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Evolution of European carnivorous mammal assemblages through the Paleogene

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ABSTRACT

The rise of Carnivora (Mammalia, Laurasiatheria) is an important evolutionary event that changed the structure of terrestrial ecosystems, starting at the dawn of the Eocene, 56 million years ago. This radiation has been mainly analysed in North America, leaving the evolution of carnivoran diversity in other regions of the globe poorly known. To tackle this issue, we review the evolution of terrestrial carnivorous mammal diversity (Mesonychidae, Oxyaenidae, Hyaenodonta, and Carnivoramorpha) in Europe. We reveal four episodes of intense faunal turnovers that helped establish the dominance of carnivoramorphans over their main competitors. We also identify two periods of general endemism. The remaining time intervals

are characterized by dispersals of new taxa from North America, Asia, and Africa. The European Paleogene carnivorous mammal fauna appears to have been almost constantly in a transient state, strongly influenced by dispersals. Many of the bioevents we highlight for European carnivorous mammals are probably best seen as ecosystem-wide responses to environmental changes. In contrast to the North American record, European hyaenodonts remain more diverse than the carnivoramorphans for the entire Eocene. The replacement of hyaenodonts by carnivoramorphans as the most diverse and dominant predators only occurred after the ‘Grande Coupure’ at 33 Ma, about 16 Myr later than in North America.

KEY WORDS

Paleogene, Predators, Taxonomic diversity, Carnivora, Hyaenodonta

INTRODUCTION

The fossil record reveals several cases of inferred ecological competition between mammal clades over long timescales (Janis *et al.*, 1994; Meng & McKenna, 1998; Maas *et al.*, 1998; Van Valkenburgh, 1999; Prufrock *et al.*, 2016). An iconic example is the evolution of terrestrial carnivorous mammals during the Paleogene (66-23 Ma), which involves the Carnivoramorpha (the clade that includes the modern order Carnivora) and the extinct clades Hyaenodonta, Mesonychia and Oxyaenidae (Savage, 1977; Radinsky, 1982; Van Valkenburgh, 1999; Friscia & Van Valkenburgh, 2010). These clades independently evolved a series of guild-defining dental and locomotor adaptations (Muizon & Lange-Badré, 1997; Rose, 2006), most notably carnassial teeth: a labio-lingually compressed, bladelike morphology that cuts through skin, muscles, and tendons by generating intense shearing forces (Savage, 1977; Flynn & Wesley-Hunt, 2005; Rose, 2006; Solé & Ladevèze, 2017). Mesonychia did not possess carnassial teeth, but are regarded as carnivorous (Szalay & Gould, 1966; Rose, 2006). All these clades were sympatric in many ecosystems during the Paleogene in North America, Asia, and Europe (Savage, 1977; Flynn & Wesley-Hunt, 2005; Rose, 2006). It has thus been proposed that they were competitors (Van Valkenburg, 1999; Morlo & Nagel, 2007; Friscia & Van Valkenburgh, 2010; Morlo *et al.*, 2010). However, only carnivoran carnivoramorphan would eventually prevail and give rise to a myriad of forms including cats, dogs, raccoons, bears, and seals, for a total of more than 281 species extant (Wilson & Mittermeier, 2009).

How carnivoramorphan radiated and eventually outcompeted hyaenodonts, oxyaenids, and mesonychids on a global scale is unclear, as few studies have focused on this question beyond North America. Since the 1990's, the success of the carnivorans in North America has been investigated in extraordinary detail, showing that carnivorans outcompeted hyaenodonts and oxyaenids during the Eocene, beginning around 50 Ma (late Ypresian), when carnivorans became the most diverse clade of carnivorous mammals (Van Valkenburgh, 1999, 2007; Flynn & Wesley-Hunt, 2005; Friscia & Van Valkenburgh, 2010). Friscia & Van Valkenburgh (2010) hypothesized that the pattern in Europe, Asia, and Africa would be similar to that of North America. This hypothesis is supported by the numerous carnivorous mammal taxa shared between Europe and North America following the Mammal Dispersal Event (MDE; Hooker, 1996, 1998, 2015; Smith & Smith, 2001, 2010; Solé *et al.*, 2011, 2013a, 2013b, 2014a), but it remains to be tested in Europe.

The evolution of the carnivorous mammals in Africa has been recently studied by Borths & Stevens (2017c) and Friscia *et al.* (2020). Throughout the Paleogene, most terrestrial carnivore niches in Afro-Arabia were occupied by hyaenodonts, but in the Neogene carnivorans seem to have displaced hyaenodonts after their dispersals into Africa, pushing hyaenodonts into more specialized forms, in terms of both body size and carnivory (Borths & Stevens, 2017c; Friscia *et al.*, 2020). The transition from a hyaenodont fauna to a carnivoran fauna coincides with other ecological changes in Afro-Arabia as tectonic conditions in the African Rift System altered climatic conditions and facilitated faunal exchange with Eurasia (Borths & Stevens, 2017c). This transition occurred around the Paleogene–Neogene boundary (ca. 23 Ma), so later than in North America (27 Ma) and Europe (11 Ma).

To address the success of the carnivorans in Europe, we analyse the taxonomic evolution of carnivorous mammals during the Paleogene of Europe and compare it to: (1) the faunal and

climatic events affecting European ecosystems during the Paleogene; and (2) the evolution of taxonomic diversity of carnivorous mammals in North America in order to evaluate the hypothesis of Friscia & Van Valkenburgh (2010).

MATERIAL AND METHODS

DEFINITION OF SUPRAGENERIC CLADES

Hyaenodontidae and Oxyaenidae were previously grouped within ‘Creodonta’, but several studies suggest that these two groups are ecomorphologically convergent rather than closely phylogenetically related (Polly, 1994; Rose, 2006; Morlo *et al.*, 2009). The use of the clade Hyaenodonta (order level) rather than Hyaenodontidae (family level) has thus been proposed (Solé, 2013) and this approach is followed here. This notably differs from Friscia & Van Valkenburgh (2010) who still use ‘Creodonta’ as a clade.

The subfamily Proviverrinae has been redefined as an endemic European clade of hyaenodonts that evolved in relative isolation (Solé, 2013; Solé *et al.*, 2014a). However, some recent phylogenetic analyses recovered Proviverrinae as paraphyletic (Borths *et al.* 2016; Borths & Seiffert, 2017; Borths & Stevens, 2017a,b,c). Some phylogenetic analyses recovered some proviverrine taxa as early diverging taxa among Hyaenodonta and proposed to name Hyaenodontoidea for the clade that includes the last common ancestor of Proviverrinae and Hyaenodontinae (Solé & Mennecart, 2019; Solé *et al.*, 2019a). Throughout this paper, the term “endemic hyaenodontoid” is used to focus on the early hyaenodontoids autochthonous to Europe, prior to the arrival of *Hyaenodon*. The subfamilies ‘Sinopinae’ and ‘Arfiinae’ are possibly paraphyletic (Borths *et al.*, 2016) but will be retained here for practical reasons.

Carnivoramorpha includes Carnivora and its closest relatives (i.e., Viverravidae and ‘Miacidae’) (Wyss & Flynn, 1993). Carnivoraformes also includes Carnivora and its closest relatives (i.e., ‘Miacidae’) but excludes Viverravidae (Flynn *et al.*, 2010). The term ‘early carnivoraform’ replaces the term ‘miacid’ herein.

