Fossil Fishes of Great Britain

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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 (Säve-Söderberg, 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 labyrinthodonts 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 ichthyostegid 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

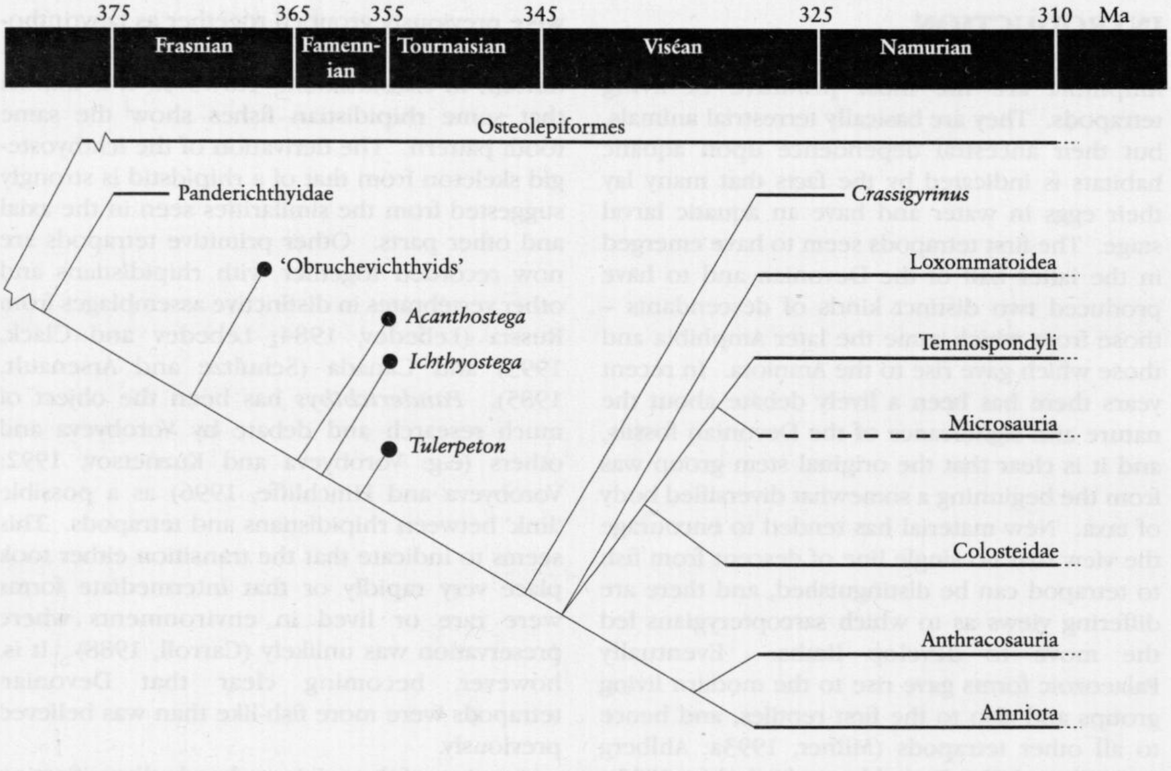

Figure 15.1 Cladogram of the fish–tetrapod transition in Late Devonian–Early Carboniferous times (after Ahlberg and Milner, 1994). The taxa are grouped on the basis of shared derived characters. The characters shared by the panderichthyids and the tetrapods appear to be adaptations to shallow-water habitats. 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.

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 modern 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 Aïstopoda, 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

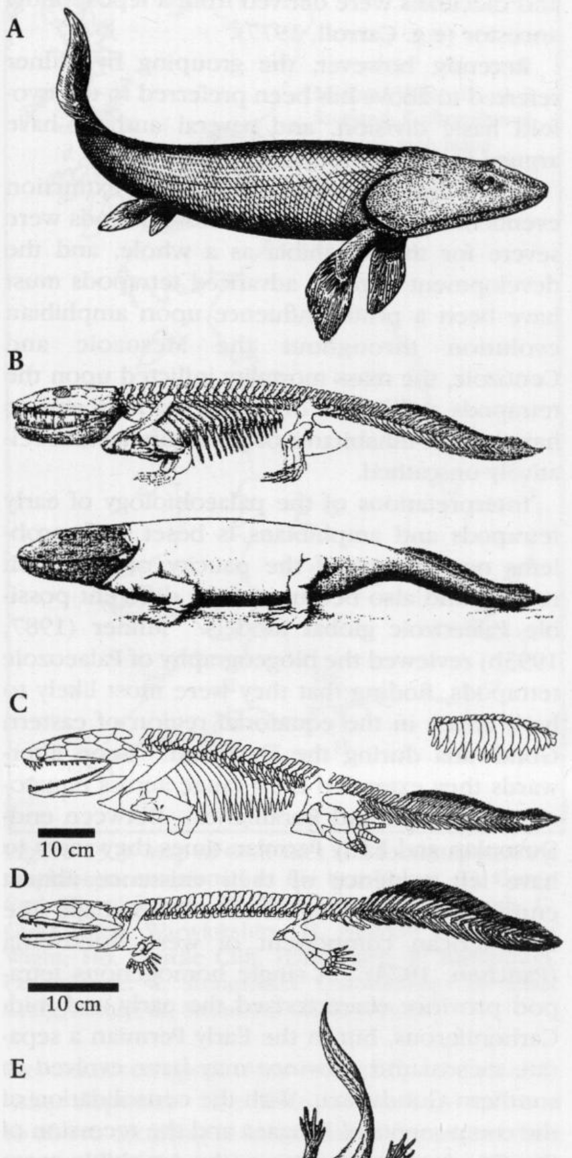

Figure 15.2 Devonian tetrapods: (A) the sarcopterygian *Panderichthys* (after Janvier, 1996); (B), (C) *Ichthyostega*; (D) *Acanthostega* (both after Coates and Clack, 1995); (E) *Tulerpeton* (after Lebedev, 1990; Janvier, 1996). These animals were all up to *c.* 1 m long.

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 temnospondyls) 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 two-fold 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

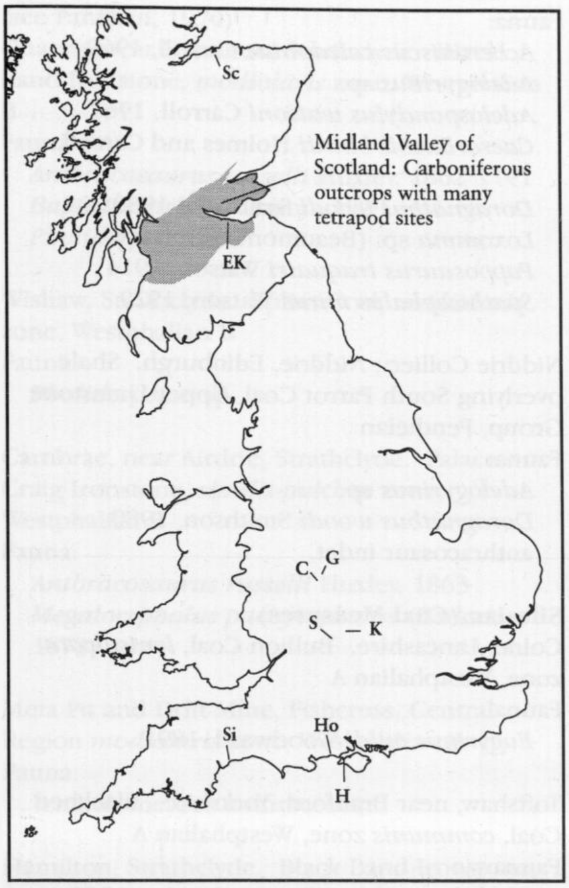

Figure 15.3 Map of GCR sites and localities yielding amphibians mentioned in the text below. C, Coton End, Warwickshire; EK, East Kirkton, Edinburgh; G, Guy's Cliffe, Warwickshire; H, Headon Hill, Isle of Wight; Ho, Hordle Cliff, Hampshire; K, Kirtlington, Oxfordshire; S, Stonesfield, Oxfordshire; Sc, Scaat Craig, Moray; Si, Sidmouth Cliffs, Devon.

