Mesozoic and Tertiary Fossil Mammals and Birds of Great Britain

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Chapter 3

British Tertiary fossil mammal GCR sites

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INTRODUCTION

The term 'Tertiary', although replaced in current global chronostratigraphical parlance by the Paleogene Period and earlier parts of the Neogene Period, spans an important interval of Earth history between the end of the Mesozoic Era and the beginning of the Quaternary Sub-era (Gradstein et al., 2004). As such, it is only the name that is archaic, not the concept. In the GCR Series, the Tertiary is accorded the rank of sub-era like the Quaternary and ends two thirds of the way through the Pliocene Epoch at the beginning of the Gelasian Stage (see Balson in Daley and Balson, 1999, pp. 237-9). The youngest mammaliferous Tertiary deposit is accordingly the Red Crag of late Piacenzian (Middle Pliocene) age and is succeeded by the early Quaternary Norwich Crag of Gelasian (Late Pliocene) age. Quaternary mammals, including those from Gelasian sediments are described in a separate volume of the GCR series (Schreve, in prep.).

TERTIARY STRATIGRAPHY AND SEDIMENTARY SETTING

During the latest part of the Cretaceous Period, Britain experienced an episode of tectonic uplift. This resulted in slight deformation (folding) of the chalk sediments and exposure of most of the British Isles as land (Anderton et al., 1979). The modern tectonic context of the British Isles developed at this time: uplift in the north-west and subsidence in the south-east, and this pattern of exposure continued throughout most of the Tertiary Sub-era. By late Paleocene times the basic shape of the modern coastline had evolved (Murray, 1992) and it differed from that of today mainly in that the North Sea incorporated much of south-east England from Dorset to Norfolk. Moreover, late in the Paleocene Epoch and early in the Eocene Epoch there was an intermittent land bridge to North America via Greenland, the North Atlantic being at an early stage of rifting.

Early Tertiary (Paleogene) sediments accumulated in one large depositional basin that is now divided by folding into the London and Hampshire tectonic basins (Figure 3.1). The succession spans some 26 million years, and it accumulated either in, or offshore from, a lowlying coastal area (Daley, 1972; King, 1981). The sedimentary environments represented range from shallow marine through brackish and freshwater to subaerial (Buurman, 1980; King, 1981; Plint, 1983, 1984). Detailed mapping and stratigraphical investigation throughout the London and Hampshire basins has led to the establishment of detailed local lithostratigraphical schemes, and these have been securely correlated in most cases by extensive biostratigraphical work, both within the British successions, to neighbouring parts of continental Europe and in one case to North America (Figure 3.2; Curry *et al.*, 1978; Schmidt-Kittler, 1987; Hooker, 1991b, 1996a,b, 1998; Hooker and Millbank, 2001; Hooker *et al.*, 2004).

The sediments of the London and Hampshire basins have proved to be rich in vertebrate, especially mammal, fossils (Hooker, 1989b) in latest Paleocene, Eocene and early Oligocene strata, with less abundant specimens (mainly reworked) from the Miocene and Pliocene sediments in East Anglia. The vertebrate record for the earlier Paleocene and later Oligocene intervals is missing, along with the sediments. The British mammal sites include good representatives of the Mammal Paleogene Reference Levels MP7–9 and MP16–21 (Schmidt-Kittler, 1987) and reference localities for biozones of Early, late Mid and Late Eocene age (Hooker, 1986, 1987, 1996a).

Earliest Paleocene sediments in continental Europe include marine chalks and bioclastic limestones. If such sediments were ever deposited in Britain, they were subsequently removed by erosion. The first preserved sediments (the Thanet Formation) of late Paleocene (Thanetian) age in Britain are restricted to eastern parts of the London Basin, and the fullest sequence occurs in eastern Kent. These sediments are marine in origin and comprise finegrained sands, silts and clays (Murray, 1992). Further transgression during the youngest part of the Paleocene Epoch led to the short-term spread of shallow marine environments across the entire London and Hampshire basins. The resulting thin unit is the Upnor Formation (formerly known as the Woolwich/Reading Bottom Bed; Ellison et al., 1994). A single mammal specimen is known from the Upnor Formation, indicative of the Cernaysian European Land Mammal Age (Hooker and Millbank, 2001.)

There has been much past discussion on where best to place the Paleocene–Eocene epoch boundary. This debate reached its peak during the last decade with International

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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.

Geological Correlation Programme Project 308. Previously, most workers distributed those strata between the Upnor Formation and division A2 of the London Clay Formation to either the Paleocene or the Eocene epochs or some to each. Some workers, however, preferred to regard these strata as belonging to the 'Paleocene-Eocene boundary interval' in anticipation of a final decision on placement by the International Union of Geological Sciences (IUGS). The latter standpoint was taken for the purposes of one earlier published GCR volume on fossil plants (Cleal et al., 2001), whereas in another (Daley and Balson, 1999) the boundary was placed between the Woolwich and Reading formations below and the 'Harwich Formation'

above. The IUGS has now ratified the global position of the Paleocene-Eocene boundary as being marked by the beginning of the Carbon Isotope Excursion (CIE) and fixed the Global Standard Stratotype-section and Point (GSSP) at Dababiya, Egypt. Recognition of the Paleocene-Eocene boundary in Britain relies on recognition of the CIE and/or the associated biotic proxies. The CIE marks an abrupt 200 thousand-year long warming event that co-incided with, and was apparently the cause of, widespread extinction of deep marine benthos, especially foraminifera, known as the 'Benthic Foram Extinction' (BFE); a near global acme in marine dinoflagellates of the genus Apectodinium; and the Mammalian Dispersal Event (MDE) that saw

the sudden appearance of many modern mammalian groups in the Northern Hemisphere and which represented their earliest global records (Berggren *et al.*, 1995). In Britain, the CIE has been recognized in soil nodules in the lower part of the Reading Formation in the Jubilee Line borehole 404T in central London (Thiry *et al.*, 1998) and in the Cobham Lignite Bed at Cobham, Kent (Collinson *et al.*, 2003). Both underlie the lower shell beds of the Woolwich Formation that contain the *Apectodinium* acme. We can now therefore be more precise about which units in the London and Hampshire basins are the late Paleocene and which are early Eocene in age.

The latest Paleocene times in Britain (the top of the Upnor Formation) were marked by widespread regression, leading to deposition of the Woolwich and Reading formations. During the deposition of these strata all of the British Isles except the extreme south-east of England was land, although generally of low relief. It is thought that the overall pattern of fluvial drainage was towards the south-east. The Reading Formation sediments are predominantly mottled green and red clays, with local developments of sandy pebble beds. Palaeosols are present and are thought to represent deposition under fluviomarine conditions with a predominantly warm, seasonally dry climate (Murray, 1992; Newell, 2001). Low-energy, brackishwater environments are represented by the Woolwich Formation, which interdigitates with the Reading Formation. Vertebrates are very rare in the Reading Formation, but a few mammals are known from the Woolwich Formation.

The succeeding London Clay Formation crops out in the London and Hampshire basins. It represents the spread of fully marine conditions over the whole area. The sediments form a thick sequence of dark-grey muds, which shows five transgression-regression cyclical events. Arenaceous horizons are found locally at the base (Murray, 1992), namely the Oldhaven Formation, Blackheath Beds, Suffolk Pebble Beds. The London Clay Formation is extremely fossiliferous and preserves many plant (Chandler, 1978; Collinson, 1983a; Cleal et al., 2001), invertebrate and vertebrate taxa. In the London Basin the maximum water depth during the deposition of the London Clay Formation has been estimated at some 200 m. In the neighbouring Hampshire Basin the environment of deposition is thought to have been one of shallow, occasionally brackish, seas (Murray, 1992).

Towards the end of Early Eocene (late Ypresian) times, and during the early Mid Eocene (Lutetian Stage), sedimentation was more arenaceous in nature, resulting in the deposition in the eastern Hampshire Basin of the Bracklesham Group. Similar sediments in the London Basin are often referred to informally as the 'Bagshot Beds'. In the western Hampshire Basin, continental time-equivalents of the Bracklesham Group are called the 'Bournemouth Group'. The two groups interdigitate on the Isle of Wight (Murray and Wright, 1974; Edwards and Freshney, 1987).

In late Mid Eocene (Bartonian) times, renewed westerly spread of marine environments began, represented by the Barton Clay Formation, and ended with a major regression, represented by the Becton Sand Formation (Hooker, 1986). A non-marine representative of this time interval is the Creechbarrow Limestone Formation of Dorset.

The Late Eocene (Priabonian) and early Oligocene (Rupelian) strata have a restricted outcrop area: they are found only in Hampshire and on the Isle of Wight. Widespread sea-level fall at the end of Mid Eocene time (Plint, 1988) meant that Priabonian and Rupelian sediments are dominantly non-marine, with a few restricted marine intercalations.

The sequence of mammal faunas in the Late Eocene and Early Oligocene sediments of the Hampshire Basin offers a unique opportunity to erect a relatively continuous biostratigraphical scheme spanning some 4 million years. The relative continuity of deposition and the succession of mammal-bearing horizons are not matched anywhere in continental Europe, where most of the localities are more isolated (Hooker, 1987; Hooker *et al.*, 2004).

The Miocene and Pliocene epochs are poorly represented in Great Britain by sediments. Probably the only existing Miocene deposits are the marine late Messinian Lenham Beds of Kent and possibly the continental Brassington Formation of Derbyshire. Both lack vertebrates. The pre-Gelasian Pliocene is represented only by the Coralline and Red Crags and by their shared Basement Bed, whose outcrop is restricted to north-east Essex and south-east Suffolk (Balson in Daley and Balson, 1999). Both formations are marine. The Coralline Crag (late Zanclean to early Piacenzian stages) has yielded only cetaceans, but the Red Crag (late Piacenzian)

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Figure 3.2 Summary of British Paleogene stratigraphy, showing the British formations and their main members calibrated to the timescale via biostratigraphy. Abbreviations: BB = Blackheath Beds; ELMA = European Land Mammal Age; EO-RHIN = Palaeotherium eocaenum-Lophiodon rhinocerodes Zone; FS = Palaeotherium curtum frohnstettense-P. medium suevicum Zone; LAUT-SID = Lophiodon lautricense-Lophiotherium siderolithicum Zone; Ma = millions of years before present; MBR = member; MC = Palaeotherium medium medium-P. curtum curtum Zone; MP = Paleogene Mammalian Reference level; NP = standard Paleogene calcareous nannoplankton zonation; P = standard Paleogene planktonic foram zonation; PE = mammal zones spanning the Neustrian; PT = Isoptychus pseudosiderolithicus-Palaeotherium muehlbergi thaleri Zone; SD = Palaeotherium magnum stehlini-Tarnomys depereti Zone; SPB = Suffolk Pebble Beds; VN = Tarnomys quercyi vectisensis-Heterobyus nanus Zone. For space reasons, the SPB are shown overlying the Woolwich Formation; in fact they overlie the Reading Formation. (Modified from Schmidt-Kittler, 1987; Hooker, 1992; 1996a; Hooker et al., 2004; Collinson, 1996.)

and the Basement Bed have yielded a diverse fauna of land and marine mammals. Most, but not all of the latter appear to occur as reworked fossils in the Basement Bed (also known as the 'Suffolk Bone Bed', 'Nodule Bed', 'Coprolite Bed', 'Boxstone Bed' and 'Sub-Crag Detritus Bed': Balson in Daley and Balson, 1999), although stratigraphical data associated with the mainly 19th Century collections are poor. The fauna was recorded in a monograph by Newton (1891) but remains largely unrevised today. It has long been recognized that fossils from the Basement Bed (and in some cases in the main mass of the Red Crag) are reworked from older deposits that have all but been removed by sub-Crag erosion. Some fossils retain matrix attributable to one deposit, which consists largely of reworked nodules. This deposit has been named the 'Trimley Sands' (incorporating also the term 'Boxstones'). Most of the fossils, including those with 'Trimley Sands' matrix, are thought to be of early Pliocene age, whereas others may date from Miocene times (Balson, 1990; Balson in Daley and Balson, 1999). Some are even older, dating clearly from the Early Eocene, namely the dawn horses Hyracotherium leporinum and Pliolophus vulpiceps (Hooker, 1980, 1994a) and the pantodont Coryphodon, reworked from the underlying London Clay Formation. The unique enigmatic

toothless cranium of 'Xipbodon' platyceps is possibly from a later Eocene deposit now completely eroded away. Together with these reworked fossils are a few that are autochthonous, e.g. the proboscidean *Mammuthus* cf. *rumanus* (Lister and Van Essen, 2004) and the giant deer, *Megaloceros*, which have apparently been found in the main mass of the Red Crag (Spencer, 1971).

MAMMAL EVOLUTION IN THE BRITISH TERTIARY SUB-ERA

The outlines of mammal evolution have been given in Chapter 1. In summary, the time-span represented by British fossil mammal-bearing beds, from the latest Palaeocene to early Oligocene times, encompasses some major changes in mammalian faunas. This time-span documents the maximum ordinal diversity of mammals, when both archaic and modern mammalian orders were present. The archaic orders are those that arose in the Paleocene Epoch or earlier and became extinct relatively early in the Tertiary Sub-era, whereas modern orders and families were still undergoing their initial diversification. Further details of the typical mammal groups are given in Chapter 1 and in general texts such as Savage and Long (1986), Carroll (1988), Benton (2005) and Rose and Archibald (2005). Krause (1984) and Rose (1984) gave detailed accounts of the mammal groups of the Paleocene and Eocene epochs respectively, essentially based on the North American record. More up-to-date accounts of the Paleocene radiation (Alroy, 1999) and of the carnivores and hoofed mammals (Janis et al., 1998) are now available. However, there is much of relevance to Europe also, because there were several phases of faunal interchange between the two continents during these two epochs.

Major changes in habitats and in mammalian adaptations occurred during the Eocene to early Oligocene interval (Collinson and Hooker, 1987; Hooker *et al.*, 1995, 2004). Collinson and Hooker (1987) gave an account of these changes, based on extensive study of fruits, seeds and megaspores and of mammalian bones and teeth.

Latest Paleocene and earliest Eocene floras in southern England indicate open and disturbed environments with limited wooded/forested areas but with mammalian communities that today are typical of closed forest vegetation (few large mammals or herbivore browsers). This incongruence probably results from the plants and mammals being provenanced from different areas or local habitats.

In southern England dense forest of tropical aspect characterized the Early to early Mid Eocene environments, and mammals showed a high ratio of small to large ground-dwelling forms, a relatively high percentage of arboreal species and adaptations to eating soft fruit and low-fibre-content leaves. By early Late Eocene times many tropical taxa had been lost and the vegetation was characterized by reed marshes and swamps with patches of woodland or forest. In latest Eocene times, an extensive and persistent reed marsh developed. These changes were accompanied by extinctions of many earlier mammalian adaptive types, a reduction in arboreal species and an increase in large grounddwelling forms, especially herbivores with specializations for a higher-fibre diet.

In more detail, Collinson and Hooker (1987) showed the evolution of dietary preferences among rodents and perissodactyls through the English Eocene to early Oligocene interval (Figure 3.3). Among rodents, there was a complete turnover in diets, from a fauna dominated by microparamyines and paramyines with mixed insectivorous-frugivorous diets in the earliest Eocene times to faunas dominated by manitshine (now pseudoparamyine) paramyids and pseudosciurids that specialized in a soft-fruit diet in Mid Eocene time. The associated palaeobotanical evidence bears this out, with abundant finds of taxa that today bear soft fruits and are components of tropical forest vegetation, and this is supported by fruits from the Middle Eocene Messel locality in Germany that have the fleshy parts preserved. In Late Eocene times, theridomyid rodents with adaptations for browsing became important, as did glirids, with their mixed insectivore-granivore adaptations. Finally, in earliest Oligocene times, eomvids and cricetids, which specialized in eating harder fruits and seeds, appeared in low abundances.

The perissodactyls show a more dramatic oneway change, from a mixed frugivore-herbivore diet to a purely browsing herbivorous one. The Early Eocene horses and their extinct European relatives, the palaeotheres, fed on fruit as well as browsing leaves from low bushes. They belonged to the genera *Pliolophus*, *Hyracotherium* and *Cymbalophus*. Later relatives of

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Figure 3.3 History of the ecology of mammals in southern England during the Eocene and Oligocene epochs. Dietary shifts of the major groups are indicated as percentage abundance, based on numbers of specimens, within particular faunas (indicated at the side of each column). Two major groups, the rodents and perissodactyls, are shown. Among rodents, the generalist insectivore/frugivores gave way to more specialist frugivores and browsers in Middle Eocene times and to dominantly frugivore/browsers by Late Eocene times. Among perissodactyls, partly frugivorous early horses were replaced gradually by browsers. (Based on Collinson and Hooker, 1987.)

Hyracotherium, species of the palaeothere genus Propalaeotherium, had teeth with longer crests that were adapted for a greater component of browsing in the diet, although these horses still ate fruits, as is confirmed by preserved stomach contents in specimens from Messel (Franzen, 2001). During Early and Mid Eocene times, new genera of larger perissodactyls with stricter adaptations to browsing became dominant. Genera such as Lophiodon and Hyrachyus were at first minor components of the faunas. With their bilophodont teeth, they were adapted to bulk feeding in an environment with a year-round supply of leaves (Hooker, 2000a). Later in the Eocene Epoch, new genera such as Palaeotherium and Plagiolophus, with teeth of a selenolophodont pattern, showed increasing crown height and molarization of their premolars, thus providing increased surface area for chewing and hence a firmer adaptation to a solely browsing diet. Several of the named perissodactyl genera became extinct in late Mid Eocene time, and Palaeotherium and Plagiolophus took over as the dominant forms until earliest Oligocene times, when the rhinoceros Ronzotherium replaced them.

These changes in generic dominance through Mid and Late Eocene times also document a major change in the dominant large browsing herbivores, from the hyrachyids and lophiodonts to the palaeotheres Palaeotherium and Plagiolophus. This switch is associated with a change in tooth type from the bilophodont to the selenolophodont type (Collinson and Hooker, 1987). The bilophodont cheek tooth bears two transverse crests (lophs), and it is seen today in the tapir Tapirus, which specializes in eating the leaves of forest trees. The bilophodont tooth shears the leaves coarsely, and they are swallowed in relatively large frag-The selenolophodont tooth of the ments. palaeotheres is more complex, bearing sharpedged ridges made from upright plates of enamel, which wear against the opposing teeth to produce a series of shearing surfaces. Such teeth are seen today in the hyrax Heterohyrax, which generally is a browser and feeds on tough dry leaves, twigs and bark, which it shears, crushes and grinds into a very fine mush before swal-This comparison suggests a major lowing. change in browsing pattern in the British and continental European Eocene herbivorous perissodactyls, from soft to tough vegetation and to a relatively more efficient feeding mode.

The Hampshire Basin sequence of mammalbearing sediments spans the Eocene-Oligocene boundary. The earliest Oligocene was a time of major extinctions among mammals in Europe, termed the 'Grande Coupure'. The extinction event occurs within the Hamstead Member of the Bouldnor Formation; it is marked by the loss of numerous mammalian species and followed by the origins of new taxa of lipotyphlan insectivorans, rodents and ungulates (Hooker et al., 2004). This event had been dated previously to lie precisely at the Eocene-Oligocene boundary, and to be caused perhaps by climate change or by competition with new mammal species dispersing into Europe from Asia. Close study of the sequences in the Hampshire Basin shows first that the major event happened in earliest Oligocene time, and that it was preceded by a smaller extinction event that correlated with vegetational change. The 'Grande Coupure' itself co-incided with the earliest Oligocene glaciation, so it is likely that climate change, as well as competition with the new Asian mammals, combined to produce the faunal turnover (Hooker et al., 2004).

After a gap of some 25 million years, we get a glimpse of British late Tertiary mammals from the Basement Bed of the Coralline and Red Crags. Dated as early Pliocene (and/or possibly late Miocene) in age, the fauna is very different from that of the latest preserved Paleogene and much more modern in character. Land mammals are represented by large proboscideans such as the gomphothere Anancus arvernensis and the mammutid Mammut borsoni, the threetoed horse 'Hipparion', a tapir, Tapirus arvernensis?, a large rhino, deer, a bovid, a large relative of the Red Panda (Parailurus anglicus) and several other carnivorans belonging to modern families, namely a cat, a hyaena, an otter and two bears, a monkey (?Mesopithecus cf. monspessulanus), and a few large rodents (size here almost certainly resulting from a preservational bias), namely the beavers Castor and Trogontherium and the porcupine Hystrix (including evidence from gnawed bones - Sutcliffe and Collings, 1972). Marine mammals are represented by a diversity of whalebone and toothed cetaceans, identified mainly from ear bones, rostra and teeth. They belong to the modern families Balaenopteridae (rorquals), Balaenidae (right whales), Physeteridae (sperm whales), Ziphiidae (beaked whales), Delphinidae (dolphins) and the extinct Cetotheriidae and Squalodontidae.

