

# MAMMALIAN FAUNAL TURNOVER ACROSS THE PALEOCENE-EOCENE BOUNDARY IN NW EUROPE: THE ROLES OF DISPLACEMENT, COMMUNITY EVOLUTION AND ENVIRONMENT

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## KEYWORDS

Ecological diversity  
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understorey  
extinction  
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## ABSTRACT

Improved knowledge of the diversity of Late Paleocene mammal faunas of NW Europe indicates a higher level of turnover at the Paleocene-Eocene boundary than previously recognized. Possible causes of the large number of extinctions in Europe are investigated through ecological diversity analysis of the mammals and the plant fossil record. Predation by incoming ground- and tree-dwelling specialized carnivores has been previously considered the main cause of the extinctions. However, the preferential extinction of small terrestrial and semiterrestrial insectivore-frugivores, (mainly stem macroscelideans and multituberculates), which are inferred to have inhabited forests with dense understorey in the Paleocene, is also linked to the arrival in Europe of a new ecological type, the large terrestrial browsing herbivore, namely the pantodont *Coryphodon*, which would have reduced understorey by feeding and physical disturbance. It is suggested that there was a delay in community evolution in Europe, which in North America had previously produced large herbivorous and specialized carnivorous types. The cause of the delay may have been the persistence throughout the Paleocene in Europe of thermophilic evergreen forests despite the cooling in the middle of the epoch. This contrasted with North America, where more open deciduous forests developed in the continental interior and provided the selection pressure for the new ecological types of mammal.

## 1. INTRODUCTION

Mammal faunas of Late Paleocene and Early Eocene age in Europe are best known in the north west of the continent, in the Anglo-Paris-Belgian Basin. The only succession in the area that yields mammals on either side of the Paleocene-Eocene (Thanetian-Ypresian) boundary is in the eastern Paris Basin. Early Eocene faunas are also known from sites in southern France, Spain and Portugal, but Paleocene faunas there are almost entirely restricted to the very end of the epoch in the Spanish Tremp Basin (López-Martínez and Peláez-Campomanes, 1999). It has been shown that the mammalian faunal turnover at the Paleocene-Eocene boundary in NW Europe was large (Hooker, 1996, 1998), with many extinctions of endemic European species and genera. 32 species originated from outside the area, mainly from outside the continent. Recognition of new genera and species of primitive macroscelideans (Hooker and Russell, 2012) increases the fauna of the late Thanetian (Cernaysian European Land Mammal Age) of the Paris Basin from 34 to 45 species. With this increase in knowledge of Late Paleocene diversity, we update the details of this turnover and investigate its causes.

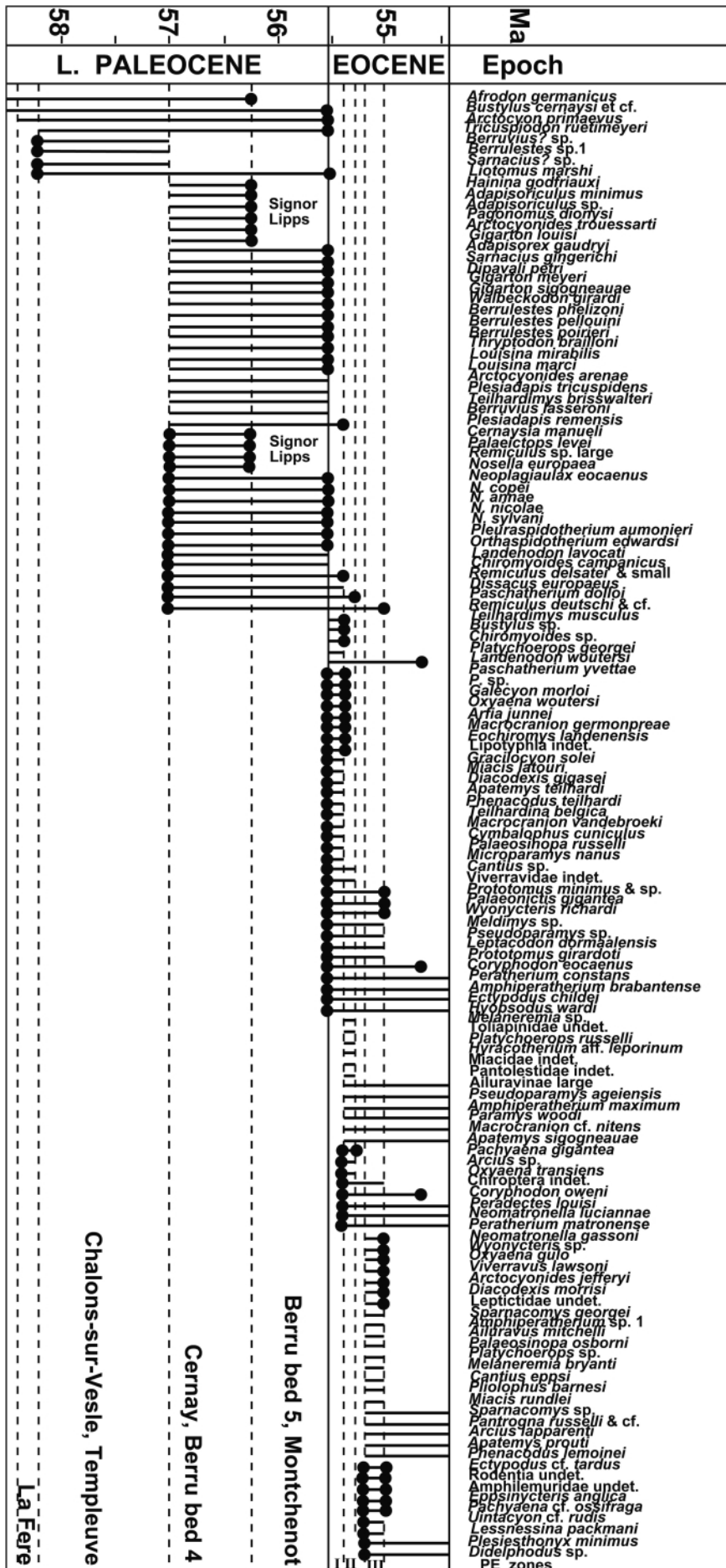
## 2. FAUNAL TURNOVER

The number of species extinctions between the youngest Paleocene level (latest Thanetian bed 5 of Laurent and Meyer, 1986) at Berru and the earliest Eocene zone PE I faunas is 23. However, the slightly older level, but still late Thanetian, at Cernay and Berru (bed 4 of Laurent and Meyer, 1986) has a near identical fauna. Eleven species that are rare at Cernay

