Eocene–Oligocene mammalian faunal turnover in the Hampshire Basin, UK: calibration to the global time scale and the major cooling event

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Abstract: A new high-resolution, *c.* 1 Ma mammalian record in continental Eocene–Oligocene strata in the Hampshire Basin is used to investigate the nature and timing of the major Europe-wide mammalian faunal turnover termed the Grande Coupure. Whether this was caused by climate change or by competition with taxa dispersing from Asia is controversial. The mammalian faunas in this record, after rarefaction analysis, show a sharp reduction in diversity only after the Grande Coupure. Improved correlation of NW European successions to global events confirms the Grande Coupure as earliest Oligocene. It shows that a *c.* 350 ka hiatus interrupts the Hampshire and Paris Basin sequences prior to the first record of post-Grande Coupure Asian taxa. Hiatus-bridging faunas from elsewhere in Europe record mainly post-Grande Coupure taxa, suggesting that the turnover occurred early in the hiatus, minimizing bias to the turnover pattern. A previously unrecorded, second, smaller turnover, involving European mammals only, immediately precedes the Grande Coupure in the Hampshire Basin, coinciding with vegetational change. This turnover is judged not to represent cooling. It is concluded that the Grande Coupure coincides with the earliest Oligocene Oi-1 glaciation and that climate change combined with competition to produce the turnover.

Keywords: Paleogene, mammals, diversity, correlation, climate.

The Grande Coupure (meaning 'big break') is a major faunal turnover, affecting mammals in Europe in the late Paleogene. It was first recognized and named by Stehlin (1910). It has frequently been equated with the Eocene–Oligocene boundary, although more recent work has suggested that it is earliest Oligocene (e.g. Hooker 1992; De Coninck 2001). The Paris and Hampshire Basins figured strongly in Stehlin's account because of their superpositional evidence. The Grande Coupure is characterized by much true extinction and dispersal-generated origination. It marks a sudden change from the endemic European faunas to ones with major components of Asian origin (e.g. Heissig 1987; Hooker 1987, 1992; Remy *et al.* 1987). Pre-Grande Coupure faunas are dominated by the perissodactyl family Palaeotheriidae (distant horse relatives), six families of artiodactyls (cloven-hoofed mammals) (Anoplotheriidae, Xipho-dontidae, Choeropotamidae, Cebochoeridae, Dichobunidae and Amphimerycidae), the rodent family Pseudosciuridae, the primate families Omomyidae and Adapidae, and the archontan family Nyctitheriidae. Post-Grande Coupure faunas include the true rhinos (family Rhinocerotidae), three artiodactyl families (Entelodontidae, Anthracotheriidae and Gelocidae) related respectively to pigs, hippos and ruminants, the rodent families Eomyidae, Cricetidae (hamsters) and Castoridae (beavers), and the lipotyphlan family Erinaceidae (hedgehogs). The speciose genus *Palaeotherium* plus *Anoplotherium* and the families Xi-phodontidae and Amphimerycidae were observed to disappear completely. Only the marsupial family Herpetotheriidae, the artiodactyl family Cainotheriidae, and the rodent families Theridomyidae and Gliridae (dormice) crossed the faunal divide undiminished.

Opinions as to the causes of this faunal turnover tend to be polarized between climatic deterioration at the beginning of the Oligocene (e.g. Legendre 1989) and competition following dispersal into Europe of taxa from Asia (e.g. Hooker 1989).

Critical to this are suggestions that the major cooling preceded the Grande Coupure, based on pollen studies in the Paris Basin (Chateauneuf 1980). It is particularly important to be able to distinguish between the alternative causes of the turnover event. This is because in North America mammalian turnover at the time of the earliest Oligocene global climatic deterioration is demonstrated to be minimal, although it is preceded by a long-term decline in diversity in the course of the late Eocene (Prothero & Heaton 1996). Conversely, climate is invoked as the cause of major contemporaneous turnover in the Mongolian Plateau (Meng & McKenna 1998).

When assessing causes of past global events, the first requirement is a high-resolution stratigraphic record. Much of the European sequence of Paleogene mammal faunas has been pieced together from geographically isolated short stratal sections or fissure-fill faunas in central and southern parts of the continent. In contrast, the Belgian and Paris Basins have long stratal successions, but the former has only one mammal fauna relevant to the Grande Coupure, that of Hoogbutsel, whereas the latter has mainly 19th-century collections of mammals, which show much collecting bias and relatively low stratigraphic resolution. The Hampshire Basin, on the other hand, has the benefit of superposition, good exposure, relatively high depositional rate and a few points of calibration to the standard marine sequence. Pre- and post-Grande Coupure faunas have long been known from the Hampshire Basin (Stehlin 1910; Cooper 1925; Jackson 1926, 1933) but with relatively little recorded stratigraphic precision, many specimens being *ex situ* beach-collected. Long-term collecting by both prospecting and screen-washing have progressively improved the precision (e.g. Bosma & Insole 1972; Bosma 1974; Hooker 1992; Hooker *et al.* 1995). It has usually been accepted that the Grande Coupure lies between the Bembridge Marls and Hamstead Members of the Bouldnor Formation (e.g. Cavelier 1979), but with a 14 m interval barren

of mammals between the top of the Bembridge Marls and the lowest post-Grande Coupure fauna in the Hamstead Member (Hooker 1992). Intense sampling in this interval has now brought to light new levels as well as established more accurately the stratigraphic positions of previously known faunal elements (Hooker in prep.). As a result, only 4 m of section, which consist of brackish sediments that have not yielded mammals, namely the Nematura Bed (Bristow *et al*. 1889) plus superjacent strata with *Polymesoda* shell beds, now separate the highest pre- and lowest post-Grande Coupure faunas.

This paper uses improved faunal data to document mammalian turnover leading up to and across the Grande Coupure, which it dates more precisely in terms of global events. The faunal compositions are based on current systematic study in which pseudo-extinctions and pseudo-originations have been eliminated (Hooker in prep.). Thus, all species recognized have autapomorphies (with two exceptions discussed below). Improved correlation between the Hampshire Basin and the Paris and Belgian Basins raises the question of potential biases in the pattern of turnover at the Grande Coupure. Using this dual approach, we evaluate hypotheses of palaeoenvironmental change at this critical time.

