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Mammalian biostratigraphy across the Paleocene–Eocene boundary in the Paris, London and Belgian basins

J. J. HOOKER
Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK

Abstract: Problems of resolution and poor superpositional evidence in mammalian biostratigraphy through Paleocene–Eocene boundary strata in NW Europe are solved by applying parsimony analysis to taxa shared between localities. On this basis, five biozones are established in the area for the interval formerly delineated by mammalian biostratigraphers as MP7–MP9. Integration with other biostratigraphies (dinocyst, calcareous nannoplankton, charophytes) aids correlation between the London, Belgian and Paris Basins, and supports the earlier idea of diachronism of the 'argile à lignites' facies. The advent of 'Sparnacian' mammal faunas in Europe may coincide with a carbon isotope excursion recently recognized in the Paris Basin. This would support recent views on essential synchronism of the beginnings of both the North American Wasatchian and European 'Sparnacian' land mammal ages.

One of the most important events in mammalian history during the Cenozoic, and certainly the most important within the Northern Hemisphere Paleogene, was that which took place at or around the Paleocene–Eocene boundary. This event was a rapid faunal turnover with large numbers of extinctions in mammal groups that had been dominant in the Paleocene, accompanied by origins at ordinal and family level. The event is best represented and documented in western North America, where long continental sequences contain an essentially continuous record of mammalian fossils (Gingerich 1989; Gingerich *et al.* 1980; Rose 1981; Schankler 1980). In Asia, the event is best documented in Mongolia, where continental sequences have a more sporadic mammalian record (Dashzeveg 1988). Europe has the most disjointed mammalian record (Russell 1975; Russell *et al.* 1982*a,b*; Hooker 1991), but the event is striking and the area is classic for containing all the stratotypes of the globally recognized Paleocene and Eocene stages (Pomerol 1981).

In Europe (as in North America), the main Paleocene groups to suffer decimation were the order Multituberculata, the Plesiadapiformes (primate relatives) and the archaic ungulates (paraphyletic order 'Condylarthra'). The incoming groups in both continents were the orders Perissodactyla, Artiodactyla, Primates (s.s.), probably Chiroptera (although not recorded in the very earliest post-event faunas) and the family Hyaenodontidae (order Creodonta). The suddenness and morphological distinctness of the appearances imply dispersal from elsewhere, but the source has not been identified, although 'the south' is usually invoked, e.g. Africa, Central America (Gingerich 1976) or India (Krause & Maas 1990). Other incoming European groups, the orders Rodentia and Apatotheria, the marsupial family Didelphidae (Paleocene records no longer upheld: Gheerbrant 1991) and the pantodont genus *Coryphodon*, are thought to have their origin in North America, because of distinctly earlier appearances there (Gingerich 1989; Rose 1981). Interchange was probably via land bridges connecting Greenland to each continent (McKenna 1983). The new fauna in Europe is often termed the *Hyracotherium–Coryphodon* fauna, after the dominant elements in old collections, and is taken to characterize the 'Sparnacian Stage', but there are problems with this definition (see below).

Biostratigraphic problems

In 1987, at the International Symposium on Mammalian Biostratigraphy and Palaeoecology of the European Paleogene, in Mainz, a mammalian biochronology was established for the Paleogene of Europe (Brunet *et al.* 1987). It consists of numbered units with the prefix MP. Workers are unanimous that MP6 is Paleocene and MP10 is Eocene on the criteria of any of the main organisms used to define the Paleocene–Eocene boundary (i.e. planktonic or benthic forams, calcareous nannoplankton, dinocysts, mammals). MP7–9 lie in a transition zone, with the major mammalian faunal turnover between MP6 and MP7. There is currently poor biostratigraphic resolution within the important MP7–MP9 interval mainly for two reasons. Firstly, although workers have normally

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accepted that the fauna from the Paris Basin locality of Mutigny is older than that of nearby Avenay, the consensus opinion in Mainz was that the differences were minor and that the combined faunas should be designated MP8+MP9 (Godinot in Brunet *et al.* 1987). Secondly, the Paris Basin localities of Pourcy and Meudon were placed in MP7, but the former was already known to have yielded several MP8+MP9-defining taxa and the latter was later shown to yield such taxa too (Russell *et al.* 1988) (see Hooker 1991).

Russell *et al.* (1982*b*, fig. 2) show the location of all the major mammal localities of late Paleocene and early Eocene age in the London, Belgian and Paris Basins. The Paris Basin has the largest cluster, but despite this the superpositional evidence for faunal succession here is extremely difficult to find. This is because of a combination of rapid lateral facies change and poor exposure. Nevertheless, certain superpositional evidence is well established. *Coryphodon*, whose earliest occurrence is in MP7, was recorded in shelly lignitic sands and clays stratigraphically well above the Conglomérat de Cernay, yielding the main MP6 fauna, in the small outlier of Mont de Berru (Depéret 1906). The Sables à Unios et Térédines, which at several sites in the vicinity of Epernay yield MP10 faunas, consistently overlie an 'argile à lignites' facies, which in its upper part yields the MP8+MP9 fauna of Mutigny (Feugueur 1963; Riveline 1984). A complication is that the MP8+MP9 Avenay fauna occurs in sands of Sables à Unios et Térédines facies, immediately overlying the argile à lignites. Michaux (1964), however, considered that the lithofacies at Avenay was subtly different from that of typical Sables à Unios et Térédines.

Biostratigraphic solutions

Methods

To avoid circular reasoning in considering the age relationships of these MP7-MP9 faunas, I have subjected them to parsimony analysis, and subsequently examined the available evidence for superposition to assess its support or otherwise for the analysis. Alroy (1992) has introduced the use of parsimony into taxonomic distributional studies. His statistical method involves the distinction between overlapping (conjunct) ranges and nonoverlapping (disjunct) ranges, together with the creation of hypothetical distributional spaces to overcome the inaccuracies caused by absent records ('apparent disjunctions') due to taphonomic or collecting biases. I have instead used a program called Phylogenetic Analysis Using Parsimony (PAUP 3.0: Swofford 1990). This program is much employed in phylogenetic analysis, but has been adopted for ecological analysis too (Lambshead & Patterson 1986). It avoids the need for hypothetical distributional spaces by simply expressing 'apparent disjunctions' as homoplasies. In the data matrix (Table 1), in contrast to a phylogenetic analysis, the locality names take the place of taxa, and taxa (numbered) take the place of characters, as in an ecological analysis. Only taxa that occur in more than one and fewer than all the localities have been used, as it is the principle of shared taxa that is being applied in order to relate the localities. A

Table 1. *Data matrix of taxa and localities*

	00000000011111111112222222222333333333344444444 12345678901234567890123456789012345678901234567
Sezanne-B.	00000000000000000000001011000011000001001111111
Conde-en-Brie	00000000000000000000011111000101001101111111111
Avenay	00000000000000000000111111000101111111011111110
Mutigny	00010000000000101101110111001011110111111100000
Pourcy	00100000111011100001110110111111111110000000000
Abbey Wood	00000000110000100000010100111111000000000000000
Soissons	000000010110000100?0000101000000000000000000000
Meudon	00010001111000010011111100000000000000000000000
Dormaal	00000111001111011100000000000000000000000000000
Suffolk P.B.	00001111101111100000000000000000000000000000000
Erquelinnes	00001101011000000000000000000000000000000000000
Try	11101111110000000000000000000000000000000000000
Berru	11110000000000000000000000000000000000000000000

Localities span MP6–MP9. Taxa are restricted to those which occur in more than one and fewer than all localities within the MP7–MP9 group. Numbers attached to taxa relate to those listed in Fig. 3.

taxon occurring at only one locality would simulate an autapomorphy in phylogenetic analysis and thus would not aid the analysis, but misleadingly increase the consistency index. Thus, the relationships between localities are established on the basis of taxa shared amongst them, minimizing the number of 'apparent disjunctions' that need to be invoked (i.e. it identifies the most parsimonious pathway linking localities). The localities are grouped into a tree, which is subsequently rooted by selection of one or more localities known to be stratigraphically the oldest (i.e. by outgroup). In this analysis, the site of Berru is used as the outgroup. This is justified because Berru together with Cernay are MP6 sites within the Sables de Rilly of the Mont de Berru outlier, which have been demonstrated to be stratigraphically below an MP7–MP9 fauna (Depéret 1906). Use of the Dollo-up character type in PAUP 3.0 (Swofford 1990, pp. 9–12) is essential since it ensures that all homoplasy takes the form of reversals, preventing a taxon from originating more than once in parallel. Thus, a synapomorphy simulates an origination and a reversal simulates an extinction. More than one reversal of the same taxon on different branches indicates either a local extinction or a collection failure due to taphonomic or methodological bias, within the total range of that taxon (i.e. = 'apparent disjunction').

