J.N.C.C.

Fossil Reptiles of Great Britain

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Access to the countryside

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12 Hope Terrace,
Edinburgh EH9 2AS.

Countryside Council for Wales,
Plas Penrhos,
Ffordd Penrhos,
Bangor,
Gwynedd LL57 2LQ.

Museum abbreviations

AUGD, Aberdeen University Geology Department.
AUZD, Aberdeen University Zoology Department.
BATGM, Bath Geology Museum.
BGS(GSE), British Geological Survey, Edinburgh.
BGS(GSM), British Geological Survey, Keyworth (old Geological Survey Museum collection, London).
BMNH, Natural History Museum, London (formerly British Museum (Natural History), London).
BRSMG, Bristol City Museum and Art Gallery.
BRSUG, Bristol University Geology Department.
BUCCM, Buckinghamshire County Museum, Aylesbury.
AMMZ, Cambridge University Museum of Zoology.
CAMSM, Sedgwick Museum, Department of Earth Sciences, Cambridge University.
DORCM, Dorset County Museum, Dorchester.
ELGNM, Elgin Museum.
EXEMS, Royal Albert Memorial Museum, Exeter.
GLRCM, Gloucester City Museum and Art Gallery.
IWCMS, Isle of Wight Museum Geology, Sandown.
LEICS, Leicestershire Museums, Leicester.
LIVCM, National Museums on Merseyside, Liverpool.
MAIDM, Maidstone Museum.
MANCH, Manchester Museum.
MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts.
NEWHM, Hancock Museum, Newcastle upon Tyne.
NMS, National Museums of Scotland, Edinburgh (formerly RSM).
NMW, National Museum of Wales, Cardiff.
NORCM, Norwich Castle Museum.
OUM, University Museum, Oxford.
OXFPM, Oxford Polytechnic Geology Department.
SHRBM, Shrewsbury Borough Museum.
SHRCM, Shropshire County Museum, Ludlow.
SDM, Stroud District Museum.
WARMS, Warwickshire Museum, Warwick.
WHIMS, Whitby Museum.
YORYM, Yorkshire Museum, York.
YPM, Yale Peabody Museum, New Haven, Connecticut.

Chapter 1

Introduction

Introduction

Britain is famous for its fossil reptiles, partly for historical reasons, but also because there are so many richly fossiliferous localities that have supplied, and continue to supply, excellent material. The continuing potential of British fossil reptile sites is illustrated by recent work on such internationally important localities as the Mid Triassic localities of England (e.g. Benton, 1990c, Benton, *et al.*, in press; Milner *et al.*, 1990), the Late Triassic faunas of Elgin (e.g. Benton and Walker, 1985), the Late Triassic marine bone beds of the south-west of England (Storrs, 1994; Storrs and Gower, 1993), the Late Triassic to Early Jurassic fissures around Bristol and in south Wales (e.g. Evans, 1980, 1981; Crush, 1984; Fraser, 1982, 1985, 1986, 1988a, 1988b, 1994; Fraser and Walkden, 1983; Whiteside, 1986), the Early and Late Jurassic marine faunas of Dorset and Somerset (e.g. McGowan, 1974a, 1974b, 1976, 1986, 1989a, 1989b; Brown, 1981; Padian, 1983; Galton, 1985b; Brown *et al.*, 1986; Taylor, 1992a, 1992b), the Mid Jurassic terrestrial faunas of the Cotswolds (e.g. Galton, 1980a, 1983a, 1983b, 1985b; Evans *et al.*, 1988, 1990; Evans, 1989, 1990, 1991, 1992a; Evans and Milner, 1991, 1994; Metcalf *et al.*, 1992), the diverse small reptiles from the Purbeck of Swanage (e.g. Evans and Kemp, 1975, 1976; Gaffney, 1976; Galton, 1978, 1981b; Buffetaut, 1982; Estes, 1983; Howse, 1986; Ensom *et al.*, 1991; Sereno, 1991a; Clark, in press), the Wealden of the Weald and of the Isle of Wight (e.g. Galton, 1969, 1971a, 1971b, 1971c, 1973, 1974, 1975; Buffetaut and Hutt, 1980; Norman, 1980, 1986, 1990b; Blows, 1987; Buffetaut, 1982; Charig and Milner, 1986, 1990; Unwin, 1991; Clark, in press), the pterosaurs and other reptiles from the Cambridge Greensand (e.g. Unwin, 1991), and the various Palaeogene faunas of southern England (e.g. Moody and Walker, 1970; Moody, 1974, 1980a; Walker and Moody, 1974; Meszoely and Ford, 1976; Hooker and Ward, 1980; Rage and Ford, 1980; Milner *et al.*, 1982). The main focus in selecting sites for conservation has been to choose those which have been studied recently, and which have supplied abundant reptile specimens. An attempt was also made to balance the coverage, so that each major stratigraphic unit and facies is represented.

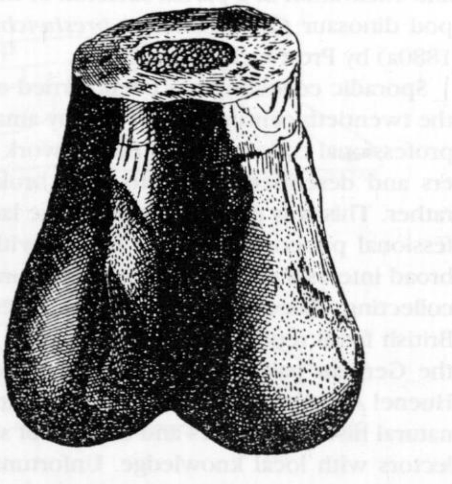

Figure 1.1 Lower end of the thigh bone of *Megalosaurus*, from Cornwell, Oxfordshire: one of the first fossil reptile bones to be illustrated from Britain, and the oldest recorded figure of a dinosaur (from Plot, 1677).

