Chapter 1 Introduction to Mesozoic and Tertiary fossil mammals and birds

M. J. Benton

A history of the study of fossil mammals and birds

Dragon's bones

Fossil mammals and birds have been found at many hundreds of localities in Great Britain, and there is a long history of collection and study, dating back to the earliest years of palaeontology. Many of the British specimens, especially of fossil mammals, have been pivotal in major developments in the history of the sciences of palaeontology, comparative anatomy and evolution.

Fossil mammals were first collected extensively in central Europe (France, Germany, Austria, Switzerland and Italy). Bones of Pleistocene mammals, such as mammoths, woolly rhinos and cave bears, frequently came to light in superficial deposits during medieval times and gave rise to intense speculation. The most popular views then were somewhat mystical. The giant bones were commonly ascribed to mythical monsters and dragons, to unicorns, or to giant humans, and many of them were even venerated as the relics of saints (Buffetaut, 1987). In China, fossil bones had been collected for a long time, often from cave deposits, and these 'dragon's bones' were ground up for use in medicine. Ivory from frozen Siberian mammoths was also widely traded from early times.

In the 17th century, British naturalists turned their attention increasingly to matters geological. There were a number of discussions at the meetings of the newly founded Royal Society about the meaning of fossils, whether they were truly the remains of once-living organisms, or whether they were some kind of inorganic 'sport of nature'. Martin Lister (1639–1712) described many fossil invertebrates but argued that they were produced by 'plastic virtues' in the rocks, whereas Robert Hooke (1635–1703) roundly opposed this notion and fully accepted that the Earth had been populated in the past by a range of organisms, many of them now extinct. John Ray (1627–1705) accepted that some fossils were petrified remains of plants and animals but argued that others were inorganic, especially those that could not be matched with living forms. His fear was that to admit the notion of extinction was to suggest that the biblical Creation had not been perfect. Edward Lhwyd (1660–1709) even argued that somehow the fossils that he described had grown within the rock, spawned from 'seeds' of living organisms that washed into the rocks through cracks.

The idea of extinction

Fossil mammals or birds were not widely collected in Britain during the 18th century, but descriptions of continental specimens of mammoths, and other mammals, were published in the *Philosophical Transactions of the Royal Society*. In addition, accounts published in French, German and Italian memoirs were also available. The general view moved haltingly from the miraculous to the scientific, with increasing recognition that the bones could be compared with those of modern animals in many cases. It seems astonishing to us now, but medieval scholars knew almost nothing of the anatomy of modern animals, and it came as a revelation that excavated bones could be compared with skeletons of modern elephants, rhinos and cows. The close similarities proved to be overwhelming evidence that fossil bones really were just that and not some kind of mysterious inorganic production of the Earth.

The identification of fossil bones of large mammals created a problem, however. How were naturalists to account for the former existence of exotic animals in Europe — elephants, rhinos, giant cattle and others? Thomas Molyneux, an Irish scholar, referred to this problem in 1697 in his memoir 'Discourse concerning the large horns frequently found under ground in Ireland…'. This was an early description of the remains of the Irish deer *Megaloceros.* Molyneux identified the antlers as coming from the American moose, which he then postulated had once lived in Ireland. He went on to argue that the fossil antlers merely proved a local extinction, presumably caused by hunting, and that the discoveries did not support a notion of general extinction, which would be contrary to divine providence.

The question arose again 50 years later. American explorers sent back to Europe the giant bones of mastodonts that they found in abundance in Ohio. Here was a major problem. In 1768, the English naturalist Collinson correctly identified the mysterious huge bones as those of a new species of elephant, or a hitherto unknown kind of animal. A year later, William Hunter, the famous British anatomist, declared that although some of the bones were elephant-like, the new American animal was an unknown 'pseudoelephant' or 'incognitum', certainly in any case a carnivore. He declared: 'if this animal was indeed carnivorous, which I believe cannot be doubted, though we may as philosophers regret it, as men we cannot but thank Heaven that its whole generation is probably extinct'. In the second half of the 18th century, dozens of reports were made of remarkable finds of this kind — mammoths from Siberia, a giant ground sloth from Argentina, elephants from Italy, Mesozoic crocodiles from England and Germany — and by 1800, most naturalists accepted that many organisms had existed on the Earth in the past that had since become extinct. This view was finally crystallized and established firmly by Georges Cuvier (1769–1832) around the turn of the 19th century.

Stratigraphy and comparative anatomy

In the early decades of the 19th century Cuvier was a leader in establishing a number of basic principles of palaeontology and comparative anatomy that were fundamental to the development of those sciences. He established that sedimentary rocks are arranged in layers that document sequences of events through time. The Scottish geologist, James Hutton (1726–1797), had shown the vastness of geological time in his famous work *Theory of the Earth,* and the English surveyor William Smith (1769–1839) independently demonstrated the sequence of rocks and the use of fossils in dating. Cuvier drew up a detailed scheme of the sequence of rocks — the stratigraphy — of the Paris Basin, with dating based on the common fossil shells. He also noted how different kinds of fossil mammals were found at different levels.

Cuvier's second major contribution was to show how isolated fossil bones could be identified by comparison with extensive arrays of modern and ancient skeletons. Cuvier's skill is encapsulated in a famous tale that he could take a single bone from any animal and reconstruct its whole skeleton and habits from that evidence alone. Apocryphal perhaps, but Cuvier showed the value of knowledge over speculation, and this facet of his ideas marked the beginning of systematic collecting, recording, and display of whole skeletons of modern and extinct animals. Indeed, this pursuit marked the beginning of another aspect of palaeontology — reconstructions of the life appearance of extinct animals. In his *Recherches sur les ossemens fossiles* (1812), Cuvier published outline reconstruction drawings of two of the early Tertiary mammals from the Paris Basin, *Palaeotheriurn* and *Anoplotherium* (Figure 1.1). This simple act attempting to create life-like skeletons of ancient animals and then putting flesh on the bones seems natural today, but it caused a sensation then. For the first time, anyone could see what the life-forms of the past actually looked like, and even though Cuvier's drawings were simple outline sketches, they were widely reproduced.

In Britain in the years from 1800 to 1830, finds of large fossil reptiles from the Mesozoic Era — the first ichthyosaurs, plesiosaurs, dinosaurs and pterosaurs — attracted most attention. In the 1830s and 1840s, new collections of Devonian fishes, from the Old Red Sandstone of Scotland became the focus. During these decades, most discoveries of fossil mammals occurred in continental Europe. However, two major discoveries in Britain by William Buckland (1784–1856), at opposite ends of the geological scale, created a sensation.

Buckland's Pleistocene and Mesozoic mammals

William Buckland was involved in the excavation of Kirkdale Cave in Yorkshire, and he published an account of the discoveries in 1822 and in 1823 (Figure 1.2). He found abundant bones of hyaenas, young and old, as well as remains of other large mammals. He argued that this had been a hyaena den, and that these scavengers had dragged carcasses back to the cave, hence building a huge accumulation of remains. These discoveries formed an important part of Buckland's attempt to reconcile the new findings of geology and palaeontology with the Bible. He argued that the cave creatures had sought refuge there at the approach of The Flood in the time of Noah (Genesis, chapter 6, of the Bible), and that they had perished under its waters. Despite this interpretation, Buckland's work at Kirkdale Cave was important as one of the first systematic excavations of a cave and the beginning of the teasing apart of the complex environmental changes during the European Quaternary Sub-era (Sutcliffe, 1985, pp. 120–1).

The second discovery was quite different: the announcement of the existence of mammals of Mesozoic age. The first specimens, two tiny jaws from the Middle Jurassic Stonesfield Slate, were collected in 1812 by William Broderip, an undergraduate at the University of Oxford. He showed them to Buckland, who eventually described one of them in 1827. By that time, Cuvier had established a broad succession of vertebrate life, with fishes and various primitive forms in the Paleozoic Era, reptiles in the Mesozoic Era and mammals in the Cenozoic Era. The discovery of mammal jaws, even those of supposed opossums (marsupials), in rocks of definite Jurassic age was quite unexpected. The announcement led to a wild debate throughout Europe, with some naturalists, such as Cuvier, accepting the discovery and others questioning either the authenticity of the dating of the rocks or the authenticity of the identification. In the end, Richard Owen (1804–1892), with the strength of his growing reputation in comparative anatomy, declared that Buckland and Broderip had been right (Owen, 1871): the jaws came from small insectivorous marsupials and they came from rocks of Jurassic age.

Evolution: birds and mammals

The field of vertebrate palaeontology and studies of fossil mammals and birds in Britain were dominated during Victorian times by two people, Richard Owen and Thomas Huxley. The rise of Huxley eclipsed Owen, and this changeover was related to changes in wider views of evolution and the history of life on Earth (Desmond, 1982).

Richard Owen was the dominant vertebrate palaeontologist and comparative anatomist in Britain from 1830 to about 1860. He rose rapidly to favour by his prodigious output of work on an enormous range of animals, living and extinct, and by his careful courting of the establishment. During these decades, Owen produced a steady flow of memoirs on fossil mammals and birds, from Britain and from the British Empire. He published the first overview of British fossil mammals and birds (Owen, 1846). Owen reached the height of his dominance in the early 1850s, when his friendship with Prince Albert gave him a key role in the Great Exhibition of 1851 and led to the display of his models of dinosaurs and other fossil animals, including mammals, at the Crystal Palace in 1854. This display caused a sensation, and Owen's name was on everyone's lips. To dominate the London scientific and social scene at that time was to experience pre-eminence on virtually a global stage.

Owen's role seemed firm and unassailable. It was, however, challenged by a rising star in the scientific firmament, Thomas Henry Huxley (1825–1895), who was 21 years younger. Huxley, like Owen, had to earn his living by his science, and, like Owen, he was intensely ambitious. Huxley began his scientific work focusing on modern marine invertebrates, and there was no clash between the two during the late 1840s and early 1850s. Two things then happened. In 1858 Huxley began to publish descriptions of British fossil amphibians and reptiles, and in these he began to pick holes in Owen's descriptions. The criticisms were minor and arcane at first, but soon became more damaging. Then in 1859 came Darwin's bombshell.

In 1859, Charles Darwin (1809–1882) published *On the Origin of Species,* and views of palaeontology changed forever. Darwin expected that the fossil record would document patterns of evolutionary change through time, and fossil birds and mammals soon yielded the evidence his supporters sought. The first finds of the Jurassic bird *Archaeopteryx* from southern Germany, in 1860 and 1861, provided a clear 'missing link' between reptiles and birds. Fossil horses from Europe and from North America became the classic mammalian evolutionary series.

Cuvier had described the horse-like *Palaeotherium* from the Eocene strata of the Paris Basin in 1804 (Figure 1.1). Later, Owen recognized this and similar mammals from the Eocene strata of the London and Hampshire basins (including the Isle of Wight). One of them, a small horse-like animal, he named *Hyracotherium* (Owen, 1841b). The Russian palaeontologist Vladimir Kovalevskii (1842–1883) published a detailed account of European fossil horses in 1873a, and he proposed that they documented an evolutionary sequence from *Palaeotherium* through various Miocene forms to *Equus* (Figure 1.3). Huxley accepted this view, until he saw the even more complete American sequence of forms in 1876, which showed that the American animals called *Eohippus,* to him the same as Owen's *Hyracotherium,* were the first horses.

Owen had developed a particular kind of evolutionary idea based on Germanic views of the anatomical archetype — an ideal model of particular broad classes of animals. He could have accepted Darwin's evolution by natural selection, by

some major modifications to his own ideas. However, Huxley apparently saw his chance and moved fast to express his public support for Darwin in a lengthy review in *The Times* and in public addresses. Owen was partly outmanoeuvred and had to oppose Huxley and Darwin. The debate continued in public, and in numerous more arcane anatomical disputes, where Huxley usually proved the victor.

During the second half of the 19th century, numerous important British fossil mammals were found. Owen himself described further Jurassic mammals, as well as mammals from the Cretaceous Purbeck Limestone Formation. Extensive new collections from the early Tertiary sediments of the Hampshire Basin and the Isle of Wight were made, and, by the 1880s and 1890s, a new generation of British experts on fossil mammals — Richard Lydekker, William Flower and others — were able to publish detailed surveys of the diverse fossil mammals that had been found by then. Isolated bird bones were reported from several Tertiary localities in the south of England during this time as well.