Choice of taxa or taxonomic rank depended largely on whether there had been a recent revision and to an extent on reliability of occurrence. For instance, tillodonts were recently revised by Baudry (1992), but the occurrence of each species is so sporadic that they have been lumped here as Esthonychidae. Carnivores have been omitted. MP7–MP9 multituberculates are only partially described and have thus not been included in the analysis. *Lophiodon* is dealt with at genus level, at which it is readily recognizable, but its species require extensive revision (Marandat 1987). The new Meudon fauna is undescribed and I here rely on the published list (Russell *et al.* 1988). Clearly, much taxonomic work remains to be done and future additions to faunal lists will improve resolution.

Results

Analysis, by means of a branch-and-bound search, of 13 localities and 47 taxa results in three maximum parsimony trees, each with 125 steps. The consistency index excluding uninformative taxa is 0.371. The successive nesting of the crown localities Sézanne-Broyes, Condé-en-Brie, Avenay and Mutigny, respectively, and the pairing of Pourcy and Abbey Wood at the next lower node are constant in all. Dormaal branches off at a node above the Suffolk Pebble Beds in one tree, but the two form sister localities in the other two. Soissons is the most unstable, being relatively poorly represented faunally. It is the sister locality to Meudon in two trees, but sister locality to Erquelinnes in the third. An Adams consensus of the three trees shows Soissons and Meudon on the one hand and Dormaal and the Suffolk Pebble Beds on the other as forming trichotomies with the respective crown groups (Fig. 1a). Analysis of the same taxa, but omitting the Soissons locality, results in four maximum parsimony trees each with 116 steps. The consistency index excluding uninformative taxa is 0.400. The only differences between them are that the relationship of Dormaal and the Suffolk Pebble Beds varies as in the original analysis and that in two trees Pourcy branches off at a node higher than Abbey Wood, the two forming sister localities in the other two. The Adams consensus is shown in Fig. 1b. Removal of Soissons has slightly destabilized the relationship between Abbey Wood and Pourcy. An Adams consensus of 16 trees including all those of 116, 117 and 118 steps is shown in Fig. 1c. It shows the three following locality pairs, Pourcy and Abbey Wood, Dormaal and the Suffolk Pebble Beds, and Erquelinnes and Try, as forming trichotomies with the respective crown groups, indicating the relative weakness of the evidence for the hierarchy of these localities in the maximum parsimony trees.

Table 2 is a chart of the mammal occurrences used in the analysis plus some MP10 ones linking St Agnan with the Sables à Unios et Térédines localities in the vicinity of Epernay. It can be used as a range chart provided that it is recognized that the order of the Suffolk Pebble Beds and Dormaal on the one hand and of Meudon and Soissons on the other is interchangeable. The chart shows that *Coryphodon* does not typify the entire MP7–MP9 span, but becomes extinct part way through the sequence. The genus *Hyracotherium* has in the past been used in a grade sense for almost any primitive horse-like perissodactyl. These are here segregated amongst the genera *Cymbalophus, Pliolophus, Propachynolophus, 'Propachynolophus'* and *Hyracotherium* s.s. (see Hooker 1994*b*). The implied time order of species of the plesiadapid *Platychoerops* coincides with the order of nodes in an independent cladistic character analysis recently conducted on this genus (Hooker 1994*a*), suggesting that it is as important biostratigraphically as its Paleocene precursor, *Plesiadapis* (Gingerich 1976).

Biozonation

To attempt some objectivity in constructing a biozonation from these data, I have summed the last

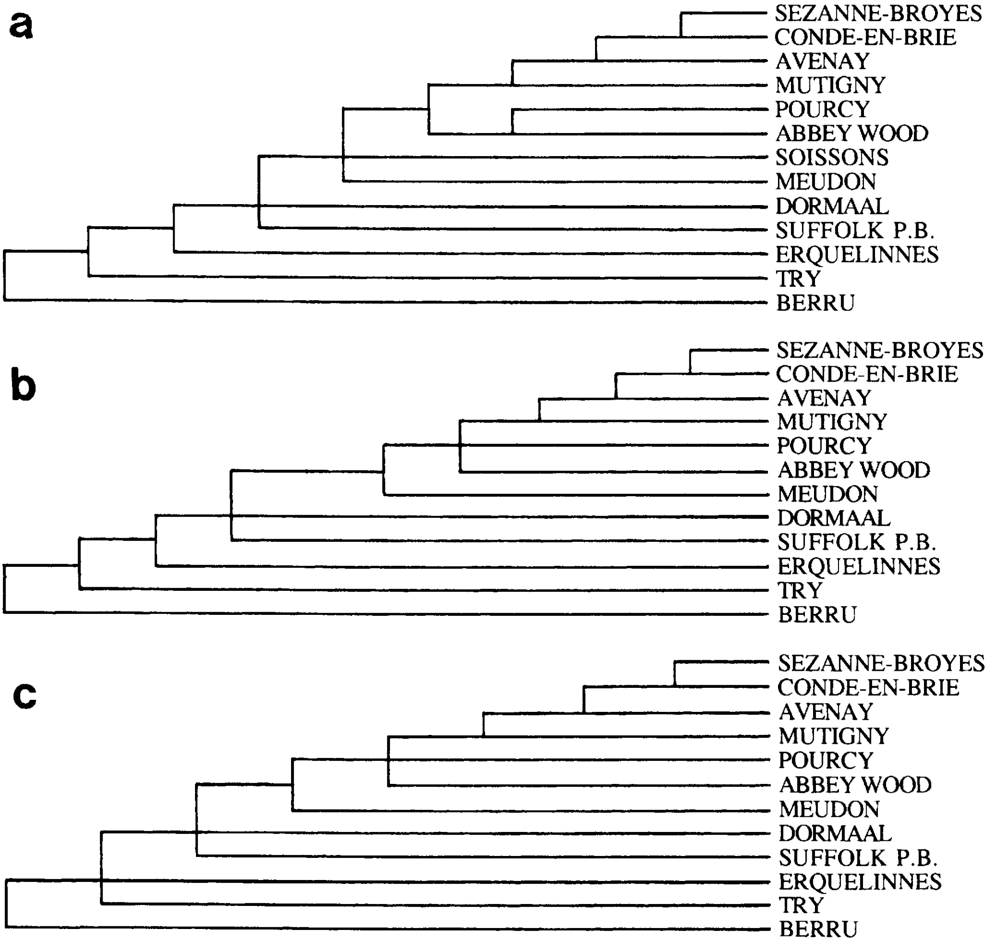


Fig. 1. Adams consensus trees derived from analysis of the data matrix in Table 1. (**a**) From three maximum parsimony trees obtained from the full data matrix; (**b**) from four maximum parsimony trees excluding the Soissons locality; (**c**) from 16 trees of 116, 117 and 118 steps excluding Soissons.

occurrences of one locality and first occurrences of the next to obtain a turnover figure between each successive pair (Fig. 2). There would be little change if the order of the Suffolk Pebble Beds and Dormaal were reversed or if Soissons were deleted. These peaks also coincide with the more robust nodes of the cladograms. I have chosen the peaks to determine the zone boundaries. The zones are concurrent range zones, named below and numbered for ease of reference as PE (for Paleocene–Eocene) I–V. They differ from the MP system in that they are biozones (*sensu* Hedberg 1976), not reference levels (*sensu* Thaler 1966), and they apply to NW Europe (onshore North Sea Basin) only, not the whole of Europe. Overlapping first appearance datum (FAD) and last appearance datum (LAD) are indicated in the definitions.