have not been found in bed 5 at Berru, probably because of their rarity. If one accepts the probability of the Signor Lipps effect here, there are instead 34 extinctions (76% of the fauna) at the Paleocene-Eocene boundary in NW Europe (Fig. 1).

Only five species survived the boundary unchanged: *Plesiadapis remensis*, *Dissacus europaeus*, *Paschatherium dolloi* (the last newly recorded in the Paleocene: Hooker and Russell, 2012) and apparently two species of *Remiculus*, whose species identifications either side of the boundary are uncertain (*R. sp. small*/*R. delseatei*; *R. deutschii*/*R. cf. deutschii*). All but the *Dissacus* became extinct within the first three mammal zones of the Eocene (PE I-III: Hooker, 1996, 2010) (Fig. 1). A further five species show evidence of having evolved (i.e. the closest Paleocene relative of a given earliest Eocene species is local and entirely primitive with respect to the latter), thus representing pseudoextinctions. Of these, *Teilhardimys musculus*, *Bustylus* sp. and *Chiromyoides* sp. did not survive zone PE I. *Landenodon woutersi* survived for longer: its last record is in the Tilehurst Member of Burghfield, London Basin (Hooker, 1991), a level apparently belonging to the Gor dinosaur zone of Powell (1992). The genus *Platychoerops* evolved from the Paleocene species *Plesiadapis tricuspiciens* and showed a modest radiation (Gingerich, 1976; Hooker, 1994; Godinot, 1998) that lasted till nearly the end of the Early Eocene. The family Toliapinidae displays a similar radiation (Russell et al., 1988; Hooker et al., 1999), but as a Lazarus clade, unknown in zone PE I. It survived until zone PE V.

Of the first appearances at the beginning of the Eocene (PE



l), the oxyaenid creodonts, apatemyids, paramyid rodents, viverravid carnivorans, nyctitheres, the pantolestid *Palaeosinopa*, the condylarths *Hyopsodus* and *Phenacodus*, the pantodont *Coryphodon*, herpetotheriid marsupials and the neoplagiaulacid multituberculate *Ectypodus* originated from North America according to the Paleocene occurrence of their nearest relatives there (Hooker, 1998). Perissodactyls, primates and probably artiodactyls show evidence of origination in Asia (Hooker and Dashzeveg, 2003; Godinot and de Lapparent de Broin, 2003; Smith et al., 2006; Ting et al., 2007). Different hyaenodontid creodonts originated in Asia and Africa (Bowen et al., 2002; Solé et al., 2009). The origin of the amphilemurid *Macrocranium* and most miacid carnivorans is obscure, although the latter do have relatives in the latest Paleocene (late Thanetian = Clarkforkian North American Land Mammal Age) of North America (Gingerich, 1989). Not all arrivals in Europe were in PE I. In particular, peradectid marsupials and

**FIGURE 1:** Range chart for Late Paleocene to earliest Eocene mammals in NW Europe. Lines represent error bars for ranges based on spot occurrences within the time interval covered. Filled circles at the top of a range indicate real extinction. Filled circles at base of range indicate originations from outside NW Europe. Range lines without filled circles at top or base indicate likely pseudo-extinctions or pseudo-originations respectively. Localities within each Paleocene time interval are given at end of chart. Similarly, PE zones (Hooker 1996, 2010) are given for Eocene time intervals. Eocene localities are: Dormaal, Erquelinnes, Kyson, Ferry Cliff (PE I), Croydon, Meudon (PE II) and Abbey Wood (PE III). The chart updates that of Hooker (1998) from the following sources: Hooker (2010); Hooker and Russell (2012); Hooker et al. (2009); López-Martínez and Peláez-Campomanes (1999); Smith, R. (1997), Smith, T. (1995, 1996, 1997a,b), Smith and Smith (2001, 2003, 2010), Smith et al. (1996). The timescale follows Westerhold et al. (2007). This is not the most up to date, but follows that used by Hooker (2010) in light of the current instability of the dating of Paleocene-Eocene boundary events (Westerhold et al., 2009).

paromyid plesiadapiforms with a clear North American origin are first known in PE II. More local originations involve two species of the lousinid *Paschatherium*, at least one of which (*P. yvettae*) originated in southern Europe (Gheerbrant et al., 1997; López-Martínez et al., 2006).

Mammalian faunal turnover at the Paleocene-Eocene boundary in western North America, largely documented in the Big-horn Basin, was much smaller in scale than in NW Europe (e.g. Gingerich and Clyde, 2001; Clyde, 2001). Of the taxa first appearing in Europe in the Eocene, rodents, tillodonts and the pantodont *Coryphodon* first appeared in North America in the late Thanetian (Clarkforkian NALMA), whilst oxyaenid creodonts appeared there in the Selandian (Tiffanian NALMA, Ti-3) (Gunnell, 1998), apatemyids in the late Danian (Torrejonian NALMA, To-3) and viverravid carnivorans in the early Danian (Puercan NALMA, Pu-2) (Flynn, 1998; Gunnell et al., 2008; Secord, 2008).

The faunal turnover at the Paleocene-Eocene boundary in NW Europe (Fig. 1) shows a large number of synchronous extinctions and originations, strongly suggestive of displacement. We investigate below the possible nature of the competition from the incoming taxa and other potential influences.