Patterns of change

Figure 1 shows occurrences of mammalian species in the Hampshire Basin, from the Bembridge Limestone Formation to the Hamstead Member of the Bouldnor Formation (upper part of the Solent Group) (see Insole & Daley 1985 for definitions). The ranges show a progressive reduction in the number of species from a peak of 47 in the lower part of the Bembridge Limestone (the 'lower fauna' of Hooker *et al*. 1995, comprising the three lowest levels in Fig. 1), to a trough of 20 in the lower part of the Hamstead Member (i.e. that part below the Nematura Bed, hereafter referred to as the lower Hamstead Member). A slight recovery to 28 species occurs a little higher in the Hamstead Member, above the Nematura Bed (hereafter referred to as the upper Hamstead Member) and after the Grande Coupure. After 19 first appearances in the lower fauna of the Bembridge Limestone, there are almost no originations until the lower Hamstead Member, where there are five newcomers, nearly all rodents. The Grande Coupure turnover (i.e. that between the lower and upper Hamstead Member faunas taken as a whole) involves the disappearance of 12 species and the appearance of 17 species. If *Pseudoltinomys cuvieri* is indeed ancestral to *P. gaillardi* (following Hartenberger 1973), one of these disappearances is a pseudo-extinction and one appearance is a pseudo-origination, reducing the true extinctions to 11 and the true
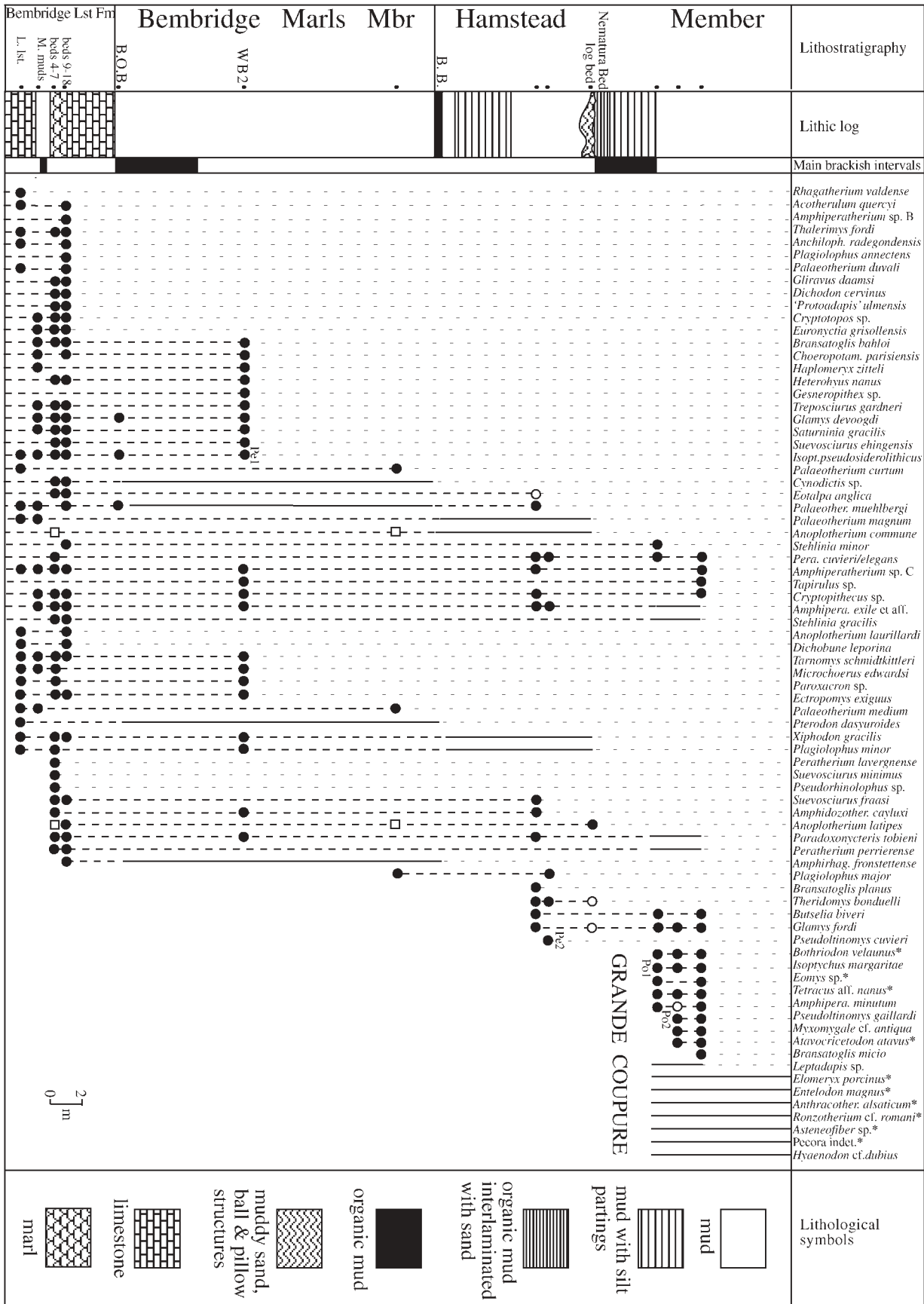
originations to 16. If Bembridge Marls *Isoptychus pseudosiderolithicus* is ancestral to *I. margaritae* (see Bosma 1974, who did not separate these species), this lineage appears after the Grande Coupure as a Lazarus taxon, there being no representative in the lower Hamstead Member. Ten of these 16 originations are of species judged to have dispersed from Asia (asterisked in Fig. 1) because they or close relatives have significant earlier ranges in that continent.
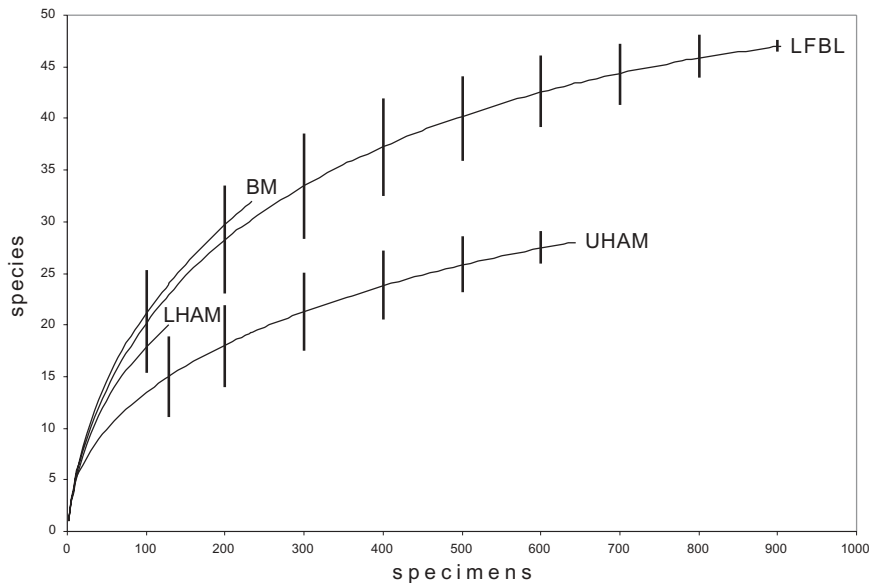
The Bembridge Limestone mammal faunas are relatively abundant and have been collected from a number of sites. Consequently, they are well known and almost certainly provide an accurate representation of the species richness in this formation. Mammals from the Bembridge Marls Member and lower Hamstead Member are rarer and are known from few sites. Although all these faunas have been collected by both prospecting and screen-washing (the former method for at least a century and a half), it is possible that the progressive reduction in species numbers between the Bembridge Limestone and the lower Hamstead Member (inclusive) is an artefact of the Signor–Lipps Effect (i.e. in this case has been enhanced by collection failure) (Signor & Lipps 1982). Except for some of the rodents and *Xiphodon*, the missing taxa are rare elements in faunas at least by the time of deposition of the Bembridge Limestone. To test this hypothesis, the faunas have been subjected to rarefaction analysis (Fig. 2). This indicates that there is no significant difference in species richness between the lower fauna of the Bembridge Limestone, the total Bembridge Marls fauna and the total lower Hamstead Member fauna. In contrast, the post-Grande Coupure, upper Hamstead Member fauna is significantly lower in species richness. This means that the number of 11 extinctions at the Grande Coupure in the Hampshire Basin is almost certainly an underestimate and that from this standpoint the abruptness of the turnover is understated.

Independent of this collection failure, however, is the small but important faunal turnover that affects the lower Hamstead Member, where three closely spaced levels record the highest pre-Grande Coupure fauna. Here, only one rodent species survives from lower strata: the pseudosciurid *Suevosciurus fraasi*. The others, the theridomyids *Pseudoltinomys cuvieri* and *Theridomys bonduelli*, the glirids *Bransatoglis planus* and *Glamys fordi*, accompanied by the 'insectivoran' *Butselia biveri*, are all newcomers. The last two represent earliest records of their respective species, previously being known only after the Grande Coupure (Butler 1972; Vianey-Liaud 1994). Despite this, the new rodents all belong to European families and thus do not represent early dispersals from Asia. On the other hand, the relationships and therefore origins of *Butselia* are obscure.

