial apparatus has been the subject of endless debate, compare Jarvik, 1942; Thomson, 1965; Fox, 1965; Bertmar, 1965, 1966) were rather less critically assigned a true choana on the basis of the reconstruction of a single fossil genus (Miles, 1977). A thorough critical review of Rosen and others (1981) is to be found in Panchen and Smithson (1987) and Yu (1990).

As is well known, while cladistic analyses and the classifications based on them are reasonably well grounded in logic, no such rigorous methodology is available for schemes of ancestry-descendent status. This leaves the evolutionist who is interested in ancestry in something of a quandary except that, whether we are dealing with sister-group or ancestor-descendent relationships, one's hypotheses are based on the same characters in the same taxa. However, there is no doubt that the place to start is with the cladogram: one can measure even *ad hoc* hypotheses of ancestry against the patterns of relationship indicated in a cladogram. Unfortunately, the current fashion (popular in some quarters, at least) of assessing cladistic relationship solely on the basis of living forms is worthless in a case like the fish-tetrapod complex, because half the possible ancestors in which one is interested are fossil forms. None of the questions raised by a cladogram of lungfishes, coelacanths, and tetrapods can be answered by those three alone (there might be some value in this approach if the coelacanths were thought to be the sister group of the osteolepiforms, as in the old "Crossopterygii" classification, but this has long since been abandoned).

Any hypothesis of the ancestry of tetrapods from lobe-fins must test on equal terms the competing claims of lungfishes, coelacanths, and osteolepiforms. Otherwise, it is, as Romer used to describe such matters, like a performance of Hamlet without the melancholy Dane. However, the inadequate approach of relying on the cladistics of living forms continues, most recently with respect to DNA data for coelacanths (Gorr, Kleinschmidt, and Fricke, 1991; Forey, 1991). The enthusiasts for this approach seem to have overlooked the fact that, if the osteolepiforms did in fact give rise to the tetrapods, then three sets of living descendent forms are available for comparison—modern lungfishes (derived from Devonian lungfishes), *Latimeria* (derived from Devonian coelacanths), and modern amphibians (derived from Devonian osteolepiforms). This makes comparisons of frogs or urodeles with lungfishes and coelacanths logically incapable of testing anything except how different modern

amphibians, lungfish, and coelacanths are from each other—which is interesting, but besides the main point.

It is also clear that a cladogram like that of Rosen and others (1981) where the characters are subjectively “fitted” is less useful than one in which the characters are simply collected and objectively analyzed by one of the several valuable computer programs now available.

Modern discussions of lobe-fin relationships are greatly illuminated by analysis of a number of newly discovered forms, principally from regions such as Arctic Canada, China, and Australia that have come to be better sampled. The result of a great deal of recent work is to show that any analysis of lobe-fin relationships must take into account the following distinct monophyletic groups of Sarcopterygii (figs. 1–6).

Coelacanthini: These are the fishes that the living coelacanth *Latimeria chalumnae* has made famous (Thomson, 1991a). In terms of morphological diversity the group is quite conservative (Schaeffer, 1952), except for the single genus *Laugia* which has modified pectoral and pelvic fins positions convergent with advanced perciform teleosts. Sample diagnostic characters include: trifold tail, rostral organ, two infradentaries, dentary absent.

Porolepiformes: This is still a poorly known group, even though *Glyptolepis* and *Holoptychius* were among the first lobe-fins to be described (from both North America and the Scottish Old Red Sandstone). New material has now been found from China that extends our knowledge of this group (Yu, 1990). A recent study of the postcranial skeleton, especially the paired fins (Ahlberg, 1989), has done a great deal to complement earlier studies of the head (review in Jarvik, 1972). Despite earlier studies, it is now known that the group does not, after all, have a choana. Key characters include the pattern of bones in the skull roof, the cheek/squamosal configuration, dendrodont teeth, and scale structure.

Dipnoi: This group is both well known and easily recognized, due to the existence of three living genera and the extreme apomorphy of the whole group. Key characters include: autostylic skull, tooth plates, skull roof, cheek, nasal apparatus, and a posteriorly extended parasphenoid.

Osteolepiformes: This group is made up of the familiar families Osteolepidae and Eusthenopteridae, together with a number of lesser known and less well-definable families such as the Megalichthyidae. The most primitive member is probably *Canowindra* from Australia (Thomson, 1973; Long, 1985, 1990). The internal relationships of the group are still confused, but they hold together fairly well as a single unit, on the basis of the following characters: a true choana, the dermal bone patterns of the skull roof and cheek, fin type, and basal scutes in the fins.

Rhizodontiformes: This is another group that has been known since at least 1835, with much taxonomic confusion (see Thomson, 1966; An-