### 3. ECOLOGICAL DIVERSITY ANALYSIS

#### 3.1 METHODOLOGY

Analysis of mammalian ecological diversity using the taxon-free categories of size, locomotor adaptation and diet can give important information on the nature of habitat (e.g. Andrews et al., 1979; Collinson and Hooker, 1987, 1991). It is used here to determine if there were environmental changes between the latest Paleocene and Early Eocene of NW Europe, which may have influenced the faunal turnover. A succession of four faunas or combinations of faunas is used to illustrate these changes, viz.: Cernay/Berru, France (latest Paleocene), Dormaal/Erquelinnes, Belgium (earliest Eocene, zone PE I: Hooker, 1996), Meudon, France (Early Eocene, zone PE II) and Abbey Wood, UK (Early Eocene, zone PE III).

Since an earlier ecological diversity study of this area (Hooker, 1998), there have been notable increases in our knowledge of the locomotor adaptation of some of the more obscure extinct mammal groups, which alter the percentages of some of the plots provided in the 1998 study. Thus, multituberculates are no longer considered arboreal (Krause and Jenkins, 1983), but to have had a largely ground-based frog-like hopping gait, although some climbing ability may have been present in some taxa (Kielan-Jaworowska and Gambaryan, 1994). They are therefore here coded as semiterrestrial. Members of the European stem macroscelidean family Louisinidae (Zack et al., 2005; Hooker and Russell, 2012) are terrestrial based on astragali and calcanea of *Paschatherium* (Godinot et al., 1996; Hooker, 2001) and *Teilhardimys* (replacement name for *Microhyus*) (Tabuce et al., 2006), backed up by more extensive postcranial bones of apheliscids (Penkrot et al., 2008). Both nyctitheres and adapisoriculids have adaptations involving

hindfoot reversal, indicating scansorial habits (Hooker, 2001; Smith et al., 2010). *Macrocranion* has apheliscid-like postcrania (Penkrot et al., 2008) and is scored here as terrestrial. This adaptation is also extrapolated to other amphilemurids. Esthonychid tillodonts have been interpreted as having climbing ability, but with limited crurotarsal mobility (Rose, 2001). The esthonychid *Plesiesthonyx* is therefore scored here as semiterrestrial. These locomotor scorings of amphilemurids and esthonychids update those of Hooker (2010).

Published sources for locomotor adaptations not cited here are given by Hooker (2010, table 20). Their definitions are given in detail in Hooker (1998).

Two approaches to ecological diversity analysis are taken here. Firstly, each of the three categories is treated separately. This follows previous studies (e.g. Hooker, 1998). In contrast to that and earlier studies, bats (Chiroptera) are no longer excluded from the size and diet categories on grounds of rarity (the reason for their exclusion from all categories by Andrews et al., 1979). Microchiropteran bats (the only ones present in the European Eocene) are thought to represent a locomotor shift from scansorial to aerial for insect-eating mammals (e.g. Hooker, 2001). Rarity of bats in the Early Eocene has more connection with their early low diversity (first representatives in Europe are in zone PE II) than with their later abundance being largely restricted to karst deposits. They are still here excluded from the locomotor category as their appearance represents an aspect of community evolution and their presence, simply by being flighted, can tell us little about the nature of the habitat. The three separate ecological diversity categories are displayed as percentages, so that, in the case of mixed diet, each fraction is attributed to its individual dietary class, rather than being treated as a mixed diet, following Andrews et al. (1979).

The second approach is to plot the categories of size against locomotor adaptation and of locomotor adaptation against diet. Here numbers rather than percentages are displayed and mixed diets are maintained as distinct. Here bats are included in both sets of biplots.

#### 3.2 PALEOCENE AND EOCENE DATA

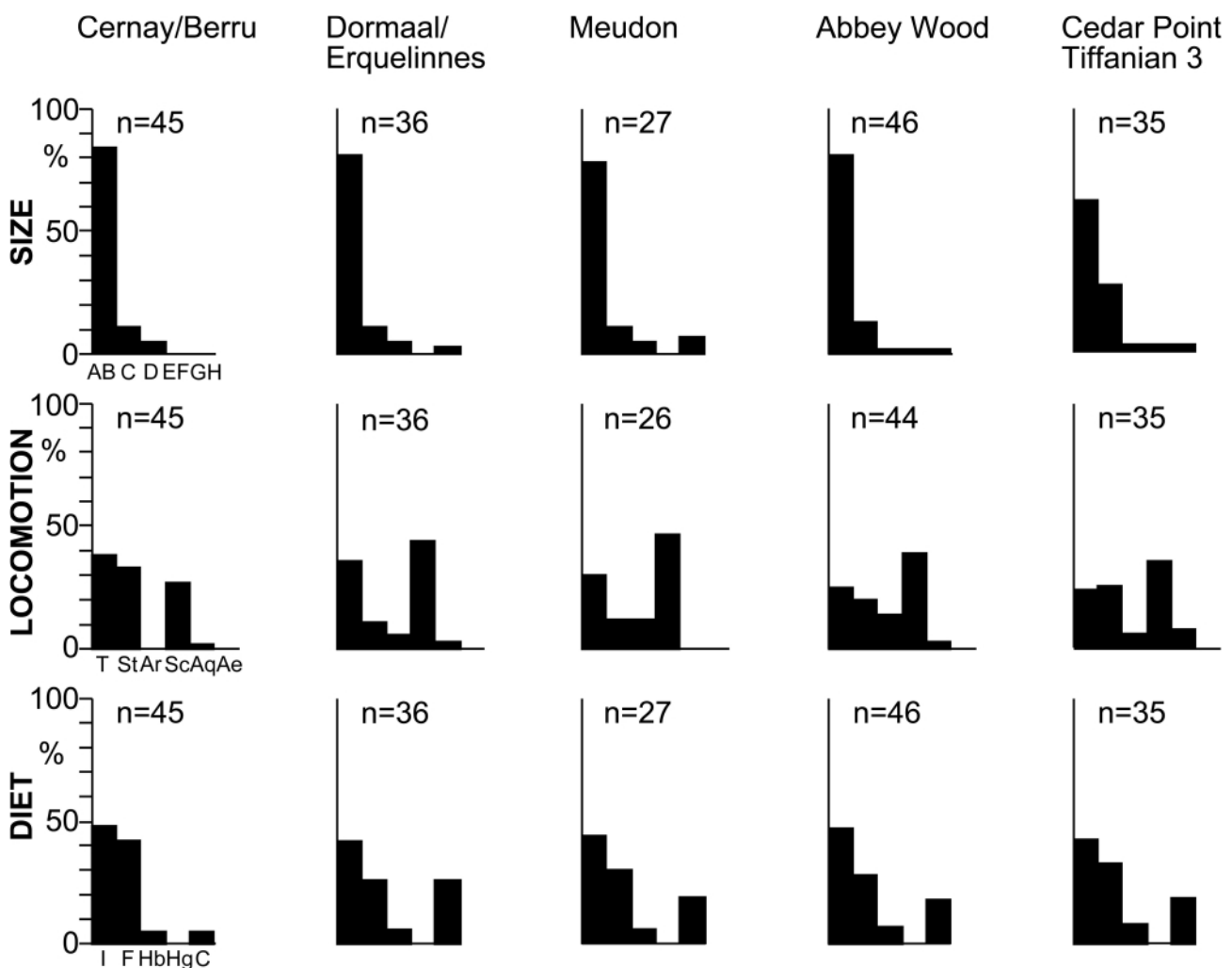
One European Early Eocene locality, Abbey Wood, London Basin, in the context of a faunal study, has recently been compared to modern ecological diversity plots in separate categories and found to compare well with broad-leaved evergreen forest habitats such as are found today in the tropics (Hooker, 2010). The comparability is based on the high percentage of the smallest size class, the large percentage of tree-living types (scansorial and arboreal), the high percentages of insectivores and frugivores and low percentages of browsing herbivores. Grazing herbivores are absent from the European Eocene (Joomun et al., 2010) and are essentially restricted to the Neogene onwards, when grasslands became widespread (e.g. Strömberg, 2011), representing an example of community evolution. Grazers are in any case usually absent from broad-leaved evergreen forests today. Unlike the Early Eocene plots,