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 miripedes 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 Cowdenbeath, Fife. 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-pulchra* 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. attheyi* 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.

Watton 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.
Batrachosauridiidae indet.
Albanerpeton sp.

Sunnydown Farm, Purbeck, Dorset. Cherty Freshwater Limestone, Purbeck Limestone Group, Tithonian
Fauna:
Discoglossidae indet.
Batrachosauridiidae indet.
salamander indet.
Lissamphibian indet.
Albanerpeton sp.

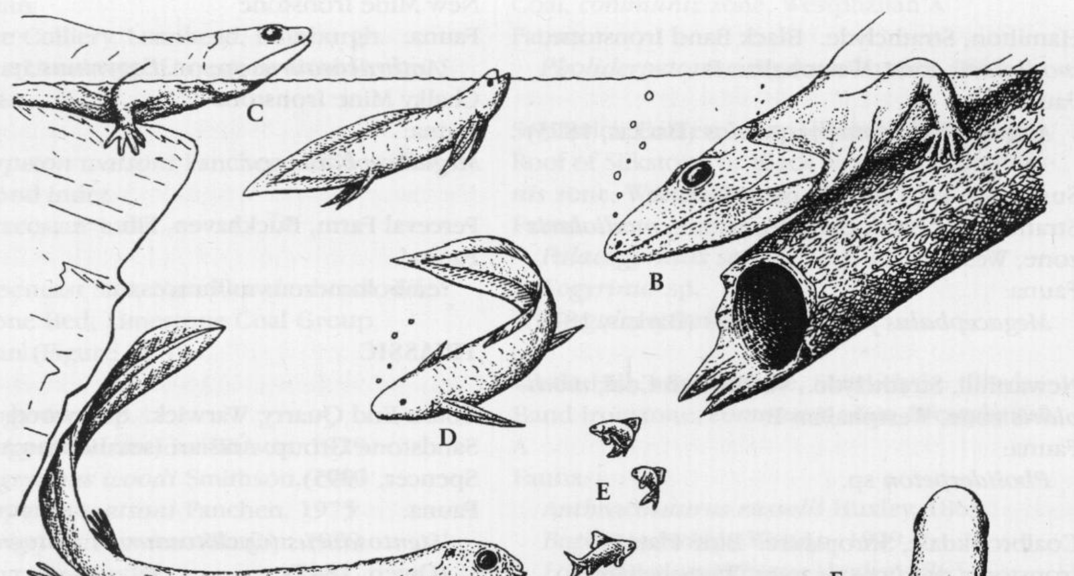

Figure 15.4 Vertebrates from Dora in a reconstruction by Janvier (1996; based on Milner *et al.*, 1986). Namurian tetrapods (A) *Crassigyrinus* and (B) *Spathicephalus* are supposedly primitive, the others are anthracosaurs: (C) *Protogyrinus* and *Eoberpeton*. Also present is the acanthodian (F) *Gyracanthus*, primitive actinopterygians (E) and lungfish (D).

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. *hinsbei* 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, Lérida, 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.

EAST KIRKTON, BATHGATE (NS 990690)

Highlights

This Viséan lacustrine deposit in Lothian preserves the remains of a predominantly terrestrial biota, including seven kinds of amphibian, fishes and a wide range of terrestrial invertebrates and plants.

Introduction

The site is a disused limestone quarry, some 27 km west of Edinburgh (Figure 15.5), where the East Kirkton Limestone dips at about 18° NE. Although rare fossil invertebrates have been known from this locality since the late 19th century, it was during the excavations initiated by Mr S.P. Wood in 1985 that tetrapod fossils were discovered. The Limestone lies near the top of the West Lothian Oil Shale Formation. This is a highly variable succession of shale with thin cherty limestones, volcanic ash bands and rare coals and marine bands. The whole is well-stratified and indicates deposition in a dominantly freshwater lake basin with variable water depth and with continuing spasmodic ash falls. It is situated close by the West Lothian volcanic centre.

During the late 1980s a series of discoveries by S.P. Wood and others aroused great interest.

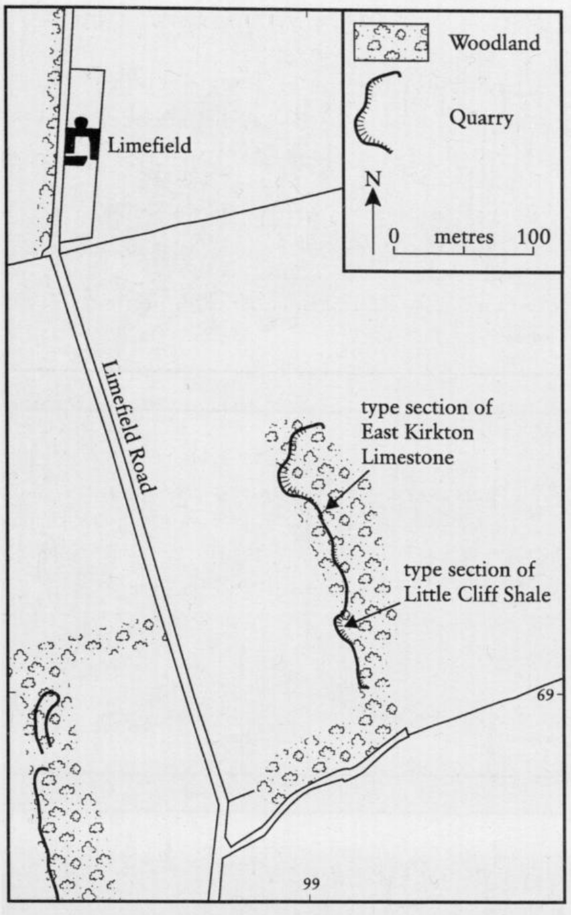

Figure 15.5 Sketch map of the GCR Site at East Kirkton Quarry (after Rolfe *et al.*, 1994).

They included several fully land-going amphibians and the oldest known stem amniote which has reptile affinities (Gee, 1988; Smithson, 1989). Subsequently a systematic investigation of the site by the National Museums of Scotland team has resulted in a special volume on this locality (Rolfe *et al.*, 1994).

The East Kirkton quarry has now yielded a rich terrestrial flora and fauna, remarkably well preserved and offering a unique view of an early Carboniferous ecosystem in a volcanic setting and a tropical wet climatic regime. The preservation and taphonomy of this biota, described by Rolfe *et al.* (1990), may be of a kind to be found elsewhere in the Midland Valley of Scotland.

Prior to the discovery of the East Kirkton amphibians, the principal tetrapod localities in the Scottish Carboniferous were in the lacustrine deposits at Cowdenbeath, Gilmerton and Loanhead (Smithson, 1985; Milner *et al.*, 1986).

Description

The section at East Kirkton has been dated as Brigantian, Upper Viséan, about 335 Ma in age. It has some 15 m of lacustrine limestones, shales, cherts and ash beds, deposited just south of the Carboniferous equator in a continental rift setting. Apart from the biota described so far, few fossils have been recorded (Rolfe *et al.*, 1994). The succession (Figure 15.6) has been extensively sampled and some 88 lithological units logged. The investigations have provided a remarkable suite of volcaniclastic lithologies and carbonate laminites (Rolfe *et al.*, 1990; Whyte, 1994). Plant fossils occur at many levels within the sequence as compressions, permineralizations or as fusain charcoal.