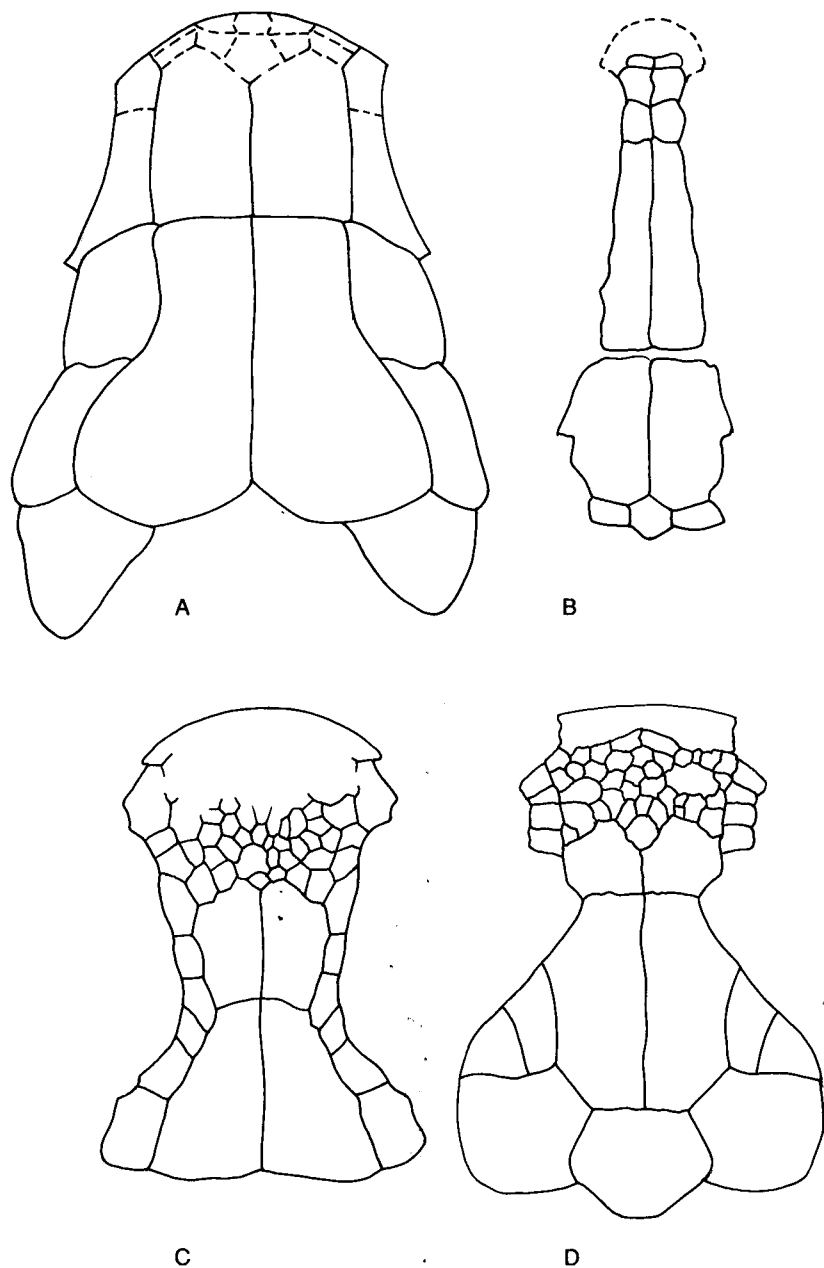


Fig. 4. Dorsal view of the skull table of (A) *Strunius* (onychodontiform), (B) *Whiteia* (coelacanth), (C) *Powichthys*, (D) *Holoptychius* (porolepiform). After Jessen (1980), and Jarvik (1980).

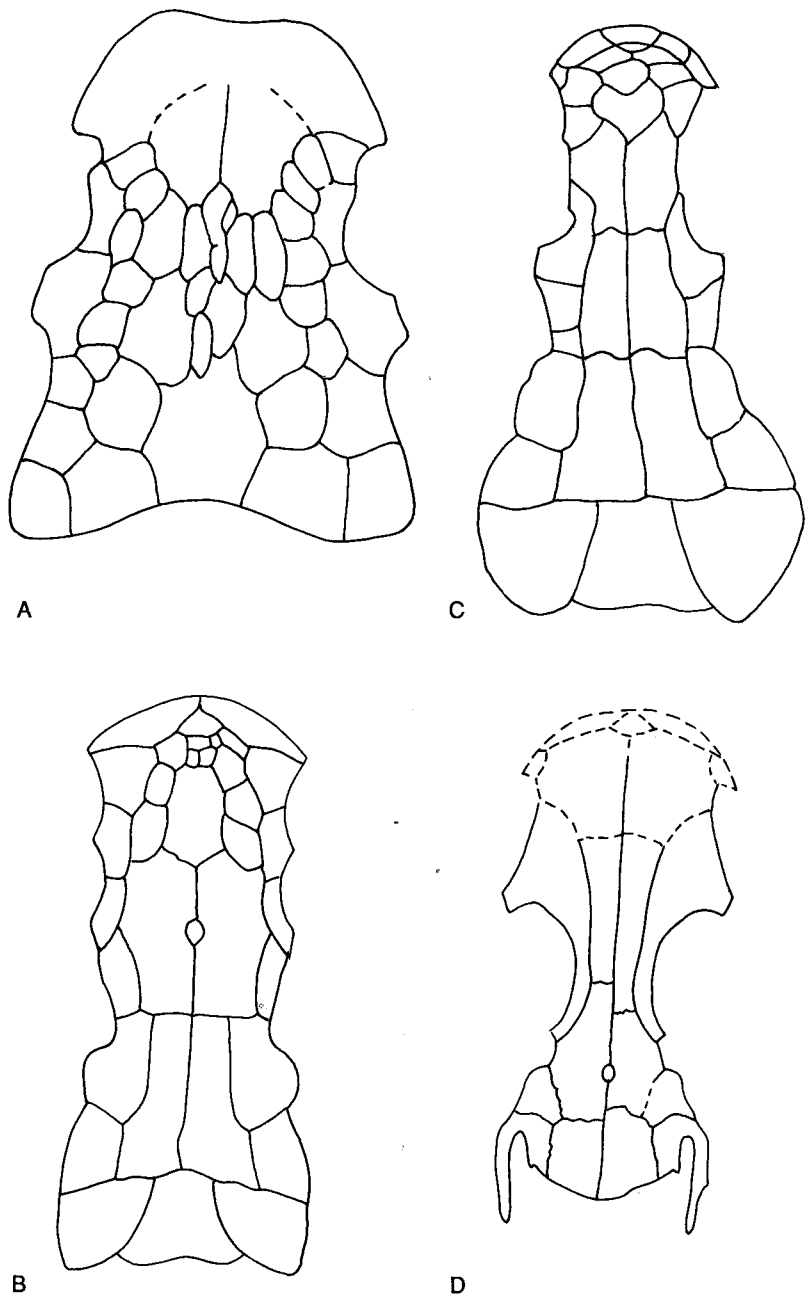


Fig. 5. Dorsal view of the skull table of (A) *Dipterus* (dipnoan), (B) *Eusthenopteron* (osteolepiform), (C) *Panderichthys*, (D) *Acanthostega* (tetrapod). After Jarvik (1980), Schultze and Arsenault (1989), and Clack (1989a).