those of the latest Paleocene (Cernay/Berru) (Fig. 2) are unusual in that they have no animals larger than the D class (10-45kg), no arboreal types and a very small percentage of carnivores. The carnivorous class is represented by a mesonychid, *Dissacus*, which was largely a scavenger (O'Leary and Rose, 1995) and by several arctocyonids, which, according to their dentitions, would have mixed carnivory with insectivory and frugivory (Collinson and Hooker, 1987). Neither group had specialized carnassial teeth, unlike the Creodonts and flesh-eating members of the order Carnivora.

The earliest Eocene (zone PE I) fauna of Dormaal/Erquelinnes shows the sudden appearance of larger mammals with the northern hemisphere Mammalian Dispersal Event, in the form of the pantodont *Coryphodon*, of arboreal types in the form of primates, and of carnivores in the form of hyaenodontid and oxyaenid creodonts and viverravid and miacid carnivorans, all with carnassial teeth (Fig. 2). At the same time there was a small reduction in terrestrial types, which continued through the first half million years of the Early Eocene.

The size/locomotor and locomotor/diet biplots show more

striking differences between the latest Paleocene and Early Eocene (Fig. 3). The most notable features in the latest Paleocene size/locomotor plots are the large numbers of small (AB, <1kg) semiterrestrials (dominated by multituberculates) and terrestrials (dominated by lousinids), of a modest number of 1-10 kg (C) semiterrestrials (two pleuraspidotheres and two *Arctocyonides* species), and of the absence of mammals >45 kg in any locomotor class. The AB terrestrial and AB and C semiterrestrial types were decimated at the Paleocene-Eocene boundary. In the first Eocene (PE I) fauna of Dormaal/Erquelinnes: there is a large increase in small scansorial (mainly rodents); appearance of two small arboreal types (a primate and an ailuravine paramyid rodent), a niche that increases through the first 500 ky of the Eocene with the addition of more primates, ailuravines and the didelphimorph marsupial *Peradectes*; great reduction in small semiterrestrials and terrestrials; and appearance of a large (GH class) terrestrial in the form of *Coryphodon*, subsequently supplemented by new mesonychids in the >45 kg classes. The first small aerial mammal is represented by a bat in the PE II site of Meu-



**FIGURE 2:** Ecological diversity spectra for size, locomotor adaptation and diet for a succession of latest Paleocene (Cernay/Berru) and earliest Eocene (Dormaal/Erquelinnes, Meudon and Abbey Wood) faunas of NW Europe and M. Paleocene fauna of Cedar Point, Wyoming, USA. Data are from Table 1. Size classes are: AB, <1kg; C, 1-10kg; D, 10-45kg; EF, 45-180kg; GH, >180kg. Abbreviations: Ae, aerial; Aq, aquatic; Ar, arboreal; C, carnivore; F, frugivore; Hb, herbivore browser; Hg, herbivore grazer; I, insectivore; Sc, scansorial; St, semiterrestrial; T, terrestrial.



don (Russell et al., 1988).

The most notable features of the latest Paleocene locomotor/diet plots are the numerous semiterrestrial insectivore/frugivores (dominated by multituberculates) and terrestrial frugivores (a niche occupied by many of the lousinids), moderate numbers of scansorial frugivores (plesiadapids) and two semiterrestrial browsing herbivores (pleuraspidotheres). At the beginning of the Eocene (Dormaal/Erquelinnes) these niches are greatly reduced, with instead the appearance of substantial numbers of terrestrial and scansorial carnivores (creodonts and carnivorans), scansorial insectivore/frugivores (mainly rodents) and a terrestrial browsing herbivore (*Coryphodon*). The aerial insectivore niche (bats) was not occupied until zone PE II (Meudon). The surviving species of scansorial plesiadapids (*Platychoerops*) shifted their diet from fruit to mixed fruit and leaves (Szalay and Delson, 1979; Hooker, 1994), inhabiting a niche not occupied by any other mammal at this time, probably accounting for their survival through much of the Early Eocene. They may have been outcompeted near the close of the Early Eocene by the arboreal ailuravine *Ailuravus*, which had developed a similar diet (Schaal and Ziegler, 1988). From PE I onwards, the scansorial insectivore/frugivore niche increased with the further diversification of rodents.