Also present are a few seals, the walrus *Trichecodon buxleyi* and the dugongid sea-cow *'Halitherium' canhami*. The Middle Pliocene strata, represented by the main Red Crag deposition saw the appearance of the first members of the elephant family in Britain (Lister and Van Essen, 2004). These late Tertiary faunas have not been recently comprehensively revised and therefore some identifications may be unreliable (for recent reviews and some up to date identifications, see Spencer, 1971; Delson, 1974; Mayhew, 1978; Stuart, 1982; Pilleri, 1987, pp. 139–41; Van Essen and Mol, 1996; Lister, 1996, 1999; Forstén, 2002; Lister and Van Essen, 2004).

BRITISH TERTIARY MAMMAL SITES

Mammals have been reported from many localities in the London and Hampshire basins (Hooker et al., 1980). Fossiliferous sites are predominantly located in extensive coastal sections, some along the northern and southern banks of the Thames Estuary and others along the south coast of Hampshire and the north and northwestern coasts of the Isle of Wight. Other sites comprised quarries or temporary construction sites. An outline of the main locations is noted here, together with the name of the fossiliferous unit. Localities are arranged according to their occurrence in the London Basin (London, Suffolk. Essex, Surrey, Sussex, Kent, Hertfordshire, Berkshire) or the Hampshire Basin (Hampshire, Isle of Wight, Dorset). Most Crag localities in Suffolk are imprecise, so grid references are mostly omitted (see Balson, 1999, for guidance).

LONDON: Dulwich (TQ 33 74; limb bones and jaw, referable to *Coryphodon* sp. and a plesiadapid respectively; Woolwich Shell Beds, Woolwich Formation; Rickman, 1861; Hooker *et al.*, 1980; Hooker, 1991b): Sydenham (TQ 34 71 or TQ 33 72; *Coryphodon* sp.; Woolwich Shell Beds, Woolwich Formation; Allport, 1841; Hooker *et al.*, 1980): Abbey Wood (see GCR site report below).

SUFFOLK: Kyson, near Woodbridge (TM 270 475; Leptictidae? indet., Pantolestidae indet., Chiromyoides sp., Cantius eppsi, Paramys sp., Meldimys? sp., Arfia junnei, Viverravidae indet., Miacidae indet., Landenodon sp., Microbyus musculus, Hyopsodus wardi, type of Cymbalophus cuniculus, Diacodexis sp.; Early Eocene (Ypresian) Suffolk Pebble Beds; Prestwich, 1850; Ward and Cooper, 1971; Hooker, 1980, 1984, 1994a, 1998; Hooker et al., 1980; Sudre et al., 1983): Ferry Cliff, near Woodbridge (see GCR site report below): Bramford (TM 130 477; Cymbalophus cuniculus; Early Eocene Suffolk Pebble Beds; Cooper, 1976b; Hooker et al., 1980; Hooker, 1984, 1994c): Ramsholt (TM 298 429-TM 297 427; Tursiops sp.; Pliocene Coralline Crag; Newton, 1891); Sudbourne (Balaenula balaenopsis, Megaptera affinis; Coralline Crag; Newton, 1891): Boyton (Castor fiber, Leptobos sp., 'Aceratherium incisivum'; Pliocene Red Crag, but mainly as reworked fossils from the Basement Bed; Newton, 1891): Bramford (Hystrix sp.; Red Crag; Spencer, 1971): Butley (Parailurus anglicus; Red Crag, but as reworked fossil from the Basement Bed; Newton, 1891): Falkenham (Mammuthus cf. rumanus; Red Crag; Spencer, 1971; Lister and Van Essen, 2004): Felixstowe (type of Trogontherium minus, Pachycrocuta perrieri, type of Parailurus anglicus, Agriotherium sp., Trichecodon huxleyi, Cervus pardinensis, Procapreolus cusanus, Balaenula balaenopsis, Balaenoptera definita, *B*. emarginata, Plesiocetus dubius, Herpetocetus scaldiensis, Balaenodon physaloides, Mammut borsoni, Anancus arvernensis, Hipparion gr. crassum, 'Aceratherium incisivum', Tapirus arvernensis; Red Crag, but mainly as reworked fossils from the Basement Bed; Newton, 1891; Lister, 1999; Forstén, 2002): Foxhall, near Waldringfield (Pannonictis pilgrimi, Trichecodon huxleyi, type of Phoca moori, Phocanella minor, type of 'Halitherium' canhami; Red Crag, but mainly as reworked fossils from the Basement Bed; Newton, 1891; Spencer, 1971): Newbourn (Castor veterior, type of Felis pardoides; Red Crag, but mainly as reworked fossils from the Basement Bed; Newton, 1891): Shotley (Choneziphius planus; Red Crag, but as reworked fossils from the Basement Bed; Owen, 1870-1889): Sutton (Castor veterior, Ursus arvernensis, Cervus perrieri, Mammut borsoni, Tapirus arvernensis; Red Crag, but mainly as reworked fossils from the Basement Bed; Newton, 1891; Lister, 1999): Trimlev (Megaloceros sp., Mesoplodon floris, Mammuthus cf. rumanus; Red Crag; Newton, 1891; Spencer 1971; Lister and Van Essen, 2004): Waldringfield (Agriotherium sp., Phoca moori,

Tapirus arvernensis; Red Crag, but mainly as reworked fossils from the Basement Bed; Newton, 1891): Woodbridge (Felis pardoides, Parailurus anglicus, Ursus arvernensis, Trichecodon buxleyi, Cervus pardinensis, Balaena affinis, B. primigenia, Balaenotus insignis, Burtinopsis similis, Balaenodon pbysaloides, Pbyseterula dubusii, Scaldicetus fusiformis, Choneziphius planirostris, Mesoplodon longirostris, M. scaphoides, 'Globicephalus' uncidens, Squalodon antwerpiensis, Mammut borsoni, Tetralophodon longirostris, Anancus arvernensis, Tapirus arvernensis, Coryphodon sp.; Red Crag, but mainly as reworked fossils from the Basement Bed; Newton, 1891; Lister, 1999): no locality, Suffolk (?Mesopithecus cf. monspessulanus; Red Crag; Delson, 1974).

ESSEX: Harwich Harbour area (TM 26 32; submarine exposures act as a source for material collecting in beach gravels: Landenodon sp., Microbyus musculus, Early Eocene Suffolk Pebble Beds; Thompson, 1911; Elliott, 1970; Hooker et al., 1980; type of Coryphodon eocaenus; ?Harwich Member, London Clay Formation, dredged offshore between Harwich and St Osyth; type of Pliolophus vulpiceps; Early Eocene Harwich Stone Band, Harwich Member, London Clay Formation; Elliott, 1970; Hooker, 1980, 1991b; Hooker et al., 1980): Walton-onthe-Naze (TM 266 234-TM 266 238; Pliolophus vulpiceps; Early Eocene high division A1 or low division A2, London Clay Formation; Daniels, 1971; see site report Chapter 4; Red Crag mammals, including whales; Owen, 1870-89; Daley and Balson, 1999, pp. 291, 317-22).

SURREY: Croydon (TQ 340 655; Coryphodon sp.; Early Eocene Woolwich Shell Beds, Woolwich Formation; Klaassen, 1883; Hooker et al., 1980; Lucas, 1998).

SUSSEX: East Wittering, Bracklesham Bay (SZ 777 973–SZ 793 966; Ailuravus michauxi; Saturninia sp., Nannopithex zuccolae; Early Eocene Wittering Formation, Bracklesham Group; Hooker, 1996b): Bracklesham, Bracklesham Bay (SZ 805 962; Hyrachyus aff. stehlini; early Mid Eocene (Lutetian) Earnley Formation, Bracklesham Group; Hooker, 1996b): Earnley Marshes, Bracklesham Bay (SZ 823 951–SZ 825 947; Amphiperatherium sp., Saturninia sp., Pachynolophus aff. boixe*datensis*; early Mid Eocene Marsh Farm Formation, Bracklesham Group; Hooker 1996b).

KENT: Studd Hill, Herne Bay (TR 152 677; type of Hyracotherium leporinum; vicinity of the Isselicrinus horizon, Early Eocene division B, London Clay Formation; Richardson, 1841; Cooper, 1977; Hooker, 1980, 1991b; Hooker et al., 1980; see Figure 3.8i): Herne Bay coastal section (TR 187 683-TR 197 684; type of Platychoerops richardsonii; Early Eocene divisions A2-B, London Clay Formation; Gingerich, 1976): Beltinge, near Herne Bay (TR 203 689; Arctocyonides arenae tooth; Late Paleocene, Upnor Formation; Hooker and Millbank, 2001); Sheppey (TL 955 738-TM 024 717; Leptacodon sp., type of Toliapina lawsoni, Platychoerops richardsonii, type of Argillotherium toliapicum, Hyracotherium leporinum; Early Eocene divisions D-E, London Clay Formation; Davis, 1936; Hooker, 1994a; Hooker et al., 1999; Hooker, 2000b; Smith and Smith, 2003: Upnor (TQ 765 714; 'Paramys ageiensis'; basal Swanscombe Member, London Clay Formation; Hooker, 1991b).

HERTFORDSHIRE: Bignell's Corner, South Mimms (TL 227 007; indeterminate insectivoran tooth; Early Eocene Tilehurst Member, Oldhaven Formation; Ward, 1976).

BERKSHIRE: Burghfield, near Reading (SU 67 68; *Landenodon*; Early Eocene Tilehurst Member, Oldhaven Formation; Hooker, 1991b).

HAMPSHIRE: Royden, near Brockenhurst (SU 319 004; Zygorbiza sp. Late Eocene (Priabonian) Brockenhurst Bed, Colwell Bay Member, Headon Hill Formation; Judd, 1880; Kellogg, 1936; Halstead and Middleton, 1972; Cray, 1973; Hooker et al., 1980): Dummer's Copse, near West End (SU 45 15; Peratherium sp., Amphiperatherium maximum, Pantrogna marandati, Buxolestes sp., Saturninia sp., Nannopithex zuccolae, Hyracotherium leporinum, Early Eocene Wittering Formation, Bracklesham Group; Hooker, 1996b; Escarguel, 1999): Lee-on-the-Solent (SU 551 016-SZ 569 999; 'Propalaeotherium' aff. parvulum early Mid Eocene; Selsey Formation, Bracklesham Group; Hooker et al., 1980; Hooker, 1996b): Elmore, near Lee-on-the-Solent (SU 563 001-SZ 565 996; 'Propalaeotherium'

British Tertiary mammal sites

aff. parvulum, Palaeotherium sp., Lophiodon cf. cuvieri; early Mid Eocene Elmore Member, Barton Clay Formation; Hooker, 1986): Barton Cliff, Barton, near Christchurch (SZ 218 930– SZ 252 952; Zygorbiza wanklyni, Basilosaurus sp., Plagiolophus curtisi curtisi, Palaeotherium aff. ?muehlbergi, Cebochoerus belveticus; late Mid Eocene (Bartonian) Barton Clay Formation; Halstead and Middleton, 1972; Hooker, 1972, 1986; Hooker et al., 1980; Sudre, 1978): Hordle Cliff (see GCR site report below).

ISLE OF WIGHT: Totland Bay (SZ 323 873-SZ 323 874; Amphiperatherium spp., Cryptotopos woodi, Scraeva batherwoodensis, Microchoerus erinaceus, Suevosciurus bosmae, Treposciurus mutabilis, Sciuroides ebrensteinensis, Tarnomys quercyi vectisensis, Thalerimys fordi; Late Eocene Totland Bay Member, Headon Hill Formation; Bosma, 1974; Hooker, 1991a; Hooker et al., 1980; Hooker and Weidmann, 2000): Colwell Bay (SZ 327 878-SZ 328 881; Thalerimys fordi; Late Eocene Colwell Bay Member, Headon Hill Formation; Hooker et al., 1980): Fishbourne area, including Wootton Creek, Kingsquay, Chapelcorner Copse (SZ 537 941-SZ 556 934; Amphiperatherium spp., Thalerimys fordi, Isoptychus sp., Plagiolophus annectens; Late Eocene Fishbourne Member, Headon Hill Formation; Colenutt, 1888; Hooker, 1987; Hooker et al., 1980): Binstead (SZ 57 92; Plagiolophus annectens, Palaeotherium magnum, Palaeotherium muehlbergi, Palaeotherium cf curtum, Anoplotherium sp., type of Dichodon cervinus, Dichodon cuspidatus; Late Eocene Seagrove Bay Member, Headon Hill Formation; Forbes, 1856; Hooker et al., 1980; Hooker, 1992): Seafield (SZ 625 915; Palaeotherium magnum, Choeropotamus parisiensis; Late Eocene Seagrove Bay Member, Headon Hill Formation; Forbes, 1856; Colenutt, 1893; Hooker et al., 1980): Tapnell Quarry, near Shalcombe (SZ 3770 9639; Amphiperatherium spp., Glamys devoogdi, Isoptychus sp., Anoplotherium cf laurillardi; Late Eocene Bembridge Limestone Formation; Insole, 1972; Hooker et al., 1980; Hooker, 1994b): Prospect Quarry (SZ 385 866; Anchilophus radegondensis, Plagiolophus minor, Palaeotherium medium medium; Late Eocene Bembridge Limestone Formation; Insole, 1972; Hooker et al., 1980): Cliff End (Sconce) (SZ 333 892; Palaeotherium magnum magnum, Palaeotherium muehlbergi

mueblbergi, Palaeotherium medium medium; Late Eocene Bembridge Limestone Formation; Forbes, 1856; Hooker et al., 1980): Gurnard Point (SZ 463 946; Amphiperatherium sp., Isoptychus sp., Glamys devoogdi; Late Eocene Bembridge Limestone Formation; Collinson et al., 1993): Yarmouth (SZ 364 899; Plagiolophus major, Palaeotherium medium suevicum, Anoplotherium sp.; Early Oligocene Bembridge Marls Member, Bouldnor Formation; Forbes, 1856; Franzen, 1968; Hooker, 1987; Hooker et al., 1980, 2004); ?Thorness Bay (SZ 440 929-SZ 464 946; Pterodon dasyuroides, Amphirhagatherium fronstettense, Anoplotherium sp.; Early Oligocene Bembridge Marls Member; Daley, 1973; Hooker et al., 1980; Hooker and Thomas, 2001): Headon Hill, Lacey's Farm Quarry, Whitecliff Bay and Bouldnor Cliff (see GCR site reports below).

DORSET: Hengistbury Head (SZ 175 905; Lophiodon cf. lautricense; 'Hengistbury Beds', Barton Clay Formation; Hooker, 1977a, 1986; Hooker *et al.*, 1980); Creechbarrow Hill (see GCR site report, below).

From these potential locations, eight are selected as GCR sites for their fossil mammal remains, two being Early Eocene in age (Ferry Cliff, Abbey Wood), one late Mid Eocene (Creechbarrow Hill), four Late Eocene (Hordle Cliff, Headon Hill, Lacey's Farm Quarry, Whitecliff Bay, the last site also Early Oligocene) and one Early Oligocene (Bouldnor Cliff). The Mammal Paleogene (MP) reference level numbers, Paleocene–Eocene (PE) zones and other biozonations are indicated for each site (based on Schmidt-Kittler, 1987; Hooker, 1986, 1987, 1996a).

- 1. Ferry Cliff, Suffolk (TM 278 486). Early Eocene (Ypresian) Suffolk Pebble Beds (MP7, Zone PEI).
- Abbey Wood, Greater London (TQ 480 786). Early Eocene (Ypresian) Blackheath Beds (MP8–9, Zone PEIII).
- 3. Creechbarrow Hill, Dorset (SY 922 824). Late Mid Eocene (Bartonian) Creechbarrow Limestone Formation (MP16, *lautricensesiderolithicum* Zone).
- 4. Hordle Cliff, Hampshire (SZ 254 925–SZ 270 921). Late Eocene (Priabonian) Totland Bay Member, Headon Hill Formation (MP17, *steb-lini–depereti* to *vectisensis–nanus* zones).

- Headon Hill, Isle of Wight (SZ 305 856–SZ 319 865). Late Eocene (Priabonian) Totland Bay Member to Lacey's Farm Limestone Member, Headon Hill Formation and Bembridge Limestone Formation (MP17–19, stehlini– depereti to medium–curtum zones).
- 6. Lacey's Farm Quarry, Totland, Isle of Wight (SZ 323 862). Late Eocene (Priabonian) Lacey's Farm Limestone Member, Headon Hill Formation (MP18, *pseudosiderolitbicus-thaleri* Zone).
- 7. Whitecliff Bay, Isle of Wight (SZ 643 864). Late Eocene (Priabonian) Totland Bay and Osborne members, Headon Hill Formation (MP17, *steblini-depereti* Zone and MP19 respectively); and early Oligocene (Rupelian) Bembridge Marls Member, Bouldnor Formation (MP20, *frohnstettense-suevicum* Zone).
- 8. Bouldnor Cliff, Isle of Wight (SZ 375 902–SZ 403 919). Early Oligocene (Rupelian) Hamstead Member, Bouldnor Formation (MP 20–21).

FERRY CLIFF, SUFFOLK (TM 278 486)

Introduction

The GCR site of Ferry Cliff, near Woodbridge in Suffolk preserves a sequence of Early Eocene sediments, including the mammal-bearing Suffolk Pebble Beds. The site was discovered by George and Vincent (1976) in the 1970s, and a fauna of molluscs, shark teeth and (probably reworked) mammal bones and teeth was obtained (Hooker, 1980, 1991b; Hooker *et al.*, 1980; King, 1981). The site is geographically close and stratigraphically identical to the classic site of Kyson, which has long been unavailable and built over.

Description

The Suffolk Pebble Beds are exposed along the banks of the River Deben on the foreshore (George and Vincent, 1976; Figure 3.4). There is



Figure 3.4 The riverside exposure of the Suffolk Pebble Beds at Ferry Cliff, Suffolk. The notebook is resting on the 25–35cm-thick pebble unit that overlies Reading Formation sands (Photo: J.J. Hooker.).

Ferry Cliff

a prominent stone band in the cliff, the Harwich Stone Band, and some 6.7 m below it in the foreshore section is a pebble bed, the 'Suffolk Pebble Bed' of George and Vincent (1976). This horizon is a thin (1-3 m) glauconitic sand that contains rounded flint pebbles as well as clay and limonite clasts. In places it is cemented to form a conglomerate. It occurs sandwiched between the London Clay Formation (above) and the Reading Formation (below), and it is interpreted to represent the initial transgressive phase of London Clay Formation deposition similar to the Blackheath Beds at Abbey Wood (Figure 3.5; see the Abbey Wood GCR site report in the present chapter).

Fauna

The Suffolk Pebble Beds at this site have produced many fossil specimens, including shark teeth and rarer molluscs and mammal teeth (King, 1981). Mammal names are taken from the listing in Hooker (1998).

MAMMALIA Marsupialia Herpetotheriidae Herpetotheriidae indet. Leptictida Leptictidae?

Leptictidae? indet. Rodentia Paramvidae 'Microparamys' nanus (Teilhard, 1927) Paramys sp. Pseudoparamys sp. Meldimys sp. Lipotyphla Adapisoriculidae Pontifactor sp. Amphilemuridae cf. Macrocranion sp. Archonta undiff. Nyctitheriidae Nyctitheriidae indet. Plesiadapiformes Plesiadapidae Platychoerops georgei Hooker, 1994c Chiromyoides sp. Primates Omomyidae Teilhardina belgica (Teilhard, 1927) Pantolesta Pantolestidae Pantolestidae indet. Carnivora Miacidae Miacidae indet. Viverravidae Viverravidae indet.



Figure 3.5 The Paleocene and Eocene sediments of the London Basin shown in a cross-section running from west to east across London. The Suffolk Pebble Beds are projected in from farther north. (After Savage and Russell, 1983.)