Work on the Pleistocene caves and bedded deposits had also produced extensive mammalian faunas, described by William Boyd Dawkins and E.T. Newton. Dawkins described mainly Late Pleistocene sites, and he produced the first detailed monographic descriptions of British Pleistocene cats, rhinoceroses, cattle and deer (Dawkins, 1867a; Dawkins and Reynolds, 1872; Dawkins and Sanford, 1866). Newton (1882, 1891) published accounts of the important faunas of the Pleistocene Cromer Forest Bed, as well as descriptions of younger Pleistocene faunas. The Pleistocene mammal GCR sites are described in a companion GCR volume (Schreve, in prep.).

Twentieth century

Much of the 20th century development of vertebrate palaeontology has been dominated by work in previously unexplored parts of the world, by advances in technology, and by greater attention to broad-scale questions in evolution, systematics and taphonomy (Buffetaut, 1987). By the year 1900, most of the major British fossil bird and mammal localities that we know today had been identified. Indeed, in those years the British record was unique in some respects, providing, for example, the best evidence of Mesozoic mammals, with material representing much of the Jurassic Period and the early part of the Cretaceous Period (reviewed by Simpson, 1928). It was only later discoveries in Mongolia, Uzbekistan, China, North America, Africa, South America and Australia that showed the true global diversity of Mesozoic mammals. Nevertheless, new collections of Triassic–Jurassic mammals and mammal-like reptiles from south-west England and Wales have provided material for a number of highly significant monographic studies (Kühne, 1956; Kermack *et al.,* 1973, 1981). The Middle Jurassic mammals and mammal-like reptiles of the Cotswolds, and of Skye, also still fill an important stratigraphical gap in global knowledge of the groups (Sigogneau-Russell, 2003a,b).

In the 1970s and 1980s, British Mesozoic, Tertiary and Quaternary birds were restudied and revised in a number of papers by C.J.O. Harrison and C.A. Walker, and further work is continuing on these important fossils.

British Tertiary mammals have been studied extensively during the 20th century, although some of the work has focused on revisions of older material. Newer approaches have, however, been applied by Collinson and Hooker (1987) and Hooker *et al.* (2004) in their studies of the successions of faunas and floras through the early Tertiary sediments of the south of England and their significance for the understanding of palaeoclimate evolution. Various faunas, and individual taxa, also have been described or revised in monographic works in the past 50 years (e.g. Cray, 1973; Bosma, 1974; Hooker, 1979, 1986, 1996b).

Several Victorian experts on the Pliocene and Pleistocene epochs, including Boyd Dawkins and Newton, continued their endeavours into the early years of the 20th century. Other workers took over in the first half of the century: S.H. Reynolds (1902–12) described British Pleistocene small carnivores, and M.A.C. Hinton produced a series of papers on monkeys (Hinton, 1908), insectivores (Hinton, 1911) and rodents (Hinton, 1926a). British Pleistocene studies then revived again around 1960, with huge advances in the understanding of stratigraphy, palaeoclimates, floras and faunas. New techniques of dating (radiometric, dendrochronolo-gy, isotope), geochemical approaches to palaeoclimate determination, and international drilling and correlation programmes, provided a firm framework for understanding the faunas. New excavations, sometimes in association with archaeologists and using much improved precision techniques, have expanded knowledge of the British Pleistocene vertebrate faunas enormously. These more recent studies are reviewed by Stuart (1982a) and Sutcliffe (1985).

Bird evolution

Knowledge of early bird evolution has been revolutionized in the past 20 years, especially by new discoveries of fossils from the Cretaceous rocks and by the application of new methods in systematics (cladistics and molecular phylogeny reconstruction).

It seems clear now that birds are a subgroup of Dinosauria, with closest relatives being modest-sized theropod dinosaurs such as the dromaeosaurids and troodontids, forms with bulbous heads, good eyesight and elongate forelimbs. The evidence for this proposed relationship is extensive and focuses on cladistic analysis of character information on skeletal structures in the forelimb, pelvis, hindlimb and skull (reviewed by Ostrom, 1976; Chiappe, 1995; Chiappe and Witmer, 2002; Benton, 2005). The main alternative view, that birds evolved in the Triassic Period directly from basal archosaur reptiles, although expressed firmly in a recent text on fossil birds (Feduccia, 1999), is not supported by any evidence.

The oldest confirmed fossil bird is *Archaeopteryx,* from the late Jurassic rocks of Germany, although an older form, *Protoavis,* from late Triassic deposits of Texas, has been proposed. The status of *Protoavis* is controversial (Chiappe and Witmer, 2002). Until 1990, very few bird specimens were known from the subsequent 60 Ma or more of the Cretaceous Period, before the appearance of the extinct hesperornithiforms and ichthyornithiforms of the Niobrara Chalk of late Cretaceous age in North America. Since 1990, spectacular discoveries of toothed and untoothed birds of Early Cretaceous age in Spain and China, found in conditions of exceptional preservation, with feathers and some other soft parts intact, have filled many gaps in the evolutionary tree. Other discoveries of birds in late Cretaceous material from Mongolia and South America have further helped develop a fuller picture of the first half of bird evolution (Chiappe, 1995; Chiappe and Witmer, 2002; Benton, 2005).

The phylogeny of birds is not yet fully established. Cladistic studies of the older and newer fossils, where a search is made for shared derived characters (those that uniquely link groups together), show that the majority of Mesozoic birds formed side branches from the line to modern birds (Neornithes). Whereas *Archaeopteryx* retains primitive reptilian characters, such as teeth, separate fingers with claws on its forelimb, an unfused wrist, a low sternum, an unfused lower leg and ankle and a long bony tail, modern birds lack all of these structures, and others. The Cretaceous fossils document the loss of these primitive features and the acquisition of 'modern bird' characters, and it is possible to draw up a fairly clear cladogram of relationships (Chiappe, 2002; (Figure 1.4)).

Modem birds radiated in the latest part of the Cretaceous Period and divided in Tertiary times into around 19 main lineages. Fossils of most of the orders are known from at least the Eocene Epoch, some 50 million years ago, especially from the British sites in the London Clay Formation. Some unusual extinct groups survived for a while, especially some large flightless flesh eaters, both in the Northern Hemisphere and in South America. Cladistic and molecular evidence of the relationships within Neornithes are limited, and the cladogram (Figure 1.5) is tentative (Cracraft *et al.,* 2004). Ducks and chickens form a basal clade Galloanserae that is separated from the remainder, and some further divisions among modem birds have been recognized, but evidence is sometimes contradictory. Further fully cladistic studies of modern and extinct birds are required, as well as fuller molecular phylogeny studies.

An evolutionary tree of birds (Figure 1.6) shows how a number of small groups branched off in the Cretaceous Period, and one of them, the Enantiornithes, became relatively abundant and diverse. However, the Enantiornithes, and the others, disappeared by the end of the Cretaceous Period, and the Neornithes prevailed thereafter. Most neornithine orders remained at low diversity in the early Tertiary Sub-era and built up to modern diversities during mid- and late Tertiary times. The main change in the Tertiary Sub-era was the huge radiation of the perching birds or songbirds — the Passeriformes — from the Miocene Epoch onwards. Today, the songbirds make up about half the overall diversity of some 7000 living bird species. The cladograms are translated into a classification of living and extinct birds in (Figure 1.7).

Further details of bird evolution may be found in Feduccia (1999) and in general textbooks such as Carroll (1988) and Benton (2005). The last of these references gives a fully up-to-date cladistic treatment of the phylogenetic information.

Mammal evolution

The mammals arose during Late Triassic times from a reptile group commonly termed the 'mammal-like reptiles'. Mammals and mammal-like reptiles together form the lade Synapsida, one of the major divisions of terrestrial vertebrates. Tetrapods, the four-limbed vertebrates, arose in the Devonian Period from ancestors among the lobe-finned fishes, the Sarcopterygii. The first tetrapods lived an amphibious lifestyle, as do modern amphibians such as frogs and salamanders, breathing air and feeding largely on land but laying their eggs in water and having fish-like larvae. During the Carboniferous Period there arose a new group of tetrapods, the amniotes, which had broken the link with the water. Amniotes lay eggs that act as small 'private ponds', so they no longer have to lay their eggs in water. The amniotic, or cleidoic ('closed'), egg has a semi-permeable outer membrane and shell that allow gases, but not water, to pass through, a supply of food (yolk) and a waste-disposal system. Amniotes include reptiles, birds and mammals.

(Figure 1.7) Table showing the classification of the major groups of birds, based on the cladograms summarized in (Figure 1.4), (Figure 1.5), (Figure 1.6). (From Benton, 2005.) [†] = extinct group

Class Ayes

[†]Family Archaeopterygidae

[†]*Rahonavis*

[†]*Jeholornis*

[†]Family Confuciusornithidae

Infraclass Ornithothoraces

[†]Order Enantiornithes

Supercohort Ornithomorpha

[†]*Patagopteryx*

[†]*Vorona*

Cohort Ornithurae

[†]Order Hesperornithiformes

Subcohort Carinatae

[†]Order Ichthyornithi formes

Superdivision Neornithes

Division Palaeognathae

[†]Order Lithornithiformes

Order Ratites

Division Neognathae

Subdivision Galloanserae

Order Anseriformes

Order Galliformes

Subdivision Neoaves

Superorder unnamed ('waterbird assemblage')

Order Gruiformes

Order Ralliformes

Order Pelecaniformes

Order Ciconiiformes

Order Charadriiformes

Order Phoenicopteriformes

Order Podicepidiformes

Order Falconiformes

Order Procellariiformes

Order Gaviiformes

Order Sphenisciformes

Order Strigiformes

Superorder unnamed

Order Apodiformes

Order Caprimulgiformes

Order Musophagiformes

Order Columbiiformes

Order Psittaciformes

Order Cuculiformes

Superorder unnamed ('higher land birds')

Order Piciformes

Order Coliiformes

Order Trogoniformes

Order Bucerotiformes

Order Coraciiformes

Order Passeriformes

The basal Amniota divided during the Carboniferous Period into three main branches, the Anapsida, which led to modern turtles, the Diapsida, which led to modern crocodiles, birds and lizards, and the Synapsida. British sites that are important in documenting these early phases of amniote, and synapsid, evolution are documented in a companion GCR volume covering reptile sites (Benton and Spencer, 1995).

In retrospect, it is possible to track the appearance of a number of specifically mammalian features during this long span of synapsid evolution from the Carboniferous Period to the Triassic Period. For example, Late Permian synapsids already had well-differentiated teeth, with the incisors, canines and cheek teeth of mammals, that were quite unlike the rather uniform teeth of typical reptiles. Early Triassic synapsids had an upright, rather than sprawling, posture and some of them may have been warm-blooded. Brain expansion continued during this time, and there was no major increase in brain size with the first mammals.

Mammals arose from cynodonts, a group of largely carnivorous synapsids that are first encountered in the latest Permian times. Early Triassic cynodonts were dog-sized predators that showed a mix of characters. During the Middle and Late Triassic epochs, certain smaller cynodonts showed the key transitions to mammals in the nature of the lower jaw. Classically, reptiles have five or more bones in their lower jaws, whereas mammals have one, the dentary. In Triassic cynodonts, the posterior elements of the lower jaw became smaller and the dentary larger. The posterior elements shifted more and more towards the middle ear region, and they took on auditory functions. In the end, the lower jaw joint switched from a contact of the articular in the lower jaw and the quadrate in the cranium (typical of reptiles), to a contact of the dentary and the squamosal. The old reptilian jaw joint, the articular–quadrate hinge, is now subsumed into mammalian ears as the joint between malleus and incus (hammer and anvil).

Most cynodonts, and other remaining synapsids, died out at the end of the Carnian Stage, some 225 million years ago, but the modest-sized tritheledonts and tritylodonts survived into the Jurassic Period, side-by-side with the first mammals. The tritylodonts, possibly the closest reptilian relatives of the mammals, lasted until the Callovian Stage, and some of the last ones are known from the British Middle Jurassic strata.

Mammals are distinguished by a number of features, notably their expanded brain that fills the whole posterior portion of the cranium; the braincase bony-elements that are fused to the outer cranial bones; double-rooted cheek teeth (premolars, molars); and a jaw articulation between the dentary (lower jaw) and squamosal (cranium). These features contrast with tritylodonts and other reptiles, which have a much smaller brain, and the braincase elements generally remain separate from the outer cranial bones, single-rooted cheek teeth, and a jaw articulation between the articular (lower jaw) and quadrate (cranium). The expansion of the brain-case and the shift of the jaw joint happened in several stages through the Triassic Period (Kemp, 1982; Benton, 2005).