The invertebrate fossils are largely arthropods such as harvestman 'spiders', millipedes, scorpions and large eurypterids (Rolfe, 1988; Clarkson *et al.*, 1994).

Fauna

Elasmobranchi: Hybodontoidea: Tristychiidae
Tristychius arcuatus Agassiz, 1837
Elasmobranchi: Xenacanthida
Diplodoselache woodi Dick, 1981
Acanthodii: Acanthodiformes: Acanthodidae
Acanthodes indet.
Climatiidae
gen. et sp. indet.
Actinopterygii: Actinopteri: Elonichthyidae:
Species C cf. ?*Elonichthys robinsoni* (scales)
Species E cf. ?*Cosmoptychius* (scales)
Watsonichthys sp.
Species B Actinopterygian of no specified affinity
Species A cf. ?*Rhadinichthys carinatus* (scales) Traquair, 1977
Species D ?*Mesopoma* Traquair, 1890
Platysomida
Eurynotus sp.
Sarcopterygii: Rhizodontidae
Scales, gen. et sp. indet.

TETRAPODA
?Loxommatidae
gen. et sp. indet.
Temnospondyli:
Balanerpeton woodi Milner and Sequeira, 1994
Type specimen from this locality

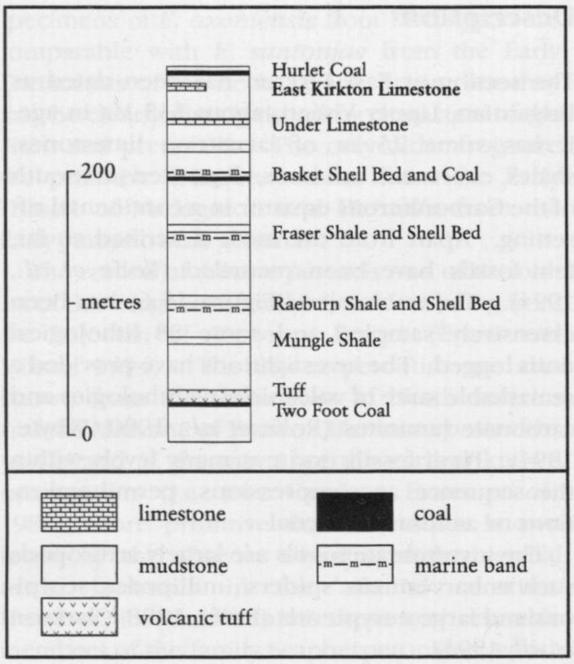

Figure 15.6 Succession in the top 250 m of the West Lothian Oil Shale Formation (after Whyte, 1994).

Aistopoda
Ophiderpeton kirktonense Milner, 1994
Type specimen from this locality
Anthracosauria *incertae sedis*
Eldeceeon rolfei Smithson, 1994
Silvanerpeton miripedes Clack, 1994
Type specimen from this locality

REPTILOMORPHA
Westlothiana lizziae Smithson *et al*., 1994
Type specimen from this locality

The elasmobranchs come from units 32–37 (Paton, 1994). Spines of the xenacanth *Diplodoselache arcuatus* Agassiz, are from a fish 30–40 cm long, which may have been a versatile predator feeding upon invertebrates and small fishes. In units 26 and 36 occur small spines from small acanthodians. Units 26–38 have produced at least six actinopterygian taxa (Coates, 1994); two are probably juveniles of uncertain affinities. One is a deep-bodied species. The sarcopterygians are represented by large patches of rhizodont scales in unit 36.

The tetrapod fauna is impressive not only for the number of individuals and taxa present but also for the remarkable preservation. For example, over 30 complete or partial skeletons of the newly discovered temnospondyl amphibian *Balanerpeton woodi* have been found at East

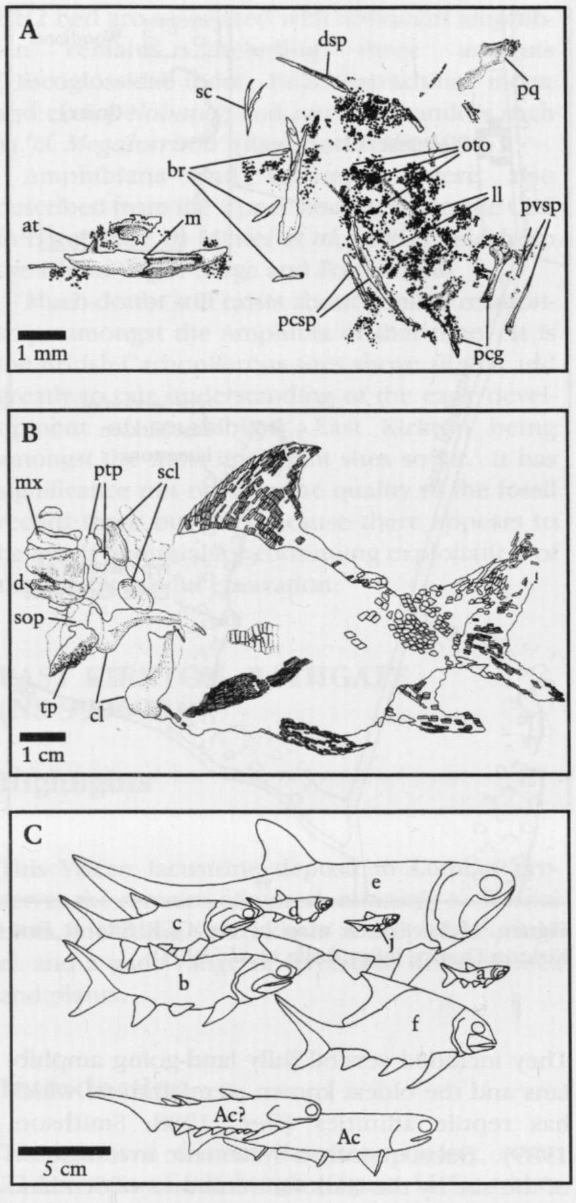

Figure 15.7 Fossil acanthodian and actinopterygian fishes from East Kirkton. (A) A very small acanthodian (RSM G 1993.6.1) from the Little Cliff Shale: Br, branchiostegal rays; dsp, dorsal spine; ll, lateral line; m, mandible; oto, otoliths; pcg, pectoral girdle; pcsp, pectoral spine; pq, palatoquadrate; pvsp, pelvic spine; sc, scapula; at, anchylosed tooth. (B) An articulated specimen of *Eurynotus* with head bones, tooth plates and scales (after Coates, 1994): cl, cleithrum; d, dentary; mx, maxillary; ptp, pterygoid; scl, supracleithrum; sop, suboperculum, tp, tooth plate. (C) a diagrammatic representation of the total acanthodian and actinopterygian fauna, based on scales and drawn to estimated proportional sizes: Ac, acanthodian material; Ac?, possible climatiid tesserae; a, actinopterygians; b, isolated scales; c, spp. of *Elonichthys*; d, spp. of *Mesopoma*; e, *Cosmoptychius*; f, eurynotid material; j, juvenile specimens.