PE I – *Platychoerops georgei–Cymbalophus cuniculus* Concurrent Range Zone

Definition: Total range of *Platychoerops georgei*, coincident with that of one or more of the following: *Cymbalophus cuniculus*, *Arfia* cf. *junnei* and *Microparamys nanus*. The zone can also be recognized by concurrence of *Teilhardina belgica*, *Cantius eppsi* and *Coryphodon* (FAD) with *Pleuraspidotherium aumonieri* and *Orthaspidotherium edwardsi* (LAD), provided that the last two taxa are truly contemporaneous (see

Table 2. *Occurrence chart for main localities ranging from MP6 to MP10 in the Paris, London and Belgian Basins*

	BER	TRY	ERQ	SUF	DOR	MEU	SOI	ABB	POU	MUT	AVE	CON	SEZ	STA	GRA
1. *Pleuraspidotherium aumonieri*	×	×													
2. *Orthaspidotherium edwardsi*	×	×													
3. *Plesiadapis remensis*	×	×							×						
4. *Berruvius lasseroni* et cf.	×					×				×					
5. *Cymbalophus cuniculus*		×	×	×											
6. *Platychoerops georgei*		×	×	×	×										
7. *Arfia* cf. *junnei*		×		×	×										
8. *Teilhardina belgica*		×	×	×	×	×	×								
9. *Cantius eppsi*		×		×		×		×	×						
10. *Coryphodon*		×	×			×	×	×	×						
11. *Paschatherium dolloi*			×	×	×	×	×		×						
12. *Microparamys nanus*				×	×										
13. *Microhyus musculus*				×	×				×						
14. *Landenodon woutersi*				×	×				×						
15. *Hyopsodus wardi*				×				×	×	×					
16. *Palaeonictis gigantea*					×	×	×								
17. *Peratherium constans*					×					×					
18. *Amphiperatherium brabantense*					×					×					
19. *Platychoerops russelli*						×	?								
20. *Hyracotherium* aff. *leporinum*						×			×	×					
21. *Apatemys sigogneaui* et cf.						×			×	×	×				
22. *Paramys ageiensis* et cf.						×		×	×	×	×	×			
23. *Peratherium matronense*						×					×	×	×		
24. *Neomatronella*						×	×	×	×	×	×	×		×	
25. *Amphiperatherium maximum*						×			×	×	×	×	×	×	×
26. *Peradectes louisi*							×			×	×	×	×		×
27. *Palaeonictis* cf. *occidentalis*								×	×						
28. *Pliolophus vulpiceps*								×	×						
29. *Arcius fuscus*								×	×	×					
30. *Microparamys russelli* s.s.								×	×		×	×			
31. *Phenacodus lemoinei*								×	×	×			×		
32. Esthonychidae								×	×	×	×	×	×	×	×
33. *Bunophorus cappettai*									×	×	×				
34. *Placentidens lotus*									×	×	×				
35. *Microparamys chandoni*									×		×	×			
36. *Platychoerops daubrei*									×	×	×	×			
37. *Apatemys mutiniacus*									×	×	×			×	
38. *Diacodexis varleti* et cf.									×	×	×	×	×	×	
39. *Lophiaspis maurettei*										×		×			
40. *Peradectes mutigniensis*										×	×	×			
41. '*Propachynolophus*' *maldani* et aff.										×	×	×	×	×	×
42. *Cantius savagei*										×	×	×	×		×
43. *Propachynolophus levei*											×	×	×		
44. *Arcius lapparenti*											×	×	×	×	×
45. *Donrussellia gallica*											×	×	×	×	×
46. *Amphiperatherium bourdellense*											×	×	×		H
47. *Lophiodon*												×	×	×	×
Nannopithex zuccolae														×	×
Ailuravus michauxi														×	×
Buxolestes														×	×
Propachynolophus gaudryi														×	×
Cuisitherium lydekkeri														×	×
Protodichobune oweni														×	×
Platychoerops richardsonii														×	×

Numbered taxa are those used in the cladistic analysis (Table 1). Those unnumbered are additional MP10 taxa. H means unrecorded but occurs in higher strata. *Palaeonictis gigantea* and *Coryphodon* are added to the Soissons list as they are recorded from the Argile à Lignites du Soissonnais in the Soissons area, although not specifically from Soissons. Relevant taxonomic works are listed in Hooker (1991, p.77). More recent additions are: Baudry (1992), Gunnell & Gingerich (1991) and Hooker (1994*a*, *b*).

Abbreviations: BER, Berru; ERQ, Erquelinnes; SUF, Suffolk Pebble Beds localities (Kyson and Ferry Cliff); DOR, Dormaal; MEU, Meudon; SOI, Soissons; ABB, Abbey Wood; POU, Pourcy; MUT, Mutigny AVE, Avenay; CON, Condé-en-Brie; SEZ, Sézanne-Broyes; STA, St Agnan; GRA, Grauves and other MP10 localities in the Epernay area in the Sables à Unios et Térédines.

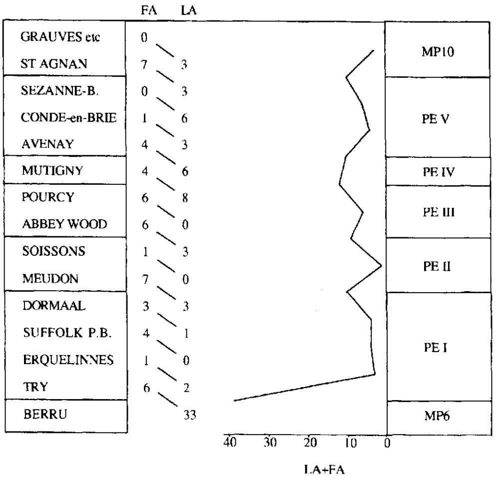


Fig. 2. Graph of taxonomic turnover between sites as listed in Table 2. Turnover figures are obtained by summing last appearances (LA) at one site with first appearances (FA) at the next. That between Berru and Try includes the entire fauna of Berru; that between the other localities is derived from Table 2. seudoextinctions are not accounted for as it is the morphological change that is here considered important for biostratigraphic purposes.

below). FAD and acme of *Paschatherium dolloi* occurs in this zone.

Reference localities: Try (Marne), France ('Conglomérat à *Coryphodon*', at the base of the Marnes Blanches de Dormans); Erquelinnes, Belgium (Erquelinnes Sand Member, Landen Formation); Kyson/Ferry Cliff, England (Suffolk Pebble Beds); Dormaal, Belgium (Dormaal Sand Member, Landen Formation). (Note: only *Platychoerops georgei* occurs at all the localities.)

PE II – *Platychoerops russelli–Teilhardina belgica* Concurrent Range Zone

Definition: Total range of *Platychoerops russelli*. Concurrence of *Hyracotherium* aff. *leporinum, Apatemys sigogneaui, Paramys ageiensis, Peratherium matronense, Amphiperatherium maximum* and *Neomatronella* (FAD) with *Teilhardina belgica* and *Palaeonictis gigantea* (LAD).

Reference localities: Meudon (Paris), France (Conglomérat de Meudon at the base of the Argile Plastique Bariolée); Soissons (Aisne), France (Argile à Lignites du Soissonnais). Sinceny (Aisne) (Sables de Sinceny) may also belong to this zone although it contains none of the zonal indicators (see below).

PE III – *Platychoerops daubrei–Cantius eppsi* Concurrent Range Zone

Definition: Coincident ranges of *Palaeonictis* cf. *occidentalis* and *Pliolophus vulpiceps*. Concurrence of *Arcius fuscus, Phenacodus lemoinei, Microparamys russelli* (s.s.), *M. chandoni*, Esthonychidae, *Bunophorus cappettai, Diacodexis varleti, Placentidens lotus, Platychoerops daubrei* and *Apatemys mutiniacus* (FAD) with *Plesiadapis remensis, Cantius eppsi, Coryphodon, Paschatherium dolloi, Microhyus musculus* and *Landenodon woutersi* (LAD).

Reference localities: Pourcy (Marne), France (Falun de Pourcy, within the Argile à Lignites d'Epernay); Abbey Wood, England (Blackheath Beds); Harwich, England (Harwich Stone Band in Harwich Member, London Clay Formation).

PE IV – *Cantius savagei–Arcius fuscus* Concurrent Range Zone

Definition: Concurrence of '*Propachynolophus*' aff. *maldani, Lophiaspis maurettei, Peradectes mutigniensis* and *Cantius savagei* (FAD) with *Hyopsodus wardi, Peratherium constans, Amphiperatherium brabantense, Arcius fuscus* and *Hyracotherium* aff. *leporinum* (LAD).

Reference locality: Mutigny (Marne), France (near the top of the Argile à Lignites d'Epernay).