TAXONOMIC SAMPLING, TEMPORAL DATA, AND PERCENTAGE OF RENEWAL

Our dataset incorporates all carnivoramorphans, hyaenodonts, viverravids, and oxyaenids from the Paleogene of Europe that have been found in a locality that can be assigned to an MP (Mammal Paleogene) reference level of the mammalian biochronological scale for the European Paleogene (Schmidt-Kittler *et al.*, 1987; BiochroM’97, 1997) and that are determinable at the species level. Our dataset has been built based on the literature; we focused on the most recent studies and did not question the taxonomy of the carnivorous mammals. The core of the dataset is the record from the Quercy Phosphorites Formation in France, which provided numerous upper Eocene and Oligocene fossiliferous localities (e.g., Escarguel & Legendre, 2006). Our sampled localities are also largely drawn from Western Europe, notably from France, Germany, Belgium, Spain, Switzerland, and England. We treated cf. and aff. species designations as a valid occurrence of a species if this species is already recorded in this MP/locality. Finally, we used Lazarus ranges to populate our time bins and reduce the influence of sampling biases: even if not recorded, a species was thus regarded as present within an MP if both older and younger occurrences of that species exist in Europe.

The dataset comprises 167 species representing 86 genera. The Supplementary Table 1 provides the stratigraphic distribution of carnivorous mammal genera and species recorded in Europe. Based on these data, we reconstructed the evolution of taxonomic diversity through time at the species and genus levels (species level: Figs. 1-2; genus level: Supplementary Figure 1; Supplementary Table 2). We derived the First Appearance Datum (FAD) and Last Appearance Datum (LAD) for all taxa at the species level through time (Supplementary Table 3, Supplementary Text 1, and Supplementary Figure 2); we also established the evolution through time of taxic renewal (as a percentage) based on these data (see Supplementary Table 4, Supplementary Text 2, and Supplementary Figure 3).

Each MP reference level from MP6 (late Thanetian, ca. 57 Ma) to MP30 (latest Chattian, ca. 23 Ma) was defined as an independent time point. It should be noted that MPs mainly represent roughly contemporaneous faunal assemblages rather than precise bio- and chronostratigraphic units. Each MP reference level is defined by the whole fauna of a reference locality (Schmidt-Kittler *et al.*, 1987; BiochroM'97, 1997, p.770). MP8 and MP9 are provisionally grouped together due to insufficient information on the mammal faunas between MP7 and MP10 (Schmidt-Kittler *et al.*, 1987, p. 16, 21; BiochroM'97, 1997, p. 774). MP15 has a questionable definition as it likely represents a reworked deposit (Comte *et al.*, 2012). Our sampling of carnivorous mammals at this MP level is null and is thus uninformative. The trends seen between MP14 and MP16 must be considered cautiously. Following BiochroM'97 (1997), MP17 is divided in MP17a and MP17b. For the absolute ages of the Paleogene stages and estimated ages of the MP levels, we used the Paleogene dates compiled by Speijer *et al.* (2020) and plotted our data by using Time Scale Creator version 7.4 (TSCreator, 2020).

We performed simple linear regressions accompanied by a t-test and a F-test between the number of taxa (including Lazarus ranges), the number of localities, and the estimated MP ages with the 'lm' functions in the *stats* package in the R statistical environment (R Core Team, 2019). These methods were used to assess the importance of sampling biases in our dataset. We found no significant correlation between the number of taxa and the estimated MP ages, but there is a weak but significant correlation between the number of taxa and the number of localities: $R^2 < 0.31$; $p\text{-value} < 0.004$ (see also Supplementary Table 5 and Supplementary Figure 4).

POLY-COHORT ANALYSES

The individual poly-cohort analysis, or survivorship poly-cohorts, helps investigations of taxon survivorship over a given time span (Escarguel & Legendre 2006; Scherler *et al.*, 2013; Mennecart, 2015) by visualizing origination/immigration and extinction/emigration proportions. We used the 'nested' analyses, in which the survivorship curves illustrate the percentage of taxa present between an initial taxonomical assemblage and the last appearance of the assemblage's last representative (Scherler *et al.*, 2013). These curves show the progressive disappearance of the original assemblage as its constituent taxa go extinct (Escarguel & Legendre 2006; Scherler *et al.*, 2013). We conducted the poly-cohort analyses at the genus and species levels on Paleogene carnivore taxa (Supplementary Table 6).

DICE SIMILARITY

We performed cluster analysis based on the Dice similarity indices using the PAST software (Hammer *et al.* 2001) in order to define the consistency of our palaeocommunities through time. Our method is based on Scherler *et al.* (2013). The Dice index for the presence/absence of data puts more weight on joint occurrences than on mismatches. When comparing two columns (or associations), a match is counted for all taxa present in both columns. The Dice index is expressed as $2M/(2M + N)$, where M is the number of matches and N the total number of taxa present in only one column. We constructed the clusters for the Dice similarity index using two methods: (1) with an unweighted pair-group method with arithmetic mean (UPGMA), the clusters are joined based on the average distance between all members of both groups, and (2) with the Single Linkage or Nearest Neighbour method (SINGL), the clusters are joined based on the smallest distance between both groups (Hammer *et al.*, 2001).

RESULTS

EVOLUTION OF TAXONOMIC RICHNESS

The species richness of European carnivorous mammal faunas generally increased through the Paleogene (Fig. 1A). However, this increase was not constant, and the diversity of carnivorous mammals fluctuated widely during the interval. There were few species of carnivorous mammals during the Thanetian (MP6), with only carnivoraforms and mesonychids recorded in Europe. The species richness of carnivorous mammal faunas boomed in the earliest Ypresian. The oldest hyaenodont and oxyaenid species are known from MP7, and are joined by new carnivoraform and mesonychid species. Diversity continued to increase with the appearance of one viverravid, and new mesonychids and oxyaenids in MP8+9. In summary, numerous clades were present in Europe during the early to middle Ypresian (MP7-MP8+9): Mesonychidae, Oxyaenidae, Hyaenodonta, and Carnivoramorpha.

Diversity slightly decreased at the end of the Ypresian partly because of the disappearance from Europe of the viverravids, oxyaenids, ‘sinopine’ hyaenodonts (last occurrence at MP8+9), and mesonychids (last record at MP10) (Fig. 1B-C). As a consequence of these disappearances, only endemic hyaenodontoids and early carnivoraforms persisted into the Lutetian of Europe. Thus, carnivoraforms decreased in diversity during the Ypresian and Lutetian. In contrast, endemic hyaenodontoids diversified during the Ypresian and at MP13-MP14. Hyaenodonts were thus more speciose than carnivoramorphans during the Lutetian (Fig. 1B).

The MP16 (Bartonian) records a modest increase in species diversity relative to MP14 (Fig. 1A). Subsequently, diversity remained stable during most of the Priabonian (MP17a-MP19). Some new groups appeared in Europe at that time: hyainailourines (Hyaenodonta) are first recorded at MP16, hyaenodontines (Hyaenodonta) at MP17a (Fig. 1C), and amphicyonids (Caniformia) at MP18 (Fig. 2B). Hyaenodonts remained more diverse during this period than the carnivoraforms (Fig. 1B).