There is a semantic issue over the definition of Mammalia. Some recent commentators have restricted the term 'Mammalia' to the immediate ancestors of modern mammals only, hence excluding many Mesozoic groups traditionally called 'mammals'. We use the traditional definition here, and we accept that Mammalia are defined by the switch from an articular-quadrate jaw joint to a dentary–squamosal jaw joint.

The early Mesozoic mammals include 10 or so groups, known best from the Jurassic rocks of Europe and North America (see Chapter 2), with some of the earliest-known sites occurring in Britain. Modem mammal groups probably appeared during Late Jurassic times, although the oldest fossils are Early Cretaceous in age. Modern mammals fall into three subclasses: the Monotremata — the platypus and echidna from Australasia — which lay eggs; the Marsupialia the pouched mammals of Australasia and the Americas — which produce tiny young that complete their development in the pouch; and the Placentalia — placental mammals — which produce relatively developed young. All these modem mammal groups exhibit hair, warm-bloodedness (endothermy), large brains and extended parental care, and they suckle their young from milk-producing glands, or mammae, hence the name 'mammal'.

The oldest monotreme fossils are isolated jaw fragments from the Early Cretaceous Epoch of Australia. The oldest marsupial and placental fossils were until recently isolated teeth and jaws, from the mid-Cretaceous Period of North America and Asia, but spectacular new finds from China of complete specimens, often with hair and other soft parts, show that the oldest marsupial at present is *Sinodelphys* (Luo *et al.,* 2003) and the oldest placental is *Eomaia* (Ji *et al.,*

2002), both from the Early Cretaceous Liaoning beds, dated at about 125 Ma.

The relationships of the advanced mammal-like reptiles, and of the Mesozoic mammals, are controversial. Until recently, attempts to reconstruct their evolution were highly varied, and some such attempts even included the idea that mammals were polyphyletic, with separate origins at least of the monotremes and their extinct relatives, and of the therians and theirs. Cladistic analyses (Figure 1.8) show at least that the Class Mammalia is monophyletic (with a single origin) and that the most primitive mammals are *Adelobasileus, Sinoconodon* and the morganucodontids. However, the arrangement of the various Mesozoic groups beyond that is highly controversial (Kemp, 1982; Rowe, 1988, 1993; Lucas and Luo, 1993; Wible *et al.*, 1995; Luo *et al.*, 2000, 2001, 2002; Kielan-Jaworowslca *et al.*, 2004).

The phylogenetic scheme shown in (Figure 1.8), based mainly on Kielan-Jaworowska *et al.*, (2004), shows a split into a southern and a northern clade of basal Mesozoic mammals. The Australosphenida, monotremes and extinct relatives, presumably evolved in Gondwana in the Jurassic Period, whereas the Boreosphenida, marsupials, placentals and extinct relatives) originated perhaps in Asia, and radiated across Europe and North America in the Jurassic Period. Monotremes today lay eggs and suckle their young in a primitive way, and presumably the Mesozoic mammals at that part of the clado-gram retained such primitive habits also. Marsupial and placental mammals today do not lay eggs, and it is likely that their Mesozoic forebears also had moved to live birth. The situation in more primitive mammals is unclear.

By the end of the Cretaceous Period the marsupials and placental mammals were relatively diverse, although good specimens are known only from a few localities in Mongolia, Uzbekistan and North America. Most of the more primitive mammal groups had long disappeared, although many marsupials in two families died out during the Cretaceous–Tertiary mass extinction, 65.5 million years ago, which saw the end of the dinosaurs and other large reptiles.

During Tertiary times, the marsupials at first existed mainly in the Americas. They spread to Europe, including Britain, where they occur commonly in Eocene and Oligocene faunas, and they also dispersed to Asia and north Africa. In the Americas, the marsupials diversified during Tertiary times, especially in South America, where they became important components of the faunas, especially as small to large carnivores. By early Eocene times, marsupials had spread across Antarctica to Australia, where they evolved into a diverse array of familiar animals, from wombats to kangaroos. Marsupials became extinct everywhere by the end of Miocene times, except in South America and Australia, and they subsequently re-invaded parts of North America more recently. Both Australia and South America were largely isolated from the rest of the world during Tertiary times, so their mammals evolved independently, marsupials in Australia and marsupials and unusual placental mammals, including sloths and armadillos, in South America.

Mammalian evolution in North America, Europe, Asia and Africa shows a fairly common pattern during Tertiary times. In the Paleocene Epoch (65.5–55.8 Ma), an array of strange mammals evolved, probably part of an experimental phase of rapid evolution after the extinction of the dinosaurs and the resulting clearing of eco-space. Paleocene faunas contain a mix of familiar groups, as well as some unusual forms (Figure 1.10), and the mammals were mostly small, with few larger than a sheep. Larger plant-eaters included the pantodonts, which were up to bear-sized and fed on leaves. The arctocyonids were dog- to bear-sized animals with broad molars for crushing plant food, and they showed a range of adaptations, some for ground dwelling, some for climbing. These, together with a large group of lithe, modest-sized plant-eaters, including the periptychids, the hyopsodontids and the phenacodontids, are traditionally grouped together as the 'condylarths'. At first, the main meat-eaters were the mesonychids (another 'condylarth' family), ranging in size from a dog to a hyaena, and smaller primitive true carnivorans. They were joined late in the epoch by oxyaenid creodonts, which superficially would have looked somewhat like cats, but are only distantly related to modern carnivorans. In Europe, there were the otter-like pantolestids, with long sharp canines, the small, insect-eating adapisoricids and adapisoriculids, the primate-like plesiadapiforms, the herbivorous pleuraspidotheres and a diversity of multituberculates. Europe lacked creodonts and carnivorans at this time.

About five of the approximately 25 modern orders of mammals were on the scene during the Paleocene Epoch, but almost all had appeared by the early part of the Eocene Epoch, around 50 million years ago. The various bizarre Paleocene groups largely survived into the Eocene Epoch and some continued for a little longer than that, but they all eventually disappeared. Most of the modern orders are known in the fossil record from Eocene sediments onwards in Europe, including the excellent Eocene sequences of the south of England, and only brief comments on their evolution

are given here.

The relationships of the major groups of placental mammals are controversial. Intense efforts have been made, using cladistic analysis of hard-part and soft-part anatomical characters and, increasingly now, molecular sequencing evidence, to disentangle eutherian relationships. Morphologists and palaeontologists had succeeded in establishing a number of subclades among the placental mammals (Figure 1.9), notably Xenarthra, Anagalida, Glires, Archonta, Euarchonta, Paenungulate, and Tethytheria, all based on shared morphological characters (Novacek, 1992, 1999). However, the deepest divisions within the tree have so far not been resolved on the basis of morphology.

The deep branching pattern has seen greater resolution from molecular evidence, although disagrees in certain important areas with the morphology. The molecules suggest that there was a unique radiation of mammals in Africa —modern mammals as different as elephants, golden moles, tenrecs, and aardvarks all appear to share a common ancestry, and indeed this clade, termed the 'Afrotheria', appears to have been one of the first to diverge from the other placental mammals (Springer *et al.,* 1997, 2003; Murphy *et al.,* 2001; Murata *et al.,* 2003). This happened some time in the Cretaceous Period, perhaps 100–88 million years ago. During this interval, a further mammalian superorder, Xenarthra, split off in South America, leaving the Boreoeutheria, or 'northern placentals'. These in turn divided into Laurasiatheria and Euarchontoglires some time from 88–79 million years ago (Archibald, 2003). The current understanding of placental relationships (Figure 1.11) represents a complete revolution of views since 1997.

The Afrotheria are the oddest collection of mammals, as noted. One subclade consists of the aardvark, the tenrecs, the golden moles, and the elephant shrews. The aardvark, sole-surviving member of the Order Tubulidentata, is an ant-eating form that was hitherto associated with the ungulates. The tenrecs and golden moles were formerly classed as true insectivorans, members of the order Lipotyphla, side-by-side with moles, shrews and hedgehogs. However, the molecular analyses pair them as Afrosoricida, dose relatives of the aardvark. The golden moles, formerly assigned to the Order Macroscelidea, and of disputed affinities, are now seen to be close relatives of the Afrosoricida.

The Proboscidea — elephants and their relatives — evolved largely in Africa and expanded worldwide as a diverse and successful group in the Miocene Epoch. Early forms were of course smaller than their modern relatives, with small tusks and small trunks. Extinct forms include the deinotheres, with curved tusks in the lower jaws, the gomphotheres, with four tusks, the mammutids and the mammoths. These groups disappeared as the world became colder, although the mammutids and mammoths adapted to the cold of the Pleistocene ice ages and then mostly disappeared 10 000 years ago as the ice receded. Some mammoths survived on Arctic islands until around 3700 years ago. Close relatives of the proboscideans are the Sirenia (the sea cows) and the Hyracoidea, the small rabbit-like hyraxes of Africa and the Middle East.

The Xenarthra have always been restricted mainly to South America, where sloths, anteaters and armadillos evolved many weird and wonderful forms.

The northern mammals, Boreoeutheria, split during the Cretaceous Period into two major clades, Laurasiatheria and Euarchontoglires. Laurasiatheria consists of lipotyphlans, bats, cetartiodactyls, perissodactyls, carnivorans, and pholidotans.

The Lipotyphla, represented today by shrews, hedgehogs, moles and their relatives, are all small, insect-eating forms, and they are known from most good Tertiary localities. The Chiroptera — the bats — are further basal laurasiatherians, with a long history dating back to the early Eocene Epoch, when the oldest bats looked very like modern forms.

Among modern mammals, the 'ungulates', or hoofed mammals, include all the large plant-eaters. After separation of the elephants and lynxes, these were classically subdivided into artiodactyls and perissodactyls, on the basis of foot symmetry and the numbers of toes (Owen, 1848c). The validity of these two orders are confirmed by modern studies. But an unexpected finding is that whales, Order Cetacea, are dose relatives of artiodactyls, perhaps even of hippos, within Artiodactyla. Hence, whales and artiodactyls are grouped together as Cetartiodactyla.

Feet of the Artiodactyla have even numbers of hooves: two in modern camels, deer and cattle, but four in many Eocene forms and in modern pigs and hippos. Extinct relatives of the pigs include some unusual forms, especially the huge,

rather terrifying entelodonts from the mid-Tertiary Sub-era. Camels, cattle and deer came to the fore especially after the Miocene Epoch. These groups are characterized by a complex digestive system that allows them to ruminate their food ('chew the cud') so as to extract maximum nutritive value from it. Whales arose in early Eocene times, and in Pakistan some small forms that retain their limbs have been found recently, proving what had been postulated, that whales evolved from land-living mammals. Surprisingly, these early land-living whales have the 'double-pulley' astragalus, a specialized ankle bone designed to improve locomotor efficiency, and formerly thought to be unique to artiodactyls. There were some primitive long, serpent-like whales in the Eocene Epoch, the archaeocetes (such as *Basilosaurus).* After the Eocene Epoch, whales evolved into their two modern groups, the odontocetes or toothed whales (flesh-eating dolphins, porpoises and killer whales) and the mysticetes, or whalebone whales, the giants that feed on plankton.

The Perissodactyla usually have an odd number of hooves on each foot (one in horses, three in rhinoceroses), and the axis of the foot passes through the middle toe. Horses had a mainly Northern Hemisphere distribution, and much of their evolution took place in North America, with frequent emigrations to Eurasia. The earliest dog-sized *Pliolophus* (formerly included in *Hyracotherium),* from the beginning of the Eocene Epoch, evolved through larger Oligocene to Pliocene forms to the modern *Equus,* and this well-documented story has become an evolutionary classic (Figure 1.3), the early parts of which are well-documented in British Eocene fossil mammal sites. Fossil rhinoceroses were once much more widespread and diverse than they are today. Extinct perissodactyls include the large brontotheres, with forked nose horns, and the strange gorilla-like chalicotheres.

