Chapter 15 Sites of British Fossil stem Tetrapoda and Amphibia

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Introduction

Amphibia are the most primitive of living tetrapods. They are basically terrestrial animals, but their ancestral dependence upon aquatic habitats is indicated by the facts that many lay their eggs in water and have an aquatic larval stage. The first tetrapods seem to have emerged in the latter half of the Devonian and to have produced two distinct kinds of descendants –those from which came the later Amphibia and those which gave rise to the Amniota. In recent years there has been a lively debate about the nature and significance of the Devonian fossils, and it is clear that the original stem group was from the beginning a somewhat diversified body of taxa. New material has tended to encourage the view that no single line of descent from fish to tetrapod can be distinguished, and there are differing views as to which sarcopterygians led the move to develop limbs. Eventually Palaeozoic forms gave rise to the modern living groups and also to the first reptiles, and hence to all other tetrapods (Milner, 1993a; Ahlberg and Milner, 1994; Daeschler and Schubin, 1995). The earliest signs of the existence of these stem tetrapods are track marks in the Mid- and Late Devonian in Europe (Milner *et al.,* 1986, 1990; Rogers, 1990; Stössel, 1995) and Australia (Warren and Wakefield, 1972; Warren *et al.,* 1986). These fossils indicate creatures, which walked on efficient limbs with well-differentiated fore and hind extremities bearing four, five or more digits and with a trailing tail. Skeletal evidence of these particular animals is, so far, still to be found.

On the other hand, bones and teeth of undoubted limb structures of later tetrapods (Ahlberg referred to them as 'near-tetrapods) are now coming to light from various late Devonian rocks in Scotland, the eastern Baltic and Russia (Ahlberg, 1991, 1995; Ahlberg and Milner, 1994; Ahlberg *et al.,* 1994; Alekseev *et al.,* 1994; Lebedev and Coates, 1995). These fossils are beginning to show that in the Late Devonian the tetrapods were well set upon the road to terrestrial adaptation. From the uppermost Devonian of East Greenland (Save-Soderberg, 1932; Jarvik, 1980, 1996) have come the most complete and intensively studied remains of a very primitive tetrapod, *Ichthyostega.* Many of the early tetrapods possessed teeth in which the enamel was infolded in a complex labyrinthine pattern; these fossils were previously grouped together as labyrintho-donts but the term is no longer regarded as significant in classification. However, it is known that some rhipidistian fishes show the same tooth pattern. The derivation of the ichthyoste-gid skeleton from that of a rhipidstid is strongly suggested from the similarities seen in the axial and other parts. Other primitive tetrapods are now recorded together with rhipidistians and other vertebrates in distinctive assemblages from Russia (Lebedev, 1984; Lebedev and Clack, 1993) and Canada (Schultze and Arsenault, 1985). *Panderichthys* has been the object of much research and debate by Vorobyeva and others (e.g. Vorobyeva and Kuznetsov, 1992; Vorobyeva and Hinchliffe, 1996) as a possible 'link' between rhipidistians and tetrapods. This seems to indicate that the transition either took place very rapidly or that intermediate forms were rare or lived in environments where preservation was unlikely (Carroll, 1988). It is, however, becoming clear that Devonian tetrapods were more fish-like than was believed previously.

A review of the origin and early diversification of tetrapods by Ahlberg and Milner (1994) pointed out that debate about the origins of tetrapods is now focusing upon the Family Panderichthyidae, a previously rather obscure group of sarcopterygians. The cladistic analysis of old and new data is beginning to delineate the origins of tetrapods as a documented sequence of character acquisition. Ahlberg and Milner's cladogram is given in (Figure 15.1). The Lower Frasnian panderichthyids actually look like early tetrapods with paired fins, though they may have been capable of 'walking' to an extent similar to that in the living catfish *Clarias.*

In the Carboniferous rocks there is now evidence of several different tetrapod lineages with clearer amphibian characteristics. Perhaps the group underwent rapid radiation on entering the new terrestrial habitats; alternatively we may have only a few highly specialized types present in the fossil record. Of singular importance is what Ahlberg and Milner (1994) identify as the 20 Ma 'Tournasian Gap', wherein the vertebrate record is extremely poor. It is an interval during which the foundations of a new and successful radiation were set in place. In any event, amphibians were firmly established by mid-Viséan time and their fossils are found most commonly in deposits associated with tropical or

subtropical coastal lagoons and swamps. All seem to have been powerfully constructed animals, presumably with functional lungs, well-developed senses of sight and smell and an improving sense of hearing. They probably fed on local invertebrates, and returned to the water for breeding. They would have been good swimmers, some with strong limbs for (terrestrial) locomotion, others snake-like with secondarily reduced limbs.

All modem amphibians need to guard against water loss through the mouth, lungs and body surface. The most primitive amphibian genera retained heavy scales (a rhipidistian inheritance) which may have slowed water loss from the body surface, but water loss could have been a serious problem for all the early amphibians and they were inhibited from leaving the vicinity of the water. A few larval (tadpole) fossil forms are known; emergence onto the land probably took place only when the basic adult morphology had been gained.

Classification and evolution

Milner (1993a) divided the amphibians, fossil and extant, into four groups — stem tetrapods of the Palaeozoic; the Aistopoda, of enigmatic origins and relationships; the Amphibia *sensu stricto,* i.e. the living Lissamphibia and their predecessors; the stem Amniota (reptiles, birds and mammals). The first group is mainly known from Late Devonian fragments and footprints — *Obruchevichthys* in Latvia (Vorobyeva, 1977), the Scaat Craig fossils (Ahlberg, 1991, 1995) and *Metaxygnathus* (Campbell and Bell, 1977) and *Elpistostege* in Canada (Schultze and Arsenault, 1985).