'Condylarthra'

Arctocyonidae Landenodon woutersi Quinet, 1968 Hyopsodontidae Hyopsodus wardi Hooker, 1979 Family and order attribution uncertain Paschatherium dolloi (Teilhard, 1927) Microbyus musculus Teilhard, 1927 Perissodactyla Equoidea Cymbalophus cuniculus (Owen, 1842)

To date, 8 named mammal species have been described from Ferry Cliff, together with 12 other less precisely identified mammalian taxa. The fauna is diverse and includes a typical array of Neustrian forms (cf. Savage and Russell, 1983, pp. 65-70), including an opossum-like marsupial (Herpetotheriidae indet.), a few primitive insectivorans, two plesiadapiforms (Figure 3.6a), a basal primate, two early carnivorans and Europe's oldest horse relative, Cymbalophus cuniculus (Owen, 1842) (Figure 3.6b,c), together with a number of other archaic mammalian types. Cymbalophus cuniculus was originally considered to be a species of Hyracotherium, but Hooker (1984) erected the new genus Cymbalophus for it, originally relating it to tapirs and rhinoceroses, but subsequently returning it to the equoid clade (Hooker, 1994a).

Interpretation

Problems have been encountered in determining the age of the Suffolk Pebble Beds. The mammalian fauna from Ferry Cliff compares best with that from Dormaal in Belgium, which is the reference locality for Mammal Paleogene Reference Level MP7 (Schmidt-Kittler, 1987). Try in France and Erquelinnes on the French-Belgian border also have similar faunas. All four are reference localities for the Zone PEI (Hooker, 1996a), which immediately post-dates the Mammalian Dispersal Event (MDE). The Suffolk Pebble Beds share the following taxa with Dormaal: Paschatherium dolloi. Landenodon woutersi, Platychoerops georgei, Teilhardina belgica, Microbyus musculus and 'Microparamys' nanus. However, the stratigraphical position of the Suffolk Pebble Beds at the base of the London Clay Formation implies an age nearly a million years younger than the mammal fauna (Hooker, 1998).

The reason for the discrepancy is probably that the mammal remains in the Suffolk Pebble Beds are reworked from a level of Dormaal age, perhaps the Reading Formation, into a level equivalent in time to the Blackheath Beds (which have a PEIII Zone mammal fauna). Hooker (1991b, p. 80; 1996a, p. 213) listed seven pieces of evidence for the proposal that the Suffolk Pebble Beds mammalian fauna is reworked:

- the Suffolk Pebble Beds specimens are robustly preserved, unlike the delicate bones from Abbey Wood, and many of them seem to have been rolled and abraded;
- 2. there are large clay clasts in the Suffolk Pebble Beds that could have been reworked from the underlying Reading Formation;



Figure 3.6 Mammal specimens from the Suffolk Pebble Beds of Ferry Cliff, Suffolk. (a) Internal view of upper incisor tooth of the plesiadapid *Platychoerops georgei* from the Suffolk Pebble Beds of Ferry Cliff, Suffolk; (b,c) Left lower jaw fragment of the early horse relative *Cymbalophus cuniculus* in internal (b) and external (c) views. (After Hooker, 1984, 1991b.)

- 3. there are rare charophytes and bithyniid oper-
- cula with oysters and shark teeth an unlikely assemblage in a near-shore marine highenergy depositional environment;
- 4. charophytes and bithyniid opercula are found together elsewhere in the London Basin only in the Reading Formation;
- 5. an old find of specimens of a plesiadapiform and of *Coryphodon* suggest an MP7 age for the Woolwich Formation, and the Woolwich Formation interdigitates with the Reading Formation, which perhaps suggests an MP7 age for them too;
- 6. Dormaal, and other MP7 mammal faunas from the continent, all occur below, not above, transgressive Ypresian deposits – this suggests perhaps a similar age assignment for the Reading Formation and an interpretation of the Suffolk Pebble Beds as a transgressive unit reworking previously deposited material.
- 7 The Suffolk Pebble Beds contain an abundance of Woolwich Formation pollen (Jolley and Spinner, 1991).

Comparison with other localities

The mammal assemblage preserved at Kyson and Ferry Cliff is approximately the same age as the faunas described from Dormaal and Erquelinnes in Belgium and Try in France. These faunas are the oldest of the Eocene, representing the first elements of the MDE. These five sites have produced some of the oldest examples of artiodactyls, perissodactyls and primates in the world, and certainly the oldest in Europe. Of these five, the mammal-producing unit at Ferry Cliff has the benefit of being the one intercalated in the least incomplete succession but at the same time suffers from the problem of reworking. The creodont species Arfia junnei is shared with earliest Eocene faunas of Wyoming, USA (A. gingerichi Smith and Smith, 2001, named for the European assemblages, is doubtfully distinct), and other species, although distinct, are very similar in the two continents (Hooker, 1998).

Conclusions

Ferry Cliff is an important locality as it is one of a few sites in Britain where the Suffolk Pebble Beds can be seen in surface exposures and is the only place where well-preserved material can be collected. The fauna preserved in the Suffolk Pebble Beds shares with only a handful of sites in Europe and North America the oldest world records of primates, artiodactyls and perissodactyls (Hooker, 1998), giving it international importance. It also is the oldest mammal fauna of Eocene age in Britain. Thus, the fauna includes the oldest British records of marsupials, rodents, insectivorans (Lipotyphla), primates, carnivorans, artiodactyls and perissodactyls, as well as the oldest British records of a number of archaic orders, in particular plesiadapiforms, pantolestans, and creodonts. The Suffolk Pebble Beds at nearby Kyson was the type locality for the equoid Cymbalophus cuniculus (Owen, 1842), one of the oldest European horse relatives. It is quite likely that continued study at Ferry Cliff will produce more species of mammal.

ABBEY WOOD, GREATER LONDON (TQ 480 786)

Introduction

Abbey Wood is one of the most important Early Eocene sites in Britain. The site is a temporary excavation in a wooded hillside (Figure 3.7) and has produced a wide range of mammals, birds, reptiles and fishes (White, 1931; Hooker *et al.*, 1980; Hooker, 1998). Despite the bulk sampling techniques being used to collect, continued careful excavation will preserve this site for many years to come.

The first excavations at Abbey Wood took place during the early part of the 20th century (White, 1931; Cooper, 1932a,b). Since then interest in the site waned until the 1960s, when renewed collecting brought to light new mammalian taxa (Simons, 1962; Van Valen, 1965; Kühne, 1969; Hooker, 1979, 1980). Since 1992, the Tertiary Research Group has run a programme of annual excavations (Dineley and Metcalf, 1999), and much new material is coming to light (Hooker, 1996c, 1998; Hooker and Dashzeveg, 2003).

Description

The site displays a sequence of sediments that range from the Chalk (Late Cretaceous) to the Blackheath Beds (Early Eocene), although intervening strata have not been exposed. The fossiliferous horizon, the Lessness Shell Bed, occurs in the lower part of the Blackheath Beds.

British Tertiary fossil mammal sites



Figure 3.7 The exposure of the fossiliferous Blackheath Beds at Abbey Wood, Greater London. Shown here is the Lessness Shell Bed, overlain by non-shelly sand. (Photo: J.J. Hooker.)

The Blackheath Beds belong to the diverse series of sediments that form basal transgressive deposits of the Thames Group. They consist of cross-bedded unconsolidated pebble beds and cemented conglomerates that commonly fill deep depressions within older units (Thanet, Upnor and Woolwich formations; Figure 3.5). At Abbey Wood the Blackheath Beds perhaps fill a large channel cut into the underlying units (Epps and Priest, 1933; Rundle, 1970; Hooker, 1975, 1991b). These facies are overlain by sands with a more marine shelly fauna (the Oldhaven Formation) further east in Kent (Chandler, 1923; Collinson et al., 2003). At Abbey Wood the upper part of the Blackheath Beds takes the form of massive pebble beds. The lower part is composed of sands with scattered pebbles that interdigitate with the Lessness Shell Bed, an intermittent shell coquina with fine-grained sand and scattered well-rounded black flint pebbles derived from lower units (Durkin and Baldwin, 1968). The Lessness Shell Bed reaches a maximum thickness of c. 2 m and is seen approximately 1.5 m below ground level (Durkin and Baldwin, 1968).

Fauna

The fauna at Abbey Wood consists of a variety of molluscs, as well as fishes, reptiles and birds. The fishes include seven or eight species of shark. The reptiles are fragments of the soft-shelled turtle *Trionyx* (Walker and Moody, 1974). Although the early years of collecting at Abbey Wood produced only a few fossils representing a limited faunal diversity, recent changes in collecting techniques, including bulk sampling, screen-washing to 0.5 mm mesh size and acid preparation, have increased the numbers of specimens and species diversity. The mammal fauna listed below is from Collinson and Hooker (1987) and Hooker (1998).

MAMMALIA
Multituberculata
Neoplagiaulacidae
Ectypodus childei (Kühne, 1969)
Marsupialia
Herpetotheriidae
Amphiperatherium brabantense Crochet,
1980
A. maximum? Crochet, 1980
Rodentia
Paramyidae
Paramys ageiensis Michaux, 1964
Meldimys? sp.
Pantrogna russelli (Michaux, 1964)
'Microparamys' sp.
Lipotyphla
Amphilemuridae
Macrocranion cf. nitens
Neomatronella sp.
Chiroptera
Emballonuridae
Eppsinycteris anglica (Cooper, 1932b)
Plesiadapiformes
Paromomyidae
Arcius fuscus (Russell, Louis and Savage,
1967)
Primates
Adapidae
Cantius eppsi (Cooper, 1932b)
Omomyidae
Omomyidae undet.

Abbey Wood

Didelphodonta Cimolestidae Didelphodus? sp. Pantolesta Pantolestidae Palaeosinopa? sp. Apatotheria Apatemyidae Apatemys sp. Tillodontia Esthonychidae Esthonychidae indet. Pantodonta Coryphodontidae Coryphodon eocaenus Owen, 1846 Creodonta Oxyaenidae Oxyaena gulo Matthew, 1915 Palaeonictis cf. occidentalis Osborn, 1892 Hyaenodontidae Prototomus? sp. Carnivora Miacidae 'Miacidae' indet. 'Condylarthra' Arctocyonidae Arctocyonides sp. Hyopsodontidae Hyopsodus wardi Hooker, 1979 Lessnessina packmani Hooker, 1979 Phenacodontidae Phenacodus lemoinei Thewissen, 1990 Artiodactyla 'Diacodexeidae' Diacodexis sp. Perissodactyla Equidae Pliolophus vulpiceps Owen, 1858

The mammalian fauna from Abbey Wood is especially diverse, although early collections represented mainly larger animals such as the primitive horse *Pliolophus* and the pantodont *Corypbodon*, but jaw material of the primitive primate *Cantius* and a tooth of a creodont (Cooper, 1932b; Epps and Priest, 1933) were also found. Abbey Wood is the type locality for five mammalian species, namely the multituberculate *Ectypodus childei*, the primate *Cantius eppsi*, the condylarths *Hyopsodus wardi* and *Lessnessina packmani* and the bat *Eppsinycteris anglica*.

The primate '*Protoadapis*' *eppsi* Cooper (Figure 3.8a,b) was made type of the new genus

Cantius by Simons (1962), distinct from similar small 'lemuroid' primates of France and Germany.

An unusual faunal element was added by Kühne (1969) when he described the multituberculate *Charlesmooria childei*, since reassigned to the neoplagiaulacid genus *Ectypodus*. This is a late-surviving genus of multituberculate, ranging from Paleocene to Eocene times and occurring in Europe and North America.

More recently, two new species of condylarths (primitive ungulates) have been discovered in the Blackheath Beds at Abbey Wood. These taxa, *Lessnessina packmani* (Figure 3.8c,d) and *Hyopsodus wardi* (Figure 3.8e,f), are represented by several fragments of jaw and isolated teeth (Hooker, 1979). Abbey Wood is the type locality for both species. Recent finds of *L. packmani* have resulted in the genus being located also in France and Mongolia, leading to the idea of dispersal across the Turgai Straits in Russia (Hooker and Dashzeveg, 2003).

'Adapisorex' anglicus Cooper, 1932b, originally was described as an insectivoran but recently reinterpreted as the oldest emballonurid (sheath-tailed) bat (Hooker, 1996c) and the species recombined as *Eppsinycteris anglica*.

The horse *Pliolophus vulpiceps* is reported from Abbey Wood (Figure 3.8h) on the basis of several jaw fragments, teeth and some postcranial elements (Hooker, 1980, 1984, 1989a, 1994a). The type of *P. vulpiceps* Owen, 1858, was named from the Harwich Stone Band (London Clay Formation) of Harwich (Figure 3.8i). Abbey Wood has produced teeth that although but not completely identical are judged to be within the range of variation of a single species.

Interpretation

The sedimentary characteristics and invertebrate fauna of the shell lens suggest a high-energy, low-salinity marine shoreface environment. The terrestrial fauna is generally well-preserved, which suggests that the palaeoshoreline was fairly close to their habitats. The clasts in the pebble-rich Blackheath Beds are mainly reworked chalk flints. They are well rounded and may be secondarily reworked from the underlying Reading and Upnor formations, and they form the coarse basal nearshore units heralding the



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Abbey Wood



Figure 3.8(a-f) Mammal specimens from the Blackheath Beds of Abbey Wood, Greater London. (a,b) Right maxilla (a) and right lower jaw (b) of the primate *Cantius eppsi*, both in crown view. (c,d) Left maxilla of the hyopsodontid *Lessnessina packmani*, in crown (c) and external (d) views. (e,f) Right maxilla (reversed) of the hyopsodontid *Hyopsodus wardi* in crown (e) and external (f) views. (g-j) Teeth from a succession of horses in stratigraphical order from southern England (in each case, from left to right, lower molar 3, upper molar 1, upper premolar 3); (g) *Cymbalaphus cuniculus* from the Suffolk Pebble Beds of Kyson, Suffolk; (h) *Pliolophus vulpiceps* from the Blackheath Beds of Abbey Wood, Greater London; (i), *P. vulpiceps* from the Harwich Stone Band (London Clay Formation) of Harwich, Essex; (j), *Hyracotherium leporinum* from divisions D and B of the London Clay Formation of Sheppey and Herne Bay, Kent. (After Simons, 1962; and Hooker, 1979, 1980, 1994a.)

London Clay Formation sea. The molluscs are brackish and nearshore marine forms; brackish taxa are the more common.

The fossil horse remains from Abbey Wood form part of a succession of early forms in Europe (Figure 3.8g–j) that reflect a combination of evolutionary trends and dispersal events (Hooker, 1980, 1994a).

The Abbey Wood fauna traditionally was classed as 'Sparnacian', one of an extensive series of faunas in France, Belgium and England, which was assigned an earliest Eocene age (e.g. Savage and Russell, 1983, pp. 65–70). This age

assignment was based largely on lithological and mapping criteria and comparisons of mammalian faunas between Europe and North America. The Sparnacian faunas, dominated by 'Hyracotherium', Cantius and Paramys, are directly comparable with the Wasatchian faunas, dominated by these three taxa plus the artiodactyl Diacodexis, which is also present at Abbey Wood. However, re-dating of the type Sparnacian in the Paris Basin has shown it to be equivalent in age only to lower and middle parts of the London Clay Formation (Laurain et al., 1983) and thus younger than either Abbey Wood or Ferry Cliff. The Neustrian European Land Mammal Age (Fahlbusch, 1976) is used instead to typify these earliest Eocene mammal faunas.

Re-assessments of the ages of European Paleogene faunas (Schmidt-Kittler, 1987; Hooker, 1991b) assigned the Abbey Wood fauna to Mammal Palaeogene Reference Level MP8-9, which equates to the French localities Avenay, Mutigny, Pourcy and Meudon and covers a broad time-span. However, a more detailed biostratigraphical calibration of Neustrian mammal faunas (Hooker, 1996a) places Abbey Wood in Zone PEIII, younger than Meudon but older than Mutigny or even Pourcy. Thus the Abbey Wood fauna occurs at a time unrepresented by mammals elsewhere in Europe. A number of independent biostratigraphical indicators (nannoplankton, dinocysts, charophytes) in the London Clay Formation and associated units confirm the position of the Blackheath Beds in Early Eocene time (King, 1981; Riveline, 1984; Knox, 1990; Hooker, 1998).

Comparison with other localities

Several of the mammal species from Abbey Wood (e.g. Cantius eppsi, Pantrogna russelli, Lessnessina packmani, Hyopsodus wardi, Pliolophus vulpiceps) are known from other localities in continental Europe, in particular the French site of Pourcy. In addition, many of the genera also are common to North America, namely Cantius, Coryphodon, Diacodexis, Didelphodus, Ectypodus, Hyopsodus, Pliolophus, Macrocranion, Apatemys, Oxyaena, Palaeosinopa, Phenacodus and Prototomus. Significantly, the species Ectypodus childei, Coryphodon eocaenus and Oxyaena gulo occur also in North America. The short range of O. gulo allows a detailed correlation with part of the North American Wasatchian Land Mammal Age (Hooker, 1998). The extensive Early Eocene faunas shared by both continents show the possibility of extensive interchange of terrestrial faunas at the time, probably largely via a land connection through Greenland that bridged the still narrow North Atlantic Ocean. An additional dispersal route has been identified from Asia to Europe via the Turgai Straits (a southern narrowing of the West Siberian sea that divided Asia and Europe in Paleocene and Eocene times) based on the shared presence of Lessnessina at Abbey Wood (and in France) and in Mongolia (Hooker and Dashzeveg, 2003). In contrast, few species are represented at other British sites, restricted to *Pliolophus vulpiceps* and *Coryphodon eocaenus* in lower parts of the London Clay Formation and *Hyopsodus wardi* in the Suffolk Pebble Beds.

There are therefore two significant Early Eocene mammalian faunas from the London Basin: Abbey Wood and that recovered from the Suffolk Pebble Beds. These faunas contain different taxa of different ages, that from the Suffolk Pebble Beds being older than that from Abbey Wood. The apparent contradiction posed by the contemporaneity of the Suffolk Pebble Beds and the Blackheath Beds is most likely to result from reworking of the mammals in the former.

Conclusions

Abbey Wood is the most important Early Eocene fossil mammal site in Britain and has produced many specimens of birds, reptiles and mammals. The fossil mammals described from this locality are diverse and include multituberculates, insectivorans, a bat, primates, rodents, condylarths, artiodactyls and perissodactyls (including Pliolophus: the oldest known ancestor of modern horses). The site is also the type locality for five mammalian species and the only site where Eppsinycteris anglica and Lessnessina packmani, and the genus that the aforementioned defines, are known. Eppsinycteris anglica is also the oldest known emballonurid bat. The Abbey Wood fauna is internationally important in that it fills a gap in the European mammal record between Meudon and Pourcy and forms the closest link so far between the European faunas and those in North America and Asia.

The site has great potential for future study, provided it is excavated carefully. Techniques of bulk sampling and sieving will ensure that our understanding of this fauna continues to grow.

CREECHBARROW HILL, DORSET (SY 922 824)

Introduction

The site of Creechbarrow Hill in Dorset has produced a rich and abundant late Mid Eocene (Bartonian) vertebrate assemblage. The fossils are preserved in a pisolitic and tufaceous sandy



Figure 3.9 The exposure of the Creechbarrow Limestone Formation in an excavation in 1976 at Creechbarrow Hill, Dorset. The hole delimits the Creechbarrow Limestone, above which can be seen beds A–C of the superficial deposits. (Photo: J.J. Hooker.)

limestone, the Creechbarrow Limestone Formation.

The first work at Creechbarrow Hill was undertaken by Hudleston (1901, 1902a,b, 1903), who discovered the capping limestone. Subsequent investigations of the site included studies of the bivalves and vertebrates (Keeping, 1910) and correlation and comparison with the Bembridge Limestone Formation of the Isle of Wight (Bury, 1934; Arkell, 1947; Curry, 1958). The first mammal bone, 'part of the tooth of a Palaeotherium', was reported by Keeping (1910). As a result of excavations by a team from the British Museum (Natural History) in 1975-1978, many mammals are now known from the site, including marsupials, insectivorans (lipotyphlans), primates, rodents, artiodactyls and perissodactyls (Hooker, 1977b, 1986).

Description

Creechbarrow Hill is a conical hill that forms an easily identified landmark in the Purbeck landscape (Hooker, 1986). The Creechbarrow Limestone Formation consists of a white to cream sandy limestone with a pisolitic and tufaceous texture. These sediments rest conformably on sands, clays and gravels of the lower and middle sections of the Creechbarrow Beds. The upper surface of the Creechbarrow Limestone Formation is truncated by an erosion surface (Hooker, 1977b; Collinson and Hooker, 1987). The sedimentary log shown in Table 3.1 is taken from Hooker (1986, pp. 209–10).