The historical records of fossil reptiles from Britain extend back a long way. Earliest finds included fossils that we now recognize as dinosaur bones (Figure 1.1) from the Mid Jurassic of Oxfordshire (Plot, 1677; Lhuyd, 1699; Woodward, 1728; Platt, 1758; more details in Delair and Sarjeant, 1975) and a marine crocodile from the Early Jurassic of Whitby, Yorkshire (Chapman, 1758; Wooller, 1758). More intensive collecting began only in the 19th century, and large numbers of marine ichthyosaurs and plesiosaurs were obtained from the Early Jurassic of Lyme Regis, Dorset and Whitby, Yorkshire (e.g. Home, 1814, 1819a; Conybeare, 1822, 1824; Young and Bird, 1822; more details in Benton and Taylor, 1984). More dinosaur specimens were found in the Mid Jurassic of Oxfordshire (Buckland, 1824) and in the Early Cretaceous of south-east England (Mantell, 1822, 1825), and footprints of Permian age came to light in Scotland (Buckland, 1828; Grierson, 1828; details in Sarjeant, 1974).

Throughout the remainder of the nineteenth century, large collections were amassed, and most of the localities noted in the present work were identified. Locality information for nineteenth century collections may be problematic in many cases, because of a lack of direct contact between the collectors and the palaeontologists who made the descriptions. Prolific authors such as Owen, Huxley, Seeley, Lydekker and others seem to have worked largely in their institutions on material that was sent to them from a network of local natural history and geological societies throughout the country. Only rarely did these biologically trained palaeontologists record geographic or geological details of the context of their specimens. A notable exception is the account of the discovery and excavation of a partial skeleton of the ornithopod dinosaur *Camptosaurus prestwichii* (Hulke, 1880a) by Prestwich (1879, 1880).

Sporadic collecting has been carried out during the twentieth century, much of it by amateurs and professional collectors, but the network of suppliers and describers seems to have broken down rather. This was partly because of the lack of professional palaeontologists in Britain with suitably broad interests and the desire to encourage active collecting: indeed, the most prolific describer of British fossil reptiles between 1900 and 1930 was the German palaeontologist Baron Friedrich von Huene! A further problem was the decline of local natural history societies and the loss of skilled collectors with local knowledge. Unfortunately, this has meant that many finds were recorded only rather poorly, if at all, and much of the material has been inadequately curated, or even lost altogether. In addition, many of the small local museums set up by natural history societies in the 1830s and 1840s declined into disuse and were either closed or handed over to local authorities. In most cases, there was no longer anyone with any knowledge or appreciation of the local specimens, and a tremendous amount of fossil reptile material must have been lost or damaged during this time, or abandoned in such a way that curatorial information was lost (see Torrens and Taylor, 1990 for a typical example, the sorry story of the Cheltenham museums).

It is only in the last 10 or 20 years that local museum standards in geology have improved dramatically, and that serious excavations by amateurs and professional scientists have been renewed in any numbers. These factors have led to the discovery and exploitation of several important sites, as noted above. The collections made during these years are to be seen in a large number of museums (listed at the end of this introduction).

REPTILIAN EVOLUTION

Reptiles today are readily identifiable: they are of course the turtles, crocodilians, lizards, snakes and the tuatara. However, the diversity of reptiles in the past was much greater than these surviving lineages would suggest. Without the fossil record, we could not begin to guess at the evolutionary history of the group. In phylogenetic terms, the Class Reptilia is a paraphyletic group, meaning that it arose from a single ancestor (among the amphibians), but that the Class does not include all of its descendants, namely the birds and the mammals. The reptiles are a part of the larger monophyletic group, the Amniota (= reptiles + birds + mammals).

Modern amniotes are defined by the possession of a cleidoic (= closed) or amniotic egg, an egg that has an outer protective coating or shell, and a complex system of membranes around the embryo within the egg. Unlike the amniotic eggs of fishes and amphibians (e.g. frog spawn), the cleidoic egg can be viewed as a 'private pond' in which the embryo can develop in relative safety on land, and with all nutritional supplies (the yolk) available. Waste materials are collected in the allantois, and the embryo can breathe through the semipermeable eggshell, which may be leathery or calcareous. The cleidoic egg allows amniotes to lay their eggs away from water, and this may have been an important advantage when the group arose, in Carboniferous times, in allowing them to occupy upland and dry areas.

The oldest reptiles have been known from the early Late Carboniferous of Nova Scotia, Canada, since the 1850s, and these include 'protorothyridids' and synapsids. A major discovery in Scotland in 1988 (Smithson, 1989; Smithson and Rolfe, 1991) has pushed the origin of amniotes back even further into the Carboniferous than had been suspected: the Nova Scotia animals date from about 300–310 Ma, while the new Scottish find, dubbed 'Lizzie' by its discoverer, Mr Stan P. Wood, is dated as about 330 Ma old. The exact affinities of 'Lizzie' are not yet certain.

Over the past 100 years, it has become clear that the major lines of amniote evolution were clearly laid out during the Late Carboniferous. The amniotes split into three main lineages, the synapsids (mammal-like reptiles and ultimately, the mammals), the diapsids (early forms, dinosaurs, extinct marine reptiles, lizards, snakes, crocodilians and ultimately birds), and the anapsids (primitive groups and turtles). Traditionally, the amniotes have been divided into four groups on the basis of their skull openings (Figure 1.2). The opening(s) behind the orbit (eye socket), termed the temporal opening(s), are present in various arrangements: no temporal opening in the anapsids, two temporal openings in the diapsids, a lower temporal opening only in the synapsids, and an upper temporal opening in the euryapsids. The first three of these groups is still regarded as having taxonomic validity, but the 'euryapsids'