The stem tetrapods of the Palaeozoic also include the better-known *Ichthyostega, Acanthostega* (Clack and Coates, 1995; Coates, 1996) and *Tulerpeton* (Lebedev, 1990; Lebedev and Coates, 1995), in all of which it now seems that the hind limbs were the more powerful in locomotion. Beyond the 'Tournaisian Gap', evolution now brought about a remarkable diversification in which the more familiar groups made their appearance (Figure 15.2).

A two-fold grouping of the Palaeozoic Amphibia was previously favoured — the 'labyrinthodonts' and the lepospondyls', but they are no longer regarded as valid entities (Milner, 1993a). *Ichthyostega* seems to be the kind of ancestor that gave rise to all late amphibians, having evolved directly from the rhipidistian fishes. In fact a single common ancestor may have given rise to all labyrinthodonts'. The lepospondyls were a heterogeneous group, each member of which probably evolved independently from early 'labyrinthodonts'. The skulls possess large fangs and receiving pits on the margins of the jaws, and the vertebral centra have more than one element per segment. The well-developed limbs clearly separate 'labyrinthodonts' from rhipidistians, and the same basic pattern of structure is found in all other tetrapods.

The fossils that have been called lepospondyls commonly lack the labyrinthine structure of the teeth and also the conspicuous fangs with their replacement pits. There is typically only one single central element to each (vertebral) segment, although some forms are said to have possessed intercentra. Many other differences exist but need not be mentioned here. Lepospondyls are generally smaller than the 'labyrinthodonts'.

'Labyrinthodonts' were conveniently divided into two groups — temnospondyls and anthracosaurs (or batrachosaurs) — which appear to have achieved about the same degree of advancement from the rhipidistian condition. Some possess a more rhipidistian character while others are more specialized. The ichthyostegids seem to retain primitive characteristics in the head which distinguish them from the other groups.

Temnospondyls appeared in the Lower Carboniferous as several distinct groups, some of which were probably secondarily aquatic, i.e. they had reduced limbs quite unsuitable for life on land. Others were clearly well-adapted terrestrial types. In later Carboniferous time several semi-aquatic kinds had evolved; they range in size from a few tens of centimetres long to large ungainly temnospondyls about 2 m long. Their terrestrial heyday was in the Early Permian, after which competition from the increasingly dominant early reptiles reduced their numbers drastically. Both large and small temnospondyls persisted into the later Permian and Triassic, especially in Gondwanaland and Russia. The largest of all, with skulls almost 1 m long, existed in the Triassic Period. By the end of the Early Jurassic, however, all labyrinthodonts' were extinct.

Anthracosaurs were an altogether less numerous and diverse group than the temnospondyls, and they include some well-known elongated aquatic forms (embolomeres) in the Carboniferous (Panchen, 1970). The vertebral column was

constructed so as to allow great lateral flexibility, thus facilitating undulatory swimming motion. Some even developed a dorsal tail fin. In Britain the group is well represented in the Carboniferous and seems to have occupied rather deep-water habitats. Other anthracosaurs were more terrestrial with short, stout and powerful limbs. Several families of amphibians from the later Carboniferous and Early Permian may be related to the anthracosaurs, but all died out within the Early Triassic.

The lepospondyls were held to comprise a varied assemblage of families of animals generally smaller than the 'labyrinthodonts' and including Palaeozoic amphibians rather like modern newts, salamanders, lizards and snakes. They possessed distinctive spool-shaped centra in the vertebrae. They are conspicuous members of the Late Carboniferous tetrapod fauna, having made their debut in the middle part of that period. Lepospondyls show no obvious affinities with the rhipidistians. It has been thought that different lepospondyl groups may have arisen from different stocks of 'labyrinthodonts' during the Late Devonian and Early Carboniferous. By the end of the Early Permian all were extinct. In fact, by the end of the Triassic time all the Palaeozoic amphibian groups (except tem-nospondyls) were extinct.

Modern Amphibia (the Lissamphibia, comprised of the frogs, salamanders and Gymnophiona) first appeared in the Triassic period and throughout the ensuing time seem to have evolved rather little. All are small animals dependent upon cutaneous respiration and are confined to damp habitats. Arguments about the origins of this big group are many, largely because of the shortage of fossil evidence. While it is possible that they all evolved from a common ancestor, it seems equally likely that each of them is descended from a different Palaeozoic taxon. Many palaeontologists have held that frogs almost certainly evolved from a temnospondyl 'labyrinthodont', while salamanders and caecilians were derived from a lepospondyl ancestor (e.g. Carroll, 1977).

Recently, however, the grouping by Milner referred to above has been preferred to the twofold basic division, and several authors have argued for a monophyletic origin.

While the biological crises and extinction events of the Permian and Triassic periods were severe for the Amphibia as a whole, and the development of more advanced tetrapods must have been a prime influence upon amphibian evolution throughout the Mesozoic and Cenozoic. the mass mortality inflicted upon the tetrapods at the end of the Mesozoic seems to have left the inhabitants of the damp habitats relatively unscathed.