To summarize, the Bembridge Limestone to lower Hamstead

Fig. 1. Range chart of mammalian species-group taxa in the Hampshire Basin from the Bembridge Limestone Formation and the Bembridge Marls and Hamstead Members of the Bouldnor Formation. ●, undoubted record; ○, doubtful identification; □ in the *Anoplotherium commune* and *A. latipes* columns indicates uncertainty as to which of these species is present. A continuous line represents an error bar indicating a doubtful horizon; heavy dashed lines join individual records; faint, widely spaced dashed lines align ranges with taxonomic names. The lithic log is representative of the succession at the western end of the Isle of Wight, and horizons from other localities are inserted according to correlations made on non-mammalian markers (Daley 1973*b*; Daley & Edwards 1990). Small filled circles to left of lithic log indicate specific mammal-bearing horizons. The highest Bembridge Marls Member and Hamstead Member horizons are all from the Yarmouth–Bouldnor Cliff locality. The lower two Bembridge Marls horizons are from Whitecliff Bay. The fauna from the horizon in the middle muds of the Bembridge Limestone is combined from the Cliff End (Sconce) and Whitecliff Bay localities. All other Bembridge Limestone horizons are from Headon Hill (see Hooker *et al*. 1995, for explanation of bed numbers). Asterisks against taxonomic names indicate origin from Asia. Abbreviations: *Amphidozother.*, *Amphidozotherium*; *Amphipera.*, *Amphiperatherium*; *Amphirhag.*, *Amphirhagatherium*; *Anchiloph.*, *Anchilophus*; *Anthracother.*, *Anthracotherium*; B.B., Black Band; B.O.B., Bembridge Oyster Bed; *Choeropotam.*, *Choeropotamus*; *Isopt.*, *Isoptychus*; *Palaeother.*, *Palaeotherium*; Pe, pseudo-extinction; Po, pseudo-origination; *Pera. cuvieri/elegans*, *Peratherium cuvieri* and *P. elegans* combined; WB2, Whitecliff Bay 2 (sampling level of Bosma 1974).

Lithostratigraphy
Bembridge Lst Fm · Bembridge Marls Mbr · Hamstead Member
L. lst. · M. muds · beds 4-7 · beds 9-18 · B.O.B. · WB2 · B.B. · Nematura Bed log bed

Lithic log

Main brackish intervals

Rhagatherium valdense
Acotherulum quercyi
Amphiperatherium sp. B
Thalerimys fordi
Anchiloph. radegondensis
Plagiolophus annectens
Palaeotherium duvali
Gliravus daamsi
Dichodon cervinus
'Protoadapis' ulmensis
Cryptotopos sp.
Euronyctia grisollensis
Bransatoglis bahloi
Choeropotam. parisiensis
Haplomeryx zitteli
Heterohyus nanus
Gesneropithex sp.
Treposciurus gardneri
Glamys devoogdi
Saturninia gracilis
Suevosciurus ehingensis
Isopt.pseudosiderolithicus
Palaeotherium curtum
Cynodictis sp.
Eotalpa anglica
Palaeother. muehlbergi
Palaeotherium magnum
Anoplotherium commune
Stehlinia minor
Pera. cuvieri/elegans
Amphiperatherium sp. C
Tapirulus sp.
Cryptopithecus sp.
Amphipera. exile et aff.
Stehlinia gracilis
Anoplotherium laurillardi
Dichobune leporina
Tarnomys schmidtkittleri
Microchoerus edwardsi
Paroxacron sp.
Ectropomys exiguus
Palaeotherium medium
Pterodon dasyuroides
Xiphodon gracilis
Plagiolophus minor
Peratherium lavergnense
Suevosciurus minimus
Pseudorhinolophus sp.
Suevosciurus fraasi
Amphidozother. cayluxi
Anoplotherium latipes
Paradoxonycteris tobieni
Peratherium perrierense
Amphirhag. fronstettense
Plagiolophus major
Bransatoglis planus
Theridomys bonduelli
Butselia biveri
Glamys fordi
Pseudoltinomys cuvieri
*Bothriodon velaunus**
Isoptychus margaritae
Eomys sp.*
Tetracus aff. *nanus**
Amphipera. minutum
Pseudoltinomys gaillardi
Myxomygale cf. *antiqua*
*Atavocricetodon atavus**
Bransatoglis micio
Leptadapis sp.
*Elomeryx porcinus**
*Entelodon magnus**
*Anthracother. alsaticum**
Ronzotherium cf. *romani**
Asteneofiber sp.*
Pecora indet.*
Hyaenodon cf. *dubius*

GRANDE COUPURE

Po1 · Po2 · Pe1 · Pe2

2
0 ⊐ m

Lithological symbols
marl
limestone
muddy sand, ball & pillow structures
organic mud
organic mud interlaminated with sand
mud with silt partings
mud

Fig. 2. Rarefaction curves for mammalian assemblages from the lower fauna of the Bembridge Limestone Formation (LFBL) (= lower limestone to beds 4–7 in Fig. 1), the Bembridge Marls Member (BM) (total of the three horizons), the lower Hamstead Member (LHAM) (total) and the upper Hamstead Member (UHAM) (total). Several horizons have been lumped to combine those for which collecting has been dominated by screen-washing with those dominated by prospecting, thereby reducing collecting bias. The vertical error bars represent 95% confidence intervals.

Member mammal record, after rarefaction analysis, shows high species richness, faunal continuity being punctuated near the top by a turnover in the rodent fauna and the appearance of *Butselia*, the newcomers being entirely from Europe. This is succeeded in the upper Hamstead Member by a sudden drop in diversity, accompanied by a major turnover with most incoming taxa emanating from Asia, marking the Grande Coupure.

Dating and calibration

Another possible source of bias in the record is missing strata, causing truncation of taxonomic ranges and thereby overstating the abruptness of the turnover. This section attempts to test the completeness of the Hampshire Basin succession by detailed correlation and dating and to position more precisely the Grande Coupure.

History of dating of the Grande Coupure

In the 1980s and earlier, the Grande Coupure was usually placed at the Eocene–Oligocene boundary (e.g. Cavelier 1979), which was considered to coincide with a major global cooling event (e.g. Legendre 1989). As correlation became more resolved, the extinction datum of the planktonic foraminiferal family Hantkeninidae became generally accepted as marking the Eocene–Oligocene boundary (e.g. Pomerol & Premoli Silva 1985; Nocchi *et al.* 1988; Pomerol 1989), although this was not formalized until later, by designation of Massignano in Umbria, central Italy, as the Global Stratotype Section and Point (GSSP) (Luterbacher & Schmitz 1998). Detailed work in marine sections combining biostratigraphy with stable isotope studies has shown that the major cooling event (marking the Oi-1 glaciation of Antarctica) postdates the hantkeninid extinction and therefore took place in the earliest Oligocene (Zachos *et al.* 1992) at the beginning of Chron C13n (Salamy & Zachos 1999). This raised problems for precise dating of the Grande Coupure in view of the paucity of adequate biostratigraphic markers in the NW European basins. Chateauneuf (1980) judged the major cooling event, based on impoverishment of the pollen flora and increase in abundance of conifers, to occur in the Paris Basin within the Marnes Blanches