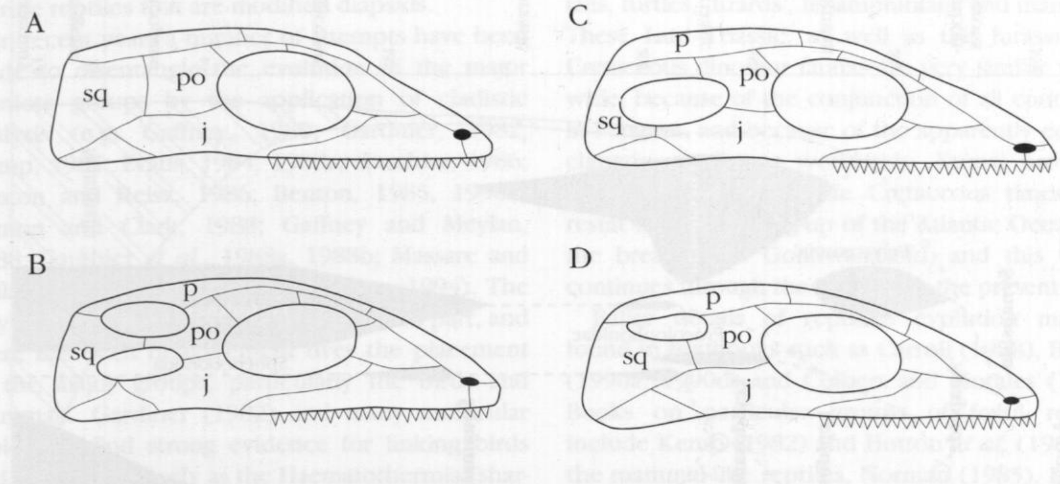

Figure 1.2 The skull patterns, in side view, of the major lineages of reptiles. The anapsid pattern (A) is plesiomorphic (primitive), being present also in fishes and amphibians, while the diapsid (B) and synapsid (C) patterns define two major clades of amniotes, the Diapsida (thecodontians, dinosaurs, pterosaurs, crocodiles, birds) and the Synapsida (mammal-like reptiles and mammals). The euryapsid pattern (D) may have arisen more than once, in different marine groups, and appears to be a derivative of the diapsid pattern. Abbreviations: j – jugal, p – parietal, po – postorbital, sq – squamosal. After Benton (1990a).

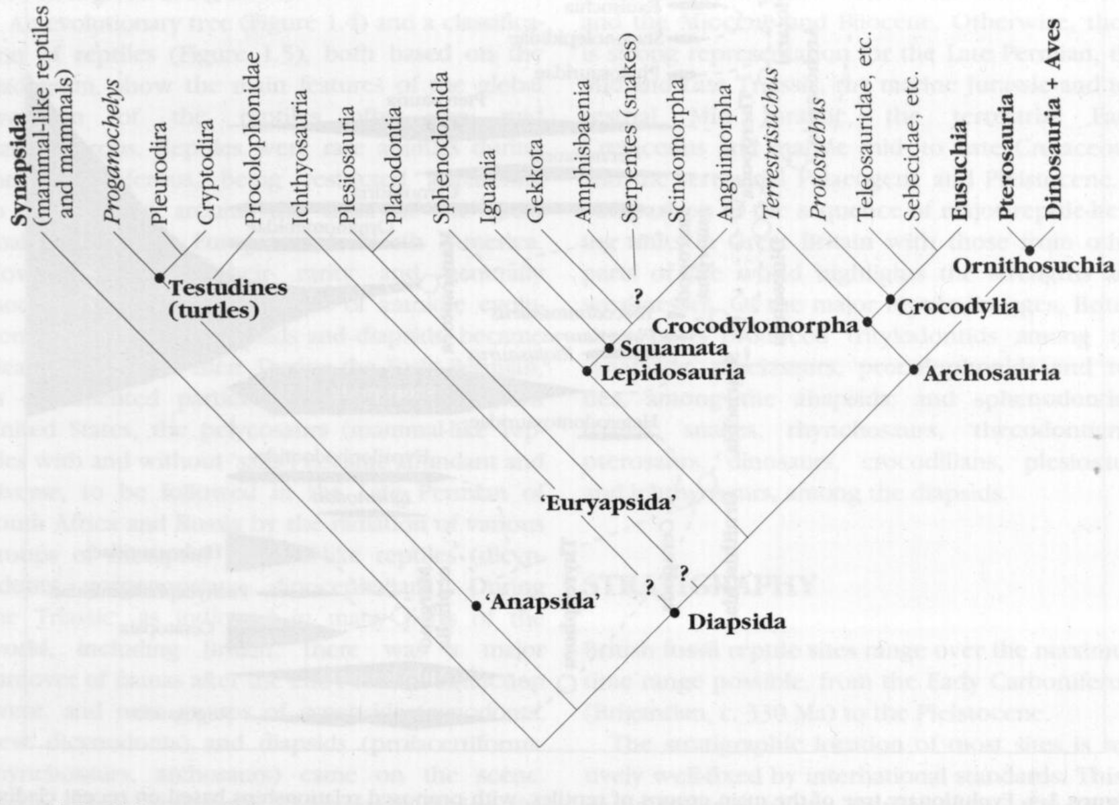

Figure 1.3 Cladogram of the major groups of reptiles, based on recent analyses (after Benton, 1990a).