Interpretations of the palaeobiology of early tetrapods and amphibians is beset with problems on account of the paucity of the fossil record, and also because of the different possible Palaeozoic global models. Milner (1987, 1993b) reviewed the biogeography of Palaeozoic tetrapods, finding that they were most likely to have arisen in the equatorial region of eastern Gondwana during the Devonian. Soon afterwards they extended their range across equatorial Gondwana and Euramarica. Between end-Devonian and Early Permian times they seem to have left evidence of their existence almost entirely within Euramerica and perhaps the Euramerican component of west Gondwana (Panchen, 1973). A single homogenous tetrapod province characterized the early and mid-Carboniferous, but in the Early Permian a separate mesosaurid province may have evolved in southern Gondwana. With the consolidation of the components of Pangaea and the recession of the Gondwanan glaciation, the Amphibia seem to have differentiated by vicariance into distinct northern and southern faunal provinces. From here on, amphibian development was primarily influenced by climate, continental dispersal and local ecological factors.

Stem tetrapods and amphibians in the British palaeontological record

As the report on Scaat Craig (Chapter 8) shows, the first known tetrapods appear in the British Upper Devonian, and further remains of that age may be expected as work continues in Scotland. These are very important fossils, but even older Devonian tetrapods may eventually be found in other deposits. The 'Tournaisian Gap' referred to above certainly is indicated in the succeeding strata throughout Great Britain. In the Viséan, however, the record is renewed in the Midland Valley of Scotland with several important sites to emphasize the diversity of tetrapods that existed there during the Carboniferous Period. The table below is compiled from data from Smithson (1985) and others. This is a significant part of the world list of known tetrapods (about 20 families) of that timespan and is based upon lagoonal, littoral and lacustrine environments (see also Wood *et al.,* 1985). The new East Kirkton site is unquestionably the most important of the Carboniferous localities in its assemblage of fishes and amphibians. The following table shows the sites for fossil

amphibians in Britain (see also (Figure 15.3)).

DEVONIAN

Scaat Craig, Fife. Scaat Craig Beds, Frasnian Fauna: *Elginerpeton pancheni* Ahlberg, 1995

CARBONIFEROUS

Tournaisian

Foulden, Berwick-on-Tweed, Berwickshire. 'Fish Bed' siltstone, Cementstone Group, Courceyan (= Ivorian)

Fauna: ?anthracosaur *incertae sedis*

Viséan

Broxburn, Lothian. Oilshale in Curly Seam, Lower Oil Shale Group, Asbian

Fauna:

Palaeomolgophis scoticus Brough and Brough, 1967

Pitcorthie, Anstruther, Fife. Calcareous Sandstone Measures, Asbian

Fauna:

Dolichopareias disjectus Watson, 1929

Doragnathus woodi Smithson, 1980

Wardie, Edinburgh. Wardie Shale Group, Holkerian

Fauna:

Lethiscus stocki Wellstead, 1982

Burdiehouse, Edinburgh. Burdiehouse Limestone, Upper Oil Shale Group, Asbian

Fauna:

Dolichopareias disjectus Watson, 1929

Pholidogaster pisciformis Huxley, 1862

Cheese Bay, East Lothian. Lower Oil Shale Group, Calciferous Sandstone Series, Asbian

Fauna:

anthracosaur *incertae sedis*

East Kirkton Quarry, near Bathgate, Lothian. East Kirkton Limestone, Upper Oil Shale Group, Brigantian

Fauna:

Loxommatidae *incertae sedis*

Balanerpeton woodi Milner and Sequeira, 1994

Ophiderpeton kirktonense Milner, 1994

Eldeceeon rolfei Smithson, 1994

Silvanerpeton miri pedes Clack, 1994

Westlothiana lizziae Smithson *et al.,* 1994

Inchkeith, Firth of Forth, Fife. Middle Oil Shale Group, Asbian

Fauna:

Doragnathus woodi Smithson *et al.,* 1980

Adelogyrinus sp.

cf. *Palaeomolgophis*

Pentland Oil Works, Edinburgh. Dunnet Shale, Upper Oil Shale Group, Asbian

Fauna:

Adelogyrinus simorhynchus Watson, 1929

Straiton, Edinburgh. Dunnet Shale, Upper Oil Shale Group, Asbian

Fauna:

Adelogyrinus simorhynchus Watson, 1929

Venturefair Pit, Gilmerton, Edinburgh.

Gilmerton Ironstone, Lower Limestone Group, Brigantian

Fauna:

Crassigyrinus scoticus Watson, 1929

Eoherpeton watsoni Panchen, 1975

Loxomma allmanni Huxley, 1862

Pholidogaster pisciformis Huxley, 1862

Namurian

Burghlee Colliery, Loanhead, Edinburgh.

Burghlee Limestone, Limestone Coal Group,

Pendleian

Fauna:

Eoherpeton watsoni Panchen, 1975

aistopod indet.

anthracosaur indet.

Dora Opencast Site, Near Cowdenbeath, Fife. Dora Bone Bed, Limestone Coal Group, Pendleian (Figure 15.4)

Fauna:

Adelogyrinus sp.

Crassigyrinus scoticus Watson, 1929

Doragnathus woodi Smithson, 1980

Eoherpeton watsoni Panchen, 1975

Spathicephalus mirus Watson, 1929

anthracosaur indet.

Dora Opencast Site, near Cowdcnbcath, Fifc. Lochgelly Blackband Ironstone, Limestone Coal Group, Pendleian

Fauna:

Adelogyrinus sp.

Ramsay Colliery, Loanhead, Edinburgh. Blackband, Rumbles and Burghlee Ironstones, Limestone Coal Group, Pendleian

Fauna:

Acheroniscus caledoniae Carroll, 1969

Adelogyrinus sp.