### 3.3 INTERPRETATION

The most diverse group of mammals in the latest Paleocene of the Paris Basin is the macroscelidean family Louisinidae with 13 species (Hooker and Russell, 2012). All are characterized as small terrestrials. Most are classed here as frugivores, although some are insectivore/frugivores. Modern macroscelideans are fully terrestrial and mainly insectivorous, alt-

hough some also feed on fallen fruit. They feed entirely at ground level (Kingdon, 1971-82). Their nests are in shallow depressions rather than burrows and their main protection from predation is through their occupation of habitats (forested and more open) with dense undergrowth/understorey. Given that the ancient macroscelideans appear to have had locomotor adaptations similar to those of their modern relatives (Penkrot et al., 2008; Tabuce et al., 2006), it is inferred that their habitat in the latest Paleocene in NW Europe would similarly have had dense understorey.

High latitude broadleaved evergreen *Nothofagus* forests of southern Argentina and Chile have a dense understorey, which consists largely of bamboo and their rather restricted fauna of mammals lacks any larger than 45 kg, the largest being the Pudu deer (*Pudu puda*). It has only one strict carnivore, a smallish (size C) semiterrestrial cat (*Felis guigna*). Most of the rest of the fauna consists of small semiterrestrial cricetid rodents, which are mostly mixed insectivore/frugivores, although the 'fruit' component in this case consists mainly of fungi (Pearson and Pearson, 1982; Redford and Eisenberg, 1992). Clearly these *Nothofagus* forests provide at best only a partial analogue for the NW European latest Paleocene. Nevertheless, the size restriction and the minimal carnivore activity are supportive of the idea of an important understorey component in the ancient forests.

Such a dense understorey is unlikely to have been such a major component of the Early Eocene forests in NW Europe in view of the smaller number of small terrestrial and semiterrestrial mammals. The change may have been effected by the appearance of the large terrestrial browsing *Coryphodon*. Although only a single species, *C. eocaenus*, was present in

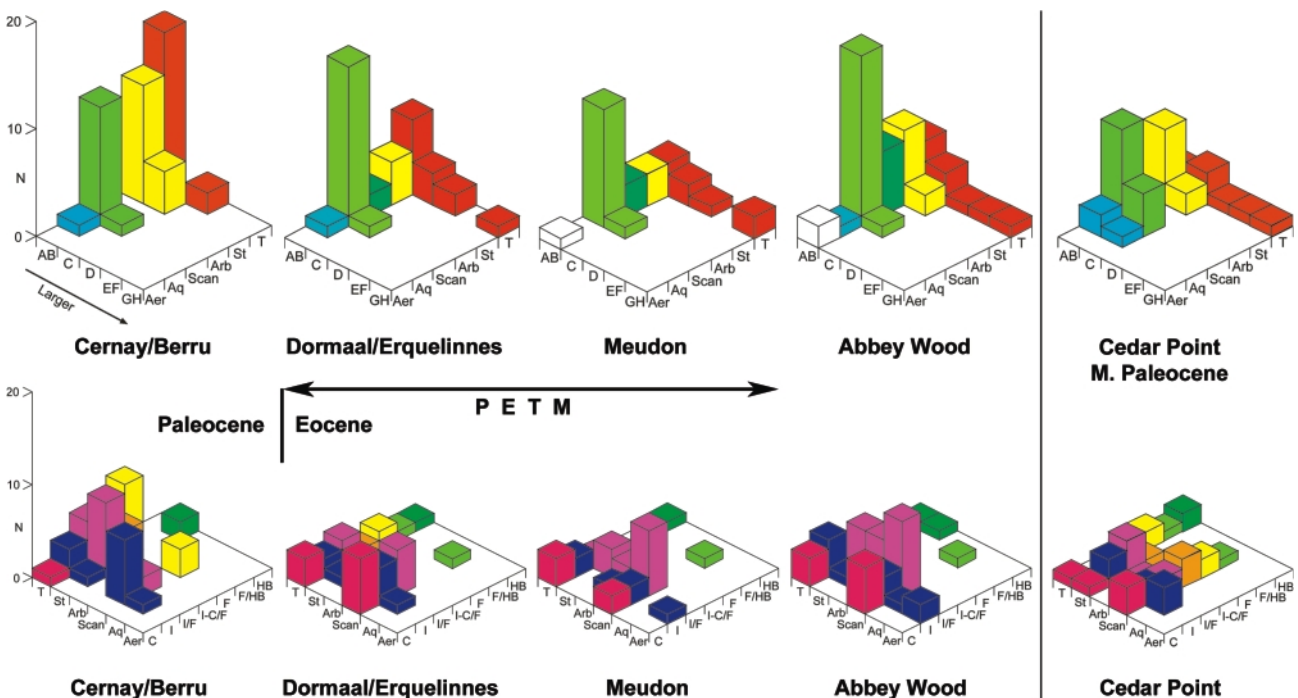


FIGURE 3: Biplots of size/locomotor adaptation and locomotor adaptation/diet for the same sites as in Fig. 2. Data are from Table 1. Size classes and abbreviations are as for Fig. 2.