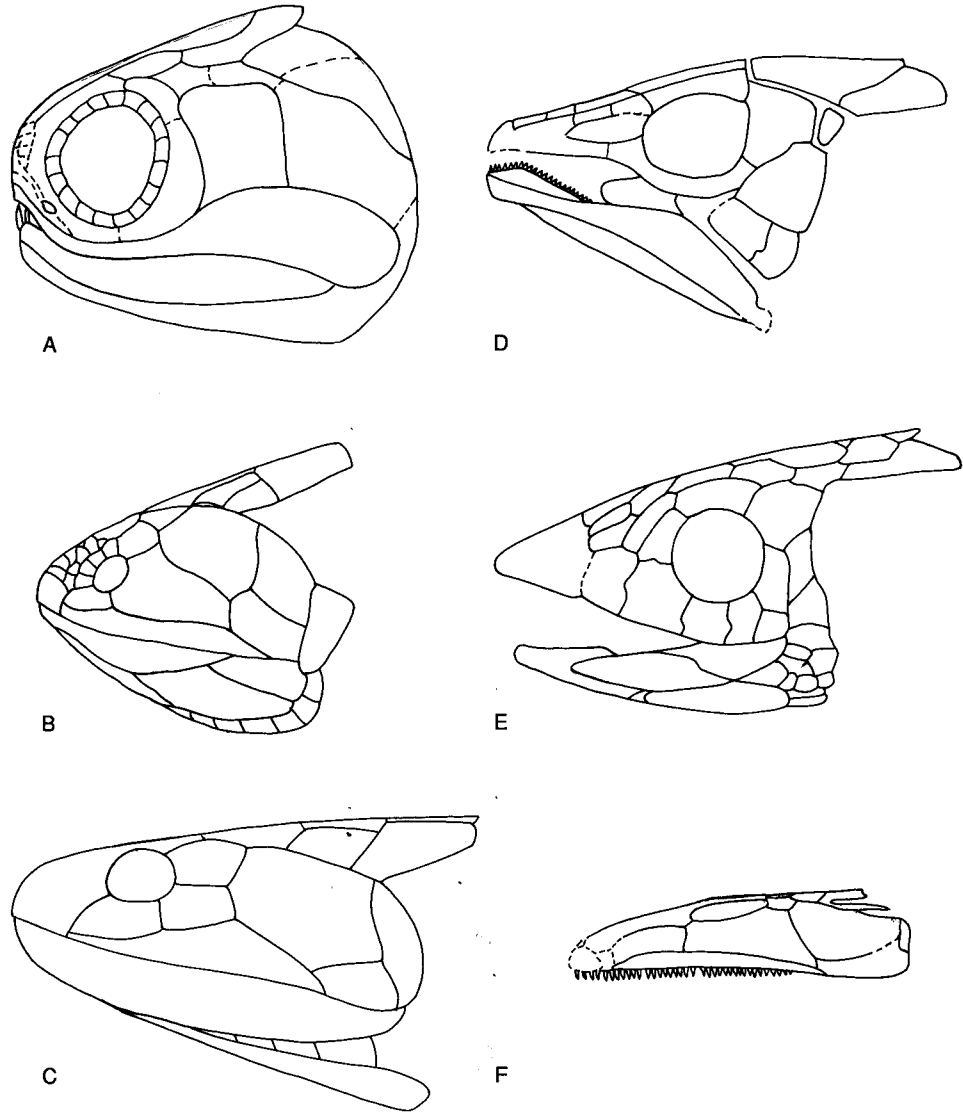


Fig. 6. Left lateral view of the cheek region of (A) *Strunius* (onychodontiform), (B) *Holoptychius* (porolepiform), (C) *Eusthenopteron* (osteolepiform), (D) *Whiteia* (coelacanth), (E) *Dipterus* (dipnoan), (F) *Acanthostega* (tetrapod). After Jarvik (1980).

drews 1985). Recently a partial study of *Strepsodus* has been completed by Andrews (1985), but the group as a whole is very poorly known. *Rhizodopsis*, of which considerable Coal Measures material exists, has never been properly described. Except for a superb fin (fig. 2), *Sauripterus* is completely unknown. Key features include: a long ventral portion of cleithrum, folding of the teeth, scale pattern.

Panderichthys: This genus was named by Pander for material from the Soviet Union (see Vorobeja, 1962, 1973, 1977). Recently discovered material from the lowermost Upper Devonian Escuminac Formation of Canada shows that the fish which Westoll (1938) called *Elpistostege* is closely allied to (perhaps even congeneric with) *Panderichthys* (Schultze and Arsenault, 1985). These two genera are particularly important because, of all lobe-finned fishes, they are most closely similar to the early amphibians. Key features include: the skull roof pattern with frontals, parietals and postparietals, low position of the external naris at the mouth margin, absence of extratemporal.

Onychodontiformes: This group has been known since 1857 on the basis of material of *Onychodus*, from the Middle Devonian of North America and Late Devonian of Europe. More recently, Jessen (1966) discovered a second genus, *Strunius*, from which a great deal of information has been gathered (and for which the group has, by some people, been unnecessarily renamed *Strunioformes*). A full description of some superb material of *Onychodus* from Australia is currently under preparation by S. M. Andrews. While *Strunius* is a smallish fish, *Onychodus* reaches the length of one meter or more. The body shape of *Onychodus* has not yet been described, but that of *Strunius* shows a pointed trifid tail not unlike either an adult coelacanth or a juvenile osteolepiform (see Thomson and Hahn, 1968). Key features include: single submandibular, fused infradentaries, deep lobe of posterior maxilla, single coronoid:

Powichthys: This genus is known from a very few specimens from Arctic Canada (Jessen, 1980). Only parts of the skull are known, the skull in general has a mixture of lungfish and porolepiform features. The intracranial joint is present.

Youngolepis: This genus from China (Zhang and Yu, 1981) is very closely related to *Powichthys*.

Diabolepis: This is another genus from China with characteristics that are somewhat "mosaic" in nature (Zhang and Yu, 1984). There has been considerable difficulty in knowing whether it is related to the Dipnoi or the Porolepiformes. The material is still incomplete.

Various schemes of lobe-fin relationships proposed in the last 10 yrs. are summarized in figures 7 and 8. The most complete cladistic analysis currently available (Yu, 1990) is shown in figure 9. Yu's analysis (like most of the others) shows a close relationship between tetrapods and osteolepiforms. *Panderichthys* plus *Elpistostege* form the closest sister group of tetrapods, although the number of characters available for analysis is

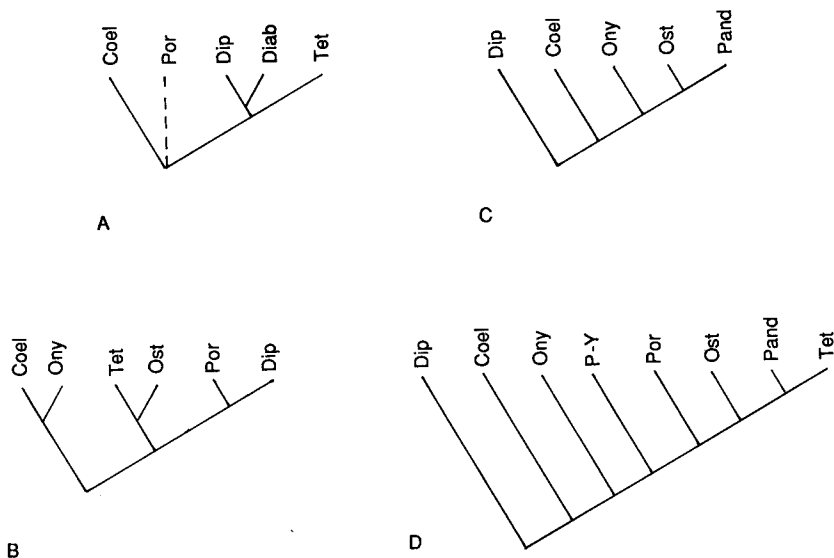


Fig. 7. Cladograms of fish-tetrapod relationships, redrawn after (A) Forey, (B) Maisey, (C) Lund and Lund, (D). Schultze. In this and later cladograms, abbreviations as follows: COEL-Coelacanthiformes, ONY Onchydontiformes, POR-Porolepiformes, POW-YOUNG or P-Y-*Powichthys* + *Youngolepis*, DIP-Dipnoi, DIAB-*Diabolepis*, RHZ-Rhizodontiformes, OST-Osteolepiformes, PAND-*Panderichthys*, TET-Tetrapoda.

