

Mesozoic and Tertiary Fossil Mammals and Birds of Great Britain

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Chapter 2

*British Mesozoic
fossil mammal GCR sites*

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INTRODUCTION: MESOZOIC STRATIGRAPHY AND SEDIMENTARY SETTING

The British Mesozoic record is represented by a full succession of Triassic, Jurassic and Cretaceous rocks. Fossil birds and mammals are found mainly in continental sediments, and such deposits, representing terrestrial and freshwater conditions, are known from the Late Triassic, the Jurassic and the Early Cretaceous sedimentary record. Rarer remains of terrestrial vertebrates such as dinosaurs have been reported from some marine units, such as the Lias (Early

Jurassic in age) and the Chalk (Late Cretaceous) deposits, but mammals and birds have not been found in the British representatives of those units. In addition to mammals, this chapter covers also the family of mammal-like reptiles: the Tritylodontidae.

The British Triassic System occurs over a wide area of the English Midlands (Figure 2.1) and has smaller outcrops in southern Wales, Devon, north-west England, Northern Ireland and Scotland. The sediments are dominantly terrestrial in origin, although limited marine and biogenic deposits are known (Warrington and Ivimey-Cook, 1992).

The Early and early Middle Triassic phase of deposition (Figure 2.2) was dominated by largely unfossiliferous clastic sediments of continental origin – the Sherwood Sandstone Group. By Late Triassic times, the dominantly terrestrial arenaceous facies deposited during Mid Triassic times were being replaced by shales and limestones of marine origin (Anderton *et al.*, 1979). These sediments, the Mercia Mudstone Group, are best known in southern Wales, south-west England and the Midlands. They are overlain by the Penarth Group, marine limestones and mudstones deposited by the Rhaetic transgression. At this time also, karst surfaces on the underlying Carboniferous limestones began to be infilled with Triassic deposits, and most of this phase of sedimentation took place in Late Triassic and Early Jurassic times (Warrington and Ivimey-Cook, 1992).

Sediments of Jurassic age crop out along a line roughly extending from Dorset to Yorkshire (Figure 2.1); more-localized developments of Jurassic lithologies occur in north-east Scotland and certain of the islands off the west coast of Scotland. The majority of the Jurassic rocks of Britain (Figure 2.2) were deposited under marine conditions. Abundant and diverse ammonite faunas have enabled detailed stratigraphical sequences to be constructed for these facies.

The marine transgression (Rhaetian) that marks the end of the Triassic Period continued into Early Jurassic (Lias) times, when Europe was dominated by a large, epicontinental shallow sea (Anderton *et al.*, 1979; Bradshaw *et al.*, 1992). Lias seas deposited thick repetitive sequences of limestones and dark anoxic mudstones, while at the same time the upland karsts of southern Wales and south-west England were occupied by early mammals as well as reptiles,

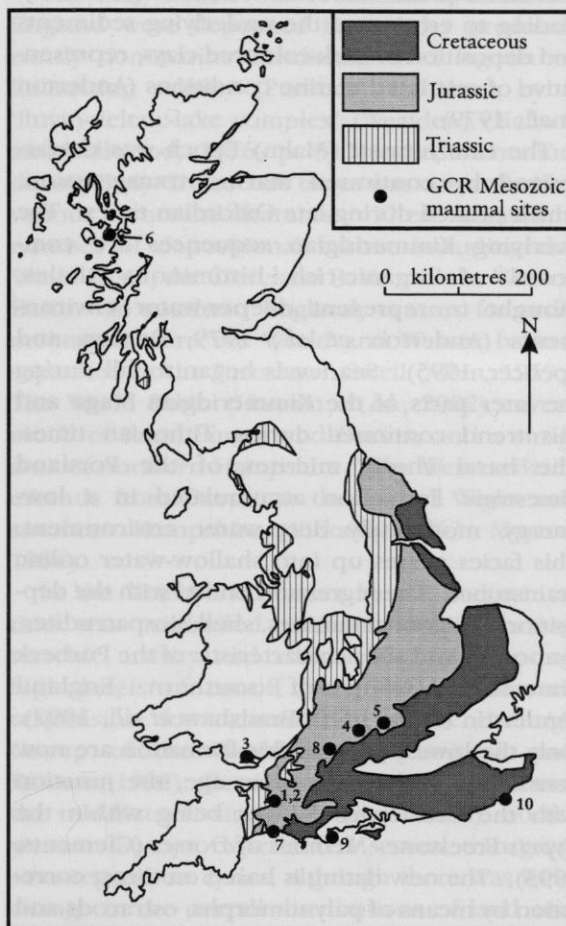


Figure 2.1 Map showing the distribution of Mesozoic rocks in Great Britain. GCR Mesozoic mammal sites:

- 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 Chicks Grove Quarry;
- 9 – Durlston Bay;
- 10 – Cliff End.

some of which were preserved in cave-fill sediments.

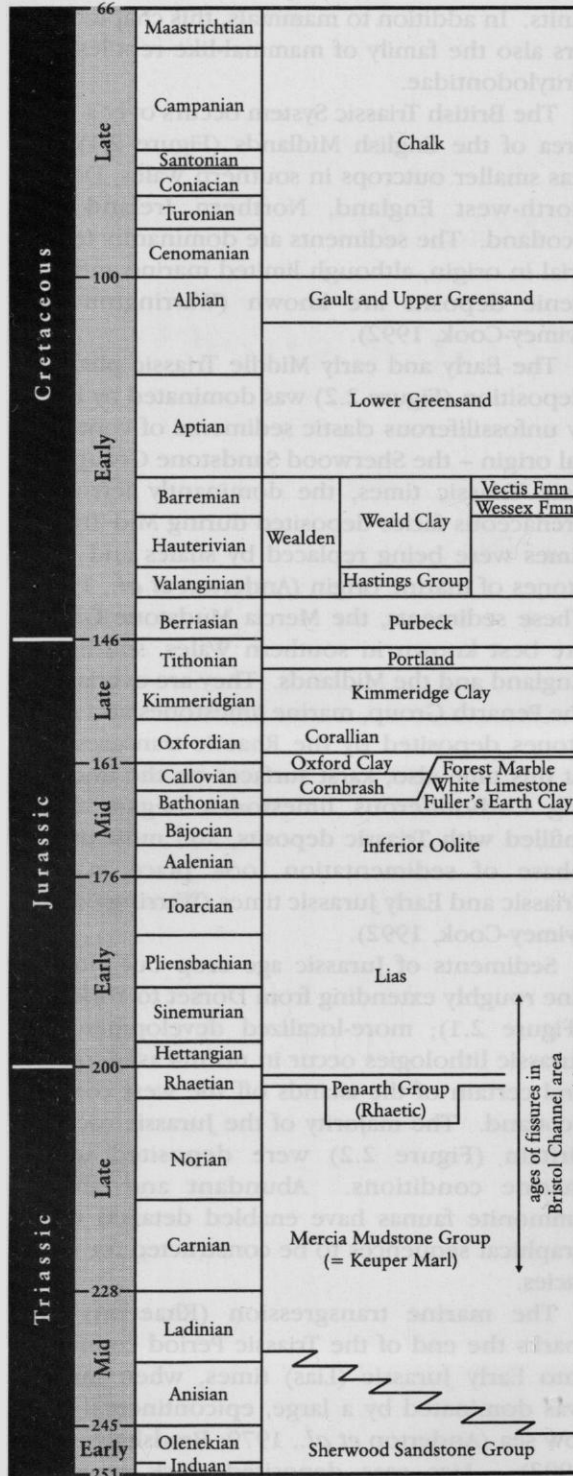


Figure 2.2 Summary of British Mesozoic stratigraphy, showing the major British lithostratigraphical units. (Modified from Benton and Spencer, 1995; and other sources, using the timescale of Gradstein *et al.*, 2004.)

The Mid Jurassic (Dogger) Epoch opened with a phase of regression (Anderton *et al.*, 1979). The Bathonian Stage, midway through Middle Jurassic times, was dominated by this large-scale regression (Bradshaw *et al.*, 1992): fluvio-deltaic environments spread across southern Britain, and lagoons, for example the Great Estuarine Group, developed in central England and western Scotland. The sediments of this age from southern England are composed of carbonates and minor clays. There is some evidence for subaerial exposure at this time (Benton and Spencer, 1995). A major transgression event affected much of Great Britain during the subsequent Callovian Stage (Figure 2.2), leading to erosion of the underlying sediments and deposition of dark-coloured clays, representative of restricted marine conditions (Anderton *et al.*, 1979).

The Late Jurassic (Malm) Epoch was characterized by continued marine transgression, which peaked during late Oxfordian times. The overlying Kimmeridgian sequences are composed of organic-rich bituminous shales, thought to represent deeper-water environments (Anderton *et al.*, 1979; Benton and Spencer, 1995). Sea levels began to fall during the later parts of the Kimmeridgian Stage and this trend continued during Tithonian times. The basal cherty micrites of the Portland Limestone Formation accumulated in a low-energy, moderately deep-water environment. This facies passes up into shallow-water oolitic grainstones. The regression ended with the deposition of lagoonal micrites, shell biosparrudites, evaporites and soils characteristic of the Purbeck Limestone Group of southern England (Anderton *et al.*, 1979; Bradshaw *et al.*, 1992). Only the lowest parts of this formation are now considered to be Jurassic in age, the junction with the Cretaceous System being within the *Cypris* Freestones Member of Dorset (Clements, 1993). The new dating is based on direct correlation by means of palynomorphs, ostracods and charophytes to the marine Tethyan sequences (Hunt, 1987; Allen and Wimbledon, 1991; Hoedemaeker, 1991; Feist *et al.*, 1995). Further support for this correlation has been provided by co-occurrence of palynomorphs and boreal ammonite zones in the southern North Sea (Abbink *et al.*, 2001).

The Cretaceous System of Great Britain represents two main phases of sedimentation (Figure 2.2). Firstly, there are the dominantly freshwater

Mammal evolution during the Mesozoic Era

Early Cretaceous (Berriasian–Barremian) Purbeck and Wealden deposits of the Weald, the Isle of Wight and Dorset, with marine strata restricted to north of the London Platform. These are followed by the widespread transgression and deposition of the marine Lower Greensand, Gault, Upper Greensand and Chalk deposits of late Early and Late Cretaceous (Aptian–Maastrichtian) age. Fossil mammals are known only from the Early Cretaceous continental facies. Cretaceous sediments crop out over south-eastern England and in a belt that runs roughly from Dorset to East Anglia, Lincolnshire and Yorkshire (Figure 2.1).

The Early Cretaceous sediments of southern England were deposited first under predominantly non-marine conditions in a lagoon of fluctuating salinity (Purbeck) and later by a 'fluvio-deltaic-lake complex' (Wealden) (Hallam and Sellwood, 1976, p. 317). Sedimentation during Early Cretaceous times was controlled by various structural features. These created a number of depositional basins, including the Weald Basin, the Cleveland Basin and the Wessex Basin. In southern England, centres for sedimentation were the Weald and Wessex basins, separated by the Portsdown Swell (Allen, 1959). The Weald Basin (Hansen *et al.*, 2002) covers much of Kent, Surrey and Sussex, and a small area of northern Hampshire. The Wessex Basin extends from Dorset to the Isle of Wight and southern Hampshire (Kirkaldy, 1963; Morter, 1984).

In the Weald and Wessex basins, sedimentation was controlled primarily by increasing tectonic activity and climatic factors, creating high levels of runoff from the land-masses responsible for accumulation of the Hastings Group of the Weald Basin (Hancock and Rawson, 1992). Between the late Berriasian and the mid-Hauterivian stages (Figure 2.2), north-western Europe experienced several transgression–regression cycles, although there was little change in the overall distributions of land and sea (Hancock and Rawson, 1992). During the early part of the Hauterivian Stage, tectonic activity that had centred on the landmasses surrounding the Weald Basin declined. This led to a reduction in overall sedimentation rates and a change from arenaceous to argillaceous facies, producing the Weald Clay Group of the Weald and the Wessex Formation of the Isle of Wight.

The beginning of the Aptian Stage (the penultimate stage of the Early Cretaceous Epoch) wit-

nessed a significant rise in sea level, leading to a return to marine environments in southern Britain. Marine sediments include 'greensands', glauconitic sandstones and clays, and then great thicknesses of chalk, a soft limestone composed largely of microfossil debris.

MAMMAL EVOLUTION DURING THE MESOZOIC ERA

Mammal evolution in Mesozoic times is reasonably well-known in parts (Lillegraven *et al.*, 1979; Kielan-Jaworowska, 1992; Kielan-Jaworowska *et al.*, 2000, 2004; Luo *et al.*, 2001, 2002; Benton, 2005). For a time, the oldest known mammals were from the Penarth Group (formerly the 'Rhaetic'; latest Triassic, c. 215–210 Ma) and earliest Jurassic in age, until a small tooth was found in ?Norian age (Late Triassic, ?223–215 Ma) deposits of Emborough fissure, Somerset (Fraser *et al.*, 1985). This has now been supplanted by a more complete mammal braincase, named *Adelobasileus*, from an even older horizon of Late Triassic age (late Carnian Stage, ?231–223 Ma) in Texas, USA (Lucas and Luo, 1993).

The tritylodonts, one of the reptilian groups most closely related to the mammals, are known from about ten genera from the Early and Mid Jurassic deposits of Europe, China and North America (Kemp, 1982; Hopson and Barghusen, 1986; Rowe, 1988; Luo and Sun, 1993). Tritylodonts were herbivores with skulls 80–220 mm long and unusual differentiated teeth. There were a number of sharp incisors and canines at the front of the jaws, a broad diastema, or gap, behind, and then four or five broad, square or rectangular molars forming parallel cheek-tooth rows. The massive multi-cusped molars are particularly characteristic fossils. Tritylodonts survived long after the extinction of most other mammal-like reptiles, and their record in Britain is particularly notable.

Ten or more groups of Mesozoic mammals are now known, but their relationships are hard to determine, partly because they are usually so incomplete and partly because the teeth, ear region and postcranial skeleton often provide conflicting characters (e.g. Rougier *et al.*, 1996). Relatively few complete skulls and skeletons are known. The best known basal mammals are the morganucodontids, represented by the fairly completely known *Morganucodon* from the

Early Jurassic fissures of south Wales and south-west England (Kermack *et al.*, 1973, 1981; Jenkins and Parrington, 1976). These shrew-sized animals were transitional forms, with both jaw joints but with mammalian-sized expanded braincase, teeth and skeleton. They were small insect-eaters and probably hunted at night and had the ability to forage in the trees (Jenkins and Parrington, 1976). Another group, the sinocondonts, are known only from China and are even more primitive than morganucodontids (Rougier *et al.*, 1996; Luo *et al.*, 2001, 2002).

During the Jurassic Period, a further seven or eight mammal groups radiated (Benton, 2005). The haramiyids, until recently known only from isolated teeth, largely from Britain, are now more fully known as a result of discoveries in the Triassic deposits of Greenland (Jenkins *et al.*, 1997). The docodonts are known mainly from isolated jaw bones and teeth from the Mid- and Late Jurassic deposits in Europe (Sigogneau-Russell, 2003a) and North America, and from one partial skeleton from Portugal (Martin and Nowotny in Martin and Krebs, 2000). The triconodonts, from the Mid Jurassic to the Late Cretaceous sedimentary record of Europe, North America and Asia, are known mainly from isolated teeth and jaw bones, although a complete skeleton has been found in China (Ji *et al.*, 1999). The group is characterized by the possession of three main cusps (hence 'triconodont') in a line on the shearing molar teeth. Once included in the triconodonts, the family Amphilestidae is of uncertain affinities and equally poorly represented except for two partial skeletons from the Early Cretaceous deposits of North America (Jenkins and Schaff, 1988).

Some other Late Jurassic and Early Cretaceous mammals show the first appearance of a different tooth pattern in which the three main cusps on the molars form a low triangular shape, a hint of the molar pattern developed in later therian mammals. They have been referred to a group called the Symmetrodonta. There have been lengthy and involved debates about whether the teeth of these Jurassic and Cretaceous forms indicate therian ancestry (e.g. Butler and MacIntyre, 1994) or are homoplastic (Rougier *et al.*, 1996; Luo *et al.*, 2001, 2002). Late Jurassic and Early Cretaceous members show such a pattern (where one cusp is offset to the side) and other incipient therian characters (Hu *et al.*, 1997). The current consensus is that the Symmetrodonta is polyphyletic. These late

members, belonging to the family Spalacotheriidae, are now classified as primitive members of the clade Trechnotheria. Cladotheres, such as the dryolestids from Europe and North America, show a zalambdodont molar pattern like modern tenrecs (placental lipotyphlans); although not specifically related to this group, other features, such as an angular process on the lower jaw, show that they are therians. Peramurids (another cladotherian family) are even closer to modern therians in having longitudinally twinned paracone and metacone on upper molars, and therians with tribosphenic molars are first known from the earliest Cretaceous rocks (Berriasian Stage) of England (Sigogneau-Russell and Ensom, 1994; Sigogneau-Russell *et al.*, 2001) and Morocco (Sigogneau-Russell, 1992).

One major Mesozoic mammal group, the multituberculates, had arisen by Mid-Jurassic times (Butler and Hooker, 2005) and lived successfully side-by-side with modern mammal groups until the end of the Eocene Epoch (Kielan-Jaworowska and Hurum, 2001). The multituberculates were successful plant-eaters, which were adapted for splitting seeds and extracting the contents with their specialized teeth. These consisted of long incisors and one or more enlarged blade-like lower premolars, rather like the modern Mountain Pygmy Possum of Australia. Multituberculates are known best from spectacular skeletons of Late Cretaceous age from Mongolia and the Paleocene sediments of North America. Originally thought to have been arboreal (Krause and Jenkins, 1983), they are now interpreted as being terrestrial (Kielan-Jaworowska and Gambaryan, 1994). Critically important jaw material of earlier forms comes from English Early Cretaceous deposits.

Further information about the relationships of the earliest mammals, and about the first representatives of the modern mammalian orders, is outlined in Chapter 1.

BRITISH MESOZOIC MAMMAL GCR SITES

Historically, the first Mesozoic mammals from anywhere in the world were reported from Middle Jurassic rocks of Oxfordshire (Broderip, 1827), an unexpected discovery at the time, because mammals were then thought to have been exclusively Cenozoic in age. The classic monographs on mammal fossils were produced

during the latter part of the 19th century and the early part of the 20th century. These monographs concentrated on sites with a long history of exploration, such as the Middle Jurassic sediments around Stonesfield, Oxfordshire, and the Early Cretaceous sediments of Swanage, Dorset. For many decades little was added to our knowledge of British mammalian sites. However, in the 1950s to 1970s several new sites were discovered. These include the Early Jurassic fissure-fill sites in Glamorgan (Evans and Kermack, 1994; see Figure 3.1), Middle Jurassic sites on Skye (Waldman and Savage, 1972), at Watton Cliff, Dorset (Freeman, 1976b, 1979), and at Kirtlington Old Cement Works, Oxfordshire (Freeman, 1976a, 1979), and Early Cretaceous sites such as Paddockhurst Park, West Sussex (Clemens and Lees, 1971). A renaissance in study through the 1990s and into the new millennium has brought to light many new specimens and re-interpretations of older material.

Further excavation at these sites, and continued prospecting in likely mammal-bearing lithologies, will enhance the existing British Mesozoic mammal collections and increase our understanding of lineages during this important phase of mammalian evolution.

Late Triassic mammal sites

Only one mammal-bearing site, Emborough Quarry, near Wells, Somerset (ST 623 505), has been described from the Triassic System of Great

Britain, although others are known from continental Europe (Sigogneau-Russell, 1983). This site preserved the first pre-Rhaetian therian mammal (Fraser *et al.*, 1985; Clemens, 1986). A full description of this site appears in Benton and Spencer (1995, pp. 90–2).