de Pantin. This is below the Grande Coupure, which lies between the latter and the overlying Calcaire de Brie (whose basal part is a lateral equivalent of the Argiles Vertes de Romainville) (Stehlin 1910). This stratigraphic position for the cooling seemed to be supported by recognition of calcareous nannoplankton zone NP22 in the Argiles Vertes de Romainville (Aubry 1985), which, as it is calibrated to Chron C12r (Berggren *et al.* 1995), should postdate the cooling. This correlation was followed by Hooker (1992). However, calcareous nannofloras in the Argiles Vertes de Romainville are impoverished and, as recognition of NP22 (an interval zone) relies on absence of a taxon (namely *Coccolithus formosus*;Martini 1971), the zonal attribution of this unit is more accurately rendered as NP22 or older (NP21?) (Aubry 1986, p. 307). Steurbaut (1992), De Coninck (2001) and Vandenberghe *et al.* (2003) have correlated the Grande Coupure to the major TA4.3–4.4 sequence boundary (Haq *et al.* 1987) (or Pr3–Ru1 of Hardenbol *et al.* 1998), which has been causally related to the Oi-1 (ORi-1) glaciation (Abreu & Anderson 1998; Zachos *et al.* 2001) of earliest Oligocene age. In eastern Belgium, however, the relevant mammal record is restricted to a single early post-Grande Coupure fauna (Hoogbutsel), so that calibration of the Grande Coupure to global events here is via recognition of the TA4.3–4.4 sequence boundary in the Paris Basin between the Marnes Blanches de Pantin and the Argiles Vertes de Romainville, both mammaliferous (Gély & Lorenz 1991). Despite these developments, many European Paleogene mammal workers still equate the Grande Coupure with the Eocene–Oligocene boundary (e.g. Aguilar *et al.* 1997). Extension of pre-Grande Coupure mammal faunas from the Bembridge Marls up into the Hamstead Member reported here raises serious doubts over calibration of the basal Hamstead Member Black Band to the TA4.3–4.4 (Pr3–Ru1) sequence boundary by Pomerol (1989, pp. 319–320) and Vandenberghe *et al.* (2003, fig. 24.7).

The Hampshire Basin

Biostratigraphy. Late Eocene–early Oligocene correlation between the Hampshire, Paris and Belgian Basins and deep marine successions has improved in recent decades with the advent of dinoflagellate cyst and calcareous nannoplankton studies. Pro-

blems still remain, however, mainly in the Paris and Hampshire Basins, because of the dominance of freshwater or nearshore deposits, which hampers wider correlation to the deep-sea realm. In the Hampshire Basin, two occurrences of standard calcareous nannoplankton zones broadly bracket the upper part of the Solent Group sequence. NP19–20 is recorded at the base of the Colwell Bay Member of the Headon Hill Formation (a unit lying about 80 m below the Bembridge Limestone Formation) (Aubry 1986) and NP23 in the upper part of the Cranmore Member of the Bouldnor Formation (overlying the Hamstead Member) (Martini 1972). Some dinocyst occurrences help to refine the correlations, but zonal charophytes are too sparsely represented (Riveline 1984) and their definitions too suspect (Sille *et al*. in prep.) to provide further resolution. The occurrence of the rodent *Theridomys bonduelli* in the lower Hamstead Member is only the second record of the species. Its type and only other authenticated occurrence is in the Marnes Blanches de Pantin in the Paris Basin (Brunet 1979; Cavelier 1979, p. 158) and establishes a firm correlation between these two units (Fig. 3). It also supports the earlier correlation, on the basis of abundance of the dinocysts *Phthanoperidinium flebile* and *Adnatosphaeridium reticulense*, of the immediately overlying units in each basin, i.e. of the Nematura Bed with the Glaises à Cyrènes at the base of the Argiles Vertes de Romainville (Liengjarern *et al*. 1980). Various other occurrences of calcareous nannoplankton, dinocysts and mammals help to correlate relevant units in the three NW European basins (Fig. 3).

Magnetostratigraphy. Curry (1992, table 13.2) showed a magnetostratigraphic scale for the entire British Paleogene succession. That relating to the Solent Group had not previously been published and is presumably the part sourced from 'E. A. Hailwood (pers. comm.)' (Curry 1992, p. 393). The normal episodes are not attributed chron numbers and their stratigraphic position is approximate. However, the correlation proposed here suggests that the normal interval within the 'Hamstead Beds' could be C13n1n and that within the Bembridge Limestone could be C13n2n (see Brinkhuis & Visscher 1995, for calibration of magnetochrons to their dinocyst zonation in Italy). A detailed study of Solent Group magnetostratigraphy is currently being undertaken (A. S. Gale, pers. comm.) and will, it is hoped, further elucidate correlation.

Sea-level changes. On the basis of ostracodes, Keen (1990, p. 156, fig. 2) produced a broad salinity curve for the Solent Group, which he then interpreted in terms of the Haq *et al*. (1987) eustatic curve. He recognized four transgressive events: the Colwell Bay Member (= Middle Headon Beds), Bembridge Oyster Bed, Nematura Bed and Cranmore Member (= Upper Hamstead Beds). He identified the Colwell Bay Member, the Bembridge Oyster Bed and the Nematura Bed with the maximum flooding surfaces of sequences TA4.1, 4.2 and 4.3, respectively, and the Cranmore Member with the transgressive part of TA4.4. However, NP23 should calibrate the Cranmore Member to a higher sequence as Brinkhuis & Visscher (1995, fig. 4) correlated NP22, via the higher part of the Mediterranean dinocyst zone Cin, to the lower part of TA4.5 (although see below). Moreover, the Colwell Bay Member with NP19–20 has been calibrated to Pr2 (TA4.2) by Vandenberghe et al. (2003). This indicates that Keen calibrated both the Bembridge Oyster Bed and Nematura Bed each one sequence too low. Biostratigraphic correlations to the Paris Basin support this view. There is a strong correlation on mammals between the Bembridge Limestone and the Première Masse du Gypse (Brunet *et al*. 1987;

Collinson 1992). The Première Masse du Gypse was interpreted by Gély & Lorenz (1991, plate 1) as late highstand deposits of their sequence 16, which they correlated to TA4.2 according to the pattern of the Haq *et al*. (1987) eustatic and coastal onlap curves in their plate. On this basis, the Bembridge Oyster Bed and Nematura Bed should be recalibrated to the maximum flooding surfaces of TA4.3 and TA4.4, respectively, as interpreted by Brinkhuis & Visscher (1995). This implies a significant hiatus between the Bembridge Limestone and Bembridge Marls (Fig. 3).

The major early Oligocene sea-level fall. A major unconformity is recognized to be associated with the TA4.3–4.4 sequence boundary in the Belgian Basin (e.g. De Coninck 2001) and Paris Basin (e.g. Gély & Lorenz 1991, their 17–18 sequence boundary; Pomerol 1989, hiatus HP11). In the Tienen and Tongeren areas of eastern Belgium, the unconformity is marked by erosion of the top of the Neerrepen Sand, where a soil is developed (Steurbaut 1992). In the Paris Basin, the Marnes Blanches de Pantin are also eroded, the unit varying in thickness from 5.5 m to zero (Chateauneuf 1980). In the western Hampshire Basin, the brackish Bembridge Oyster Bed is succeeded first by mainly brackish and then by freshwater beds for the rest of the Bembridge Marls (Daley 1972, 1973b; Collinson 1983). The base of the succeeding Hamstead Member is marked by a freshwater organic clay, the Black Band (Forbes 1856), from whose base rootlets often descend, and below which a line of calcrete nodules occurs. Succeeding clays are at first much like those of the underlying freshwater parts of the Bembridge Marls, but higher up include silt partings. The highest unit below the Nematura Bed is a muddy sand, in contrast to all lower beds of the Bouldnor Formation, which are muds (Fig. 1). This muddy sand unit is loaded and shows ball-and-pillow structures (Fig. 4a and b). It also contains large coniferous logs up to 5 m in length (Fig. 4c and d). The overlying brackish Nematura Bed rests sharply and erosively on this muddy sand and contains much probably reworked wood (Fig. 4e and f). A boulder-sized clast consisting of palaeosol penetrated by rootlets descending from a lignite was found in the shelly basal unit of the Nematura Bed (Fig. 4e and f) and suggests the former presence of a soil bed subsequently removed by erosion.