PE V – *Donrussellia gallica–Apatemys sigogneaui* Concurrent Range Zone

Definition: Total range of *Propachynolophus levei*. Concurrence of *Arcius lapparenti, Donrussellia gallica* and *Amphiperatherium bourdellense* (FAD) with *Bunophorus cappettai, Apatemys sigogneaui, Placentidens lotus, *Peradectes mutigniensis, *Phenacodus lemoinei, *Lophiaspis maurettei, *Platychoerops daubrei, *Microparamys chandoni, *M. russelli* (s.s.) and **Paramys ageiensis* (LAD); and of *Lophiodon* (FAD) with the asterisked taxa only.

Reference localities: Avenay (Marne), France (Sables à Unios et Térédines); Condé-en-Brie (Aisne), France (Sables de Cuise); Sézanne-Broyes (Marne) (Sables à Unios et Térédines).

Minor faunas

Harwich. The Harwich Stone Band within the Harwich Member of the London Clay (= Wrabness Member, Harwich Formation of Jolley 1996) has yielded *Pliolophus vulpiceps* (the holotype) which is restricted to PE III. Between Harwich and St Osyth, the holotype jaw of *Coryphodon eocaenus* was found by offshore dredging. Although no horizon is recorded for this specimen, dredging was in the last century used to mine the Harwich Stone Band for cement manufacture (Whitaker 1885, p.17), so it is likely that the *Coryphodon* came from a nearby horizon within the Harwich Member.

Sinceny. Amongst the small fauna from the Sables de Sinceny, only *Pliolophus* aff. *vulpiceps* (see Hooker 1994*b*) and *Dipsalidictis* cf. *transiens* (see Gunnell & Gingerich 1991, p. 177) give a clue to the age. *P.* aff. *vulpiceps* otherwise occurs only at Soissons, whilst *D.* cf. *transiens* otherwise occurs in Europe only at Meudon, both PE II (personal observation).

Evidence for superposition

Paris Basin

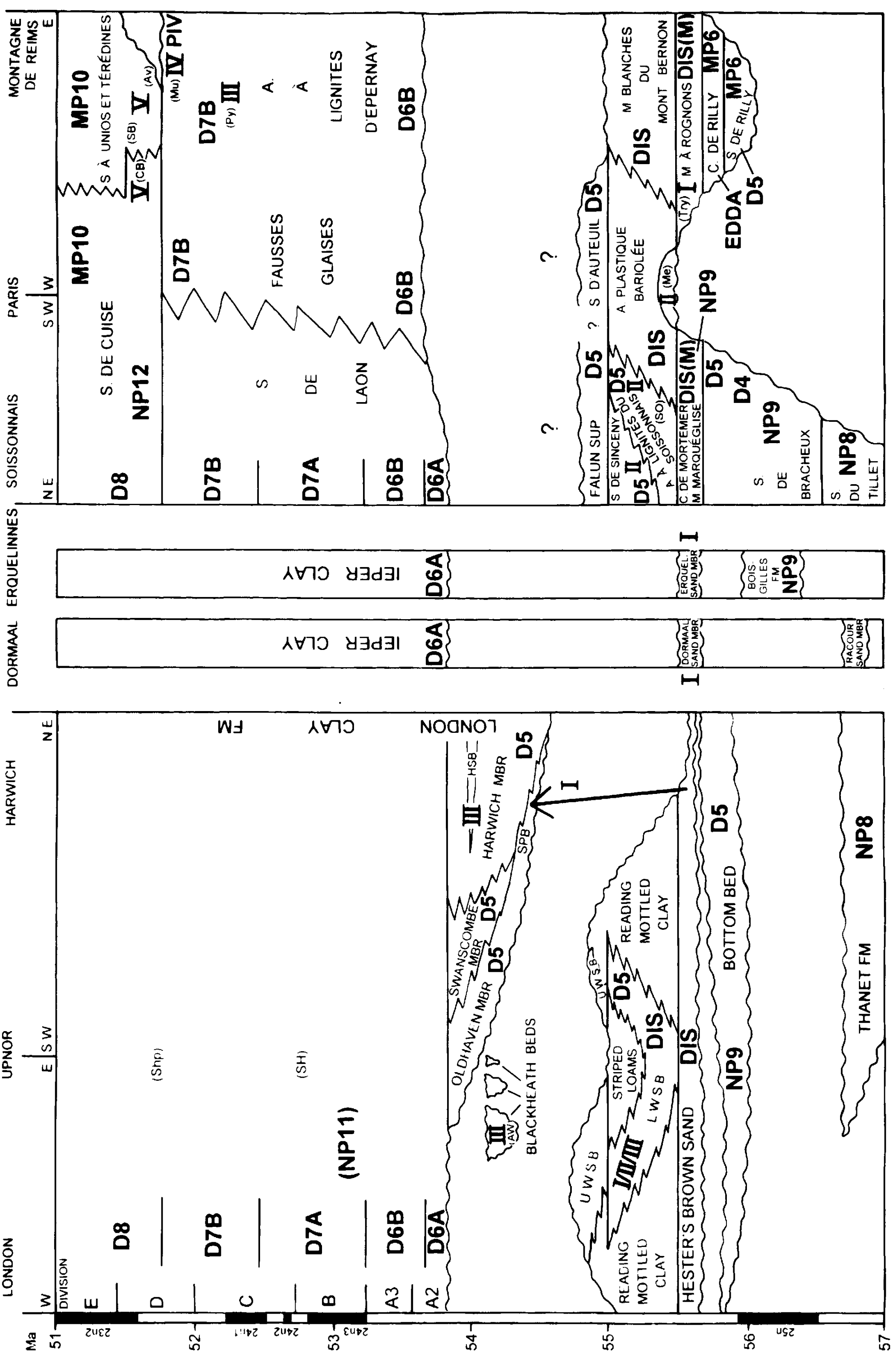
The Avenay (PE V) fauna occurs in Sables à Unios et Térédines facies immediately overlying Argile à Lignites facies (Guernet 1981); the Mutigny (PE IV) fauna occurs 3 m below the top of the Argile à Lignites (Riveline 1984, p. 145–146) at a lateral distance of 1.5 km from the Avenay quarry. The Pourcy (PE III) fauna occurs in a sandy coquina (falun) within Argile à Lignites facies (Laurain & Barta 1985, p. 42–43) 13 km from the Mutigny locality and so is impossible to stratify with respect to the latter.

The best way of demonstrating mammal succession seems to be by means of associated dinocyst and charophyte zonal taxa, whose succession is documented. Thus, Pourcy (PE III) has yielded two species of dinocyst (D. E. Russell, pers. comm.) that, according to Powell (1992), occur no earlier than zone D7B (= W5), the highest dinocyst zone recorded from the Argile à Lignites facies of the Montagne de Reims area (i.e. at Verzenay and Mailly; Gruas-Cavagnetto *et al.* 1980). On this basis, it is likely to be close in level to Mutigny. The suggested partial reworking of the Pourcy fauna, thus giving it an overall older aspect (Cavelier 1987, p. 263–264) is a possibility, but the rolled appearance of the isolated teeth is insufficient evidence on its own and should in any case affect only certain faunal elements.

Mutigny (PE IV) has yielded the charophyte *Peckichara piveteaui* (see Riveline 1984). This has also been recorded in the upper part of the Argile à Lignites of the Fosse-Parisis quarry at Mt Bernon, Epernay (Grambast 1977), where, in a borehole, a different species, *P. disermas*, occurs throughout the underlying Marnes Blanches du Mt Bernon (Riveline 1984). *P. disermas* also occurs in the Cendrier and Argile Plastique Bariolée at Passy in the Paris area (Riveline 1984) just above the horizon with the Meudon mammal fauna (PE II).

At Soissons, the Argile à Lignites with the PE II mammal fauna near the top (apparently in the Sables à Paludines at the Grande Séminaire pit; de Lapparent 1939) are overlain by the Sables de Sinceny (Faluns Sableux) with a diversity of dinocysts of the genus *Apectodinium*. In the overlying Falun Supérieur (Argiles à Cyrènes et à Huitres), *Apectodinium* dominates the dinocyst assemblage (Bignot *et al.* 1981). The same stratigraphic distribution of dinocysts is present at Sinceny (Gruas-Cavagnetto 1968, p. 21–22), where two mammals uniquely shared with the PE II Soissons locality occur in the Sables de Sinceny. At neither locality is there any sign of *Wetzeliella*, which occurs at Mt Bernon near the base of the Argile à Lignites (namely, *W. meckelfeldensis*, a D6B indicator; Laurain *et al.* 1983); so these strata at Soissons and Sinceny must pre-date D6. The dinocysts therefore demonstrate that PE II is below PE III.