The mammal specimens come from bed 12, Creechbarrow Limestone Formation the (Hooker, 1986). Specimens are disarticulated, and some show signs of abrasion. The mammalian remains are dominated by teeth; only a few bones have been described. The teeth display a variety of preservational characteristics: some are fresh, with mahogany enamel and dark-brown dentine, others are very worn. The bones also range from well- to poorly-preserved. It is thought that the land vertebrate remains were brought into a paludal to lacustrine depositional environment by periodic flooding events (Hooker, 1986). Some of the bones show the parallel tooth patterns produced from gnawing by rodents (Hooker, 1986).

Fauna

The Creechbarrow Limestone Formation has produced a mixed fossil assemblage, including reworked Cretaceous bryozoans (marine) as well as indigenous shelled terrestrial gastropods (Preece, 1980), prosobranch snail opercula, slug plates, bivalves, fishes and reptiles (crocodile). The faunal list is taken from Hooker (1986), with minor emendations from Hooker (1989b, 1991a; Hooker and Weidmann, 2000) and Harrison (2002).

MAMMALIA

Marsupialia

Herpetotheriidae

Amphiperatherium aff. goethei Crochet, 1980

Amphiperatherium fontense Crochet, 1980 Rodentia

Paramyidae

Plesiarctomys curranti Hooker, 1986

British Tertiary fossil mammal sites

Mar	nmal Age (Pahibusch, 1976) is used to read.	Thickness (m)
Sup	perficial deposits	
D.	Modern topsoil	0.01-0.4
C.	Soil horizon with limestone fragments and artefacts	0.2-0.4
B.	Fine sandy soil horizon, no artefacts	0-0.3
A.	Limestone rubble	0-0.3
Cre	echbarrow Limestone Formation	
12.	Buff marl with variable-sized limestone clasts and fossils including shells of	
	land and freshwater snails, snail opercula, slug plates, vertebrates and	
	reworked silicified Cretaceous bryozoans	max. 1.6
Uni	named sands and clays	
11.	Pale-brown, sandy silty clay with occasional angular flint fragments	1.0
10.	Pale-brown, clayey silty sand	0.3
9.	Pale-brown, very sandy silty clay	0.16
8.	Pale-grey, silty clay with low sand content	0.16
7.	Pale-brown, very sandy silty clay	0.2
6.	Pale-grey, very silty clay with low sand content	0.2
5.	Pale-grey, sandy silty clay	0.31
4.	Pale-brown, slightly clayey silty sand, the clay content reduced in the middle	
	of the bed	0.5
3.	Pale-brown, very clayey silty sand	0.18
2.	Very pale-grey, calcareous silty sand	0.14
1.	Whitish buff, very calcareous sand with small ovoid and tubular calcareous	
600	concretions 2–5 mm in diameter	0.14

Table 3.1 The sedimentary log for the Creechbarrow GCR site, from Hooker (1986)

Plesiarctomys buerzeleri Wood, 1970	Pseudoloris cf. crusafonti Louis and Sudre,
Manitshinae indet.	1975
Ailuravus steblinschaubi Wood, 1976	Microchoerus wardorum Hooker, 1986
Gliridae	Microchoerus creechbarrowensis Hooker,
Glamys bookeri Harrison, 2002	1986
Pseudosciuridae	Pantolesta
Sciuroides rissonei Hooker, 1986	Pantolestidae
Treposciurus preecei Hooker, 1986	Pantolestidae indet.
Suevosciurus authodon Hooker, 1986	Apatotheria
Lipotyphla	Apatemyidae
Amphilemuridae	Heterobyus cf. sudrei Sigé, 1975
Gesneropithex figularis Hooker, 1986	Heterobyus aff. nanus Teilhard, 1922
Chiroptera	Heterohyus morinionensis Hooker, 1986
Hipposideridae	Carnivora
?Pseudorhonolophus sp.	'Miacidae'
Family indet.	Paramiacis sp.
Three genera and species indet.	?Miacidae indet.
Archonta undiff.	'Condylarthra'
Nyctitheriidae	Paroxyclaenidae
Nyctitheriidae indet.	Vulpavoides cooperi Hooker, 1986
Primates	Artiodactyla
Adapidae	Cebochoeridae
Europolemur collinsonae Hooker, 1986	Cebochoerus robiacensis Depéret, 1917
Leptadapis aff. magnus (Filhol, 1874)	Acotherulum campichii (Pictet, 1857)
Omomyidae	Choeropotamidae
Nannopithex quaylei Hooker, 1986	Haplobunodon venatorum Hooker, 1986
Nannopithex sp. 1	Choeropotamus sp. indet.

Mixtotheriidae

Mixtotherium aff. gresslyi Rütimeyer, 1891 Mixtotherium sp. indet.

Mixtotheriidae gen. et sp. nov

Anoplotheriidae

Dacrytherium elegans (Filhol, 1884)

Xiphodontidae

Dicbodon cf. *biroi* Hooker and Weidmann, 2000

Dichodon sp. indet.

Dichobunidae

Mouillacitherium cf. elegans Filhol, 1882 Hyperdichobune sp. 1

Amphimerycidae

Pseudamphimeryx? sp. indet.

Perissodactyla

Palaeotheriidae

Propalaeotherium aff. parvulum A (Laurillard, 1849) Propalaeotherium aff. parvulum B (Laurillard, 1849) Lophiotherium siderolithicum (Pictet, 1857) Plagiolophus curtisi creechensis Hooker,

1986

The marsupials - two species of Amphiperatherium - are represented by numerous teeth (Figure 3.10a,b); they differ in size and cusp arrangement. A pantolestid is represented by a single tooth. Rodents make up more than 50% of the individuals represented by the specimens from Creechbarrow Hill. Seven rodent taxa were described by Hooker (1986), again all based on teeth, and these included four species named from there: Plesiarctomys curranti Hooker, 1986 (Figure 3.10c); Sciuroides rissonei Hooker, 1986 (Figure 3.10d); Suevosciurus authodon Hooker, 1986 (Figure 3.10e); and Treposciurus preecei Hooker, 1986 (the latter was later raised from subspecies level by Hooker, 1991a). An eighth rodent, a dormouse, Glamys bookeri was described by Harrison (2002).

A species of amphilemurid, *Gesneropithex figularis*, was named by Hooker (1986) for a fragmentary jaw and isolated teeth of this hedgehog-like animal (Figure 3.10f,g). Amphilemurids were once classed as primates, but reconstruction of the dentition of the Creechbarrow Hill species (Hooker, 1986), together with complete skeletons of a related form from Germany (Koenigswald and Storch, 1983), showed them to be erinaceomorph lipotyphlans. The tiny insectivorous nyctitheres and four species of bats also were identified on the basis of broken isolated teeth (Hooker, 1986). Only one of the specimens was good enough for a closer tentative assignment, that of the bat *Pseudorbinolophus* (Hooker, 1989b).

The Creechbarrow Hill site has yielded a remarkable seven species of primates. There are five omomyids, small arboreal insectivores and frugivore-herbivores, including three species for which Creechbarrow Hill is their type locality: Nannopithex quaylei Hooker, 1986 (Figure 3.10h), Microchoerus wardorum Hooker, 1986 (Figure 3.10i), and Microchoerus creechbarrowensis Hooker, 1986 (Figure 3.10j), all of them based on isolated teeth. There are two species of adapid primate, including one species unique to Creechbarrow Hill, Europolemur collinsonae Hooker, 1986 (Figure 3.10k); both of them are larger than the omomyids and are adapted more for a browsing leaf-eating and fruit-eating diet.

Unusually, three species of apatemyid are identified, including the species Heterobyus morinionensis Hooker, 1986 (Figure 3.101). Apatemyids were small tree-climbing insecteaters, but with extraordinary long curved incisor teeth, superficially like a rodent but not evergrowing. These dental attributes as well as features of the skeleton are convergent with the modern Aye-Aye (Koenigswald and Schierning, 1987). Flesh-eating mammals are rare, with only a few teeth of miacid carnivorans reported. A paroxyclaenid 'condylarth', Vulpavoides cooperi Hooker, 1986, was named on the basis of a couple of teeth. From what we know of other representatives of the family, this was a civet-like climbing animal that may have had a diet of insects, flesh and/or fruit.

Ungulates from Creechbarrow Hill include at least three species of perissodactyls (one of them a subspecies unique to the site, *Plagiolophus curtisi creechensis* Hooker, 1986), all of them small to medium-sized terrestrial browsers or mixed frugivore/browsers that fed on leaves of bushes and low trees and on fallen fruits. *Plagiolophus curtisi creechensis* is based on an associated upper and lower dentition, although more complete material of the type subspecies from Barton allowed a partial skull reconstruction (Figure 3.10m–o; Hooker, 1986, fig. 51). Artiodactyls are the most diverse group, with up to 13 species reported so far, mostly founded on teeth but with a few fragmentary jaw



• Roccalgewald and Starch, with up to 15 species reported so the mostly be created and reach but with a feet fright fire and



Figure 3.10 Mammal specimens from the Creechbarrow Limestone Formation of Creechbarrow Hill, Dorset and Barton Clay Formation of Barton, Hants. (a) Upper molar tooth 1 of the marsupial *Ampbiperatherium* aff. *goethei* in crown view. (b) Upper molar tooth 1 of the marsupial *Ampbiperatherium fontense* in crown view. (c) Lower molar tooth 1 of the rodent *Plesiarctomys curranti* in crown view. (d) Lower molar tooth 1 or 2 of the rodent *Sciuroides rissonei* in crown view. (e) Upper deciduous premolar 4 of the rodent *Suevosciurus autbodon* in crown view. (f,g) Lower jaw of the lipotyplan insectivoran *Gesneropithex figularis* in external (f) and internal (g) views. (h) Upper premolar tooth 4 of the primate *Nannopithex quaylei* in crown view. (i) Upper molar tooth 1 of the primate *Microchoerus wardorum* in crown view. (j) Upper molar tooth 1 of the primate *Microchoerus wardorum* in crown view. (j) Upper molar tooth 1 of the primate *Collinsonae* in crown view. (l) Upper molar tooth 3 of the apatothere *Heterobyus morinionensis* in crown view. (m–o) Skull in lateral (m) and palatal (n) views and lower jaws in crown view (o) of the perissodactyl *Plagiolophus curtisi curtisi*. (p) Lower jaw fragment with molar tooth 3 of the artiodactyl *Haplobunodon venatorum*. m–o are from Barton, the remainder from Creechbarrow Hill. (After Hooker, 1986).

bones also and a single astragalus. One new species of artiodactyl has been established from Creechbarrow Hill: *Haplobunodon venatorum* Hooker, 1986 (Figure 3.10p), a close relative of *Choeropotamus* in the Choeropotamidae (Hooker and Thomas, 2001).

Creechbarrow Hill preserves specimens of taxonomic groups that normally are rare in European Eocene localities, for example a paroxyclaenid, three apatemyids and two *Plesiarctomys*. The size of mammals from Creechbarrow Hill is strongly skewed to smaller animals (Hooker, 1992). This could represent a collecting bias, because the Creechbarrow Limestone Formation was largely sieved for microvertebrate specimens, but it is more likely that the skew to small size is real (Hooker, 1986, 1992). The fauna is heavily dominated by planteaters (rodents, artiodactyls, perissodactyls), whereas carnivores (carnivorans) are extremely rare. However, this is typical of other correlative faunas in Europe (Savage and Russell, 1983, p. 104) and may reflect a bias to preservation of the rodents and ungulates, which should have had larger populations.

The Creechbarrow Hill locality has provided type materials of 13 species and one subspecies of mammal, namely the amphilemurid *Gesneropithex figularis* Hooker, 1986; the omomyid primates *Nannopithex quaylei* Hooker, 1986; *Microchoerus wardorum* Hooker, 1986; and *Microchoerus creechbarrowensis* Hooker, 1986; the adapid primate *Europolemur collinsonae* Hooker, 1986; the rodents *Plesiarctomys curranti* Hooker, 1986; *Glamys bookeri* Harrison, 2002; Sciuroides rissonei Hooker, 1986; Suevosciurus authodon Hooker, 1986; and Treposciurus preecei Hooker, 1986; the apatemyid Heterohyus morinionensis Hooker, 1986; the condylarth Vulpavoides cooperi Hooker, 1986; the perissodactyl Plagiolophus curtisi creechensis Hooker, 1986; and the artiodactyl Haplobunodon venatorum Hooker, 1986.

Most of the mammals in the assemblage are typical of the preceding Lutetian Stage, representing holdover taxa. Differences from the preceding Lutetian Stage are mainly at the species level, whereas some differences from the younger Headonian faunas are at genus level. This interval does not mark a time of major evolution among the mammals on an intercontinental scale, nor, apparently, was there any interchange with faunas outside Europe, a typical feature of the times before and after (Savage and Russell, 1983, p. 104). It represents a time of transition between typical middle and late Eocene European faunas. Thus Creechbarrow Hill has the last member of the primate genus Europolemur and one of the last paroxyclaenids. It also has the first members of the rodent genera Treposciurus and Suevosciurus, which dispersed widely in Europe at the beginning of Late Eocene times. The Bartonian faunas of Creechbarrow Hill, and correlatives in continental Europe, include many essentially endemic taxa, including the cebochoerid, anoplotheriid and xiphodontid artiodactyls. Likewise, the perissodactyls, mainly equoids and tapiromorphs, continued at their previous abundance. One perissodactyl group, the giant lophiodontids, is absent from Creechbarrow Hill, although present in correlative faunas elsewhere in Europe (Hooker and Weidmann, 2000) and in penecontemporaneous strata at Hengistbury (Hooker, 1977a); this was their last appearance before extinction.

Interpretation

Different theories have been devised to explain the environment of deposition of the Creechbarrow Limestone Formation. Initially Hudleston (1901) considered the sediments to have been deposited under lacustrine conditions, although the discovery of gastropods (Keeping, 1910) characteristic of terrestrial conditions appeared to deny the lacustrine model. Bury (1934) considered the site to represent deposition in a lime-rich swamp with high levels of evaporation. Preece (1980) reviewed the sedimentological and molluscan evidence and concluded that any interpretation should be tentative, although the presence of features such as a shallow water body, the close proximity of forest cover and flowing water or water seepage indicate a lake. Hooker (1986) concluded that the mammals from Creechbarrow Hill inhabited a forest environment, probably close to the lake where their remains are preserved. The sediments indicate a complex of fluvial, lacustrine and terrestrial deposition. The distribution of body sizes of mammals, with a skew to small size, indicates a forest habitat with a complex structure (Hooker, 1992). The distribution of locomotory modes among the mammals, and the relative abundance of arboreal forms, suggests closest parallels with lowland tropical forests today. Hooker (1992, p. 500) summarized the Creechbarrow Hill habitat as a tropicaltype, high-stature forest with glades.

The mammals form the most rapidly evolving taxonomic group seen at Creechbarrow Hill, and they have been used to date the sediments. Key taxa for correlation with continental European sites are Ailuravus steblinschaubi, Pseudoloris cf. crusafonti, Lopbiotherium siderolithicum and Acotherulum campichii. The British endemic Plagiolophus curtisi establishes a correlation with the marine stratotype Bartonian Stage. Creechbarrow Hill is dated to Mammal Paleogene Reference Level MP16 and the lautricense-siderolithicum Zone, by comparison with continental European faunas. It is close to the well-known Robiac fauna from France (Sudre, 1969), sharing with it a number of species: Amphiperatherium fontense, Heterohyus cf. sudrei, Heterobyus aff. nanus, Cebochoerus robiacensis and Dichodon cf. biroi (Hooker and Weidmann, 2000). Many genera also are shared: nearly half the species that were named as new taxa from Creechbarrow Hill belong to typical Robiac genera. The Robiacian European Land Mammal Age traditionally has been correlated with the global Bartonian Stage, although recent evidence suggests that it also extends into the Stage (Hooker and preceding Lutetian Weidmann, 2000).

Comparison with other localities

No other mammal locality in Britain compares with Creechbarrow Hill. Other Bartonian sites include Hengistbury, Dorset (Hooker, 1977a),

Hordle Cliff

and Barton itself, but fossil mammal finds are rare. Barton has yielded only six taxa of whales, terrestrial ungulates and a bat (Halstead and Middleton, 1972; Hooker, 1986) and does not approach Creechbarrow Hill in diversity and abundance of mammalian finds, although the remains are generally more complete. Further afield, comparisons between the mammalian fauna at Creechbarrow Hill and European sites suggest that similarities exist with the locality of Grisolles in northern France (Hooker, 1986), with the famous Robiac locality in southern France (Sudre, 1969; Savage and Russell, 1983, p. 100; Schmidt-Kittler, 1987) and with the lautricense-siderolithicum Zone faunas of Mormont (Hooker and Weidmann, 2000). The Robiac locality has produced 55 mammalian species (Sudre, 1969; Mathis, 1987; Legendre, 1989), using prospecting and screenwashing techniques (Sudre, 1969), a comparable diversity of mammals and a comparable relative abundance of specimens.

Conclusions

The mammalian fauna preserved in the Creechbarrow Limestone Formation is abundant and diverse. The use of bulk sampling techniques to study Creechbarrow Hill means that all sizes of fossils have been recovered, not just the more obvious large specimens. This is one of the few late Mid Eocene (Bartonian) faunal assemblages from Britain and is much richer than any other British site of the same age. It is the source of type materials of 13 species and one subspecies, the northernmost Bartonian mammal fauna site in Europe and it has last and first occurrences for several important European genera. It rivals the famous Robiac locality in France, of similar age, and this confirms the national and international significance of Creechbarrow Hill. The wide range of animals, including artiodactyls, perissodactyls, primates, rodents and carnivores, represent a complex forest-dwelling community.

HORDLE CLIFF, HAMPSHIRE (SZ 254 925–SZ 270 921)

Introduction

Hordle Cliff has produced one of the richest early Late Eocene (early Priabonian) mammalian faunas in Europe, belonging to the Headonian European Land Mammal Age. Other taxa, for example turtles, crocodilians, lizards, snakes and birds, are also well-represented (Benton and Spencer, 1995; Holman, 1996; see Chapter 4). What also makes the site exceptional is the exquisite preservation of fragile bones, especially in the Mammal and Crocodile beds.

The Hordle (formerly Hordwell) Cliff locality (Figure 3.11) exposes a sequence of Late Eocene sediments in the low sea cliffs between Becton Bunny and Milford-on-Sea. The lithostratigraphical units seen here are the Totland Bay Member (formerly known as the 'Lower Headon Beds') and the base of the Colwell Bay Member (formerly known as the 'Middle Headon Beds') of the Headon Hill Formation.

Fossils have been recovered from Hordle Cliff since the 19th century, when Searles Wood and the Marchioness of Hastings made extensive collections of vertebrate material. The Hastings Collection is held at the Natural History Museum, London. Hordle Cliff also has a long history of geological investigation and has been studied by Hastings (1848, 1852, 1853), Tawney and Keeping (1883), Gardner et al. (1888), Curry (1958), Cray (1973), Milner et al. (1982), Plint (1984), Edwards and Daley (1997) and Hooker (1992). Early accounts of the fossil mammals from Hordle Cliff were published by Wood (1844, 1846), Owen (1848a,b 1857b), Lydekker (1884a, 1885a,b) and Cooper (1926b). Stehlin (1910) provided an overview of the fauna, and he listed 16 species from Hordle Cliff. Further revisions and additions of individual mammals from Hordle Cliff were made by Butler (1946), Simons (1961), Franzen (1968), Hooker (1991a, 2001), Harrison et al. (1995), Norris and Harrison (1998a,b) and Hooker and Thomas (2001). Cray (1973) provided an overview of the fauna and revised the non-ungulate mammals in some detail. Comprehensive revised faunal lists have been provided by Hooker et al. (1980), Collinson and Hooker (1987) and Hooker (1987, 1992).

Description

Since the 19th century, the sedimentary sequence exposed at Hordle Cliff has been successively described by Hastings (1852), Tawney and Keeping (1883), Gardner *et al.* (1888), Cray (1973) and Plint (1984). The most recent account is by Edwards and Daley (1997), from

British Tertiary fossil mammal sites



Figure 3.11 Totland Bay Member resting on Becton Sand Formation, Hordle Cliff, looking towards Becton Bunny. (Photo: D.L. Harrison.)

whom the following composite sequence (Table 3.2) is taken in abbreviated form.