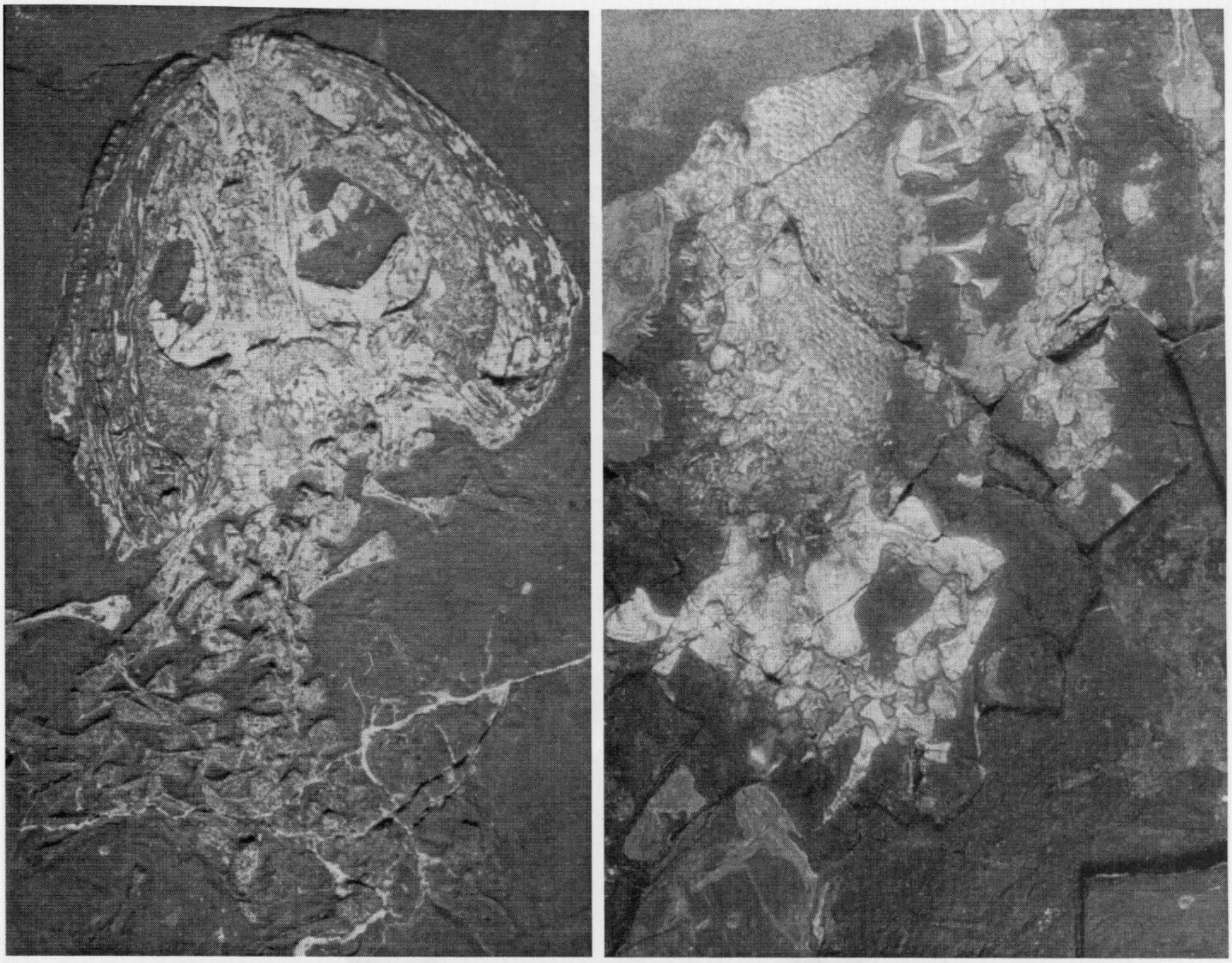

Figure 15.8 *Balanerpeton woodi* Milner and Sequiera; photographs under UV light (× 1) of (A) the skull and anterior part of the axial skeleton in dorsal view (GLAHM V2051) and (B) posterior part of the axial skeleton, hind limb and squamation in dorsal view (GLAHM V 2052). From the Upper Viséan, Bathgate. (Photographs courtesy of the Hunterian Museum, Glasgow.)

Kirkton (Milner and Sequeira, 1994). It is the commonest tetrapod in the assemblage and grew to about 50 cm in length. Superficially it is like the later genus *Dendrerpeton*, but has a more advanced structure of the skull (Figures 15.8 and 15.9). The lower jaw has fewer but larger teeth than the corresponding upper jaw. There have also been found two straight ribs from a much larger form, a probable second temnospondyl at East Kirkton. The temnospondyls are comprised of some 160 genera and are more numerous than all the other early non-amniote tetrapod groups combined.

In contrast, the aistopod *Ophiderpeton kirktonense* Milner, 1994 is amongst the rarest of the East Kirkton tetrapods (Figure 15.10). The holotype is an articulated skull and anterior part of the trunk in counterpart blocks of shale from unit 82 of the section. Other material is partly disarticulated and very poorly preserved. Aistopods are a group of limbless vertebrates with very long bodies and short tails. They are clearly specialized with their snake-like form and terrestrial mode of life. They show no sign of having possessed a sensory lateral line system which is present in aquatic tetrapods. As many as 200 vertebrae may be present in the axial skeleton. The aistopod skull is highly derived

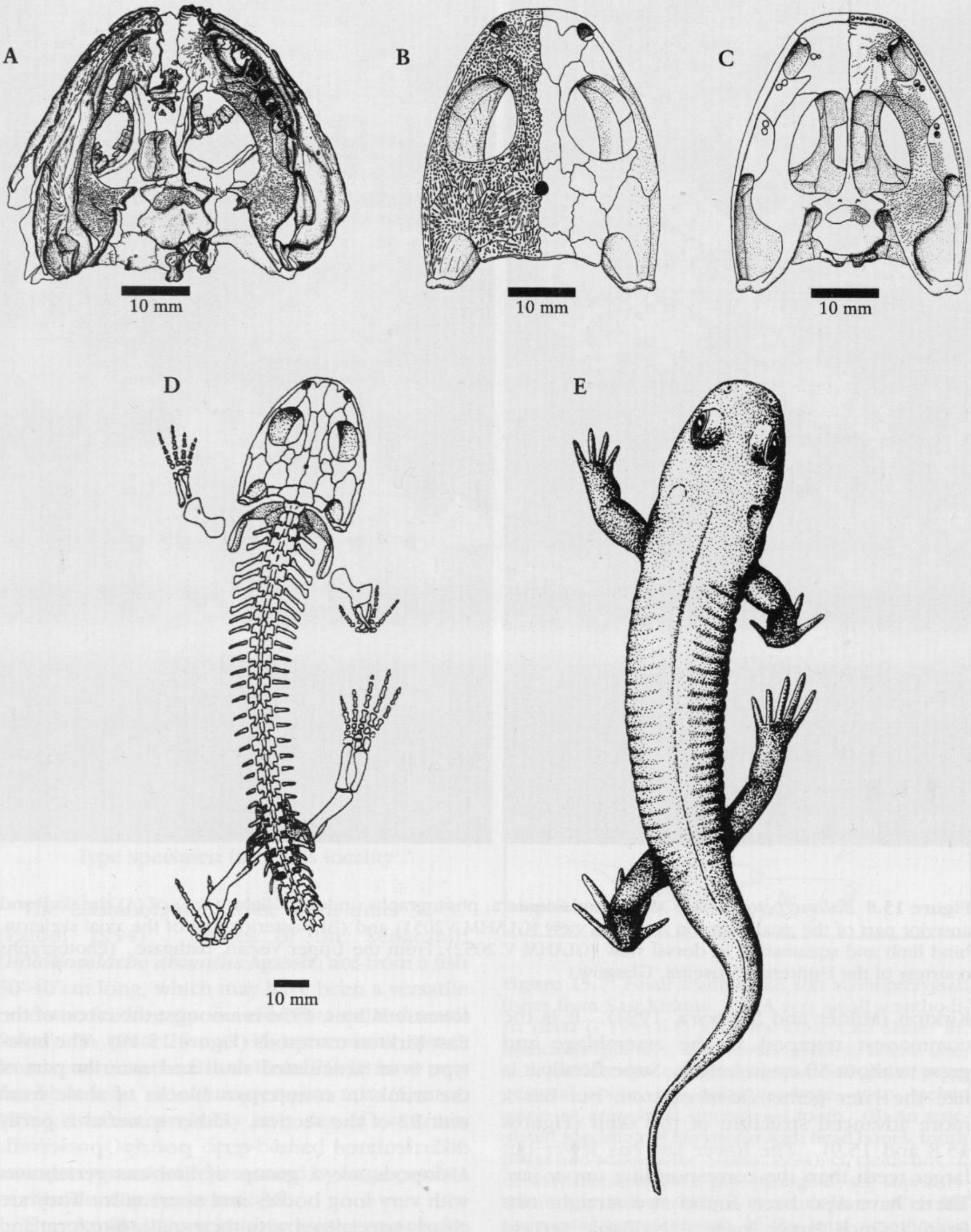

Figure 15.9 *Balanerpeton woodi* Milner and Sequiera (based on GLAHM V 2051): (A) the dorso-ventrally compressed skull in palatal view; (B) restoration of the skull in dorsal view showing ornamentation on the outer surface of bones; (C) the skull restored in palatal view with marginal teeth and fangs and surface ornamentation indicated; (D) restoration of the incomplete skeleton in dorsal view; (E) the animal restored in dorsal view (after Milner and Sequiera, 1994).