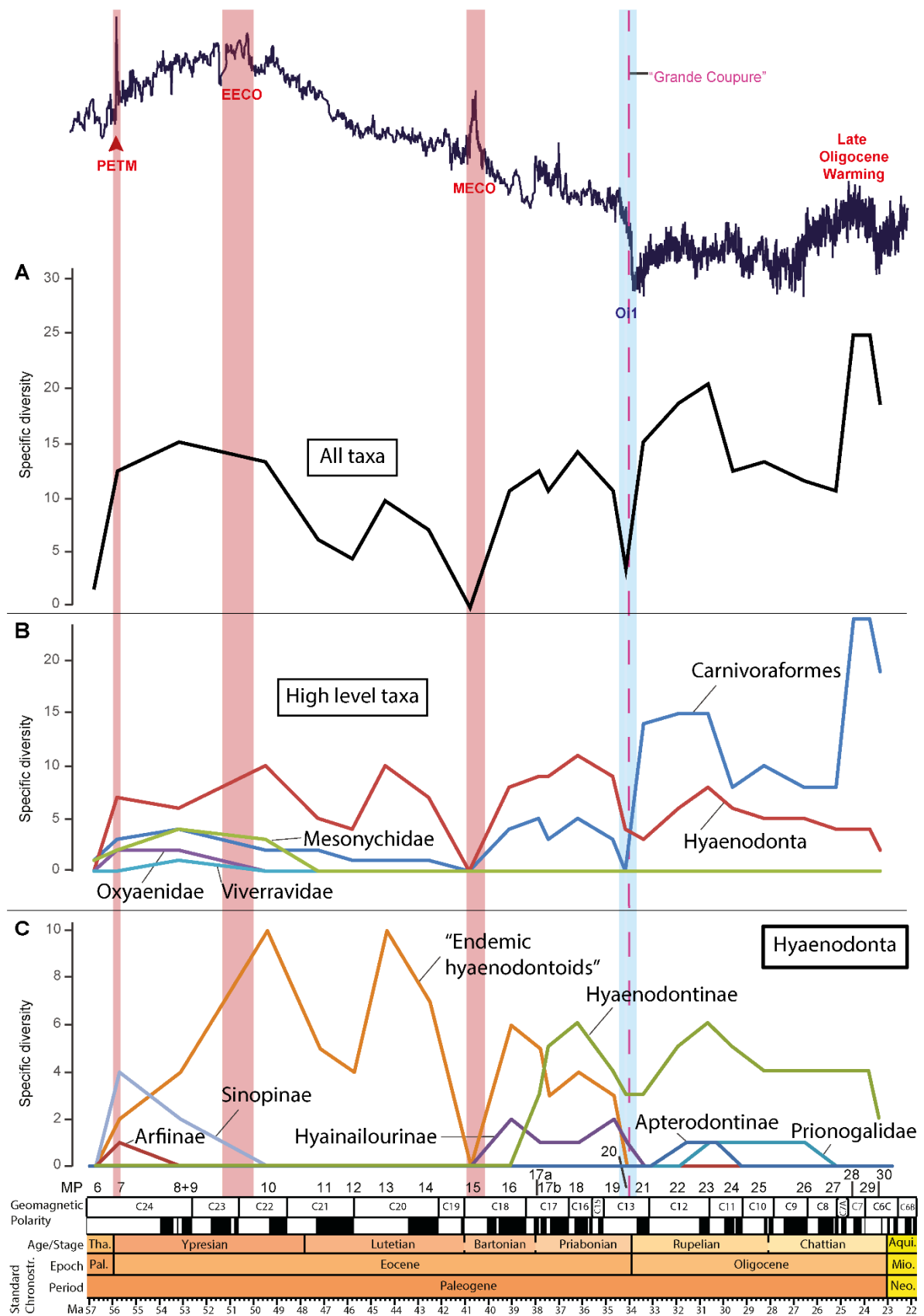


Figure 1. Evolution of specific diversity of carnivorous mammals during the Paleogene in Europe. A. All taxa. B, Higher level taxa: Mesonychidae, Oxyaenidae, Hyaenodonta, Carnivoraformes, Viverravidae. C, Hyaenodonta: Apterodontinae, Arfiinae, Hyaenodontinae,

Hyainailourinae, Prionogalidae, “Endemic hyaenodontoids”, Sinopinae. Orange bars: most notable Eocene climatic warming phases; blue bar: climatic cooling at the onset of the Oligocene. Abbreviations: EECO, Early Eocene Climatic Optimum; PETM, Paleocene-Eocene Thermal Maximum; MECO, Middle Eocene Climatic Optimum; Oi-1, Oligocene Oi-1 event.

Total taxonomic richness strongly decreased just before the end of the Eocene (MP20) and bounced back in the earliest Oligocene (MP21) (Fig. 1A). More importantly, the ratio between the hyaenodonts and carnivoramorphs reversed (Fig. 1B). Hyaenodonts were more numerous than carnivoramorphans during the entire Eocene. This situation inverted at the onset of the Oligocene after the ‘Grande Coupure’ (Fig. 1B). Moreover, during the Eocene, hyaenodonts were mainly represented by endemic hyaenodontoids, but by the Oligocene most hyaenodonts belong to Hyaenodontinae (Fig. 1C).

During the Oligocene (MP21-MP30), hyaenodonts remain relatively limited in their diversity. Their highest diversity is reached at MP23 with the presence of the enigmatic hyaenodontid *Thereutherium* (Prionogalidae) and two hyaenodont subfamilies: Apterodontinae and Hyaenodontinae (Fig. 1B-C). Caniformia represented the most diverse clade of carnivorans at MP21 (Fig. 2A), partially due to the abundance of Ursidae (Fig. 2B). However, at MP22 the feliformians became the most diverse group, a trend that lasts until the end of the Rupelian (MP25) (Fig. 2A). The ratio between feliformians and caniformians changes once again during the early Chattian at MP26. This change is related to the disappearance of the Nimravidae (Fig. 2C). The diversity of Caniformia is further increased in the late Chattian by the high number of ursid and amphicyonids species (MP28-30) (Fig. 2A-B).

POLY-COHORT ANALYSIS

Only one of the two carnivorous genera recorded at MP6 (late Thanetian) persisted until MP10 (late Ypresian). MP7 shows an almost complete faunal turnover, and this assemblage survived only until the middle Ypresian (MP8+9). Some genera – but none of the species – of MP8+9 and MP10 faunas persisted until the end of the Eocene (Fig. 3). The Lutetian faunas (MP11-MP14) were partially replaced, especially at the species level. For instance, the species of the MP11 faunas are unknown from the overlying MP levels (Figure 3). A drastic modification of the cohorts occurred in the Bartonian (at MP16). A small fraction of the genera of the MP8+9, MP10, and MP13 faunas, but none of MP11 and MP12, are recorded in the Bartonian and Priabonian. Some genera even survive until the end of the Eocene (Fig. 3). The Bartonian and Priabonian faunas (MP16-MP19) were continuously renewed at the species and genus levels until the end of the Eocene (Fig. 3).