The Carnivora, represented by modern cats, dogs, bears, seals and sealions, came to the fore between the Eocene and Miocene epochs. The feliforms, or cats, civets, mongooses and hyaenas, include many extinct forms that were similar to living representatives, but also many sabre-toothed cats, a style of carnivory that is now extinct. The caniforms — dogs, bears, racoons and weasels and the marine forms also included some unusual extinct forms — the amphicyonids, something like giant bear-dogs. The marine carnivorans — the pinnipeds, including the seals, sealions and walruses — form a monophyletic group, despite earlier suggestions of polyphyly, and they evolved in the Oligocene Epoch from terrestrial caniforms. Their closest relatives are bears (Ursidae). Close relatives of the carnivora are the Pholidota — the pangolins — known today from Africa and south-east Asia.

The second boreoeutherian clade, Euarchontoglires, consists of a diverse assemblage of smaller northern mammal groups, divided essentially into the clades Euarchonta and Glires.

Euarchonta includes Scandentia, or tree shrews, which are a small group of squirrel-like animals from Asia. The Dermoptera, or flying lemurs, include two species from south-east Asia, a single Eocene fossil from Thailand and the North American Paleocene and Eocene families Mixodectidae and Plagiomenidae. Close relatives are the extinct Plesiadapiformes from early Tertiary times: tree-dwelling insect and plant-eaters that were once erroneously classified as primates. The primates themselves include an array of forms: the lemurs, lorises and bushbabies, the tarsiers, the Old World and New World monkeys and the apes. The apes evolved from Old World monkeys, and they have a rich fossil record, especially in Miocene deposits in Africa. Humans of course belong here, and the oldest humans are from rocks dated as over 4 million years old, in East Africa.

The clade Glires consists of rodents, rabbits and relatives. The largest modern order of mammals, the Rodentia, consists of 1800 species today — about 40% of all mammal species. Most of these are myomorphs — mice, rats and their relatives — a group that radiated explosively in the past 20 million years. Other rodent groups include the sciuromorphs (squirrels and beavers) and the hystricognaths (guinea pigs, capybaras and chinchillas), a group restricted to South America. Most fossil rodents probably looked pretty much like mice or squirrels, but there were a couple of oddities: the Miocene mylagaulids from North America, with small horns on their snouts, and the giant capybara *Phoberomys,* from the late Miocene and Pliocene epochs, as large as a pigmy rhinoceros. The Lagomorpha — rabbits and hares — are dose relatives of the rodents.

When the cladograms (Figure 1.9) and (Figure 1.11) are translated into phylogenies (Figure 1.10) and (Figure 1.12), the rapid radiation of mammals in the Paleocene and early Eocene epochs becomes evident. A number of early groups became extinct in mid-Tertiary times, and others can be seen to have declined somewhat in diversity (Sirenia, Perissodactyla, Proboscidea). The cladogram also can be represented by a list-form classification (Figure 1.13).

There are many books on fossil mammals, including Savage and Long (1986), illustrated with beautiful colour paintings, and Benton (1991), with abundant colour photographs and diagrams. The textbook by Carroll (1988) offers a fully documented account of the fossil mammal groups, and Benton (2005) gives a briefer but more up-to-date account, with a fully dadistic approach. Mesozoic mammals are presented more fully by Kemp (1982), Lillegraven *et al.* (1979) and Kielan-Jaworowska *et al.* (2004). Savage and Russell (1983) offer detailed listings of mammalian faunas from around the world, and papers in Szalay *et al.* (1993) present detailed phylogenies of various mammalian groups. Rose and Archibald (2005) provide an up-to-date account of placental phylogeny. Stuart (1982a) and Sutcliffe (1985) provide good accounts of Pleistocene mammals, which will also be the subject of a companion GCR volume to the present one.

Fossil mammal and bird sites: distribution and range

British fossil mammal sites (Figure 1.14) have a long range, from Late Triassic (*c.* 215 Ma) to Pliocene times. Representation is especially good in the Jurassic Period and early in the Cretaceous Period, and in the Eocene and Oligocene epochs.

Fossil birds are much less well-represented in the known British fossil record (Figure 1.14), with equivocal Mesozoic remains and good materials from the early Tertiary Sub-era and the Pleistocene Epoch, but with a Miocene–Pliocene gap. Although some Mesozoic birds have been reported from Great Britain, most have turned out to be equivocal, and the valid reports are relatively unimportant finds, so no GCR sites for Mesozoic birds could be established. Supposed bird remains have been described from the Cambridge Greensand (Albian—Cenomanian) of Cambridge — isolated limb elements named *Enaliornis barretti* and *E. sedgwicki* (Seeley, 1876) — which may indeed be avian and, possibly, hesperornithiform (Olson, 1985; Elzanowski and Galton, 1991; Unwin, 1993). Another taxon, *Wileyia valdensis* Harrison and Walker, 1973, based on a worn humerus from the Weald Clay (Barremian) of Henfield, Sussex, and described as a bird, may indeed be an enantiornithid, or it could be reptilian (Olson, 1985; Unwin, 1993).

The sites described in the present volume are largely clustered in southern England, associated with the main belts of outcrop. One exception is the important Middle Jurassic site on Skye in the Scottish Inner Hebrides.

(Figure 1.13) The classification of the major groups of mammals. The scheme for placental mammals is modified from McKenna and Bell (1997) using numerous recent sources including Janis *et al.,* (1998); that for marsupials is from Kirsch *et al.* (1997); the nontherian mammal scheme is from various sources including Kielan-Jaworowslca and Hurum (2001) and Kielan-Jaworowslca *et al.* (2004). Families represented at British sites are in bold typeface. A breakdown into families is provided only when a given order is represented in Britain. Only the ranks class, subclass, infraclass, superorder, order and family are used, except in the Cetacea where a subordinal breakdown is given. Intervening ranks are shown hierarchically but without rank names as these vary greatly among authors. t = extinct group; '?' against a family indicates doubt as to position. Inverted commas indicate a paraphyletic group.

Class Mammalia

†Family Sinoconodontidae

†Family Morganucodontidae

†Family Amphilestidae

†Family Kuehneotheriidae

†Family Thereuodontidae

†Family Tmodontidae

†Order Docodonta

†Family Docodontidae

†Order Triconodonta s.s.

†Family Triconodontidae

†Order Shuotheridia

†Family Shuotheriidae

†Subclass Allotheria

†Order 'Haramiyida'

†Family Theroteinidae

†Family Haramiyidae

†Family Eleutherodontidae

†Order Multituberculata

†Family Kermackodontidae

†Family Hahnotheriidae

†Family Allodontidae

†Family Zofiabaataridae

†Family Paulchoffatiidae

†Family Pinheirodontidae

†Family Plagiaulacidae

†Family Albionbaataridae

†Family Eobaataridae

†Family Arginbaataridae

†Family Eucosmodontidae

†Family Microcosmodontidae

†Family Taeniolabididae

†Family Kogaionidae

†Family Neoplagiaulacidae

†Family Ptilodontidae

†Family Cimolodontidae

†Family Cimolomyidae

†Family Boffiidae

Subclass Australosphenida

Order Monotremata

Family Ornithorhynchidae

Family Tachyglossidae

†Order Ausktribosphenida

Subclass Trechnotheria

†Family Spalacotheriidae

Cladotheria

†Family Amphitheriidae

†Family Dryolestidae

†Family Paurodontidae

†Family Donodontidae

†Family Mesungulatidae

†Family Brandoniidae

†Family Arguitheriidae

†Family Arguimuridae

†Family Vincelestidae

†Family Peramuridae

Boreosphenida

†Family Aegialodontidae

Theria

Metatheria

†Family Deltatheridiidae

†Family Deltatheroididae

†Family Asiatheriidae

Infraclass Marsupialia

†Boreometatheria

†Order Peradectemorphia

Notometatheria

Order Didelphimorphia

Family Didelphidae

Family Caluromyidae

†Family Sparassocynidae

†Family Herpetotheriidae

†Order Sparassodonta

Order Paucituberculata

†Order Polydolopimorphia

Order Peramelina

Order Dasyuromorphia

Order Notoryctemorphia

Order Microbiotheria

Order Diprotodontia

†Order Yalkaparidontia

Eutheria

Infraclass Placentalia

Order Xenarthra

†Order 'Leptictida'

†Family Gypsonictopidae

†Family Didymoconidae

†Family Leptictidae

†Family Pseudorhynchocyonidae

†Order Pantolesta

†Family Pantolestidae

†Family Pentacodontidae

†Family Ptolemaiidae?

†Order Palaeanodonta

Order Pholidota

Order Tubulidentata

†Order Bibymalagasia

Order Lipotyphla

†Family Palaeoryctidae?

Family Tenrecidae

†Family Adapisoriculidae?

Family Soricidae

†Family Proscalopidae

Family Talpidae

†Family Dimylidae

†Family Geolabididae

†Family Nesophontidae

†Family Micropternodontidae

†Family Apternodontidae

Family Solenodontidae

†Family Plesiosoricidae

†Family Adapisoricidae?

†Family Amphilemuridae

Family Erinaceidae

†Order Didelphodonta

†Family Cimolestidae

Order Carnivora

†Family Viverravidae

†Family 'Miacidae'

†Family Nimravidae

Family Fefidae

Family Viverridae

Family Herpestidae

Family Hyaenidae

Family Canidae

†Family Amphicyonidae

Family Ursidae

Family Otariidae

Family Odobenidae

Family Phocidae

Family Ailuridae

Family Mephitidae

Family Mustelidae

Family Procyonidae

†Order Creodonta

†Family Oxyaenidae

†Family Hyaenodontidae

†Order Pantodonta

†Family Bemalambdidae

†Family Harpyodidae

†Family Pastoralodontidae

†Family Titanoideidae

†Family Pantolambdidae

†Family Barylambdidae

†Family Pantolambdodontidae

†Family Coryphodontidae

†Family Cyriacotheriidae?

†Order Tillodontia

†Family Esthonychidae

†Order Taeniodonta

†Order Notoungulata

†Order Astrapotheria

†Order Xenungulata

†Order Pyrotheria

†Order Arctostylopida

Superorder Anagalida

†Order Nimotonida'

Order Lagomorpha

†Order Mixodontia

Order Rodentia

†Family Alagomyidae

†Family Laredomyidae

†Family 'Paramyidae'

†Family Allomyidae

Family Aplodontidae

†Family Mylagaulidae

†Family Pseudosciuridae

†Family Theridomyidae

Family Gliridae

†Family Reithroparamyidae

Family Sciuridae

Family Castoridae

†Family Protoptychidae

†Family Armintomyidae

Family Dipodidae

†Family Simimyidae

Family Cricetidae

Family Muridae

Family Arvicolidae

Family Spalacidae

Family Rhizomyidae

†Family Eomyidae

†Family Florentiamyidae

Family Geomyidae

Family Heteromyidae

Family Pedetidae

†Family Zegdoumyidae

Family Anomaluridae

†Family Ivanantoniidae

†Family Sciuravidae

†Family Chapattimyidae

†Family Cylindrodontidae

Family Ctenodactylidae

†Family Tsaganomyidae

Family Hystricidae

Family Erethizontidae

†Family Myophiomyidae

†Family Diamantomyidae

†Family Phiomyidae

†Family Kenyamyidae

Family Petromuridae

Family Thryonomyidae

Family Bathyergidae

Family Agoutidae

†Family Eocardiidae

Family Dinomyidae

Family Caviidae

Family Hydrochoeridae

Family Octodontidae

Family Echimyidae

Family Capromyidae

†Family Heptaxodontidae

Family Chinchillidae

†Family Neoepiblemidae

Family Abrocomidae

Order Macroscefidea

†Order Dinocerata

Superorder Archonta

Order Chiroptera

†Family Archaeonycteridae

'Family Icaronycteridae

†Family Palaeochiropterygidae

†Family Hassianycteridae

†Family Tanzanycteridae

†Family Philisidae

Family Pteropodidae

Family Rhinolophidae

Family Hipposidcridae

Family Megadermatidae

Family Rhinopomatidae

Family Craseonycteridae

Family Nycteridae

Family Emballonuridae

Family Myzopodidae

Family Mystacinidae

Family Phyllostomidae

Family Mormoopidae

Family Noctilionidae

Family Thyropteridae

Family Furipteridae

Family Naralidae

Family Molossidae

Family Vespertilionidae

Corder uncertain

†Family Nyctitheriidae

Order Scandenfia

Order Dermoptera

†Order Apatotheria?