The lowest part of the section, seen just east of Becton Bunny, exposes the Mammal Bed, which dips approximately 2.5° to the south-east across the cliff face. The Crocodile Bed is seen as a similar feature higher up in the cliff. The highest beds, the *Limnaea* marl/Rodent bed and associated horizons, occur discontinuously below the gravels capping the cliffs, farther to the east.

The fossil vertebrates have been found mainly in the Totland Bay Member (Cray, 1973; Milner *et al.*, 1982; Benton and Spencer, 1995, pp. 285–7), although a few occur in the overlying Colwell Bay Member (Hooker *et al.*, 1980). Older specimens in collections bear generalized labels, such as 'Upper Eocene, Hordwell', which do not indicate the horizon more closely, although some are embedded in a characteristic matrix, sometimes with an associated shelly fauna, which often can be used to recognize the Mammal Bed, Crocodile Bed or Rodent Bed. The early accounts of Hastings (1848, 1852, 1853) indicate that most of her finds came from two main horizons, the Mammal Bed and the Rodent Bed, and from a fossiliferous pocket in the Crocodile Bed.

The Rodent Bed consists predominantly of grey clays and marls. It has produced an extensive fauna of rodent jaws, turtle carapace, teeth and bone fragments of crocodiles, snake vertebrae, and teeth and bones of other mammals (Hastings, 1852). Cray (1973) noted occasional rodent teeth and turtle fragments from this horizon and observed that all of the specimens were small and fragmentary and presumably transported and water-sorted.

The Crocodile Bed is composed of an upper, soft, white sandy layer and a lower brownish indurated layer. Fossils from this horizon included crocodile and turtle remains (Hastings, 1852), with spectacular nearly complete crocodile skulls and turtle carapaces.

The Mammal Bed (Curry, 1958; Cray, 1973) yielded fossils from white sand, which also

Table 3.2 The sedimentary sequence at Hordle Cliff (after Edwards and Daley, 1997)

C. Farder	35. Birtles, hirds and orammal,	Thickness (m)
obvell P	w Mombos ('Middle Headen Bade')	
olwell B	ay member ('Middle Headon Beds')	recent collection
Sand,	fine; carbonaceous mottles and streaks (Millord Marine Bed)	seen to 1.25
otland B	ay Member ('Lower Headon Beds')	
33.	Marl, grey-green, weathering rusty, with intercalated lenticular fine-grained sand	0.85
32c.	Mud, carbonaceous, weathering pale pinky-grey; shell debris and bone	
	fragments (Rodent bed in part)	0.04
32b.	Marl, sandy, pale-green; abundant shell debris and bone fragments;	
	Lymnaea, theridomyid teeth (Limnaea marl, Rodent bed in part)	0.10
32a.	Marl, sandy, pale-green to rusty, to marly sand; scattered shell fragments	0.20
31c.	Sand, fine-grained	0.60
31b.	Muddy silt, thin bedded, passing up into fine-grained sand	0.80-1.07
31a.	Muddy silt, thin bedded with marl and thin black mud intercalations; lenses	
	of Viviparus lentus, Potamaclis turritissima, Unio solandri, ostracods;	
	bands of seeds at base (Limnocarpus band)	0.40-0.46
30b.	Grevish marls and clays, with intercalated fine-grained sand beds	2.80
30a.	Muds, thin bedded, with intercalated fine-grained sand, especially near	
n iero	base, with U. solandri, V. lentus, seeds of Stratiotes, charophytes	c. 2.50
29.	Muds: seam of fine-grained sand with <i>P. turritissima</i> , basal sand resting on	
	strongly burrowed junction	0.50
28.	Sand, fine-grained, pale-brown to purplish: black muds with sand-filled	Holman and
(71.189)	burrows: humic muds at base (Chara bed)	0.50
26.	Marl with sand-filled burrows passing down into sandy limestone	0.25-1.12+
25	Sand medium-fine grained: thin marl near top	0.58
24	Marl with calcareous mottles	0.75
23	Sand fine-grained passing up into muddy silt: black mud lenses in upper	0.53
-0.	part	NS 2200001 boo
22	Mud silty blue: carbonate mottles common	0.36
21	Mud, shelly fine-grained sand layers: Potamomva blana	0.25
20	Sand very fine-grained passing up into mud with carbonate mottles: black	0.2)
20.	mud lenses in upper part	0.28
19/18	Mud blue carbonate mottles at top: shelly layers: P blana Lymnaea at	0.20
17/10.	base	0.10
17	Limestone: Ivmnaea, Australorhis (Ivmnaean limestone)	0.10
16	Mud_greenish: thin black mud at top_rusty-weathering mudstone: podules	
10.	towards base	0.95
15c	Silt muddy P plana	0 10-0 20
15b	Sand very fine-grained or silt: greenish mud bands: calcareous cementation	0.10 0.20
190.	near top: shell bed at base with <i>P plana</i> (Crocodile bed)	136
15a	Thin bedded muddy silt and silty mud brown and black: <i>P</i> bland and	0.32
	seeds	Codentia
14	Mud_silty: sand-filled burrows	0.04
13	Sand medium-grained: shell debris at base (Rolled Bone Bed)	0 20-0 70
12	Muds mainly very dark-grey interbedded with layers and lenses of grey	0.20 0.70
12.	medium-grained sand; and sand, medium-grained; lignite layers; plant	0.50-1.90
	debris and seeds	0.90-1.90
11	Sand medium-grained	130
10	Mud silty in situ carbonaceous woody roots (Leaf bed)	1.50
10.	Mud, siny: in-situ carbonaccous woody roots (Lear bed)	0.40
9.	silt towards base: V lentus bones (Mammal bed)	2 51
0	Mud. massive, grow blue: large must weathering calesroous mudstone	2.30
0.	Mud, massive, grey-blue; large rusty-weathering calcareous mudsione	1.0/
6	Silt or very fine sand, mottled with blue mud	1.00
0. 5	Mud massive gree blue brown mottles silts near base	0.1
5.	Mud, massive, grey-blue, brown motiles, shity near base	1.70
1-4.	alternations of black and grey muds, some sitty or sandy; some levels with	al provincial and
Deet	rooticts and burrows; r. plana, corotical deperatia	1.2
Rests	comorniably on becton sand Pornation (barton sand)	

contained abundant remains of shells, and from lower bluish-green sandy clays. Fossils include fishes, crocodiles, turtles, birds and mammal bones, sometimes partly articulated. More recent collecting and sieving of pockets of fossiliferous sediment in the Mammal Bed have yielded thousands of small bones of fishes, reptiles, birds and mammals (Milner *et al.*, 1982; Collinson and Hooker, 1987; Benton and Spencer, 1995; Norris and Harrison, 1998a,b; Hooker, 2001).

Fossil vertebrates also have been found in the Rolled-Bone Bed and above and below the Lower Ironstone Band (Hastings, 1852; Cray, 1973).

Fauna

The extensive faunas from various horizons at Hordle Cliff include molluscs, fishes, some 40 taxa of reptiles (Benton and Spencer, 1995; Holman and Harrison, 1998a,b), birds (see Chapter 4) and over 40 mammals. The list of mammals below is taken from Hooker (1987, 1992), with additions from Hooker (1991a, 2001), Hooker and Weidmann (2000), Hooker and Thomas (2001) and Harrison *et al.* (1995). Letters at the end of a name distinguish occurrences in the mammal bed (M), Crocodile Bed (C) and Rodent Bed (R).

MAMMALIA
Marsupialia
Herpetotheriidae
Amphiperatherium spp. (M, C, R)
Leptictida?
Pseudorhynchocyonidae
Pseudorbynchocyon sp. (M)
Rodentia
Pseudosciuridae
Sciuroides ehrensteinensis Schmidt-Kittler,
1971 (R)
Treposciurus mutabilis Schmidt-Kittler,
1970 (R)
Treposciurus gardneri Hooker, 1991a (M)
Suevosciurus bosmae Hooker, 1991a (M, R)
Tarnomys depereti (Stehlin and Schaub,
1951) (M)
Tarnomys quercyi vectisensis Bosma, 1974
(R)
Theridomyidae
Thalerimys headonensis (Bosma, 1974) (M
Thalerimys fordi (Bosma and Insole, 1972)
(R)

Gliridae

Glamys priscus (Stehlin and Schaub, 1951)(M) *Gliravus* cf. *daamsi* Bosma and de Bruijn, 1982 (M)

Miniglis minor (Bosma and de Bruijn,

1982) (R)

Lipotyphla

Talpidae

Eotalpa anglica Sigé, Crochet and Insole, 1977 (M)

Amphilemuridae

Gesneropithex grisollensis Louis and Sudre, 1975 (M, R)

Archonta undiff.

Nyctitheriidae Cryptotopos woodi (Cray, 1973) (M) Cryptotopos beata Crochet, 1974 (M) Saturninia gracilis Stehlin, 1941 (R) Paradoxonycteris tobieni? (Sigé, 1976) (M) Primates Adapidae Leptadapis magnus (Filhol, 1874) (M, R) Omomvidae Pseudoloris parvulus (Filhol, 1890b) (M, R) Microchoerus erinaceus Wood, 1844 (M, C, R) Microchoerus creechbarrowensis Hooker, 1986 (M/C) Pantolesta Pantolestidae Opsiclaenodon major (Lydekker, 1887) (M, C, R)

Apatotheria

Apatemyidae

Heterobyus sp. 1 (M, R)

Creodonta

Hyaenodontidae

Hyaenodon minor Gervais, 1852 (M/C)

Carnivora

'Miacidae' *Paramiacis* sp. (M)

Viverravidae

Quercygale angustidens (Filhol, 1872)

(M/C) Artiodactyla

Cebochoeridae

Acotherulum saturninum Gervais, 1850 (R) Acotherulum pumilum (Stehlin, 1908) (R) Choeropotamidae

Haplobunodon lydekkeri Stehlin, 1908 (M/C) Amphirhagatherium edwardsi Hooker and

Amphirhagatherium eawarasi Hooker and Thomas, 2001 (C)

Rhagatherium valdense Pictet, 1857

Choeropotamus depereti Stehlin, 1908 (M/C)

Tapirulus cf. *perrierensis* Sudre, 1978 (R) Anthracotheriidae

Diplopus aymardi Kovalevskii, 1873b (M/C) Anoplotheriidae

Dacrytherium ovinum (Owen, 1857b) (M/C)

Xiphodontidae

Dichodon cervinus (Owen, 1846) (R) Dichodon cuspidatus Owen, 1848b (M, C) Amphimerycidae

Pseudamphimeryx hantonensis Cooper, 1928 (M)

Perissodactyla

Palaeotheriidae

Plagiolophus annectens (Owen, 1848b)(M, C)

Palaeotherium magnum stehlini Depéret, 1917 (M/C)

Palaeotherium muehlbergi praecursum Franzen, 1968 (M/C) Palaeotherium duvali priscum Franzen,

1968 (M/C)

Pachynolophidae

Anchilophus dumasi (Gervais, 1849) (M/C) Anchilophus radegondensis gaudini Pictet and Humbert, 1869 (M/C).

The marsupials, species of Amphiperatherium, opossum-like forms, are known from jaws with teeth (Figure 3.12a). The rodents from Hordle Cliff are important, as a relatively diverse assemblage of 11 species is known. Bosma (1974) and Bosma and de Bruijn (1979, 1982) described several taxa that are unique to the Headon Hill Formation. The species Treposciurus gardneri was established by Hooker (1991a) for an upper jaw (Figure 3.12b) and a number of isolated teeth from Hordle Cliff, as well as material from Headon Hill and Whitecliff Bay, which Bosma (1974) had ascribed to the French species T. intermedius. It differs from this species in being a smaller animal with different patterns of cusps on the molar teeth. The theridomyid Thalerimys headonensis also is known from jaw fragments with teeth (Figure 3.12c). Collinson and Hooker (2000) reported seeds of the aquatic floating plant Stratiotes bearing predation holes from the Chara bed (Bed 28 of the Totland Bay Member). The gnaw marks resemble those made today on hazelnuts by wood mice, but according to size they are attributed to one of the glirids (dormice) in the fauna, probably *Glamys*. These are the oldest examples of rodent seed-gnawing yet reported.

The tiny nyctitheres are known from teeth and jaws (Figure 3.12d,e), as well as ankle bones ascribed to Cryptotopos by Hooker (2001). These ankle bones show that nyctitheres are not primitive shrews as had previously been thought, but stem members of the superorder Archonta, to which primates, treeshrews, colugos and possibly bats belong. The ankle bones also show that nyctitheres could invert their feet, allowing them to climb trees. The pantolestid Opsiclaenodon major is represented by jaws and teeth; it was a larger animal, probably semiaquatic, and may have fed on fish like its relative Buxolestes from Messel. The amphilemurid Gesneropithex grisollensis is represented by jaws (Hooker, 1986) and a probable ear bone (Norris and Harrison, 1998b), indicating distant relationships with hedgehogs. Hordle Cliff also records the oldest mole (Talpidae), Eotalpa anglica, described first from Headon Hill (see GCR site report; Sigé et al., 1977)

Four taxa of primates, three omomyids and one adapid, have been recorded, two of them species that were already known from France. *Microchoerus erinaceus*, a small fruit-eater and browser, was the first mammal to be described from Hordle Cliff (Wood, 1844); it is represented by jaws, cranial fragments and isolated teeth (Cray, 1973; Figure 3.12f,g). The tiny related *Pseudoloris parvulus* has been identified from lower jaws similar to the French type specimen. *Leptadapis magnus*, an indri-sized, treedwelling, browsing herbivore, also is represented by jaw and tooth material (Cray, 1973; Figure 3.12h).

The apatemyid *Heterohyus* sp., based on a single worn molar tooth, was the first apatemyid from Britain when Cray (1973) reported it, although several specimens of this genus were later identified from Creechbarrow Hill and Headon Hill. The hyaenodontid creodont *Hyaenodon* cf. *minor* is known from several jaws and teeth, including a beautiful complete paired lower jaw (Figure 3.12i,j). It was a wolfsized carnivore with powerful carnassial molars for slicing flesh. The true carnivoran, the viverravid *Quercygale angustidens*, was a smaller foxsized flesh-eater, represented by a single partial skull (Cray, 1973).

The ungulates from Hordle Cliff are diverse, consisting of 12 artiodactyls and six perissodactyls, and they include several taxa unique to



Figure 3.12 Fossil mammal specimens from the Totland Bay Member, Headon Hill Formation of Hordle Cliff, Hampshire. (a) Partial right lower jaw of the marsupial *Amphiperatherium* in external view. (b) Partial maxilla of the rodent *Treposciurus gardneri* in crown view. (c) Partial maxilla of the rodent *Thalerimys beadonensis* in crown view. (d,e) Partial left lower jaw of the nyctithere *Cryptotopos woodi* in crown (d) and internal (e) views. (Based on Cray, 1973; Bosma, 1974; Hooker, 1991a.)



Figure 3.12 Fossil mammal specimens from the Totland Bay Member, Headon Hill Formation of Hordle Cliff, Hampshire – *continued*. (f,g) The primate *Microchoerus erinaceus*, palate and upper dentition (f) and partial left lower jaw in external view (g). (h) Partial left lower jaw of the primate *Leptadapis magnus* in external view. (Based on Cray, 1973.)



Figure 3.12 Fossil mammal specimens from the Totland Bay Member, Headon Hill Formation of Hordle Cliff, Hampshire – *continued*. (i,j) Complete pair of lower jaws of the creodont *Hyaenodon minor* in crown (i) and external (j) views. (Based on Cray, 1973.)

the Headon Hill Formation, but the majority belong to taxa reported from France and Germany. The perissodactyls were all mediumsized terrestrial browsing herbivores, whereas *Palaeotherium magnum* was large – one of the largest mammals of its day, about the size and build of a modern tapir. Most of the artiodactyls were more modest in size, most of them terrestrial browsing herbivores, but *Cebochoerus* was a fruit-eater, and the choeropotamids had mixed browsing and fruit-eating diets (Collinson and Hooker, 1987; Hooker and Thomas, 2001). *Pseudamphimeryx* was a tiny leaf-eating ruminant, weighing less than 1 kg. The rare cebochoerid *Acotherulum pumilum* recently was described from the Rodent Bed (Harrison et al., 1995).

Hordle Cliff is the type locality for 10 mammalian species and two subspecies: *Treposciurus* gardneri Hooker, 1991a; Cryptotopos woodi (Cray, 1973); Microchoerus erinaceus Wood, 1844; Opsiclaenodon major (Lydekker, 1887); Haplobunodon lydekkeri Stehlin, 1908; Diplopus aymardi Kovalevskii, 1873b; Dacrytherium ovinum (Owen, 1857b); Dichodon cuspidatus Owen, 1848b; Pseudamphimeryx hantonensis Cooper, 1928; Plagiolophus annectens (Owen, 1848b), Palaeotherium muehlbergi praecursum Franzen, 1968 and Palaeotherium duvali priscum Franzen, 1968.

Interpretation

The Totland Bay Member (previously the 'Lower Headon Beds'), consisting of clays, sands and marls with occasional lignite beds, has been interpreted as a coastal sequence. The sediments represent brackish and freshwater lagoons, distributary-channel and floodplainlake environments (Plint, 1984) that developed following a major sea-level fall at the end of Mid Eocene times (Plint, 1988). The lagoonal sediments show a trend of decreasing salinity through time, with the eventual removal of any marine influence. Deposition was then dominated by fluvial systems and shallow floodplain lakes. During this time several brackish incursions took place, probably because of the low topography (Plint, 1984).

Analysis of the mammal faunas suggests a more balanced range of body sizes than from the older Creechbarrow Hill fauna (see GCR site report). From ecological diversity analysis, the suggested habitat is open forest or one with glades, but of a less tropical type than Creechbarrow Hill. The arboreal percentage, however, implies a fairly complex structure (Hooker, 1992, p. 500).

The section is dated by using non-marine biostratigraphical indicators. The mammal faunas belong to the Headonian European Land Mammal Age (ELMA) (Bosma, 1974), shared with deposits of the same age on Headon Hill (see GCR site report), and comparisons with equivalents in southern France establish a clear sequence of assemblages immediately following those of the Bartonian Stage at Creechbarrow Charophytes from the Totland Bay Hill. Member, Hordle Cliff, are indicative of the Gyrogona tuberosa Zone, which occurs in the Marnes de Verzenay, overlying the marls with Pholadomya ludensis (type Ludian local stage) from the Paris Basin. The zone indicates an early Priabonian age mammal.

The Hordle Cliff faunas from the Totland Bay Member are equated with Mammal Paleogene Reference Level MP17 (Schmidt-Kittler, 1987) and belong to the *steblini-depereti* and *nanus-vectisensis* zones, which allow detailed correlation across Europe.

Comparison with other localities

The sedimentary sequence preserved at Hordle Cliff spans in age the lowest two horizons at Headon Hill on the Isle of Wight (see GCR site report), and so the mammalian faunas can be compared (e.g. Hooker, 1987). Although there are many similarities in the faunal compositions of the two sites, the assemblages recorded from Hordle Cliff have a greater proportion of large animals, especially artiodactyls and perissodactyls. Generally the specimens collected at Hordle Cliff are better preserved.

Farther afield, the mammal faunas of the Totland Bay Member can be compared with those in continental Europe. The classic site of Euzet-les-Bains in southern France has long been recognized as age-equivalent to some of the Hordle Cliff levels (e.g. Savage and Russell, 1983, pp. 104–8). Mammal Paleogene Reference Level MP17 encompasses numerous mammal faunas from sites in continental Europe, including Roc de Santa and Sossis in Spain, Aubrelong 2, La Bouffie, Baby 1, Les Clapies, Fons 1–7, Salème, Les Pradigues, Les Sorcières, Perrière, Malpérié, Rosières 5 and Euzet in France, and La Cantine 2 and Lebratières 1 in Switzerland (Schmidt-Kittler, 1987).

Conclusions

Hordle Cliff is important internationally for having one of the most taxonomically diverse early Late Eocene mammalian faunal suites in Europe. It is the type locality for 10 species and two subspecies of mammal. On a national scale, it has yielded many taxa of Late Eocene mammals, especially artiodactyls, perissodactyls and rodents, whose osteological remains are often exquisitely preserved and provide a wide range of anatomical information. The co-occurrence of diverse non-mammalian faunas and especially of floras (and including the oldest evidence for seed-gnawing by rodents in the world), together with the laterally well-exposed sequence, facilitating sedimentological study, allow for detailed palaeoenvironmental reconstruction. Coastal erosion here means that new material will be continually available for future study.