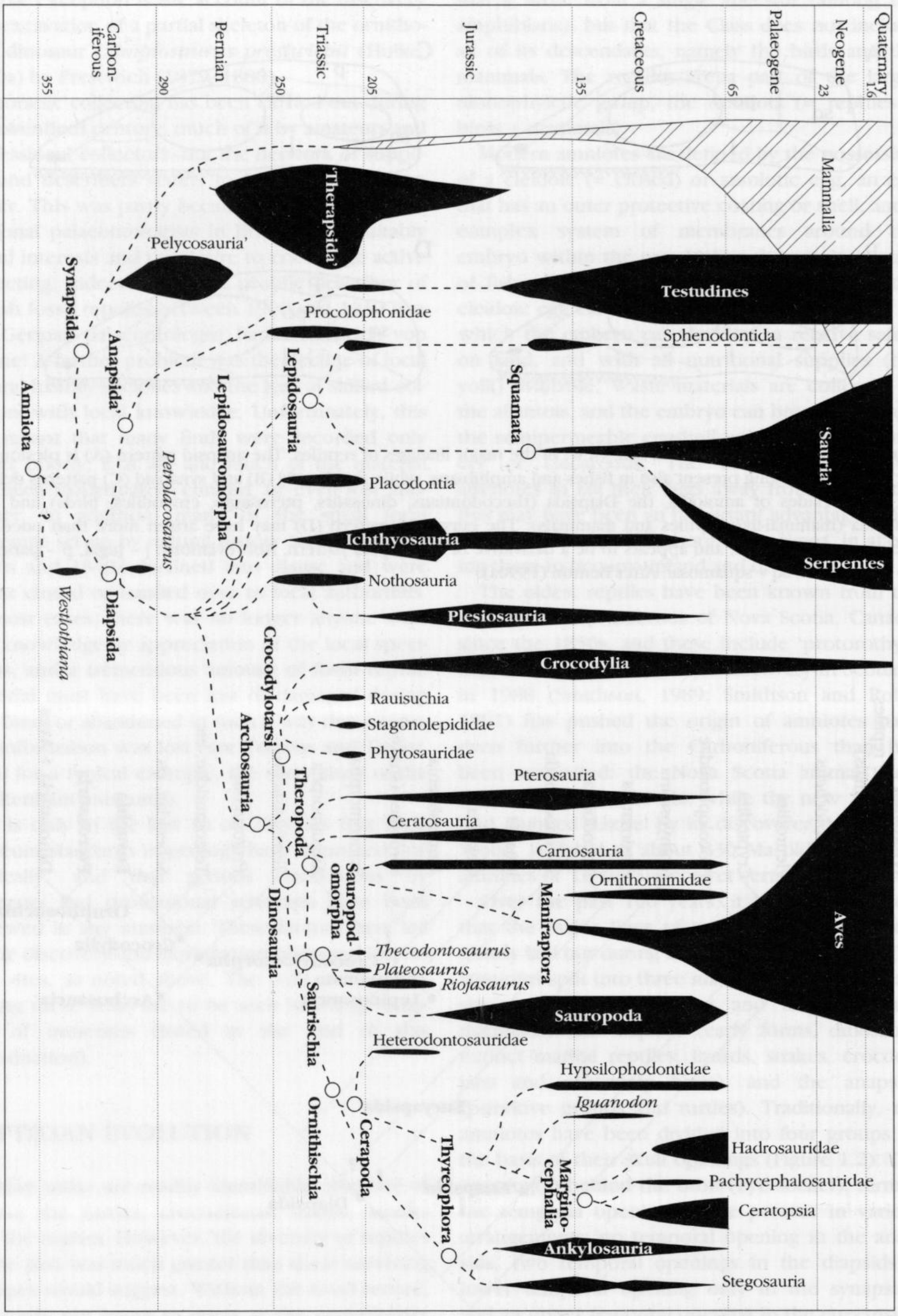

Figure 1.4 Evolutionary tree of the main groups of reptiles, with proposed relationships based on recent cladistic analyses, and the stratigraphical distributions based on global data. The width of the 'spindles' represents diversity of the groups (after Benton, 1990a).

appear to be an artificial assemblage of extinct marine reptiles that are modified diapsids.

In recent years a number of attempts have been made to disentangle the evolution of the major amniote groups by the application of cladistic analysis (e.g. Gaffney, 1980; Gardiner, 1982; Kemp, 1982; Evans, 1984, 1988a; Gauthier, 1986; Heaton and Reisz, 1986; Benton, 1985, 1990b; Benton and Clark, 1988; Gaffney and Meylan, 1988; Gauthier *et al.*, 1988a, 1988b; Massare and Callaway, 1990; Storrs, 1991; Spencer, 1994). The phylogenetic analyses are still tentative in part, and there has been disagreement over the placement of the major groups, particularly the birds and mammals. Gardiner (1982) and many molecular biologists, find strong evidence for linking birds and mammals closely as the Haematothermia (sharing a common ancestor presumably in the Triassic), while most other authors accept a more 'traditional' view, followed here also, that the phylogenetic split between birds and mammals lies in the Carboniferous (i.e. the diapsid/synapsid split). A cladogram, based on the work of the above-noted authors, and updated from those in Benton (1990a, 1990b), based on the work of Massare and Callaway (1990), Storrs (1991) and Spencer (1994), is given in Figure 1.3.

An evolutionary tree (Figure 1.4) and a classification of reptiles (Figure 1.5), both based on the cladogram, show the main features of the global evolution of the reptiles after the mid Carboniferous. Reptiles were rare animals during the Carboniferous, being restricted apparently to life in and around the trees of the great coal forests of Europe and North America. However, despite their rarity and generally modest size, the main lineages of amniote evolution, the anapsids, synapsids and diapsids, became clearly established then. During the Early Permian, as documented particularly in the mid-western United States, the pelycosaurs (mammal-like reptiles with and without 'sails') became abundant and diverse, to be followed in the Late Permian of South Africa and Russia by the radiation of various groups of therapsid mammal-like reptiles (dicynodonts, gorgonopsians, dinocephalians). During the Triassic, as indicated in many parts of the world, including Britain, there was a major turnover of faunas after the end-Permian extinction event, and new groups of synapsids (cynodonts, new dicynodonts) and diapsids (prolacertiforms, rhynchosaurs, archosaurs) came on the scene. These faunas apparently disappeared during the Late Triassic, to be replaced by a global 'modern' fauna, consisting of dinosaurs, pterosaurs, crocodilians, turtles, 'lizards', lissamphibians and mammals. These Late Triassic, as well as the Jurassic and Cretaceous dinosaur faunas are very similar worldwide, because of the conjunction of all continents in Pangaea, and because of the apparently equable climatic conditions worldwide. Faunal provinces become evident by Late Cretaceous times as a result of the opening-up of the Atlantic Ocean and the break-up of Gondwanaland, and this theme continues through the Tertiary to the present.

