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 modem 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 low-lying 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 ed.,* 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-Kitder, 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 biodastic 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 fine-grained 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 WoolwichlReading 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 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 (Cleat *et al.,* 2001), whereas in another (Daley and Batson, 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 coincided 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 dinofiagellates 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, brackish-water 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 cyclical transgression-regression 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 shal low, 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) 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 'Tritnley 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 *Mphodon' platyceps* is possibly from a later Eocene deposit now completely eroded away. Together with these reworked fossils are a few that are autochtho-nous, 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 dosed 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 ground-dwelling 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, eomyids and cricetids, which specialized in eating harder fruits and seeds, appeared in low abundances.

The perissodactyls show a more dramatic one-way 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 *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 fragments. The selenolophodont tooth of the palaeotheres is more complex, bearing sharp-edged 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 swallowing. This comparison suggests a major 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 mammal-bearing 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 coincided 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 three-toed 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 huxleyi* 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; Forsten, 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 funnel,* 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]748; *Tursiops* sp.; Pliocene Coralline Crag; Newton, 1891); Sudbourne (*Balaenula bataenopsis, 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 pbysaloides, 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; Forster', 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): Trimley (*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 huxleyi, Cervus pardinensis, Balaena affinis, B. primigenia, Balaenotus insignis, Burtinopsis similis, Balaenodon physaloides, Physeterula 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., *Microhyus 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-on-the-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. *boixedatensis;* 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 3.8)j): 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]; *Zygorhiza* 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'* aft *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'* 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]; *Zygorhiza wanklyni, Basilosaurus* sp., *Plagiolophus curtisi curtisi, Palaeotherium aff. ?muehlbergi, Cebochoerus helveticus;* 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 hatherwoodetzsis, Microchoerus erinaceus, Suevosciurus bosmae, Treposciurus mutabilis, Sciuroides ehrensteinensis, 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, Chapelcomer 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 muehlbergi, 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, Whitediff Bay and Bouldnor cur (see GCR site reports below).

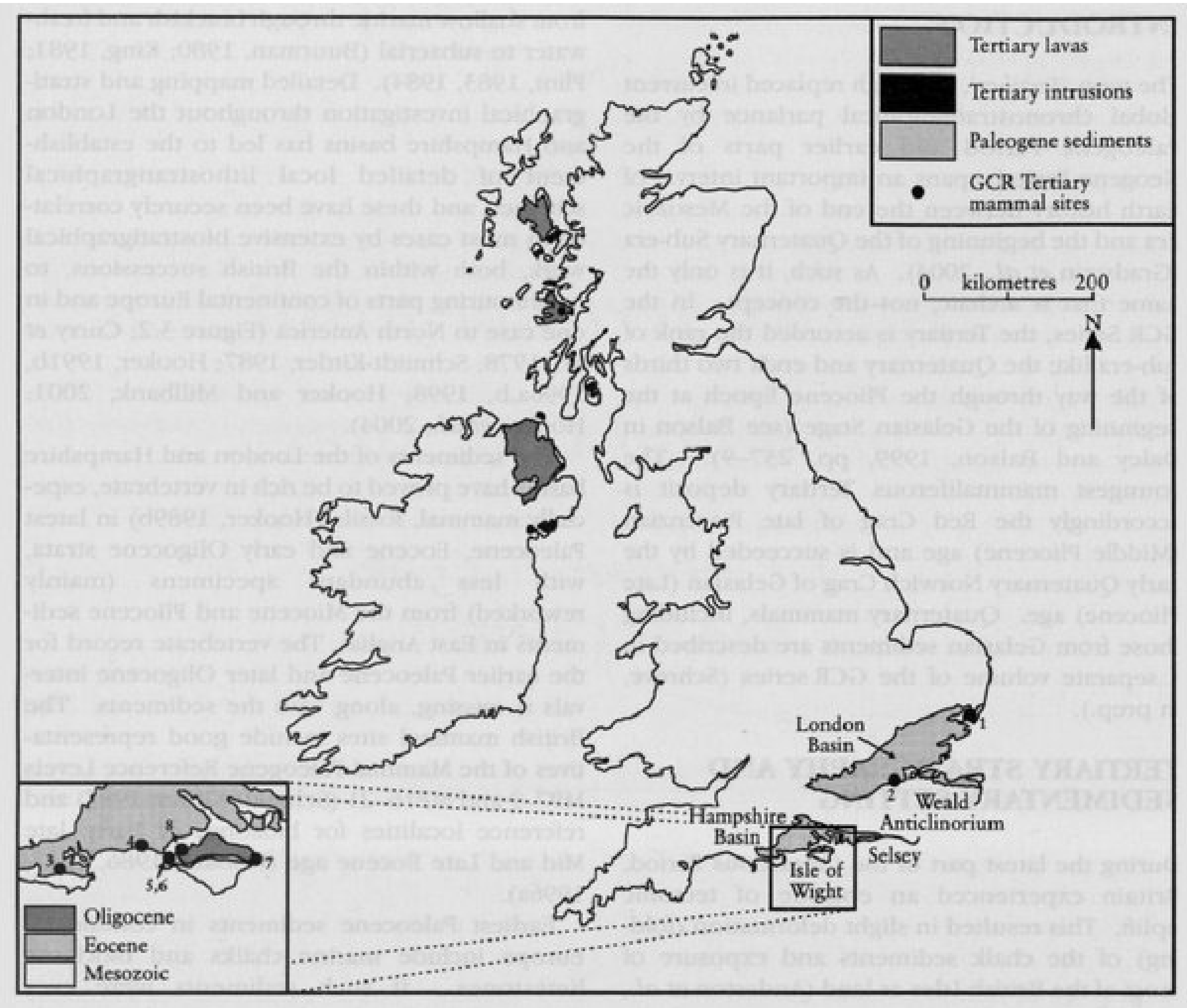
DORSET: Hengistbury Head ([SZ 175 905]; *Lophiodon* cf. *lautricense*; 'Hengistbury Beds', Barton Clay Formation; Hooker, 1977a, 1986; Hooker *et al.,* 1980); Creechbarrow Hill (see GCR site report, below).