Try (PE I) is the most difficult site to relate stratigraphically. Its fauna is presumed to have come from the vertebrate-rich 'conglomérat à *Coryphodon*', although, apart from this taxon, the remaining elements were found in quarry spoil (Louis *et al.* 1983). Suggestions by these authors of mixed ages for the fauna were based on the association of three Cernaysian and two Sparnacian taxa. One of the former, *Plesiadapis tricuspidens,* has now been reidentified as *Platychoerops georgei* (Hooker 1994*a*) and typifies PE I. Bearing in mind the rarity of mammaliferous horizons and the consistency of preservation type in the assemblage, it seems equally likely that the fauna is homogeneous and that the two remaining MP6 representatives (*Pleuraspidotherium aumonieri* and *Orthaspidotherium edwardsi*), as well as a champsosaur (D. E. Russell, pers. comm.), are survivors from an earlier time. A final resolution to the problem can only come from recollecting *in situ.* Whichever the outcome, a PE I locality with MP6 survivors, or closely superposed MP6 and PE I faunas at the same site, Try has great biostratigraphic potential. The 'conglomérat à *Coryphodon*' is sandwiched between 15 m of Marnes Blanches de Dormans above and the marnes calcaires à *Paludina aspersa* (a probable equivalent of the Calcaire de Rilly) below (Hébert 1853; Feugueur 1963, p. 334). The Marnes Blanches are capped by Argile à Lignites with brackish molluscs (Hébert 1853). The succession of thick white marls followed by lignitic shelly clays is similar to that documented at Mt Bernon (Laurain *et al.* 1983). The 'conglomérat à *Coryphodon*' has been equated with the Conglomérat de Meudon (Feugueur 1963) as it occurs at the base of a 'Sparnacian' succession.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MONTAGNE DE REIMS
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D7A
D6B
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(NP11)
(Shp)
(SH)
LONDON CLAY FM
OLDHAVEN MBR
SWANSCOMBE MBR
HARWICH MBR
HSB
SPB
III
(AW)
BLACKHEATH BEDS
D5
I
UWSB
LWSB
STRIPED LOAMS
I/II/III
READING MOTTLED CLAY
DIS
HESTER'S BROWN SAND
BOTTOM BED
NP9
NP8
THANET FM
IEPER CLAY
DORMAAL SAND MBR
ERQUEL. SAND MBR
RACOUR SAND MBR
BOIS GILLES FM
S. DE CUISE
NP12
S DE LAON
FAUSSES GLAISES
MP10
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M MARQUÉGLISE
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S DU TILLET
C. DE RILLY
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EDDA
MP6

However, the mammal faunas are distinctly different (as noted above). An alternative interpretation has been offered by Laurain & Meyer (1986, p. 108–110). These authors equated the 'conglomérat à *Coryphodon*' with the Marnes à Rognons, which at various sites overlie Calcaire de Rilly/Marnes de Chenay with an MP6 mammal fauna and *Sphaerochara edda* zone charophytes. The Marnes à Rognons themselves can frequently be shown to belong to the base of the *Peckichara disermas* charophyte zone by the occurrence of *P. microcarpa*, which is restricted to this horizon (sites of Banthelu and Guitrancourt: Riveline 1984). *P. microcarpa* also occurs in the apparently lateral equivalent, the Calcaire de Mortemer. Both the Marnes à Rognons and the Calcaire de Mortemer underlie (depending on the site) either Argile Plastique Bariolée or Argile à Lignites du Soissonnais, both of which contain PE II mammals. It is probable therefore (although unproven) that the Try (PE I) mammals come from the Marnes à Rognons Calcaire de Mortemer level. Discovery of charophytes at Try could provide the necessary tests.

London Basin

At Ferry Cliff the Harwich Member with the Harwich Stone Band (containing the PE III indicator *Pliolophus vulpiceps* at Harwich) directly overlies the Suffolk Pebble Beds with a PE I fauna. However, I have already argued (Hooker 1991) that the latter fauna is reworked on the basis of an associated assemblage of charophytes and bithyniid opercula which otherwise co-occur in a clay lens within a cross-bedded sand unit (the 'brown sand' of Hester 1965, fig. 3) overlying the Bottom Bed at Harefield, Berkshire. The reworking hypothesis is supported by the presence of large clay clasts in the Suffolk Pebble Beds (Hooker 1991) and an abundance of Woolwich Beds pollen (Jolley & Spinner 1991).

Another PE III locality is Abbey Wood. The mammals are in sandy shelly Blackheath Beds that fill channels, or at least valleys, eroded in the underlying Woolwich Beds. Similar but better exposed Blackheath Beds channel fills at Swanscombe, Kent, have a basal pebble bed that is confluent with that at the base of the Oldhaven Member that overlies them. The Blackheath Beds can thus be shown to be younger than the Woolwich Beds, which contain a *disermas* zone charophyte (*Stephanochara curryi*), and slightly older than at least one of the pre-*Wetzeliella* London Clay members (namely the Oldhaven Member) (Costa & Downie 1976; Costa *et al.* 1978, Knox *et al.* 1983). Thus, both the Harwich and Abbey Wood PE III faunas are relatively close in age but apparently much older than Pourcy. The Woolwich Shell Beds also contain the mammal *Coryphodon*, so indicate no greater accuracy than PE I–III.

Belgian Basin

The only accurately datable Belgian Basin mammal faunas are from Dormaal and Erquelinnes (PE I), so no superposition is demonstrable here.

Fig. 3. Correlation scheme for lithostratigraphic units in the London, Belgian and Paris Basins, calibrated to the geomagnetic polarity timescale of Cande & Kent (1992). Magnetostratigraphy has so far only been documented in the London Basin and in the Ieper Clay of the Belgian Basin (Ali *et al.* 1992; Ellison *et al.* 1996) and correlation elsewhere is by means of biostratigraphy alone. Time calibration of London Basin strata within Chron 24r is based largely on Berggren & Aubry (1996). The correlation framework relies heavily on the dinocyst zonation (Costa & Manum 1988; Chateauneuf & Gruas-Cavagnetto 1978; Gruas-Cavagnetto 1968, 1974, 1976; Knox *et al.* 1983; Laurain *et al.* 1983; Powell 1992) backed up by calcareous nannoplankton (NP) (Aubry 1983; De Coninck *et al.* 1981; Siesser *et al.* 1987) and charophytes (Riveline 1984). Mammal zones (PE) and relevant reference levels (MP) are added to this framework, which they support and in the lower part of the sequence help to refine. In particular they support the idea of diachronism of the Argile à Lignites facies (Cavelier 1987). Lateral equivalence of Argile à Lignites du Soissonnais with Argile Plastique Bariolée and Marnes Blanches du Mont Bernon in the Paris Basin is supported by charophytes and mammals and parallels that of the Woolwich Shell Beds and Reading Mottled Clay in the London Basin. However, whereas the tectonically controlled hiatus between the Woolwich Shell Beds and the London Clay in the London Basin is well established, the equivalent hiatus shown in the Paris Basin may alternatively have been partly or completely filled by the Falun Supérieur and/or the Sables d'Auteuil. Although the complete thickness of the London Clay is shown, erosion has reduced its thickness progressively northeastwards until only the lower units are present in the Harwich area. Major unconformities are indicated by a wavy line. Abbreviations: A, Argiles; BB, Blackheath Beds; C, calcaire; HSB, Harwich Stone Band; L, lower; M, Marnes; Mbr, Member; S, Sables; SL, striped loams; SPB, Suffolk Pebble Beds; U, upper; WSB, Woolwich Shell Beds. Charophyte zones: EDDA, *Sphaerochara edda*; DIS, *Peckichara disermas*; (M), range of *P. microcarpa* within DIS; PIV, *P. piveteaui*. Mammal localities: (Av), Avenay; (AW), Abbey Wood; (CB), Condé-en-Brie; (Me), Meudon (Conglomérat de Meudon); (Mu), Mutigny; (Py), Pourcy; (SB), Sézanne-Broyes; (SH), Studd Hill; (Shp), Sheppey; (So), Soissons.