small. The crucial features linking osteolepiforms (*sensu lato*) and tetrapods are those of the limb skeleton and skull roof.

Rosen and others (1981) concluded that previous attempts to discuss lobe-fin/tetrapod relationships had been led astray by two factors—a blind adherence to an evolutionary view of systematic relationships and the unsuspected plesiomorphy of tetrapod and osteolepiform characters. While many of their methodological criticisms were refreshingly correct (and amply, if unwittingly, confirmed by some typically reactionary reviews), it is now clear that their analysis was woundingly theory-laden. And it seems to be the case that the anomalous factor in the analysis of lobe-fins is, in fact, *apomorphy* of the lungfish skeleton, together with plesiomorphy of features of lungfish soft anatomy.

Yu's analysis shows that the porolepiforms do not have a close relationship to the osteolepiforms but that their closest relatives are the lungfishes. The choana is a synapomorphy of osteolepiforms and tetrapods and is lacking in all other lobe-fin groups. The lungfishes have a narial condition convergent with that of tetrapods. The intracranial joint may be plesiomorphous for all lobe-fins and therefore was lost more than once.

The result of all this work is an extremely strong case for a cladogram that is fully consistent with the hypothesis of an ancestral osteolepiform/

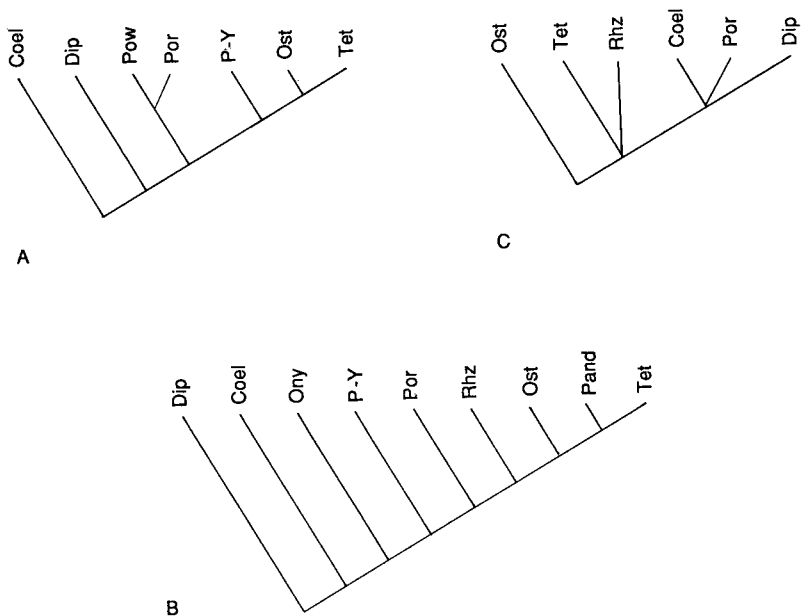


Fig. 8. Cladograms of fish-tetrapod relationships, redrawn after (A) Panchen and Smithson (1987), (B) Ahlberg (1989), (C) Long (1990). For abbreviations, see figure 7.

tetrapod relationship, to the exclusion of other lobe-fin groups. A revised classification based on this analysis (should one be necessary) would have to look something like that shown in figure 10 (which is hopelessly clumsy, especially when the new names are chosen to be both recognizable and disposable).

WHEN

Over the last few decades, the date of earliest record for most of the lobe-finned fish groups has been pushed back to the Early Devonian

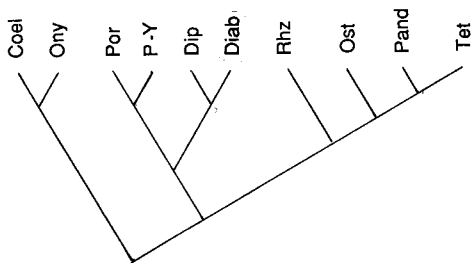


Fig. 9. Cladogram of fish-tetrapod relationships, redrawn after Yu (1990); see also figure 13. For abbreviations, see figure 7.

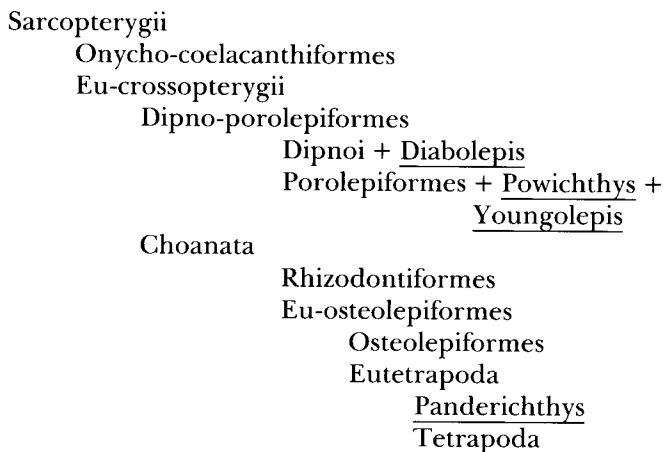


Fig. 10. Classification of lobe-finned fishes and tetrapods resulting from Yu's (1990) cladogram of relationships.

(figs. 11 and 12). None has yet been found in the Silurian, although a probable sister group, the Lophosteidae, is now known from the Late Silurian of Europe. In looking at the range of available cladograms of lobe-fin relationships (figs. 7-9; compare fig. 13), it is obvious that the split between Actinopterygii and Sarcopterygii must have occurred at least in the Late Silurian and that the major lineages of lobe-fin were separate in the Early Devonian. However, it is not clear when the lobe-fin/tetrapod divergence occurred. The problem lies in the fossil record of the tetrapods. The East Greenland, Russian, and Brazilian records are all Late Devonian (Famennian). The Australian jaw (if it is tetrapod) is also Famennian. The plesiomorphic sister-group of tetrapods (*Panderichthyidae*) is Late Devonian (Frasnian) in age. But the Australian trackway is inconclusive both as a record of tetrapods (however "good" the track, a definitive set of skeletal remains is still needed) and with respect to age. It is listed as "possible Early Devonian" (Warren, Jupp, and Bolton, 1986).