	Cernay/Berru					Locomotion	Diet	Dormaal/Erquelimnes					Locomotion	Diet			
	Cernay/Berru	Dormaal/Erquelimnes	Meudon	Abbey Wood	Cedar Point			Cernay/Berru	Dormaal/Erquelimnes	Meudon	Abbey Wood	Cedar Point					
<i>Afrodon germanicus</i>	X				AB	Scan	I					X			C	T	F/HB
<i>Bustylus cernaysi</i>	X				AB	Scan	I					X			AB	Scan	C
<i>Arctocyon primaevus</i>	X				D	T	I-C/F					X			AB	Scan	I/F
<i>Tricuspidon ruetimeyeri</i>	X				C	St	I-C/F					X	X		AB	St	I/F
<i>Liotomus marshi</i>	X				AB	St	I/F					X			AB	Scan	I/F
<i>Hainina godfriauxi</i>	X				AB	St	I/F					X			AB	Scan	I/F
<i>Adapisoriculus minimus</i>	X				AB	Scan	I					X			AB	Scan	I/F
<i>Adapisoriculus</i> sp.	X				AB	Scan	I					X	X		AB	T	I
<i>Pagonomus dionysi</i>	X				AB	Aq	I					X			AB	Scan	I/F
<i>Arctocyonides trouessarti</i>	X				C	St	I-C/F					X			GH	T	C
<i>Gigartion louisi</i>	X				AB	T	I/F					X			AB	Scan	I/F
<i>Adapisorex gaudryi</i>	X				AB	T	I/F					X			C	T	C
<i>Samacius gingerichi</i>	X				AB	Scan	I					X	X		AB	Aer	I
<i>Dipavali petri</i>	X				AB	T	F					X			GH	T	HB
<i>Gigartion meyeri</i>	X				AB	T	F					X	X		AB	Arb	I/F
<i>Gigartion sigogneauae</i>	X				AB	T	F					X			AB	T	I
<i>Walbeckodon girardi</i>	X				AB	T	I					X			AB	St	I/F
<i>Berrulestes phelizoni</i>	X				AB	T	I/F					X			AB	T	I
<i>Berrulestes pelouini</i>	X				AB	T	I					X			AB	Scan	I
<i>Berrulestes poirieri</i>	X				AB	T	I/F					X			C	T	C
<i>Thryptodon braillonii</i>	X				AB	T	F					X			AB	Scan	C
<i>Louisina mirabilis</i>	X				AB	T	F					X			C	St	I-C/F
<i>Louisina marci</i>	X				AB	T	F					X			AB	T	I-C/F
<i>Arctocyonides arenae</i>	X				C	St	I-C/F					X			AB	T	I
<i>Plesiadapis tricuspidentis</i>	X				C	Scan	F					X			AB	Scan	I/F
<i>Teilhardimys brisswalteri</i>	X				AB	T	F					X			AB	St	I/F
<i>Berruvius lasseroni</i>	X				AB	Scan	I					X			AB	Arb	I/F
<i>Plesiadapis remensis</i>	X				AB	Scan	F					X			AB	Aq	I
<i>Cernaysia manueli</i>	X				AB	St	I/F					X			C	Scan	F/HB
<i>Palaeictops levei</i>	X				AB	T	I					X			AB	Arb	I
<i>Remiculus</i> sp. large	X				AB	Scan	I/F					X			C	T	F/HB
<i>Nosella europaea</i>	X				AB	St	I					X			AB	Scan	C
<i>Neoplagiaulax eocaenus</i>	X				AB	St	I/F					X			AB	Scan	I/F
<i>N. copei</i>	X				AB	St	I/F					X			AB	Scan	I/F
<i>N. annae</i>	X				AB	St	I/F					X			AB	Scan	I/F
<i>N. nicolae</i>	X				AB	St	I/F					X			AB	Scan	I/F
<i>N. sylvani</i>	X				AB	St	I/F					X			C	T	F
<i>Pleuraspidothorium aumonieri</i>	X				C	St	HB					X			AB	St	I/F
<i>Orthaspidothorium edwardsi</i>	X				AB	St	HB					X			AB	Arb	I/F
<i>Landenodon lavocati</i>	X				AB	St	I-C/F					X			AB	Scan	I/F
<i>Chirmyoides campanicus</i>	X				AB	Scan	F					X			AB	T	I
<i>Remiculus delatei</i> + small	X	X			AB	Scan	I					X			AB	Aer	I
<i>Dissacus europaeus</i>	X	X			D	T	C					X			EF	T	C
<i>Paschatherium dolloi</i> + cf.	X	X	X		AB	T	I/F					X			AB	Scan	C
<i>Remiculus deustchi</i> + cf.	X	X	X		AB	Scan	I/F					X			AB	St	F
<i>Teilhardimys musculus</i>	X				AB	T	F					X			AB	St	I/F
<i>Bustylus</i> sp.	X				AB	Scan	I					X			C	St	HB
<i>Platychoerops georgei</i>	X				AB	Scan	F/HB					X			AB	St	I
<i>Landenodon woutersi</i>	X				AB	St	I-C/F					X			C	St	C
<i>Paschatherium yvettae</i>	X				AB	T	I/F					X			GH	T	HB
<i>P. sp.</i>	X				AB	T	I/F					X			C	Scan	I-C/F
<i>Galecyon morloi</i>	X				AB	Scan	C					X			AB	Scan	C
<i>Oxyaena woutersi</i>	X				C	T	C					X			AB	St	I/F
<i>Arfia junnei</i>	X				C	Scan	C					X			AB	Scan	C
<i>Macrocranium germonpreae</i>	X				AB	T	I					X			C	Scan	C
<i>Eochiromys landenensis</i>	X				AB	Scan	I/F					X			AB	Scan	F
<i>Lipotyphla</i> indet.	X				AB	St	I					X			C	T	F
<i>Gracilocyon solei</i>	X				AB	Scan	C					X			AB	Arb	I
<i>Miacis latouri</i>	X				AB	Scan	C					X			C	Aq	I
<i>Diacodexis gigasei</i>	X				AB	T	I-C/F					X			AB	St	I/F
<i>Apatemys teilhardi</i>	X				AB	Scan	I/F					X			AB	St	I/F
<i>Phenacodus teilhardi</i>	X				C	T	F					X			AB	T	I/F
<i>Teilhardina belgica</i>	X				AB	Arb	I					X			C	Scan	I-C/F
<i>Macrocranium vandebroeki</i>	X				AB	T	I					X			AB	St	I
<i>Cymbalophus cuniculus</i>	X				C	T	F/HB					X			AB	Aq	I
<i>Palaeosinops russelli</i>	X				AB	Aq	I					X			AB	Scan	I
<i>Microparamys nanus</i>	X				AB	Scan	I/F					X			AB	Scan	I
<i>Prototomus minimus</i> + sp.	X		X		AB	Scan	C					X			AB	Scan	I/F
<i>Palaeonictis gigantea</i>	X	X	X		D	T	C					X			AB	Scan	I/F
<i>Wyonycteris richardi</i>	X	X	X		AB	Scan	I					X			AB	Scan	F/HB
<i>Meldimys</i> sp.	X	X	X		AB	Arb	I/F					X			C	T	F/HB
<i>Pseudoparamys</i> sp.	X	X	X		AB	Scan	I/F					X			EF	T	C
<i>Leptacodon dormaalenensis</i> + sp.	X	X	X		AB	Scan	I					X			C	Scan	I-C/F
<i>Prototomus girardoti</i> + cf.	X	X	X		AB	Scan	C					X			AB	St	I
<i>Coryphodon eocaenus</i>	X		X		GH	T	HB					X			AB	Arb	I/F
<i>Peratherium constans</i>	X				AB	St	I/F					X			D	T	HB
<i>Amphiperatherium brabantense</i>	X				AB	St	I/F					X			AB	St	I/F
<i>Ectypodus childei</i> + cf.	X	X	X		AB	St	I/F					X			AB	Aq	I
<i>Cantius eppsi</i> + sp.	X	X	X		AB	Arb	I/F					X			C	T	I-C/F
<i>Viverravidae</i> indet.	X	X			AB	Scan	C					X			C	St	I-C/F
<i>Melaneremia</i> sp.	X	X			AB	Arb	I					X			AB	T	F
<i>Tolapiniidae</i> indet.	X	X			AB	Scan	I					X			AB	St	I
<i>Platychoerops russelli</i>	X				C	Scan	F/HB					X			AB	Scan	F