Integrated zonation

Thus, the order of mammal zones indicated by the PAUP analysis fits with the known sequence of dinocyst and charophyte zones. Only two slight anomalies exist. Firstly, PE III appears very long, spanning five dinocyst zones (D5B to D7B). One possible explanation that would be worth investigating is as follows. The absence of a record of zone D7A between D6B and D7B in either the Fausses Glaises or Argile à Lignites d'Epernay (Gruas-Cavagnetto 1976; Gruas-Cavagnetto *et al.* 1980; Laurain *et al.* 1983) might mean a major hiatus in this sequence, which could have allowed reworking of much of the Pourcy fauna from D6B into D7B sediments, thus potentially shortening the timespan of PE III.

Secondly, of two mammal species known from London Clay B at Studd Hill, Herne Bay, one *Platychoerops richardsonii* occurs for the first time in the Paris Basin in MP10, following its possible ancestor, *P. daubrei* in PE III–V. According to the dinocyst zones, this should equate with about the middle of the Argile à Lignites d'Epernay below the level of Pourcy (PE III). There seems a much stronger case for the integrity of the dinocyst zones than for one hypothetical mammalian ancestor–descendant relationship; and it is likely that *P. richardonii* originated earlier in southern England and dispersed to France in MP10 times, where it first occurs at Saint-Agnan (Louis *et al.* 1983). In fact, a degree of endemism in southern England is suggested by the presence of *Hyracotherium leporinum* s.s. at both Studd Hill and higher parts of the London Clay at Sheppey, but not in the Paris Basin (Hooker 1994*b*).

Figure 3 shows correlation of the major lithostratigraphic units of the London, Belgian and Paris Basins in the late Paleocene and early Eocene, based on integration of the dinocyst, charophyte, calcareous nannoplankton and mammal zonations. The dinocysts form the major framework, but the mammals have the potential to improve resolution in the region of zones PE I–II if their stratigraphical relationships can be better established. This could be important as this is a time interval when dinocysts seem less reliable, because of relatively long ranges, and are lacking from the more alkaline sediments where mammals are often best represented. Figure 4 shows calibration of the mammal zones with the other zonations based on this study.

The proposed correlation of PE I faunas across the three basins as discussed above (see Fig. 3) leads to several observations. In the London and Belgian Basins they are associated with cross-bedded fluvial sands (Dormaal Sand and Erquelinnes Sand Members of the Landen Formation and the 'brown sand' of Hester 1965). It implies that there is a large hiatus in the Dormaal and Erquelinnes areas of Belgium between the Landen and Ieper Clay Formations. This gap is probably filled, in part at least, further north in Belgium by the Knokke Member, which is of Woolwich Shell Beds facies (Laga & Vandenberghe 1990).

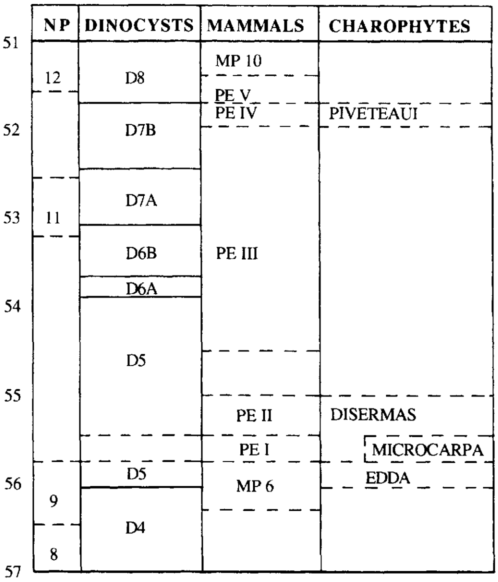

Fig. 4. Calibration of mammal zones with those of dinocysts, calcareous nannoplankton (NP) and charophytes against the timescale as in Fig. 3.

Wider implications

Correlation has long been made between the early Wasatchian of western North America and the 'Sparnacian' (as defined by mammal faunas here distributed between zones PE I–V) of Europe on the basis of many shared mammal genera (e.g. Savage 1971). Very few species, however, have been recognized to be in common [until recently only *Pachyaena gigantea* (Cope); see Boule 1903], which is strange in view of the degree of intercontinental interchange invoked for this period of time.

One reason for this could be a slow diachronous dispersal event, allowing time for speciation. Diachronism has often been invoked for the dispersal event leading to the advent of the earliest Wasatchian or 'Sparnacian' faunas. It has often been claimed that base 'Sparnacian' is significantly earlier than base Wasatchian, overlapping most of the late Paleocene North American Clarkforkian age (e.g. Godinot 1982; Hooker 1980; Rose 1980).

Table 3. *Closely related species in Wasatchian 0 (WaO in the Clarks Fork Basin, Wyoming, North America, and in zone PE I in NW Europe (see Gingerich, 1989, 1993; Hooke 1994*a).

North America	Europe
Cantius torresi	*Cantius eppsi*
Teilhardina brandti	*Teilhardina belgica*
Arfia junnei	*Arfia* cf. *junnei*
Diacodexis ilicis	*Diacodexis* sp. (Dormaal)
'Hyracotherium' sandrae	*Cymbalophus cuniculus*

The discovery of an earlier fauna of Wasatchian type (Wa0) with some species either very similar or identical to ones in Europe reinstated the idea of synchrony of Wasatchian-base 'Sparnacian' (Gingerich 1986, 1989, 1993). In Europe, close relatives of some of these restricted Wa0 species occur in zone PE I (Table 3). However, the extrapolation of the NP9–NP10 boundary from the North American Atlantic coast to the Bighorn Basin, Wyoming, via the first occurrence of *Platycarya* pollen (Wing *et al.* 1991) seemed to favour once again the diachronism idea. This is because this datum in the Bighorn Basin lies just below the base of Wa0, whereas the NP9–NP10 boundary of the North Sea Basin, as extrapolated from the Atlantic via the −17 ash, lies at the base of the London Clay Formation (Knox 1990) approximately coincident with the PE II–III boundary.

A hopefully independent source of correlation comes from carbon isotope stratigraphy. The brief strong negative excursion documented in the deep sea by Kennett & Stott (1991) has been recognized from tooth enamel and soil carbonate at the Clarkforkian–Wasatchian boundary in the Bighorn Basin (Koch *et al.* 1992). A similar excursion has been recognized in a sandy calcrete (Marne à Rognons) at the base of the main Argile Plastique Bariolée sequence at Limay in the Paris Basin (Sinha & Stott 1994; Stott *et al.* 1996; Thiry 1981, pp. 19–21, pers. comm.). Three kilometres away at Guitrancourt, the Marne à Rognons contains *Peckichara microcarpa* (Thiry 1981, p. 23; Riveline 1984, pp. 101–102), thus providing a tentative link between the carbon isotope excursion and mammal zone PE I and supporting essential synchroneity of the mammal dispersal event in North America and Europe. The short-lived nature of the warming event deduced from the excursion could have allowed the rapid northward expansion of mammalian ranges, normally invoked to allow the intercontinental exchange via Greenland. It could equally rapidly have caused their contraction when temperatures cooled again a few thousand years later, resulting in isolation and rapid speciation in the respective continents.

The MP6 mammal faunas occur in the Marnes de Chenay at Montchenot (Louis in Laurain & Meyer 1986, p. 117) and in the underlying Sables de Rilly (including the Conglomérat de Cernay) at Cernay and Berru (Russell 1964). The Sables de Rilly at Montchenot are recorded as containing *Apectodinium homomorphum* and *A. parvum* (Gruas-Cavagnetto 1974, p. 5). The first occurrence of *A. parvum* is associated with D5A (Aau) (Powell 1992, pp. 169, 177) and in the London Basin (Powell *et al.* 1996) the Bottom Bed, thus within the lower part of NP9. As the bases of both NP9 (Aubry 1985) and the Clarkforkian (Butler *et al.* 1987) occur within Chron 25N, MP6 must be coeval with a part of the Clarkforkian.

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References

ALI, J. R., KING, C. & HAILWOOD, E. A. 1992. Magnetostratigraphic calibration of early Eocene depositional sequences in the southern North Sea Basin. *In*: HAILWOOD, E. A. & KIDD, R. B. (eds) *High Resolution Stratigraphy*. Geological Society, London, Special Publication, **70**, 99–125.

ALROY, J. 1992. Conjunction among taxonomic distributions and the Miocene mammalian biochronology of the Great Plains. *Paleobiology*, **18**, 326–343.