Fuller details of reptilian evolution may be found in textbooks such as Carroll (1988), Benton (1990a, 1990d) and Colbert and Morales (1991). Books on particular groups of fossil reptiles include Kemp (1982) and Hotton *et al.* (1986) on the mammal-like reptiles, Norman (1985), Benton (1989), Weishampel *et al.* (1990) and Carpenter and Currie (1990) on the dinosaurs, and Wellnhofer (1991) on the pterosaurs.

The British record of fossil reptiles illustrates a remarkably high proportion of the evolution of the group (Figures 1.6 and 1.7). Missing portions are the Late Carboniferous to Early Permian, known only from footprints and sporadic body fossils, virtually the whole of the evolution of mammal-like reptiles before the latest Triassic, and the Miocene and Pliocene. Otherwise, there is strong representation for the Late Permian, the Mid and Late Triassic, the marine Jurassic and terrestrial Mid Jurassic, the terrestrial Early Cretaceous and marine mid- to Late Cretaceous, and the terrestrial Palaeogene and Pleistocene. A comparison of the sequence of major reptile-bearing units in Great Britain with those from other parts of the world highlights the strengths and weaknesses. Of the major reptile lineages, British sites have produced tritylodontids among the synapsids; pareiasaurs, procolophonids and turtles, among the anapsids; and sphenodontids, lizards, snakes, rhynchosaurs, 'thecodontians', pterosaurs, dinosaurs, crocodilians, plesiosaurs and ichthyosaurs, among the diapsids.

STRATIGRAPHY

British fossil reptile sites range over the maximum time range possible, from the Early Carboniferous (Brigantian, *c.* 330 Ma) to the Pleistocene.

The stratigraphic location of most sites is relatively well-fixed by international standards. This is partly because of the mature state of local biostratigraphy in Britain. In addition, it has been

- Series Amniota
  - *Class Reptilia
    - Subclass Synapsida
    - 'Family Protorothyrididae'
    - †Family Mesosauridae
      - *†Order Pelycosauria
      - Order Therapsida
        - †Suborder Biarmosuchia
        - †Suborder Dinocephalia
        - †Suborder Dicynodontia
        - †Suborder Gorgonopsia
        - Suborder Cynodontia
          - †Family Procynosuchidae
          - †Family Galesauridae
          - †Family Cynognathidae
          - †Family Diademodontidae
          - †Family Chiniquodontidae
          - †Family Tritylodontidae
          - †Family Tritheledontidae
          - Class Mammalia
    - Subclass Anapsida (*sensu stricto*)
      - †Family Captorhinidae
      - †Family Procolophonidae
      - †Family Pareiasauridae
      - Order Testudines (Chelonia)
        - †Family Proganochelyidae
        - Suborder Pleurodira
        - Suborder Cryptodira
          - Superfamily Baenoidea
          - †Family Meiolaniidae
          - Superfamily Chelonioidea
          - Superfamily Trionychoidea
          - Superfamily Testudinoidea
      - †Family Protorothyrididae
    - Subclass Diapsida
      - †Family Millerettidae
      - †Family Petrolacosauridae
      - †Family Weigeltisauridae
      - Infraclass Lepidosauromorpha
        - †Order Younginiformes
        - Superorder Lepidosauria
          - Order Sphenodontida
            - Family Sphenodontidae
            - †Family Pleurosauridae
          - Order Squamata
            - *Suborder Sauria (Lacertilia)
              - Infraorder Gekkota
              - Infraorder Iguania
              - Infraorder Scincomorpha
              - Infraorder Anguimorpha
              - Infraorder Amphisbaenia
            - Suborder Serpentes (Ophidia)
      - Infraclass Archosauromorpha
        - †Family Trilophosauridae
        - †Family Rhynchosauridae
        - †Order Prolacertiformes
        - Division Archosauria
          - Family Proterosuchidae
          - Family Erythrosuchidae
          - Family Euparkeriidae
          - Subdivision Crocodylotarsi
            - †Family Phytosauridae
            - †Family Stagonolepididae
            - †Family Rauisuchidae
            - †Family Poposauridae
            - Superorder Crocodylomorpha
              - †Family Saltopusuchidae
              - †Family Sphenosuchidae
              - Order Crocodylia
                - †Family Protosuchidae
                - *†Suborder Mesosuchia
                  - Family Teleosauridae
                  - Family Metriorhynchidae
                  - Family Sebecidae, etc.
                - Suborder Eusuchia
                  - Family Gavialidae
                  - Family Crocodylidae
                  - Family Alligatoridae
          - Subdivision Ornithosuchia
            - †Family Ornithosuchidae
            - †Family Lagosuchidae
            - †Order Pterosauria
              - *Suborder Rhamphorhynchoidea
              - Suborder Pterodactyloidea
            - *†Superorder Dinosauria
              - Family Herrerasauridae
              - Order Saurischia
                - Suborder Theropoda
                  - Infraorder Ceratosauria
                  - Infraorder Carnosauria
                  - Family Ornithomimidae
                  - Infraorder Maniraptora
                    - Family Compsognathidae
                    - Family Coeluridae
                    - Family Oviraptoridae
                    - Family Dromaeosauridae
                    - Family Troodontidae
                    - Class Aves
                - Suborder Sauropodomorpha
                  - *Infraorder Prosauropoda
                    - Family Thecodontosauridae
                      - Family Plateosauridae
                      - Family Melanorosauridae
                    - Infraorder Sauropoda
                      - *Family Cetiosauridae
                      - Family Camarasauridae
                      - Family Brachiosauridae
                      - Family Diplodocidae
                      - Family Titanosauridae
              - Order Ornithischia
                - Family Pisanosauridae
                - Family Fabrosauridae
                - Suborder Cerapoda
                  - Infraorder Ornithopoda
                    - Family Heterodontosauridae
                    - Family Hypsilophodontidae
                    - *Family Iguanodontidae
                    - Family Hadrosauridae
                  - Infraorder Pachycephalosauria
                  - Infraorder Ceratopsia
                    - Family Psittacosauridae
                    - Family Protoceratopsidae
                    - Family Ceratopsidae
                - Suborder Thyreophora
                  - Family Scelidosauridae
                  - Infraorder Stegosauria
                  - Infraorder Ankylosauria
                    - Family Nodosauridae
                    - Family Ankylosauridae
      - Diapsida *incertae sedis*
        - †Superorder Sauropterygia
          - Order Placodontia
          - Order Nothosauria
          - Order Plesiosauria
            - Family Plesiosauridae
            - Family Cryptoclididae
            - Family Elasmosauridae
            - Family Pliosauridae
          - Order Ichthyosauria