Adelospondylus watsoni Carroll, 1967

Caerorhachis bairdi Holmes and Carroll, 1977

Doragnathus woodi Smithson, 1980

Loxomma sp. (Beaumont, 1977)

Papposaurus traquairi Watson, 1914

Spathicephalus mirus Watson, 1929

Niddrie Colliery, Niddrie, Edinburgh. Shale overlying South Parrot Coal, Upper Limestone Group, Pendleian

Fauna:

Adelogyrinus sp.

Doragnathus woodi Smithson, 1980

anthracosaur indet.

Silesian (Coal Measures)

Colne, Lancashire. Bullion Coal, *lenisulcata* zone, Westphalian A

Fauna:

Eugyrinus wildi Woodward, 1891

Toftshaw, near Bradford, Yorkshire. Blackbed Coal, *communis* zone, Westphalian A

Fauna:

Pholiderpeton scutigerum Huxley, 1869

Swanwick Colliery, near Alfreton, Derbyshire. Roof of Silkstone or Black Shale Coal, *communis* zone, Westphalian A

Fauna:

Palaeogyrinus sp.

Eogyrinus sp.

?Megalocephalus

Castle Hill, near Carluke, Strathclyde. Black Band Ironstone, *communis* zone, Westphalian A

Fauna:

Anthracosaurus russelli Huxley, 1863

Baphetes kirkbyi Watson, 1929

Loxomma acutirhinus Huxley, 1863

Pholiderpeton sp.

Pirnie, near Leven, Fife. Earl David's Parrott Coal, *modiolaris* zone, Westphalian A

Fauna:

Baphetes kirkbyi Watson, 1929

Megalocephalus pachycephalus (Barkas, 1873)

Palaeoherpeton decorum (Watson, 1926) (see Panchen, 1970)

Quarter, near Hamilton, Strathclyde. Black Band Ironstone, *modiolaris* zone, Westphalian B

Fauna:

Anthracosaurus russelli Huxley, 1862

Baphetes kirkbyi Watson, 1929

Pholiderpeton sp.

Wishaw, Strathclyde. Splint Coal, *modiolaris* zone, Westphalian B

Fauna:

Pholiderpeton sp.

Carnbrae, near Airdrie, Strathclyde. Palace Craig Ironstone, *similis–pulcbra* zone, Westphalian B

Fauna:

Anthracosaurus russelli Huxley, 1863

Megalocephalus pachycephalus (Barkas, 1873)

Meta Pit and Drift Mine, Fishcross, Central Region *modiolaris* zone, Westphalian B Fauna:

?embolomerous anthracosaur

Hamilton, Strathclyde. Black Band Ironstone, *modiolaris* zone, Westphalian B

Fauna:

Megacephalus pachycephalus (Barkas, 1873)

Sunnyside Pit, Larkhall, near Wishaw,

Strathclyde. Black Band Ironstone, *modiolaris* zone, Westphalian B

Fauna:

Megacephalus pachycephalus (Barkas, 1873)

Newarthill, Strathclyde. Vurtuewell Coal, *modiolaris* zone, Westphalian B

Fauna:

Pholiderpeton sp.

Coalbrookdale, Shropshire. Blue Flats Ironstone, *modiolaris* zone, Westphalian B Fauna:

Megalocephalus ('*Orthosaurus*')

Pirine Colliery, near Leven, Fife. Earl David's Parrot Seam, *modiolaris* zone, Westphalian B

Fauna:

Palaeogyrinus decorus Watson, 1924

Baphetes kirkbyi Watson, 1929

Megacephalus sp.

Airdrie, Lanarkshire. Black Band Ironstone, *modiolaris* zone, Westphalian B

Fauna:

Anthracosaurus russelli Huxley, 1863

Baphetes latirostris Watson, 1929

Loxomma acutirhinus Watson, 1929

?Pholiderpeton

Newsham, Northumberland. Base of *similis–pulchra* zone, Westphalian B Fauna:

Pteroplax cornuta Hancock and Atthey, 1868

?Eogyrinus sp. (*E. attbeyi* Watson, 1926)

Megalocephalus sp.

Airdrie district, Lanarkshire. Palacegraig Limestone, lower *similis–pulchra* zone, Westphalian B and C

Fauna:

Megalocephalus sp.

Fenton, North Staffordshire. Rag Mine Ironstone, *phillipsi* zone, Westphalian C

Fauna:

Eogyrinus sp.

Megalocephalus sp.

New Mine Ironstone

Fauna:

?Anthracosaurus sp. or *?Eogyrinus* sp.

Chalky Mine Ironstone

Fauna:

Megalocephalus sp.

Perceval Farm, Buckhaven, Fife

Fauna:

?embolomerous anthracosaur

TRIASSIC

Coton End Quarry, Warwick. Sherwood Sandstone Group, Anisian (see Benton and Spencer, 1995)

Fauna:

'*Stentosaurus* (*Cyclotosaurus*) *leptognathus*' (Owen, 1842)

Mastodonsaurus sp.

Guy's Cliffe, Warwick. Sherwood Sandstone Group, Anisian (see Benton and Spencer, 1995)

Fauna:

Mastodonsaurus sp.

Sidmouth Cliffs, Sidmouth, Devon. Otter Sandstone Formation, Anisian (see Benton and Spencer, 1995)

Fauna:

Eocyclotosaurus sp.

Mastodonsaurus lavisi (Seeley, 1876) Capitosauridae *incertae sedis* Temnospondyl indet.