AUBRY, M.-P. 1983. Biostratigraphie du Paléogène épicontinental de l'Europe du nord-ouest. Etude fondée sur les nannofossiles calcaires. *Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, **89**, 1–317.

—— 1985. Northwestern European Paleogene magnetostratigraphy, biostratigraphy, and paleogeography: calcareous nannofossil evidence. *Geology*, **13**, 198–202.

BAUDRY, M. 1992. Les tillodontes (Mammalia) de l'Eocène inférieur de France. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, (C4)**14**, 205–243.

BERGGREN, W. A. & AUBRY, M.-P. 1996. A late Paleocene–early Eocene NW European and North Sea magnetobiochronological correlation network: a sequence stratigraphic approach. *This volume.*

BIGNOT, G., GRUAS-CAVAGNETTO, C., GUERNET, C., PERREAU, M., RENARD, M., RIVELINE, J. & TOURENQ, J. 1981. Le Sparnacien de Soissons (Aisne, France): étude sédimentologique et paléontologique. *Bulletin d'Information des Géologues du Bassin de Paris,* **18**(4), 3–19.

BOULE, M. 1903. Le *Pachyaena* de Vaugirard. *Mémoires de la Société Géologique de France,* **10**(4), 1–16.

BRUNET, M., FRANZEN, J. L., GODINOT, M., HOOKER, J. J., LEGENDRE, S., SCHMIDT-KITTLER, N. & VIANEY-LIAUD, M. (coordinators) 1987. European reference levels and correlation tables. *Münchner Geowissenschaftlicher Abhandlungen,* (A)**10**, 13–31.

BUTLER, R. F., KRAUSE, D. W. & GINGERICH, P. D. 1987. Magnetic polarity stratigraphy and biostratigraphy of Middle–Late Paleocene continental deposits of south-central Montana. *Journal of Geology,* **95**, 647–657.

CANDE, S. C. & KENT, D. V. 1992. A new geomagnetic polarity timescale for the late Cretaceous and Cenozoic. *Journal of Geophysical Research,* **97**(B10), 13 917–13 953.

CAVELIER, C. 1987. Diachronisme des faciès et discontinuités dans le Paléogène. Exemple du Thanétien et de l'Yprésien en Ile-de-France. Essai de généralisations et corrélations dans les bassins anglais, belge et parisien. *Bulletin d'Information des Géologues du Bassin de Paris, Mémoire Hors Série,* **6**, 243–270.

CHATEAUNEUF, J.-J. & GRUAS-CAVAGNETTO, C. 1978. Les zones de Wetzeliellaceae (Dinophyceae) du bassin de Paris. *Bulletin du Bureau de Recherches Géologiques et Minières,* (2)**4**(2), 59–93.

COSTA, L. I. & DOWNIE, C. 1976. The distribution of the dinoflagellate *Wetzeliella* in the Palaeogene of north-western Europe. *Palaeontology,* **19**, 59–64.

—— & MANUM, S.B. 1988. The description of the interregional zonation of the Paleogene (D1–D15) and the Miocene (D16–D20). *In*: VINKEN, R., VON DANIELS, C. H., GRAMANN, F., KOTHE, A., KNOX, R. W. O'B., KOCKEL, F., MEYER, K.-J. & WEISS, W. (eds) *The Northwest European Tertiary Basin. Results of the IGCP Project No 124.* Geologisches Jahrbuch, (A)**100**, 321–330.

——, DENISON, C. & DOWNIE, C. 1978. The Palaeocene/Eocene boundary in the Anglo–Paris Basin. *Journal of the Geological Society, London,* **135**, 261–264.

DASHZEVEG, D. 1988. Holarctic correlation of non-marine Palaeocene–Eocene boundary strata using mammals. *Journal of the Geological Society, London,* **145**, 473–478.

DE CONINCK, J., DE DECKER, M., DE HEINZELIN, J. & WILLEMS, W. 1981. L'age des faunes d'Erquelinnes. *Bulletin de la Société Belge de Géologie,* **90**, 121–154.

DE LAPPARENT, A. F. 1939. Une coupe du Sparnacien à Soissons (Aisne). *Annales de la Société géologique du Nord,* **64**, 7–18.

DEPÉRET, C. 1906. Relations stratigraphiques des faunes de Cernay et de Meudon au mont de Berru. *Bulletin de la Société Géologique de France,* (4)**6**, 442–443.

ELLISON, R. A., ALI, J. R., HINE, N. M. & JOLLEY, D. W. 1996. Recognition of Chron 25n in the upper Paleocene Upnor Formation of the London Basin, UK. *This volume.*

FEUGUEUR, L. 1963. *L'Yprésien du Bassin de Paris. Essai de monographie stratigraphique.* Mémoire du Service de la Carte Géologique de France, Paris, 1–568.

GHEERBRANT, E. 1991. *Bustylus* (Eutheria, Adapisoriculidae) and the absence of ascertained marsupials in the Palaeocene of Europe. *Terra Nova,* **3**, 586–592.

GINGERICH, P .D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *Papers on Paleontology, Museum of Paleontology, University of Michigan,* **15**, 1–145.

—— 1986. Early Eocene *Cantius torresi* – oldest primate of modern aspect from North America. *Nature,* **320**, 319–321.

—— 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. *Papers on Paleontology, Museum of Paleontology, University of Michigan,* **28**, 1–97.

—— 1993. Early Eocene *Teilhardina brandti*: oldest omomyid primate from North America. *Contributions from the Museum of Paleontology, University of Michigan,* **28**, 321–326.

——, ROSE, K. D. & KRAUSE, D. W. 1980. Early Cenozoic mammalian faunas of the Clark's Fork Basin-Polecat Bench area, northwestern Wyoming. *Papers on Paleontology, Museum of Paleontology, University of Michigan,* **24**, 51–68.

GODINOT, M. 1982. Aspects nouveaux des échanges entre les faunes mammaliennes d'Europe et d'Amérique du Nord à la base de l'Eocène. *Géobios, Mémoire Spécial,* **6**, 403–412.

GRAMBAST, L. 1977. Etude sur les charophytes tertiaires d'Europe occidentale. II Espèces nouvelles de l'Eocène inférieur. *Paléobiologie Continentale,* **12**(2), 1–35.

GRUAS-CAVAGNETTO, C. 1968. Etude palynologique des divers gisements du Sparnacien du Bassin de Paris. *Mémoires de la Société Géologique de France,* **110**, 1–114.

—— 1974. Associations sporopolliniques et microplanctoniques de l'Eocène et de l'Oligocène inférieur du Bassin de Paris. *Paléobiologie Continentale,* **5**(2), 1–20.

—— 1976. Etude palynologique du sondage de la Défense (Paris). *Revue de Micropaléontologie,* **19**, 27–46.

—— , LAURAIN, M. & MEYER, R. 1980. Paysage végétal et position stratigraphique du sommet des Lignites du Soissonnais dans la Montagne de Reims (Yprésien, Bassin de Paris). *Géobios,* **13**, 947–952.

GUERNET, C. 1981. Ostracodes sparnaciens du Bassin de

Paris (France). *Revue de Micropaléontologie*, **24**, 51-56.

GUNNELL, G. F. & GINGERICH, P. D. 1991. Systematics and evolution of late Paleocene and early Eocene Oxyaenidae (Mammalia, Creodonta) in the Clarks Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, University of Michigan*, **28**, 141–180.

HÉBERT, E. 1853. Note sur l'age des sables blancs et des marnes à *Physa gigantea* de Rilly, en réponse à la communication faite par M. Prestwich, dans la séance du 21 février 1853. *Bulletin de la Société Géologique de France*, (2)**10**, 436–454.

HEDBERG, H. D. 1976. *International Stratigraphic Guide*. John Wiley & Sons, New York.

HESTER, S. W. 1965. Stratigraphy and palaeogeography of the Woolwich and Reading Beds. *Bulletin of the Geological Survey of Great Britain*, **23**, 117–137.

HOOKER, J. J. 1980.The succession of *Hyracotherium* (Perissodactyla, Mammalia) in the English early Eocene. *Bulletin of the British Museum (Natural History)* (Geology), **33**, 101–114.

—— 1991. The sequence of mammals in the Thanetian and Ypresian of the London and Belgian Basins. Location of the Palaeocene-Eocene boundary. *Newsletters on Stratigraphy*, **25**, 75–90.