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).

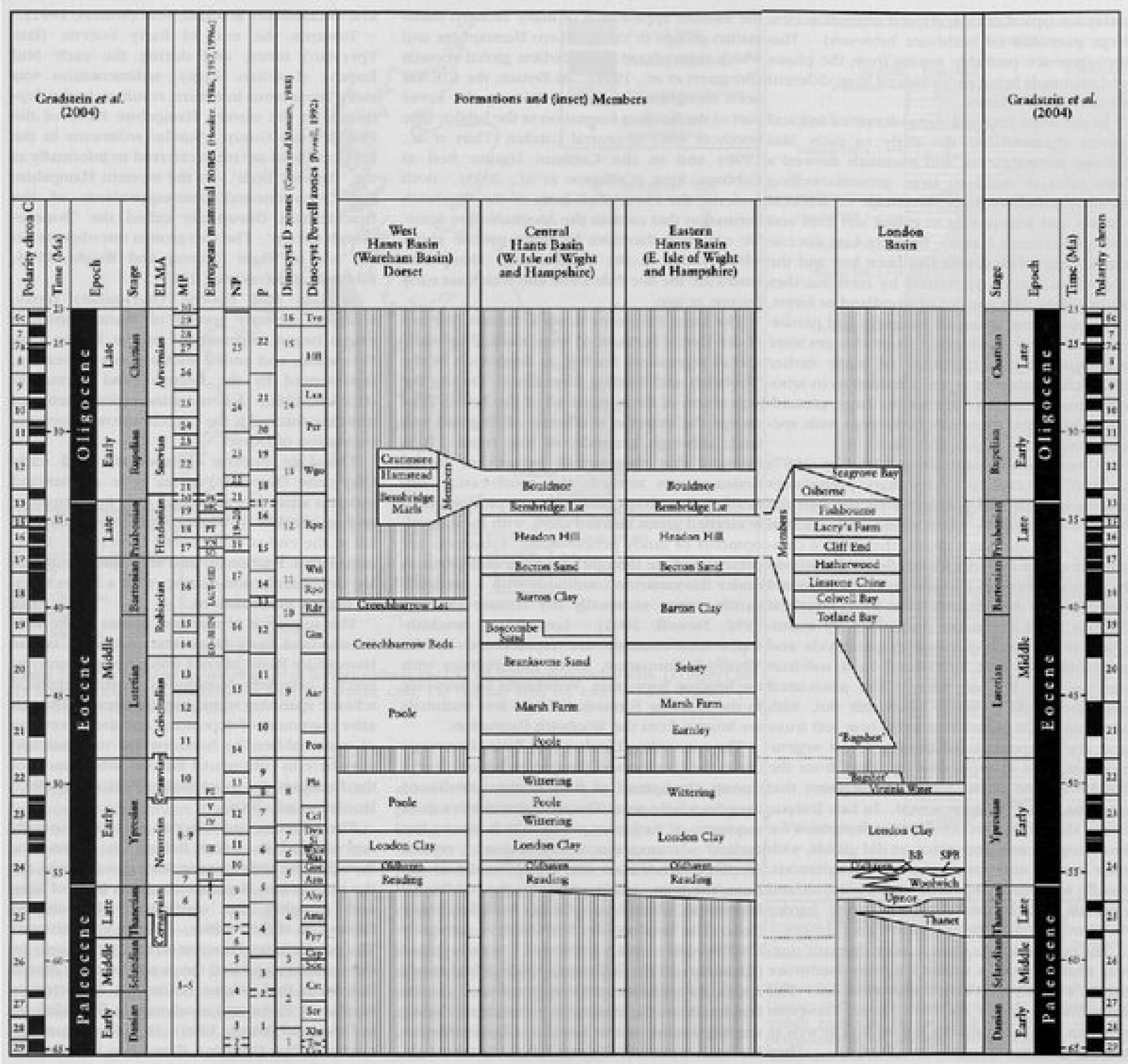
1. Ferry Cliff; Suffolk [TM 278 486]. Early Eocene (Ypresian) Suffolk Pebble Beds (MP7, Zone PEI).
2. Abbey Wood, Greater London [TQ 480 786]. Early Eocene (Ypresian) Blackheath Beds (MP8–9, Zone PEIII).
3. Creechbarrow Hill, Dorset [SY 922 824]. Late Mid Eocene (Bartonian) Creechbarrow Limestone Formation (MP16, *lautricense–siderolithicum* Zone).