Emborough Quarry is no longer worked; it contains a fissure, where sediments have infilled a collapsed cave in the Mendip Hills. The sediments are generally poorly sorted, with locally derived boulders and coarse conglomerates held in a red marl matrix. Although Emborough Quarry fissure material, like many fissure deposit sites, contains no palynomorphs, relative dating has been achieved by lithostratigraphical comparisons with nearby outcrops (Fraser *et al.*, 1985), and is here assumed to be Norian in age (Clemens, 1986).

The vertebrate fauna from Emborough Quarry includes lepidosaurs, archosaurs, sphenodontids and the mammal *Kuebneotherium*. Two teeth have been described. The first is a lower molar, the second a premolar (Fraser *et al.*, 1985).

EARLY JURASSIC MAMMAL AND TRITYLODONT SITES

Mammal and tritylodont fossils of ‘Rhaeto-Liassic’ age are relatively well known and have been recovered from a number of localities in southern Africa, Europe, China, western North America and India (Clemens *et al.*, 1979). The

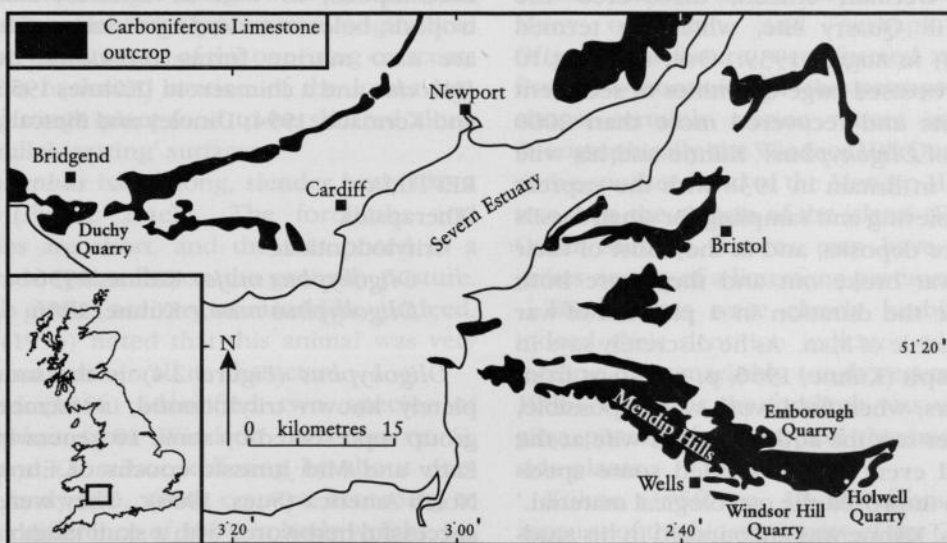


Figure 2.3 Map showing the distribution of Carboniferous Limestone and of tetrapod-bearing GCR fissure sites in south-west England. (After Fraser, 1985.)

British Early Jurassic fissure sites are among the most important in the world. These fissures were produced by solution in karst on upland regions that formed an archipelago in the Bristol Channel region during latest Triassic and Early Jurassic times (Robinson, 1957; Fraser, 1985; Figure 2.3). Mammals, tritylodonts and other small tetrapods occupied the islands and occasionally fell into the open fissures, where they were eventually covered by soils and other debris that washed in.

The three key British Early Jurassic fissure sites that have yielded remains of mammals and tritylodonts are selected as GCR sites:

1. Windsor Hill Quarry, Somerset (ST 615 452). Early Jurassic (Hettangian–Sinemurian) fissure fill.
2. Holwell Quarries, Somerset (ST 727 452). Early Jurassic (Hettangian–Sinemurian) fissure fill.
3. Bridgend Quarries, Glamorgan (SS 906 757). Early Jurassic (Hettangian–Sinemurian) fissure fill.

WINDSOR HILL QUARRY, SHEPTON MALLET, SOMERSET (ST 615 452)

Introduction

Windsor Hill Quarry is the type site for the mammal-like reptiles *Oligokyphus major* and *Oligokyphus minor* (Kühne, 1956). Walter Kühne, a German citizen, discovered the Windsor Hill Quarry site, which he termed 'Mendip 14', in August 1939. Over the next 10 years, he processed large quantities of sediment from the site and recovered more than 2000 specimens of *Oligokyphus*. Kühne and his wife had arrived in Britain in 1938 with the express purpose of sieving and sampling for small fossils in the fissure deposits, and in the midst of their work the war broke out and they were both interned for the duration in a prisoner-of-war camp on the Isle of Man. As he discretely says in his monograph (Kühne, 1956, p. 4), 'Apart from the war years, when field work was impossible, each summer saw the author and his wife at the locality, and every season yielded some specimens which improved the osteological material.' Nonetheless, Kühne was encouraged in his studies during his internment years and was enabled to finish the work after the war.

Description

Kühne (1956, pp. 5–6) noted that the *Oligokyphus* bones came from a single fissure that had a strike oriented East–West. 'The fissure is only one foot wide or less and is exposed for about 50 yards. It was fortunate that the outcrop of the fissure was so near the road that quarrying had to stop...'

The fissure was filled with light-brown, pebbly, iron-rich sandy limestone showing faint signs of lamination. The pebbles in the fissure were a mixture mainly of Carboniferous chert and limestone, with rarer silica and phosphatized Lias clasts. The *Oligokyphus* bones ranged in size up to 60 mm, and 'as many as 200 specimens per cubic foot' were recovered in some places. The bones showed signs of abrasion and had evidently been washed into the fissure from another site where the animals died.

The site preserved a mixture of reworked Penarth Group ('Rhaetic') taxa as well as in-situ Hettangian marine fishes (Dineley and Metcalf, 1999). For example, about half the brachiopods were reworked from 'Rhaeto-Liasic' sediments, and the others apparently were contemporaneous. The ammonites (*Arnioceras* sp., *Promicroceras* sp.) indicate a Sinemurian age.

Fauna

Taxa present at Windsor Hill Quarry include marine invertebrates, fishes and the tritylodonts. Marine invertebrates include some 15 taxa of brachiopods, as well as bivalves, small gastropods, belemnites and ammonites. The fishes are also marine forms: *Lissodus*, *Acrodus*, *Hybodus* and a chimaeroid (Kühne, 1956; Evans and Kermack, 1994; Dineley and Metcalf, 1999).

REPTILIA

'Therapsida'

Tritylodontidae

Oligokyphus major Kühne, 1956

Oligokyphus minor Kühne, 1956

Oligokyphus (Figure 2.4) is the most completely known tritylodontid, a member of a group represented by some 10 genera from the Early and Mid Jurassic epochs of Europe and North America (Sues, 1986). They were highly successful herbivores with a skull length ranging from 80 to 220 mm.

Oligokyphus has the typical superficially

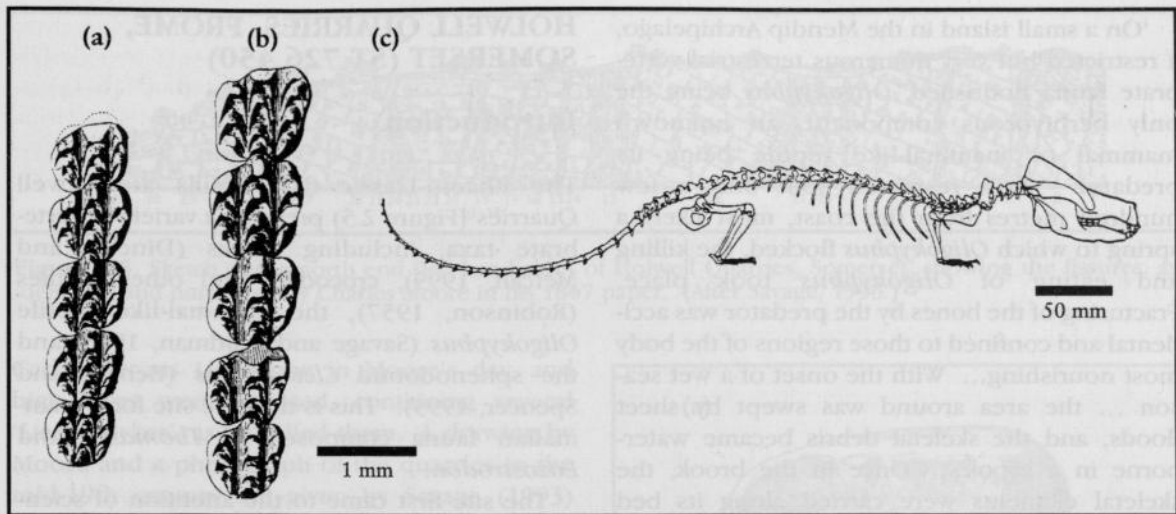


Figure 2.4 Specimens of the tritylodont *Oligokyphus* from the Early Jurassic deposits of Windsor Hill Quarry, Somerset: (a) and (b) upper cheek dentitions of *Oligokyphus minor* and *O. major* respectively (anterior is to the bottom of the diagram); (c) skeletal reconstruction of *Oligokyphus*. (Based on Kühne, 1956.)

rodent-like tritylodontid skull, with a deep lower jaw and a high sagittal crest, indicating powerful jaw muscles that plastered the outside of the lower jaw and the side of the skull to the crest. The dentition is highly specialized: elongate incisor teeth at the front and four to six massive cheek teeth in straight rows (Figure 2.4a, b). The upper cheek teeth all bear three longitudinal rows of crescent-shaped cusps, whereas the lower cheek teeth bear two rows. When the jaws close, the two lower rows cut into grooves between the three upper rows. The tight arrangement of ridges and grooves restricted the jaw movement of *Oligokyphus* to a longitudinal one. The orientations of the opposing crescents indicate a backward motion of the lower jaw, allowing tough plant food to be sheared along four parallel 'grating' surfaces.

Oligokyphus had a long, slender body like a weasel (Figure 2.4c). The forelimbs and hindlimbs are short, and the feet posed in a plantigrade (palm flat on the ground) posture. The limb girdles are very mammal-like. Indeed, Kühne (1956) noted that this animal was very nearly a mammal in all its characters.

Kühne (1956) identified two species of *Oligokyphus* from Windsor Hill Quarry, *O. major* and *O. minor*, differing by about one-third in body size, which equates, according to him, to a difference of 100% in body weight, i.e. *O. minor* weighed half as much as *O. major*. Kühne (1956, p. 98) noted that these genuinely

might be two different species, or they simply might be males and females of a single species.

Interpretation

The fissures from Windsor Hill Quarry are classified as Neptunian dykes: they were formed below sea level and have been infilled with a sediment containing a highly variable invertebrate and vertebrate fauna. The mode of formation of the Windsor Hill Quarry fissure, and indeed the other fissures to be seen elsewhere on the Mendip Hills, is debated (Simms, 1990). Many of them, and perhaps also the *Oligokyphus* fissure, were formed as solutional fissures – conduits for the passage of waters, almost certainly marine waters in this case. (Geographically, the Windsor Hill Quarry site lies at the southern end of the Mendip Hills, at what was then the margin of the island (Figure 2.1).) Other Mendip fissures may have formed as grikes on top of a limestone pavement.

Tritylodonts were clearly herbivores, and indeed their dentition indicates adaptation to feeding on remarkably tough vegetation (Sues, 1986). Perhaps the forelimb was used in digging, possibly for roots and rhizomes of water-side plants.

Kühne (1956, pp. 10–18) offers a detailed account of the biostratigraphy of the *Oligokyphus* remains. He summarizes his conclusions graphically, as follows:

British Mesozoic fossil mammal GCR sites

'On a small island in the Mendip Archipelago, a restricted but very numerous terrestrial vertebrate fauna flourished, *Oligokyphus* being the only herbivorous component, an unknown mammal or mammal-like reptile being its predator. At a restricted spot only a few hundred metres from the coast, most likely a spring to which *Oligokyphus* flocked, the killing and eating of *Oligokyphus* took place. Fracturing of the bones by the predator was accidental and confined to those regions of the body most nourishing... With the onset of a wet season ... the area around was swept by sheet floods, and the skeletal debris became waterborne in a brook... Once in the brook, the skeletal elements were carried along its bed right into the sea. Into the open fissure in the sea floor there would fall mainly heavy skeletal elements, the majority of the small and light elements, as well as small debris of bone, traversed the fissure and passed out to sea to be dispersed by currents.'

Comparison with other localities

The Windsor Hill Quarry site is most comparable with the Holwell Quarries GCR site in terms of age and sedimentary setting. No other site in the region yields *Oligokyphus* in such quantities, however, and indeed no other site presents such a monospecific assemblage. *Oligokyphus* also has been reported from Pant Quarry in South Glamorgan (SS 896 760) (part of the Bridgend Quarries GCR site), in association with the mammals *Thomasia*, *Kuehneotherium* and *Morganucodon* (Benton and Spencer, 1995, p. 82). The genus *Oligokyphus* was not established for the Windsor Hill Quarry material but for some teeth from a Rhaeto-Liassic bone bed in Baden-Württemberg, south-west Germany.

Conclusions

Windsor Hill Quarry has produced some of the best tritylodontid specimens in the world. The abundant specimens of *Oligokyphus* described by Walter Kühne in 1956 provided the first detailed knowledge of this extraordinary group of mammal-like reptiles. The tritylodontids are probably the closest reptilian relatives of the mammals, and yet specimens are rare and usually fragmentary. Understanding of *Oligokyphus* gave a key to understanding the origin of mammals.

HOLWELL QUARRIES, FROME, SOMERSET (ST 726 450)

Introduction

The Rhaeto-Liassic fissure fills at Holwell Quarries (Figure 2.5) preserve a variety of vertebrate taxa, including sharks (Dineley and Metcalf, 1999), crocodiles and other reptiles (Robinson, 1957), the mammal-like reptile *Oligokyphus* (Savage and Waldman, 1966) and the sphenodontid *Clevosaurus* (Benton and Spencer, 1995). This is the type site for a mammalian fauna composed of *Thomasia* and *Eozostrodon*.

The site first came to the attention of scientists in the middle of the 19th century, when Charles Moore discovered the remains of extinct mammals. Moore began work at Holwell Quarries in 1855 or 1856, and he was perhaps the first palaeontologist ever to use a systematic campaign of sieving and washing sediment samples to recover microvertebrate remains (Savage, 1993). Moore presented his initial results to the meeting of the British Association for the Advancement of Science in 1858, noting finds of fishes and reptiles. He also reported rare mammal teeth similar to *Microlestes antiquus* recorded from the Rhaetic of Germany by Plieninger in 1847. Moore continued his sieving campaign at Holwell Quarries, recovering in total nearly a million individual fossils, including over 45 000 teeth of *Acrodus* and 29 mammalian teeth. The results of all this work were eventually presented in a lengthy paper to the Geological Society of London (Moore, 1867). Owen (1871) and Simpson (1928) provided formal descriptions of the *Microlestes* teeth.

In 1939, Walter Kühne visited Holwell Quarries and collected two tonnes of sediment, which he washed and sieved, extracting 20 mammalian teeth. He worked a different fissure to that studied by Moore, as the earlier fissures had since been quarried away. After this work, Kühne prospected around the Mendips and discovered the new site of Windsor Hill Quarry (see GCR site report). Kühne (1946, 1949a) described his finds of mammal teeth from Holwell Quarries, and Parrington (1941, 1946) provided additional information.

Description

Holwell Quarries were actively worked for the

Holwell Quarries

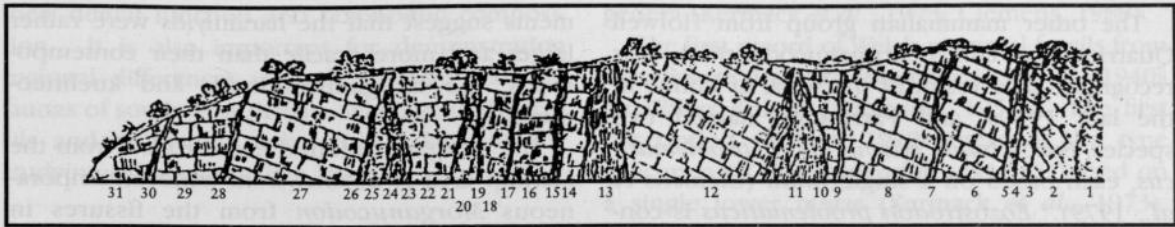


Figure 2.5 Sketch of the north end (left-hand side) of Holwell Quarries, Somerset, showing the fissures, as identified and numbered by Charles Moore in his 1867 paper. (After Savage, 1993.)

Carboniferous Limestone in Moore's day, and high faces were exposed, containing several 'Liassic dykes', as he called them. A drawing by Moore and a photograph of the quarries in the mid-19th century are given by Savage (1993) (Figure 2.5). However, Moore (1867) clearly understood that the 'Liassic dykes' at Holwell Quarries were fissures filled with sediment. He realized that in early Mesozoic times there were a number of islands in the Bristol Channel region made from Carboniferous limestone and that small reptiles and mammals lived on the islands. The upland regions of the islands were fissured as limestone pavements, and soils, debris and bones were washed into the fissures.

Fauna

Robinson (1957) listed the fauna from Holwell Quarries as consisting of five named species of mammal, as well as unnamed mammalian remains, 'unidentified fragments' of reptiles and 'a few specimens' of placodont teeth and crocodilian teeth; taxonomic revisions have reduced the accepted number of mammals to three.

REPTILIA

'Therapsida'

Tritylodontidae

Oligokyphus sp.

MAMMALIA

Haramiyidae

Thomasia moorei (Owen, 1871)

Thomasia antiqua (Plieninger, 1847)

Morganucodontidae

Eozostrodon parvus Parrington, 1941

Moore (1867) identified most of the mammal teeth from Holwell Quarries as belonging to the genus *Microlestes*, known already from the 'Rhaetic' deposits of Germany. In his formal description of the 29 mammalian teeth collected by Moore, Owen (1871) accepted this identifica-

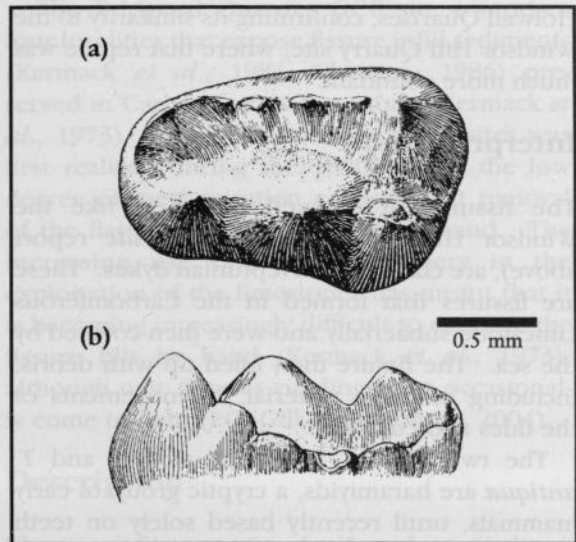


Figure 2.6 Upper molar of the haramiyid mammal *Thomasia moorei* from the Early Jurassic fissure filling of Holwell Quarries, Somerset, in crown (a) and internal (b) views. (From Simpson, 1928.)

tion and named the teeth *Microlestes moorei*. Simpson (1928), in his review of British Mesozoic mammals, considered that there were in fact three taxa present, and he named two additional species, *Microcleptes fissurae* and *Thomasia anglica*. The name *Microlestes* derives from the Greek for 'little thief', but it was found to have been given earlier to a beetle, so it was changed to *Microcleptes*, but that too was found to be pre-occupied, so eventually it was changed to *Haramiya*, deriving from Arabic word with the same meaning (Simpson, 1947). More recently, from a study of the occlusal relationships of haramiyid teeth, Butler and MacIntyre (1994) have shown that *Haramiya* represents upper teeth and *Thomasia* lower teeth of the same taxon, the prior name being *Thomasia*. Two different size groups at Holwell Quarries were recognized as different species of *Thomasia*.