—— 1994*a*. A new species of *Platychoerops* (Plesiadapiformes, Mammalia), from the latest Palaeocene of the Paris, London and Belgian Basins. *Géobios*, **27**, 343–352.

—— 1994*b*. The beginning of the equoid radiation. *Zoological Journal of the Linnean Society*, **112**, 29–63.

JOLLEY, D. W. 1996. The earliest Eocene sediments of eastern England: an ultra-high resolution palynological correlation. *This volume*.

—— & SPINNER, E. 1991. Spore-pollen associations from the lower London Clay (Eocene), East Anglia, England. *Tertiary Research*, **13**, 11–25.

KENNETT, J. P. & STOTT, L. D. 1991. Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature*, **353**, 225–229.

KNOX, R. W. O'B. 1990. Thanetian and early Ypresian chronostratigraphy in south-east England. *Tertiary Research*, **11**, 57–64.

——, HARLAND, R. & KING, C. 1983. Dinoflagellate cyst analysis of the basal London Clay of southern England. *Newsletters on Stratigraphy*, **12**, 71–74.

KOCH, P. L., ZACHOS, J. C. & GINGERICH, P. D. 1992. Correlation between isotope records in marine and continental carbon reservoirs near the Palaeocene/Eocene boundary. *Nature*, **358**, 319–322.

KRAUSE, D. W. & MAAS, M. C. 1990. The biogeographic origins of late Paleocene–early Eocene mammalian immigrants to the Western Interior of North America. *Geological Society of America Special Paper*, **243**, 71–105.

LAGA, P. & VANDENBERGHE, N. (eds) 1990. The Knokke well (11E/138) with a description of the Den Haan (22W/276) and Oostduinkerke (35E/142) wells. *Mémoires pour servir à l'Explication des Cartes Géologiques et Minières de la Belgique*, **29**, 1–118.

LAMBSHEAD, P. J. D. & PATERSON, G. L. J. 1986. Ecological cladistics – an investigation of numerical cladistics as a method for analysing ecological data. *Journal of Natural History*, **20**, 895–909.

LAURAIN, M. & BARTA, L. 1985. Journées d'étude 13–14 Octobre 1984, Paléogène de la Montagne de Reims et de la Montagne d'Avize. *Bulletin d'Information des Géologues du Bassin de Paris*, **22**(1), 17–45.

—— & MEYER, R. 1986. Stratigraphie et paléogéographie de la base du Paléogène champenois. *Géologie de la France*, **1986**, 103–123.

——, BARTA, L., BOLIN, C., *ET AL*. 1983. Le sondage et la coupe du Mont Bernon à Epernay (Marne). Etude sédimentologique et paléontologique du stratotype du Sparnacien et de la série éocène. *Géologie de la France*, **3**, 235–254.

LOUIS, P., LAURAIN, M., BOLIN, C. & BARTA, L. 1983. Nouveau gisement de vertébrés dans le Cuisien supérieur de Saint-Agnan (Aisne) ses relations stratigraphiques avec les autres gisements yprésiens du Bassin parisien. *Bulletin d'Information des Géologues du Bassin de Paris*, **20**(4), 3–20.

MCKENNA, M. C. 1983. Cenozoic paleogeography of north Atlantic land bridges. *In*: BOTT, M. H. P., SAXOV, S., TALWANI, M. & THIEDE, J. (eds) *Structure and Development of the Greenland-Scotland Ridge*. Plenum Press, New York, 351–399.

MARANDAT, B. 1987. La biostratigraphie mammalienne de l'Eocène continental du versant sud de la Montagne Noire. Reconsidération d'après les nouvelles données. *Münchner Geowissenschaftlicher Abhandlungen*, (A)**10**, 149–158.

MICHAUX, J. 1964. Age des Sables à Unios et Térédines (Eocène inférieur) d'Avenay (Marne) et leurs relations avec les sables du meme nom des gisements classiques d'Epernay. *Comptes Rendus Sommaires des Séances de la Société Géologique de France*, **1964**, 103.

POMEROL, C. (ed.) 1981. Stratotypes of Paleogene stages. *Bulletin d'Information des Géologues du Bassin de Paris, Mémoire Hors Série*, **2**, 3–301.

POWELL, A. J. 1992. Dinoflagellate cysts of the Tertiary System. *In*: POWELL, A. J. (ed.) *A Stratigraphic Index of Dinoflagellate Cysts*. Chapman & Hall, London, 155–229.

——, BRINKHUIS, H. & BUJAK, J. P. 1996. Upper Paleocene – Lower Eocene dinoflagellate cyst sequence biostratigraphy southeast England. *This volume*.

RIVELINE, J. 1984. Les gisements à charophytes du Cénozoique (Danien à Burdigalien) d'Europe occidentale: lithostratigraphie, biostratigraphie, chronostratigraphie. *Bulletin d'Information des Géologues du Bassin de Paris, Memoire Hors Série*, **4**, 1–523.

ROSE, K. D. 1980. Clarkforkian Land-Mammal Age: revised definition, zonation, and tentative intercontinental correlations. *Science*, **208**, 744–746.

—— 1981. The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene–Eocene boundary. *Papers on Paleontology, Museum of Paleontology, University of Michigan*, **26**, 1–197.

RUSSELL, D. E. 1964. Les mammifères paléocènes d'Europe. *Mémoires du Muséum National d'Histoire Naturelle, Paris*, (C)**13**, 1–321.

—— 1975. Paleoecology of the Paleocene–Eocene transition in Europe. *Contributions to Primatology*, **5**, 28–61.

——, Galoyer, A., Louis, P. & Gingerich, P. D. 1988. Nouveaux vertébrés sparnaciens du Conglomérat de Meudon à Meudon, France. *Comptes Rendus Hébdomadaires des Séances de l'Académie des Sciences, Paris*, (II)**307**, 429–433.

—— & 32 others. 1982*a*. Tetrapods of the Northwest European Tertiary Basin. *Geologisches Jahrbuch*, (A)**60**, 5–74.

——, Hartenberger, J.-L., Pomerol, C., Sen, S., Schmidt-Kittler, N. & Vianey-Liaud, M. 1982*b*. Mammals and stratigraphy. *Palaeovertebrata, Mémoire Extraordinaire*, 1–77.

Savage, D. E. 1971. The Sparnacian–Wasatchian mammalian fauna, Early Eocene, of Europe and North America. *Abhandlungen des Hessischen Landesamtes für Bodenforschung*, **60**, 154–158.

Schankler, D. M. 1980. Faunal zonation of the Willwood Formation in the central Bighorn Basin, Wyoming. *Papers on Paleontology, Museum of Paleontology, University of Michigan*, **24**, 99–114.

Siesser, W. G., Ward, D. J. & Lord, A. R. 1987. Calcareous nannoplankton biozonation of the Thanetian Stage (Palaeocene) in the type area. *Journal of Micropalaeontology*, **6**, 85–102.

Sinha, A. & Stott, L. D. 1994. New atmospheric $p\mathrm{CO}_2$ estimates from paleosols during the late Paleocene/early Eocene global warming interval. *Global and Planetary Change*, **9**, 297–307.

Stott, L. D., Sinha, A., Thiry, M., Aubry, M.-P. & Berggren, W.A. 1996. Global δ^{13}C changes across the Paleocene–Eocene boundary: criteria for terrestrial–marine correlations. *This volume.*

Swofford, D. L. 1990. *PAUP, Phylogenetic Analysis Using Parsimony, Version 3.0.* User's manual, Illinois Natural History Survey, Champaign.

Thaler, L. 1966. Les rongeurs du Bas-Languedoc dans leurs rapports avec l'histoire du Tertiaire d'Europe. *Mémoires du Muséum National d'Histoire Naturelle, Paris*, (C)**17**, 1–296.

Thiry, M. 1981. Sédimentation continentale et altérations associées: calcitisations, ferruginisations et silicifications. Les Argiles Plastiques du Sparnacien du Bassin de Paris. *Sciences Géologiques*, **64**, 1–173.

Whitaker, W. 1885. *The Geology of the Country around Ipswich, Hadleigh, and Felixstow.* Memoir of the Geological Survey of England and Wales, 1–156.

Wing, S. L., Bown, T .M. & Obradovich, J. D. 1991. Early Eocene biotic and climatic change in interior western North America. *Geology*, **19**, 1189–1192.