TABLE 1: Mammalian faunal lists for Cernay/Berru, Dormaal/Erquelimnes, Meudon, Abbey Wood and Cedar Point, with scorings for size, locomotor adaptation and dietary categories used in Figs 2-3. The Cedar Point list is taken from Secord (2008, fig. 8). See Fig. 1 caption for other sources. Size classes and abbreviations are as for Fig. 2.

the earliest Eocene faunas, its impact on an easily accessible low growing vegetation through browsing and its sheer bulk is likely to have been major. This would have facilitated predation by the larger terrestrial carnivorous creodonts, which in combination could have been the main cause of the massive extinctions (all the multituberculates and pleuraspidothers, most of the lousinids). The increase in low level browsing could also have reduced the availability of fruit at this stratum. This, together with competition from incoming primates and rodents targeting fruit at source in the trees, may have caused the demise of the arctocyonids, whether terrestrial or semiterrestrial.

There is some support from modern European forests and woodlands for the contention that a large terrestrial herbivore like *Coryphodon* would have adversely affected small terrestrial mammals by reducing their ground cover. In the Bialowieza Forest of Poland, where the large herbivorous European Bison (*Bison bonasus*) exists, ground and shrub-nesting birds have much lower density populations than in many British woodlands where large herbivores are largely absent (Tomialojc et al., 1984). An exception to the situation in British woodlands is the New Forest, Hampshire, where there is a high density of deer, including *Cervus elaphus* (up to 300 kg), and free-ranging horses and where the density of shrub-nesting birds is closer to that of Bialowieza than to other British woodlands (Yalden and Albarella, 2009, p. 63). Additional evidence can be adduced from the often damaging impact on native vegetation by introduced herbivores like goats and deer (e.g. Courchamp et al., 2003).

Judging the relative influences of incoming predators and the large terrestrial herbivore *Coryphodon* in NW Europe at the beginning of the Eocene is difficult. Studies of modern ecosystems indicate that alien predators (meaning those introduced to new areas by humans, but analogous to the natural immigrations of the past) have twice the impact on prey species than do native predators (Salo et al., 2007). Important to this impact is the frequent behavioural naivety of the prey species to the new, highly adaptable predators. The impact has been particularly severe in Australia, where hunting tactics of the native marsupial predators may differ from those of the distantly related alien placental predators (Salo et al., 2007). This would seem comparable to the introduction of creodonts and carnivorans with carnassial teeth into Europe at the beginning of the Eocene, where predation would previously have been restricted to arctocyonids and a mesonychid, which lack carnassials, and the former of which were also frugivorous.

The impact of *Coryphodon* versus the new carnivores is potentially testable since *Coryphodon* appears not to have dispersed as far south as southern Europe, whereas hyaenodontid (although not oxyaenid) creodonts and carnivorans did (Antunes and Russell, 1981; Godinot, 1981). Unfortunately, the succession of mammals across the Paleocene-Eocene boundary is poorly known in southern Europe. Those from the latest Paleocene are restricted to the Tremp Basin, Spain (López-Martínez and Peláez-Campomanes, 1999; López-Martínez et

al., 2006) and none are known unequivocally from the very beginning of the Eocene (Hooker, 1998). In the Tremp Basin, of the ten species known from the latest Paleocene, *Nosella*, *Adapisorex*, *Paschatherium*, *Teilhardimys*, *Pleuraspidotherium* and *Hainina* (the last two with cf. qualifications) are shared with the late Thanetian Cernay and Berru faunas. As in the north, except for *Paschatherium* and *Teilhardimys*, these genera also did not survive into the known Early Eocene faunas of southern Europe.