JURASSIC

Kirtlington Old Cement Works, Oxfordshire. Kirtlington Mammal Bed, Forest Marble, Upper Bathonian

Fauna:

Eodiscoglossus oxoniensis Evans, Milner and Mussett, 1990

Marmorerpeton freemani Evans, Milner and Mussett, 1990

M. kermacki Evans, Milner and Mussett, 1990

Salamander A

Salamander B

Celtedens sp.

Watson Cliff, Dorset. Mammal Bed, Forest Marble, upper Bathonian Fauna:

Eodiscoglossus oxoniensis Evans, Milner and Mussett, 1990

Marmorerpeton sp.

'Kirtlington Salamander A'

albanerpetonid indet.

Durlston Bay, Purbeck, Dorset. Cherty Freshwater Member, Purbeck Limestone Group, Tithonian.

Fauna:

Discoglossidae indet.

Batrachosauridae indet.

Albanerpeton sp.

Sunnydown Farm, Purbeck, Dorset. Cherty Freshwater Limestone, Purbeck Limestone Group, Tithonian

Fauna:

Discoglossidae indet.

Batrachosauridae indet.

salamander indet.

Lissamphibian indet.

Albanerpeton sp.

CENOZOIC

Hordle Cliff, Hampshire. Mammal Bed, Headon Hill Formation, Priabonian, Eocene

Fauna:

'discoglossid 1' of Milner *et al.* (1982)

'discoglossid 2' of Milner *et al.* (1982)

Eopelobates cf. *hinshei* Estes, 1970

Albiobatrachus wightensis Meszoely *et al.,* 1984

Salamandra sansaniensis Lartet

Chelotriton cf. *paradoxus*

Triturus sp.

Headon Hill, Isle of Wight. Cliff End Member, Headon Hill Formation, Priabonian, Eocene

Fauna:

'discoglossid 2' of Milner *et al.* (1982)

Eopelobates sp.

Albionbatrachus wightenesis Meszoely *et al.,* 1984

Salamander indet. cf. *Megalotriton*

Elsewhere in Britain the record is enhanced by fossils from the Namurian–Westphalian deposits, principally coal measures. At Newsham, in Northumberland, coal measure facies of the Westphalian *modiolaris* zone have produced the largest taxonomically diverse assemblage of well-preserved tetrapods of that age in northwestern Europe (Boyd, 1984). Benton and Spencer (1995) listed several Late Carboniferous and Permian reptile sites at which amphibain remains are also known. From the Keele Beds of Shropshire, footprints indicate a local amphibian fauna but at the Middridge fossil fish site (q.v., above) in the Permian of County Durham the so-called amphibian remains (Hancock and Howse, 1870c) are now discounted. These rare and somewhat obscure fossils are much overshadowed in importance by occurrences in North America and central Europe. Amphibians are present in the fossil assemblages now retrieved from the Triassic of the Midlands and southwest England (Benton and Spencer, 1995). Here larger animals are present together with fossil reptiles, and the truly terrestrial nature of the vertebrate community is apparent. Recently reviewed (Milner *et al.,* 1990; Benton *et al.,* 1994) from Coton End Quarry, Warwick, are a ?mid-Triassic lungfish (*Ceratodus laevissimus*)*,* the temnospondyl capitosaurus '*Stenotosaurus* (*Cyclotosaurus*) *leptognathus*'

(Owen, 1842) and the mastodonsaur *Mastodonsaurus* sp. From Guy's Cliffe, also at Warwick, *Mastodonsaurus* sp. has been reported by the same authors. Benton and Spencer (1995, p. 58) also remark on the fauna from the Otter Sandstone Formation at Sidmouth, south Devon, as follows:

'The remains of three forms of temnospondyl amphibian (M. *lavisi, Eocylotosaurus* sp., capitosaur *incertae sedis*) are abundant in the Otter Sandstone Formation. These were all aquatic, superficially crocodile-like forms, and were probably carnivores or piscivores which fed at the waterside. The new eocyclotosaur material represents the first find of a benthosuchid from the Middle Triassic in Britain. It is similar to *Eocyclotosaurus* species from two European formations: *E. lehmani* from the *Voltzia* Sandstone of the Vosges in France and *E. woschmidti* from the Lower Röt of the

Schwartzwald in Germany. There is also undescribed eocyclotosaur material from the Moenkopi Formation of Arizona (Welles and Estes, 1969; Morales, 1987). The remains of *Mastodonsaurus lavisi* show some resemblance in interorbital proportions and dermal sculpture to material from Coton End and Bromsgrove (Paton, 1974a [sic], pp. 265–82) [Paton, 1975] and these show closest resemblance to *M. cappelensis* from the Upper Buntsandstein (Anisian) of Baden-Württemburg, Germany (Milner *et al.,* 1990). *M. lavisi* is the largest temnospondyl in the Otter Sandstone herpetofauna with an estimated skull length of 500–600 mm, and a body length of 2 m or more.'

Britain's oldest salamanders and frogs have been discovered in the mid-Jurassic rocks of Kirklington. The following is given by Benton and Spencer (1995, p. 161):

'The amphibians, reptiles and mammals from the Kirklington Mammal Bed have been summarized by Freeman (1979) and Evans and Milner (1991, 1994). Details of the collecting and preparation techniques are given in Freeman (1976, 1979), Kermack *et al.* (1987) and Evans (1989).'