†Family Apatemyidae

†Order Plesiadapiformes

†Family Purgatoriidae

†Family Microsyopidae

†Family Toliapinidae

†Family Paromomyidae

†Family Micromomyidae

†Family Carpolcstidae

†Family Plesiadapidae

†Family Picromomyidae

†Family Picrodontidae

Order Primates

†Family Adapidae

Family Lemuridae

Family Daubentoniidae

Family Lorisidae

Family Galagidae

Family Cheirogaleidae

†Family Archaeolemuridae

†Family Palaeopropithecidae

Family Indriidae

†Family Omomyidae

Family Tarsiidae

†Family Eosimiidae

†Family Parapithecidae

†Family Pliopithecidae

Family Cercopithecidae

Family Hylobatidae

Family Hominidae

Family Callitrichidae

Family Atelidae

Superorder Linguine

†Order 'Condylarthra'

†Family Arctocyonidae

†Family Paroxyclaenidae

†Family Mesonychidae

†Family Periprychidae

†Family Hyopsodontidae

†Family Didolodontidae

†Family Phenacodontidae

Order Artiodactyla'

†Family 'Diacodexcidae'

†Family Leptochoeridae

†Family 'Helohyidae'

†Family 'Anthracotheriidae'

Family Hippopotamidae

†Family Raoellidae

†Family Entelodontidae

Family Suidae

Family Tayassuidae

†Family Sanitheriidae

†Family Cebochocridae

†Family Choeropotamidae

†Family Mixtotheriidae

†Family Cainotheriidae

†Family Anoplotheriidae

†Family Xiphodontidae

†Family Homacodontidae

†Family Agriochoeridae

†Family Merycoidodontidae

†Family Protoceratidae

†Family Oromerycidae

Family Camclidae

?Family Dichobunidae

†Family Amphimerycidae

†Family Hypertragulidae

Family Tragulidae

†Family Leptomerycidae

†Family Bachitheriidae

†Family Lophiomerycidae

†Family Gelocidae

Family Moschidae

Family Cervidae

Family Antilocapridae

†Family Palaeomerycidae

Family Giraffidae

Family Bovidae

Order Cetacea

Suborder Archaeoceti'

†Family Palticetidae

†Family Protocetidae

†Family Ambulocetidae

†Family Remingtonocetidae

†Family Basilosauridae

Suborder Mysticeti

†Family Aetiocetidae

†Family Llanocetidae

†Family Mammalodontidae

†Family Eomysticetidae

†Family Cetotheriidae

Family Balacnoptcridae

Family Eschrichtlidae

Family Neobalaenidae

Family Balaenidae

Suborder Odontoceti

†Family Agorophiidae

†Family Simocctidae

†Family Patriocetidae

Family Physeteridae

Family Kogiidae

Family Ziphiidae

†Family Squalodontidae

†Family Squalodelphinidae

†Family Waipatiidae

†Family Dalpiazinidae

Family Platanistidae

†Family Eurhinodelphinidae

†Family Eoplaranistidae

Family Iniidae

Family Pontoporiidae

Family Lipotidae

†Family Kentriodontidae

†Family Albirconidae

Family Delphinidae

Family Phocaenidae

Family Monodontidae

†Family Odobenocetopsidae

†Order Litoptema

Order Sirenia

†Family 'Prorastomidae'

†Family 'Protosirenidae'

Family Trichechidae

Family Dugongidae

†Order Desmostylia

†Order Embrithopoda

Order Proboscidea

†Family Numidotheriidae

†Family Barytheriidae

†Family Moeritheriidae

†Family Deinotheriidae

†Family Palaeomastodontidae

†Family Mammutidae

†Family 'Gomphotheriidae'

Family Elephantidae

Order Hyracoidea

Order Perissodactyla

†Family Lambdotheriidae

†Family Brontotheriidae

†Family 'Isectolophidae'

†Family Chalicotheriidae

†Family Lophiodontidae

†Family Pachynolophidae

†Family Lophialetidae

†Family 'Helaletidae'

†Family Deperetellidae

Family Tapiridae

Family 'Hyrachyidae'

†Family Amynodontidae

†Family Rhodopagidae

†Family Hyracodontidae

Family Rhinoccrotidae

Family Equidae

†Family Palaeotheriidae

The selection of Mesozoic and Tertiary fossil mammal and bird GCR sites

This volume contains descriptions of all of the sites that were selected for the Geological Conservation Review (GCR) for their special significance to the study and understanding of fossil mammals and birds in the Mesozoic Era and the Tertiary Sub-era (for a discussion of the point taken for the boundary between the end of the Tertiary Sub-era and the beginning of the Pleistocene Epoch for the purposes of the present volume, see below). Whereas Pleistocene fossil sites were selected for all aspects of their vertebrate palaeontology: for finds of birds and/or mammals, and also for their content of (usually rarer) fishes, amphibians and reptiles, pre-Pleistocene GCR sites that were selected for the GCR for their content of fossil reptiles and post-Paleozoic amphibians have been presented elsewhere in the GCR Series by Benton and Spencer (1995), and for fishes and Paleozoic amphibians by Dineley and Metcalf (1999).

The general principles guiding GCR site selection are described in the introductory GCR volume (Ellis *et al.,* 1996), but can be encapsulated in three broad components:

- International geological importance (e.g. palaeontological 'type' sites and other sites that have achieved informal, but widely held, international recognition).
- Presence of 'classic' or exceptional features that are scientifically important (e.g. 'textbook' examples of particular features or exceptionally rare occurrences).
- Presence of representative geological features (e.g. characteristic or typical British palaeontological assemblages) that are essential in comprehensively portraying the fossil mammal and bird record of Britain.

However, in order to ensure true national importance in the selected *representative* sites, site selection was underpinned by the premise that the particular 'GCR Block' (site selection category; of which three are relevant here, Mesozoic Mammalia, Tertiary Mammalia and Ayes) should be represented by the *minimum number* of sites. Only those sites absolutely necessary to represent the most important aspects of Britain's Mesozoic to Tertiary mammals and birds were

therefore selected.

On an entirely practical level, all selected sites must be conservable, meaning in essence:

1. that development planning consents do not exist or else amendments can be negotiated; and
2. that sites are physically viable, for example, in terms of the long-term stability of exposures.

To compile the ultimate site lists for the Mesozoic Mammalia, Tertiary Mammalia and Ayes GCR Blocks, extensive consultations were carried out with appropriate Earth scientists, and a large number of sites were assessed before the final listing was produced.

The initial site selections were made around 1980–1982 by a number of contributors: Professor K.A. Kermack for the Mesozoic mammal sites, Drs C.J.O. Harrison and C.A. Walker for the Tertiary bird sites, and Dr A.N. Insole for the Tertiary mammal sites. The total numbers of selected GCR sites are:

Mesozoic mammals	10
Tertiary mammals	8
Tertiary birds	8
TOTAL	26

These GCR sites are a small sub-set of the hundreds of fossiliferous locations that were considered before selection.

The final phase of the project took place during 1997–1999, with final revision in 2004, when the authors of this volume prepared the fully documented site descriptions and introductory materials that are included in the present volume. Liz Cook was responsible for drafting the site descriptions, and Mike Benton wrote the introductory materials on geology, stratigraphy and bird and mammal evolution, and carried out the final revisions. Jerry Hooker edited the Mesozoic and Tertiary chapters, updating the mammalian faunal lists, the criteria for mammal site recognition and the stratigraphy.

The present volume is to be accompanied by a companion title encompassing the Pleistocene mammal and bird sites.

The Pliocene–Pleistocene boundary

The position of the Pliocene and Pleistocene boundary is important in dividing the scope of the present volume from that of the companion GCR volume on Pleistocene vertebrates. There has been considerable debate over the location, and date, of the definitive boundary.

Since the International Geological Congress in London in 1948, the Pliocene–Pleistocene boundary in Britain has traditionally been placed either at the base of (Baden-Powell, 1950; Boswell, 1952; Lagaaij, 1952) or within (Movius, 1949; Van der Vlerk, 1950) the 'Red Crag' of East Anglia. The placing of this boundary was based on the first appearance of elephant and horse within the Red Crag and the general indications of climatic deterioration inferred from the molluscan fauna (Harmer, 1900, 1902). The first indication of climatic deterioration was regarded as the key factor in defining the boundary (Oakley, 1949). The Red Crag therefore occupies a key position in the definition of the Pliocene–Pleistocene boundary in British stratigraphy.

However, in an effort to resolve inconsistencies with the recommendations of the 1948 Congress (Oakley, 1949) a proposal for a Pliocene–Pleistocene stratotype section at Vrica, Italy, was eventually agreed by the IUGS Commission on Stratigraphy (ICS) (Aguirre and Pasini, 1985). The Pliocene–Pleistocene boundary was defined as the base of a bed of silty marly claystone conformably overlying sapropelic bed 'e'. The base of this bed was chronologically calculated (based on geomagnetic calculations) to be at 1.64 Ma before present. Revision of the geomagnetic polarity time-scale (Cande and Kent, 1995) re-dated the Pliocene–Pleistocene boundary at approximately 1.74 Ma. The most-recent dating is 1.81 Ma (Gradstein *et al.,* 2004).

Objectors to the Vrica definition in northern Europe (e.g. Zagwijn, 1992) point to difficulties in the recognition of this boundary in sequences elsewhere and believe that a climatic definition, which was specifically rejected by the

Commission, offers a more workable solution.

The implications of placing the Pliocene-Pleistocene boundary in Britain at or close to the same level as the Vrica boundary, using geomagnetic polarity correlation, is that this is stratigraphically much higher than that traditionally used and therefore deposits previously regarded as being of early Pleistocene age would now be considered as Pliocene.