HEADON HILL, ISLE OF WIGHT (SZ 305 856–SZ 319 865)

Introduction

The locality of Headon Hill displays a section of sediments spanning all of Late Eocene

British Tertiary fossil mammal sites



Figure 3.13 Hatherwood Point, at the south-western end of the Headon Hill Formation outcrop on Headon Hill, Isle of Wight. The Hatherwood Limestone Member with lignite bed is shown (Photo: M.J. Benton.)

(Priabonian) time (Figures 3.13 and 3.14). The mammal fossils preserved at Headon Hill are distributed through several facies, each characterized by a different fossil assemblage. Six major faunas have been identified, two from the Totland Bay Member and one each from the Linstone Chine Member, the Hatherwood Limestone Member, the Lacey's Farm Limestone Member and the Bembridge Limestone Formation. These six horizons are included in the GCR locality. Some of them (e.g. that from the Bembridge Limestone Formation) are composed of several closely spaced horizons (Hooker et al., 1995), and in addition there are minor intermediate horizons recorded (Cray, 1973; Hooker, 1987). That from the Lacey's Farm Limestone Member is represented better faunally in the Lacey's Farm Quarry GCR site, but there the stratigraphical relationships are less clear than at Headon Hill.

Headon Hill has been studied extensively, initially during the 19th century, with the first report of mammal specimens from the site in a stratigraphical account by Prestwich (1846) and a description of one of the artiodactyls by Owen (1857a).Further new records from the Bembridge Limestone Formation were announced by Lydekker (1884a) and Stehlin (1910), but without mention of the locality; the specimens concerned, however, are almost all from Headon Hill. Franzen (1968) listed the species of Palaeotherium from the site. New taxa were described from Headon Hill by Cray (1973), Bosma (1974), Gingerich (1977), Sigé et al. (1977), Bosma and de Bruijn (1979, 1982), Hooker (1991a), and Hooker and Thomas (2001) and the mammalian faunas were reviewed by Hooker (1992) and Hooker et al. (1995). The stratigraphy and history were reviewed by White (1921), and further sedimentological and stratigraphical work has been completed more recently, for example by Edwards (1966), Daley and Edwards (1974), Bosma (1974), Daley and Insole (1984), Insole and Daley (1985), Insole et al. (1998) and Daley (1999b).

Description

At Headon Hill Late Eocene sediments are exposed in the cliff, although vegetation and landslips obscure parts of the succession (Figure



Figure 3.14 Field sketch of the south-western end of Headon Hill, showing the major stratigraphical divisions. (Based on Insole *et al.*, 1998.)

3.14). The sequence is the most complete representation of the Headon Hill Formation, and it has been designated as the stratotype of that unit (Insole and Daley, 1985).

The following simplified sedimentary log (Table 3.3) is based on a composite of the exposure seen in the south-western and north-eastern corners of Headon Hill and is simplified from Cray (1973) and Insole and Daley (1985), for the Headon Hill Formation, and Hooker *et al.* (1995), for the Bembridge Limestone Formation.

The exact provenance of most of the older Headon Hill specimens is not recorded in detail. Cray (1973, pp. 19–27) analysed existing records, and he himself discovered some relatively productive horizons.

1. Totland Bay Member, green clay at base of section, 2.1 m above the Becton Sand Formation ('Headon Hill Sands'): a fragmentary lower jaw of *Dicbodon cuspidatus* (Wright, 1852; Owen, 1857a). Bosma (1974) described six species of rodents from the green silty clay with shell fragments that occurs approximately 2.5 m above the base of the Totland Bay Member, her locality HH1. Two of these were named as new species by Hooker (1991a) and a seventh species was added by Bosma and de Bruijn (1979). The fauna totals 18 species and belongs to the *steblini–depereti* Zone (Hooker, 1987) and Mammal Paleogene Reference Level MP17A (Legendre and Hartenberger, 1992).

2. Totland Bay Member, green marl immediately below the How Ledge Limestone: a partial skeleton, as yet undescribed (Cray, 1973). Bosma (1974), Bosma and de Bruijn (1979, 1982) and Hooker (1991a) described 11 species of rodents from grey-green marls below the How Ledge Limestone, from Bosma's locality HH2. The fauna totals 29 species and belongs to the *vectisensis-nanus* Zone (Hooker, 1987) and Mammal Paleogene Reference Level MP17B (Legendre and Hartenberger, 1992). Table 3.3 Simplified sedimentary log for Headon Hill (based on Cray, 1973, Insole and Daley (1985) and personal observations by the present author, JJH, for the Headon Hill Formation, and Hooker *et al.* (1995), for the Bembridge Limestone Formation)

1.0 1.4
1.0 1.4
1.4
c 50
c. J.0
6.8
4.0
0.7
3.7
0.5
2.5
9.0
2.8
0.7
3.5
0-2.0
2.0
0.2
4.4
3.0
2.6
3.7
0.4
3.0
1.8
1.9
0.3
3.5

- 3. Linstone Chine Member, *Microchoerus* Bed, a small lenticular horizon of buff clay-rich sand containing wood debris at the base of the unit, some 100 m in lateral extent and located at the south-west corner of Headon Hill: 16 species, generally small in size (Hooker, 1987), site found in 1962 (Cray, 1973).
- 4. Hatherwood Limestone Member, Lignite Bed, a 0.4–0.7 m thick unit of carbonaceous clay and lignitic shell marl, filling an eroded surface, located about a third of the way up the vertical cliff formed by the limestone on the

south-west seaward face of Headon Hill: 33 species, the most extensive fauna from the Headon Hill Formation, found since 1961 (earlier isolated finds, including that noted by Prestwich (1846) also probably came from this member). Bosma's (1974, p. 26) localities HH3 and HH4, respectively below and above a 0.5 m lignite bed, produced rodent remains from brown silty marls. A few larger mammals have also been found in the upper limestone unit of the member (Franzen, 1968; Hooker and Thomas, 2001)

- 5. Lacey's Farm Limestone Member, lower part of the unit, exposed near the top of the cliff (SZ 3065 8595), a succession of grey-green and brown marls with thin shelly sand seams passing up into green marls with calcareous concretions. The marls are transitional upwards into a rubbly arenaceous limestone, the main unit of the member, which is overlain by laminated grey-green clays of the Fishbourne Member. Mammal remains were found at two levels, University of Bristol sites 7103 and 7106, the latter being equivalent to University of Utrecht site HH5. Teeth of the rodent Isoptychus pseudosiderolithicus were found (Bosma and Insole, 1972; Bosma, 1974). Subsequent collecting has yielded eight other taxa too (Hooker, 1987; 1992) but preservation is poor.
- 6. Bembridge Limestone Formation. Bosma and Schmidt-Kittler (1972, p. 182) and Bosma (1974, pp. 26-7) noted fossil mammals from her localities HH6 and HH7 (SZ 317 863), located on the north-eastern slope of Headon Hill, near the top of the cliff. The fossils came from a 1 m-thick unit above the main lower limestone succession of the Bembridge Limestone Formation. The unit is composed of marls and black muds, and it is overlain by a fine pale-yellow sand of probable Quaternary age. The fossils were found in the black muds with shell fragments in the upper part of the unit. Specimens included isolated teeth of the rodent Ectropomys exiguus Bosma and Schmidt-Kittler, 1972, a species founded on specimens from Whitecliff Bay (see GCR site report). More extensive collecting, summarized by Hooker et al. (1995, 2004), indicated a large fauna of 51 small and large mammals, found both in the main lower limestone unit and in nine separate horizons in the overlying muds and marls. The fauna belongs to the medium-curtum Zone (Hooker (1987) and Mammal Paleogene Reference Level MP19 (Schmidt-Kittler, 1987).

Fauna

The fossil mammals are found in horizons that also contain plant remains, as well as fishes (Dineley and Metcalf, 1999) and reptiles (turtles, crocodiles, lizards, snakes; Benton and Spencer, 1995). The combined faunal list for all six major units is compiled from Cray (1973), Bosma (1974), Hooker (1992) and Hooker *et al.* (1995, 2004). Records from individual units are indicated by the initials of the units in brackets following the taxonomic name: lower Totland Bay Member (LTB), upper Totland Bay Member (UTB), Linstone Chine Member (LC), Hatherwood Limestone Member (HL), Lacey's Farm Limestone Member (LF) and Bembridge Limestone Formation (BL).

MAMMALIA

Marsupialia

Herpetotheriidae

Amphiperatherium spp. (LTB, UTB, LC, HL, LF, BL)

Peratherium cuvieri (Fischer, 1829) (UTB, HL, BL)

Peratherium perrierense Crochet, 1979 (BL)

Peratherium lavergnense Crochet, 1980 (BL)

Rodentia

Paramyidae

Plesiarctomys curranti Hooker, 1986 (LTB)

Pseudosciuridae

Sciuroides ehrensteinensis Schmidt-Kittler, 1971 (LTB, UTB)

Treposciurus mutabilis Schmidt-Kittler, 1970 (LTB, UTB, HL, LF)

Treposciurus gardneri Hooker, 1991a (LTB, UTB, HL, BL)

Suevosciurus bosmae Hooker, 1991a (LTB, UTB, LC, HL)

Suevosciurus minimus (Major, 1873) (BL) Suevosciurus fraasi (Major, 1873) (BL)

Suevosciurus ebingensis Dehm, 1937 (BL) Tarnomys quercyi vectisensis Bosma, 1974 (UTB)

Tarnomys 'quercyi quercyi' (Schlosser, 1884) (LC, HL, LF)

Tarnomys schmidtkittleri Hooker and Weidmann, 2000 (BL)

Theridomyidae

Isoptychus euzetensis (Depéret, 1917) (UTB)

Isoptychus pseudosiderolithicus de Bonis, 1964 (HL, LF)

Isoptychus sp. (LC, BL)

Thalerimys headonensis (Bosma, 1974) (LTB)

Thalerimys fordi (Bosma and Insole, 1972) (UTB, LC, HL, LF, BL)

Ectropomys exiguus Bosma and Schmidt-Kittler, 1972 (BL)

Gliridae Glamys priscus (Stehlin and Schaub, 1951) (LTB, UTB, LC, HL, LF) Glamys devoogdi (Bosma and de Bruijn, 1979) (BL) Miniglis minor (Bosma and de Bruijn, 1982) (LTB, UTB, HL) Gliravus daamsi Bosma and de Bruijn, 1982 (LTB, UTB, HL, BL) Bransatoglis babloi Bosma and de Bruijn, 1982 (UTB, LC, HL, BL) Lipotyphla Talpidae Eotalpa anglica Sigé, Crochet and Insole, 1977 (LTB, UTB, LC, HL, BL) Amphilemuridae Gesneropithex grisollensis (Louis and Sudre, 1975) (LTB, UTB) Chiroptera Hipposideridae Pseudorbinolophus sp. (BL) Vespertilionidae Stehlinia gracilis Revilliod, 1919 (BL) Stehlinia minor (Revilliod, 1922) (BL) Archonta undiff. Nyctitheriidae Saturninia gracilis Stehlin, 1941 (UTB, LC, HL, BL) Euronyctia grisollensis (Sigé, 1976) (UTB, BL) Scraeva hatherwoodensis Cray, 1973 (LC, HL) Cryptotopos woodi (Cray, 1973) (UTB, LC, HL) Cryptotopos sp. (BL) Paradoxonycteris tobieni (Sigé, 1976) (BL) Paradoxonycteris aff. tobieni (Sigé, 1976) (UTB, LC, HL) Amphidozotherium cayluxi Filhol, 1877 (BL) Primates Omomvidae Microchoerus erinaceus Wood, 1844 (LTB, UTB, LC, HL) Microchoerus edwardsi (Filhol, 1880) (BL) Pseudoloris parvulus (Filhol, 1890b) (UTB) Adapidae Leptadapis stintoni (Gingerich, 1977) (UTB, HL) Leptadapis magnus (Filhol, 1874) (LTB, UTB, HL) Protoadapis ulmensis (Schmidt-Kittler, 1971) (UTB, HL, BL)

Apatotheria Apatemyidae Heterobyus nanus Teilhard, 1922 (UTB, LC, HL, BL) Pantolesta Pantolestidae Opsiclaenodon major (Lydekker, 1887) (LTB, UTB) Dyspterna bopwoodi Cray, 1973 (HL) Cryptopithecus sp. (BL) Creodonta Hyaenodontidae Hyaenodon brachyrbynchus Blainville, 1841 (HL) Pterodon dasyuroides Blainville, 1839 (BL) Carnivora Amphicyonidae Cynodictis lacustris Gervais, 1852 (BL) Cynodictis sp. (LC) Artiodactyla Cebochoeridae Acotherulum saturninum Gervais, 1850 (HL) Acotherulum quercyi (Stehlin, 1908) (BL) Choeropotamidae Rhagatherium cf. valdense Pictet, 1857 (LTB, BL) Amphirhagatherium edwardsi Hooker and Thomas, 2001 (HL) Amphirhagatherium fronstettense (Kovalevskii, 1874) (BL) Choeropotamus parisiensis Cuvier, 1821 (BL) Cainotheriidae Paroxacron sp. (BL) Anoplotheriidae Dacrytherium ovinum (Owen, 1857b) (HL) Anoplotherium commune? Cuvier, 1804 (BL) Anoplotherium latipes (Gervais, 1852) (BL) Anoplotherium laurillardi? Pomel, 1851 (BL) Diplobune sp. (BL) Xiphodontidae Xiphodon gracilis Cuvier, 1822 (BL) Dichodon cuspidatus Owen, 1848b (LTB, HL) Dichodon cervinus (Owen, 1841a) (BL) Dichobunidae Dichobune leporina Cuvier, 1822 (BL) Amphimervcidae Pseudamphimeryx hantonensis Cooper, 1928 (LTB, HL, LF)

Perissodactyla

Palaeotheriidae

Plagiolophus annectens (Owen, 1848b) (UTB, HL, LF, BL)

Plagiolophus minor (Cuvier, 1804) (BL)

Palaeotherium magnum Cuvier, 1804 (BL) Palaeotherium muehlbergi Stehlin, 1904 (UTB, LC, HL, BL)

Palaeotherium duvali Pomel, 1853 (BL)

Palaeotherium curtum Cuvier, 1812 (HL, BL)

Palaeotherium medium Cuvier, 1804 (BL) Pachynolophidae

Anchilophus radegondensis radegondensis (Gervais, 1852) (BL)

The mammal faunas from Headon Hill are comparable in the relative abundance of the different mammalian taxa with the fauna of equivalent age from Hordle Cliff, although the material generally is less completely preserved. The pantolestid Dyspterna hopwoodi was named from a lower jaw specimen (Figure 3.15a,b) and two isolated teeth from the Lignite Bed in the Hatherwood Member (Cray, 1973). It was a medium-sized carnivore that may have been aquatic. The nyctithere Scraeva batherwoodensis is based on a tiny lower jaw from the Microchoerus Bed (Figure 3.15c,d) and is smaller than the related species Cryptotopos woodi from Hordle Cliff (Cray, 1973). The adapid primate Leptadapis stintoni also was founded on fragmentary jaws from the Lignite Bed and was identified at first as Adapis parisiensis (Cray, 1973) but was named as a new species by Gingerich (1977) and recombined by Hooker (1986). It may alternatively be conspecific with L. assolicus (see Godinot, 1984). It was a modest-sized arboreal browsing herbivore. The omomyid primate Microchoerus erinaceus is best known from Hordle Cliff, but teeth from the Totland Bay Member, Microchoerus Bed and Lignite Bed have been identified to this species (Cray, 1973; Hooker, 1987). The apatemyid Heterohyus was not recorded from Headon Hill by Cray (1973; Hooker, 1987), but was listed subsequently by Collinson and Hooker (1987). The creodont Hyaenodon also is recorded on the basis of a fragment of a left maxilla (Cray, 1973) from the Lignite Bed.

The rodents from Headon Hill are more diverse than those from Hordle Cliff, and most of the glirid species recorded have their type specimens from the locality. The species Suevosciurus bosmae was established by Hooker (1991a) on teeth (Figure 3.15e) from the green clay in the How Ledge Limestone (including Bosma's locality HH2) and from Bosma's (1974) localities HH3 and HH4 (Hatherwood Limestone) that Bosma (1974) had included in S. palustris. The perissodactyls and artiodactyls from Headon Hill are similar to those from Hordle Cliff, but of lower diversity. Five species of Palaeotherium have been identified (Collinson and Hooker, 1987), all of them relatively large terrestrial browsing animals. Four of these, P. curtum, P. medium, P. muehlbergi and P. magnum show microevolutionary changes through the sequence. The stages have been given stratigraphical subspecies names and are important in correlation (Franzen, 1968).

Eleven mammal species and one subspecies have their type specimens from Headon Hill, namely the pantolestid Dyspterna bopwoodi Cray, 1973, the mole Eotalpa anglica Sigé, Crochet and Insole, 1977 (the oldest recognized from anywhere in the world), the nyctithere Scraeva hatherwoodensis Cray, 1973, the adapid primate Leptadapis stintoni (Gingerich, 1977), the rodents Suevosciurus bosmae Hooker, 1991a, Thalerimys headonensis (Bosma, 1974), Miniglis minor (Bosma and de Bruijn, 1982), Gliravus daamsi Bosma and de Bruijn, 1982, Glamys devoogdi (Bosma and de Bruijn, 1979), Bransatoglis babloi Bosma and de Bruijn, 1982, and Tarnomys quercyi vectisensis (Bosma, 1974), and the artiodactyl Amphirhagatherium edwardsi Hooker and Thomas, 2001.

Interpretation

The sedimentary environments displayed by the succession on Headon Hill are similar to those at Hordle Cliff (see GCR site report). The succession also is dated by the same criteria as used at Hordle Cliff, although only the lower mammalbearing units within the Totland Bay Member are directly comparable in age, based on the succession of restricted-range rodents (Bosma, 1974; Hooker, 1987) and to some extent by lithostratigraphical and mapping considerations.

Two mammal assemblages from Headon Hill, those from the How Ledge Limestone green clay (upper Totland Bay Member) and from the Lignite Bed (Hatherwood Limestone Member), are dominated by small mammals with body weights of less than 1 kg (Hooker, 1992). This



Figure 3.15 Fossil mammal specimens from the Headon Hill Formation of Headon Hill, Isle of Wight. (a,b) Right lower jaw of the pantolestid *Dyspterna hopwoodi* in crown (a) and internal (b) views. (c,d) Partial left lower jaw of the insectivore *Scraeva batherwoodensis* in crown (c) and internal (d) views. (e) Fourth upper milk premolar of the rodent *Suevosciurus bosmae* in crown view. (Based on Cray, 1973; Bosma and de Bruijn, 1979; Hooker, 1991a.)

bias to small size may be partly the result of selective preservation and of collecting, mainly by sediment sieving, during which larger specimens are rarely encountered. Arboreal mammals make up about 20% of the fauna, the rest being ground-dwellers: roughly the same proportions as at Hordle Cliff. There are more frugivores than at Hordle Cliff, and the How Ledge Limestone green clay has yielded more insectivores.

The depositional environments of the Headon Hill Formation range from coastal floodplain to low-salinity lagoon and freshwater lakes and marshes, with one interval of more marine

Headon Hill

conditions (Colwell Bay Member). The mammal types indicate a forest habitat that was slightly more closed than at Hordle Cliff (and less tropical than in the Bartonian Stage of Creechbarrow Hill), but of similar complexity and structure. The Hatherwood Limestone Member fauna might represent a local forest patch, partly because of the limited lateral extent of the unit. The How Ledge Limestone green clay, however, extends apparently unchanged for at least 4 km, and it appears to be directly laterally equivalent to the Hordle Cliff Rodent Bed, some 7 km distant, so this may be a less local assemblage (Hooker, 1992).

The Bembridge Limestone Formation has the most diverse fauna and is interpreted as representing a range of environments from open wooded to dense forest (Hooker, 1994b; Hooker *et al.*, 1995). The oldest assemblage (from the lower limestone) indicates open wooded habitats, and the higher assemblages (from the marls and black mud bands) suggest more-closed wooded conditions.

Comparison with other localities

The Totland Bay Member at Headon Hill shares many taxa with the contemporaneous Hordle Cliff, although there are differences, especially in the composition of the rodent faunas. The overall fauna from this member is somewhat smaller than that from Hordle Cliff, although the complete faunal list for the locality is much larger (over 73 species). The Headon Hill Totland Bay Member faunas also can be compared with the same ones attributed to Mammal Paleogene Reference Level MP17 in continental Europe as for Hordle Cliff (see GCR site report).