'The amphibians include a frog referable to the family Discoglossidae (*Eodiscoglossus oxoniensis*)and five species of salamander (*Albanerpeton, Marmorerpeton kermacki, M. freemani* and two unnamed forms). *Eodiscoglossus oxoniensis* is the earliest identifiable discoglossid frog known, and one of the oldest frogs of any sort (Evans *et al.,* 1990). The specimens of *E. oxoniensis* from Kirtlington are comparable with *E. santonjae* from the Early Cretaceous of Montech, Lerida, Spain, but they may be clearly distinguished by characters of the ilium and premaxilla. The only older frogs are the primitive *Triadobatrachus* from the Early Triassic of Madagascar and *Vieraella* from the Early Jurassic of Argentina.

The record of *Albanerpeton* is one of the oldest of this enigmatic family, the oldest being from the Bajocian of Averyron, France (Evans and Milner, 1994). The albanerpetontids are also known from the Cretaceous of North America and the Miocene of France. *Marmorerpeton kermacki* and *M. freemani* are the earliest known salamanders (i.e. true Caudata; Evans *et al.,* 1988), more primitive than any other known forms by the absence of intravertebral spinal nerve foramina in the atlantal centrum. However, in other features these taxa resemble members of the family Scapherpetonidae, which comprises neotenous forms otherwise known only from the Late Cretaceous and Palaeocene. Salamanders A and B are yet to be described.'

Later Mesozoic and Cenozoic amphibian records in Britain are few and scattered and are of no great significance in the history of this class of vertebrates. Most modern amphibian families can be traced back to the early Cenozoic, and some to the early Cretaceous. Palaeogene amphibian occurrences are rather rare (Milner, 1986) and are almost exclusively from freshwater communities of the Headon Beds (Upper Eocene–Lower Oligocene) of the Hampshire coast and the Isle of Wight (Meszoely and Ford, 1976; Rage and Ford, 1980; Meszoely *et al.,* 1984; Insole and Daley, 1985). Unpublished amphibian material has also been reported from the freshwater clays and marls of the Hampstead Member of the Bouldner Formation (Oligocene) at Hampstead on the Isle of Wight (A.R. Milner, pers. comm., 1995).

The Late Eocene of Headon Hill and Totland Bay has yielded both amphibians and reptiles: the locality description by Benton and Spencer (1995) includes the following:

'The Headon Hill Formation falls in the Headonian European mammal age and is equated with the upper part of this age, dated as Late Eocene (Priabonian) by Curry *et al.* (1978). The environments are interpreted as floodplain and lagoonal, as for Hordle (q.v.), and the vertebrates are associated with close, subtropical forests (Hooker, 1992). The squamates from the HH2 bed are associated with abundant amphibian remains, including three anurans (Discoglossidae indet., Palaeobatrachinae indet. and cf. *Eopelobates*)and rare salamanders such as 'cf. *Megalotriton*' (Rage and Ford, 1980).'

Amphibians and squamates were also described from the Upper Eocene of Hordle Cliff in Hampshire by Milner *et al.* (1982), and from the Isle of Wight (Rage and Ford, 1980).