with respect to the basic tetrapod pattern. There appears here to be a loss of bone so that in the extreme the skull is reduced to a set of struts articulating the lower jaw against the braincase. The maxillary dentition is of widely spaced sturdy pointed fangs. The lack of limbs and limb girdles adds to the difficulty of determining the relationship to the other tetrapods. Seven genera are known so far, allotted to three families and the group ranges from the Middle Viséan to the Permian in Eurasia (Milner, 1993b). In Britain their provenance is from the Scottish Viséan – the oldest being *Lethiscus stocki* Wellstead (1982) from the Wardie Shale – and from the Westphalian of Northumberland.

Anthracosaurids are represented by several new forms. *Silvanerpeton miripedes* is a small, gracile form, the holotype of which is an almost complete articulated specimen in black shale (Unit 82; Figure 15.11). A second specimen is the natural mould of the skull and anterior postcranium. There are also some disarticulated large limb bones and vertebral elements. Clack's (1994) description of this material, amongst the earliest of the anthracosaurs, reveals it as very different from previously described early articulated anthracosaur remains, such as *Proterogyrinus* from the Upper Viséan of West Virginia. *Silvanerpeton* has the anthracosaur characters of tabular–parietal bone contact, a tabular horn and a moderate surangular crest, gastrocentrous vertebrae with poorly ossified centra and neural arches. There are over 30 presacral vertebrae, a closed palate, mobile basal articulation and an intertemporal bone in the skull. This new genus differs from *Eldeceeon*, the other species of anthracosaur at East Kirkton, in the number of ribs and vertebrae, interclavicle shape, relative limb length, in having an unossified tarsus, and a pedal phalangeal count of 23 455.

The new species of *Eldeceeon rolfei* (Figure 15.12) was described by Smithson (1994) as a primitive, moderately sized anthracosaur (overall length 35 cm) represented by two specimens from Unit 76. These fossils present a combination of characters which do not fit readily into either of the two suborders of anthracosaurs, and moreover this includes the restriction of the ribs to the front half of the presacral column. Fortunately the well-ossified appendicular skeleton is preserved to show a phalangeal count of 23 454 in fore and hind extremities.

Westlothiana lizziae (Smithson and Rolfe, 1990) is the earliest known reptilomorph and Smithson *et al.* (1994) were able to describe an almost complete skeleton, as well as a second nearly complete but disarticulated skeleton and other remains. These represent a skink-like animal with a long body and small limbs (Figure 15.13). The skull is short and compact, with a

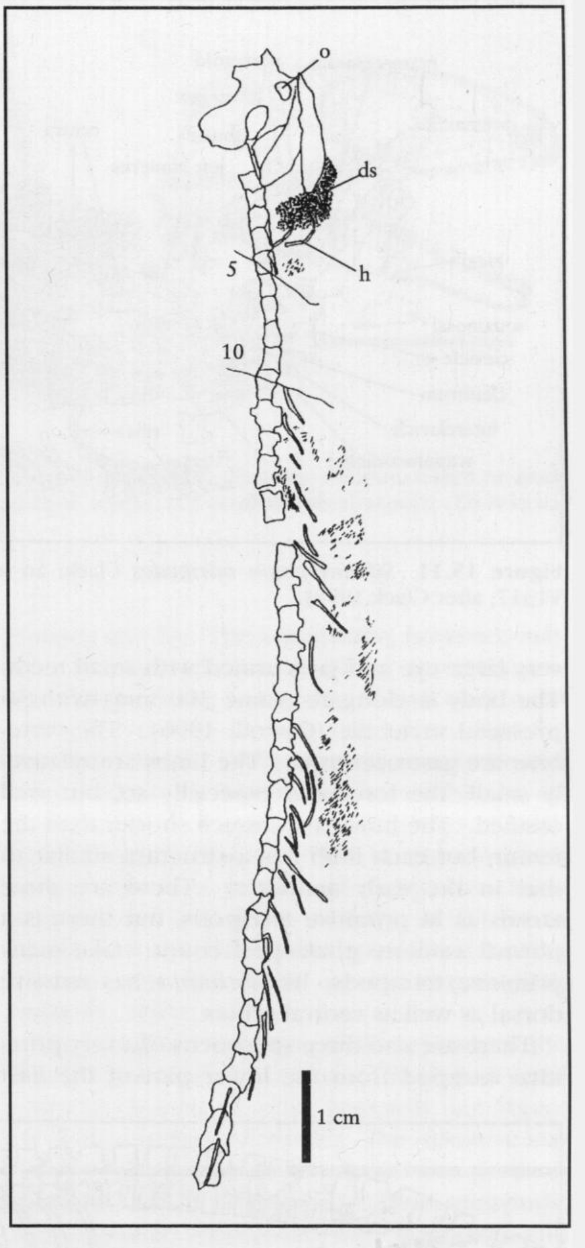

Figure 15.10 *Ophiderpeton kirktonense* Milner, holotype RSM G 1988.3.1; part of skull and vertebral column, the vertebrae 5–10 are restored from counterpart; ds, dorsal scales; h, hyoid; o, orbit (after Milner, 1994).

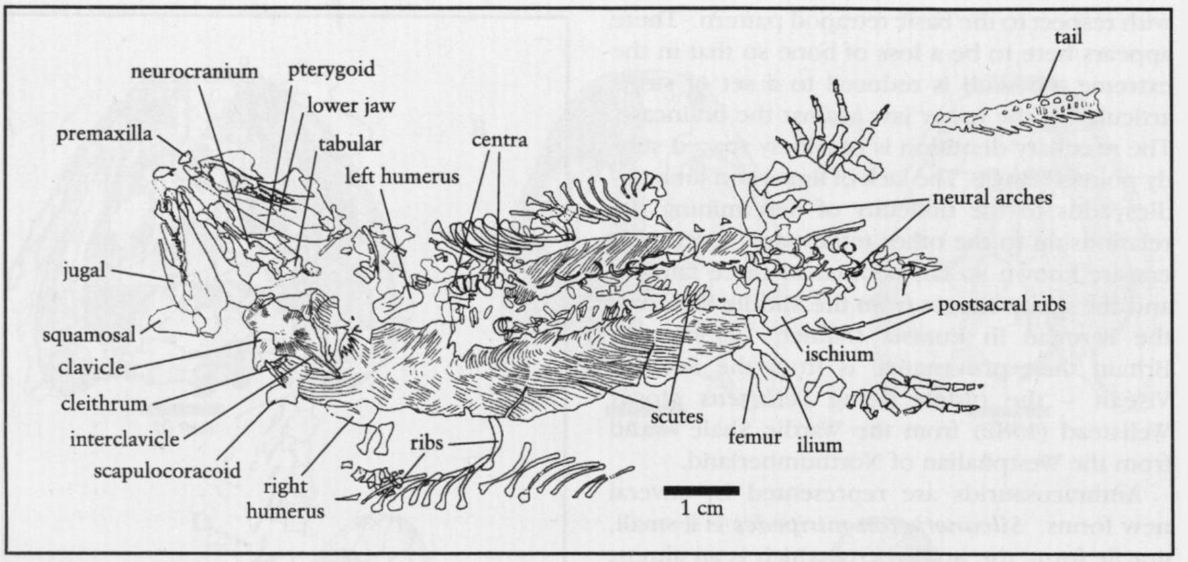

Figure 15.11 *Silvanerpeton miripedes* Clack; an interpretative drawing of the skeleton (specimen UMXC V1317; after Clack,1994).