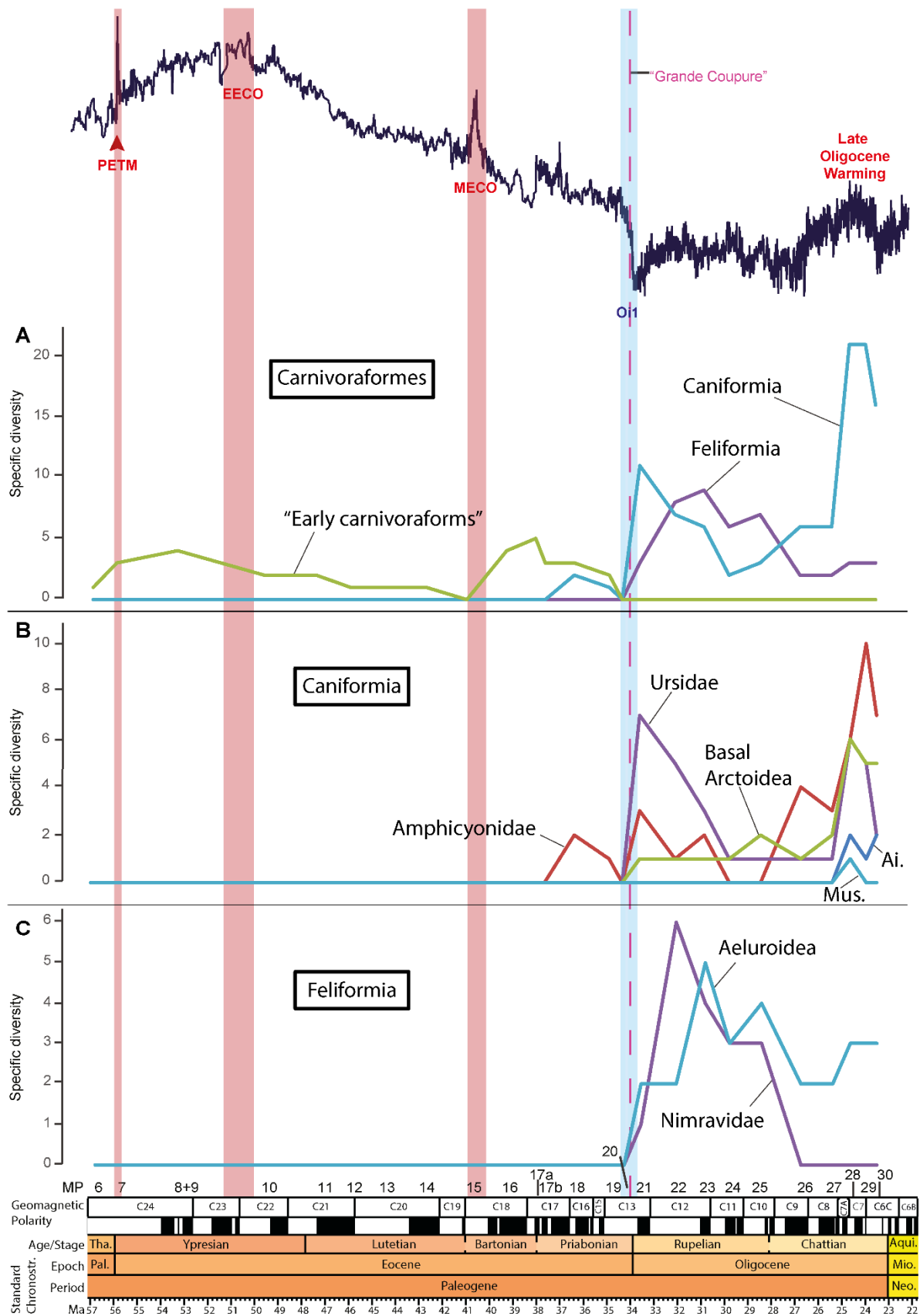


Figure 2. Evolution of specific diversity of carnivoraformes during the Paleogene in Europe. A. Carnivoraformes: “Early carnivoraformes”, Caniformia, Feliformia. B. Caniformia: Basal Arctoidea, Amphicyonidae, Ailuridae, Ursidae, Mustelidae. C. Feliformia: Aeluroidea,

Nimravidae. Orange bars: most notable Eocene climatic warming phases; blue bar: climatic cooling at the onset of the Oligocene. Abbreviations: Ai., Ailuridae; EECO, Early Eocene Climatic Optimum; Mus., Mustelidae; PETM, Paleocene-Eocene Thermal Maximum; MECO, Middle Eocene Climatic Optimum; Oi-1, Oligocene Oi-1 event.

The faunas changed dramatically in the earliest Oligocene (early Rupelian, MP21). Only a tiny fraction of the species of the Priabonian (MP17a-MP17b, not MP18-19) persisted until MP21. The genera of MP17a, MP18, and MP19 persisted slightly longer, but their constituent species changed. The MP21 cohort is very persistent: it lasts until the late Chattian (MP28) for the species cohort and the end of the Oligocene (MP30) for the genus cohort. The slightly younger MP22 and MP23 cohorts also survived until the end of the Oligocene. The MP24 to MP27 faunas show very limited modification of the cohort, especially for the genera. Only the early Chattian MP26 fauna contains new taxa, but a lot of these taxa disappeared rapidly (after MP27). The MP28, MP29, and MP30 faunas include numerous newcomers among the carnivorous taxa, along with representatives of the older MP levels, including some taxa from the early Rupelian.

DICE SIMILARITY

We recover a fairly similar pattern for all taxa (Fig. 4). The lower MP levels (MP6, MP7, MP8+9, and MP10) in some cases cluster together but the groups vary slightly depending on the carnivore clade and taxonomic level analysed (i.e., species or genera) (Fig. 4C-F). Based on these analyses, we recognize several groups that are supported by all taxa combined (Fig. 4A-B), as well as by the hyaenodonts (Fig. 4E-F) and carnivoramorphans (Fig. 4C-D) separated: One group clusters the Lutetian MP12, MP13, and MP14 faunas; another clusters the Bartonian-Priabonian MP16 to MP19 faunas; the final group clusters MP21-MP30, corresponding to the entire Rupelian-Chattian interval. The relationships between these three groups is variable depending on the analysed criteria.

