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, some of which were preserved in cave-fill sediments.

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 (Maim) 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 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), northwestern 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 southwest 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 sinoconodonts, 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 'tricondont') in a line on the shearing molar teeth. Once included in the triconoconts, 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 Maclntyre, 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.

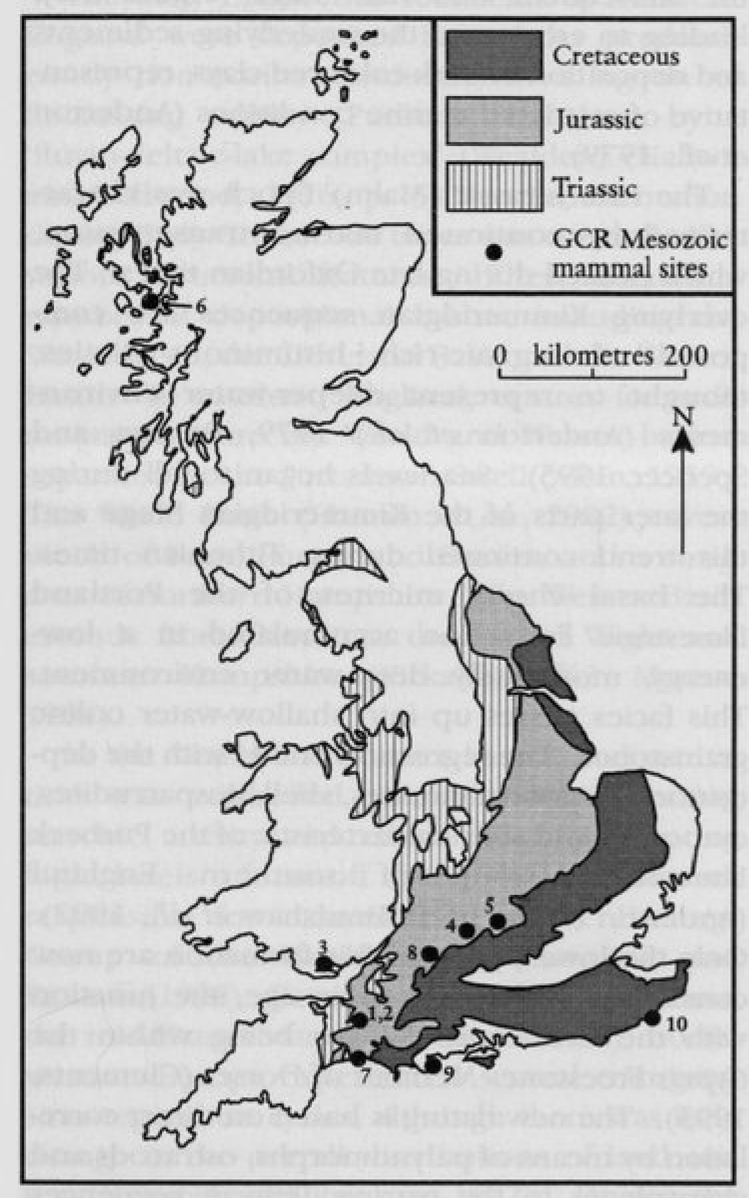
Late Triassic mammal sites

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).

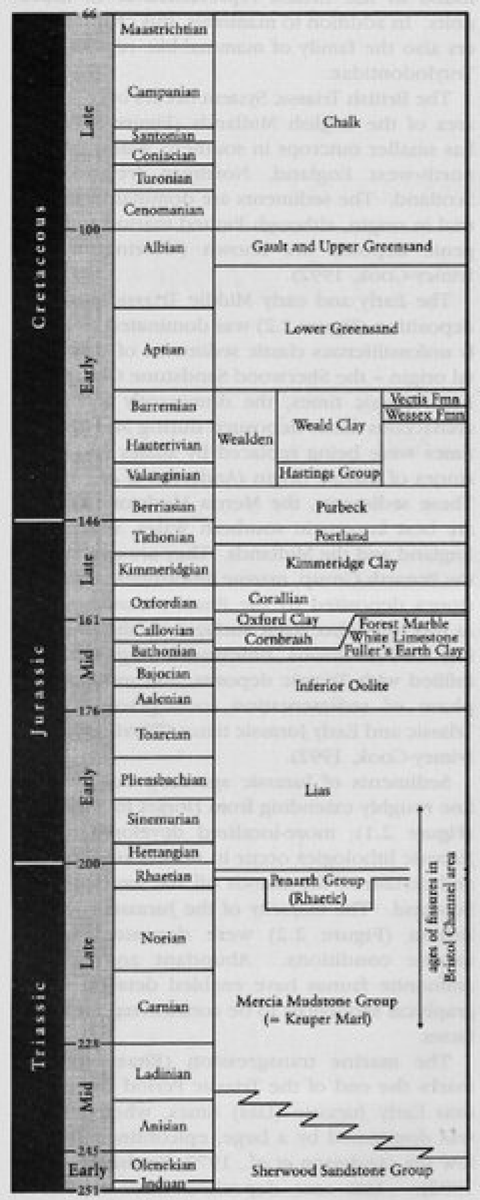
Emborough Quarry is no longer worked; it contains a fissure, where sediments have infilled a collapsed cave in the Mendip Hills. The sediments are generally poorly sorted, with locally derived boulders and coarse conglomerates held in a red marl matrix. Although Emborough Quarry fissure material, like 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 *Kuehneotherium.* Two teeth have been described. The first is a lower molar, the second a premolar (Fraser *et* ed., 1985).