very large eye and jaws armed with small teeth. The body is elongate (some 300 mm) with 36 presacral vertebrae (Carroll, 1996). The vertebrae are gastrocentrous. The limbs are relatively small, the forelimbs especially so, but well ossified. The humerus is much shorter than the femur, but each limb has a structure similar to that in the early amniotes. There are three tarsals as in primitive tetrapods, but there is a normal amniote phalangeal count. Like many primitive tetrapods, *Westlothiana* has massive dorsal as well as ventral scutes.

There are also three specimens of a very primitive tetrapod from the lower part of the East Kirkton Limestone. These animals were elongated and loxommatid-like, and possessed skulls that were up to 10 cm long, broad-snouted and alligator-like in shape. They may have been fish-eating predators.

Interpretation

The model of the East Kirkton environment proposed by Durant (1994) comprises volcanic vents surrounded by a thickly vegetated hinterland with streams carrying pyroclastic detritus to lakeside deltas and beaches. Rainfall was intermittent but sufficient to maintain a strong

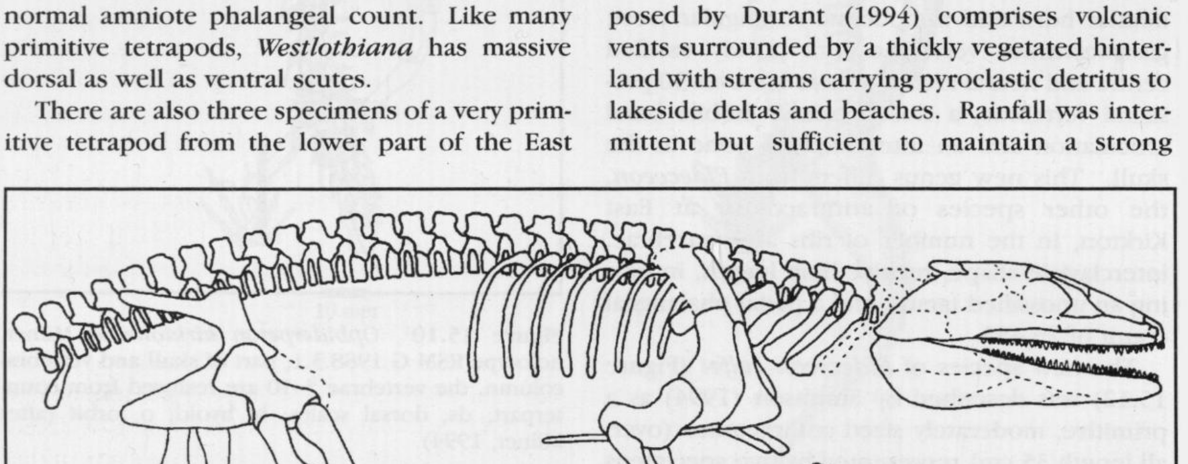

Figure 15.12 *Eldeceeon rolfei* Smithson; the skull and most of the post-cranial skeleton in a provisional restoration, based mainly on the holotype (RSM G 1990.7.1) from the East Kirkton Limestone (after Smithson, 1994).

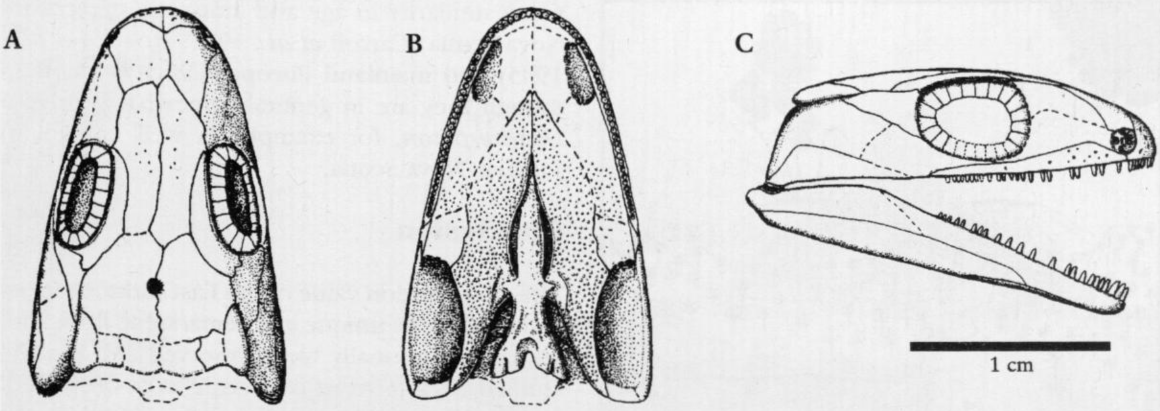

Figure 15.13 *Westlothiana lizziae* Smithson and Rolfe; reconstruction of the skull and skeleton based on both known specimens. (A) Skull in dorsal aspect; (B) skull in palatal aspect; (C) skull in lateral aspect; (D) restoration of incomplete skeleton (after Smithson *et al.*, 1994.)

drainage pattern (Figure 15.14). There seems to be no direct link between the death and subsequent preservation of organic remains and the volcanic activity. Whether the burning of plants to provide the fusain was from contact with hot ejecta or lava or from ignition by lightning is not known.

Clarkson *et al.* (1994) suggest that the lake was generally cool, though occasionally temperature may have been raised by localized hot spring activity. When acidity was reduced, calcium carbonate was precipitated, covering wide areas of the lake floor and the remains lying upon it. From time to time some sediment was slumped into deeper water, triggered perhaps by local earth tremors.

During the existence of the East Kirkton lake it underwent profound faunal changes. Its early stage seems to have been as a fish-free pond full of newt- or salamander-like amphibians. Volcanic activity perhaps then put an end to the aquatic vertebrate population and only terrestrial tetrapods are found. Towards the end of the record the lake reverted to a productive body of water but with only fish representing the vertebrates.

Apart from the fishes, the bulk of the biota consists of plants, land-living invertebrates and amphibians and reptilomorphs that are amongst the oldest known. The vertebrates seem to have been largely carnivorous in habit. The elasmobranchs and palaeonscid actinopterygians were active swimmers, probably inhabiting middle depths within the lake and feeding upon invertebrates and fry. The xenacanths, however, may have fed upon bottom-dwelling invertebrates. The acanthodians, on the other hand, were most probably plankton-feeders, with ostracods as the principle food. Amongst the palaeonscid actinopterygians, *Eurynotus* is notable in its dentition which suggests a durophagous (mollusc-browsing) habit. The sarcopterygians, known only from patches of scales, have been estimated to have been as large as 0.5 m in length, and may have been specialized lurking predators in this lake, as elsewhere (S.M. Andrews, 1985).