The Black Band has long been thought to mark a major environmental change, emergence and hiatus (e.g. Aubry 1985; Pomerol 1989; Vandenberghe *et al*. 2003). This has been due partly to misinterpretation of its main features and partly to miscorrelation with unconformities at the top of the Neerrepen Sand and of the Marnes Blanches de Pantin. The rootlet horizon that descends from its base is by no means unique to the lower part of the Bouldnor Formation. Rootlets are also associated with organic muds at two levels within the Bembridge Marls (Collinson 1983, pp. 186–187). Moreover, these do not necessarily indicate terrestrial conditions, as they may belong to one of several rooted aquatic species in the flora. A lithic log by Curry & Hailwood (1986, table 1) implies a pebble bed at the base of the Black Band (no symbol explanation given, but resembles those by Curry 1965, fig. 4). This is erroneous, although occasional small angular fragments of flint are recorded (Bristow *et al*. 1889, p. 191). These provide no evidence of hiatus or transgression, but the possibility that they sank from floating vegetation is not inconsistent with the plant fossil evidence (Collinson 1983, p. 208). The calcrete nodule horizon below the Black Band is the only evidence of terrestrial conditions and is also not unique to the Hamstead Member. Two other horizons with calcrete nodules occur 2.5–3.0 m below the Nematura Bed. The sediments immediately above the Black Band are identical
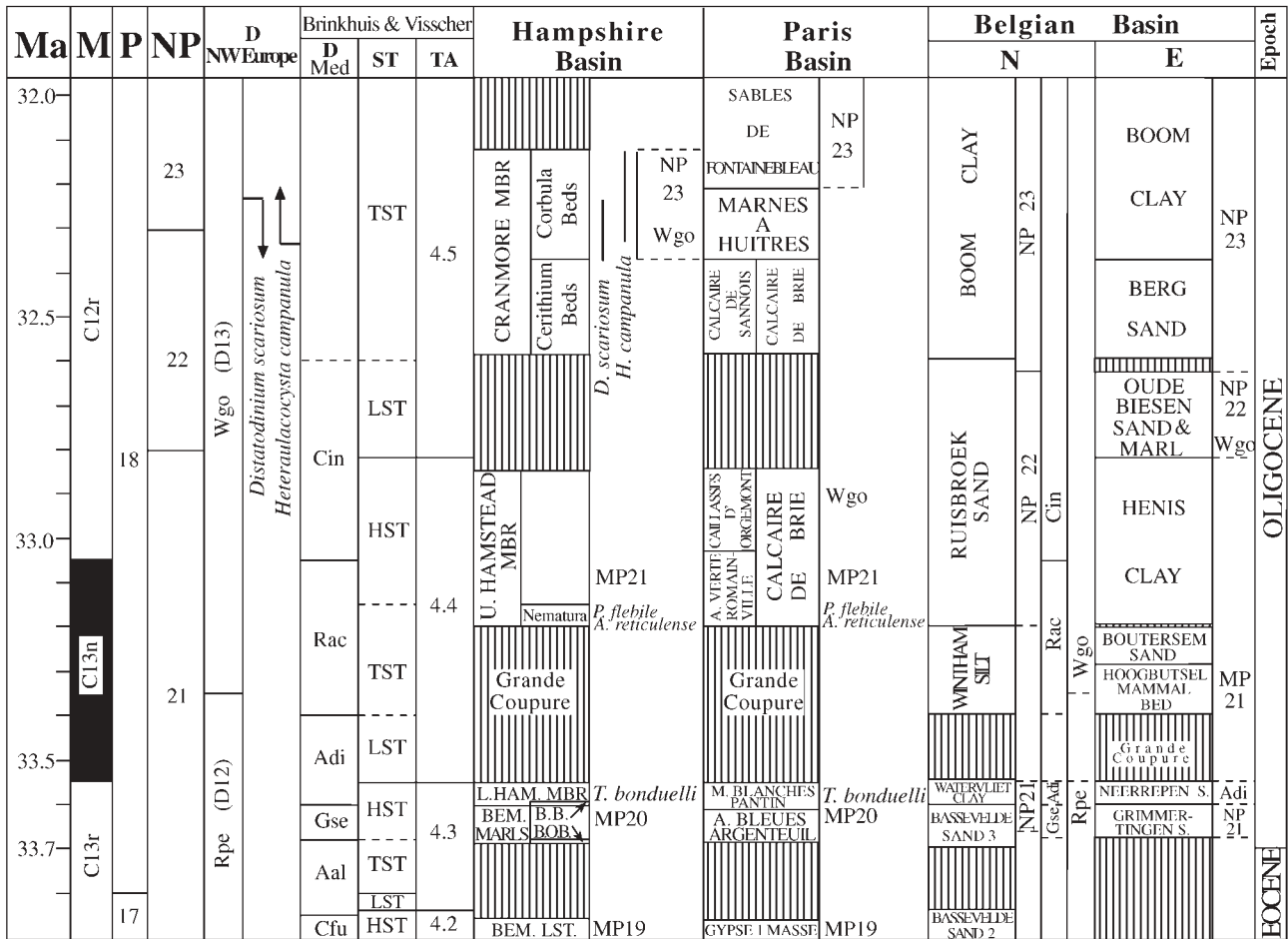
Fig. 3. Correlation chart of strata of latest Eocene and early Oligocene age in the Hampshire, Paris and Belgian Basins. The first four columns show millions of years before present (Ma), magnetochrons (M), standard planktonic foraminiferal zones (P) and standard calcareous nannoplankton zones (NP) from Berggren *et al.* (1995). The fifth column shows NW European dinocyst zones (D); those represented by letter abbreviations are from Powell (1992), as are the overlapping ranges of *D. scariosum* and *H. campanula*, which indicate a precise interval within zone Wgo; the numbered D zones are from Costa & Manum (1988). The sixth, seventh and eighth columns show the Mediterranean dinocyst zones of Brinkhuis & Biffi (1993) (D Med) and their calibration by Brinkhuis & Visscher (1995) to the various systems tracts (ST) and sequences (TA) of Haq *et al.* (1987). The ninth, tenth and eleventh main columns show the lithostratigraphy in the Hampshire, Paris and Belgian Basins, respectively (the last divided into northern and eastern areas), together with the biostratigraphic markers that govern the correlations. Vertical hatching indicates hiatus. MP refers to Mammalian Paleogene Reference Levels (Brunet *et al.* 1987), and these as numbered mark point occurrences. Dinocyst zone Wgo marks its lowest local occurrence in each case. It should be noted that Brinkhuis & Visscher (1995) have calibrated the base of NP22 to a position within dinocyst Zone Cin in Umbria, central Italy, thus conforming to the position of NP22 at 32.8 Ma in the lower part of Chron C12r (Berggren *et al.* 1995). However, at the Contessa Highway section in Umbria, base NP22 (= CP16c) clearly calibrates to a position within the underlying dinocyst Zone Rac (Brinkhuis & Biffi 1993, fig. 2) and to a position high in Chron C13n (Nocchi *et al.* in Pomerol & Premoli Silva 1985). The latter calibration matches that of Brinkhuis & Biffi's zones with NPs in northern Belgium (Stover & Hardenbol 1994; Vandenberghe *et al.* 2003) followed herein. The discrepancy is due to diachronism of disappearance of the NP21 zonal indicator (Cavelier 1975; Aubry 1992). A., Argiles; *A.*, *Adnatosphaeridium*; B.B., Black Band; BEM., Bembridge; B.O.B., Bembridge Oyster Bed; HAM., Hamstead; M., Marnes; Nematura, Nematura Bed; *P.*, *Phthanoperidinium*; S., Sand; *T.*, *Theridomys*.

to those below, indicating a rapid return to the depositional environment of the Bembridge Marls. Rather than indicating a fall in sea level, a more likely interpretation of the Black Band and associated calcretes is a pause in subsidence of a shallow lake environment that may not have exceeded 4 m in depth and sometimes may have been as shallow as 0.3 m (Daley 1972; Collinson 1983).