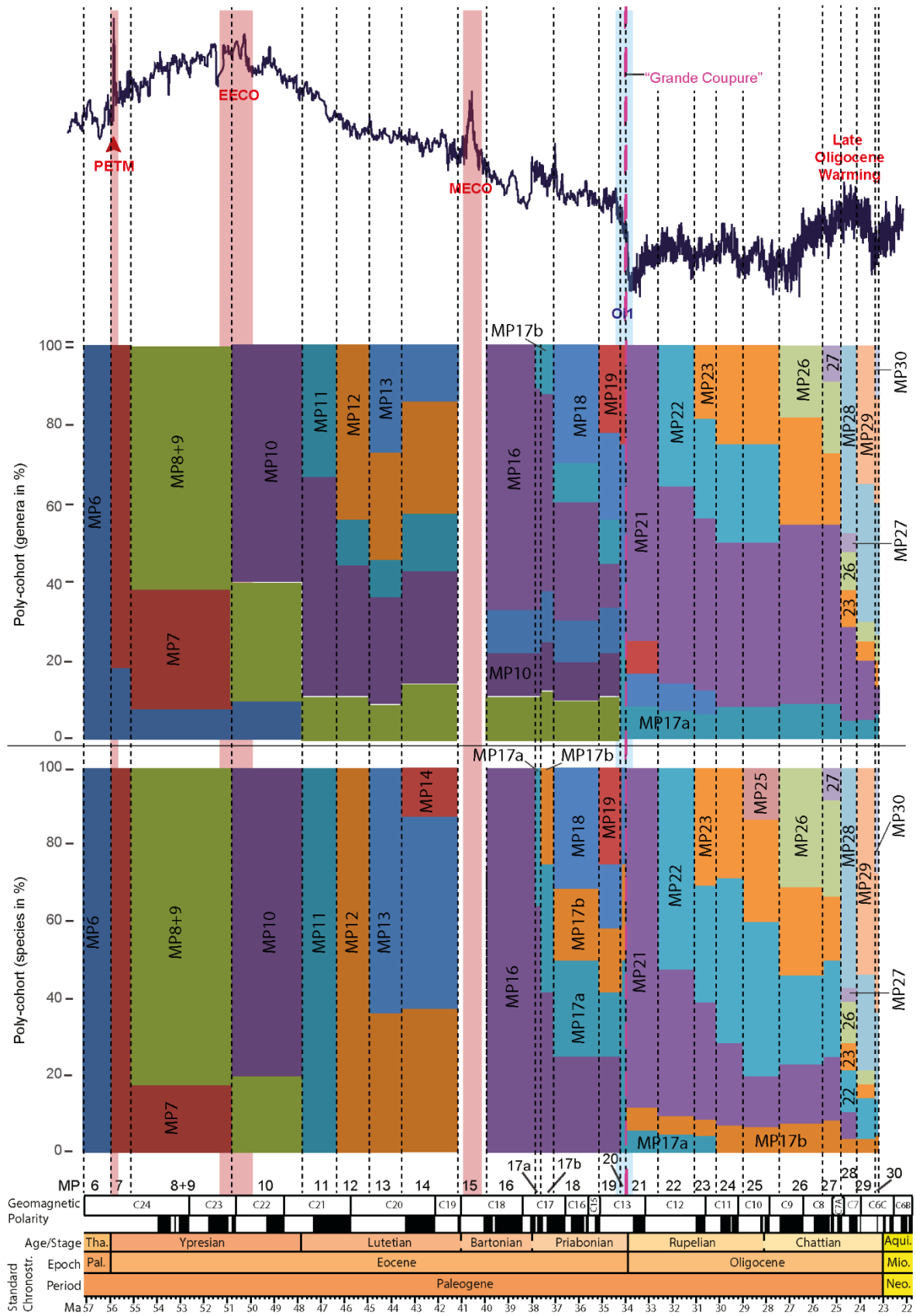


Figure 3. Survivorship poly-cohort for the genera and species of carnivorous mammals (in %). It illustrates the percentage of carnivorous taxa still present from an initial taxonomical assemblage (i.e., the carnivorous taxa recorded in an MP level) until the last

appearance of its last representative; these curves show the on-going decay of the assemblage by extinction of its constituent taxa. The colours used for the MP taxonomical assemblages are different from those used in Figs 1 and 2; they are not symbolic but were chosen for ease of reading. Orange bars: most notable Eocene climatic warming phases; blue bar: climatic cooling at the onset of the Oligocene. Abbreviations: EECO, Early Eocene Climatic Optimum; PETM, Paleocene-Eocene Thermal Maximum; MECO, Middle Eocene Climatic Optimum; Oi-1, Oligocene Oi-1 event.

DISCUSSION

THE EVOLUTION OF EUROPEAN CARNIVOROUS MAMMALS AND ITS REGIONAL CONTEXT

Our results highlight a series of important turnovers and dispersals that punctuated the evolution of European carnivorous mammals during the Paleogene. These bioevents are contemporaneous with other phenomena such as climate change and dispersals of other mammalian groups (Figure 5), suggesting that these phenomena affected several trophic levels in terrestrial Paleogene ecosystems. These changes can be summarized as follows:

Thanetian

Thanetian European floras indicate the existence of subtropical (*i.e.*, warm and subhumid) and tropical (*i.e.*, warm and humid) environments in Europe as well as the presence of forested vegetation with dense understory during this interval (Hooker & Collinson, 2012; Smith *et al.*, 2014; see also Wolfe, 1975). For instance, the flora of Rivecourt (France) shows affinities with the modern tropical and subtropical floras of Asia (notably Indo-Malaysian flora; Del Rio *et al.*, 2019). MP6 (ca. 57 Ma, late Thanetian) is characterized by the first occurrence of carnivorous mammals in Europe (Fig. 5). However, the carnivorous mammal fauna is not very diverse with only a few carnivoraforms and mesonychians known from MP6 (Fig. 1B). These mammals probably followed distinct routes to disperse to Europe: mesonychids might have come from North America around the Selandian along with neoplagiaulacid multituberculates (De Bast & Smith, 2016), or during the Thanetian (Solé *et al.*, 2018); and the early carnivoraforms recorded at Rivecourt might have dispersed from Asia, together with rodents, at the end of the Thanetian (Smith *et al.*, 2014; Solé *et al.*, 2016). In general, the latest Thanetian European fauna appears to be transitional, comprising late Thanetian and earliest Ypresian taxa, including the first representatives of the modern orders of Carnivoraformes and Rodentia (Gheerbrant *et al.*, 1999; Smith *et al.*, 2014; Solé *et al.*, 2016).