Much doubt still exists about familial relationships amongst the Amphibia of that time. It is the British Carboniferous sites above all that add greatly to our understanding of the early development of amphibians, East Kirkton being amongst the most important sites so far. It has significance not only for the quality of the fossil record there but also because there appears to be much potential for continuing exploitation of the site by careful excavation.
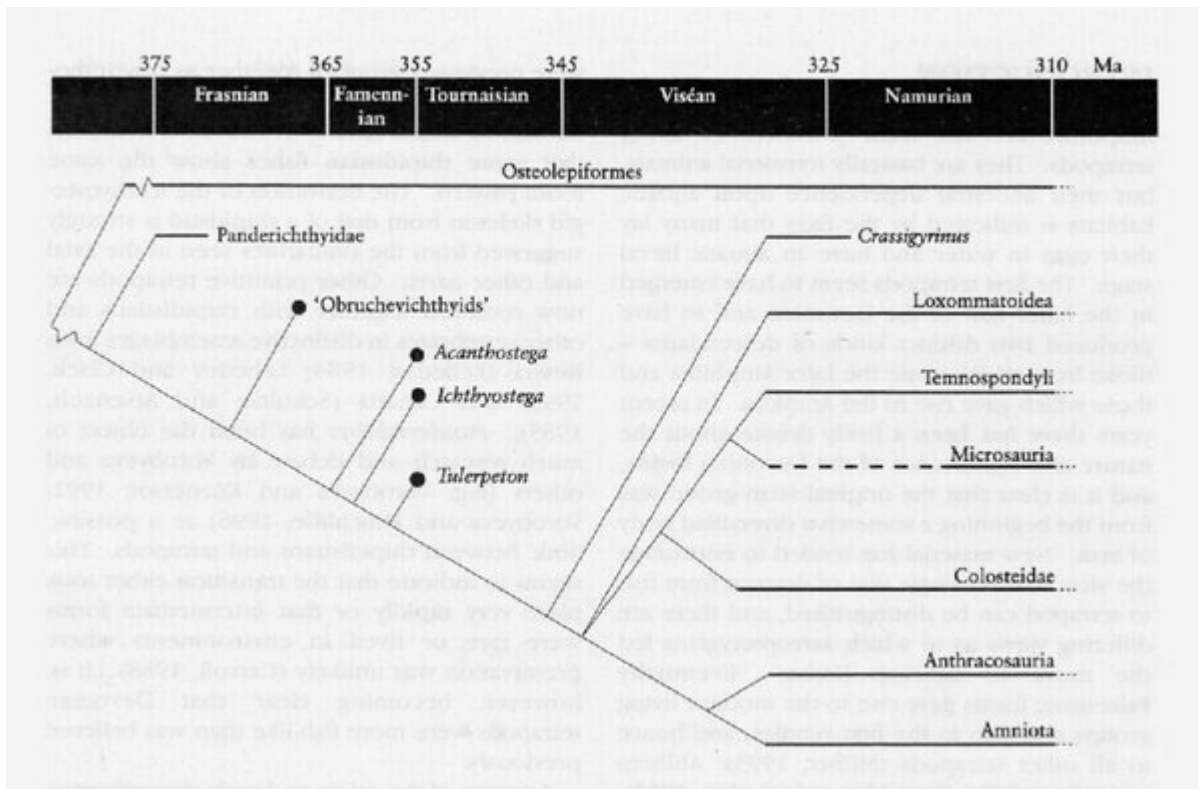
(Figure 15.1) Cladogram of the fish–tetrapod transition in Late Devonian–Early Carboniferous times (after Ahlberg and Milner, 1994). The taxa are grouped on the basis of shared derived characters. The characters shared by the panderichthyids and the tetrapods appear to be adaptations to shallow-water habitats. Devonian tetrapods retained lateral line systems and so must have been at least semi-aquatic. The black dots represent taxa known from a single locality; bars show the stratigraphical range of taxa known from several levels. The osteolepiformes originated in Middle Devonian times, perhaps some 10 Ma earlier.