The other mammalian group from Holwell Quarries, the family Morganucodontidae, was recognized as a result of the work of Kühne in the late 1930s, and Parrington named two species, *Eozostrodon parvus* and *E. problematicus*, each based on a single tooth (Clemens *et al.*, 1979). *Eozostrodon problematicus* is considered to be a junior synonym of *E. parvus* (Parrington, 1978; Clemens, 1979).

Savage and Waldman (1966) noted isolated remains of the tritylodont *Oligokyphus* from Holwell Quarries, confirming its similarity to the Windsor Hill Quarry site, where that reptile was much more abundant.

Interpretation

The fissures at Holwell Quarries, like the Windsor Hill Quarry fissure (see site report above), are classified as Neptunian dykes. These are fissures that formed in the Carboniferous Limestone subaerially and were then covered by the sea. The fissure then filled up with debris, including biogenic material, by movements of the tides and currents.

The two species *Thomasia moorei* and *T. antiqua* are haramiyids, a cryptic group of early mammals, until recently based solely on teeth from England, France, Switzerland, Belgium and Germany. Such limited fossil evidence of course led to wild speculation about the role of these mammals. Their great age implied that they were important in mammalian evolution, and they have often been allied with the multituberculates. New finds in Greenland now show more about the anatomy and affinities of the group (Jenkins *et al.*, 1997). These new finds, from Late Triassic sediments of East Greenland, include maxillae and dentaries (tooth-bearing elements), as well as teeth (the only elements known before), together with isolated postcranial remains. These specimens confirm the tooth positions and orientations postulated when only isolated teeth were known (Butler and MacIntyre, 1994). Mastication was effected differently from the contemporaneous morganucodontids and kuehneotheriids, but like the multituberculates the lower jaw moved posteriorly during occlusion. Unlike multituberculates, however, where the main shearing is horizontal, in haramiyids shearing took place as the opposing cusps entered and left their receiving basins, with less intervening horizontal movement (Butler, 2000). The postcranial ele-

ments suggest that the haramiyids were rather larger and more gracile than their contemporaries, the morganucodontids and kuehneotheriids.

The morganucodontid *Eozostrodon* from the Mendip area is distinct from penecontemporaneous *Morganucodon* from the fissures in southern Wales (Clemens, 1979), which is a primitive non-therian mammal – a small insect-eating form. The morganucodontids fall very low on recent cladograms of mammalian relationships (e.g. Kemp, 1982; Rowe, 1988, 1993; Wible *et al.*, 1995; Luo *et al.*, 2001, 2002). The material from Holwell Quarries is very incomplete compared with more complete specimens of *Morganucodon* from southern Wales and of its relative *Megazostrodon* from Lesotho.

Comparison with other localities

This site is of a similar age to the Windsor Hill Quarry fissure fill from nearby in the Mendip Hills and the Bridgend Quarries fissures in southern Wales. The haramiyids are well represented at Holwell Quarries by dental material, although the new discoveries in Greenland (Jenkins *et al.*, 1997) are of more complete haramiyid remains. However, some dental features of the Greenland taxon appear atypical of haramiyids (Kermack *et al.*, 1998). Thus, the importance of the Holwell Quarries assemblage is undiminished. The isolated Holwell Quarries teeth are most comparable with material from Rhaetic bone beds in south-west Germany and Switzerland (Clemens and Kielan-Jaworowska, 1979; Clemens, 1980). Morganucodontids are better known from the Bridgend Quarries, but the genus there is different. The find of isolated *Oligokyphus* remains (Savage and Waldman, 1966) confirms a certain similarity with the Windsor Hill Quarry site.

Conclusions

Holwell Quarries preserve one of the most important Mesozoic mammal faunas from Britain. Species present include *Thomasia moorei*, *T. antiqua* and *Eozostrodon parvus*. The type specimens of *T. moorei* and of *E. parvus* came from Holwell Quarries, as did the species now considered junior synonyms of all three species in the fauna. It is thus a critically important site for haramiyids, forming the basis for the first comprehensive understanding of

their dental function and taxonomic composition. It is also important for demonstrating regional differences in Early Jurassic mammal faunas of south-west Britain. The age of the fossils and sediments makes this a key site for studying early mammalian faunas.

BRIDGEND QUARRIES, GLAMORGAN (SS 895 760, SS 899 765, SS 902 768, SS 906 757)

Introduction

The Glamorgan area has a selection of early Jurassic fissure infills preserved in Triassic karstic features in Carboniferous limestones (Figure 2.7). The fissure sediments have preserved a range of taxa, including sphenodonts and mammals (Benton and Spencer, 1995). Four quarries – Ewenny Quarry (SS 902 768), Duchy Quarry (SS 906 757), Pont Alun (or Pontalun or Litalun) Quarry (SS 899 765) and Pant Quarry (SS 895 760) – have produced four mammalian

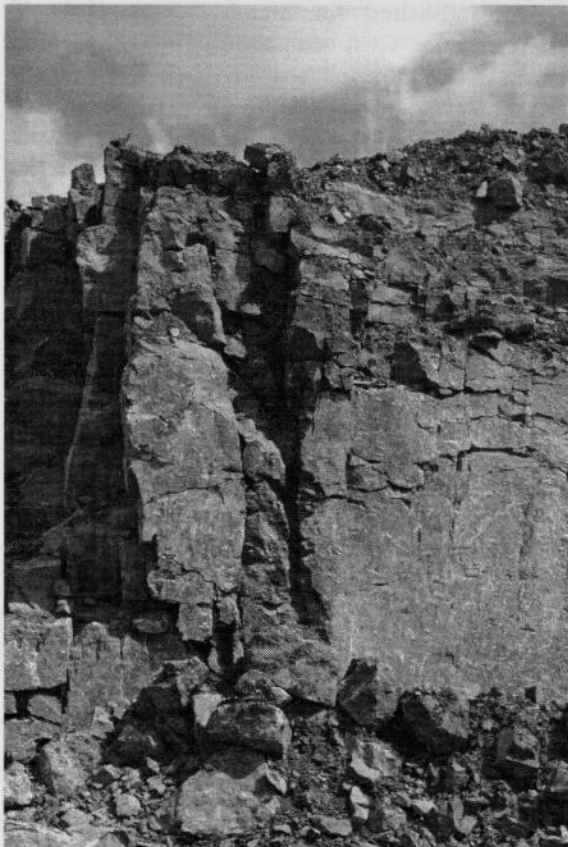


Figure 2.7 Bridgend Quarries GCR site, Glamorgan. Example of an Early Jurassic fissure fill in the Carboniferous Limestone. (Photo: W.A. Wimbledon.)

genera (Kermack *et al.*, 1973; Clemens, 1986).

The first record of Welsh mammal fossils from cave fissure deposits was made in the late 1940s by Walter Kühne (Robinson, 1957). The first description (Kühne, 1949b) was of the type specimen of *Morganucodon watsoni*, based on a single lower molar (Kermack *et al.*, 1973). Since then many more specimens have been recovered, thanks to extensive collecting in the 1950s, 1960s and 1970s by Kenneth Kermack, Frances Mussett and Pat Lees.

The Bridgend Quarries GCR site comprises four localities that expose fissure infill sediments (Kermack *et al.*, 1981; Clemens, 1986) preserved in Carboniferous Limestone (Kermack *et al.*, 1973). The importance of these sites was first realized during the 1950s, when the low degree of mechanization ensured that removal of the fissure-fill sediments was by hand. The increasing use of heavy machinery in the exploitation of the limestones has meant that it is becoming increasingly difficult to excavate the fissure fills by hand (Kermack *et al.*, 1973), although new fissures yielding bone occasionally come to light (P.G. Gill, pers. comm., 2004).

Description

The cave fissures are developed in Carboniferous Limestone. The fissures take the form of narrow slots that follow the joint planes and are thought to represent immature solution features (Robinson, 1971). These slots are up to 1.0 m wide but are generally somewhat narrower (Kermack *et al.*, 1973; Evans and Kermack, 1994).

The sediments infilling the caverns and fissures range in composition from soft plastic clays to hard marls. A variety of sediment colours also have been recorded from the sites, including red, green, yellow and dark grey. Haematite grains and pebbles and plant (*Hirmeriella muensteri*) remains are common (Robinson, 1971; Kermack *et al.*, 1973; Evans and Kermack, 1994). The bone material ranges in colour from white to dark grey and brown, although white bone in a red matrix is most common. There is no evidence to suggest that the bones were reworked (Evans and Kermack, 1994).

Unlike many fissure-fill sites, the Bridgend Quarries sediments have been dated – on the basis of *Hirmeriella (Cheirolepis)* spores at Duchy, Pont Alun and Pant quarries – as

British Mesozoic fossil mammal GCR sites

Hettangian–Sinemurian in age (Evans and Kermack, 1994).

Fauna

The majority of the specimens preserved in the Bridgend Quarries fissures are attributable to the lepidosaur *Gephyrosaurus bridensis*, described by Evans (1980, 1981), and the remainder are mammalian. Fraser (1985) also noted 'unidentified archosaurs' from Pont Alun Quarry. *Oligokyphus*, *Thomasia*, archosaurs and sphenodontians have also been recorded from Pant quarry (Evans and Kermack, 1994).

MAMMALIA

Morganucodontidae

Morganucodon watsoni Kühne, 1949b

?*Morganucodon* sp.

Kuehneotheriidae

Kuehneotherium praecursoris Kermack, Kermack, and Mussett, 1968

?Kuehneotheriidae

"*Kubneon duchyense* Kretzoi, 1960"

'Haramiyida'

Haramiyidae

Thomasia sp.

The dominant mammal is *Morganucodon watsoni* (Evans and Kermack, 1994), a shrew-sized insectivore with a skull 26 mm long (Figure 2.8). *Morganucodon* has a lower jaw composed mainly of the dentary bone; however, the jaw joint comprises contacts of both the dentary with the squamosal and the articular with the quadrate, the latter also functioning as a 'middle' ear. It also retained several remnants of other reptilian jaw bones, and in these respects it is more primitive than any modern mammal (Kermack *et al.*, 1973, 1981). The cheek teeth are divided into molars and premolars, a fully mammalian character, and tooth replacement appears to have been fully mammalian also, with a milk set and an adult set (reptiles replace their teeth many more times). The cheek teeth of *Morganucodon* occlude, and jaw movement was more complex than in advanced cynodont reptiles: it was rather triangular, with a certain amount of back-and-forwards movement, but a sideways component also. The skeleton of *Morganucodon* is incompletely known, but details of this portion of the anatomy are complemented by its relative *Megazostrodon* from Lesotho (Jenkins and Parrington, 1976).

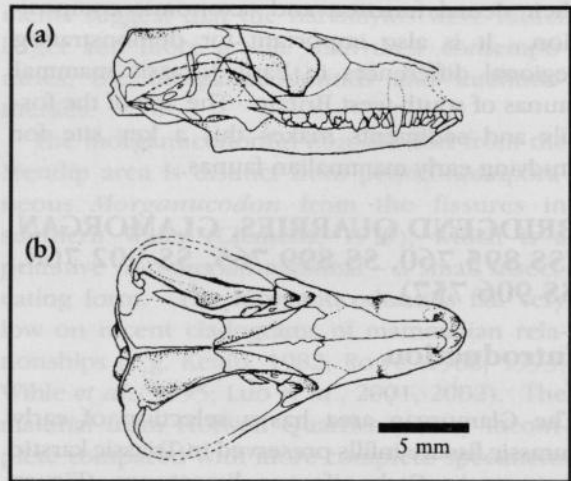


Figure 2.8 The skull of the basal mammal *Morganucodon* in lateral (a) and dorsal (b) views. (After Kermack *et al.*, 1981.)

There has been some confusion concerning the use of the names *Morganucodon* Kühne, 1949b, established for material from the Bridgend Quarries, and *Eozostrodon* Parrington, 1941, established for material from Holwell Quarries (see GCR site report). The former name was championed by Kermack and the latter by Parrington. Clemens (1979), in an attempt to attain nomenclatural stability, showed that the two were different at least at species level. He recommended that the name *Eozostrodon parvus* should be used only for the poorly known morganucodontid material from Holwell Quarries, and the name *Morganucodon* should be used for the more complete material from South Wales.

Kuehneotherium praecursoris is represented by isolated teeth and rare jaw fragments (Kermack *et al.*, 1968; Gill, 1974). *Kuehneotherium* was also a small insectivore, equipped with delicate three-cusped teeth. The occurrence of isolated teeth is explained by the fragile bones and tapering roots: the teeth fall out of the jaws easily, and once the teeth have been lost the jaw quickly fragments (Evans and Kermack, 1994). It is possible that the specimens of *Kuehneotherium* from Pant Quarry and Pont Alun Quarry are specifically different (Evans and Kermack, 1994).

The first tooth of a new group was noted by Kühne (1950) from Duchy Quarry as 'Duchy 33', identified at the time as a symmetrodont, (Cassiliano and Clemens, 1979). It was named *Kubneon duchyense* by Kretzoi (1960). Kermack

et al. (1968), in describing *Kuebneotherium*, noted that their new genus was distinct from *Kubneon* but that the original tooth on which the latter had been based was probably an upper not a lower molar and had since been lost. Their recommendation that *Kubneon duchyense* be considered a *nomen vanum* is adopted here (P.G. Gill pers. comm., 2004).

The record of *Thomasia* is based on one tooth fragment from Pant (Kermack *et al.*, 1981, p. 135).

Interpretation

Before the transgression of the Rhaetic Sea, the Vale of Glamorgan was an area of low-lying land with ephemeral freshwater playas. The Carboniferous Limestone formed low hills. The Rhaetic transgression flooded this low-lying plain, leaving the hills as small islands, including St Bride's Island south of Bridgend Quarries (Robinson, 1971; Kermack *et al.*, 1973; Simms, 1990). St Bride's Island was relatively small, with a maximum area of 20 km², and may have formed part of an archipelago. The palaeoclimate has been reconstructed as tropical/sub-tropical with heavy seasonal rains; the island lay at approximately 15°N latitude (Evans and Kermack, 1994). Continued subsidence eventually resulted in the complete submergence of the islands during the Sinemurian Stage (Kermack *et al.*, 1973).

Several theories have been put forward in order to account for the preservation of the vertebrate fossils in the Welsh fissures. The first suggests that the creatures were washed into the caves during periods of heavy rain. However, it is unlikely that this would so effectively concentrate the vertebrate remains. An alternative is that forest fires or flash floods killed large numbers of animals, which were washed into the fissures. These theories fail to account for the absence of invertebrates. Finally, the fossil assemblage may represent a predator accumulation. This hypothesis is supported by the patterns of bone damage and modification (for example, the tooth marks on the surfaces of some of the bones), the relative proportions of the bones preserved and the general small body size of the taxa represented (Evans and Kermack, 1994).

The two main mammal groups represented at Bridgend Quarries were once thought to document a major split in mammalian evolution, with

the morganucodontids documenting the first prototherians, a group represented today by the monotremes. *Kuebneotherium*, by contrast, has three-cusped teeth that have an offset central cusp, allowing uppers and lowers to interlock because of their 'reversed triangle' pattern in crown view. This cusp pattern was considered to represent the first stage in evolution of complex occlusion, such as is found in typical therians. Thus, *Kuebneotherium* was seen as the first therian mammal, that is, a distant ancestor of marsupials and placentals.

More recent work, however, using only derived characters and studying more of the anatomy than just teeth, has produced a more complex phylogeny (reviewed by Benton, 2005). Indeed, current cladograms (e.g. Rowe, 1988, 1993; Wible *et al.*, 1995; Luo *et al.*, 2001, 2002) place the morganucodontids as second-most basal mammal group, with *Kuebneotherium* as third most basal (see Chapter 1). The symmetrodonts, now recognized as polyphyletic occur scattered through the phylogenetic tree (Kielan-Jaworowska *et al.*, 2004).

Comparison with other localities

The faunas from the Bridgend Quarries are comparable in age to those preserved at Holwell Quarries and Windsor Hill Quarry. However, more taxa are represented, although there is little overlap between the faunas. This possibly reflects the increased opportunities for collecting provided by four quarries all within a small geographical area.

Morganucodon has also been described from the Rhaetic bone beds at Hallau, Kanton Schaffhausen, in Switzerland (Clemens, 1980). *Kuebneotherium* is known from Late Triassic sites at Emborough, Saint-Nicholas-de-Port, France (Godefroit and Sigogneau-Russell, 1999), Syren, Luxembourg (Godefroit *et al.*, 1998) and Jameson Land, East Greenland (Jenkins *et al.*, 1994).

Conclusions

The Late Triassic–Early Jurassic Welsh fissure-fill sediments provide incomparable evidence about early mammal evolution. *Morganucodon watsoni* and *Kuebneotherium praecursoris* are unique basal mammals (Clemens *et al.*, 1979). The good degree of preservation and relative abundance of the mammalian remains has

British Mesozoic fossil mammal GCR sites

allowed detailed reconstructions of significant parts of the anatomy of these Early Jurassic mammals, and *Morganucodon*, together with the African *Megazostrodon*, are the most completely known early mammal fossils in the world. This is a key site of undisputed international importance.

MIDDLE JURASSIC MAMMAL SITES

Fossil mammal sites of Middle Jurassic age are rare globally, although Great Britain has five well-documented sites of this age. Localities such as Stonesfield Slate Mines in Oxfordshire have been producing mammal fossils since the 19th century. Others, for example Kirtlington Old Cement Works, Oxfordshire, and Loch Scavaig, Skye, are more recent discoveries that have proved valuable sources of fossil materials and consequently have greatly increased our understanding of the evolutionary relationships of early mammals.

Most of Britain's Middle Jurassic mammal sites are limited to the sediments associated with the Bathonian marine regression, which were deposited under lagoonal, deltaic and swamp conditions (Evans and Milner, 1994). British Middle Jurassic mammal sites are listed below, county by county, based on published records.

DORSET: Watton Cliff (also known as 'West Cliff'), near West Bay (Bridport Harbour) (SY 451 908–SY 453 907; haramiyidan tooth and tritylodontid tooth; Forest Marble Formation; Ensom, 1977; Clemens *et al.*, 1979; Evans and Milner, 1994); see GCR site report below. In the vicinity of Bothenhampton (the tritylodontid *Stereognathus*; Forest Marble Formation: Ensom *et al.*, 1994).

GLOUCESTERSHIRE: Hornsleasow Quarry (also known as 'Snowhill Quarry'), near Cheltenham (SP 131 322; three orders of mammals, Docodonta, Eupantotheria and Multituberculata; clay lens in the Chipping Norton Limestone Formation; Metcalf *et al.*, 1992). Tarlton Clay Pit, near Cirencester (SO 970 001; one mammalian incisor, two fragments of molars, representing a docodontid and a triconodontid; Forest Marble Formation; Evans and Milner, 1994). Ready Token, near Cirencester (SP 100 050; one indeterminate mammalian incisor; Wychwood Beds, Forest Marble Formation; Evans and Milner, 1994).

OXFORDSHIRE: Woodeaton, near Oxford (SP 534 122; possible mammalian incisor; Hampen Marly Formation; Clemens *et al.*, 1979; Evans and Milner, 1994). Stonesfield Slate Mines, west of Woodstock (SP 387 171; *Amphilestes*, *Phascolotherium*, *Amphitherium*; Stonesfield Slate; Clemens *et al.*, 1979; Butler and Clemens, 2001); see GCR site report below. Kirtlington Old Cement Works (SP 494 199; see GCR site report for list; Freeman, 1979; Evans and Milner, 1994; Sigogneau-Russell, 2003a,b).