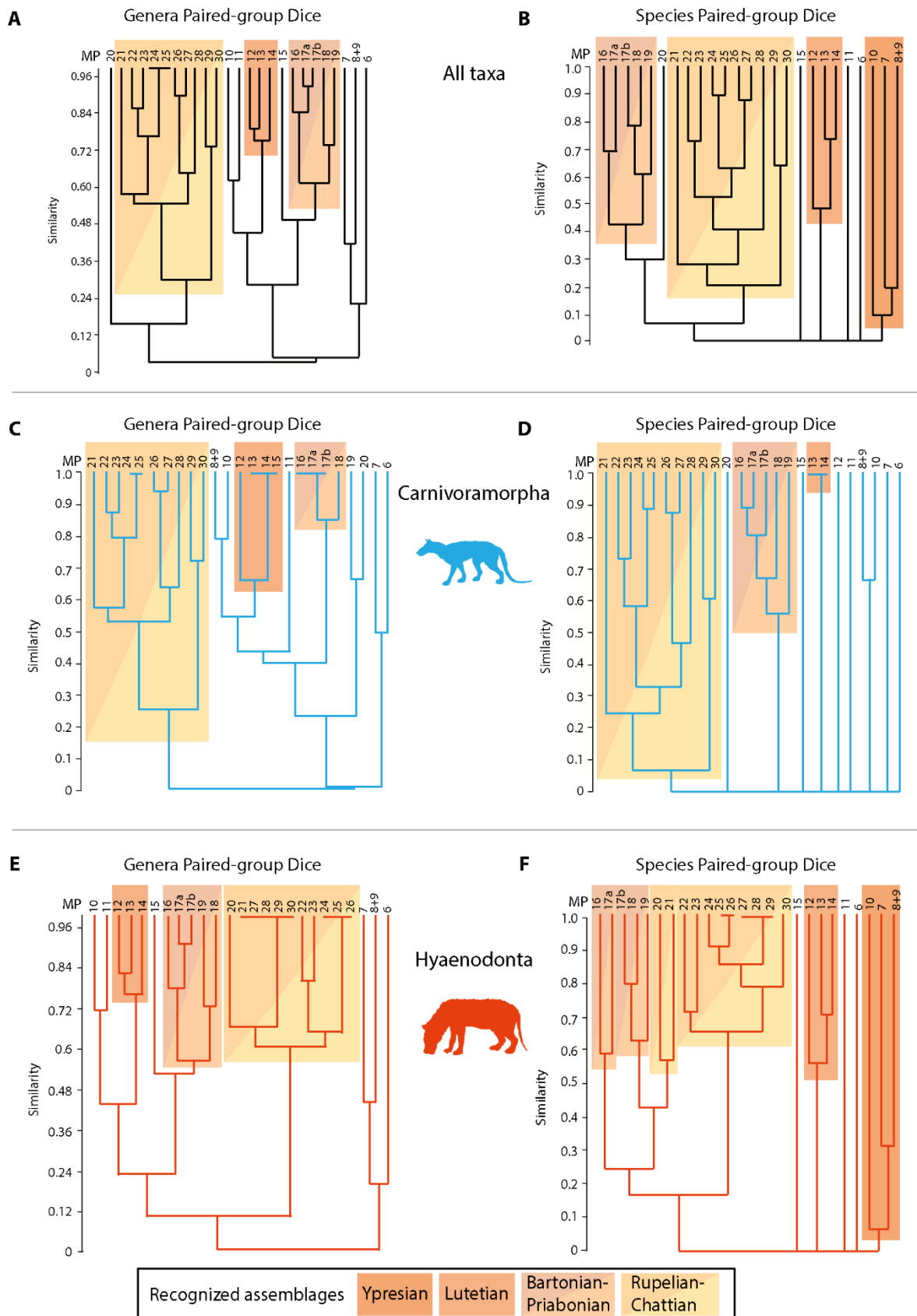


Figure 4. Results of the Paired-group Dice analysis. A-B: all taxa; C-D: Carnivoramorpha; E-F: Hyaenodonta. The boxes highlight the recognized assemblages among the Paleogene, i.e., the similarity of the carnivorous faunas identified for each MP level.

Carnivoramorphan silhouette: *Daphoenus*, (credit: Robert Bruce Horsfall, vectorised by T. Michael Keeseey, phylopic.org), hyaenodontan silhouette: *Hyaenodon "horridus"* (credit Robert Bruce Horsfall, phylopic.org). Abbreviations: EECO, Early Eocene Climatic Optimum; PETM, Paleocene-Eocene Thermal Maximum; MECO, Middle Eocene Climatic Optimum; Oi-1, Oligocene Oi-1 event.

Ypresian

The earliest Eocene floras do not suggest a radical change in vegetation from the late Paleocene (Hooker & Collinson, 2012), although there are some differences in the assemblages, especially the rise of *Aulacoxylon*, a dominant species in the Ypresian Paris Basin (De Franceschi & De Ploëg, 2003; Smith *et al.*, 2014). *Aulacoxylon* and the other components of the palaeoflora indicate the presence of closed forests as well as a warm and wet seasonal climate in Europe (Fairon-Demaret & Smith, 2002; Fairon-Demaret *et al.*, 2003). In contrast, European mammal assemblages changed greatly around the Paleocene-Eocene boundary (ca. 56 Ma). The mammal fauna that lived in Laurasia at that time was profoundly affected by the Paleocene-Eocene Thermal Maximum (= PETM), a period of ~150 Kyr of climate warming (Zachos *et al.*, 2001, 2008; Hollis *et al.*, 2019). The numerous dispersal events to Europe that originated from Asia, North America, and Africa that mark the MDE notably brought the first primates, artiodactyls, and perissodactyls into Europe (e.g., Hooker & Dashzeveg, 2003; Smith *et al.*, 2006; Gheerbrant & Rage, 2006; Hooker, 2015). This resulted in a homogenization of mammal faunas across the continents of the Northern Hemisphere. During this interval, numerous carnivoramorphan taxa, as well as the first hyaenodonts, and oxyaenids dispersed into Europe (Smith & Smith, 2001; Solé *et al.*, 2011, 2013a, 2014b) (Fig. 1B-C, Fig. 5). The carnivoraform and mesonychid genera of MP6 survived into the early Ypresian (MP7) and mixed with the newcomers (Fig. 3). Dispersals continued for some groups of mammals for ~500,000 years after the PETM (MP8+9; ca. 55 Ma) (Hooker, 2010). Among carnivorous mammals, the first viverravids as well as new mesonychids dispersed into Europe, probably from North America (Hooker, 2010; Solé *et al.*, 2018) (Fig. 1B, Fig. 5). Carnivorous mammals then evolved endemically into the Bartonian, despite the possible continuation of intercontinental connections (e.g., Smith, 2001).

As indicated by both the FAD/LAD and the percentage of renewal (Supplementary Texts 1-2), the Ypresian as a whole was a period of instability for carnivorous mammal diversity – notably for hyaenodonts, which experienced higher turnover rates than carnivoramorphans. Other clades underwent profound changes as well, illustrated by the disappearances of viverravids and oxyaenids around 54-52 Ma (Intra-Ypresian Mammal Turnover; Solé *et al.*, 2011, 2019b), and mesonychids at the end of the Ypresian (ca. 48 Ma; Ypresian–Lutetian Mammal Turnover; Solé *et al.*, 2018, 2019b) (Fig. 1B, Fig. 5). Their disappearances may be connected to the diversification of hyaenodonts in Europe around the Ypresian-Lutetian transition (Solé *et al.*, 2014a) (Fig. 1B-C). Other mammal groups radiated at the end of the Ypresian (MP10): perissodactyls, artiodactyls, rodents, and pantolestids (Savage *et al.*, 1966; Sudre & Erfurt, 1996; Smith, 2001). However, these events are best seen as turnovers, being associated with a series of contemporaneous extinctions (Solé *et al.*, 2019b). These extinctions and radiations might be related to the Early Eocene Climatic Optimum (EECO, ca.

53–49 Ma; Zachos *et al.*, 2008; Hollis *et al.* 2019) (Fig. 5), a global warming period that had a drastic impact on the composition of the mammal fauna in North America (Woodburne *et al.*, 2009). The EECO produced a major increase in habitat complexity, but a subsequent climatic cooling event (49–46 Ma) resulted in major mammal diversity loss: the Bridgerian Crash (Woodburne *et al.*, 2009). Woodburne *et al.* (2009) suggested that the EECO began the greatest episode of land mammal faunal turnover of the first part of the Cenozoic.

Lutetian

During the Lutetian (MP11–MP14), European ecosystems experienced increased aridity and increased seasonality. This is illustrated by the appearance of perissodactyl palaeotheriids at MP13, which have more hypsodont teeth than the perissodactyls recorded in the older faunas (Franzen, 2003; Badiola *et al.*, 2009). This period is known as the First Intra-Eocene Mammal Turnover (Franzen, 2003) (Fig. 5). It is also marked by a floristic change, which reflects a cooling and drying during the MP13–MP14 interval (Collinson *et al.*, 1981). An important and drastic change in global temperatures occurred after the EECO as global temperature decreased (Zachos *et al.*, 2008). Cooling in Central Europe around 45 Ma was stepwise and primarily driven by cooler winters, which also increased seasonality (Mosbrugger *et al.*, 2005).

For carnivorous mammals, the Lutetian corresponds to a period of relative stability characterized by speciation within endemic genera of carnivoraforms and hyaenodonts, an observation supported by our poly-cohort analysis and Dice similarity results (Figs 3–4). Despite the stability of genera during the Lutetian in Europe, there is an overall decrease in the diversity of carnivorous mammals, which might be related to aridification and increased seasonality during the interval. However, the specific origin of this decline in diversity remains to be tested.