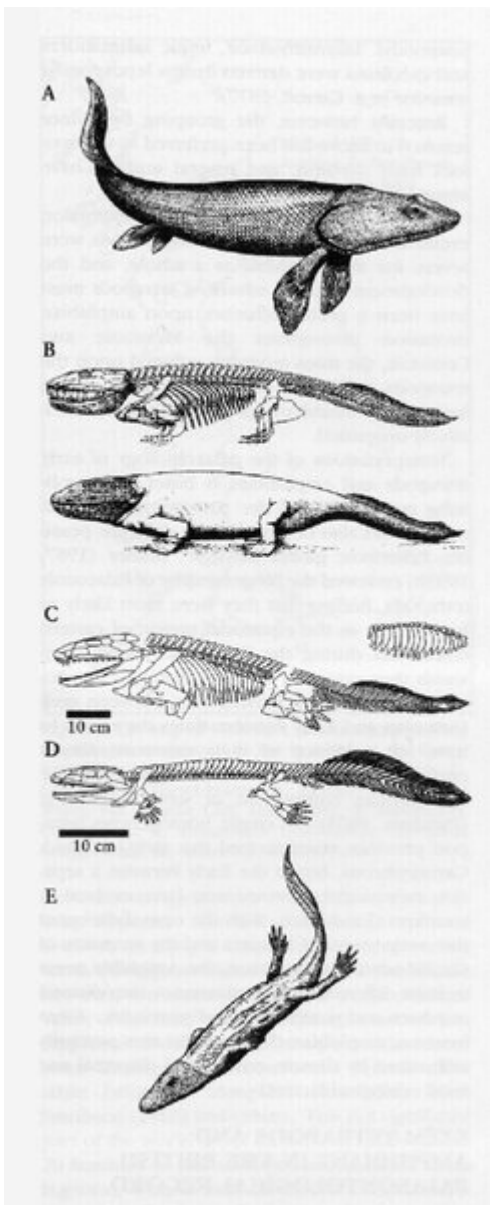
(Figure 15.2) Devonian tetrapods: (A) the sarcopterygian Panderichthys (after Janvier, 1996); (B), (C) Ichthyostega; (D) Acanthostega (both after Coates and Clack, 1995); (E) Tulerpeton (after Lebedev, 1990; Janvier, 1996). These animals were all up to c. 1 m long.
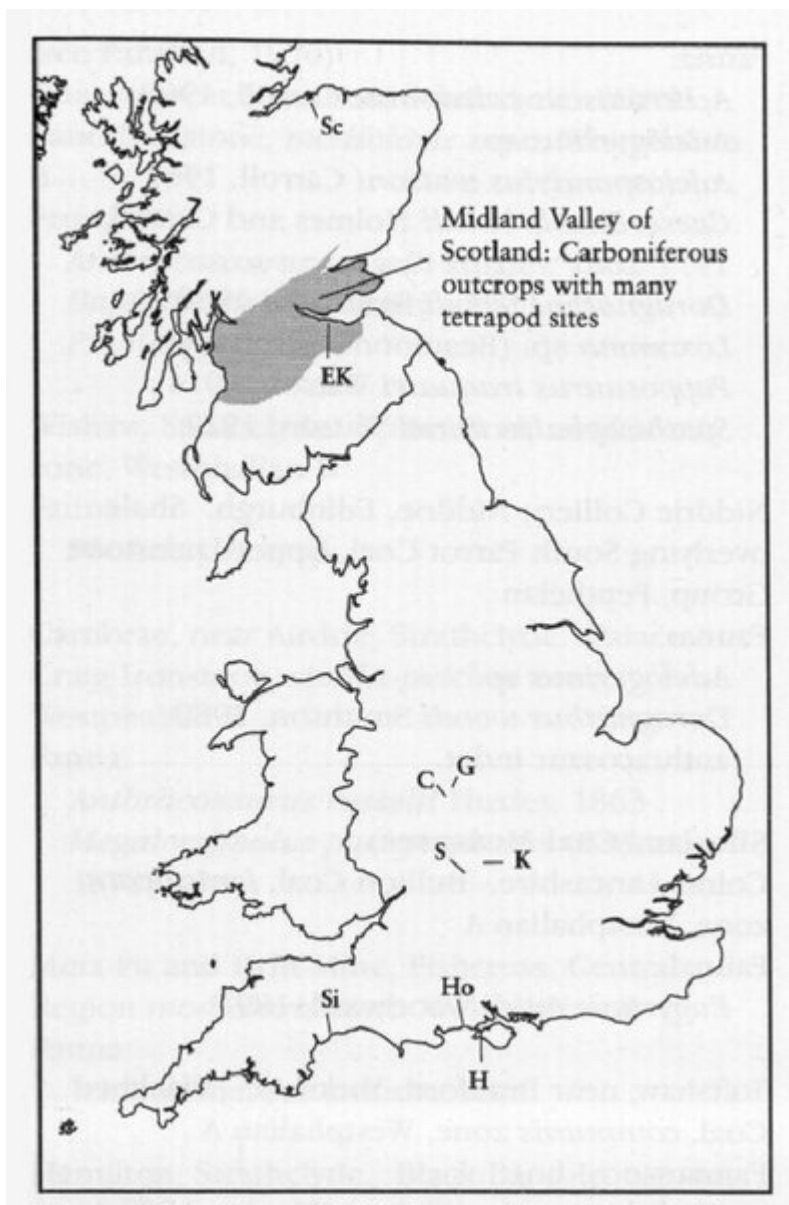
(Figure 15.3) Map of GCR sites and localities yielding amphibians mentioned in the text below. C, Coton End, Warwickshire; EK, East Kirkton, Edinburgh; G, Guy's Cliffe, Warwickshire; H, Headon Hill, Isle of Wight; Ho, Hordle Cliff, Hampshire; K, Kirtlington, Oxfordshire; S, Stonesfield, Oxfordshire; Sc, Scaat Craig, Moray; Si, Sidmouth Cliffs, Devon.
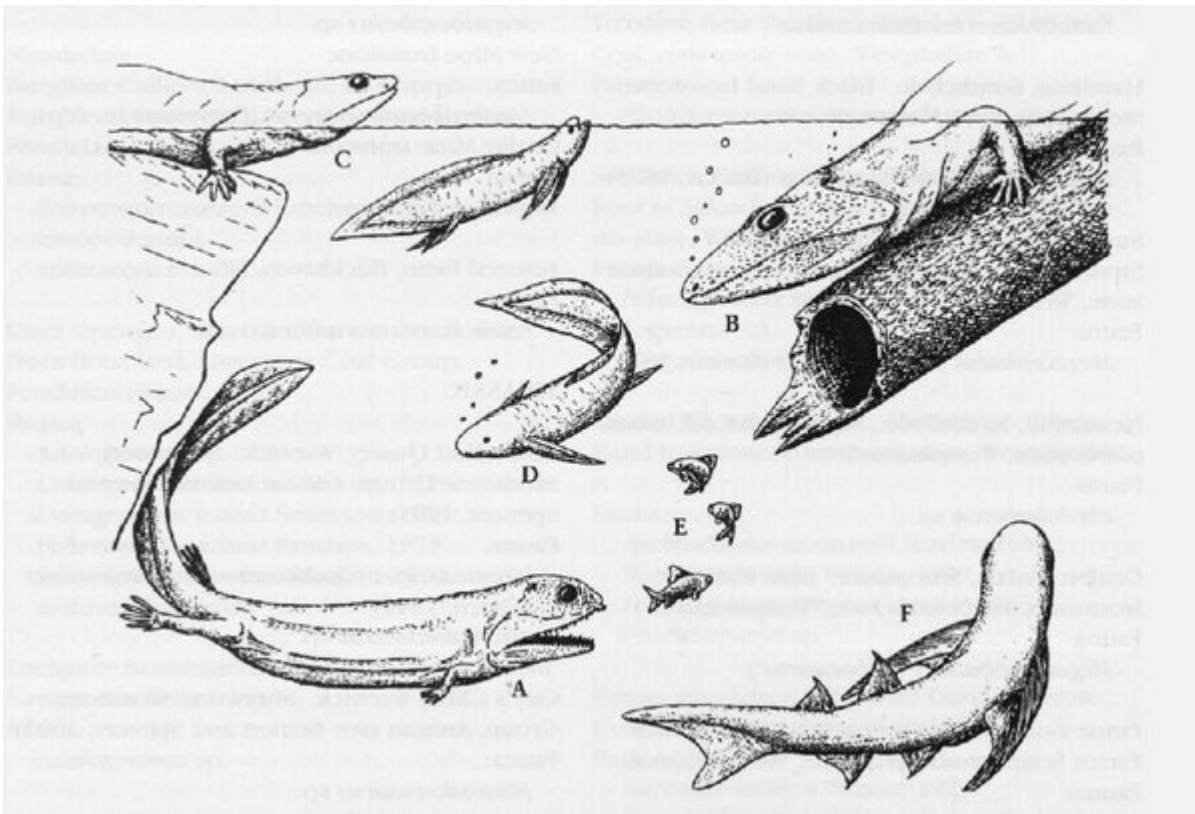
(Figure 15.4) Vertebrates from Dora in a reconstruction by Janvier (1996; based on Milner et al., 1986). Namurian tetrapods (A) Crassigyrinus and (B) Spathicephalus are supposedly primitive, the others are anthracosaurs: (C) Protogyrinus and Eoherpeton. Also present is the acanthodian (F) Gyracanthus, primitive actinopterygians (E) and lungfish (D).