The tetrapods were almost all dependent ultimately upon aquatic sources of food and upon water for their mode of life generally (see Figure 15.15 for a suggested model). The primitive loxommatid-like tetrapods may have been predatory upon small fishes and other tetrapods. Temnospondyl amphibians were abundant, and those at East Kirkton are the oldest known. *Balanerpeton* was a relatively terrestrial animal, like a large salamander. The aistopod may have occupied a niche comparable to that of recent snakes, living in the plant litter or even underground. Its few, large teeth suggest that it preyed on organisms almost as large as its own head – arthropods and small vertebrates in the cryptofauna. The anthracosaurs were active animals, terrestrial or aquatic, predatory on small or larval tetrapods and arthropods (Figure 15.15).

The presence of the lake, its surrounding vegetation and the warm climate were prime factors

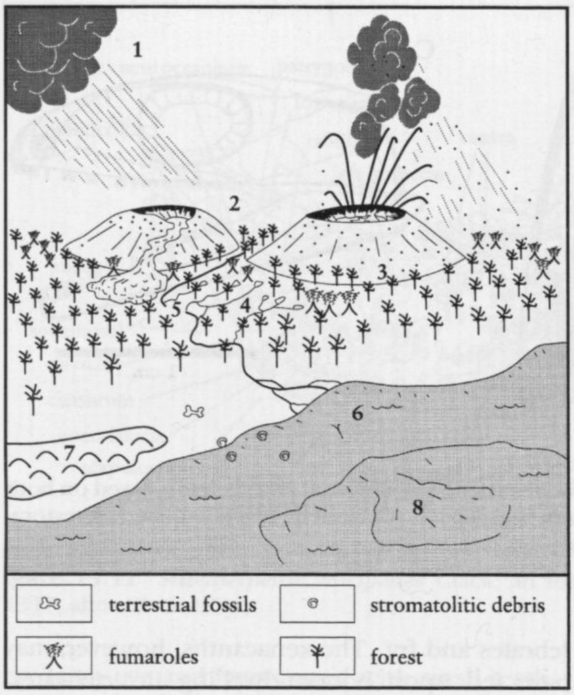

Figure 15.14 Reconstruction of the environments represented in the vicinity of the East Kirkton Lake (after Durant, 1994). 1, intermittent rainfall; 2, recently expired volcano with lava flows; 3, erupting basaltic volcano with associated heavy rainfall; 4, fumaroles and hot springs emitting mineral-rich waters; 5, intermittent stream in flood transporting volcanic detritus from flanks of volcanoes; 6, terrestrial fossils incorporated in sediment during transport; 7, exposed lake shallows or floodplain with limestone and stromatolite debris; 8, deposition of graded units in lake.

in the palaeoecology. Most of the tetrapods were essentially terrestrial in habit. For much of the time the lake waters were toxic from mineral contaminants, and may also have been cut off from other water bodies. However, for the later part of its existence somewhat less hostile conditions prevailed and the fishes entered the lake. This was accompanied by a change in the land flora, which now became lycopod-dominated, and perhaps also by a wetter climate.

Comparison with other localities

The East Kirkton site is alone in the quality of preservation of and extent of the tetrapod fauna; the fishes in contrast are not very well preserved. There are also more detailed palaeoenvironmental data available here than there is at other localities of comparable age in Britain. Sites of some similarity in age and fauna are present in Nova Scotia (Carroll *et al.*, 1972; Holmes *et al.*, 1995) and mainland Europe (Czech Republic), though they are in general somewhat younger. *Dendrerpeton*, for example, is well known at Joggins, Nova Scotia.

Conclusion

The conservation value of the East Kirkton site is provided by its unique and remarkable flora and fauna, exceptionally well preserved and closely studied by a team of experts in a co-ordinated team effort. It is clear that there is still much potential for further excavation and study of the remarkable tetrapods which have extended back to Viséan time the record of the reptilomorphs. Comparable early but less productive sites or sets of localities are known in the Carboniferous of mainland Europe (Milner, 1980, 1993b), eastern USA and Canada (Carroll *et al.*, 1972) and elsewhere in southern Scotland (Smithson, 1985).

HEADON HILL (SZ 315858–SZ 318862) (POTENTIAL GCR SITE)

Highlights

Early Cenozoic amphibian fossils are recorded from the epicontinental–continental sequence of this site in the Isle of Wight, Hampshire. They occur in the sands and clays of the Headon Hill Formation (Late Eocene).

Introduction

The Late Eocene (Priabonian) Headon Hill Formation in the type area in the degraded coastal sections of Headon Hill, Isle of Wight, has produced an abundant fauna of turtles, crocodiles, snakes and lizards. Large parts of the section (Figure 15.16) are obscured by mud flows, but the relevant beds may easily be cleared for further excavation.

The Headon Hill Formation between Alum Bay and Totland has been described by Prestwich (1846), White (1921), Stinton (1971), Cray (1973), Daley and Insole (1984) and Insole and Daley (1985). Accounts of the reptilian faunas have been given by Cray (1973), Meszoely and Ford (1976) and Rage and Ford (1980), but there is as yet no complete overview.

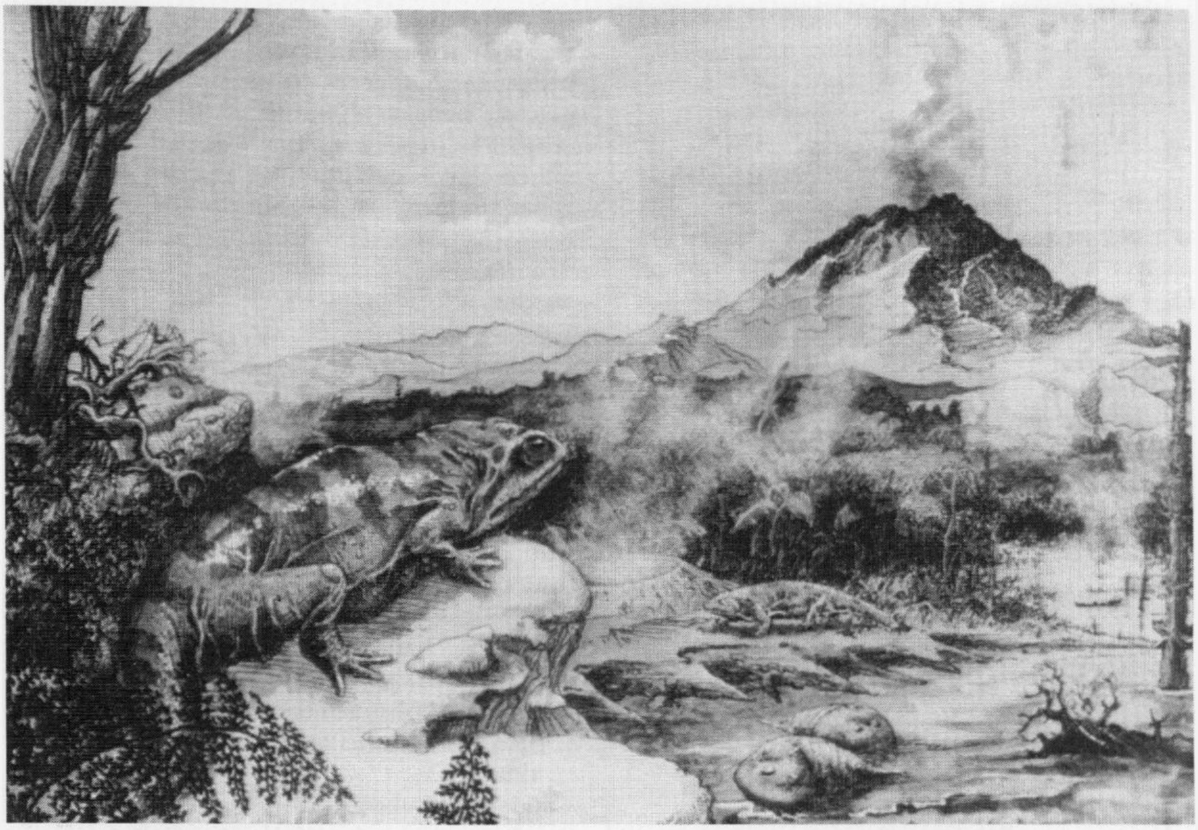

Figure 15.15 Reconstruction of the hot springs environment that is indicated in the East Kirkton Limestone. The temnospondyl *Balanerpeton* is in the foreground while an *Eoherpeton*-like anthracosaur (*Eldeceeon*) is in the middle distance, next to a fumarole. The eurypterid *Hibbertopterus* is at the water's edge and the pteridosperm *Sphenopteris* is shown in the bottom-left corner. (From Milner *et al.*, 1986; Courtesy of the Hunterian Museum/Modern Geology.)