The succession of litho- and biofacies from the base of the Bembridge Marls to the log bed underlying the Nematura Bed strongly suggests a single upward shallowing sequence, with only minor fluctuations in water depth (the calcretes below the Black Band being the largest). The top is marked by a sequence boundary. The biota of the Nematura Bed records the highest salinity of the entire Hamstead Member. The White Band, some 10 m higher, has ostracodes suggesting salinities similar to those of the Nematura Bed (namely 9–16‰) (Keen 1972), but, unlike the latter, lacks marine dinoflagellates (Liengjarern *et al.* 1980). Between the two horizons, occasional bands of brackish corbiculids intercalate with sediments containing freshwater gastropods and charophytes (pers. obs.). Moreover, unlike the Nematura Bed, the White Band is restricted in distribution, apparently passing laterally into a sand with freshwater gastropods (Bristow *et al.* 1889, p. 203). Higher parts of the upper Hamstead Member are almost entirely freshwater (Keen 1972). The implication is that the entire lowstand and most of the transgressive systems tracts of the sequence overlying the log bed are missing at the
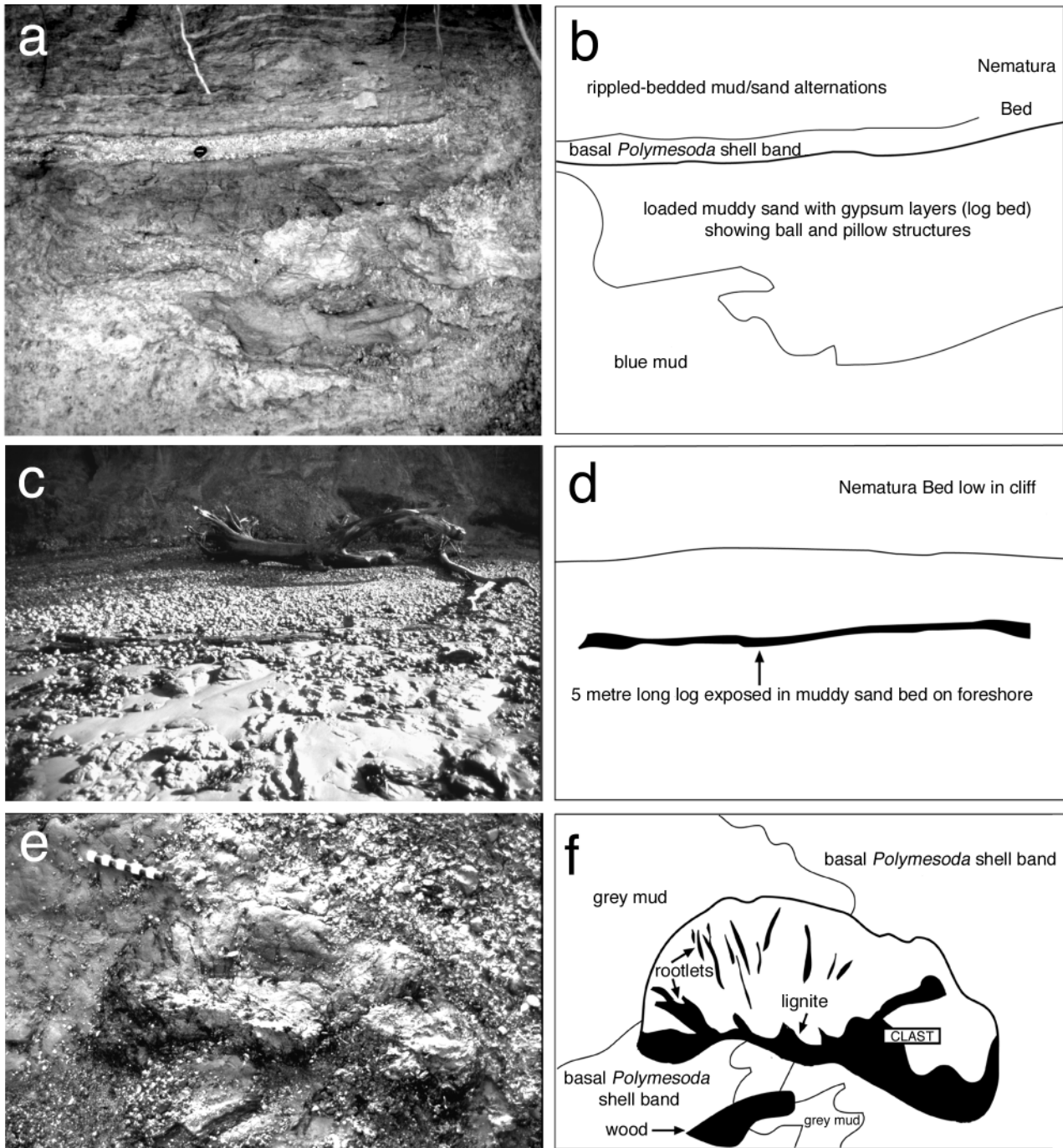
Fig. 4. (**a**) Section of Hamstead Member, Bouldnor, showing Nematura Bed sharply overlying loaded muddy sand with ball-and-pillow structures; lens cap is 50 mm in diameter and is resting on basal *Polymesoda* shell band of Nematura Bed. (**b**) Interpretation of (**a**). (**c**) *In situ* coniferous log, 5 m in length, in muddy sand bed (foreshore) below Nematura Bed (exposed in cliff behind), Bouldnor. (**d**) Interpretation of (**c**). (**e**) Clast, with palaeosol penetrated by rootlets descending from lignite, embedded in basal *Polymesoda* shell band of Nematura Bed with probably reworked wood fragment, viewed from above, foreshore, Bouldnor; grey mud overlies the shell band; scale with centimetre divisions. (**f**) Interpretation of (**e**).

sub-Nematura Bed unconformity (Fig. 3). Correlations of the relevant successions in the Hampshire, Paris and Belgian Basins, using available markers, support the idea that the Grande Coupure coincides with this major hiatus and that it equates with the TA4.3–4.4 sequence boundary (Fig. 3).

Differing interpretations. It is important to note here that the Haq *et al.* (1987) sequence stratigraphic scale has not been tied to tightly time-constrained reference sections. Therefore, published interpretations tend to vary. Of relevance here are differences in recognizing the temporal extent of TA4.4 (Ru1). Brinkhuis & Visscher (1995), working on sections in northern Italy, placed the TA4.4–4.5 sequence boundary near the top of NP21, equated by them with the lower part of dinocyst zone Cin of Brinkhuis & Biffi (1993). They positioned the maximum flooding surface of TA4.4 within the underlying dinocyst Zone Rac, which in

northern Belgium is recognized in the Wintham Silt and lowest parts of the Ruisbroek Sand (Vandenberghe et al. 2003). This segment of the north Belgian succession is correlated with the nonmarine Hoogbutsel Mammal Bed, Boutersem Sand and Henis Clay in eastern Belgium, by being bracketed by the overlying Oude Biesen Sand and Marl, which record NP22, and by the underlying Neerrepen Sand, which contains the dinocyst *Areosphaeridium dictyoplokum* and must thus be no younger than Brinkhuis & Biffi's Adi Zone (underlying Rac) (Fig. 3; Vandenberghe et al. 2003). On the basis of the sequence stratigraphic interpretation of Brinkhuis & Visscher (1995), the Nematura Bed (recognized by Keen as the maximum flooding surface) and the Argiles Vertes de Romainville correlate well with a position high in Zone Rac as recorded in northern Belgium and perhaps with a minor, short-lived transgressive phase at the base of the Henis Clay in eastern Belgium (Steurbaut 1992).Vandenberghe et al. (1998, 2003), in contrast, interpreted Brinkhuis & Visscher's concept of the TA4.4–4.5 sequence boundary as the transgressive surface of TA4.4 (Ru1) and placed the TA4.4–4.5 (Ru1–2) sequence boundary higher in the succession of the Boom Clay within the lower part of Chron C12n.