Setting aside the Australian trackway, the shape of the cladogram places the split between the osteolepiforms and *Panderichthys* plus tetrapods as no later than in the early Middle Devonian. If the trackway is genuinely Early Devonian in age, then all the divergences within the osteolepiform plus tetrapods group must have happened in the Early Devonian. A conservative view would be to reserve judgement on the age of the trackway, and this would then place the split between the *Panderichthys* and tetrapod lineages as most probably having occurred at some point between the late Early Devonian and earliest Late Devonian and probably no more recently than the Givetian (Middle Devonian).

This means that the search for the earliest tetrapods, which has hithertofore been largely concentrated on the latest Devonian rocks,

| | | N.Am-Eu | S.Am | S.China | Ant | Aust |
|-----------------|-----------|---------------------|------|---------|---------|----------|
| UPPER DEVONIAN | Fammenian | Tet Rhiz Pand | Tet | | | Tet |
| | Frasnian | | | | | Ony |
| MIDDLE DEVONIAN | Givetian | Coel | | | Rhz Ost | |
| | Couvinian | Ost Ony | | | | Ost |
| LOWER DEVONIAN | Emsian | | | | | Dip ?Tet |
| | Sieginian | Por Dip | | | | |
| | Gedinnian | P-Y | | P-Y Por | | |

Fig. 12. Time distribution of Devonian lobe-finned fishes and tetrapods, by continent. For abbreviations, see figure 7.

assumed to be primarily freshwater forms, both in origin and distribution, with only secondary excursions into marine conditions. It had been almost universally assumed that the fish-to-tetrapod transition had occurred in fresh water, not only because of the lobe-fins but also because virtually all modern amphibians are freshwater organisms.

The prevailing view used to be that the origin of tetrapods had occurred in shallow fresh water, driven by tropical conditions, and at least seasonal drying and hence lack of dissolved oxygen in the water (see further discussion below). This view was questioned by Packard (1974, 1976) who pointed out that all the physiological/ecological arguments concerning dissolved oxygen would apply even more strongly in salt-water conditions.

In 1969 (Thomson, 1969b, see also Thomson, 1980) I showed that, far from being primary freshwater fishes, all lobe-finned groups are in fact first marine in distribution and only later diversified from coastal

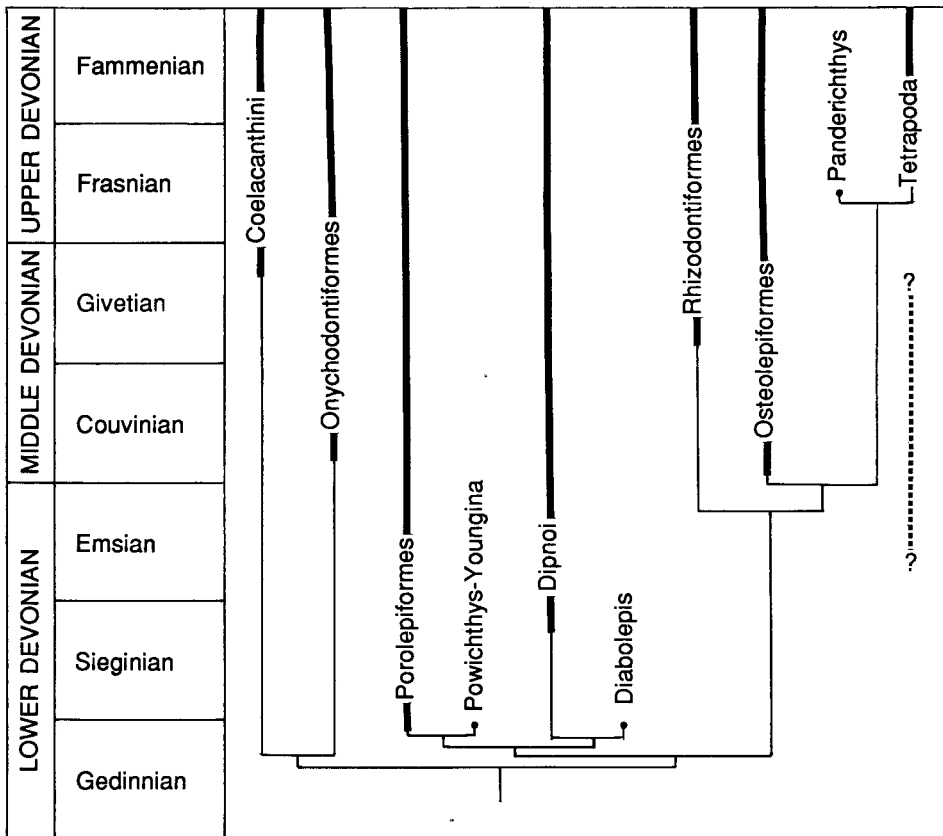


Fig. 13. Cladogram of fish-tetrapod relationships redrawn after Yu (1990) showing possible time of divergences; see also figure 9. Note that if the report of an Emsian tetrapod trackway is correct, then the point of divergence between *Panderichthys*+Tetrapoda and Osteolepiformes is pushed back to the early Emsian, but the shape of the cladogram is not violated. For abbreviations, see figure 7.

marine conditions to coastal plain freshwater (rivers and marshes, with possibility of anadromy) and purely inland freshwater drainage basins.

Furthermore, comparative physiological evidence points in the same direction. We now know that both the living coelacanth *Latimeria* (marine) and the living lungfishes (fresh water) can synthesize urea in the liver, thus giving a mechanism (potential in the case of living lungfishes) for osmoregulation in sea water. (There is a strange convergence in that, for any advanced fish with a low total serum osmolarity from dissolved electrolytes, living in the sea is much like living on land—in both cases they are living in a physiological desert.) The living lungfishes use a mechanism of urea retention as a device for saving water during estiva-

tion (to *avoid* terrestrial conditions). Tetrapods use the same device to accommodate *to* terrestrial conditions (Thomson, 1969b).

This information then greatly informs the question of the origins and paleogeographical distributions of lobe-fins and tetrapods.