Description

A generalized section of the Headon Hill Formation taken from the south-west corner of Headon Hill, based on Cray (1973) and Insole and Daley (1985), is:

	Thickness (m)
Cliff End Member (part of 'Upper Headon Beds')	
Clays and marls	seen to 6.6
Hatherwood Limestone Member (part of 'Upper Headon Beds')	
Limestones	2.8
Lignite (Lignite Bed)	0.7
Limestones	2.7
Linstone Chine Member (part of 'Upper Headon Beds')	
White and grey sands (*Microchoerus* Bed at base)	0.8
Colwell Bay Member ('Middle Headon Beds')	
Blue-green clays and sands	2.0
Limnaea Limestone	0.2
Blue, green and brown sandy clays (*Venus* Bed)	*c.* 4.4
Sands, clays and lignites (*Neritina* Bed)	2.5
Totland Bay Member ('Lower Headon Beds')	
Limnaea Limestone (How Ledge Limestone)	*c.* 2.0
Marls, clays, sands and lignites	4.6
Limnaea Limestone	0.4
Green clays and pale sands	4.4
Limnaea Limestone	0.8
Blue and green clays	1.0
Limnaea Limestone	0.25
Green sandy clays	0.7
Green clays	seen 1.1

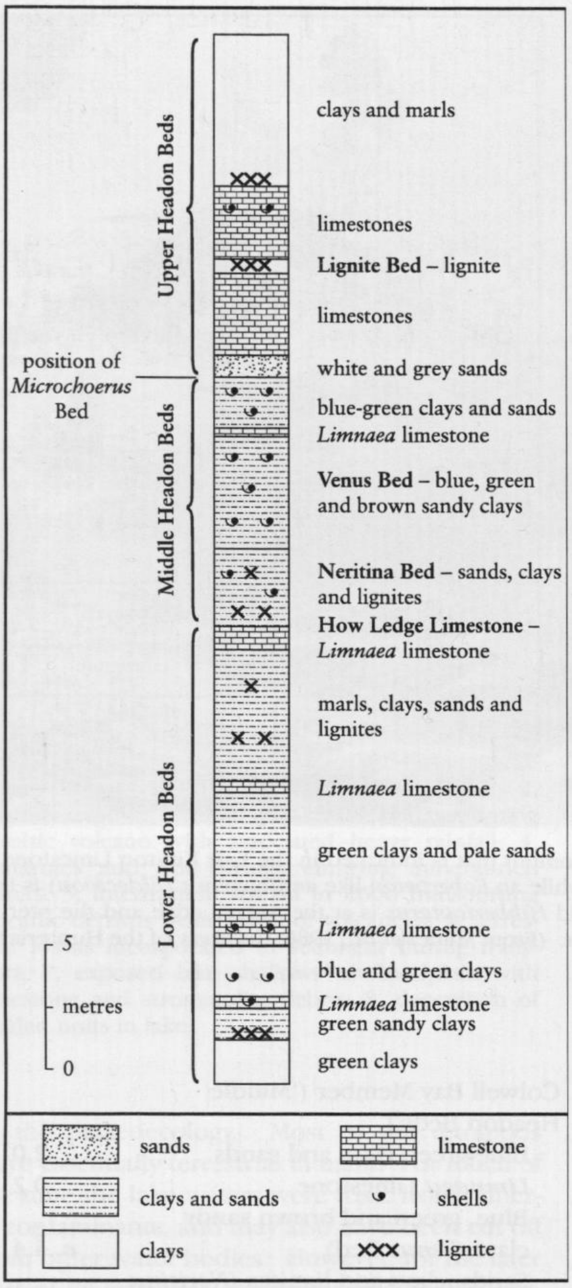

Figure 15.16 Section through the Headon Hill Formation at Headon Hill, Isle of Wight (after Cray, 1973).

In the early 1970s, large collections of reptiles (particularly squamates) and amphibians were obtained by Mr R.L.E. Ford from units in the Totland Bay Member, in particular from Bed HH2 (Bosma, 1974, fig. 9) beneath a unit of hard limestone named the 'How Ledge Limestone', from a series of green-grey clays. Two localities have yielded herpetofaunas from this stratum: in the undercliff at Headon Hill and in Totland Bay. The How Ledge Limestone occurs along the coast between Hatherwood Point and How Ledge, and it appears that the amphibians occur patchily beneath the entire length of the outcrop. The fossils are all represented by disarticulated, and frequently abraded and fragmented, elements that indicate considerable predepositional disturbance.

Fauna

The main collection of fossil reptiles from Headon Hill are in the NHM, Museum National d'Histoire Naturelle (MNHN) Paris and the Stuttgarter Museum für Paläontologie (Ford Collection). The collections include many mammal amd reptile taxa, as well as amphibians.

Anura: Discoglossidae
'discoglossid 2' of Milner *et al.* (1982)
Anura: Pelobatidae
Eopelobates sp.
Anura: Palaeobatrachidae
Albionbattrachus wightensis Meszoely *et al.*, 1984
Caudata: Salamandridae
salamandrid indet. cf. *Megalotriton*

Interpretation

The interpretation of the Headon Hill section is essentially that given for the Hordle Cliff (q.v.) outcrop – a basin infilling with a final depositional phase above sea level. The land surface was heavily vegetated and supported a considerable vertebrate fauna. For the latter to have been so apparently abundant, there was probably a substantial invertebrate fauna as well, all dependent upon extensive bodies of freshwater. The climate was subtropical or Mediterranean.

Comparison with other localities

Geographically and stratigraphically, the nearest comparable units to the Totland Bay Formation at Headon Hill are the same stratigraphical unit as at Hordle Cliff (SZ 263923–SZ 273918) and Wootton Creek, Fishbourne, on the Isle of Wight (SZ 551927). In the 'Osborne Beds' the large discoglossid frog 'discoglossid 2' of Milner *et al.* (1982) is present (Rage and Ford, 1980). All of the amphibians recorded from Headon Hill are known from the directly correlative sequence at Hordle, but there are many genera known from

Hordle that are absent on the Isle of Wight (see above), possibly the result of taphonomic differences (Milner *et al.*, 1982). Elements of the Headon Hill fauna are found in a well-preserved assemblage of anurans and caudates from the Oligocene Lower Hamstead Beds exposed along the foreshore at Cranmore Ledge, Bouldnor, on the Isle of Wight (SZ 370900–SZ 405920; Milner, 1986). This assemblage has yielded 'discoglossids 1 and 2' of Milner *et al.* (1982), ***Eopelobates*** cf. ***hinschei*** and the salamanders ***Salamandra sansaniensis*** and ***Chelotriton*** cf. ***paradoxus***. The '*Venus*' Bed and Oyster Bed of the Middle Headon Beds exposed along the foreshore at Colwell Bay, Isle of Wight (SZ 327878–SZ 328881), yield good fish fossils.

Conclusion

The conservation value of the Headon Hill section lies in its great potential for future collecting, since it has been much less exploited than the equivalent-age units at Hordle Cliff (q.v.).