It is not clear which is the correct calibration to the sequence stratigraphic scale, but we have chosen to follow Brinkhuis & Visscher (1995) as their interpretation relates to a deep, marine, mainly continuous succession, well calibrated by biostratigraphy and magnetostratigraphy. This is also consistent with the recognition by Stover & Hardenbol (1994) of a sequence boundary within the upper part of the Ruisbroek Sand in north Belgium. Thus, a deepening, implying sea-level rise, recorded by dinocyst assemblages in the Mediterranean about the middle of Zone Rac (Brinkhuis 1994), equates on biostratigraphic grounds with a brackish interval in the Hampshire, Paris and eastern Belgian Basins. According to temporal calibration (Fig. 3), the gap between the log bed and the Nematura Bed in the Hampshire Basin, and between the Marnes Blanches de Pantin and the Argiles Vertes de Romainville in the Paris Basin is likely to represent about 350 ka.

The presence of a major gap in the Hampshire Basin, together with differences in lithology, within what is currently classed as a member (Hamstead Member) suggests that the Bouldnor Formation should be more finely subdivided. One way of achieving this might be to restrict the Hamstead Member to either the upper or lower part and to rename the remainder. In fact, the lower Hamstead Member is difficult to distinguish from the Bembridge Marls Member in that both are greyish laminated muds. In contrast, the upper Hamstead Member is dominated by green, poorly bedded muds with frequent colour mottling. However, the western Isle of Wight Bembridge Marls succession is rather different from that of the stratotype in the east at Whitecliff Bay (Daley 1973a, b; Insole & Daley 1985). Therefore, any lithostratigraphic revision of the Bouldnor Formation needs to cover the entire Isle of Wight outcrop and is clearly outside the scope of the present paper.

Implications for the Grande Coupure

The sub-Nematura Bed and sub-Argiles Vertes de Romainville gaps will have the effect of enhancing the abruptness of the faunal turnover at the Grande Coupure noted by Stehlin and subsequent workers in the Hampshire and Paris Basins. Some idea of how artificial or real this abruptness might be can be gained by considering other key mammal faunas that, on grounds of concurrent ranges of taxa, fill this gap. Thus, there are several post-Grande Coupure faunas in southern Germany (namely, the fissure fillings of Möhren 19, 31, 7/16 and 20; Heissig 1987) and one in southern France (Soumailles; Brunet 1979), where incoming Asian taxa are accompanied by a few surviving European endemics. These endemics are ones that are missing from other examples of locally earliest post-Grande Coupure faunas. Also, the hiatus in the Belgian Basin may be shorter in the Tienen area (Fig. 3). Here, the post-Grande Coupure Hoogbutsel Mammal Bed occurs in deposits interpreted as lowstand (Steurbaut 1992), although in view of the major extent of the sea-level fall envisaged at this time, they are more likely to be early transgressive. In either case, the Hoogbutsel Mammal Bed would be older than the mammal-bearing parts of the upper Hamstead Member. This may explain the presence at Hoogbutsel of the artiodactyl *Cebochoerus* and the pseudosciurid *Suevosciurus* as surviving endemics (Misonne 1957, where the *Cebochoerus* is misidentified, in plate 2, fig. 13, as *Dichobune*). These are missing from the upper Hamstead Member. It may also explain the absence of any anthracotheres at Hoogbutsel, in contrast to their abundance in the upper Hamstead Member, as Cavelier (1979, p. 161) recognized. This artiodactyl family is known to have arrived late in southern Germany (Heissig 1987). These bridging faunas are not composed of equally mixed pre- and post-Grande Coupure elements. The dispersing elements are diverse, whereas the briefly surviving endemics are in fact few and often different in the different European regions, e.g. *Anoplotherium* in Germany, *Palaeotherium* in Germany (three species) and France (one species), *Cebochoerus* in France and Belgium. This suggests that most of the turnover occurred early in the period represented by the hiatus in the NW European basins. The degree to which the hiatus in the Hampshire and Paris Basins is enhancing the abruptness of the Grande Coupure is therefore likely to be small, suggesting that the turnover was indeed major and rapid.

Evidence from sedimentation rate

Correlation suggests that the Grande Coupure coincides with the TA4.3–4.4 sequence boundary, and thus approximately with the earliest Oligocene cooling event Oi-1. However, correlation of the lower Hamstead Member within the upper part of TA4.3 is imprecise. In view of biotic evidence for earlier cooling, what other evidence can improve the precision of the dating here? According to oxygen isotope data from deep-sea benthic foraminifera (Zachos et al. 1992, 2001; Salamy & Zachos 1999), the 350 ka interval from 33.90 to 33.55 Ma begins with a relatively warm phase that crosses the Eocene–Oligocene boundary and continues with a sharp cooling marking the beginning of the Oi-1 glaciation. The correlation chart (Fig. 3) indicates that the mammalian record from the Bembridge Limestone to the top of the lower Hamstead Member should span about 350 ka, crossing the Eocene–Oligocene boundary approximately between the Bembridge Limestone and Bembridge Marls. The segment from the Bembridge Oyster Bed upwards should then span about 150 ka. Collinson (1983, p. 188) recognized, in the western outcrop of the Bembridge Marls, alternating silty clay–clay laminae couplets, that occurred at a frequency of 52 cm^{-1}, and suggested that they might represent annual varves. If the sedimentation rate suggested by the frequency of these couplets remained constant through the entire sub-Nematura Bed Bouldnor Formation, a thickness in the western outcrops of 31 m, this would indicate a time interval of 161 200 years, broadly supporting the estimate derived from correlation. Within the remaining small correlation error, it is possible that the lower Hamstead

Member spans the very beginning of the cooling phase. The discussion below considers the evidence from the biota of all three NW European basins for environmental change at this time.

Biotic evidence for environmental change before the Grande Coupure

The lower Hamstead Member mammal fauna

Three of the four rodents that appear near the top of the lower Hamstead Member, *Theridomys bonduelli*, *Bransatoglis planus* and *Glamys fordi*, have teeth that show extra or stronger cresting than those of their nearest relatives in the Bembridge Marls (Stehlin & Schaub 1951; Bosma & de Bruijn 1979; Vianey-Liaud 1994). This suggests a slightly coarser diet, which might be the result of seasonal scarcity of high-quality food or it might simply be due to the occupation of a habitat with different vegetation. The fourth rodent, *Pseudoltinomys*, is a semibipedal, ricochetal ground dweller that probably lived in open habitats (Schmidt-Kittler & Storch 1985). *B. bahloi* and *G. devoogdi*, respectively the closest relatives of *B. planus* and *G. fordi*, are both restricted to northern Europe (Vianey-Liaud 1994). The origin of *Theridomys bonduelli* is unknown. One hypothesis is that these three species originated further north than the Hampshire Basin, where no continental deposits of relevant age survive, and spread south in response to climatic cooling.