INNER HEBRIDES: Loch Scavaig, Skye and Lochalsh (NG 519 165; *Borealestes* and an unnamed 'pantothere'; Kilmaluag Formation; Evans and Milner, 1994; Waldman and Evans, 1994); see GCR site report below.

Of these, four are selected as GCR sites for fossil mammals:

1. Stonesfield Slate Mines, Oxfordshire (SP 387 171). Middle Jurassic (middle Bathonian) Stonesfield Slate facies, Taynton Limestone Formation.
2. Kirtlington Old Cement Works, Kirtlington, Oxfordshire (SP 494 199). Middle Jurassic (late Bathonian) White Limestone Formation to lower Cornbrash Formation.
3. Loch Scavaig, Skye and Lochalsh (NG 519 165). Middle Jurassic (late Bathonian) Kilmaluag Formation.
4. Watton Cliff, Dorset (SY 453 908). Middle Jurassic (late Bathonian) Forest Marble Formation.

STONESFIELD SLATE MINES, OXFORDSHIRE (SP 387 171)

Introduction

The Stonesfield Slate Mines have been a rich source of reptile and mammal vertebrate fossils since the mid-1700s (Clemens *et al.*, 1979; Benton and Spencer, 1995). To date, three mammalian taxa have been described from this site.

The predominantly sandy limestones mined in the Stonesfield Slate Mines area (Figure 2.9) have produced one of the most diverse terrestrial middle Bathonian (Middle Jurassic) vertebrate faunas known. The site has produced many hundreds of fossils that cover a range of taxa,

Stonesfield Slate Mines

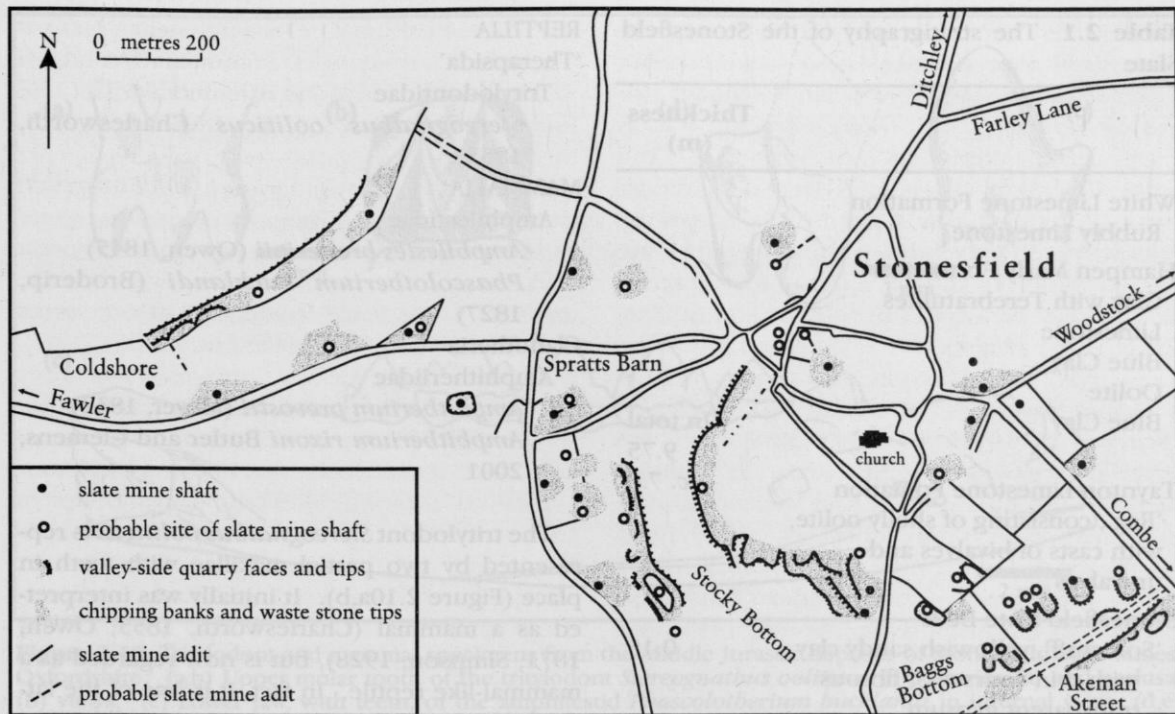


Figure 2.9 The Stonesfield Slate Mines. (Based on Aston, 1974; after Benton and Spencer, 1995.)

including dinosaurs, pterosaurs, mammal-like reptiles, turtles, crocodiles, ichthyosaurs, plesiosaurs and mammals (Benton and Spencer, 1995). The extant mines and accessible shafts have been designated an SSSI for stratigraphical and palaeontological reasons.

Stonesfield Slate has been mined at least since Roman times. Excavation of the slates from mines and small quarries continued until 1911 (Evans and Milner, 1994; Benton and Spencer, 1995). The sediments consist of a sequence of fine-grained calcarenites with shelly partings interbedded with thinly laminated, impersistent oolitic limestones (Boneham and Wyatt, 1993; Evans and Milner, 1994).

The first mammal fossil was discovered from Stonesfield Slate Mines in approximately 1764, although the significance of the material was not fully appreciated until subsequent study by Buckland some 50 years later (Buckland, 1824; Broderip, 1827; Simpson, 1928; Clemens *et al.*, 1979). Buckland's student, J.W. Broderip, had found two small mammal jaws at Stonesfield Slate Mines around 1812. He sold one to Buckland and mislaid the other, and the former eventually was described in 1828. This was the first published record of a Mesozoic mammal, and it created a sensation (see Chapter 1).

Description

Lithological and stratigraphical sections through the Stonesfield Slate have been recorded by a number of workers, for example Fitton (1836), Phillips (1871), H.B. Woodward (1894), Walford (1895, 1896, 1897), Richardson *et al.* (1946), McKerrow and Baker (1988) and Boneham and Wyatt (1993). The following description is based on Richardson *et al.* (1946, p. 30).

The Stonesfield Slate is a grey or pale-brown coloured calcareous sediment. It is generally well-laminated and fissile, with shelly partings. It contains silt- and sand-grade quartz grains. Impersistent laminae of oolitic limestone are common and are locally interbedded with fine-grained, fissile oolites (Boneham and Wyatt, 1993). A thin horizon of conglomerate sourced from the underlying Chipping Norton Limestone Formation occurs in the middle part of the section (Sellwood and McKerrow, 1974). The Stonesfield Slate has a limited distribution (within 1.5 km of Stonesfield village) and reaches a maximum thickness of 1.8 m (Aston, 1974).

Fauna

The fauna of the Stonesfield Slate is dominated

British Mesozoic fossil mammal GCR sites

Table 2.1 The stratigraphy of the Stonesfield Slate

	Thickness (m)
White Limestone Formation	
Rubbly Limestone	
Hampen Marly Formation	
Clay with Terebratulites	
Limestone	
Blue Clay	
Oolite	
Blue Clay	In total
	9.75
Taynton Limestone Formation	c. 7.6
'Rag', consisting of shelly oolite, with casts of bivalves and univalves	
Stonesfield Slate Beds	
'Soft stuff', yellowish sandy clay, with thin courses of fibrous transparent gypsum	0.15
'Upper Head', sand enveloping a course of spheroidal laminated calcareous gritstones which produce the slate. These are called 'Potlids' from their figure, and receive with the other slaty bed the name of 'Pendle' as characteristic of workable stone. The stone is partially oolitic and shelly, sometimes full of small fragmentary masses	0.45
'Manure' or 'Race', slaty friable rock	0.3
'Lower Head', sand and grit, including a course of spheroidal concretions of slate	0.45–0.6
'Bottom stuff', sandy and calcareous grit, with admixture of oolite grains	0.3
Chipping Norton Limestone Formation	

by marine taxa, for example fishes, bivalves, gastropods and rare ammonites, belemnites and corals. Terrestrial taxa are represented by reptiles, mammals, insects and plant remains, including conifers and ferns (Boneham and Wyatt, 1993; Benton and Spencer, 1995; Cleal and Rees, 2003).

REPTILIA
'Therapsida'
Tritylodontidae
<i>Stereognathus ooliticus</i> Charlesworth, 1855
MAMMALIA
Amphilestidae
<i>Amphilestes broderipii</i> (Owen, 1845)
<i>Phascolotherium bucklandi</i> (Broderip, 1827)
Cladotheria
Amphitheriidae
<i>Amphitherium prevostii</i> (Meyer, 1832)
<i>Amphitherium rixoni</i> Butler and Clemens, 2001

The tritylodont *Stereognathus ooliticus* is represented by two partial maxillae with teeth in place (Figure 2.10a,b). It initially was interpreted as a mammal (Charlesworth, 1855; Owen, 1871; Simpson, 1928), but is now regarded as a mammal-like reptile. In fact, it is one of the latest surviving tritylodontids, a group well-known from the Early Jurassic Windsor Hill Quarry site (see GCR site report).

All of the mammals recorded from the Stonesfield Slate were discovered before the publication of Simpson's (1928) review paper, and nothing has been reported since, probably because active mining of the Stonesfield Slate ceased at the beginning of the 20th century.

The amphilestids *Amphilestes* and *Phascolotherium* are known from small lower jaws (Figure 2.10c), the first two specimens found by Broderip around 1812 and later named by Owen. The 7–10 cheek teeth are similar in size along the length of the jaw and bear three sharp cusps. They differ from triconodonts, in which order they were once included, in having the central cusp larger than the other two. Since 1828, five additional small jaws have been collected (Simpson, 1928; Evans and Milner, 1994).

The records of *Amphitherium* from this locality, based on four lower jaw specimens (Simpson, 1928), are important as it is one of the earliest known occurrences of a cladotherian (i.e. stem therian but more derived than a symmetrodont). All specimens unequivocally identified as *Amphitherium* are from this site (Figure 2.10d, e). Originally named as a single species, *A. prevostii*, restudy of the four jaws has indicated that one (BMNH 36822) belongs to a distinct species called *A. rixoni* (Butler and Clemens, 2001). Unlike the more fragmentary specimens

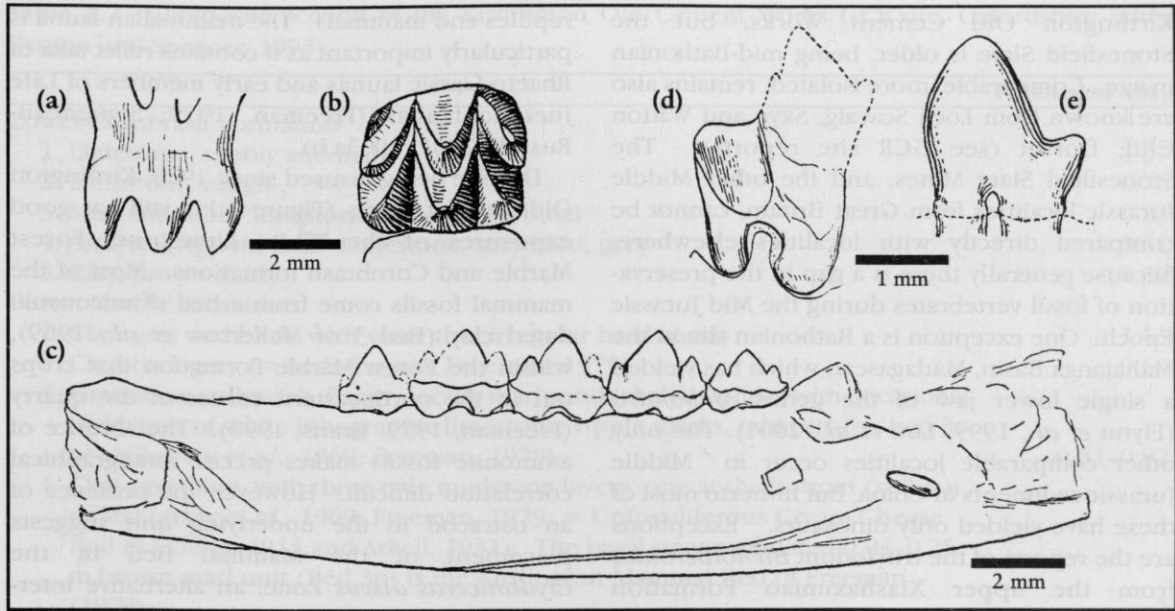


Figure 2.10 Tritylodont and mammal specimens from the Middle Jurassic deposits of Stonesfield Slate Mines, Oxfordshire. (a,b) Upper molar tooth of the tritylodont *Stereognathus ooliticus* in posterior (a) and occlusal (b) views. (c) Lower jaw, with teeth, of the amphilestid *Phascolotherium bucklandi* in internal view. (d,e) Cheek teeth of the amphitheriid *Amphitherium prevostii*; (d) broken right lower molar in external view; (e) left lower premolar 4 in external view. (Based on Owen, 1871; and Simpson, 1928.)

recovered by screenwashing techniques, these near-complete dentitions from Stonesfield Slate Mines are unique for the Bathonian Stage. *Amphitherium* was about the size of a modern shrew. The teeth indicate a diet of small invertebrates (Kraus, 1979).

Interpretation

The limited lateral extent of the Stonesfield Slate facies can be explained by the deposition of clastic sediments during transgression across a discontinuous hardground surface (Sellwood and McKerrow, 1974).

The fossils recovered from the Stonesfield Slate are indicative of shallow marine or coastal conditions. The presence of terrestrial taxa (insects, mammals and plant debris) is explained by the close proximity of the Anglo-Brabant landmass. These remains were probably washed into the sea during storm events, where they were quickly buried in sand bodies (Benton and Spencer, 1995). The diverse flora, comprising 25 morphospecies, is dominated by remains of araucariacean and cheirolepidiacean conifers, bennettitaleans, and leaves of the possible gymnosperm *Pelourdea* (Cleal and Rees, 2003). These mainly represent coastal vegetation,

including mangrove-like stands of *Ptilophyllum*, and conifers probably growing in lowland coastal habitats that were subjected to periodic water-stress.

The stratigraphical position of the Stonesfield Slate has been a source of controversy for many decades. The historical aspects of this debate have been reviewed by Benton and Spencer (1995). The most recent stratigraphical analysis of the position of the Stonesfield Slate, by Boneham and Wyatt (1993), reports that the slate facies was worked from three levels within the Taynton Limestone Formation: at the top, within, and at the base. This three-fold recurrent nature of the slate facies means that it cannot be regarded as a formal lithostratigraphical unit and therefore should be considered as an informal name for the laminated calcarenite beds that occur within the Taynton Limestone Formation. The Stonesfield Slate is no longer thought to form part of the Sharp's Hill Formation, although tilestone (slate) facies may occur.

Comparison with other localities

A similar, but wider, array of tritylodont and early mammal taxa has been reported from

Kirtlington Old Cement Works, but the Stonesfield Slate is older, being mid-Bathonian in age. Comparable, more isolated, remains also are known from Loch Scavaig, Skye and Watton Cliff, Dorset (see GCR site reports). The Stonesfield Slate Mines, and the other Middle Jurassic localities from Great Britain, cannot be compared directly with localities elsewhere, because generally there is a gap in the preservation of fossil vertebrates during the Mid Jurassic Epoch. One exception is a Bathonian site in the Mahajanga Basin, Madagascar, which has yielded a single lower jaw of the genus *Ambondro* (Flynn *et al.*, 1999; Luo *et al.*, 2001). The only other comparable localities occur in Middle Jurassic sediments in China, but hitherto most of these have yielded only dinosaurs. Exceptions are the reports of the tritylodont *Bienotheroides* from the upper Xiashaximiao Formation (Bathonian–Callovian stage; Benton, 1993) and the haramiyidan *Eleutherodon* from the Toutunhe Formation of Liuhuanguo (?Bathonian; Maisch *et al.*, 2005) of China.

Conclusions

The Stonesfield Slate Mines site is significant as a historical site, the location of the first reported Mesozoic mammal remains and the first site to yield tritylodont fossils. It also is important for continuing finds of mammal fossils at least into the 20th century and for its potential in the future on re-excavation. The Stonesfield Slate Mines site also is important for yielding a classic Middle Jurassic fauna of both reptiles and mammals that has strongly influenced our understanding of these groups since the earliest studies of vertebrate palaeontology. The Stonesfield Slate Mines helps fill an important worldwide gap in the fossil record of early mammals.

KIRTLINGTON OLD CEMENT WORKS, KIRTLINGTON, OXFORDSHIRE (SP 494 199)

Introduction

Kirtlington Old Cement Works quarry is one of the richest Middle Jurassic (late Bathonian) vertebrate sites in the world (Evans and Milner, 1994). The fauna is especially diverse and includes frogs, salamanders, lizards, turtles, crocodiles, pterosaurs, dinosaurs, mammal-like

reptiles and mammals. The mammalian fauna is particularly important as it contains relict taxa of Rhaeto-Liassic faunas and early members of Late Jurassic faunas (Freeman, 1979; Sigogneau-Russell, 2001, 2003a,b).

Despite being disused since 1929, Kirtlington Old Cement Works (Figure 2.11) still has good exposures of the White Limestone, Forest Marble and Cornbrash formations. Most of the mammal fossils come from a bed of unconsolidated clay (Bed 3 of McKerrow *et al.*, 1969), within the Forest Marble Formation that crops out in the north-eastern corner of the quarry (Freeman, 1979; Evans, 1990). The absence of ammonite fossils makes precise stratigraphical correlation difficult. However, the presence of an ostracod in the underlying unit suggests placement of the Mammal Bed in the *Clydoniceras discus* Zone; an alternative interpretation is that it belongs to the slightly older *Oxycerites aspidoides* Zone (Freeman, 1979).

Description

The sedimentary succession at Kirtlington Old Cement Works has been described by many authors, including Odling (1913), Arkell (1931), Douglas and Arkell (1932) and Richardson *et al.* (1946). The following section (Table 2.2) is taken from Benton and Spencer (1995, p. 157).

The section described here is a composite based on exposures from around the quarry and therefore does not accurately represent the large amount of lateral variation (Benton and Spencer, 1995).

The Mammal Bed at Kirtlington Old Cement Works consists of an unconsolidated brown marl. It occurs as an impersistent lens in the north-eastern corner of the quarry. The lens is of variable thickness, ranging from 40 to 250 mm, thinning at the edges. The sediments beneath the Mammal Bed are composed of a deep yellow, friable oolitic limestone that grades down into a massive coralline limestone. The sediments above the Mammal Bed are yellow limestones. The Mammal Bed is younger than the mammal-bearing horizons at the Stonesfield Slate Mines (Freeman, 1979).