As the Quaternary Period (normally incorporating the Pleistocene and Holocene epochs) has traditionally been considered to be the interval of oscillating climatic extremes (glacial and interglacial episodes) dating from about 2.6 Ma, it has been proposed, as a compromise, to decouple the beginning of the Quaternary (i.e. the end of the 'Tertiary' — see Chapter 3) from the beginning of the Pleistocene. This involves extending the Quaternary as a sub-era back in time to 2.6 Ma to the Gauss-Matuyama palaeomagnetic boundary, thus incorporating the Gelasian Stage of the Pliocene (Gradstein *et al.,* 2004: 5, fig.1.2, p. 28, p. 441). A formal decision on this proposal is pending, but it is accepted for the purposes of this volume (see also Balson, 1999, fig. 8.1, pp. 237–9). Fossil mammal and bird sites in Great Britain stratigraphically above this (2.6 Ma) horizon, but below the now accepted Global Standard Stratotype-section and Point (GSSP) for the base of the Pleistocene at Vrica (1.81 Ma, Gradstein *et al.,* 2004), will be treated in a separate volume covering all of the British Quaternary deposits, except the Holocene (Schreve, in prep.).
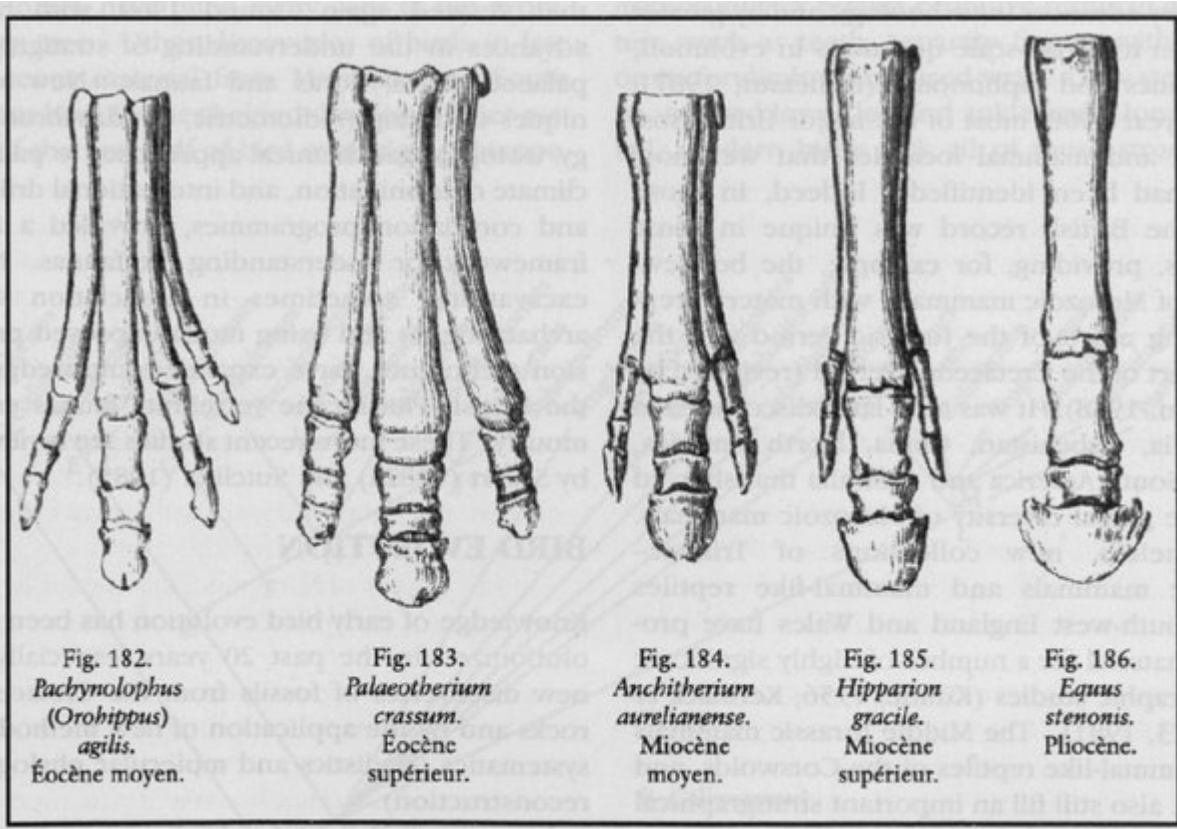
References
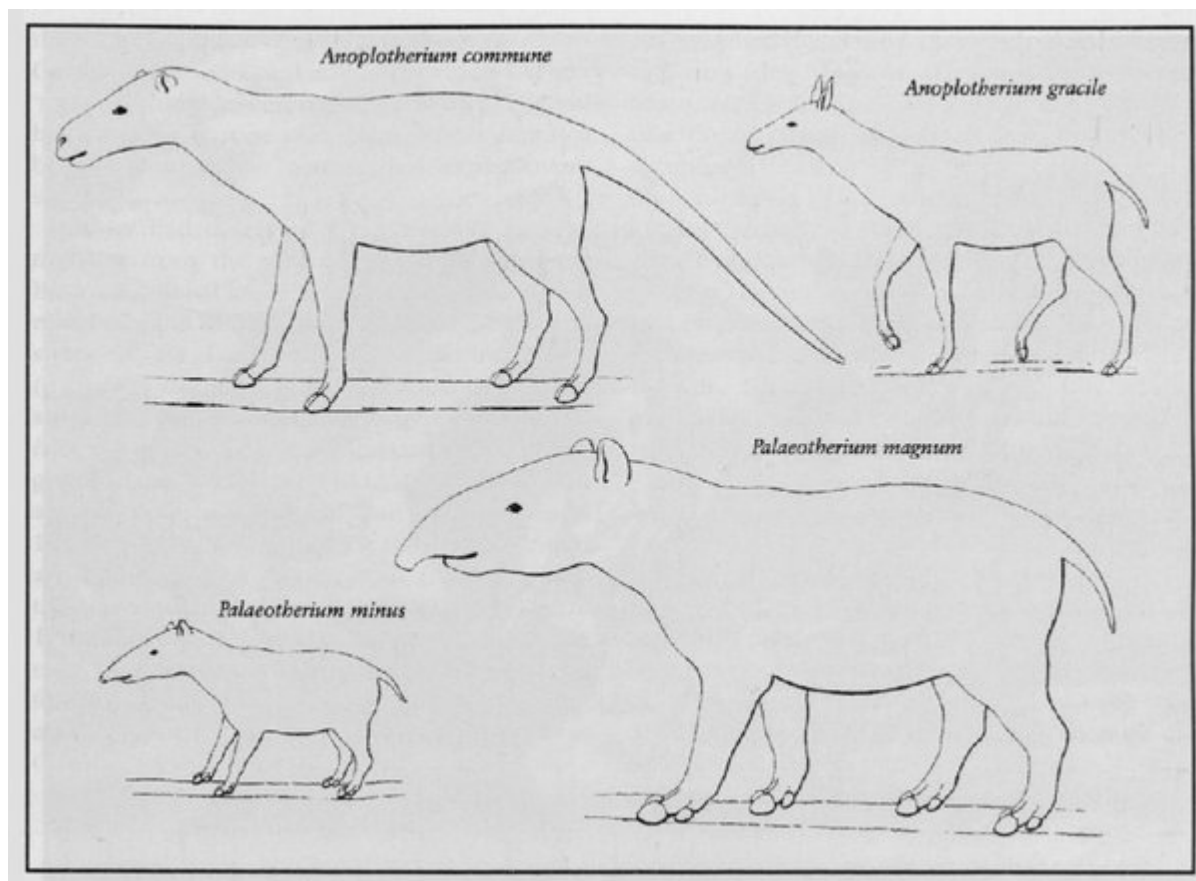
*(Figure 1.1) Reconstructions drawn by C.L. Laurillard, under the direction of Georges Cuvier, of the early mammals Anoplotherium and Palaeotherium, based on specimens he had reconstructed from the Tertiary deposits of the Paris Basin. These were some of the first, admittedly tentative, reconstructions ever made of fossil vertebrates. A. gracile is now placed in the genus Xiphodon and P minus in the genus Plagiolophus. (From Cuvier, 1834–1836.)*

(Figure 1.2) An imaginative drawing of William Buckland transported back to Pleistocene times at Kirkdale Cavern, Yorkshire — a hyaena den full of bones of Pleistocene mammals. (After Buckland, 1823.)

| Fig. 182.	Fig. 183.	Fig. 184.	Fig. 185.	Fig. 186.
Pachynolophus (Orohippus) *agilis.* Éocène moyen.	*Palaeotherium crassum.* Éocène supérieur.	*Anchitherium aurelianense.* Miocène moyen.	*Hipparion gracile.* Miocène supérieur.	*Equus stenonis.* Pliocène.

(Figure 1.3) The succession of horse evolution, from the four-toed Orohippus from Middle Eocene sediments (left) to the modern one-toed horse, Equus (right). This evolutionary scheme was worked out in the 1870s by Huxley in Britain, Kovalevskii in Russia, and Marsh in North America, and it immediately became a textbook example of evolution. (From
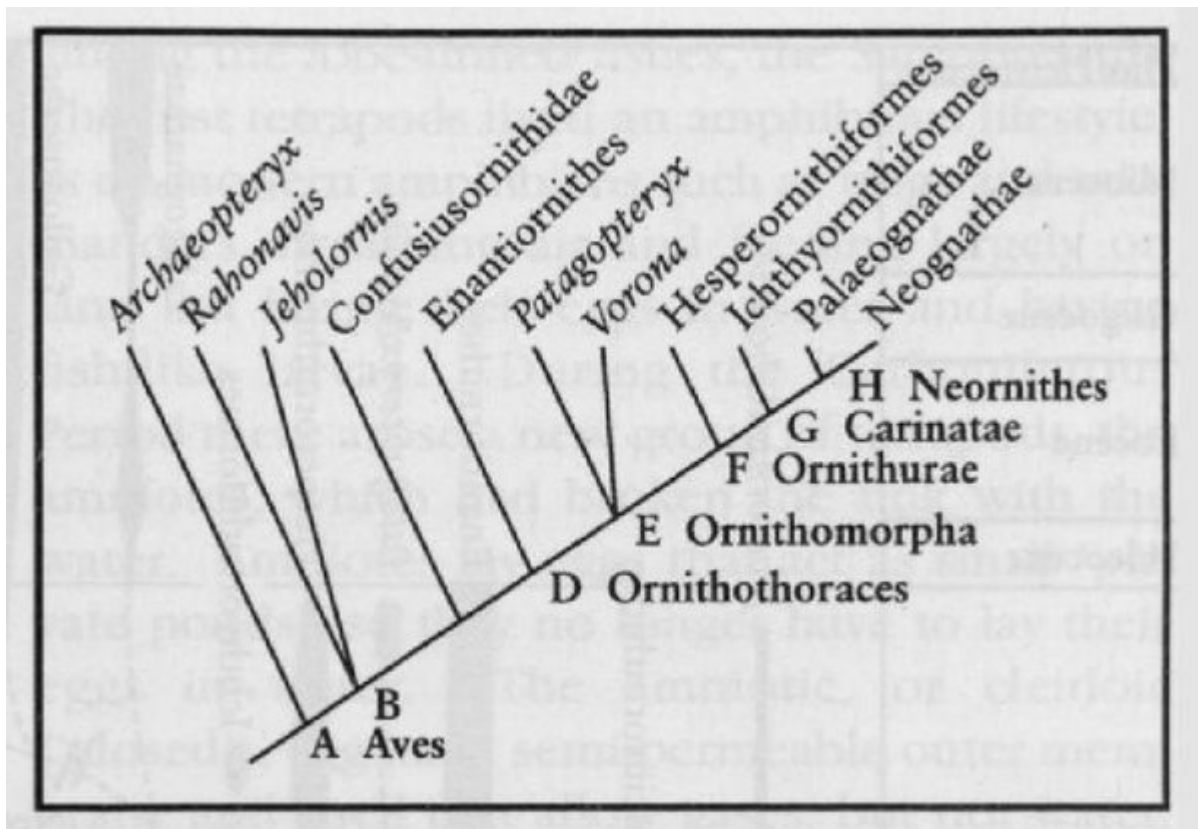
(Figure 1.4) Cladogram showing the postulated relationships of the major groups of birds, based on the work of Chiappe (1995, 2002) and others. (From Benton, 2005.)
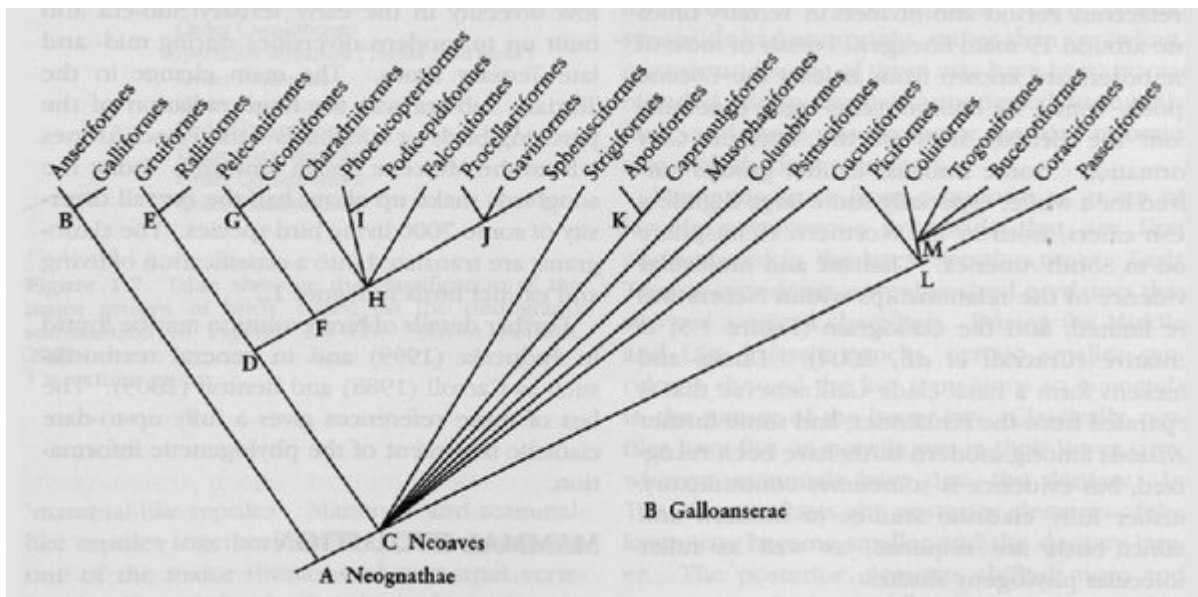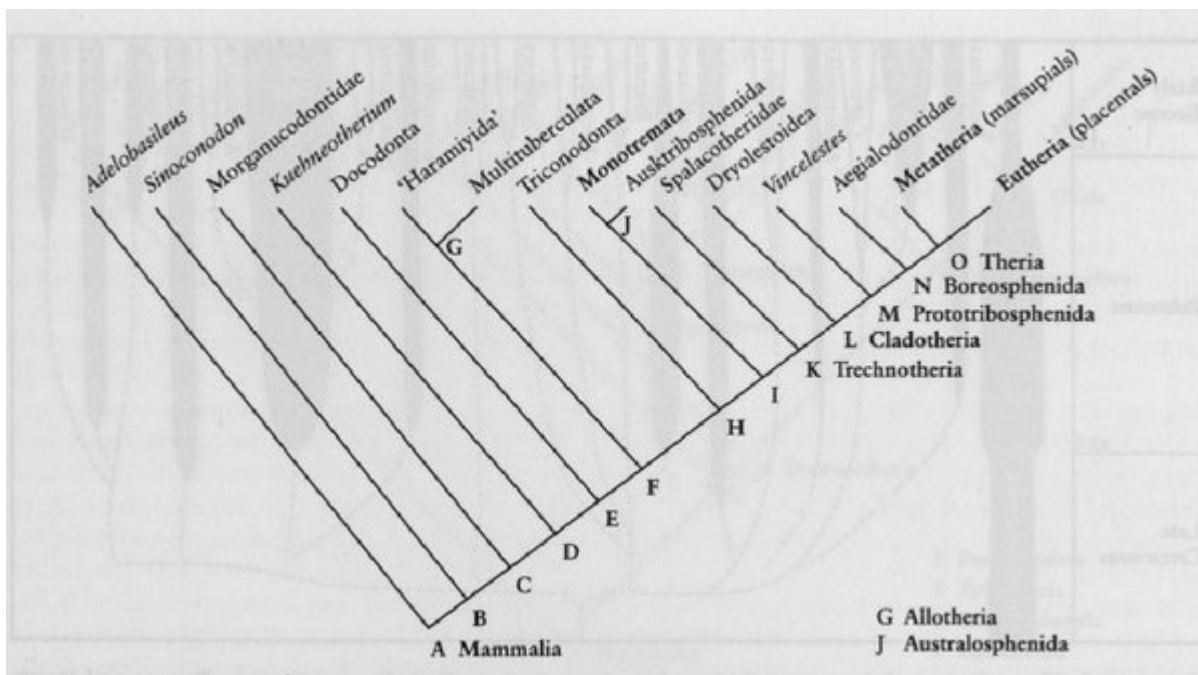