Paleogeography

In figure 12, the distributions of the first members of each of the Devonian lobe-finned fish groups and the Devonian tetrapod occurrences are plotted by geological age for each major continental mass (except for India in which no Devonian lobe-finned fishes are known). The time-sequence of the plot generally matches the cladogram; for example, porolepiforms and lungfishes appear first in the record. The obvious anomaly is the relatively late first appearance of coelacanths. However, as can be seen, it is difficult to decipher any simple geographic pattern in this scheme.

Long (1990) suggested that the fossil record supports the view that the Porolepiformes, Dipnoi, and Coelacanthini had arisen in North America/Europe and that *Youngolepis*, Rhizodontiformes, and Osteolepiformes together with tetrapods had evolved in East Gondwana. However, it is clear that *Youngolepis* (Gedinnian, South China) and *Powichthys* (Gedinnian, Canadian Arctic) are very closely related to each other and to the Porolepiformes. Further, Porolepiformes (*sensu stricto*) are in any case found in South China along with *Youngolepis* (Yu, 1990). The same South China beds also contain *Diabolepis* which is a lungfish relative, and the Early Devonian record of lungfishes in Australia is nearly as old as that in North America. The Osteolepiformes first occur at roughly the same time in North America, Europe, and Australia. Long placed weight on estimates of the relative primitiveness of the East Gondwana forms, but the argument can be turned around: if the North American/European osteolepiforms, which are older than the East Gondwana forms, are also more derived, then they must have been preceded by more primitive osteolepiforms—most economically with the same distribution.

As long as the geological age of the reported "Early Devonian" trackway from Australia is tentative and no skeletal remains are known, to conclude that tetrapods arose in, and radiated from, East Gondwana is premature. If we look at the distribution of actual skeletal remains and grant that *Metaxygnathus* is a tetrapod, then the tetrapods are found world wide during the Upper Devonian. Their closest sister group (Panderichthyidae), also Late Devonian, is North American-European.

Recent paleogeographic reconstructions for the Devonian still differ somewhat, with the main uncertainties being two-fold: the position of eastern Gondwana (and the rotation of all Gondwana) during the Devonian and the relatively proximity of the land masses (fig. 14). During the Late Silurian, North America plus most of western Europe was widely separated from the other continental masses. During the Early Devonian they approached more closely, then they separated again by the end of the Devonian. The extent to which the continents approached and the

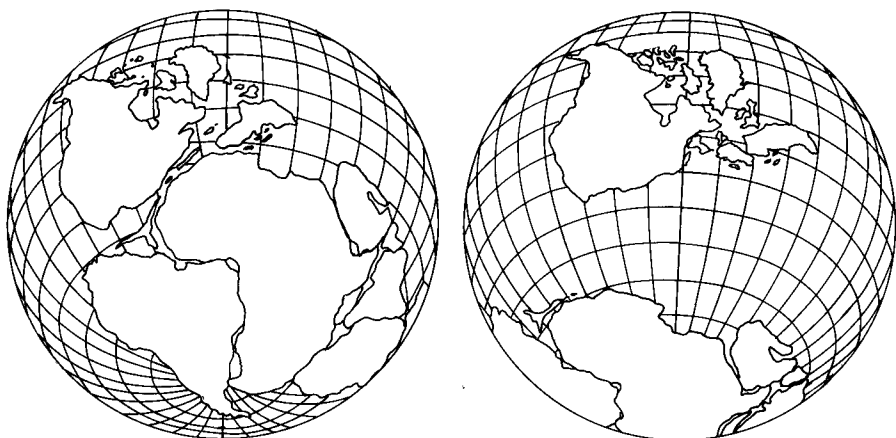


Fig. 14. Maps showing possible continental positions in (A) Early and (B) Middle Devonian. Opinions vary as to the time of close approximation of the continents and the Devonian latitude of Gondwana. After van der Voo (1986).

exact timing is still debated—most accounts have the continents separated only by a very narrow seaway either in the Early Devonian or Middle Devonian. Most reconstructions agree that the land masses were widely separated in the Late Devonian.

The question of continental position is important not only for patterns of diversification and dispersal of lobe-finned fishes but for climate as well. The best we can do at the moment is to identify an equatorial zone and a broad subtropical/temperate arid zone. The major inland basin areas where fossil lobe-fins have been found are tropical.

Putting all this together, one can tentatively conclude that the first diversification of the lobe-fins, consisting of porolepiforms, lungfishes, and coelacanths, occurred in a broad equatorial zone, in shallow seas bounding northern and eastern North America, the fragments of Europe and Asia, and the northern coasts of Gondwana. The Osteolepiformes arose slightly later in the same general zone. Subsequent diversifications of lobe-fins at lower taxonomic levels produced lineages that both invaded freshwater and dispersed to higher (southern) latitudes. One of these later diversifications produced the tetrapods. At this time it is not clear when this happened: I am personally inclined to discount the “Early Devonian” trackway from Australia and would place the origin of tetrapods at late Middle Devonian. But it could have been earlier. The first tetrapods diversified and dispersed widely and, like their lobe-finned sisters, apparently very quickly (especially if the origin is Givetian or younger). Given the present state of resolution of the record, it is not possible to fix the *place* of origin, but I suspect that (like the other lobe-fin origins) it occurred at low latitudes.

Thus paleogeography requires that migration of fish populations between, say, Greenland and Australia must have occurred at least through narrow epicontinental seas. The known tetrapod occurrences are all in fresh water deposits. If the more derived "osteolepiform plus tetrapod" assemblage really had consisted of primary freshwater organisms, then the origin of tetrapods could only have taken place at such time (possibly the early Devonian) as the plates were closely opposed, allowing migration to occur across and around land masses via fresh water—through stream capture, et cetera. However, since all Devonian lobe-fin groups evidently could live in salt water, then the question of migration of fishes (in time or space) presents no difficulty: they used the seas. In addition, we are forced to conclude that, unless the tetrapods diverged from the rest of the osteolepiforms at a time when all the continental plates were joined to the extent of having contiguous freshwater drainage (as seems unlikely), tolerance of marine conditions by the immediate ancestors of the tetrapods is also *required*. Finally, unless the tetrapods arose more than once on different continents, then tolerance of marine conditions by the first tetrapods was also required.

There is an interesting footnote to this subject. In the light of the newer discoveries from China and Australia, we are forced to recognize that the whole subject of tetrapod origins is strongly historically and therefore culturally conditioned. We had come to expect that the answer to the puzzle would come from study of European and North American fossils, because that is where both the fossils and the paleontologists were. Whether this was deliberately chauvinistic is hard to say (there was no real alternative). However, great as our knowledge of these northern faunas is, we should not be surprised to see our familiar schemes turned upside down and inside out, in the future. And it is amusing to ponder what would have been the state of the field if the nineteenth century paleontology of fishes (or, indeed, most groups of organisms) had begun in Australia and China and we now had the benefit of 150 yrs of intense collecting *there*—and knew next to nothing about the northern "Old" and "New" worlds.