Bartonian–Priabonian

Numerous changes in the carnivorous mammal fauna are observed in Europe during the Bartonian and Priabonian. They could be related to: (1) the long warming interval (~750 kyr) known as the Middle Eocene Climatic Optimum (MECO; ca. 40 Ma); and (2) the global cooling trend that started after the EECO (Zachos *et al.*, 2001, 2008). Indeed, the high FAD/LAD percentage of renewal values after the MECO clearly indicate that hyaenodonts and carnivoramorphans both experienced a high degree of turnover (Supplementary Tables 3–4, Supplementary Texts 1–2). Cenograms that document the interval before 37 Ma (early Priabonian, MP17a–MP17b) show a log-uniform distribution of body weights, typical of mammal communities inhabiting a tropical evergreen forest under warm and humid conditions (Escarguel *et al.*, 2008). From 37 Ma (MP17b) to the Eocene/Oligocene boundary (33.9 Ma; MP20), cenogram analysis indicates more arid climates (possibly the arrival of extended dry seasons?) and more open vegetation, corresponding to wooded savannah. This analysis is consistent with the climatic deterioration (i.e., greenhouse to icehouse transition) during the late Eocene (Escarguel *et al.*, 2008). Subtropical evergreens were still dominant in the Priabonian, but the vegetation was less tropical than before, indicating a transition from an equable humid climate to a more seasonal, periodically drier, subhumid climate (Collinson & Hooker, 1987; Collinson, 1992; Knobloch *et al.*, 1993; Kvaček, 2010). However,

paleoclimatic deterioration varied with latitude and palaeogeographic situation (Kvaček, 2010).

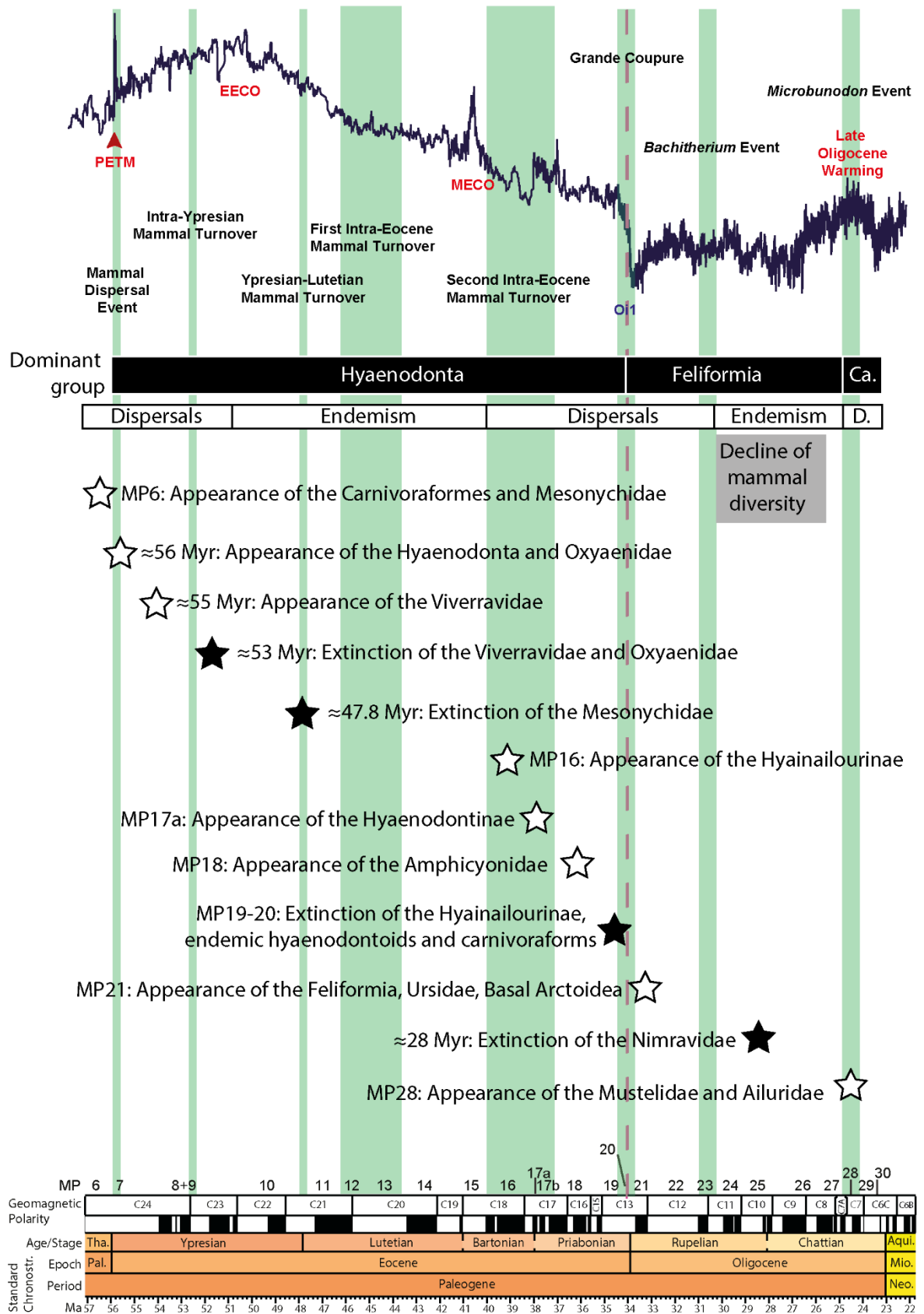


Figure 5. Summary of the faunal events (dominant group, dispersion/endemic phases, appearances, extinctions) that characterized the history of the carnivorous mammals in Europe. Green bars: faunal events recognized based on the evolution of the European mammals. Black boxes: dominant carnivorous group. White boxes: dispersal/endemic phases. Open stars: appearances; closed stars: extinctions. The grey box indicates a period of general decline of diversity among carnivorous mammals. Abbreviations: Ca., Caniformia; D., dispersals EECO, Early Eocene Climatic Optimum; PETM, Paleocene-Eocene Thermal Maximum; MECO, Middle Eocene Climatic Optimum; Oi-1, Oligocene Oi-1 event.

The fossil mammal record also suggests changes in ecosystems during the Bartonian-Priabonian. Blondel (2001) demonstrated a decrease in folivorous perissodactyls and an increase in both folivorous/frugivorous and folivorous artiodactyls during the Bartonian to early Priabonian (MP16-MP17b). During this time some groups, such as Amphimerycidae (Artiodactyla), acquired fused cuboid and navicular bones of the tarsus, suggesting the development of more open habitats and increased seasonality in this time interval. These habitat changes are also supported by the appearance of hypsodont rodents (Vianey-Liaud & Marivaux, 2017). The Bartonian-Priabonian ecosystem changes correspond to the Second Intra-Eocene Mammal Turnover first established using the perissodactyl and artiodactyl fossil record (Franzen, 2003) (Fig. 5).