Figure 1.5 Table showing the classification of the major groups of reptiles, based on the cladograms summarized in Figure 1.3. Symbols: † extinct group; * paraphyletic group (after Benton, 1990a).

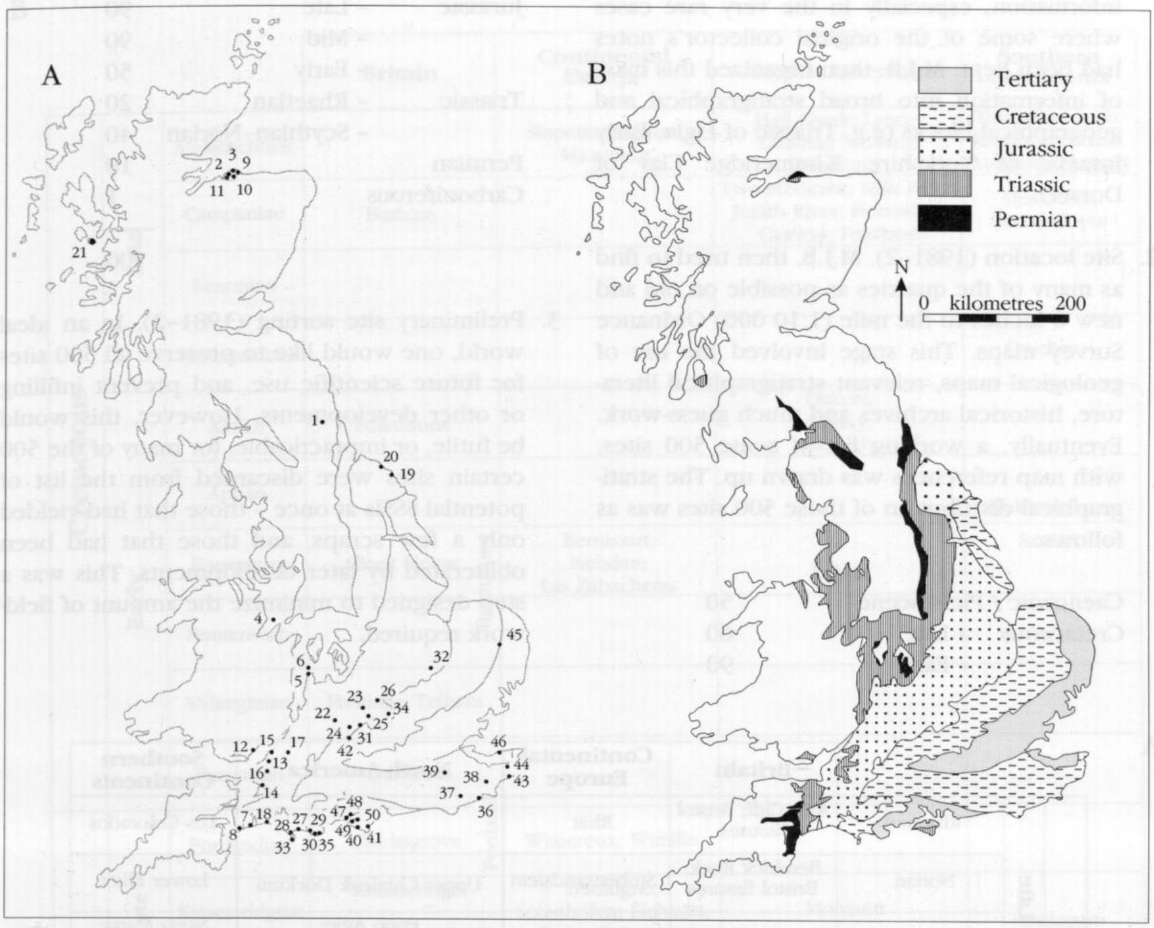

Figure 1.6 (A) Map of Great Britain showing the distribution of the 50 GCR fossil reptile sites; (B) The outcrop pattern of Permian, Triassic, Jurassic, Cretaceous and Tertiary rocks in Great Britain. After Benton (1988).

possible to correlate sites to ammonite zones, or even subzones, for most of the Jurassic and Cretaceous. Dating evidence for the terrestrial Permian, Triassic and Palaeogene sites is less secure, but is often tied to evidence from palynology, or other floral and microfossil evidence. The age of fossil reptile faunas is crucial for a proper understanding of the evolution, palaeoecology and palaeobiogeography of the group, and considerable emphasis has been placed on establishing the age of each site as precisely as possible. The evidence, and any controversial issues, are recounted in detail in the site descriptions.