The Mammal Bed contains indigenous and reworked fossils. The indigenous taxa are characteristic of a non-marine environment and include vertebrates and ostracods. Plant fossils also are common, although they are highly fragmented and poorly preserved. The reworked

Kirtlington Old Cement Works

Table 2.2 Composite section of the Kirtlington Old Cement Works GCR site, Oxfordshire (after Benton and Spencer, 1995)

	Thickness (m)
Lower Cornbrash Formation	
1. Limestone, rubbly and marly	1.07
2. Limestone, tough	0.76
3. Marl and rubby limestone, in places nodular	0.23
4. <i>Astarte-Trigonia</i> Bed. Limestone, very hard, grey	0.61
5. Clay, brown marly	0.30
Forest Marble Formation	
1. Clay, grey and bluff, with some thin irregular hard bands	1.53
2. Clay, dark-grey (= beds 3w-z of Freeman, 1979)	0.69
3. Limestone, yellowish, flaggy, locally marly and 'shaly', oolitic, with occasional inclusions of white lithographic limestone; ripple marks, rain pits (?= bed 3v of McKerrow <i>et al.</i> , 1969; Freeman, 1979)	0.61-0.92
4. Clay, grey-blue, with three pale mudstone layers, one at the bottom (= 3p-u of McKerrow <i>et al.</i> , 1969; Freeman, 1979; = Unfossiliferous Cream Cheese Bed of Odling, 1913; and Arkell, 1931). The basal unconsolidated 0.04-0.25 m brown marl unit (Bed 3p) is the Kirtlington Mammal Bed of Freeman (1979).	2
5. Coral- <i>Epithyris</i> Limestone (Upper <i>Epithyris</i> Bed or 'Fossiliferous Cream Cheese Bed of Odling, 1913; and Arkell, 1931; ?Beds 3n-o of McKerrow <i>et al.</i> , 1969). Limestone; at northern end an extremely hard white blue-hearted lithographic rock. Passes locally into unfossiliferous oolite	1.23-2.21
6. <i>fimbriatus-waltoni</i> Beds (= Bed 10 of Arkell, 1931; Beds 3k, l of McKerrow <i>et al.</i> , 1969). Clay, grey-green to greenish black, with some pellets at top; bed largely made up of bivalves; when bed 7 is absent, there is lignite at the base	1.07
7. Oyster- <i>Epithyris</i> Marl (= Bed 9; Middle <i>Epithyris</i> Bed of Arkell, 1931; Bed 3k of McKerrow <i>et al.</i> , 1969). Marl, brown. Locally, a thin layer of corals occurs below	0-0.75
White Limestone Formation	
1. Limestone, hard, blue-hearted (?= Beds 3i, j of McKerrow <i>et al.</i> , 1969)	0.92
2. Marl (?= Bed 3h of McKerrow <i>et al.</i> , 1969)	0.23
3. Limestone, similar to 8 (?= Bed 3g of McKerrow <i>et al.</i> , 1969)	0.84-0.92
4. <i>Epithyris</i> Limestone (= Lower <i>Epithyris</i> Bed of Arkell, 1931; = Beds 3a-f, Bed 1e of McKerrow <i>et al.</i> , 1969). Limestones, white at west end of pit a mass of <i>Epithyris</i> . Thins out eastwards and replaced from beneath by lenticular limestones	2.44
5. <i>Aphanoptyxis ardleyensis</i> Bed. Limestones, well bedded	0.46-0.61
6. <i>Nerinea eudesii</i> Beds. Limestones in three courses	1.68

fossils generally are abraded and include oysters, corals, brachiopods, echinoids and crinoids (Freeman, 1979).

The sediments of the Mammal Bed, in addition to the brown marl, contain fragments of oolitic limestone, with individual ooliths, fragments of shells and rare clastic grains. The sediments are well sorted and show no evidence of sedimentary structures. The palaeoenvironment of the Mammal Bed has been interpreted as a shallow pool formed during a temporary marine regression. Sediments from the surrounding oolitic limestone outcrop collected in the pool,

along with invertebrate and vertebrate debris (Freeman, 1979).

Bulk sampling of the unconsolidated brown marls produced batches of mammal teeth with similar taphonomic characteristics. The teeth appear to have been hollowed out from within, removing the root. Freeman (1979) considered this to be caused by stomach acids during digestion. However, Fisher (1981) considered loss of enamel to be characteristic of digestion; a feature not shown by the mammal fossils at Kirtlington Old Cement Works. The crowns are generally incomplete and show unabraded frac-

British Mesozoic fossil mammal GCR sites



Figure 2.11 General view of the disused Kirtlington Old Cement Works quarry, Oxfordshire. Exposures of White Limestone, Forest Marble and Cornbrash formations. (Photo: Dave Evans.)

tures. The lack of matching pieces of the teeth would suggest that the breakage occurred before fossilization (Freeman, 1979).

Fauna

The fauna from various horizons at Kirtlington Old Cement Works consists of frogs, salamanders, turtles, lizards, crocodylians, pterosaurs, dinosaurs and plesiosaurs (Freeman, 1979; Evans and Milner, 1994; Benton and Spencer, 1995). The mammalian fauna from Kirtlington Old Cement Works is represented by about 700 specimens, mainly isolated teeth, which were recovered from 10 tonnes of sediment (Kermack *et al.*, 1987). There is much uncertainty about the identification of some specimens. The list below represents the most securely recognized taxa. In addition, Freeman (1976a, 1979) has tentatively recognized the genus *Amphitherium* and a dryolestid whereas Sigogneau-Russell (2003b) has recorded several additional 'symmetrodonts' and cladotheres. Four more allotherian taxa have also been described, including the oldest multituberculates (Butler and Hooker, 2005).

REPTILIA

'Therapsida'

Tritylodontidae

Stereognathus ooliticus Charlesworth, 1855

MAMMALIA

Morganucodontidae

Wareolestes rex Freeman, 1979

Docodonta

Docodontidae

Boreolestes serendipitus Waldman and Savage, 1972

Boreolestes mussetti Sigogneau-Russell, 2003a

Cyrtlatberium canei Freeman, 1979

Krusatodon kirtlingtonensis Sigogneau-Russell, 2003a

Peraiocynodon major Sigogneau-Russell, 2003a

Simpsonodon oxfordensis Kermack, Lees and Mussett, 1987

Allotheria

'Haramiyida'

Millsodon superstes Butler and Hooker, 2005

Kirtlingtonia catenata Butler and Hooker, 2005

Eleutherodontidae

Eleutherodon oxfordensis Kermack, Kermack, Lees and Mills, 1998

Multituberculata

Kermackodontidae

Kermackodon multicuspis Butler and Hooker, 2005

Hahnotheriidae

Hahnotherium antiquum Butler and Hooker, 2005

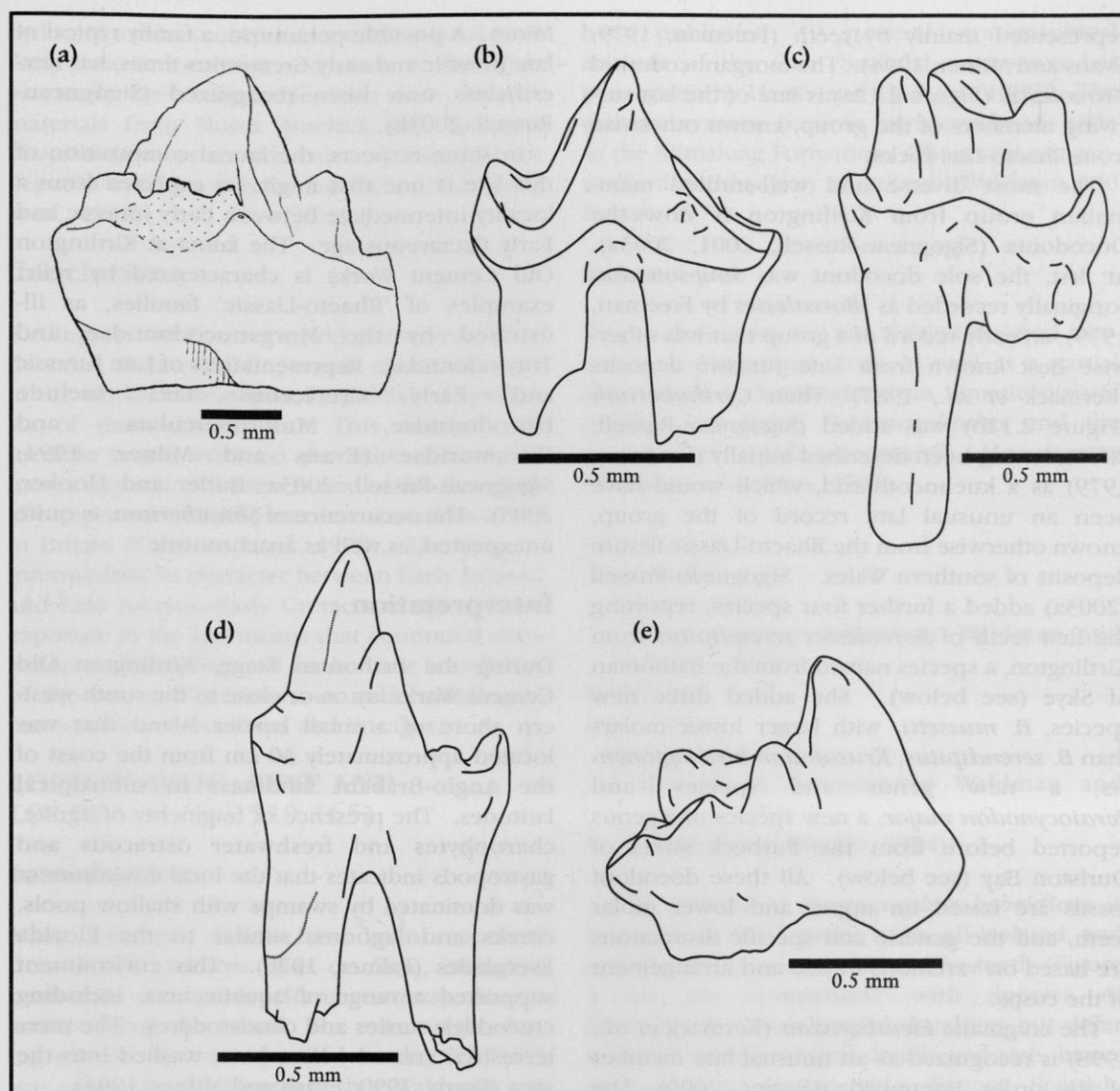


Figure 2.12 Mammal specimens from the Middle Jurassic sediments of Kirtlington Old Cement Works, Oxfordshire. (a) Lower molar of the morganucodontid *Wareolestes rex*, outer view. (b) Lower molar of the docodont *Cyrtlatherium canei*, outer view. (c) Lower molar of the amphilestid *Amphilestes* from Watton Cliff, Dorset, inner view. (d) Lower molar of the amphitheriid *Palaeoxonodon ooliticus*, inner view. (e) Upper molar of *Palaeoxonodon*, back view. (Based on Freeman, 1979.)

Shuotheridia

Shuotheriidae

Shuotherium dongi Chow and Rich, 1982

Shuotherium kermacki Sigogneau-Russell, 1998

Cladotheria

Amphitheriidae

Palaeoxonodon ooliticus Freeman, 1976a

Palaeoxonodon freemani Sigogneau-Russell, 2003b

Palaeoxonodon sp. (Sigogneau-Russell, 2003b)

?Peramuridae

genus indet. (Sigogneau-Russell, 2003b)

Family indet.

Kennetheredium leesi Sigogneau-Russell, 2003b

The tritylodont *Stereognathus* and the mammals from Kirtlington Old Cement Works are all

represented mainly by teeth (Freeman, 1979; Evans and Milner, 1994). The morganucodontid *Wareolestes* (Figure 2.12a) is one of the last surviving members of the group, known otherwise from Rhaeto-Lias rocks.

The most diverse and well-studied mammalian group from Kirtlington is now the Docodonta (Sigogneau-Russell, 2001, 2003a). At first, the sole docodont was *Simpsonodon* (originally recorded as *?Boreolestes* by Freeman, 1979), an early record of a group that was otherwise best known from Late Jurassic deposits (Kermack *et al.*, 1987). Then *Cyrtlatherium* (Figure 2.12b) was added (Sigogneau-Russell, 2001), having been described initially (Freeman, 1979) as a kuehneotheriid, which would have been an unusual late record of the group, known otherwise from the Rhaeto-Liassic fissure deposits of southern Wales. Sigogneau-Russell (2003a) added a further four species, reporting the first teeth of *Boreolestes serendipitus* from Kirtlington, a species named from the Bathonian of Skye (see below). She added three new species, *B. mussetti*, with larger lower molars than *B. serendipitus*, *Krusatodon kirtlingtonensis*, a new genus and species, and *Peraiocynodon major*, a new species of a genus reported before from the Purbeck strata of Durlston Bay (see below). All these docodont fossils are based on upper and lower molar teeth, and the generic and specific distinctions are based on variations in size and arrangement of the cusps.

The enigmatic *Eleutherodon* (Kermack *et al.*, 1998) is recognized as an unusual late member of the order Haramiyida (Butler, 2000). The presence here of *Shuotherium*, with its pseudo-tribosphenic molars, is remarkable in that *Shuotherium* is known otherwise only from China (Sigogneau-Russell, 1998).

An unexpected diversity of allotherians has only just been recognized (Butler and Hooker, 2005). These include two more 'haramiyidans' of uncertain affinities plus the earliest known multituberculates. The latter, *Kermackodon* and *Habnotherium*, are placed in their own families, considered to branch successively from the base of the multituberculate tree.

Palaeoxonodon (Figure 2.12d,e), once thought to be a peramurid (Freeman, 1976a) is now recognized to be an amphitheriid close to *Amphitherium* (Sigogneau-Russell, 2003b); the classic type of Bathonian mammal (Figure 2.12e) being known already from Stonesfield Slate

Mines. A possible peramurid, a family typical of late Jurassic and early Cretaceous times, has nevertheless now been recognized (Sigogneau-Russell, 2003b).

In some respects, the faunal composition of this site is one that might be expected from a locality intermediate between Early Jurassic and Early Cretaceous age. The fauna at Kirtlington Old Cement Works is characterized by relict examples of 'Rhaeto-Liassic' families, as illustrated by the Morganucodontidae and Tritylodontidae. Representatives of Late Jurassic and Early Cretaceous taxa include Docodontidae, Multituberculata and *?Peramuridae* (Evans and Milner, 1994; Sigogneau-Russell, 2003a; Butler and Hooker, 2005). The occurrence of *Shuotherium*, is quite unexpected, as well as anachronistic.

Interpretation

During the Bathonian Stage, Kirtlington Old Cement Works lay on or close to the south-western shore of a small barrier island that was located approximately 30 km from the coast of the Anglo-Brabant landmass in subtropical latitudes. The presence of fragments of lignite, charophytes and freshwater ostracods and gastropods indicates that the local environment was dominated by swamps with shallow pools, creeks and lagoons, similar to the Florida Everglades (Palmer, 1979). This environment supported a range of aquatic taxa, including crocodiles, turtles and choristoderes. The rarer terrestrial taxa may have been washed into the area (Evans, 1990; Evans and Milner, 1994).

Comparison with other localities

The vertebrate fauna from the Kirtlington Old Cement Works GCR site is comparable in age to the fauna preserved at Watton Cliff, Dorset (see GCR site report in the present chapter). Although the amphibians from these sites are very similar, other elements of the fauna show greater differences. The slightly older vertebrate assemblage from Stonesfield Slate Mines (Middle Bathonian in age) shows some similarities with the fauna at Kirtlington Old Cement Works, but the mammal species represented are different and the fauna at Stonesfield Slate Mines is smaller. Some of the taxa are unusual in their temporal distribution at Kirtlington Old Cement Works. If correctly identified, the morganu-

codontid tooth is comparable with material from Early Jurassic localities, and some of the other mammals are comparable with Late Jurassic materials from North America and Portugal. *Shuotherium* occurs otherwise in Late Jurassic deposits in China (Chow and Rich, 1982; Wang *et al.*, 1998).

Conclusions

Kirtlington Old Cement works preserves one of the most diverse Middle Jurassic mammal faunas in the world, with at least 19 published species, six of them docodonts. This number will increase when work on the other faunal elements appears. The site is one of the five globally important Middle Jurassic mammal localities in Britain (Clemens *et al.*, 1979). The fauna is intermediate in character between Early Jurassic and Late Jurassic–Early Cretaceous age. Good exposure at the site means that continued excavation and sampling will further our knowledge of the taxa and increase our understanding of mammalian relationships and lineages.

LOCH SCAVAIG, SKYE AND LOCHALSH (NG 519 165)

Introduction

Many vertebrate fossils have been recovered from Middle Jurassic beds on Skye, including mammals, therapsids (*Stereognathus*), lizards and a choristodere skull. The mammal-producing site on Skye (unspecified locality UB7111) was originally not identified, but Waldman and Evans (1994) gave the map reference. The fossil-bearing unit occurs within the Kilmaluag Formation, formerly the Ostracod Limestones, on the northern side of Glen Scaladal, Elgol (Benton and Spencer, 1995; Figure 2.13). The Kilmaluag Formation forms part of the upper portion of the Great Estuarine Group, formerly the Great Estuarine Series (Andrews, 1985), and is of middle Bathonian age (Waldman and Savage, 1972). The site was discovered in August 1971 by M. Waldman and J.B. Dobinson (Waldman and Savage, 1972; Waldman and Evans, 1994). This locality is situated within the Elgol Coast Site of Special Scientific Interest.

Description

The geological succession at the site has not

been published. A general stratigraphical account of the Glen Scaladal succession has been given by Harris and Hudson (1980). The mammal remains occur in marlstone bands within the Kilmaluag Formation. The marls are generally dark blue-grey in colour (Waldman and Savage, 1972).

Fauna

The Loch Scavaig site has yielded isolated tritylodont and mammal teeth, as well as a partial skeleton of a choristodere (an aquatic diapsid reptile), the lizard *Paramacellodus* and the stem-group lepidosauromorph *Marmoretta* (Waldman and Evans, 1994).

REPTILIA

'Therapsida'

Tritylodontidae

Stereognathus hebridicus Waldman and Savage, 1972

MAMMALIA

Docodonta

Docodontidae

Borealestes serendipitus Waldman and Savage, 1972

'pantothere' (Savage, 1984)

The tritylodont *Stereognathus hebridicus* is represented by 35 molar teeth, all isolated, and nothing else (Savage, 1984). The teeth (Figure 2.14a) are comparable with species of *Stereognathus* from English localities but differ in minor morphological details and size, hence warranting separation as a distinct, Scottish, species.

The mammal fauna has been reviewed by Savage (1984). The specimens of *Borealestes serendipitus* include a partial skeleton with upper and lower dentition, a fragment of maxilla with three teeth, four other mandibular fragments with teeth, and an isolated incisor tooth. The taxon was for a long time known only from this site, but Sigogneau-Russell (2003a) has reported isolated teeth of the species from Kirtlington (see GCR site report, above) and from Watton Cliff. (see GCR site report, below). Docodont mammals were mouse-sized, with long narrow snouts and burrowing adaptations (Kron, 1979; Sigogneau-Russell, 2003a; Martin and Nowotny in Martin and Krebs, 2000). The 'pantothere' from Skye is represented by less complete material (Savage, 1984).



Figure 2.13 Loch Scavaig; Skye, general view of the succession in the Kilmaluag (Mid Jurassic) Formation. (Photo: Colin MacFadyen.)

Interpretation

The sedimentology of the Great Estuarine Group rocks has been studied extensively by a number of workers; consequently a detailed picture of the sedimentary environment of deposition has been pieced together. Hudson (1962, 1966) considered the Great Estuarine Group to have been deposited under conditions of variable, but generally low, salinity in a series of shallow lagoons. Holmden and Hudson (2003) have used strontium isotope studies to confirm that the Great Estuarine Group basin was lagoonal and controlled more by seasonal changes in evaporation, precipitation, and flooding than by direct inputs of seawater or riverine water transported over large distances. Lagoons containing the oyster *Praeexogyra* in the Duntulm Formation have a higher proportion of seawater than the *Praemytilus* lagoons of the Kildonnan Member. Uniform strontium/calcium ratios in many of the Great Estuarine Group molluscs is consistent with a seasonally dry, Mediterranean-style climate for Middle Jurassic times in Britain. Evidence for subaerial exposure, including desiccation cracks, has been recorded (Harris and

Hudson, 1980).