WHY?

The radiations of lobe-finned fishes, especially of the Dipnoi and Osteolepiformes, created a range of fishes capable of living in coastal seas, in the rivers and swamps of the coastal plain, in great rivers, and in lakes large and small. Many of these fishes were small to medium-sized (up to 10 cm), living in schools like so many modern fishes. Some were huge freshwater predators—*Eusthenodon*, *Hynieria*, and *Rhizodus* reached two meters or more. *Sauripterus* (of which we really only know one great fin and a few bony plates and scales) probably exceeded three meters in length. These fishes were the equivalent of *Esox* and *Arapaima* in modern rivers.

Most of the lobe-fins were probably general carnivores, although the big ones were obviously piscivorous. The lungfishes were all bottom

feeding forms. With their massive tooth plates they crushed hard, shelly food material and soft-bodied worms and arthropods alike. Some fossil lungfishes may, like their modern descendants, also have included plant material in their diet (review in Thomson, 1969a). All the lobe-fins (despite the contorted special pleading of Campbell and Barwick, 1980) were at least partial lungbreathers.

Why did a group of osteolepiform lobe-fins invade the land; and what was the set of adaptations that allowed/created this transition? Following Barrell (1916), the view fostered by Romer and others (Romer, 1958; but compare Inger, 1957) was that the driving factor in the transition to tetrapod status was climatic. It was thought that the extensive Devonian redbeds indicated severe drying conditions in the second half of the Devonian.

Whether or not his view is geologically correct (for opposing views see Krynine, 1949), I believe it is logically inadequate. The key to the transition was not climate but ecology. The first tetrapods were at best amphibious creatures. They were certainly not terrestrial organisms. They were not fishes driven onto a hostile land, but fishes taking advantage of a newly evolved and rich semi-aquatic ecosystem—namely what we now call “wetlands.” The emergence of wetlands was due literally to the emergence of vegetation. Romer’s vision of the tetrapod ancestors as fishes driven from drying pool to drying pool along parched water courses in a semi-desert landscape must be replaced by a vision of fishes exploring the possibilities of the productive, ecologically stable, marshes of coastal and inland waterways. Here was abundant food for those fishes who had the physical equipment (respiration, locomotion) to deal with life in extremely shallow water, in conditions that nonetheless were constantly moist.

Life in and around the Devonian marshes offered the following advantages: new food resources in the form of invertebrates in the vegetation, plus fishes in the open water; escape from aquatic predators; the opportunity to lay their eggs in isolated pools and guard them from predators; and at all times the moist vegetation offered protection from desiccation and an environment in which to move around when pools dried up.

HOW

Whatever the ecological scenario, one of the most important questions in the origin of tetrapods is: how did the major morphological repatterning from fish to tetrapod condition occur? Did it occur slowly and gradually or (as the fossil record seems to indicate) quickly? Did the key morphological features change serially, or in concert?

Naturally, part of the answer must depend on the way in which the fossil data define (and refine) the question. We should not leap to conclusions, especially when the evidence is negative, but the evidence so far points to a fairly rapid change in morphology, affecting whole complexes of characters, and without a major series of broad diversifica-

tions at lower taxonomic levels (genera and species). The record is somewhat different, for example, from that of the origin of mammals from synapsid reptiles (Kemp, 1982, 1985; Thomson, 1988).

In the origin of any major group, the origin of complex morphological changes is naturally one of the prime foci of research. For example, in the "reptile to mammal" transition, the evolution of the middle ear complex has been an active area of research for more than 50 yrs. In the fish to tetrapod transition, a stumbling block to advances in this sort of area has been uncertainty over the exact nature of the transitional forms. Much good work that had previously been done with the "rhypidistian" fishes (principally *Eusthenopteron*) was effectively derailed for a while by the effort to establish a dipnoan ancestry.

In 1966 (see also Thomson, 1988, 1991c), I pointed out that the changes in morphology that characterize any major transition did not—could not—occur in isolation one from another. As we can see from the list of features given earlier, they fall naturally into a series of functional groupings (see above). Because of this, I proposed that the evolution of character complexes fitted a pattern that was termed *correlated progression*. The model of correlated progression is directly opposed to the model of *key innovation* (Bock, 1969), which involves serial acquisition of new features, each accompanied by taxonomic diversification ("postadaptational adjustment"). However, one can imagine the two modes acting at different times in the same morphological transition (Thomson, 1991c). Both models require "*preadapted*" morphology—lungs in fishes, the osteolepiform internal limb structure, and so on.

The model of correlated progression allows for the production of mosaic forms in terms of lineages in which only a subset of features potentially involved in the complex actually change. Correlated progression does not require a series of taxonomic radiations to drive and punctuate the transitional process. To this extent, at least, the rival models can be tested against the fossil record. So far, evidence of such diversifications is lacking.

A prime requirement of any observed or theoretical transition in morphology is that the whole process must be *functionally integrated*. In the skin, for example, scales were largely lost in the fish-tetrapod transition, except for those on the belly which remained for mechanical protection. They were lost at least in part because the skin had become an even more important site of respiratory gas exchange than it was in fishes. The mucus glands of fishes became even more fully developed in their semi-terrestrial descendants in order to keep the skin moist and to allow that gas exchange.

The eyes moved to a position on the top of the head. Perhaps this was because a proto-tetrapod had to watch for predators attacking from above rather than below. But it was also in part because the head was broadened and flattened to create a more powerful buccal pump for ventilating the lungs. In this case, we can trace a link between eye position,

and jaw mechanics and, therefore, to the origin of the middle ear. A flattened head shape does not work very well with the intracranial kinetics of a typical osteolepiform (Thomson, 1967). Once the jaw mechanics changed, the suspensory role of the hyomandibular was reduced. Changes in the hyomandibular were also affected by (and caused) reduction in the gill apparatus. This, then, is the basis for "correlated progression." In lungfishes the hyomandibular became a vestige when the jaws became holostylic. In the ancestors of tetrapods, the hyomandibular acquired a new role, that of stapes, but even here there is preadaptation because if, as has been proposed, the osteolepiform spiracular pouch (lying flat against the hyomandibular) contained a bubble of air (left over from air breathing) the hyomandibular would have already had a partial hearing function (Thomson, 1966).