4. Hordle Cliff Hampshire [SZ 254 925]–[SZ 270 921]. Late Eocene (Priabonian) Tolland Bay Member, Headon Hill Formation (MP17, *stehlini–depereti to vectisensis–nanus* zones).
5. 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, *pseudosiderolithicus-thaleri* Zone).
7. Whitecliff Bay, Isle of Wight [SZ 643 864]. Late Eocene (Priabonian) Totland Bay and Osborne members, Headon Hill Formation (MP17, *stehlini–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).

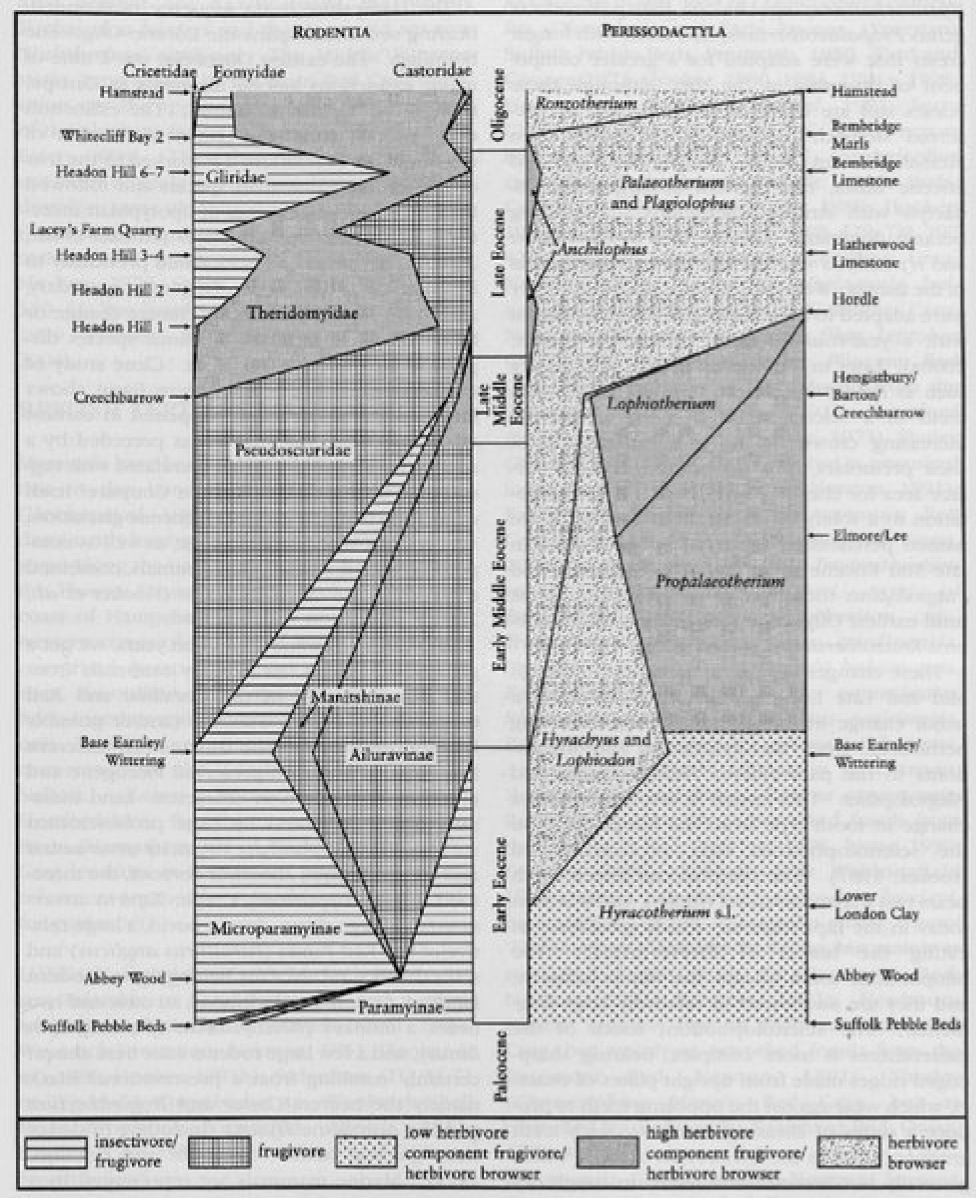
References



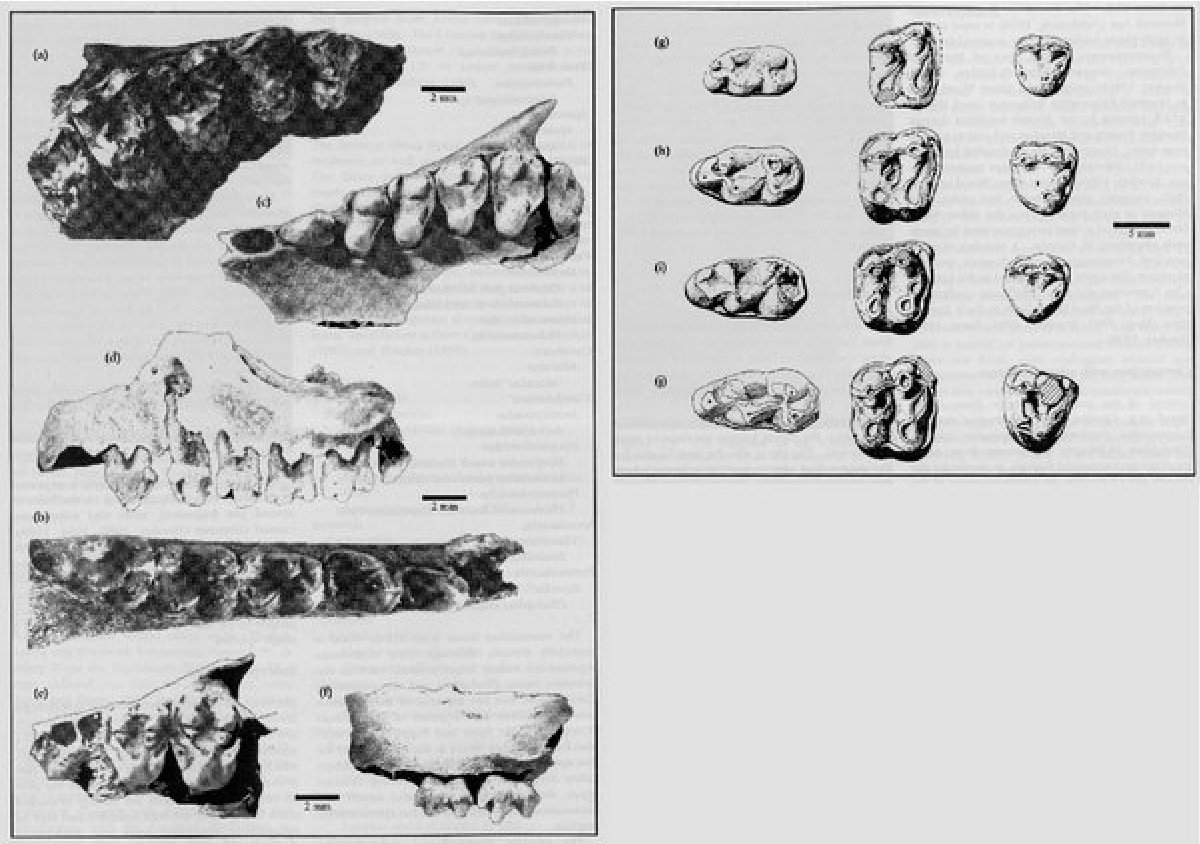
(Figure 3.1) Map showing the distribution of Tertiary rocks in the UK. GCR Tertiary mammal sites: (1) Ferry Cliff; (2) Abbey Wood; (3) Creechbarrow Hill; (4) Hordle Cliff; (5) Headon Hill; (6) Lacey's Farm Quarry; (7) Whitecliff Bay; (8) Bouldnor Cliff.



(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-S1D = Lophiodon lautricense-Lophiotherium siderolithicum Zone; Ma = millions of years before present; MBR = member; MC = Palaeotherium medium medium—I? curtum curtum Zone; MP = Paleogene Mammalian Reference level; NP = standard Paleogene calcareous nanno-plankton 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—Heterohyus 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; I looker, 1992; 1996a; Hooker et al., 2004; Collinson, 1996.)



(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.)



(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.)