(Figure 1.5) Cladogram showing the postulated relationships of the major groups of neognath birds, based on the work of Cracraft et al. (2004) and others. (From Benton, 2005.)
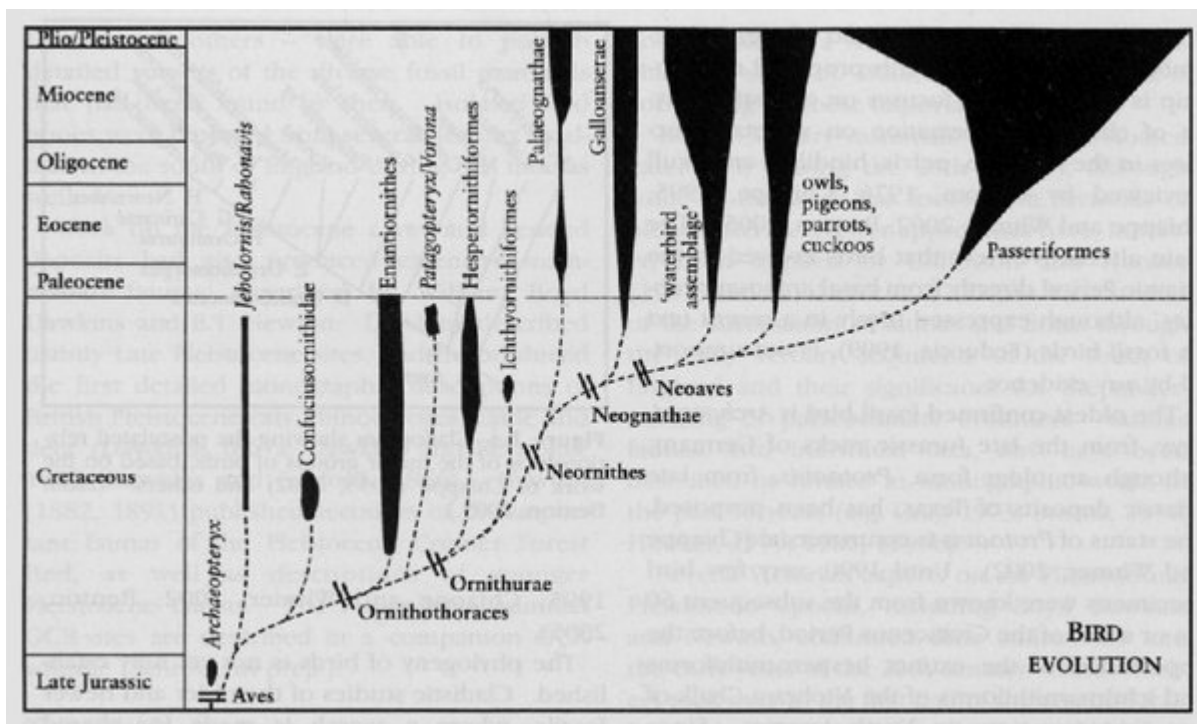
(Figure 1.6) Phylogenetic tree of birds, showing the relative importance of the different groups through time, their known fossil records, and postulated relationships, based on Unwin (1993), Chiappe (1995, 2002) and Cracraft et al. (2005). (From Benton, 2004.)

Class Aves
       †Family Archaeopterygidae
       †*Rahonavis*
       †*Jeholornis*
       †Family Confuciusornithidae
   Infraclass Ornithothoraces
       †Order Enantiornithes
     Supercohort Ornithomorpha
       †*Patagopteryx*
       †*Vorona*
      Cohort Ornithurae
       †Order Hesperornithiformes
     Subcohort Carinatae
       †Order Ichthyornithiformes
     Superdivision Neornithes
      Division Palaeognathae
       †Order Lithornithiformes
       Order Ratites
      Division Neognathae
       Subdivision Galloanserae
        Order Anseriformes
        Order Galliformes
       Subdivision Neoaves
        Superorder unnamed ('waterbird assemblage')
         Order Gruiformes
         Order Ralliformes
         Order Pelecaniformes
         Order Ciconiiformes
         Order Charadriiformes
         Order Phoenicopteriformes
         Order Podicepidiformes
         Order Falconiformes
         Order Procellariiformes
         Order Gaviiformes
         Order Sphenisciformes
         Order Strigiformes
        Superorder unnamed
         Order Apodiformes
         Order Caprimulgiformes
         Order Musophagiformes
         Order Columbiiformes
         Order Psittaciformes
         Order Cuculiformes
        Superorder unnamed ('higher land birds')
         Order Piciformes
         Order Coliiformes
         Order Trogoniformes
         Order Bucerotiformes
   Order Coraciiformes
         Order Passeriformes

(Figure 1.7) Table showing the classification of the major groups of birds, based on the cladograms summarized in Figures 1.4–1.6. (From Benton, 2005.) t = extinct group

(Figure 1.8) Cladogram showing the postulated relationships of the major groups of mammals, and of the Mesozoic groups in particular, based on the work of Rowe (1988, 1993), Luo el al. (2001, 2002) and others. It also follows the alternative interpretation of Kielan-Jaworowska et al., (2004, fig. 15.2), which accepts the integrity of the Allotheria (Butler and Hooker, 2005). Branch points B, C, D, E. F, H and I are unnamed. (After Benton, 2005.).
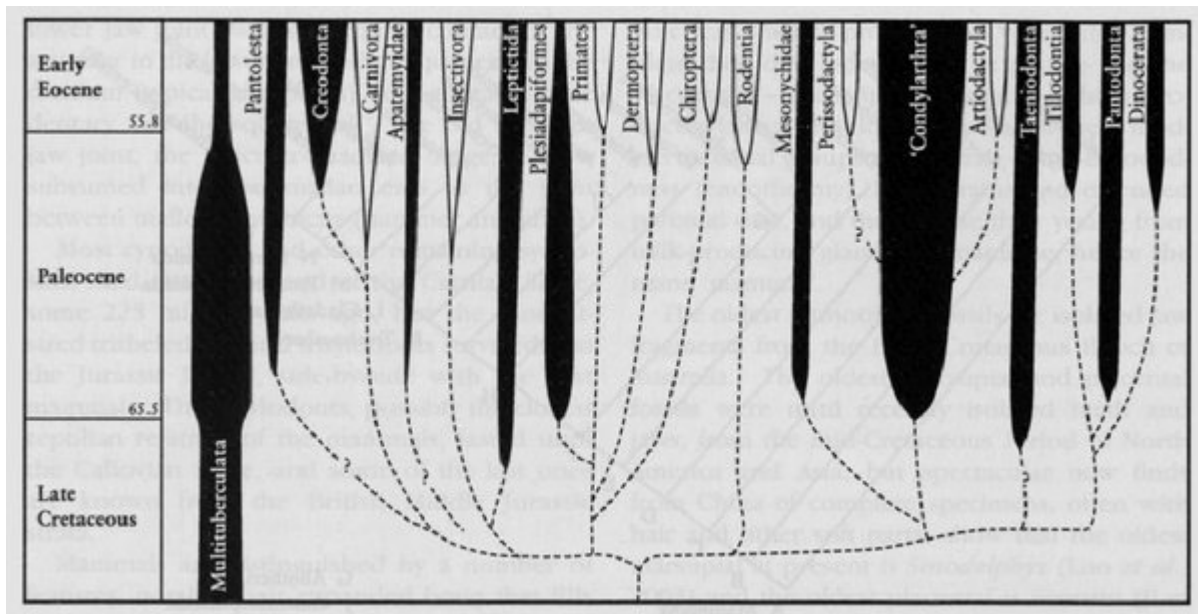