Despite our scanty knowledge of southern European Paleocene mammals, there is no evidence of much greater survival than in the north, because southern Early Eocene faunas, as in the north, are dominated by newly dispersed taxa from other continents (Godinot, 1981; Marandat, 1991). Exceptions are *Adapisoriculus*, a survivor from the northern Paleocene (Marandat, 1991) and the enigmatic *Eurodon* (Estravis and Russell, 1992) and *Ilerdoryctes* (Marandat, 1991), whose relationships and origins are obscure. However, inadequacy of the data prevents a rigorous comparison of the scale of turnover between northern and southern Europe at the Paleocene-Eocene boundary. By analogy with patterns in recent history, predation from alien carnivores is likely to have been the dominant agent of extinction in NW Europe at the Paleocene-Eocene boundary, but facilitated especially in the case of terrestrial prey by the activities of *Coryphodon*.

#### 4. PALAEOBOTANICAL CONTEXT

The question arises as to whether there is any evidence from fossil floras in NW Europe for a shift in vegetation across the Paleocene-Eocene boundary, in particular one that could be climate-related and that could have influenced the mammal turnover, for instance favouring the newcomers over the Paleocene endemics. In addition, one might ask if there is any floral evidence for a reduction in understorey vegetation at this time. The main latest Paleocene (late Thanetian) flora is from the Travertin de Sézanne, E. Paris Basin, a time equivalent of the Cernay and Berru mammal faunas (Laurain and Meyer, 1986). Several floras are known in the Paris Basin from the succeeding Vaugirard Formation (formerly Argiles Plastiques) at the sites of Bagneux, Cessoy, Meudon and Vervins; they are likely to belong to the PETM (Aubry et al., 2005), but are difficult to interpret because they have not been recently revised and are frequently poorly preserved (Fritel, 1910; Feugueur, 1963). All are leaf floras. Mai (1995, p. 144) has noted leaves in the Sézanne flora as being entire-margined and megaphyllous.

In the London Basin, equivalent-aged floras come from the Upnor Formation (late Thanetian) and Woolwich and Reading Formations (PETM) (Collinson and Cleal, 2001; Hooker et al., 2009). These are either fruit and seed (Upnor Formation) or fruit, seed and leaf floras (the rest). In the Woolwich and Reading Formation floras, there are a few distinctive, repeatedly occurring PETM elements, all seeds: one resembling that of the cucurbitacean *Trichosanthes*, another resembling that of the lythracean *Decodon* and a new genus of Theaceae. Other

floral elements include members of the families Vitaceae, Menispermaceae and Icacinaceae, probably representing lianas, and these are more widespread stratigraphically, occurring in the Paleocene and later in the Early Eocene too.

Overall, these floras do not suggest a radical change in vegetation type from the latest Paleocene to the earliest Eocene. They also do not allow us to identify understorey plants and we are not aware of a means of determining understorey habit from fossil floras.

## 5. COMMUNITY EVOLUTION

A significant number of mammals that appeared by dispersal at the beginning of the Eocene in Europe filled niches not occupied in the European Paleocene. These included specialized terrestrial and scansorial carnivores with carnassial teeth (independently evolved at least twice: creodonts and carnivorans), large terrestrial browsing herbivores, small arboreal insectivores and insectivore/frugivores and small, mainly scansorial mammals with gnawing incisors (rodents). The question arises as to why none of these ecological types had evolved in the European Paleocene. Analysis of the ecological diversity of a typical Middle Paleocene fauna from North America (Cedar Point, late Selandian, Tiffanian NALMA, Ti-3: Secord, 2008) shows individual locomotor and dietary plots much more similar to those of the earliest Eocene than of the latest Paleocene of NW Europe. This indicates that many of the ecological types that appeared in Europe at the beginning of the Eocene had already evolved in North America at least 3 million years earlier. The size plot, however, shows a lower proportion of smaller to larger types than in the European earliest Eocene, suggesting a more open habitat. This is corroborated by penecontemporaneous fossil leaf floras in the Bighorn and Great Divide basins, Wyoming, where leaf margin analysis indicates broad-leaved temperate deciduous forest (Hickey, 1980; Gemmill and Johnson, 1997). Those of the Great Divide Basin are relatively depauperate with a leaf morphotype count of 28 species.

Middle Paleocene floras in Europe for comparison are rare (Collinson and Hooker, 2003). The only one documented is that of the Marnes de Gelinden, Belgium, a leaf flora of late Selandian age. Mai (1995) noted that this flora was dominantly evergreen with few deciduous elements and interpreted it as a thermophilic broad-leaved evergreen forest or evergreen laurophyllous forest, dominated by evergreen Fagaceae and Lauraceae. Indeed, Mai (1995) took the Gelinden flora as the key representative of thermophilic vegetation in the European Paleocene. Woods associated with a slightly younger Paleocene flora show only indistinct growth rings (Gerrienne et al., 1999). This vegetation suggests a more closed structure with perhaps more consistent fruit availability than the contemporaneous forests of Wyoming. Poor preservation of the leaves and need for revision of the leaf flora suggests some reservation over the interpretation of the vegetation that the Gelinden flora represents, but it is consistent with the composition of European Paleocene mammal faunas. If correct, it is possible

that such a habitat might provide little selection pressure for dietary or increased body size shifts. In contrast, the more open deciduous forests of Wyoming might well have produced selection pressures to diversify away from a fruit diet into herbivory and carnivory. Specialized herbivory would also have entailed an increase in body size to facilitate the digestion of leaves, whilst larger body size may have been selected for in their carnivore predators. The different vegetational characteristics in the two continents could have resulted from the difference between a dominantly maritime setting in island Europe and a continental interior setting in western North America. Europe may thus have been somewhat buffered by its geography against the Middle Paleocene global cooling phase.

Persistent closed vegetation through the Paleocene is therefore a tentative hypothesis to explain the delay in mammalian community evolution in Europe compared to North America and by extrapolation also compared to Asia, where rodents appear to have originated (Meng et al., 2003). This delay in community evolution might explain why the mammalian faunal turnover at the Paleocene-Eocene boundary in NW Europe was so dramatic.

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