Plants

A good record of macroplants (especially fruits and seeds) and palynology accompanies the mammals in the Solent Group of the Hampshire Basin (Chandler 1963; Machin 1971; Collinson 1983, 1990, 1992; Collinson *et al*. 1993; Cleal *et al*. 2001). The fruit and seed record of aquatic species changes little in the interval under discussion. However, the fern *Acrostichum,* which is represented by sporangial clusters (and not just by dispersed spores whose affinity might be uncertain), occurs in very low numbers in the Black Band compared with the Bembridge Marls (Collinson 1983) and has not been recorded above the basal metre of the Hamstead Member (Collinson 2001). Monocolpate pollen, probably representing palms, undergoes a sudden reduction above the lowest plant level about a third of the way up the Bembridge Marls, disappearing entirely in the Black Band (Collinson 1983). The Black Band also marks the incoming in abundance of the inaperturate conifer pollen *Inaperturopollenites magnus* (R. Pot.) Thomson & Pflug (Collinson 1983). The taxodiaceous conifer *Quasisequoia couttsiae* (Heer) Kunzmann (Kunzmann 1999) is abundant in two horizons in the lower Hamstead Member. *Q. couttsiae* is represented by leafy shoots, seeds and ovuliferous cone fragments (Collinson & Sille in prep.). Pollen cones of Cretaceous *Quasisequoia* contain inaperturate pollen (Kvacek 2000), suggesting that *I. magnus* may have been produced by *Q. couttsiae*. *Quasisequoia* is widely distributed but sporadic and rare in the Paleogene in southern England (Cleal *et al*. 2001; as *Sequoia couttsiae*). However, intensive bulk sediment sampling of the Solent Group for plant macrofossils and mammals over 30 years (e.g. Collinson 1992; Hooker 1992) has not yielded any *Quasisequoia*-containing samples except those reported here in the lower Hamstead Member.

The plant evidence suggests that the Black Band and overlying sediments of the lower Hamstead Member contain fossils from a vegetation that differs from that of underlying beds of the Bouldnor and Bembridge Limestone Formations. This may represent a local shift in the nature of vegetation proximal to the depositional environment or it could reflect climatic cooling (affecting warm-loving palms and *Acrostichum*), or both. The time correlates of the lower Hamstead Member in the Paris Basin, the Marnes Blanches de Pantin, document a dramatic fall in diversity of pollen taxa, but with a high percentage of conifers (especially bisaccate Pinaceae), which was interpreted by Chateauneuf (1980) to suggest cooling. *Quasisequoia* is an extinct conifer whose climatic tolerances are unknown. However, the long stratigraphic range of the species *Q. couttsiae* through the Paleogene, combined with climatic tolerances of near living relatives *Sequoia* and *Sequoiadendron* of the Taxodiaceae *sensu lato* (Kunzmann 1999), do not suggest that it was a taxon favoured by cool climates. In northern Europe vegetation changed through the Eocene in response to cooling climate, with cooler-adapted vegetation (e.g. mixed evergreen and deciduous forest) gradually replacing dominantly evergreen subtropical vegetation (Collinson 1992, 2000). In southern England comparatively few warm-loving elements remain in the Bembridge Limestone or younger floras (Cleal *et al*. 2001). Thus continuing climate change might be poorly expressed in fossil floras where most warm-loving elements have already been eliminated.

Dinoflagellate cysts and molluscs from the Neerrepen Sand, Belgium

In the Tienen and Tongeren areas of the Belgian Basin, the time-equivalent unit of the lower Hamstead Member is the Neerrepen Sand (Fig. 4; De Coninck 2001). This unit is characterized by a dinoflagellate flora that includes an Arctic to low-temperature species, *Spiniferites* aff. *elongatus* (De Coninck 2001). Deville (1996) described the molluscan fauna and other biota, among which he interpreted the species *Arctica roffiaeni*, the large size of the species *Palliolum h. hausmanni* (both bivalves) and an abundance of *Pinus* (bisaccate) pollen as indications of a cold climate. Deville (1996) has also suggested that the palaeosol capping the Neerrepen Sand contains freeze–thaw structures, although this postdates the sand itself and the evidence has yet to be published.

Discussion

The ecological composition of the incoming rodent fauna of the lower Hamstead Member suggests that the animals may have been living in a habitat that was different from that of the underlying Bembridge Marls or Bembridge Limestone. Data from the associated plant fossils support this contention by indicating a different vegetation, one that was dominated by conifers and with subsidiary aquatic species. The dominance of conifer pollen in the time equivalent Marnes Blanches de Pantin in the Paris Basin gives some indication that this vegetation was not restricted to the Hampshire Basin, although the taxa involved are different. However, abundances of Pinaceae pollen (Neerrepen Sands and Marnes Blanches de Pantin) are difficult to interpret because, amongst all land plant pollen, bisaccates are the most affected by taphonomic factors (Moore *et al*. 1991). Bisaccate pollen is not above background levels in southern England at this time.

The evidence from the Neerrepen Sand for cool climate is weak at best. The range of *Arctica roffiaeni* in Belgium extends down into the Wemmel Sand of the warm late Lutetian (Deville 1996, fig. 5). This leaves only the large size of *Palliolum h. hausmanni* and a single dinoflagellate species to indicate cooling climate at this time.

It is possible that the vegetation of the lower Hamstead Member, together with its rodent fauna, represents the environment of the hinterland, brought closer to the depositional environment by regression (i.e. the late highstand systems tract of sequence TA4.3) rather than by cooling climate. Under this hypothesis, the rodents need not have undergone a southward range shift. The rarefaction analysis of the mammal faunas, which indicates no significant reduction in species richness up to and including the lower Hamstead Member, also supports the idea of little or no cooling at this time.

Conclusions

A new high-resolution record of mammals across the Grande Coupure in the Hampshire Basin drastically reduces the faunal gap between pre- and post-Grande Coupure faunas to 4 m. This record, after rarefaction analysis, shows: (1) a small but significant turnover in the rodents in the latest pre-Grande Coupure fauna (in the lower Hamstead Member); (2) a sudden fall in species richness immediately after the Grande Coupure (in the upper Hamstead Member), coincident with the appearance of numerous new taxa from Asia. Improved correlation between the Hampshire, Paris and Belgian Basins, aided by calibration of calcareous nannoplankton and dinocyst zones with sequence stratigraphy in Italy (Stover & Hardenbol 1994; Brinkhuis & Visscher 1995; Vandenberghe *et al.* 2003), shows that the Grande Coupure is characterized in the Hampshire and Paris Basins by a sedimentary hiatus of *c.* 350 ka, corresponding to the first part of sequence TA4.4 of Haq *et al.* (1987). Bridging faunas in Belgium, southern Germany and southern France, however, suggest that the abruptness of the Grande Coupure is only slightly intensified in the Hampshire and Paris Basins by this hiatus, as most of the turnover appears to have occurred near the beginning of the period represented by the hiatus.

The faunal turnover in the rodents in the latest pre-Grande Coupure fauna (lower Hamstead Member) in the Hampshire Basin coincides with a change in the vegetation from one dominated by aquatic species to one dominated by taxodiaceous conifers. Evidence from contemporaneous biota in the Paris and Belgian Basins had previously been used to suggest that this interval represented either the early Oligocene cooling event or an early phase of it. This evidence is shown to be weak and contradicted by the lack of reduction in mammalian species richness at this time. In contrast, the Grande Coupure coincides with the major TA4.3–4.4 sequence boundary and shows a rapid fall in mammalian species richness, factors that together indicate that it is the Grande Coupure that reflects the Oi-1 cooling. The Grande Coupure (a European event) also shows a major invasion of mammals from Asia, unlike North America, where contemporaneous faunal change was slight. Therefore, both global climate change (cooling) and dispersal from outside the main European landmass were likely to have had a combined influence on the Grande Coupure faunal turnover.

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