Andrews (1985) divided the Kilmaluag Formation into two lithofacies. The first, the 'clastic facies', cropping out on north Skye, consists of calcareous mudstones and shales with minor sandstones and clayey limestones. These sediments are thought to represent deposition in shallow, ephemeral lagoons, mudflats and channels isolated from the sea. The invertebrate fauna indicates low salinity. The second lithofacies association, the 'argillaceous limestone facies', is composed of alternating beds of carbonates (some dolomitic) and calcareous shales. These sediments probably reflect a similar depositional environment to the 'clastic facies', with climatic fluctuations between humid and dry conditions. The overlying Skudiburgh Formation sees a change to dominantly alluvial sedimentation with some calcrete development. The upper part of the Great Estuarine Group represents a late Bathonian regression, with a change in palaeoenvironment from near-marine salinity lagoons (Duntulm Formation), through muddy lagoons with a low-salinity fauna (Kilmaluag Formation), to alluvial mudflats and channels (Skudiburgh Formation).

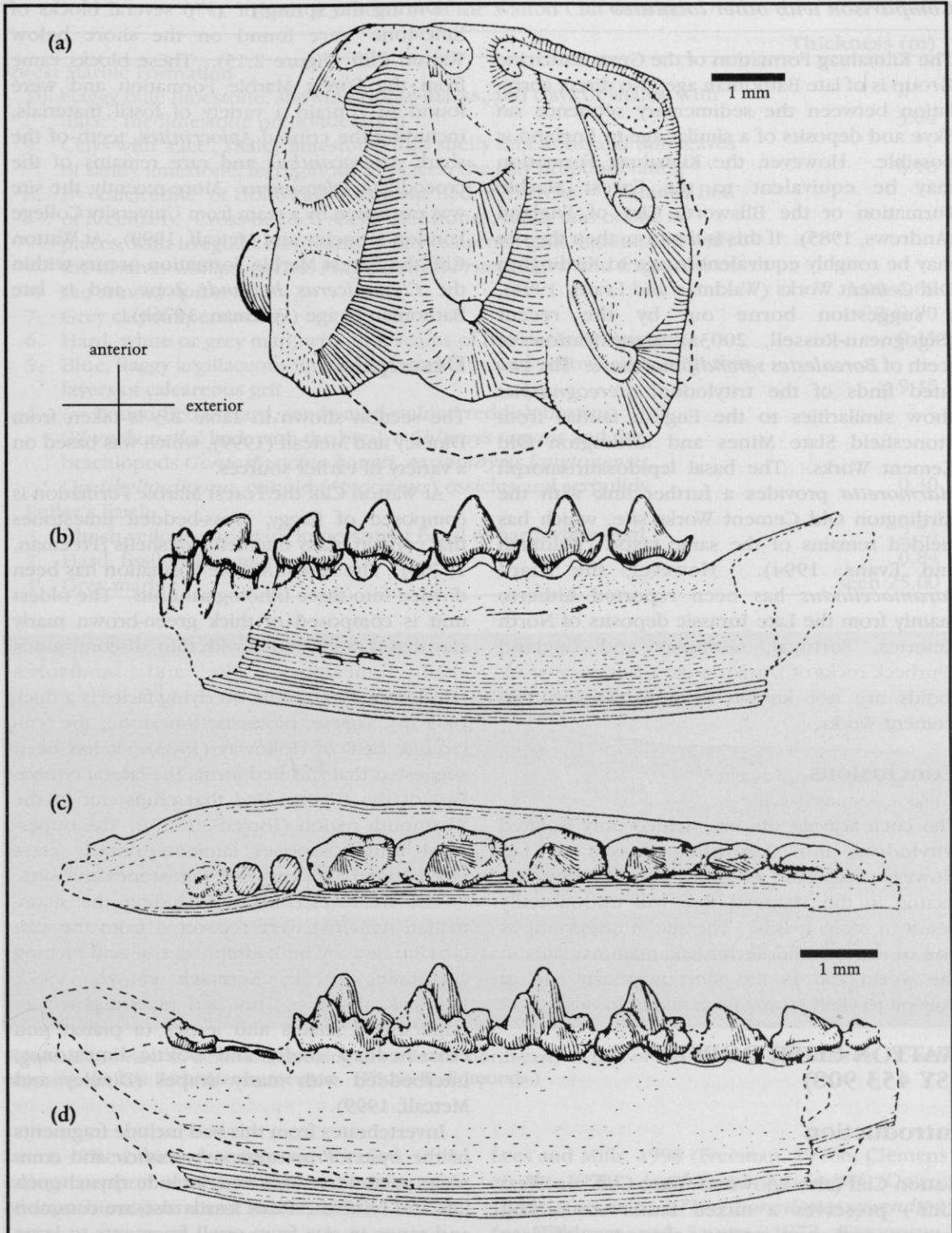


Figure 2.14 Teeth and jaws from the Middle Jurassic sediments of Loch Scavaig, Skye. (a) Upper left molar tooth of the tritylodont *Stereognathus bebridicus* in crown view. (b-d) Left lower jaw of the docodont mammal *Borealestes serendipitus* in external, crown, and internal views. (After Waldman and Savage, 1972.)

Comparison with other localities

The Kilmaluag Formation of the Great Estuarine Group is of late Bathonian age. No direct correlation between the sedimentary sequence on Skye and deposits of a similar age in England is possible. However, the Kilmaluag Formation may be equivalent to the Forest Marble Formation or the Blisworth Clay of England (Andrews, 1985). If this is the case, then the site may be roughly equivalent in age to Kirtlington Old Cement Works (Waldman and Evans, 1994), a suggestion borne out by the recent (Sigogneau-Russell, 2003a) identification of teeth of *Borealestes serendipitus* there. The isolated finds of the tritylodont *Stereognathus* show similarities to the English faunas from Stonesfield Slate Mines and Kirtlington Old Cement Works. The basal lepidosauromorph *Marmoretta* provides a further link with the Kirtlington Old Cement Works site, which has yielded remains of the same taxon (Waldman and Evans, 1994). However, the lizard *Paramacellodus* has been reported hitherto mainly from the Late Jurassic deposits of North America, Portugal, Germany and England (Purbeck rocks of Durlston Bay), but paramacellodids are not known from Kirtlington Old Cement Works.

Conclusions

The Loch Scavaig site has yielded only isolated tritylodont and mammalian fossils so far. However, exposure is good, and ongoing collecting in the Mammal Bed will undoubtedly result in more fossils. The site is important as one of the few Middle Jurassic mammal sites in the world and as the most northerly site in Europe to yield Mesozoic mammal fossils.

WATTON CLIFF, DORSET (SY 453 908)

Introduction

Watton Cliff (also known as 'Ware Cliff' or 'West Cliff') preserves a mixed fauna containing marine and non-marine elements of late Bathonian age. The fauna is diverse and includes various fishes, amphibians, mammals and mammal-like reptiles. The cliff-top exposure forms the most complete section of the Forest Marble Formation from Dorset.

During the spring of 1970 several blocks of limestone were found on the shore below Watton Cliff (Figure 2.15). These blocks came from the Forest Marble Formation and were found to contain a variety of fossil materials, including the crinoid *Apiocrinites*, teeth of the shark *Asteracanthus* and rare remains of the crocodylian *Teleosaurus*. More recently, the site was excavated by a team from University College London (Dineley and Metcalf, 1999). At Watton Cliff the Forest Marble Formation occurs within the *Clydoniceras hollandi* Zone and is late Bathonian in age (Freeman, 1976b).

Description

The section shown in Table 2.3 is taken from Dineley and Metcalf (1999), which was based on a variety of earlier sources.

At Watton Cliff the Forest Marble Formation is composed of flaggy, cross-bedded limestones that contain many fragments of shells (Freeman, 1976b). The Forest Marble Formation has been divided into three lithological units. The oldest unit is composed of thick green-brown marly clay that is interbedded with thin, discontinuous shelly limestones, silts and sandstones (Holloway, 1983). The overlying facies is a thick (3–5 m), coarse, bioclastic limestone, the 'calcirudite bed' of Holloway (1983). It has been suggested that this bed forms the lateral equivalent of the *Digona* Bed that crops out in the Weymouth region (Torrens, 1969). The uppermost unit comprises laminated marly clays interbedded with very fine sandstones and silts.

The microvertebrates (including the mammalian remains) were recovered from the 'calcirudite bed' by bulk sampling and acid etching (Freeman, 1976b; Kermack *et al.*, 1987; Kermack, 1988). This bed is composed of impersistent sheets and lenses of planar and cross-bedded shelly and oolitic limestones, interbedded with marly drapes (Dineley and Metcalf, 1999).

Invertebrates from this bed include fragments of the oyster *Praeexogyra hebridica* and complete pectinids. Rare taxa include rhynchonellids and bivalves. Plant fossils also are common and range in size from small fragments to large logs (Dineley and Metcalf, 1999).

The microvertebrate fauna is composed of two well-defined components. The first is composed of well-preserved marine fish remains. The second contains the reworked tetrapod

Watton Cliff

Table 2.3 Section of the Watton Cliff GCR site

	Thickness (m)
Forest Marble Formation	
10. Flaggy blue limestone, showing ripple-marks, and clays or shales, with 'race'; the limestone preponderating	3.04
9. Clays with 'race', shaley limestone, thin shelly limestone and thin leaves of sandy limestone, ferruginous in places; the clay preponderating	6.10
8. (= 'calcirudite' of Holloway = ? <i>Digona</i> Bed of Torrens = 'Mammal Bed' of Freeman). Cross-bedded shelly limestones, sandy and oolitic in places, with irregular clay seams, many ochreous galls, lignite; and with the bivalves <i>Camptonectes</i> , <i>Plagiostoma</i> , <i>Praeexogyra</i> and fragments of the crinoid <i>Apiocrinus</i>	3.00–4.60
7. Grey clay (impersistent)	0–0.90
6. Hard, white or grey marl, with thin seams of bluish shelly limestone	0.15
5. Blue, flaggy argillaceous limestones, and blue and yellow clays, with thin layers of calcareous grit	9.15
4. (= Boueti Bed). Hard, sandy marl stained reddish-brown; ' <i>Rhynchonella</i> ' bed, with the bivalve <i>Chlamys vagans</i> and the brachiopods <i>Goniorhynchia boueti</i> , <i>Avonothyris langtonensis</i> , <i>Ornithella digona</i> , crinoid (<i>Apiocrinus</i>) ossicles and serpulids	0.30
Fuller's Earth	
3. Bluish-yellow marl, with impersistent band of hard white marl	2.74
2. Hard, fissile white marl	0.84
1. Grey marls	seen 25.00

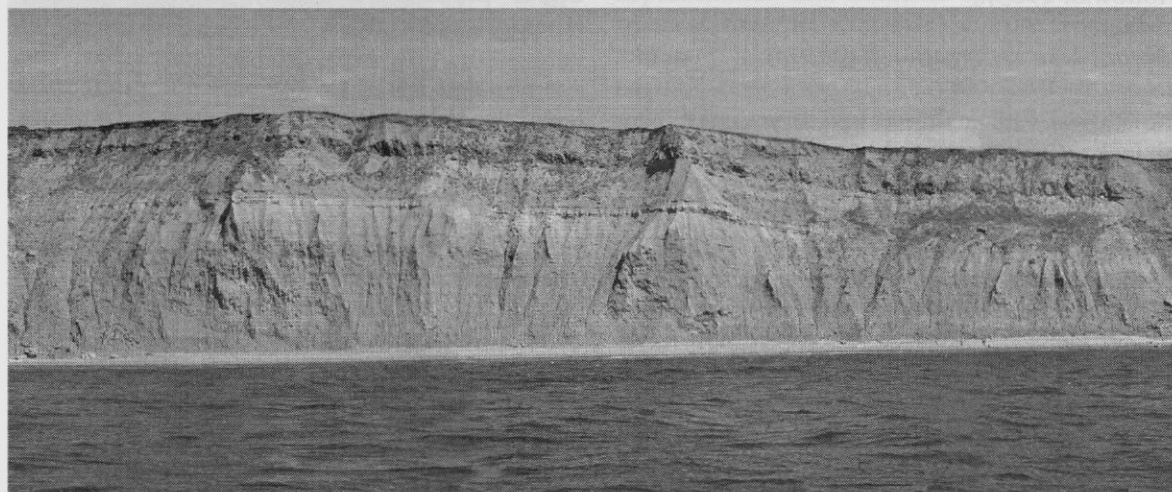


Figure 2.15 View to landward (looking towards the north-east) of part of the Watton Cliff GCR site, Dorset, exposing the late Bathonian succession. (Photo: R. Edmonds.)

fauna. The bones generally are abraded, indicating transport into the offshore environment of deposition (Evans and Milner, 1994).

Fauna

So far, only four mammalian species have been described from this site: the allotherian *Eleutherodon oxfordensis* Kermack, Kermack,

Lees and Mills, 1998 (Freeman, 1976b; Clemens *et al.*, 1979), *Amphilestes broderipii* (Owen, 1845) (Freeman, 1979), *Borealestes serendipitus* Waldman and Savage, 1972 (Sigogneau-Russell, 2003a) and Trechnotheria indet. (Sigogneau-Russell, 2003b). The record of *E. oxfordensis* is based on two teeth that closely resemble the type series from Kirtlington. The record of *A. broderipii* (Figure 2.12c) is the first

since the finding of the original specimens at Stonesfield in the 19th century. The record of *B. serendipitus* is a fragmentary molariform tooth, comparable with the original material from Loch Scavaig, and with newly reported specimens from Kirtlington. The trechnotherian is a rolled lower molar with some dryolestoid characters. (N.B. Trechnotheria is nearly synonymous with Holotheria).

A single tritylodont tooth, identified as *Stereognathus* sp., also has been described from this site (Ensom, 1977).

Interpretation

The 'calcirudite bed' has been interpreted as an offshore bank composed of shell fragments, deposited in shallow, moderate-energy waters. The shell debris is thought to be reworked from the underlying Forest Marble Formation. Individual beds may show ripple laminations; the bases of the beds generally are sharp. The terrestrial materials were deposited during storm events in cross-cutting channels (Holloway, 1983).

Comparison with other localities

The Watton Cliff mammal bed is younger than the Stonesfield Slate. The mammal-bearing lens at Kirtlington Old Cement Works also has been dated as late Bathonian in age (Evans and Milner, 1994), so Watton Cliff may be roughly contemporaneous. However, the exact stratigraphical relationship of this site with the mammal bed from the Great Estuarine Group on Skye is uncertain (Freeman, 1976b).

The amphibian faunas from Watton Cliff and Kirtlington Old Cement Works are comparable. However, the tritylodont and mammalian fauna from Watton Cliff is not sufficiently well known for detailed comparisons to be made. Continued scientific study at the site may well remedy this.

Conclusions

Although so far only four mammalian species have been described from Watton Cliff, and a fifth has now been found (Butler and Hooker in press); the cliff-top exposures will enable continued excavations of the mammal-bearing horizons. Future collecting undoubtedly will further extend our knowledge of the vertebrate faunas

from this site. Watton Cliff is selected for the GCR as one of the small number of such sites in Britain and as a site with potential for further excavation in the future. The importance of the site, as for the other British Middle Jurassic mammal sites, is that locations of this age are almost unknown elsewhere in the world.

LATE JURASSIC MAMMAL SITES

Late Jurassic mammals have been reported from several sites around the world, but such finds have been rare in Britain. The single British example is selected as a GCR site:

Upper Chicksgrove Quarry, Wiltshire (ST 962 296), exposing Late Jurassic (Tithonian) Portland Limestone Formation.

UPPER CHICKSGROVE QUARRY, WILTSHIRE (ST 962 296)

Introduction

Upper Chicksgrove Quarry yielded a diverse fauna of fossil reptiles and mammals during an excavation in the early 1980s (Figure 2.16). The site was first noted by a remarkable pioneering female geologist, Etheldred Bennett, who made one of the very first bed-by-bed stratigraphical descriptions in the literature. That section, in the east of the Chicksgrove Quarry complex, can still be accurately proved today. The site has been noted several times in the literature (Fitton, 1836; Arkell, 1933; Wimbledon, 1976, 1980) and is one of the most significant for stratigraphical studies in the Late Jurassic strata, because of its rich ammonite faunas. The site had never figured in the vertebrate palaeontological literature, and its only claim to vertebrate palaeontology had been as the source of fragmentary fish material from the basal Purbeck Limestone.

In the late 1970s and early 1980s, however, quarrying revealed new stratigraphical units that yielded common vertebrate material. Discoveries (Anon., 1983) included fishes, dinosaurs and crocodylians, in a unit lying within the otherwise marine Portland Group (Wimbledon, 1980).

Description

The site shows a thick succession of Portland Limestone and basal Purbeck Limestone strata



Figure 2.16 Collecting for research in the Portland Limestone Formation at the Upper Chicks Grove GCR site, which is important for both fossil reptiles and mammals. (Photo: W. A. Wimbledon.)

above, totalling around 27 m. The actively quarried locality was monitored by W. A. Wimbledon since the 1970s. The plant and reptile bed of the Wardour Portland Limestone was discovered in the early 1980s. Stratigraphically, the unit is the basal bed of the Wockley Member (Wimbledon, 1976), traditionally termed the 'Ragstone beds'. The bed is a fine quartz sand with many carbonate fragments, mostly shell fragments: it is laminated and shows abundant remains of current-aligned flattened carbonized plant material. In places, the sediment is silicified (Astin, 1987), as are some of the biotic contents, notably seeds, wood and gastropods. The unit was deposited in a depression in the top of the glauconitic building stone of the Tisbury Member, and is overlain by a discontinuous gastropod-rich micrite. The sand deposit lenses out rapidly eastwards, and the basal unit towards the east is a thin clay with serpulid debris. This lensing unit rests on a highly irregular erosion surface cut down into the topmost bed of the Tisbury

Member (and embedded in that surface are crushed *okusensis* zone ammonites). The deposit, up to 0.60 m thick, is of limited extent within the depression, and it was excavated in the 1980s and removed for screening for microvertebrate and other fossils. Nineteen tonnes were screened and washed on site. Sorting of the washings and acid residues is still not finished. The bare surface left by removal of the plant bed shows the extent (15 × 7 m) and shape of the trough.

The fauna of the plant-reptile bed is diverse (Anon, 1983). In addition to abundant carbonized plant remains, large reptilian bone fragments, teeth, silicified molluscs and wood also occur. The bed contains the bivalve *Myrene*, ostracods, around 20 species of gastropods, and bones and teeth of fishes, crocodylians, pterosaurs, ornithischian and saurischian dinosaurs, lepidosaurs and mammal material, as well as megaspores and microspores, conifer seeds and wood.

Vertebrate material is abundant and varied, from microscopic teeth to large limb bones. Lepidosaurian and mammal specimens are the smallest, together with many minute crocodylian and pterosaur teeth. Groups present, on the basis of teeth, include one diplodocid sauropod, a camarasaurid sauropod, small and large theropods, presumed coelurosaurs, a fabrosaurid and *Iguanodon*. In addition, armoured forms (nodosaur or stegosaur) also occur. Crocodylians are represented by three types: abundant goniopholids, theriosuchians and *Bernissartia*. There are two identifiable species of pterosaur: assigned to *Pterodactylus* and *Gnathosaurus*. Mammal remains consist of several dozen complete teeth and fragments. No precise specific assignments have yet been attempted. However, members of three orders of mammals have been positively identified (W. A. Wimbledon, pers. comm.): Multituberculata, Triconodonta and 'Eupantotheria'.