HOW THE SITES WERE SELECTED

Fifty sites were selected as Geological Conservation Review (GCR) sites for their significance in representing aspects of the evolution of reptiles (Figure 1.6). A full account of the site-selection procedure, as well as discussions of the use of sites, the detective work involved, and conservation issues are given by Benton and Wimbledon (1985) and Benton (1988). The exact procedure followed in investigating Britain's heritage of fossil reptile sites, in selecting those that should become Sites of Special Scientific Interest (SSSIs), and hence come under the protection of the Wildlife and Countryside Act (1981), and in producing the present volume were as follows (modified from Benton and Wimbledon, 1985):

1. Initial data handling (1981–2). M.J.B. examined all published papers about British fossil reptiles and noted all site information, poor as it usually was (e.g. 'Wealden, Sussex', 'Bathonian, Oxfordshire', 'Chalk, Dover'). M.J.B. then studied most of the major museum collections in Britain (listed below) and again noted site

information, especially in the very rare cases where some of the original collector's notes had been kept. M.J.B. then organized this mass of information into broad stratigraphical and geographical blocks (e.g. Triassic of Elgin, Early Jurassic of Yorkshire, Kimmeridge Clay of Dorset).

2. Site location (1981–2). M.J.B. then tried to find as many of the quarries as possible on old and new 6 inches to the mile (1:10 000) Ordnance Survey maps. This stage involved the use of geological maps, relevant stratigraphical literature, historical archives and much guess-work. Eventually, a working list of some 500 sites, with map references was drawn up. The stratigraphical distribution of those 500 sites was as follows:

Caenozoic / Pleistocene		50
Cretaceous	– Late	60
	– Early	90
Jurassic	– Late	90
	– Mid	90
	– Early	50
Triassic	– Rhaetian	20
	– Scythian–Norian	40
Permian		10
Carboniferous		1
		500

3. Preliminary site sorting (1981–2). In an ideal world, one would like to preserve all 500 sites for future scientific use, and prevent infilling or other developments. However, this would be futile, or impracticable, for many of the 500 certain sites were discarded from the list of potential SSSIs at once – those that had yielded only a few scraps, and those that had been obliterated by later developments. This was a step designed to minimize the amount of field-work required.

A

			Britain	Continental Europe	North America	Southern Continents
Triassic	Late	Rhaetian	Aust Cliff; Bristol fissures	Rhät		Los Colorados
		Norian	Bendrick Rock; Bristol fissures	Stubensandstein	Upper Chinle & Dockum	Lower Elliot
		Carnian	Elgin sites	Schilfsandstein	Popo Agie; Lower Chinle & Dockum	Santa Maria; Ischigualasto; Maleri
	Mid	Ladinian		Muschelkalk		
		Anisian	Grinshill; Coten End; Devon coast	Muschelkalk; Donguz Series	Moenkopi	
	E	Scythian		Buntsandstein		
Permian	Late	Tatarian	Cutties Hillock; Masonshaugh	Urals		Beaufort Group Karroo
		Kazanian		Zechstein		
		Ufimian	Middridge	Kupferschiefer		
	Early	Kungurian			Pease River Group	
		Artinskian		Rotliegendes	Clear Fork Group	
		Sakmarian			Wichita Group	
		Asselian				
Carboniferous	Late	Gzelian				
		Kasimovian			Garnett	
		Moscovian		Nýřany	Joggins; Florence	
		Bashkirian				
	Early	Serpukhovian				
		Viséan	(East Kirkton)			
		Tournaisian				

Figure 1.7 Generalized stratigraphic column showing the major British fossil reptile sites in sequence, and comparable sites elsewhere in the world. A: Carboniferous to Triassic; B (opposite): Jurassic to Cretaceous; C (page 12) Tertiary to Quaternary.

B

			Britain		Continental Europe	North America	Southern Continents
Cretaceous	Late	Maastrichtian			Sinpetra; Rognac; Maastricht	Hell Creek; Lance; Laramie; Scollard; Frenchman	Titanosaur beds; Kronosaur chalk, Australia; Nemegt
		Campanian	Burham			Two Medicine; Milk River; Judith River; Horseshoe Canyon; Fruitland	Djadochta; Barun Goyot
		Senonian					
		Cenomanian					Quishan
	Early	Albian	Folkestone			Dakota; Paluxy; Cloverly	
		Aptian					Kukhtekskaya
		Barremian	Clock House	Brighstone	Bernissart; Nehden; Las Zabacheras	Lakota	Santana
		Hauterivian					
		Valanginian	Hastings; Telham				
		Berriasian	Durlston				
Jurassic	Late	Portlandian	Chicksgrove	Portland	Wimereux; Wimille		
		Kimmeridgian	Kimmeridge Smallmouth		Boulogne; Solenhofen; Eichstätt; Cerin; Guimarota	Morrison	Tendaguru
		Oxfordian	Peterborough		Calvados		Shangshaximiao (Sichuan)
	Mid	Callovian			Dives		
		Bathonian	Shipton; Kirtlington; Stonesfield; New Park		Caen		Xiashaximiao (Sichuan)
		Bajocian					
		Aalenian					
	Early	Toarcian	Whitby		Holzmaden	Navajo	Khota
		Pliensbachian				Kayenta	
		Sinemurian					
		Hettangian	Lyme Regis			Wingate; Moenave	Clarens; Lower Lufeng; Upper Elliot