This brings us to one of the central and most difficult features of the fish to tetrapod transition—the first appearance of a middle ear. The general outlines of a morphological transition from the fish to tetrapod condition seemed to have been laid out in 1966 (Thomson, 1966; van Bergeijk, 1966), although many details obviously remained to be worked out. The middle ear example was in fact the source of the correlated progression model. The hyomandibular becomes the stapes, the spiracular gill pouch becomes the tympanic cavity, the otic notch supports a tympanum in the position of, and perhaps derived from, the anterior portion of the operculum. A new fenestra ovale arises where the hyomandibular articulates with the otic capsule. However, this scheme was based on the assumption that the first tetrapod had a tympanum, otic notch, and a reduced stapes, principally for sound conducting and no longer having a major role in the jaw suspension (it was still connected to the quadrate via a ligamentous process).

Lombard and Bolt, in an important series of papers (1979, 1988), have argued on the contrary that the original tetrapod "stapes" was unreduced and heavily connected to the jaw articulation in the first tetrapods, and that there was no tympanic membrane. The otic notch, tympanic membrane, fenestra ovalis, and even the sensory epithelium of the inner ear evolved later more than once in parallel. None of the very early tetrapod fossils seemed to confirm the Lombard and Bolt proposition, nor did they very strongly falsify it. However, *Acanthostega*, at least, has an otic notch, and recently Clack (1989) has described the stapes of *Acanthostega* which is associated with that notch. It has lost most if not all of its jaw suspensory functions, and, despite Clack's opinion that the stapes does not have a hearing function but is somehow connected with function of the spiracular organ, it fits surprisingly well with the older model rather than Lombard and Bolt's model (compare Fritzsche, 1990). The question of when aerial sound reception arose is, however, very much unsettled.

Ichthyostega has a well developed tail and obviously spent a lot of time in the water. But the heavy and broadly overlapping ribs testify to the fact

that it also spent time at least partially out of the water and was therefore mechanically adapted to deal with the problem of being "heavy" for the first time. It is interesting that the vertebral column is not particularly far advanced along the road toward what we now know as the tetrapod condition, and the heavy development of the rib cage seems to represent a firm stride down an evolutionary blind alley. The rigidity of the rib cage then presents interesting problems for lung ventilation. There must have been a buccal force pump—was there also a kind of piston-like motion of the viscera (Thomson, 1980)?

A prominent feature of modern models of major morphological change is "preadaptation" (Bock, 1959). In this case, function changes more rapidly than morphology, and the whole matter depends upon a special coincidence of (prior) morphology and (future) ecological opportunity. Naturally, preadaptation can only be recognized in hindsight. The lungs and limbs of lobe-finned fishes can be seen as excellent examples of preadaptation. What works well for a fish in special warm, anoxic, shallow-water conditions (use of lungs instead of gills, use of fins as limbs assisted by body flexure in locomotion) gives a foundation for change in function followed by refinement of structure (under intense selection) for the new conditions.

The limbs, of course, occupy pride of place in any analysis of tetrapod origins. The pattern of internal structure of the osteolepiform limb as in *Eusthenopteron* (Andrews and Westoll, 1970) and *Sterropterygion* (Thomson, 1972; Rackoff, 1980) is clearly homologous with that of tetrapods with respect to the humerus/femur or ulna and radius/tibia or fibula, but little else. It would also be a mistake to exaggerate the extent to which osteolepiform fishes actually used their fins as arms and legs; the fins in the forms that we know are all small and feeble (compared even with the large fins of porolepiforms, coelacanth, and the modern lung-fish *Neoceratodus*, which have a different internal structure). These fishes obviously could not live out of water because they would suddenly be unsupported and feel the force of gravity.

However, the discovery by Rackoff (1980) that the flexure of the "elbow" and "knee" joints in *Sterropterygion* (and probably *Eusthenopteron*) are the same as in tetrapods offers a functional clue as to the origin of tetrapod locomotion.

While the basic arrangement of skeletal elements in the fore and hind limbs of tetrapods are the same, the knee and elbow point in opposite directions. The origin of this may be in the different function of the limbs in fishes. The model has been proposed (Rackoff, 1980; Thomson, 1980, 1988) that the pectoral fins were used by fishes in shallow water to hold the front end of the body up, and the most effective position for the fin was to be folded forward under the head. The anterior part of the fish was then slung from the shoulder girdle, and the

lungs would not be crushed by the weight of the body. In these fishes, however, it was not necessary to hold up the posterior half of the fish. In shallow water, the pelvic fins were used to push backward, and the most efficient configuration is the backward flexure of the knee. This pattern was a legacy to all future tetrapods.

There are a number of distal elements in the paired fins of osteolepiforms, but it is not easy to find in them obvious homologues of elements of the tetrapod carpus or tarsus, let alone digits. This is because of the fundamental fact that homology is not to be found in structures alone, but in the *morphogenetic patterning mechanisms of development* that cause those structures. To find the origins of the distal parts of the limbs we have to look beyond both comparative anatomy and functional mechanics. For too long, we have ignored the fact that morphological features are not only linked functionally but also in development. A full correlated progression model must therefore take into account the hugely integrative properties of developmental cascades (Thomson, 1988, 1990, 1991c). In the end, this is more important than straining to find in the fish fin all the phenotypic homologues of tetrapod carpals, tarsals, and digits.

An approach to this question is now possible through the work of Shubin and Alberch (1986). Shubin and Alberch have worked out the basic morphogenetic patterning processes of the tetrapod limb which occurs through the growth and division of a number of cellular blastemata. Their scheme immediately clears up one of the old problems of the osteolepiform limb skeleton, namely the inequality in size and shape of the ulna and radius in certain osteolepiforms. Shubin and Alberch show that this is exactly what could have been predicted. The limb is not a symmetrically branching structure but is subtended, as it were, from the ulna. Further, it is obvious that the digits and most of the carpal and tarsal elements of the tetrapod foot are neomorphs not represented anywhere in the osteolepiform limb. These distal parts of the tetrapod limb skeleton are not created by the transformation of existing osteolepiform elements but by a further elaboration (continuation in time) of the processes of blastemata division.

While modern researches are thus starting to show an underlying ontogenetic basis to the sort of structural and functional correlations that evolutionary and functional morphologists have traditionally studied, unfortunately, the causal processes of limb development are simpler to work out than those for the head. Head development involves massively complicated migrations of neural crest cells and patterns of segmentation in the neural, branchial, and muscular systems, and the neurocranium and dermal skeleton. However, it will be necessary to unravel these complex strands if we are ever to understand fully the origin of, for example, the tetrapod middle ear.

In the meantime, for all these systems, the discovery of more fossils would help!

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