Interpretation

The plant bed is an anomalous unit; lithologically it is like no other in the Vale of Wardour Late Jurassic succession. Its facies is atypical in what is a predominantly open-water sequence with a shelled marine molluscan fauna: the norm for the Portland Group. The bed is remarkable also in that it contains a fossil fauna and flora that came from adjacent non-marine environments,

aqueous and terrestrial. Non-marine environments are typical in the Purbeck Limestone, but not in the Portland Group. Wimbledon (1976), after a revision of Portlandian stratigraphy, placed the plant–reptile bed in the *Galbanites kerberus* biozone, well down in the Portland Group. No other non-marine intercalations or biotas have been found in the British Portlandian Stage, apart from rare dinosaur teeth.

Comparison with other localities

The Late Jurassic Tithonian Stage has been split locally into two substages: the Bolonian below (spanning the upper Kimmeridge Clay) and the Portlandian above (covering the Portland and basal Purbeck Limestone Groups). This vertebrate assemblage is the only one known of its age. No land vertebrate assemblage has been recorded from the Portlandian substage, only rare isolated dinosaur teeth. The non-marine Morrison Formation faunas of dinosaurs and mammals from mid-western North America have always been vaguely described as late Jurassic in age (Clemens *et al.*, 1979). Most of the animals are from the upper Brushy Basin member (Engelmann and Callison, 1998), dated as ranging in age from late Kimmeridgian to early Tithonian (Steiner, 1998), thus slightly older than the Upper Chicks Grove fauna. The Guimarota deposit of Portugal is approximately coeval with the Morrison Formation, as is Tendaguru in Tanzania (Heinrich, 1999). The Purbeck Limestone, whose mammals are from Durlston Bay, Swanage and other localities in the Isle of Purbeck, associated with crocodylians and limited dinosaurian remains, are considerably younger, being of early to mid-Berriasian age (Allen and Wimbledon, 1991).

Thus the Upper Chicks Grove Quarry deposit and contained mammals fall approximately midway between these two clusters, of latest Kimmeridgian to early Bolonian and Berriasian age, a span of about 3 Ma. The Morrison Formation mammals fall near the Kimmeridgian–Bolonian boundary. Upper Chicks Grove Quarry is unequivocally mid-Portlandian in age, and Durlston Bay is earliest Cretaceous in age.

Conclusions

The fossil mammals from Upper Chicks Grove Quarry are apparently diverse, though rare.

They have not been studied yet, so their full import still has to be determined. However, their age lends them considerable international importance: they fall midway in age between the famous Morrison Formation mammals of North America and the Purbeck–Wealden mammals of Britain and other countries.

EARLY CRETACEOUS MAMMAL SITES

Early Cretaceous mammals are known from rich faunas at the very beginning of the period (Berriasian Stage) in the Purbeck Limestone Group and from poorer but globally important sites in Wealden strata of Valanginian and Barremian ages. Those from the Purbeck Limestone Group are listed below.

Purbeck Limestone Group mammal sites

DORSET: Durlston Bay (SZ 035 772–SZ 039 786; diverse mammalian fauna, including triconodonts, docodonts, multituberculates, symmetrodonts and ‘eupantotheres’; Lulworth Formation; Clemens *et al.*, 1979); see GCR site report below. Sunnydown Farm (SY 9822 7880) and sites in the surrounding area (SZ 020 777, SY 980 790; *Peraiocynodon*, *Gerhardodon purbeckensis*, *Sunnyodon notleyi*, *Bolodon osborni*, *Bolodon minor*, *Albionbaatar denisiae*, *Dorsetodon haysomi*, *Chunnelodon alopekodes*, *Peramus*, *Amblotherium*, ?*Peraspalax*, *Phascolestes*, *Magnimus ensomi*, *Thereuodon taraktes*, *Spalacotherium evansae* and *Tinodon micron*; Cherty Freshwater Member, Lulworth Formation; Ensom *et al.*, 1994; Sigogneau-Russell, 1999; Sigogneau-Russell and Ensom, 1994, 1998; McGowan and Ensom, 1997; Ensom and Sigogneau-Russell, 1998, 2000). Acton, small quarry (SY 990 778; *Tribactonodon bonfieldi*; Intermarine Member, Durlston Formation; Sigogneau-Russell *et al.*, 2001).

WILTSHIRE: Town Gardens Quarry, Swindon (SU 152 835; *Plagiaulax*, *Spalacotherium* and other mammals; may be contemporaneous with Dorset sites; Clemens *et al.*, 1979; Hudleston, 1876).

One Purbeck mammal locality has been selected as a GCR for its mammals: Durlston Bay, Swanage, Dorset.

Durlston Bay

DURLSTON BAY, SWANAGE, DORSET (SZ 035 772–SZ 039 786)

Introduction

The coast at Durlston Bay (Figure 2.18) exposes the finest sections of the Purbeck Limestone Group in Britain. The sediments seen here were deposited during latest Jurassic and earliest Cretaceous times. This site has produced one of the most diverse vertebrate faunas from Britain, including over 40 species of reptile (for example turtles, crocodiles, pterosaurs, dinosaurs and lizards) as well as 20 species of mammal (Benton and Spencer, 1995). Vertebrate materials have been recovered from several horizons within the Purbeck Limestone Group succession, although the occurrence of mammalian fossils is restricted to the Cherty Freshwater and Marly Freshwater Members.

Durlston Bay, or 'Durdlestone Bay' as it is known in old published accounts, has been studied for many decades. The first discoveries of mammal fossils were made around 1854 by the Reverend P.B. Brodie, who sent his finds to Richard Owen. Shortly after this, Samuel Beckles organized an excavation near the top of the cliffs. He unearthed many mammal fossils. Unfortunately there is some confusion concerning the exact stratigraphical position of these

remains. Subsequent work at 'Beckles Pit' has failed to relocate the horizon excavated by him. More-recent work has focused on collecting from the 'dirt beds' and from fallen blocks of limestone found on the foreshore (Clemens *et al.*, 1979). Furthermore, teeth have been described from the horizon represented at Sunnydown Farm, which is also in the Cherty Freshwater Member (Sigogneau-Russell and Ensom, 1994; Ensom and Sigogneau-Russell, 1998, 2000).

Description

The mammalian fauna from Durlston Bay comes from the Lulworth Formation (Figure 2.18), below the Cinder Bed (Clemens and Mills, 1971). The majority of the specimens are from the Mammal Bed in the Marly Freshwater Member, although subsequent fossils have been found slightly higher in several beds in the Cherty Freshwater Member (Simpson, 1928; Ensom and Sigogneau-Russell, 2000; Gill, 2004). Benton and Spencer (1995, p. 208) described the Mammal Bed as:

'The Mammal Bed ('Dirt Bed') of Beckles' excavations (Bed 93 of Austen (1852); Bed 22 of Bristow; bed 83 of Clements (in Torrens, 1969)); always equated with beds 14–16 of the shore

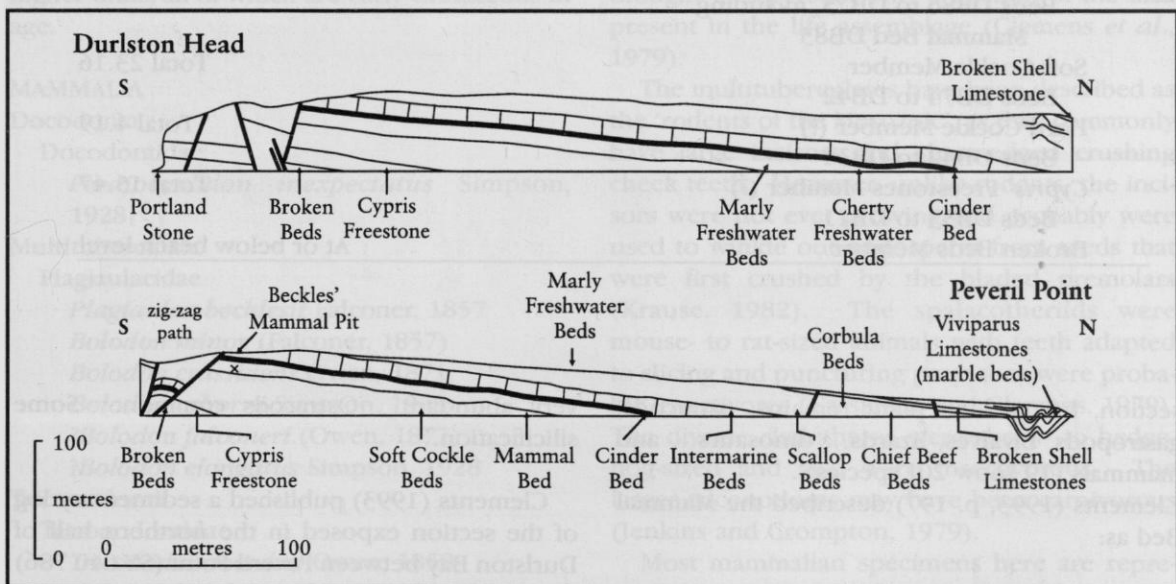


Figure 2.18 Cliff profiles of Durlston Bay showing the type section of the Durlston Formation. (After Strahan, 1898.)

British Mesozoic fossil mammal GCR sites

Table 2.4 Section of the Durlston Bay GCR site

	Thickness (m)
Purbeck Limestone Group	
Durlston Formation	
Upper 'Cypris' Clays and Shales Member	Total 12.8
Beds DB246 to DB224, including	
Upper Purbeck Marble (= Blue Marble) DB244	0.76
Lower Purbeck Marble (= Red Marble) DB241	0.81
Green Marble DB237 to DB234	0.46
'Crocodile Bed' top of DB221	
Unio Member	Total 1.14
Beds DB223 to DB221	
Broken Shell Limestone Member	Total 8.15
Bed DB220	
Chief Bed Member	Total 8.15
Beds DB219 to DB190	
Corbula Member	Total 10.27
Beds DB189 to DB154	
Scallop Member	Total 1.55
Beds DB153 to DB146	
Intermarine Member (or Upper Building Stone)	Total 15.64
Beds DB145 to DB112, including	
Leaning or Laning Vein DB144 to DB141	1.62
Royal Limestone DB140	0.30
Red Rag DB133	0.74–0.79
Under Rag DB131	0.69–0.76
Cinder Member	Total 2.95
Bed 111	
Lulworth Formation	
Cherty Freshwater Member	Total 8.12
Beds DB110 to DB87, including:	
Flint Bed (or Cherty Freshwater Bed) DB97	0.84
Marly Freshwater Member	Total 4.29
Beds DB86 to DB75, including	
Mammal Bed DB83	
Soft Cockle Member	Total 23.16
Beds DB74 to DB42	
Hard Cockle Member (?)	Total 4.19
Beds DB42 to DB34	
Cypris' Freestones Member (?)	Total 15.47
Beds DB33 to DB11	
Broken Beds Member	At or below beach level

section, has yielded plant remains, ostracods, gastropods, bivalves, lizards... dinosaurs... and mammals (19 [now 20] species)'. Clements (1993, p. 197) described the Mammal Bed as:

'Dark-grey, shelly, carbonaceous, calcareous clay and shale. Rests on an irregular surface of, and in part grades into, the bed below. Gastropods

very abundant. Ostracods common. Some silicification.'

Clements (1993) published a sedimentary log of the section exposed in the northern half of Durlston Bay between Peveril Point (SY 040 786) and the zig-zag path (SY 035 780). The sequence is dominated by calcareous beds with some clays, shales and sandstones. Much work has

Durlston Bay

been completed on this site, so highly detailed records of the sedimentary sequence are available. The description in Table 2.4 of the Durlston and Lulworth formations is a simplified version of the section from Clements (1993).

The Durlston Bay section spans the Jurassic–Cretaceous boundary. The boundary used to be placed at the top of the Lulworth Formation, below the Cinder Member. However, several authors have argued, on diverse biotic grounds, that the Cretaceous Period begins with the *Cypris* Freestones Member (see section above). This latter interpretation is followed here, making the Mammal Bed (within the Marly Freshwater Member in the section above) earliest Cretaceous (Berriasian) in age.

Fauna

The Durlston Bay section has yielded many thousands of identifiable specimens of fishes, reptiles and mammals. The reptiles include some 41 species of turtles, lizards, crocodylians, pterosaurs and dinosaurs and a rare plesiosaur and ichthyosaur. The fishes are described more fully by Dineley and Metcalf (1999) and the reptiles by Benton and Spencer (1995) in companion GCR volumes. The fishes and reptiles are found at a number of horizons, some of them near the base of the succession, in and around the Mammal Bed, but most of them from higher units, all of which are early Cretaceous in age.

MAMMALIA

Docodonta

Docodontidae

Peraiocynodon inexpectatus Simpson, 1928

Multituberculata

Plagiaulacidae

Plagiaulax becklesii Falconer, 1857

Bolodon minor (Falconer, 1857)

Bolodon crassidens Owen, 1871

Bolodon osborni Simpson, 1928

?*Bolodon falconeri* (Owen, 1871)

?*Bolodon elongatus* Simpson, 1928

Triconodonta

Triconodontidae

Triconodon mordax Owen, 1859

Trioracodon ferox (Owen, 1871)

Trioracodon major (Owen, 1871)

Trioracodon oweni Simpson, 1928

Trechnotheria

Spalacotheriidae

Spalacotherium tricuspides Owen, 1854 (including *Peralestes longirostris* Owen, 1871)

Spalacotherium evansae Ensom and Sigogneau-Russell, 2000

Spalacotherium bookeri Gill, 2004

Cladotheria

Peramuridae

Peramus tenuirostris Owen, 1871

Dryolestidae

Amblotherium nanum (Owen, 1871)

Amblotherium pusillum (Owen, 1871)

Kurtodon pusillus Osborn, 1888

Peraspalax talpoides Owen, 1871

Phascolestes mustelula (Owen, 1871)

The mammalian assemblage preserved in the sediments exposed at Durlston Bay is extremely diverse (20 species) for the Mesozoic Era (Figure 2.19), and it has been the subject of numerous descriptive works, including some major monographs (Owen, 1854, 1859, 1871; Falconer, 1857; Osborn, 1888; Simpson, 1928) and some recent revisions (Kielan-Jaworowska and Ensom, 1992; Sigogneau-Russell and Ensom, 1998; Sigogneau-Russell, 2003a). The majority of specimens are mandibles, and when Simpson (1928) wrote his influential monograph, the Purbeck assemblage was one of the best faunas of Mesozoic mammals known. The fauna is thought to represent only a fraction of the taxa present in the life assemblage (Clemens *et al.*, 1979).

The multituberculates have been described as the 'rodents of the Mesozoic', as they commonly have large incisors and sharp-edged crushing cheek teeth. However, unlike rodents, the incisors were not ever growing and probably were used to winkle out endosperm from seeds that were first crushed by the bladed premolars (Krause, 1982). The spalacotheriids were mouse- to rat-sized animals with teeth adapted to slicing and puncturing prey: they were probably insectivores (Cassiliano and Clemens, 1979). The diverse cladotheres were shrew- to hedgehog-sized and also were insectivorous. The larger triconodonts may have been carnivorous (Jenkins and Crompton, 1979).

Most mammalian specimens here are represented by upper and lower jaws and some by partial skull and skeletal elements, not just isolated teeth.

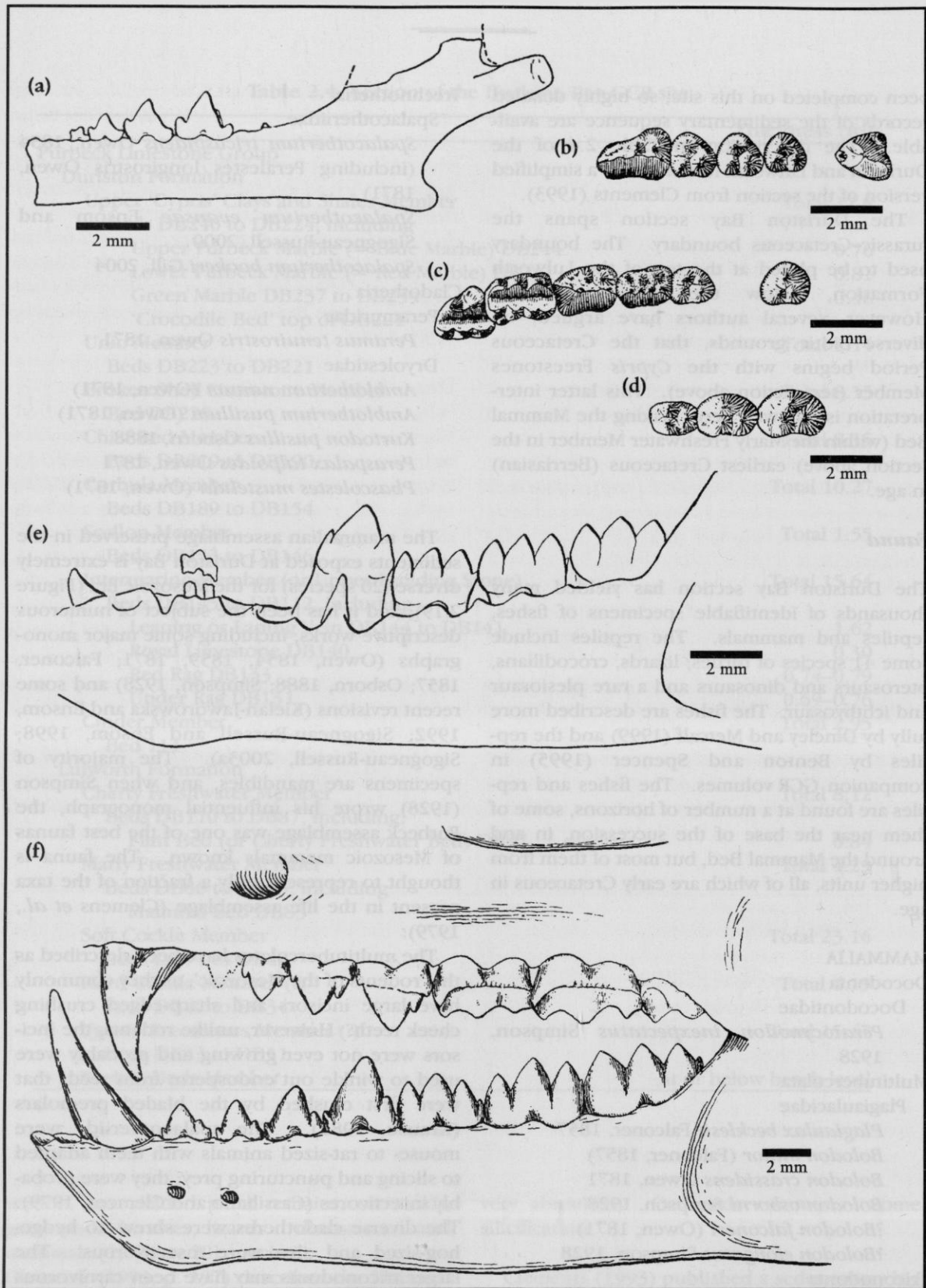


Figure 2.19 Teeth and jaws of mammals from the Early Cretaceous deposits of Durlston Bay, Dorset. (a) Left lower jaw of the docodont *Peraiocynodon inexpectatus* in external view. (b-d) Crown views of the known upper dentitions of the species of *Bolodon*: *B. crassidens* (b), *B. osborni* (c), and *B. elongatus* (d). (e) Left lower jaw of the triconodont *Triconodon mordax* in external view. (f) Composite reconstruction of the jaws and teeth of the triconodont *Trioracodon ferox*. (After Simpson, 1928.)