Figure 1.7 – *contd.*

C

				Britain	Continental Europe	North America	Southern Continents
Quaternary		Holocene		Ubiquitous	Ubiquitous	Ubiquitous	Pampas; Olduvai (part)
		Pleistocene		Ubiquitous	Ubiquitous	Ubiquitous	Omo; Olduvai (part); etc.
Tertiary	Neogene	Pliocene			Montpellier; Pikermi; Samos	Hemphill; Clarendon; Ogalalla (part)	Siwaliks (part); Montehermosa; Huayqueria
		Upper Miocene				Barstow; Ogalalla (part)	Chasico; Fort Ternan; Siwaliks (part)
		Middle Miocene			Steinheim; Oeningen	Hemingford	Chinji (Siwalik)
		Lower Miocene				Arikareean	Santa Cruz; Bugti; Turgai
	Palaeogene	Oligocene	Chattian	Bouldnor Cliff		White River (part)	Colhuehuapian
			Rupelian		Quercy (part)	White River (part); Chadron	Deseado; Fayûm (part)
		Eocene	Priabonian	Hordle; Headon Hill	Quercy (part); Robiac	Uinta; Washakie (part)	Fayûm (part)
			Bartonian	Barton Cliff			
			Lutetian		Messel; Geiseltal	Bridger; Washakie (part) Green River (part)	Musters
			Ypresian	Sheppey	Erquelinnes; Dormaal; Monte Bolca	Wind River; Willwood; Wasatch	Casa Mayor
		Palaeocene	Thanetian		Cernay	Fort Union; Tongue River; Clark Fork	Rio Chico; Itaboraí; Pernambuco
			Danian			Torrejonian	

Figure 1.7 – *contd.*

4. Site visits and further site sorting (1981–2). Every site on the reduced list of 200 or so was visited, and an attempt was made to locate the fossiliferous horizon(s). At this stage, further sites were struck off the list of potential SSSIs if they were filled in, or if the relevant horizons were completely inaccessible.

5. Selection of major sites (1981–2). The selection of key sites for each unit was then made. Each of these sites had to have demonstrated potential (i.e. major finds of international importance, whether published or not), as well as the potential for more finds from known fossiliferous horizons.

6. Publication of the work (1990–2). P.S.S., in association with M.J.B., updated all the records made in 1981–2, arranged the information in a logical format, and produced the present volume. The focus of the text is on the 50 SSSIs, but all other sites that were identified as having produced any reptile fossils are also documented in the relevant places in the text. Figure 1.6 shows the distribution of these 50 sites.

Further information on the site-selection procedure, with a detailed example, based on the Oxfordian sites, is given by Benton and Wimbledon (1985). Benton (1988) lists all 50 British fossil reptile SSSIs in synoptic form, and full details and justifications are given in this volume.

Chapter 2

British Carboniferous fossil reptile sites

Within the past decade two possible Carboniferous reptiles have come to light in Britain, one from the Lower Carboniferous of West Lothian, Scotland and the other from the Upper Carboniferous of Newsham, Northumberland. The Scottish material, collected by Mr Stanley Wood and the National Museums of Scotland, came from the Lower Carboniferous (Brigantian) East Kirkton Limestone near Bathgate, West Lothian, and forms part of an important terrestrial assemblage that includes some of the earliest recorded temnospondyl amphibians, eurypterids, myriapods, scorpions and the earliest known opilionid (harvestman). Two 'reptile' specimens have been collected from different horizons; the type from bed 82, the black shale member (Smithson, 1989), and the second from bed 76 (Smithson *et al.*, 1994). There are two further specimens (A.R. Milner, pers. comm., 1994).

The type specimen (NMS G.1990.72.1), named *Westlothiana lizziae* (Smithson and Rolfe, 1991), consists of an almost complete articulated skeleton preserved in part and counterpart. The total length of the skeleton is 180–200 mm with a presacral length of about 120 mm. Assignment to the Reptilia (Division Amniota) was based on two main criteria. Firstly, a well-developed astragalus and calcaneum are present in the pes, a character shared by all extant amniotes. Secondly, the cranial remains show clear reduction of the temporal series (intertemporal, supratemporal and tabular) permitting contact between the parietal, postorbital and the squamosal. The latter character is found in all other Carboniferous tetrapods which are regarded as true amniotes.

However, recent further study of the type specimen following preparation of the palate and braincase, and detailed examination of the second specimen (Smithson *et al.*, 1994) have revealed that *Westlothiana* has a mixture of primitive tetrapod and derived amniote characters. It shares with early amniotes the pattern of bones in the temporal series, a large vertical quadrate, gastrocentrous vertebrae, gracile humerus with distinct supinator process, and hind feet with a pedal formula 23454. But, unlike other early amniotes, it lacks a tooth-bearing pterygoid flange and, contrary to the original description, it has three proximal tarsals, tibiale, intermedium and fibulare, and not an astragalus and calcaneum.

The earliest amniote fossil identified prior to the discovery of the Scottish reptile was *Hylonomus*, a protorothyridid from the lower Westphalian B (Upper Carboniferous) of Joggins, Nova Scotia (*c.* 308 Ma) (Carroll, 1964); thus the Scottish 'reptile', if that is what it is (Brigantian, 335 Ma, Lower Carboniferous) pre-dates *Hylonomus* by 27 Ma.

The only other reptilian material reported from the British Carboniferous are the supposed remains of a reptile collected during the late 19th century from the lower Westphalian B (Upper Carboniferous) of Newsham, Northumberland (NZ 306791). The specimen (NEWHM G24.84), which consists of an incomplete skull table, was referred to the 'Romeriidae', and subsequently to the Protorothyrididae by Boyd (1984, 1985). A recent examination of the specimen, however, has demonstrated that it belongs to the skull of an acanthodian fish of a variety common at the find locality (Coates and Smithson, pers. comm. to Milner, 1987, p. 500).

Footprints of amphibians and reptiles have been recovered (Sarjeant, 1974) from Butts Quarry, Aveley, Shropshire (SO 7684) in the Keele Beds, dated as Westphalian D (Smith *et al.*, 1974, p. 9) or Stephanian (Haubold and Sarjeant, 1973, p. 897).

No reptile sites are scheduled as SSSIs from the British Carboniferous because East Kirkton has so far produced very few specimens. Should more come to light there, it would be a strong candidate for scheduling as a GCR reptile site.