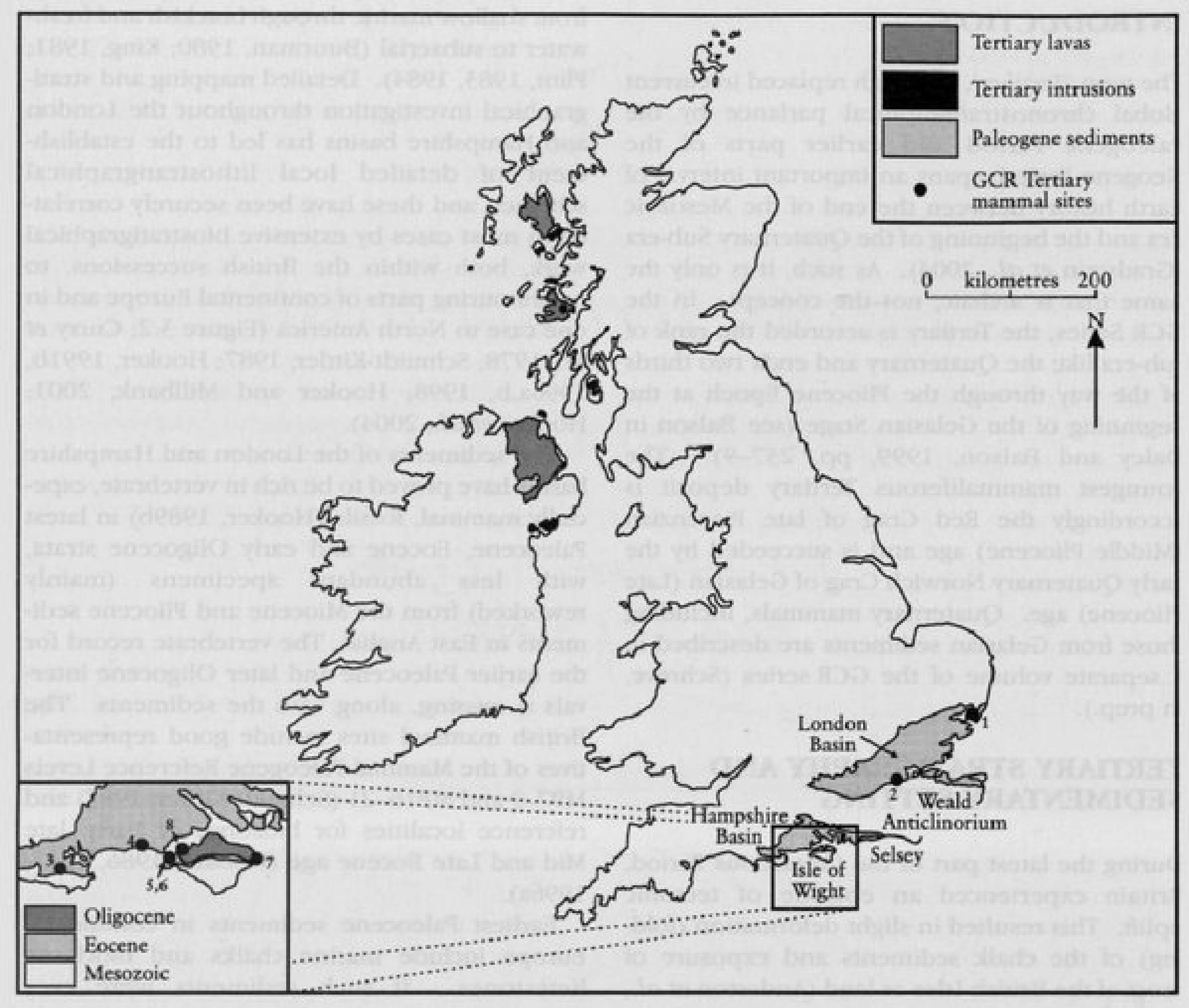
References



(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 Chicksgrove Quarry; 9 — Durlston Bay; 10 — Cliff End.



(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.)



(Figure 3.1) Map showing the distribution of Tertiary rocks in the UK. GCR Tertiary mammal sites: (1) Ferry Cliff; (2) Abbey Wood; (3) Creechbarrow Hill; (4) Hordle Cliff; (5) Headon Hill; (6) Lacey's Farm Quarry; (7) Whitecliff Bay; (8) Bouldnor Cliff.