Higher faunas at Headon Hill have no or insignificant representation at other British localities (except at Lacey's Farm Quarry – see GCR site report). They can, however, be compared with faunas in continental Europe. Thus the Hatherwood Limestone Member fauna has its closest links with the fauna of the classic locality La Débruge in the south of France and other sites attributed to Mammal Paleogene Reference Level MP18.

The Bembridge Limestone Formation fauna has long been recognized to be time-equivalent to the top gypsum level at the famous Montmartre locality near Paris (Stehlin, 1910), where Cuvier first described such well-known genera as *Palaeotherium* and *Anoplotherium*. It is also age-equivalent to Entreroches in Switzerland (Hooker, 1992; Hooker and Weidmann, 2000). The Bembridge Limestone Formation fauna is often attributed to Mammal Paleogene Reference Level MP19 (Schmidt-Kittler, 1987), although it is slightly younger than Escamps in France (the reference locality for MP19) (Hooker, 1987).

These mammal-bearing localities in continental Europe, although faunally rich, are mostly isolated geographically one from another, often occurring in different basins, and may have no superpositional information at all, such as the fissure fillings of Quercy (France), Mormont (Switzerland) and Bavaria (Germany). Therefore, the long sequence of superposed mammal levels at Headon Hill is unique and vital for demonstrating the time order of most European Late Eocene faunas.

Conclusions

Headon Hill has international importance for its a unique sequence of superposed mammal faunas spanning all of Late Eocene time that can be used to calibrate stratigraphically and geographically isolated faunas in the rest of Europe. It is the stratotype for the Headonian European Land Mammal Age (Bosma, 1974; Fahlbusch, 1976) and is the only site in the Hampshire Basin at which a succession of four European mammalian biozones (steblini-depereti, vectisensis-nanus, pseudosiderolithicus-thaleri and medium-curtum) can be observed. Early collections consist almost entirely of a few large mammals found by prospecting. Screenwashing in the 1960s and 1970s and ongoing large-scale sediment processing and sieving operations (e.g. Hooker et al., 1995) are both enlarging the faunas and increasing the density of the succession. Stratigraphical overlap with Hordle Cliff is restricted to the Totland Bay Member, and even here there are significant faunal differences. Headon Hill is the type locality for 11 species and one subspecies of mammals. One of these, Eotalpa anglica, is the oldest known member of the mole family (Talpidae) in the world. Headon Hill is also the stratotype of the British lithostratigraphical unit, the Headon Hill Formation, as well as some of its included members, the Totland Bay, Hatherwood Limestone and Lacey's Farm Limestone members (Insole and Daley, 1985).

LACEY'S FARM QUARRY, TOTLAND, ISLE OF WIGHT (SZ 323 862)

Introduction

Lacey's Farm Quarry (also known as the 'Greens Quarry') is an abandoned quarry (Figure 3.16) that exposes a sequence of sediments from the Lacey's Farm Limestone Member of the upper part of the Headon Hill Formation, in a small outlier from the main Headon Hill locality (see GCR site report). It has produced an abundant and moderately diverse mammalian fauna of 22 species that represent nine orders. The unit was sampled intensively in the 1960s and 1970s, and the rodents have been described (Bosma and Insole, 1972, 1976; Bosma, 1974; Bosma and de Bruijn, 1979, 1982). Headon Hill, and a sedimentary log of the succession in the quarry is given here from Insole and Daley (1985, p. 84; Table 3.4).

The vertebrate materials have been recovered from thin clay and sand seams in the Lacey's Farm Limestone Member in the upper part of the Headon Hill Formation (Bosma and Insole, 1972), as well as from the limestone itself (University of Bristol localities 6911 and 7105; Bosma and Insole, 1972). The fossiliferous section is at SZ 3224 8618. The main collections were made by sieving the clays and sands, and additional finds in the limestone were made by prospecting. The fossils are almost entirely isolated teeth.

Fauna

The list of mammalian taxa is based on Insole (1972) and Hooker (1992, table 25.1).

Description

The Lacey's Farm Quarry locality lies close to the stratotype section of the Lacey's Farm Limestone Member of the Headon Hill Formation at

MAMMALIA Marsupialia Herpetotheriidae



Figure 3.16 Lacey's Farm Quarry, showing exposure of the Lacey's Farm Limestone Member.

 Table 3.4 A sedimentary log of the succession in the quarry (from Insole and Daley, 1985)

	Imckness (m)
Headon Hill Formation	**************************************
Fishbourne Member	
Mud, brown-grey, with basal conglomerate	seen to 1.0
Lacey's Farm Limestone Member	
Limestone, white, rubbly with green marl lenses; Lymnaea, Australorbis	2.5
Marl, yellow-green; abundant calcareous concretions; vertebrate bones	
and teeth	0.3
Limestone, white, rubbly; base transitional into underlying mud	0.9
Mud, green; abundant calcareous concretions	seen to 0.3

Amphiperatherium spp.

Rodentia

Pseudosciuridae

Suevosciurus ebingensis Dehm, 1937

Treposciurus mutabilis Schmidt-Kittler, 1970

Tarnomys quercyi (Schlosser, 1884)

Theridomyidae

Isoptychus pseudosiderolithicus de Bonis, 1964

Thalerimys fordi (Bosma and Insole, 1972) Gliridae

Gliravus daamsi Bosma and de Bruijn, 1982

Glamys priscus (Stehlin and Schaub, 1951) *Bransatoglis babloi* Bosma and de Bruijn, 1982

Chiroptera

indet.

Archonta undiff.

Nyctitheriidae

Paradoxonycteris aff. tobieni (Sigé, 1976) Primates

Adapidae

Leptadapis stintoni (Gingerich, 1977) Omomyidae

Microchoerus erinaceus Wood, 1844 Microchoerus edwardsi? (Filhol, 1880)

Apatotheria

Apatemyidae

Heterobyus nanus Teilhard, 1922

Carnivora

Amphicyonidae

Cynodictis lacustris Gervais, 1852

Artiodactyla

Cebochoeridae

Acotherulum saturninum Gervais, 1850 Choeropotamidae

Rhagatherium sp.

the world the first the first the	and the second second second	The start
Xiphodontidae	The Martine	Aler and
Haplomeryx sp.		
Amphimerycidae		
Pseudamphimeryx	bantonensis	Cooper,
1928		
Perissodactyla		
Palaeotheriidae		
Plagiolophus annec	tens (Owen, 1	848b)
Palaeotherium mag	num Cuvier, 1	804

The fauna of 22 mammals from the Lacey's Farm Limestone Member has its closest relationships with the older Headonian fauna from the underlying Hatherwood Limestone Member of Headon Hill (see GCR site report), but the diversity and number of specimens is less. The fauna is, however, much richer and better preserved than in the Lacey's Farm Limestone Member at Headon Hill. The majority of the taxa are common to the other earlier Priabonian/ Headonian mammal faunas of southern England and of the Paris Basin.

Lacey's Farm Quarry is the type locality for one species, the rodent *Thalerimys fordi* (Bosma and Insole, 1972), based on a number of isolated teeth (Figure 3.17), which differs from its relative, *Isoptychus pseudosiderolithicus*, in being larger and having more complex infoldings on the crowns of its molars. The fauna is marked by the first appearance of the pseudosciurid rodent *Suevosciurus ehingensis*, which may have evolved in Britain from the earlier *S. bosmae* in a northern European speciation event (Hooker, 1991a).

Interpretation

The environment of deposition of the Lacey's Farm Limestone Member is that of a freshwater



Figure 3.17 Fossil mammal specimens from the Headon Hill Formation of Lacey's Farm Quarry, Isle of Wight. Teeth of the rodent *Thalerimys fordi* in crown view. (a) Upper molar 1 or 2. (b) Upper premolar 4. (c) Upper milk premolar 4. (After Bosma and Insole, 1972.)

lake, with evidence in the west of subaerial exposure and karst development (Insole, 1972).

The distribution of mammal taxa indicates a bias towards small sizes, as with the Headon Hill mammal faunas, possibly partly the result of bias in preservation and collecting (as for Headon Hill, most of the Lacey's Farm Quarry mammal specimens were found by screenwashing – see above). The Lacey's Farm Limestone Member mammal fauna includes more frugivores and fewer insectivores than the Hordle Cliff Mammal Bed. The Lacey's Farm Limestone Member mammal assemblage is probably a local accumulation, and it may indicate a forest patch where mammals have been concentrated in the fossiliferous unit.

The Lacey's Farm Limestone Member mammal assemblage has overall similarities with other Headon Hill Formation faunas but is sufficiently different from most of them that, with the fauna from the Hatherwood Limestone Member alone, it is assigned to the pseudosiderolithicus-thaleri Zone (Hooker, 1987) and Mammal Paleogene Reference Level MP18 (Schmidt-Kittler, 1987). This makes it equivalent in age and composition to a number of mammal faunas from France (Gousnat, Sainte-Néboule, St Martin de Villeréal 1, Ste Croix de Beaumont 1, Civrac, La Débruge), Switzerland (Gösgen-Kanal) and Germany (Pfaffenweiler, Ehrenstein 1A. Ehrenstein 2, 3, 6, Herrlingen 3).

Comparison with other localities

The mammalian assemblage preserved at Lacey's Farm Quarry can demonstrably be intercalated

into the sequence at Headon Hill by direct lithostratigraphical mapping of the Lacey's Farm Limestone Member over a distance of only about 1 km. Only very occasional mammal fossils are known from other sites in the Lacey's Farm Limestone Member, namely Headon Hill and Whitecliff Bay (see GCR site reports), from where six and one taxa respectively are recorded, all of which also occur at Lacey's Farm Quarry. The fauna is also comparable with a number of faunas from Spain, France and Switzerland, as detailed above.

Conclusions

Lacey's Farm Quarry is nationally important for preserving the only rich mammalian fauna from the Lacey's Farm Limestone Member of the Headon Hill Formation. It complements the nearby internationally important sequence at Headon Hill by providing a datable fauna at a level poor in mammals at Headon Hill. Although little work has so far been published on this locality, it has great potential for future study, and the fauna could be considerably augmented.

WHITECLIFF BAY, ISLE OF WIGHT (SZ 643 864)

Introduction

A section from the Reading Formation to the lower part of the Bouldnor Formation is exposed in Whitecliff Bay (Figure 3.19). Fossil



Figure 3.18 The Bembridge Marls Member of the Bouldnor Formation at Whitecliff Bay, Isle of Wight. (Photo: Dave Evans.)

vertebrates generally have been found at various horizons in Whitecliff Bay (Hooker *et al.*, 1980), but mammal remains have been found only in the Headon Hill, Bembridge Limestone and Bouldnor formations. They occur at a number of levels: in the Totland Bay, Lacey's Farm Limestone and Osborne members of the Headon Hill Formation, in the middle muds of the Bembridge Limestone Formation and in the Bembridge Marls Member of the Bouldnor Formation. The stratigraphy has been described by White (1921), Edwards (1966), Bosma (1974), Insole and Daley (1985), Daley and Edwards (1990) and Daley (1999b).

Mammal remains were reported from the Totland Bay Member by Bosma (1974), the Lacey's Farm Limestone and Osborne members (formerly 'Osborne Beds') by Bosma and Insole (1972), the Bembridge Limestone by Hooker *et al.*, (2004) and the Bembridge Marls Member by Bosma (1974), and Hooker *et al.* (2004).

Although the beach is generally covered by a substantial layer of gravel, storms often uncover the Eocene sediments. The section seen in the cliff is often leached and somewhat decalcified, except after a period of erosion, when a clean section is present.

Description

The section of Late Eocene and earliest Oligocene sediments in Whitecliff Bay (Figures 3.18 and 3.19) provides the most complete such sequence in the Hampshire Basin. Indeed, Stinton and Curry (1979) named Whitecliff Bay as the type locality for their Solent Formation, a unit that Insole and Daley (1985) raised to the rank of Solent *Group* and which includes the Headon Hill, Bembridge Limestone and Bouldnor formations. The measured section given here (Table 3.5) is simplified from Insole and Daley (1985, pp. 73, 91, 95).

The Whitecliff Bay section extends higher in the Hampshire Basin sequence than does the Headon Hill section, to include the Bembridge Marls Member of the Bouldnor Formation. It also differs in including an additional unit, the Seagrove Bay Member, at the top of the Headon



Figure 3.19 Cliff profile of the Paleogene section at Whitecliff Bay, Isle of Wight. (After Insole et al., 1998.)

Hill Formation; the Hatherwood Limestone Member is missing; the Colwell Bay Member is much thicker and fully marine at the base; and the Totland Bay Member is much thinner, through pre-Colwell Bay Member erosion. Mammal fossils have been found at six horizons through the sequence: near the base in the Totland Bay Member, in the Lacey's Farm Limestone Member, near the top of the Osborne Member, and at two levels in the Bembridge Marls Member.

The mammal remains from the Totland Bay Member occur in a lens of clay, 25 cm thick, with abundant '*Limnaea*', '*Planorbis*' and *Viviparus*, termed locality WB1 (Bosma, 1974, p. 29). The lens is situated in a green clay unit, about 2 m thick, which passes up into pure lignite. The lens is about 3 m above the base of the unit, marked by the contact with the underlying Becton Sand Formation.

Mammals have been found at three horizons in the 'Osborne Beds', in marls and muds, at University of Bristol localities 7066, 7101 and 7102 (Bosma and Insole, 1972). The first locality is about 7 m from the base, and the last two 30–35 m from the base, corresponding respectively to the Lacey's Farm Limestone Member, the upper part of the Osborne Member and the lower part of the Seagrove Bay Member, in modern terminology.

Mammal bones and teeth also have been found in the Bembridge Marls Member, both right at the base of that unit and some 10 m up the section. Bosma (1974, pp. 29-30) specified that mammal remains came from her localities WB2A and WB2B, both in the cliff at Whitecliff Bay, below Bembridge School (SZ 643 865). Site WB2A produced fossils from a white marly limestone that fills irregular depressions in the top of a solid limestone bed. The WB2B material was collected from a yellow marl about 20 cm thick, situated 5-10 m west of WB2A at about the same level. The fossiliferous horizon is about 11.5 m above the main limestone succession of the Bembridge Limestone Formation. This unit has produced remains of some 22 species of mammals (Hooker et al., 2004).

Fauna

The mammal fauna of the Totland Bay Member so far recorded is restricted to the rodent *Thalerimys headonensis* (Bosma, 1974). That from the Lacey's Farm Limestone Member is

A Contraction of the contraction	Thickness (m)
Pleistocene	
Plateau gravels	
Bouldnor Formation	
Bembridge Marls Member	
Mud, green-grey to grey, with shell bands	с. 18.0
Siltstone, grey-green, erosional structures, pseudomorphs after gypsum,	
gastropods	1.4
Mud, grey-green, occasional sandstone bands	1.2
Marl, light green-grey, some siltstone bands	0.9
Mud, green-grey mottled red, sandy lenses	9.0
Mud, dark green-grey, pyritized shell band at base	bee vel 1.2
Mud, green-black, discontinuous argillaceous limestone near middle	0.9
Muddy sand, light green-grey, marine fossils	0.4
Mud, grey-green, with shelly sands and muds	1.4
Bembridge Limestone Formation	
Marls, pale-green, burrowed top	1.2
Limestone, white, conglomeratic at base	1.4
Limestone, pale-brown, with gastropods	0.7
Marl and mud, grey, becoming darker downwards, with Corbicula	1.3
Limestone, pale-brown to pale-grey at base, lignitic near middle	2.3
Marl, pale-grey, with thin limestone at base	1.8
Headon Hill Formation	
Seagrove Bay Member	
Mud, dark green with pale green siltstone above	2.8
Sandstone and sandy limestone, with mud band	0.8
Mud, green with brown mottling, some calcareous concretions	4.8
Sandstone, vellow, with basal erosion surface	0.7
Osborne Member	
Mud, red and green mottled near top, grey in middle, grey-green with red	
mottling lower, and black at base	10.4
Fishbourne Member	
Mud, grey and grey-green, shaly with sporadic Viviparus bands	10.9
Lacey's Farm Limestone Member	
Marl, green, with concretions and calcareous bands	6.7
Cliff End Member	
Mud. green with red mottling	4.0
Mud. grev-green	8.0
Linstone Chine Member	
Fine-grained pale-green sandstone	1.5
Colwell Bay Member	in the second second
Mud. green and green-grey, with Lymnaea	5.8
Fine-grained sand, pale-green to mud, grey-green	1.6
Mud. dark-green, passing down into pale-vellow fine-grained sand	3.2
Sandy mud, blue-grey, very shelly in upper half	4.1
Mud. pale grey, abundant <i>Ostrea</i> at base	1.2
Sandy mud, blue-grey, with shell beds, basal erosion surface	12.9
Totland Bay Member	(palothed)
Marl, pale-green, with shelly bands	18
Muddy fine-grained sand, pale-grey, sandy ironstone at base	1.8
Mud. pale grey, with several lignitic layers	2.8
Mud. bright green	17
Rests conformably on Becton Sand Formation	1.1

 Table 3.5 The measured section of the Solent Group for Whitecliff Bay (after Insole and Daley, 1985; Daley and Edwards, 1990)

British Tertiary fossil mammal sites

restricted to *Isoptychus pseudosiderolithicus* (Bosma and Insole, 1972), and that from the Osborne Member includes only *Tarnomys quercyi* and *Isoptychus* (Bosma and Insole, 1972; Hooker, 1987). The Bembridge Marls Member mammals are accompanied at the base of the unit by shark teeth (Hooker *et al.*, 1980). The faunal list given is just for the Bembridge Marls Member and is from Bosma (1974), Hooker (1987) and Hooker *et al.* (1995, 2004) and includes smaller mammals found at the Whitecliff Bay microvertebrate localities, as well as larger animals found by prospecting in both Whitecliff Bay and Howgate Bay at higher horizons in the member.

MAMMALIA

Marsupialia

Herpetotheriidae

Amphiperatherium spp.

Rodentia

Pseudosciuridae

Tarnomys schmidtkittleri Hooker and Weidmann, 2000

Treposciurus gardneri Hooker, 1991a Suevosciurus ebingensis Dehm, 1937

Theridomyidae

Isoptychus pseudosiderolithicus de Bonis, 1964

Ectropomys exiguus Bosma and Schmidt-Kittler, 1972

Gliridae

Glamys devoogdi (Bosma and de Bruijn, 1979)

Bransatoglis babloi Bosma and de Bruijn, 1982

Lipotyphla

Amphilemuridae

Gesneropithex sp.

Archonta undiff.

Nyctitheriidae

Saturninia gracilis Stehlin, 1941 Paradoxonycteris tobieni (Sigé, 1976)

Amphidozotherium cayluxi Filhol, 1877

Primates Omomyidae

Microchoerus edwardsi (Filhol, 1880)

Apatotheria

Apatemyidae

Heterobyus nanus Teilhard, 1922 Pantolesta

Pantolestidae

Cryptopithecus sp.

Artiodactyla

Choeropotamidae	
Choeropotamus parisiensis Cuvier, 1821	
Tapirulus sp.	
Cainotheriidae	
Paroxacron sp.	
Anoplotheriidae	
Anoplotherium commune Cuvier, 1804	
Xiphodontidae	
Xiphodon gracilis Cuvier, 1822	
Haplomeryx zitteli Schlosser, 1886	
Perissodactyla	
Palaeotheriidae	

Plagiolophus minor (Cuvier, 1804)

The rodents from Whitecliff Bay have had an important influence on studies of early rodent evolution, forming the basis of a number of papers (Bosma and Insole, 1972; Bosma and Schmidt-Kittler, 1972; Bosma, 1974; Bosma and de Bruijn, 1979, 1982). The sequences at Whitecliff Bay and Headon Hill, together with supplementary shorter sections at Lacey's Farm Quarry and Bouldnor Cliff, have formed the basis for a detailed rodent biostratigraphy of the Late Eocene to early Oligocene time interval (Bosma, 1974; Bosma and de Bruijn, 1979, 1982).

The Osborne Member at Whitecliff Bay has so far produced only small mammals, whereas the Bembridge Marls Member fauna consists of small and large mammals, with a modest array of artiodactyl and perissodactyl remains.