(Figure 1.10) The radiation of the mammals from Late Cretaceous to Early Eocene times in Europe and North America, showing four phases, one in the latest Cretaceous, a second in the earliest Paleocene, a third in the late Palaeocene, and a fourth in the earliest Eocene times, as far as the fossil record indicates. Groups that are now extinct are shaded black, extant orders are left blank: this shows the extent of the early proliferation of diverse groups that became extinct soon after. Relationships are based on morphological evidence. (After Benton, 2005.)
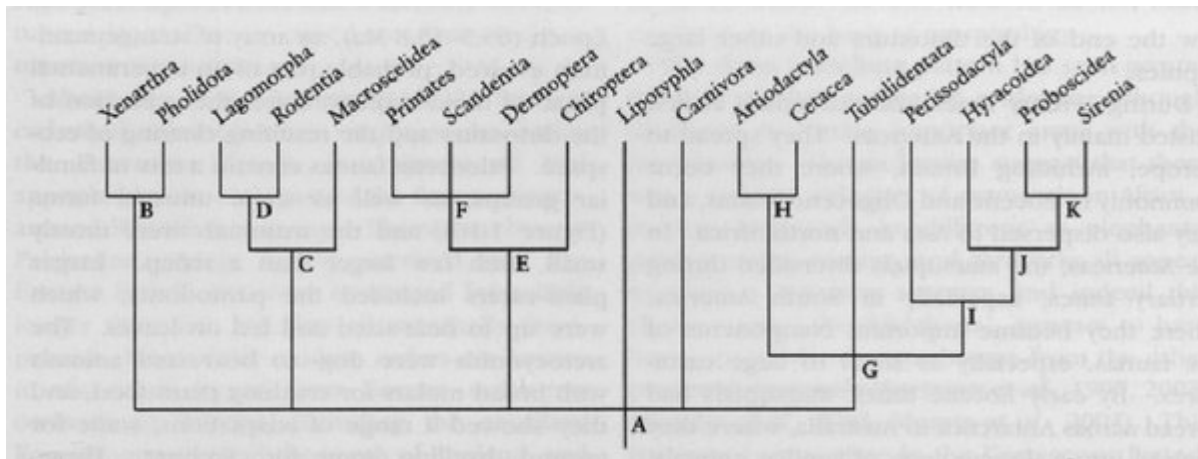
(Figure 1.9) Relationships of the modern orders of placental mammals, based on morphological evidence. Modified after Novacek (1999) by the exclusion of extinct orders and the addition of some commonly used higher groupings, namely Euarchonta, Tethytheria. The weakest supported nodes are B and E. Nodes: A, Placentalia; B, Edema; C, Anagalida; D, Glires; E, Archonta; F, Euarchonta; G, Ungulata; H, Cetartiodactyla; I, Pantomesaxonia: J, Paenungulata; K, Tethytheria.
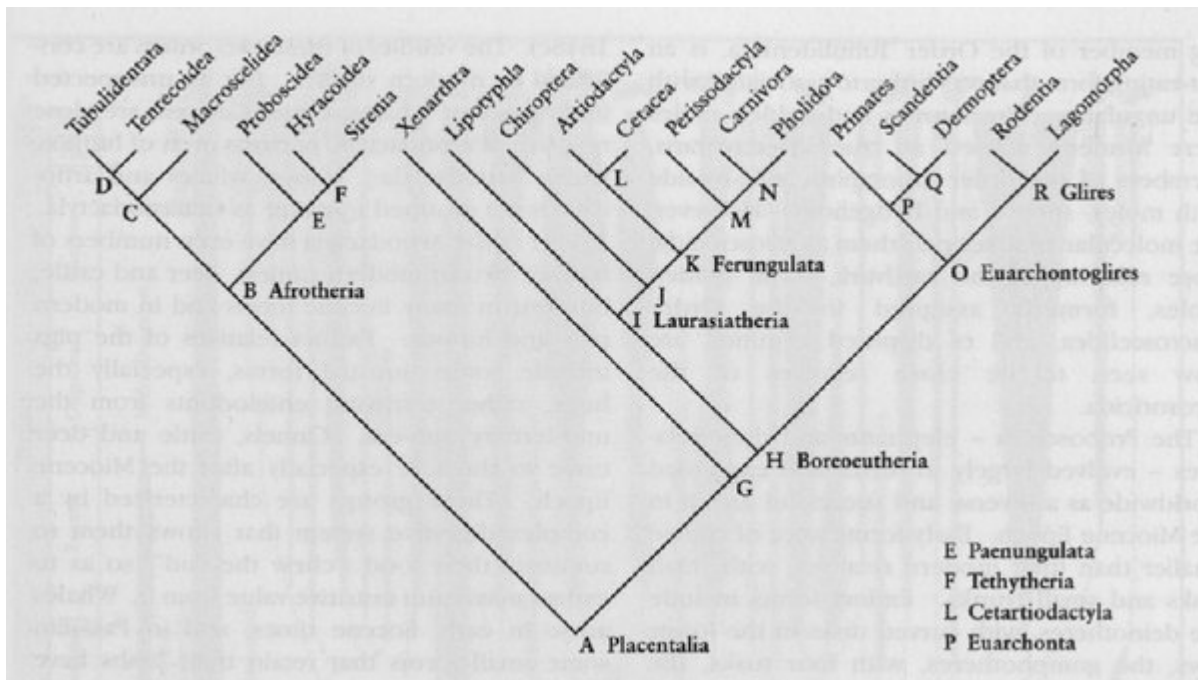
(Figure 1.11) Relationships of the modern orders of placental mammals based on molecular evidence. (From Benton, 2005.)
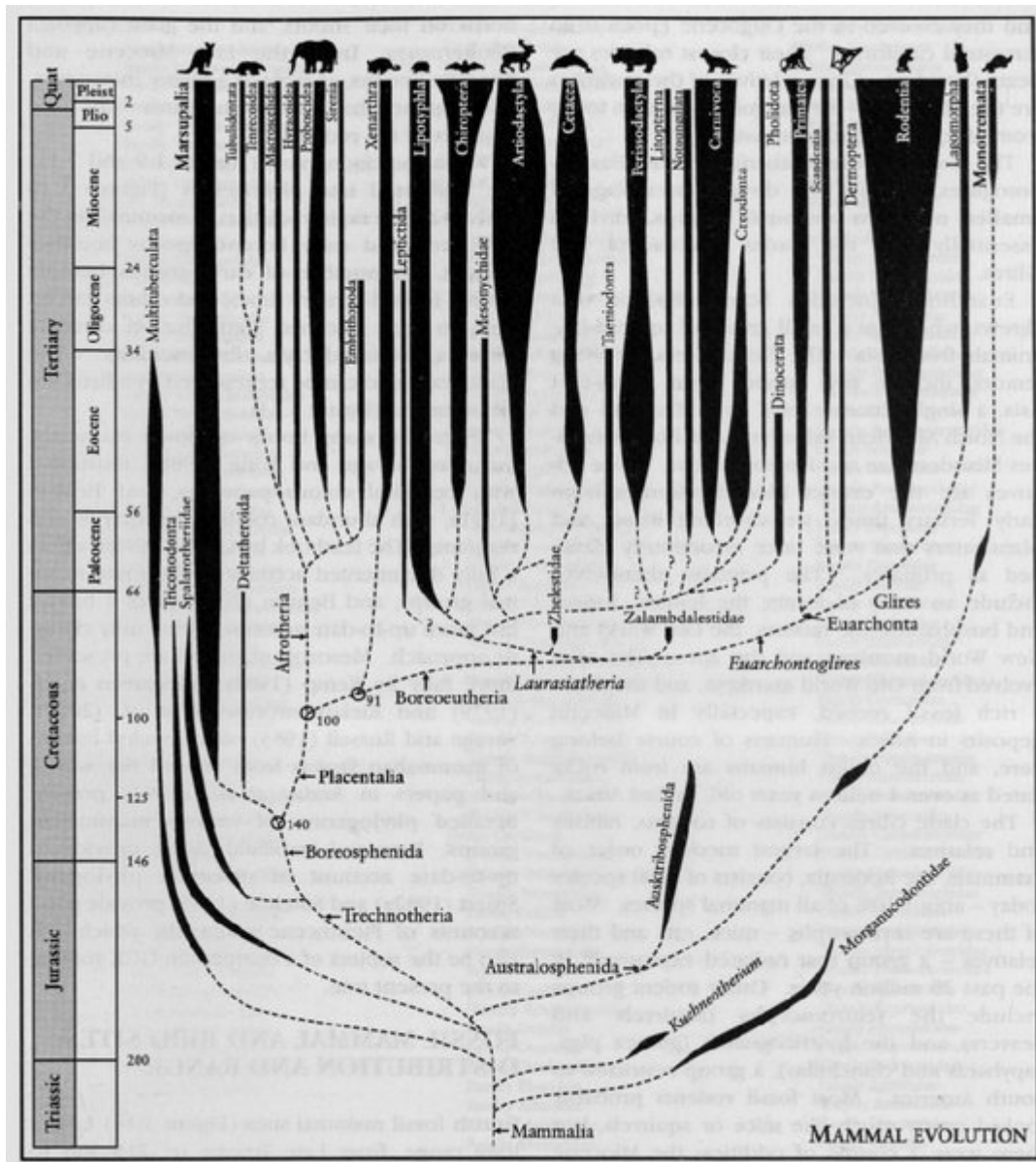
(Figure 1.12) Phylogeny of the mammals, showing relative abundance, known fossil record (solid lines) and postulated relationships (dashed lines). Relationships of modern groups based on molecular evidence. The time scale (left) is not to scale. (After Benton, 2005.)

(Figure 1.13) The classification of the major groups of mammals. The scheme for placental mammals is modified from McKenna and Bell (1997) using numerous recent sources including Janis et al., (1998); that for marsupials is from Kirsch et al. (1997); the non-therian mammal scheme is from various sources including Kielan-Jaworowslca and Hurum (2001) and Kielan-Jaworowslca et al. (2004). Families represented at British sites are in bold typeface. A breakdown into families is provided only when a given order is represented in Britain. Only the ranks class, subclass, infraclass, superorder, order and family are used, except in the Cetacea where a subordinal breakdown is given. Intervening ranks are shown hierarchically but without rank names as these vary greatly among authors. † = extinct group; '?' against a family indicates doubt as to position. Inverted commas indicate a paraphyletic group.
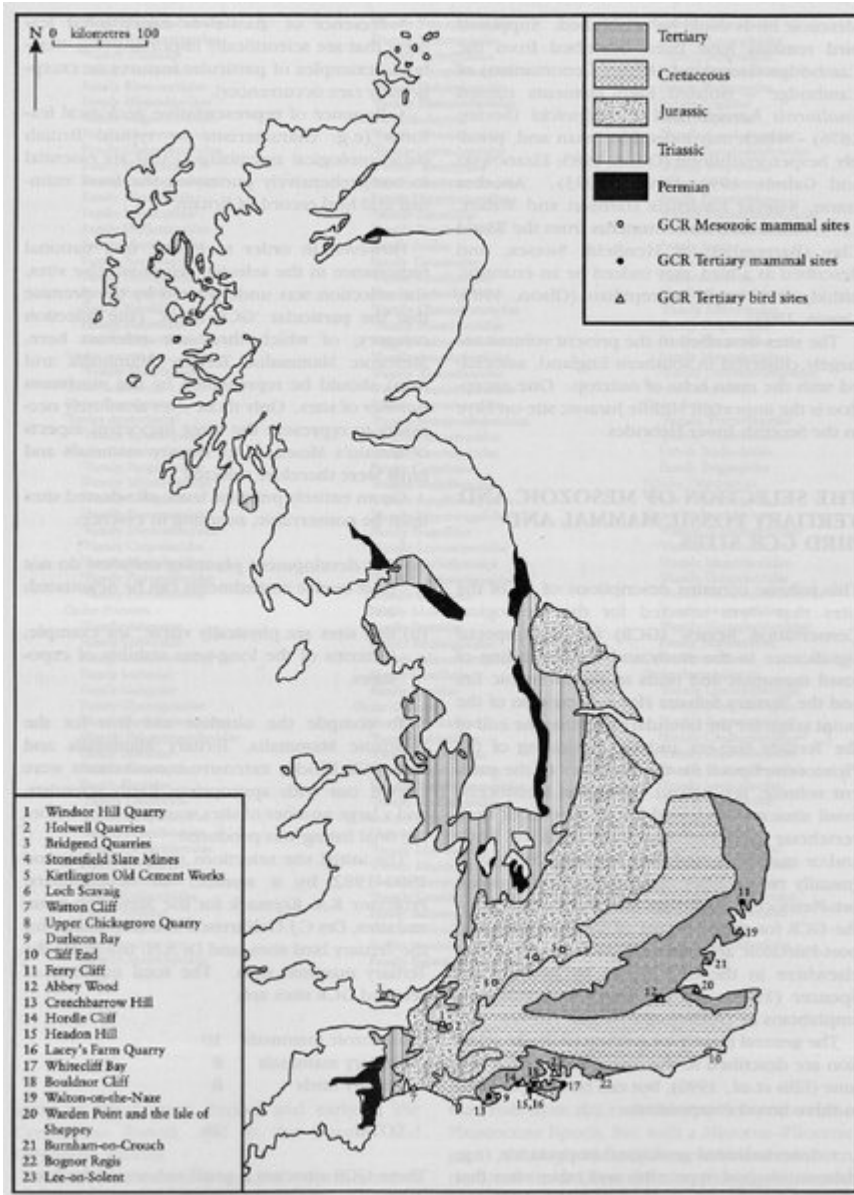
(Figure 1.14) (a) Map of Great Britain showing the distribution of the 23 discrete localities for Mesozoic and Tertiary GCR fossil bird and mammal sites, superimposed on the outcrop pattern of Permian, Triassic, Jurassic, Cretaceous, and Tertiary rocks in Great Britain. (After Benton and Spencer, 1995.)

Legend:
- Tertiary
- Cretaceous
- Jurassic
- Triassic
- Permian
- ○ GCR Mesozoic mammal sites
- ● GCR Tertiary mammal sites
- △ GCR Tertiary bird sites

1 Windsor Hill Quarry
2 Holwell Quarries
3 Bridgend Quarries
4 Stonesfield Slate Mines
5 Kirtlington Old Cement Works
6 Loch Scavaig
7 Watton Cliff
8 Upper Chicksgrove Quarry
9 Durlston Bay
10 Cliff End
11 Ferry Cliff
12 Abbey Wood
13 Creechbarrow Hill
14 Hordle Cliff
15 Headon Hill
16 Lacey's Farm Quarry
17 Whitecliff Bay
18 Bouldnor Cliff
19 Walton-on-the-Naze
20 Warden Point and the Isle of Sheppey
21 Burnham-on-Crouch
22 Bognor Regis
23 Lee-on-Solent