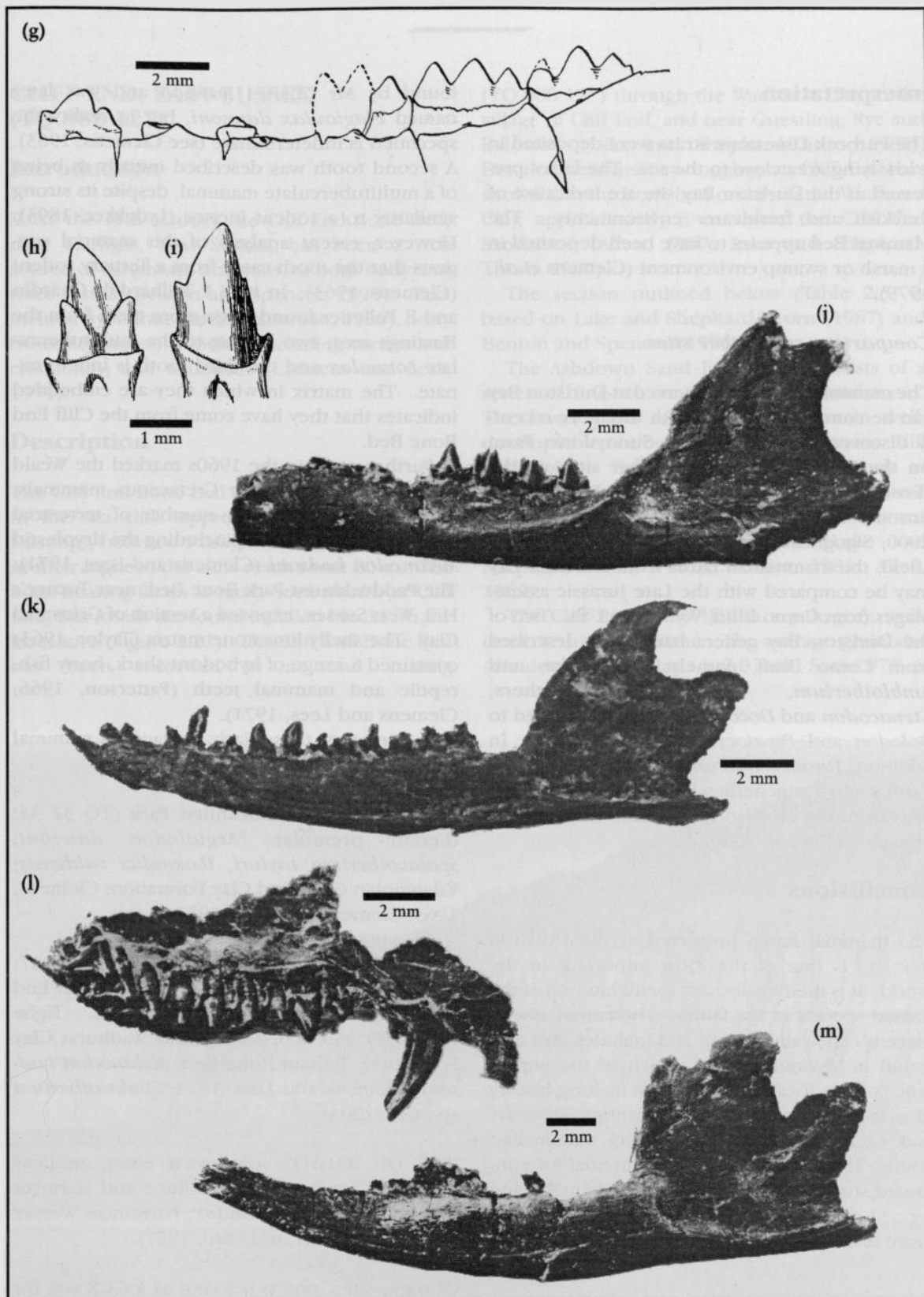


Figure 2.19 – continued. (g) Internal view of the right lower teeth of the triconodont *Trioracodon oweni*. (h,i) Left lower molar of the spalacotheriid *Spalacotherium tricuspides* in internal and external views. (j) Left lower jaw of the peramurid *Peramus tenuirostris* in external view. (k) Right lower jaw of the dryolestid *Amblotherium pusillum* in internal view. (l) Left maxilla of the dryolestid *Kurtodon pusillus* in internal view. (m) Right lower jaw of the dryolestid *Phascolestes mustelula* in internal view. (After Simpson, 1928.)

Interpretation

The Purbeck Limestone strata were deposited in a low-lying area close to the sea. The facies preserved at the Durlston Bay site are indicative of brackish and freshwater environments. The Mammal Bed appears to have been deposited in a marsh or swamp environment (Clemens *et al.*, 1979).

Comparison with other sites

The mammalian fauna preserved at Durlston Bay can be compared directly with the more recently discovered materials from Sunnydown Farm on the Isle of Purbeck and other sites nearby (Ensom *et al.*, 1994; Sigogneau-Russell and Ensom, 1994; Ensom and Sigogneau-Russell, 2000; Sigogneau-Russell *et al.*, 2001). Further afield, the mammalian fauna from Durlston Bay may be compared with the Late Jurassic assemblages from Como Bluff, Wyoming, USA. Two of the Durlston Bay genera have been described from Como Bluff, namely *Trioracodon* and *Amblotherium*, whereas two others, *Ctenacodon* and *Docodon*, are closely related to *Bolodon* and *Peraiocynodon* respectively. In addition, *Tinodon micron* from the Sunnydown Farm site is congeneric with *T. bellus* and *T. lepidus* from the Morrison Formation (Ensom and Sigogneau-Russell, 2000).

Conclusions

The mammal fauna preserved at the Durlston Bay site is one of the most important in the world. It is the type locality for all but one of the named species in the fauna. The faunal assemblage is especially diverse and includes taxa also found in Wyoming, USA. Much of the importance of this locality comes from its long history of research, but also from the unique diversity and excellent preservation of its mammalian fauna. The site also has great potential for continued study: the cliff section is constantly being eroded by the sea and undoubtedly will provide more fossils in the future.

WEALDEN MAMMAL SITES

In 1881 the first Wealden mammal fossil from southern England was discovered, a tooth from 'Old Roar Quarry' near Hastings, which was

found by Mr Charles Dawson and was later named *Plagiaulax dawsoni*, but in reality the specimen is indeterminate (see Clemens, 1963). A second tooth was described initially as being of a multituberculate mammal, despite its strong similarity to a rodent incisor (Lydekker, 1893). However, recent analysis of this material suggests that the tooth came from a Tertiary rodent (Clemens, 1963). In 1911 P. Teilhard de Chardin and F. Pelletier found three more teeth from the Hastings area; two belong to the multituberculate *Loxaulax* and the third tooth is indeterminate. The matrix in which they are embedded indicates that they have come from the Cliff End Bone Bed.

Further work in the 1960s marked the Weald as a significant area for Cretaceous mammals. Tighe Farm produced a number of terrestrial and aquatic vertebrates, including the dryolestid *Melanodon hodsoni* (Clemens and Lees, 1971). The Paddockhurst Park Bone Bed, near Turner's Hill, West Sussex, exposed a section of Grinstead Clay. The shelly limestone matrix (Taylor, 1963) contained a range of hybodont shark, bony fish, reptile and mammal teeth (Patterson, 1966; Clemens and Lees, 1971).

In summary, these Early Cretaceous mammal sites are:

WEST SUSSEX: Paddockhurst Park (TQ 32 34; therian premolar ?*Aegialodon dawsoni*, *Spalacotherium taylori*, ?*Loxaulax valdensis*; Valanginian Grinstead Clay Formation; Clemens, 1963; Clemens and Lees, 1971).

EAST SUSSEX: Cliff End (TQ 886 127; Valanginian Wadhurst Clay Formation, Cliff End Bone Bed; Clemens and Lees, 1971). Tighe Farm (TQ 936 266; Valanginian Wadhurst Clay Formation, Telham Bone Bed, *Melanodon hodsoni*; Clemens and Lees, 1971; *Spalacotherium* sp.; Gill, 2004).

ISLE OF WIGHT: south-west coast, midway between Compton Grange Chine and Hanover Point (SZ 377 840; *Loxaulax*; Barremian Wessex Formation; Butler and Ford, 1977).

Of these sites, one is selected as a GCR site for fossil mammals:

Cliff End, East Sussex (TQ 886 127). Early Cretaceous (Valanginian) Wadhurst Clay Formation, Cliff End Bone Bed.

**CLIFF END, EAST SUSSEX
(TQ 886 127)**

Introduction

Since the 19th century, the Cliff End Bone Bed, near Fairlight, East Sussex, has been a rich source of vertebrate materials, of both body and trace fossils (Benton and Spencer, 1995). Taxa include hybodont sharks (Patterson, 1966), bony fishes *Lepidotes*, reptiles (including turtles and crocodiles) and mammals (Clemens and Lees, 1971).

Description

The Cliff End Bone Bed (Figure 2.20) is exposed in the sea cliffs approximately 7 km east of Hastings, between Fairlight Cove and Pett Level. At their highest, the cliffs reach some 30 m. The bone-bearing facies is rarely seen *in situ* at Cliff End, but fossils are found in fallen blocks on the foreshore (Figure 2.21). The Cliff End Bone Bed has been recorded in a road cutting

(TQ 888 137) through the Wadhurst Clay in the village of Cliff End, and near Guestling, Rye and Baldstow (Lake and Shephard-Thorn, 1987). Detailed sedimentary logging at Cliff End has shown that the bone bed occurs in the Wadhurst Clay, approximately 3 m above the Cliff End Sandstone (Allen, 1967; Lake and Shephard-Thorn, 1987).

The section outlined below (Table 2.5) is based on Lake and Shephard-Thorn (1987) and Benton and Spencer (1995):

The Ashdown Sand Formation consists of a series of fine- to medium-grained sandstones. The lower parts of the section contain well-developed cross-bedding, especially near Cliff End Point. Smaller-scale structures such as cross-laminations, planar bedding, silt/mud drapes, slumps and penecontemporaneous folds and faults are common (Lake and Shephard-Thorn, 1987; Stewart, 1981; Allen, 1962).

The Cliff End Bone Bed is a pale-grey, well-cemented granulestone. The average grain size (diameter) of the clasts is 2.0 mm. Some 97% of



Figure 2.20 Part of the Cliff End GCR site, east of Hastings, East Sussex. The Cliff End Bone Bed occurs at the top of the section. Fossil mammal teeth and bones have been found in fallen blocks from the bone bed on the foreshore. (Photo: R. Edmonds).

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Table 2.5 Section of the Cliff End GCR site

	Thickness (m)
Hastings Group	
Tunbridge Wells Sand Formation	
Fine-grained, yellowish sandstones and silts with impersistent seams of mottled silty clay	Up to 50
Wadhurst Clay Formation	
Grey mudstones interlaminated with thin siltstones	50–57
Also: calcareous sandstone beds (Tilgate Stone), sandstone channel, fills, soils and, near the base:	
Cliff End Bone Bed	
Cliff End Sandstone	
Top Ashdown Pebble Bed	10
Ashdown Sand Formation	180–200
The upper 30–50 m are chiefly sandstones, whereas the strata below are dominantly massive mottled sideritic sandstone beds.	
Near the base:	
Lee Ness Sandstone	1–2

the clasts are quartz; the remainder are lithic (sandstone and claystone) clasts, fragments of wood and vertebrate fossils. The matrix consists of very fine-grained quartz and clay cemented by calcite (Cook, 1995a). The bone bed occurs in scours, runnels and gutters in the Wadhurst Clay; occasionally they join up forming small sheets (Allen, 1975; Lake and Shephard-Thorn, 1987). Occasionally blocks of the bone bed are found interdigitating with cross-laminated grey sandstone (Cook, 1995b).

Vertebrate material is common in the Cliff End Bone Bed, but mammal remains are rare, representing perhaps 5% of all bones (Patterson, 1966). It has been estimated that 200 kg of sediment will produce only one mammal tooth. The Cliff End Bone Bed is dated as Valanginian in age on the basis of its position within the Wadhurst Clay, its fossil content and regional considerations (Allen and Wimbledon, 1991).

Fauna

Many of the early records of mammal teeth from the Hastings area are vague and do not provide an accurate site location. In the following list, only specimens with a known locality are given.

MAMMALIA

Multituberculata

Eobaataridae

Loxaulax valdensis (Woodward, 1911)

Trechnotheria

Spalacotheriidae

Spalacotherium cf. *tricuspidens* Owen, 1854

Cladotheria

Dryolestidae

Melanodon bodsoni Clemens and Lees, 1971

Boreosphenida

Aegialodontidae

Aegialodon dawsoni Kermack, Lees, and Mussett, 1965

The Wealden mammal specimens from Cliff End were described by Woodward (1911), Simpson (1928, 1929), Kermack *et al.* (1965) and Clemens and Lees (1971). All of the mammal fossils occur as isolated teeth. The plagiaulacid *Loxaulax valdensis* is known from several molar teeth (Figure 2.22a,b) and may represent more than one species as yet too incomplete to distinguish (Clemens and Lees, 1971). The dryolestid *Melanodon bodsoni* also is represented by isolated teeth (Figure 2.22c,d). *Melanodon* is known also from the Morrison Formation of Como Bluff, Wyoming, USA, but the species are different. *Spalacotherium tricuspidens* was named from specimens from the Purbeck of Durlston Bay (see GCR site report), but a specimen from Cliff End also may be ascribed tentatively to that species. A further specimen has been reported (Gill, 2004).

The species *Aegialodon dawsoni* has special significance as the talonid of its unique lower molar is indicative of the tribosphenic grade of evolution. When named, it was the earliest

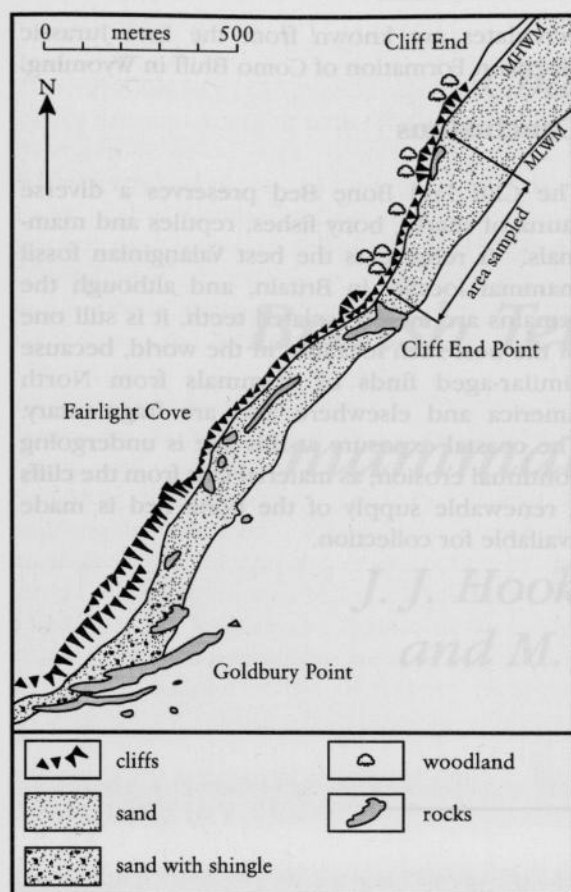


Figure 2.21 Map showing the section of foreshore where fallen blocks of the Cliff End Bone Bed may be found in Fairlight Cove, east of Hastings. (MHWM = Mean high water mark; MLWM = Mean low water mark; after Cook, 1995a.)

mammal to show such structure. It is thus a therian mammal more derived than dryolestids or peramurids, although belonging to neither the marsupial nor the placental clade (Kielan-Jaworowska *et al.*, 1979; Luo *et al.*, 2001, 2002). Since it was described, earlier tribosphenic teeth have been discovered, viz. *Tribactonodon* from the English Purbeck Limestone (Sigogneau-Russell *et al.*, 2001), *Hypomylos* from Berriasian deposits in Morocco (Sigogneau-Russell, 1992) and *Ambondro* from Madagascan Bathonian sediments (Flynn *et al.*, 1999).

Interpretation

The Hastings Group is composed primarily of arenaceous sediments, with subsidiary clay units. The sandy sediments were deposited pre-

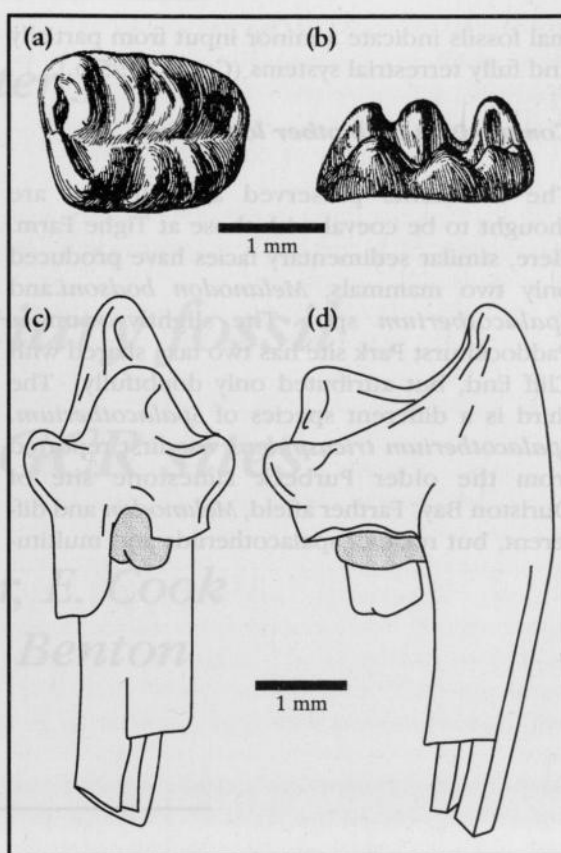


Figure 2.22 Teeth of mammals from the Early Cretaceous Cliff End Bone Bed, near Hastings, East Sussex. (a,b) Lower molar of *Loxaulax valdensis* in crown (a) and external (b) views. (c,d) Right upper molar of *Melanodon bodsoni* in external (c) and back (d) views. (Based on Simpson, 1928; and Clemens and Lees, 1971.)

dominantly on a series of braidplains (Allen, 1975, 1989). Meandering channels account for the wide lateral extent of the sandstone lithofacies (Stewart, 1983). The finer-grained sediments were deposited in swamps, lakes and brackish lagoons. The climate was warm temperate, with some degree of seasonality and humid-arid climate cyclicity (Allen, 1981; Allen *et al.*, 1998).

The Cliff End Bone Bed represents a reworked bone accumulation. Initial deposition of the bone materials was in a high-energy fluvial regime as winnowed lag deposits. The fluvial lag sediments were reworked during non-marine transgressions forming shoreline deposits (Allen, 1975; Cook, 1995a). The predominance of fish and shark remains reflects the aquatic nature of the deposit. The crocodile and mam-

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mal fossils indicate a minor input from partially and fully terrestrial systems (Cook, 1995b).

Comparison with other localities

The sediments preserved at Cliff End are thought to be coeval with those at Tighe Farm. Here, similar sedimentary facies have produced only two mammals, *Melanodon bodsoni* and *Spalacotherium* sp.. The slightly younger Paddockhurst Park site has two taxa shared with Cliff End, but attributed only doubtfully. The third is a different species of *Spalacotherium*. *Spalacotherium tricuspidentis* was first reported from the older Purbeck Limestone site of Durlston Bay. Farther afield, *Melanodon* and different, but related, spalacotheriids and multitu-

berculates are known from the Late Jurassic Morrison Formation of Como Bluff in Wyoming.

Conclusions

The Cliff End Bone Bed preserves a diverse fauna of sharks, bony fishes, reptiles and mammals. It represents the best Valanginian fossil mammal locality in Britain, and although the remains are merely isolated teeth, it is still one of the best such localities in the world, because similar-aged finds of mammals from North America and elsewhere also are fragmentary. The coastal exposure at this site is undergoing continual erosion; as material falls from the cliffs a renewable supply of the bone bed is made available for collection.