The mammal teeth and bones from the Osborne Member were obtained by sieving (Bosma and Insole, 1972). Similarly, the mammal remains from the Bembridge Marls Member, as sampled by Bosma and Schmidt-Kittler (1972), Bosma (1974) and Hooker (1991a), also were obtained by sieving sediment and subsequent concentration using acetic acid. The bones and teeth were essentially small elements, and those from Bosma's locality WB2A at least included 'polished bone fragments'.

The Bembridge Marls Member of Whitecliff Bay is the source of the type specimen of the rodent *Ectropomys exiguus* Bosma and Schmidt-Kittler, 1972 (Figure 3.20).

Interpretation

The lower parts of the succession are similar depositionally to the equivalent units at Headon Hill. An exception to this is the Colwell Bay Member, which is fully marine at its base and Bouldnor Cliff



Figure 3.20 The rodent *Ectropomys exiguus* from the Bouldnor Formation of Whitecliff Bay, Isle of Wight. (a) Upper molar 1 or 2. (b) Upper molar 3. (c) Upper premolar 4. (d) Upper milk premolar 4. All in crown view. (After Bosma and Schmidt-Kittler, 1972.)

contains calcareous nannoplankton as well as a diverse mollusc fauna, an important point of calibration to standard marine sequences. The sediments of the Osborne Member are dominantly colour-mottled clays with mudcrack horizons and occasional bone concentrations, which suggest the overbank facies of a floodplain. The overlying Seagrove Bay Member appears to be a higher-energy fluvial deposit prograding over the Osborne Member (Hooker, 1992).

The Bembridge Marls Member mammal fauna, according to its ecological diversity signal, indicates an open woodland (Collinson *et al.*, 1993). The depositional environment of the Bembridge Marls Member varies from lagoonal near the base to fluvio-lacustrine alternations higher up (Daley, 1972, 1973).

Comparison with other localities

The presence of *Thalerimys headonensis* in the Totland Bay Member indicates an age-correlation of site WB1 with the lower fauna of the Totland Bay Member at Headon Hill (Bosma, 1974).

Mammals from the other members of the Headon Hill Formation are currently too sparse to attempt correlation other than by lithostratigraphy.

The Bembridge Marls Member mammal faunas of Whitecliff Bay are attributed to Mammal Paleogene Reference Level MP20 (Schmidt-Kittler, 1987), equivalent to the sites Huermeces del Cerro in Spain, St Capraise, Tabarly, Baby 2 and Villeneuve la Comptal 2 in France, and Frohnstetten, Neustadt and Nordshausen in Germany. They also may belong to the *suevicum-frohnstettense* Zone, although this is uncertain (Hooker, 1987).

Conclusions

Mammal fossils can be found at several horizons in the rock succession at Whitecliff Bay, spanning the entire Late Eocene and earliest Oligocene times. The fauna from the Bembridge Marls Member is by far the best known in that unit from any British site and includes the type material of the rodent Ectropomys exiguus. Faunas from other levels are as yet poorly known but potentially are important, as the Standard Calcareous Nannoplankton Zone NP19/20 is recorded at the base of the Colwell Bay Member, facilitating correlation with the marine realm. Correlation thence via mammals to Headon Hill provides a vital chain of relative dating between marine and non-marine provinces in Europe. The total Whitecliff Bay section, because of its long uninterrupted timespan, is critical as a European standard for geological time through this interval, and the intercalation of several mammal faunas, although overall less diverse than at Headon Hill, is important in this broader context. The mammal-bearing horizons are still available, and ongoing intensive collecting is enhancing their importance.

BOULDNOR CLIFF, ISLE OF WIGHT (SZ 375 902–SZ 403 919)

Introduction

Bouldnor Cliff exposes the Bembridge Limestone Formation and the Bouldnor Formation (Figure 3.21). The unstable nature of the cliffs, leading to a high rate of coastal erosion, make this an excellent site for fossil collecting. Bouldnor Cliff is important globally as a source of Oligocene reptiles, birds and mammals. It is a classic British site for the larger Paleogene mammals, notably anthracotheres (e.g. Cooper, 1925). More recently, the smaller rodents have been described by Bosma (1974) and Bosma and de Bruijn (1979).

Description

The coastal section at Bouldnor Cliff (including Hamstead Cliff and Ledge) exposes the Bembridge Limestone Formation and all of the overlying Bouldnor Formation in a synclinal structure (Figure 3.21). Although the coastal section is long (3.2 km), exposure is intermittent owing to slumping. The Bembridge Limestone Formation crops out in the eastern parts of the section (SZ 401 920) and is responsible for the 'Hamstead Ledge' feature. The Bembridge Marls Member is best-exposed in the adjacent cliff and foreshore, whereas the Hamstead and Cranmore members form the cliff and foreshore farther west (Insole and Daley, 1985).

The section (Table 3.6) is taken from Benton and Spencer (1995, p. 296) and is based on White (1921), Daley (1973), Daley and Edwards (1974), Daley and Insole (1984), Insole and Daley (1985) and Daley (1999b).

Mammal remains, together with fish, turtles and crocodiles, occur at several levels in the Bouldnor Formation: near the top of the Bembridge Marls Member and within the Hamstead Member, both below and above the Nematura Bed. They have been collected from both cliff and foreshore exposures and many are found loose on the beach with no clear provenance, although preservation can often be a guide. From the Bembridge Marls at Yarmouth several species of large mammal typify the suevicum-frobnstettense Zone (Hooker 1987) and Mammal Paleogene Reference Level MP20 (Schmidt-Kittler, 1987), namely Anoplotherium sp., Palaeotherium medium suevicum and Plagiolophus major (Hooker et al., 2004).

Lower parts of the Hamstead Member, below the *Nematura* Bed, contain similar large mammals, typical of the endemic Late Eocene faunas of Europe, namely *Anoplotherium commune*, *A. latipes*, *Xipbodon gracilis*, *Plagiolophus minor*, *P. major*, *Palaeotherium magnum*, *P. muehlber*-



Figure 3.21 The fossiliferous Bembridge Limestone Formation and Bouldnor Formation at Bouldnor, Isle of Wight.

Bouldnor Cliff

(+) (conservation) and the state of the stat	Thickness (m)
Bouldnor Formation	adanta nconstanta ba
Cranmore Member (Upper Hamstead Beds of White, 1921)	
Corbula Beds	5.8
Cerithium Beds	3.4
Hamstead Member (Lower Hamstead Beds of White, 1921)	
Green and mottled clays, with lignite beds and shell beds	с. 25
Water-Lily Bed: laminated lignite with seeds, palm leaves, water-lily leaves and molluscs	0.6
Green and red marls (much obscured)	20.7
White Band: green clays with white shell-marls	1.8
Green clay with ironstone nodule band (much obscured)	10.8
Nematura Bed: black lignitic clay, full of gastropods	0.9
Green and black clavs, with bivalves and gastropods	8.1
Black Band: lignite, full of Viviparus and Unio	0.5
Bembridge Marls Member (Bed notation from Daley, 1973)	
HAM XXXI-XXXIV: freshwater clays	1.8
HAM XXX: lignite with seeds and molluscs	0.1
HAM XXVI-XXIX: clays with seeds and molluscs	5.7
HAM XXIII–XXV: lignite and clay, rich in water-plant seeds, leaf fragments	20
and gastropods	2.0
HAM XX-XXII: ITESIWATER Clays and shits	2.0
HAM AIX: green clays and white maris, with bivalves	0.5
HAM XV block clev with costronoide	1.0
HAM AV: Diack clay with gastropous	0.2
HAM AI-AIV: muds and slits, with Divalve Dand	5.0
bivalves and gastropods	2.7
HAM V: greenish-grey clay with bands containing Melanoides acuta,	
Serpula sp. and Viviparus lentus	0.3
HAM I-IV: grey and black clays with shelly partings and bands containing	
bivalves and gastropods; thin shell bed with Ostrea at the base	
(Bembridge Oyster Bed)	0.9
Rests on Bembridge Limestone Formation	derives and 19601

Table 3.6 Section for Bouldnor Cliff (after Benton and Spencer, 1995)

gi and P. curtum frobnstettense. The last is restricted to the suevicum-frobnstettense Zone and MP20. Thanks to screenwashing techniques, a fauna of small mammals has also been found in these strata. Key amongst these is the theridomyid rodent Theridomys bonduelli, whose only other correctly recorded occurrence is in the Marnes Blanches de Pantin in the Paris Basin, affording a secure correlation (Hooker et al., 2004). This correlation integrates with that of the Nematura Bed and Argiles Vertes de Romainville dated on the dinoflagellate cysts (Liengjarern et al., 1980), which form the next higher unit in both basins.

Upper parts of the Hamstead Member above the *Nematura* Bed yield a very different fauna. Amongst the large animals, there are no more

anoplotheres, xiphodonts or palaeotheres. Amongst the smaller elements, the pseudosciurid rodents, the omomyid primates, the amphilemurid lipotyphlans and nearly all of the nyctitheres have disappeared. In place of the old large mammals are artiodactyls of the families Anthracotheriidae (Bothriodon, Elomeryx and Anthracotherium) and Entelodontidae and a pecoran (advanced ruminant), and perissodactyls of the family Rhinocerotidae (Ronzotherium) (Hooker et al., 2004). Of the rodents, alongside the theridomyids and glirids (dormice), which persisted undiminished, appeared the first European beavers (Asteneofiber), hamsters (Atavocricetodon) and the extinct eomyids (Bosma, 1974; Bosma and de Bruijn, 1979). Also amongst the fauna of smaller mammals are the first European hedgehogs (*Tetracus*) and bears (a dog-sized amphicynodontine). The upper Hamstead Member has also yielded the last adapid primate in the world (*Leptadapis* sp.) and the last British nyctithere (one specimen each). In contrast, the marsupials continued almost unchanged.

The anthracotheres, distant hippo relatives, are the best-known elements of the Bouldnor Cliff post 'Grande Coupure' fauna, as they are the only large early Tertiary mammals that are relatively common fossils. Their taxonomy and nomenclature is complex (Owen, 1848c; Lydekker, 1884b, 1885a; Cooper, 1925, 1926a; Lavocat, 1952; Hellmund, 1992; Hooker, submitted). Rare elements represented by only a few isolated teeth are the giant pig-like entelodontid *Entelodon* (Brunet, 1979) and the first British true rhinoceros *Ronzotherium* (Ford, 1972).

Shark remains also have been reported from the *Ceritbium* and *Corbula* beds in the brackish and marine Cranmore Member (Hooker *et al.*, 1980), but no mammals from those levels.

Fauna

The mammalian fauna from the Hamstead Member at Bouldnor Cliff, consisting of 44 species, is listed here. It is based on information on the rodents from Bosma (1974) and Bosma and de Bruijn (1979), with nomenclatural changes from Vianey-Liaud (1994), Freudenthal (1996) and an updated list by Hooker *et al.*, (2004). The letters (L) and (U) after names distinguish between occurrences in lower and upper parts of the Hamstead Member, respectively.

MAMMALIA

Marsupialia

Herpetotheriidae

- Amphiperatherium exile Gervais, 1852 (L,U)
- Amphiperatherium minutum (Aymard, 1846) (U)

Amphiperatherium sp. (L, U)

Peratherium cuvieri (Fischer, 1829) (L) Peratherium elegans (Aymard, 1846) (U)

Peratherium cf. *perrierense* Crochet, 1979 (U)

Rodentia

Pseudosciuridae

Suevosciurus fraasi (Major, 1873) (L)

Theridomyidae Pseudoltinomys cuvieri (Pomel, 1853) (L) Pseudoltinomys gaillardi (Stehlin and Schaub, 1951) (U) Theridomys bonduelli (Lartet, 1869) (L) Isoptychus margaritae (Vianey-Liaud, 1989) (U) Gliridae Glamys fordi (Bosma and de Bruijn, 1979) (L, U) Bransatoglis planus (Bahlo, 1975) (L) Bransatoglis micio (Misonne, 1957) (U) Eomyidae Eomys sp. (U) Cricetidae Atavocricetodon atavus (Misonne, 1957) (U) Castoridae Asteneofiber sp. (U) Lipotyphla Talpidae ?Eotalpa sp. (L) Myxomygale cf. antiqua Filhol, 1890a (U) Erinaceidae Tetracus aff. nanus (Aymard, 1846) (U) Plesiosoricidae? Butselia biveri Quinet and Misonne, 1965 (L, U) Chiroptera Vespertilionidae Steblinia minor (Revilliod, 1922) (U) Stehlinia gracilis Revilliod, 1919 (U) Archonta undiff. Nyctitheriidae Paradoxonycteris tobieni (Sigé, 1976) (L, UD Amphidozotherium aff. cayluxi Filhol, 1877 (L) **Primates** Adapidae Leptadapis sp. (U) Pantolesta Pantolestidae Dyspterna woodi Hopwood, 1927 (L, U) Carnivora Ursidae ?Amphicynodon sp. Creodonta Hyaenodontidae Hyaenodon cf. dubius Filhol, 1873 (U) Artiodactyla Entelodontidae Entelodon magnus Aymard, 1846 (U) Anthracotheriidae

Bouldnor Cliff

Elomeryx porcinus (Gervais, 1852) (U) Bothriodon velaunus (Cuvier in de Blainville, 1846) (U)

Anthracotherium alsaticum Cuvier, 1822 (U)

Choeropotamidae

Tapirulus sp. (U)

Anoplotheriidae

moss de Henares). Fra Anoplotherium commune Cuvier, 1804 (L) Anoplotherium latipes (Gervais, 1852) (L)

Xiphodontidae

Xiphodon gracilis Cuvier, 1822 (L)

Pecora

Pecora indet. (U)

Perissodactyla

Palaeotheriidae

Palaeotherium magnum Cuvier, 1804 (L) Palaeotherium muehlbergi Stehlin, 1904 (L)

Palaeotherium curtum frohnstettense Franzen, 1968 (L)

Plagiolophus minor (Cuvier, 1804) (L)

Plagiolophus major (Brunet and Jehenne, 1989) (L) Rhinocerotidae

Ronzotherium cf. romani Kretzoi, 1940 (U).

A distinct change in the nature of the mammal faunas high in the early Tertiary strata in the Isle of Wight was noticed in the pioneering years (e.g. Forbes, 1856). However, it was not until early in the 20th century that the Swiss palaeomammalogist H.G. Stehlin (1910), with a European perspective, recognized the scale and significance of this faunal turnover, which he termed the 'Grande Coupure' (meaning 'big break'). During most of the Eocene Epoch, Europe had been a series of islands, intermittently linked, but separated by seaways from other continents. European mammal faunas quickly became endemic and, when Europe and Asia became reconnected early in the Oligocene Epoch, Asian species dispersed into Europe and much of the European endemic fauna (e.g. most palaeotheres, anoplotheriid, xiphodontid and choeropotamid artiodactyls, nyctitheres and primates) became extinct. How much the extinction was due to competition with the newcomers and how much to climatic change (this time was also marked by the first major glaciation of Antarctica in the Cenozoic Era) is still unclear (Hooker et al., 2004).

Until recently, the 'Grande Coupure' in the Isle of Wight was thought to occur between the Bembridge Marls and Hamstead Members of the Bouldnor Formation (e.g. Forbes, 1856; Stehlin, 1910; Hooker, 1992). Intensive collecting, especially using screenwashing, at a number of levels in the Bouldnor Formation has shown that the 'Grande Coupure' is in fact within the Hamstead Member (Hooker et al., 2004). Moreover, a number of taxa previously thought to occur only after the 'Grande Coupure' (e.g. Glamys fordi, Butselia biveri - see Bosma and de Bruijn, 1979; Butler 1972) have been found to pre-date the event, but this does not include any taxa with a clear Asian origin. Stehlin (1910) deduced his 'Grande Coupure' from study of continental European faunas, many of which occur in isolated localities, including fissure fillings, where superposition cannot easily be demonstrated. The Bouldnor Cliff section is thus unique both in having a continuous, wellexposed succession across this faunal divide and in having several discrete levels with a diversity of large and small mammal remains (Hooker et al., 2004).

The Bouldnor Cliff sections have provided the type specimens of two species: Dyspterna woodi Hopwood, 1927, and Glamys fordi (Bosma and de Bruijn, 1979).

Interpretation

The sediments preserved at Bouldnor Cliff are indicative of low-energy conditions and probably were deposited in a mainly lagoonal-lacustrine complex. Salinity ranged from brackish to freshwater. At times the water levels were low and desiccation cracks formed, for example in the lower sections of the Bembridge Marls Member (Daley, 1973). Daley (1973) distinguished three sedimentary environments in the Bembridge Marls Member: estuarine deposits in the lower part, passing up into lagoonal mudstones, and then floodplain and lacustrine sediments at the top. Collinson (1983b) reinterpreted Daley's floodplain lake environment as the upper reaches of a lagoon where salinities had dropped below 3 %.

The sample of mammal specimens from the upper part of the Hamstead Member at Bouldnor Cliff includes a relatively high proportion of large animals, which suggests an open habitat (Hooker, 1992). The distribution of dietary preferences and locomotory styles among the mammals suggests a moderately wooded woodland-bushland setting.

The dating of this dominantly non-marine sequence is complex. However, using the combination of a number of different markers (dinoflagellate cysts, mammals and sea-level changes), it is possible to correlate with successions in the Paris and Belgian basins, which have more marine intervals. From these areas, calibration with the standard marine sequences is possible (Liengjarern *et al.*, 1980; Aubry, 1986; Brinkhuis and Visscher, 1995; Steurbaut, 1992). It suggests that the Eocene-Oligocene boundary lies approximately between the Bembridge Limestone and Bembridge Marls and that the 'Grande Coupure' is therefore within the Early Oligocene (Hooker *et al.*, 2004).

Comparison with other localities

The Bembridge Marls and lower Hamstead members are assigned to the *suevicum-frohnstettense* Zone (Hooker, 1992; Hooker *et al.*, 2004) and Mammal Paleogene Reference Level MP20 (Schmidt-Kittler, 1987). As such, they are age-equivalent of continental European mammal faunas in Spain (Huermeces del Cerro, Sierra Palomera, Villarrosano 1, 12), France (St Capraise-d'Eymet, Tabarly, Baby 2, Villeneuve-la-Comptal, Paris Basin Marnes supragypseuses) and Germany (Frohnstetten, Bernloch 1A, Weissenburg 2). The lower Hamstead fauna is specifically age equivalent of the Marnes

time complexe Subangeranged from blackfught, breshrauerodar times the white lards meredom and descention crucks formed, for exampletin the lower sections of the Beninsdge Mada Member (Daiey, 1973). Daley (1923) shall and feifer three sedimentary environments in the Beninsdge Mark Member, extratoredepoint in the Bower propagation and incretion estiations, and then Boodplain and incretion estiatores, and then Boodplain and incretion estiatores, and then Boodplain and incretion estiatores, and then Boodplain lake environments in the defined Baley's Boodplain lake environment in the defined Baley's Baley's Baley's Baley's Baley's the defined Baley's Baley's Baley's Baley's the defined Baley's Baley's Baley's the Baley's the defined Baley's Baley's Baley's the Baley's the defined Baley's Baley's Baley's the Baley's the defined Baley's Baley's the Baley's the Baley's the defined Ba Blanches de Pantin in the Paris Basin on the shared presence of *Theridomys bonduelli*.

The upper Hamstead Member at Bouldnor Cliff is assigned to MP21 (Schmidt-Kittler, 1987) and as such is the age-equivalent of a number of continental European mammal faunas, in Spain (Calaf, Montalban 8, Olalla 4A, Santpedor, Espinosa de Henares), France (Ronzon, Ravet, Ruch, Lagny-Thorigny, Aubrelong 1, Soumailles), Belgium (Hoogbutsel), Germany (Möhren 19, 20, Ehrenstein 1B) and the Czech Republic (Detan (BiochroM'97, 1997)). Its fauna is particularly similar to that occurring at Hoogbutsel (Belgium), with which it shares two rodent species and one lipotyphlan species (Bosma, 1974; Butler, 1972), and with Lagny-Thorigny (Paris Basin) and Ronzon (Central France), where the distinctive anthracothere Bothriodon also occurs (Cavelier, 1979).

Conclusions

The sequence at Bouldnor Cliff is the only one in Europe that shows a well-exposed, superposed succession of multiple pre- and post-'Grande Coupure' mammal faunas, thus accurately documenting the major European faunal turnover just after the Eocene–Oligocene boundary. For this it is important internationally. It is the type locality for two mammal species. Although the cliff sections are much subject to slipping, washing by the sea continues to yield fresh sections and material.

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