Regarding the carnivorous mammals, the Bartonian-Priabonian assemblages (MP16-MP20) are very distinct from all others, consistently clustering together in our Dice similarity analyses (Fig. 4). After the Lutetian stability, the Bartonian (MP15-MP16) and the Priabonian (MP17a-MP20) record another drastic period of restructuring that is illustrated by the near absence of cohorts from the Lutetian (Fig. 3). This restructuring marks the end of a period of endemism for the European carnivorous fauna. The appearances of new subfamilies of hyaenodonts (Hyainailourinae and Hyaenodontinae), as well as the first occurrence of the caniformian family Amphicyonidae, are notable markers of this restructuring (Fig. 1C, Fig. 2B, Fig. 5). Hyaenodontines probably dispersed from Asia into Europe, while hyainailourines probably dispersed from Africa into Europe (Lange-Badré, 1979; Solé *et al.*, 2015; Borths & Stevens, 2019). The origin of Amphicyonidae is less clear (Wang *et al.*, 2005). Several new hyaenodontoids and early carnivoraforms from endemic lineages evolved in Europe during the Bartonian and early Priabonian (MP16-MP17b), mixing with the newcomers. The Bartonian and Priabonian appearance of lineages that originated outside of Europe is also observed in other mammalian clades. Notably Anthracotheriidae (Artiodactyla) dispersed from Asia into Europe in the middle Priabonian (MP18; Blondel, 2001) through dispersal corridors between Asia and southeastern Europe (Balkan archipelago, Iran, Anatolia) (Heissig, 1979; Ducrocq, 1995; Blondel, 2001; Mennecart *et al.*, 2021). Rodents also underwent several phases of diversification and dispersal during this interval time (Vianey-Liaud & Marivaux, 2017).

‘Grande Coupure’

The Eocene-Oligocene transition saw the establishment of subhumid to semi-arid summer seasons, which resulted in the disintegration of forest cover. This resulted in the withdrawal or

extinction of some paleotropical elements of the paleoflora, as well as the dispersal of deciduous trees (Ollivier-Pierre *et al.*, 1987; Leopold *et al.*, 1992; Knobloch *et al.*, 1993). In Western Europe, this boundary is marked by a spread of conifers and temperate woodlands. In some areas, even savanna-bound Umbelliferae (Ollivier-Pierre *et al.*, 1987) are recorded. The European flora thus suggests that the climate became much drier, with a marked seasonality, and that the tropical and subtropical forests were replaced by temperate, mixed deciduous floras and more open habitats (Gruas-Cavagnatto, 1974; Collinson & Hooker, 1987; Ollivier-Pierre *et al.*, 1987; Cavagnetto & Anadón, 1996). To summarize, European vegetation gradually changes around the Eocene-Oligocene boundary; characterized by the expansion of arid and more-seasonal biomes, and the decline of mangroves, swamps, and forest biomes (Kvaček *et al.*, 2014; Kunzmann *et al.*, 2016; Pound & Salzmann, 2017).

The Eocene/Oligocene boundary is marked by numerous disappearances in various vertebrate groups. As shown by Rage (2006), most of the lower vertebrate species present during the Eocene, which were mainly endemic to Europe, went extinct. Extinction ratios reached ca. 60% among late Priabonian mammalian lineages (Legendre *et al.*, 2006; Escarguel *et al.*, 2008). Many archaic frugivorous/folivorous families of endemic artiodactyls, such as Xiphodontidae, went extinct. Some artiodactyl families survived into the Oligocene, notably Cebochoeridae, Dacrytheriidae, Anoplotheriidae, and Amphimerycidae, but were extinct by the end of the Oligocene (Legendre *et al.*, 1995; Blondel, 2001, Erfurt & Métais, 2007).

The onset of the Oligocene is also marked by numerous appearances, such as that of new perissodactyl families (*e.g.*, Rhinocerotidae) (Legendre & Hartenberger, 1992; Tissier *et al.*, 2018). These new arrivals may have been facilitated by a new land connection with Asia, the product of the drying of the Turgai Strait (Pomerol, 1967) in response to glacio-eustatic sea-level fall (Haq *et al.*, 1987). This great faunal shift, as well as the modification of the floras, collectively called the ‘Grande Coupure’, was first identified by Stehlin (1909) and is coeval with the global climate cooling and large-scale Antarctic glaciation called the Oligocene Oi-1 event (Blondel, 2001; Zachos *et al.*, 2001; Escarguel *et al.*, 2008; Mennecart *et al.*, 2021) (Fig. 5).

Our results show that the diversity of endemic hyaenodontoids and early carnivoraforms dramatically decreased at the end of the Eocene (latest Priabonian) (Fig. 1C, Fig. 2A, Fig. 5). The hyaenodont decrease also includes the newly arrived the hyainailourines (MP16-MP20), which are absent from the Oligocene (Lange-Badré, 1979) (Fig. 1C). Moreover, only one species of *Hyaenodon*, the most abundant hyaenodont genus of the Priabonian and Oligocene of Europe, crossed the Eocene-Oligocene boundary (Bastl *et al.*, 2014).

Our poly-cohort analysis results are consistent with a strong modification of the carnivorous fauna around the Eocene-Oligocene boundary (Fig. 3). Essentially, MP21 marks the shift in dominance from hyaenodonts to carnivoraforms (Fig. 1B). The lower values of FADs, LADs, and percentage of renewal suggest that hyaenodonts experienced slower rates of diversification after the ‘Grande Coupure’ (see Supplementary Texts 1-2). MP21 is also crucial from an evolutionary perspective, as it records the first occurrence of Feliformia (probably dispersing from Asia) (Dashzeveg, 1996; Peigné & de Bonis, 1999; Peigné, 2000), Ursidae (Caniformia), and basal Arctoidea (Caniformia) in Europe (Fig. 5). These

appearances establish the foundation of a relatively stable fauna that spans the entire Oligocene (MP21 to MP30) (Fig. 4).

Blondel (2001) concluded that, for Western European ungulates, the Eocene-Oligocene transition is marked by different phases of extinction and origination related to environmental changes. Several other studies indicate that changes in the European ungulate fauna started in the late Priabonian (Legendre & Hartenberger, 1992). Like changes in the ungulate fauna, the carnivorous fauna transition at the ‘Grande Coupure’ is gradual: the endemic hyaenodontoids and early carnivoraforms disappeared before the end of the Eocene (MP18-MP20) and newcomers arrived in the early Oligocene (MP21-MP23) (Fig. 5). The gradual modification of the mammal communities’ parallels trends observed in the evolution of the European vegetation. However, it is important to note that the Eocene-Oligocene boundary itself is marked by a major and sudden shift in the carnivorous mammal fauna.

Rupelian

This stage corresponds to the peak of floral change that started in the late Eocene, which is characterised by the extinction of some paleotropical elements and the dispersal of deciduous trees (Knobloch *et al.*, 1993). The Quercy Phosphorites provide very few botanical data, however, De Franceschi *et al.* (2006) described a fossil assemblage that is evidence of a warm Mediterranean to subtropical paleoenvironment. Based on cenogram analysis, Escarguel *et al.* (2008) hypothesized that arid conditions with relatively low mean annual temperatures, which are associated with (sub)desert to lightly forested environments, reigned in Europe from the early Rupelian (MP21) to middle Chattian (MP26-MP27). The end of the Rupelian (ca. MP25) might correspond to a period of maximum aridity in Western Europe (Legendre *et al.*, 1991).

The appearance of new mammals in Western Europe two million years after the ‘Grande Coupure’ (ca. 31 Ma; MP23) is known as the *Bachitherium* Dispersal Event (Fig. 5), named after the oldest known European ruminant (Mennecart *et al.*, 2018a,b). Our data indicate limited dispersal of carnivorous mammals during this event (see Supplementary Texts 1-2). The most interesting Oligocene period for carnivorous mammals occurred at end of the Rupelian (MP24-MP25) (Fig. 1A, Fig. 5) as it is one of the rare periods in our dataset when the LADs outnumber the FADs (this also occurs at MP14 and MP19-MP20) (Supplementary Table 3). This reflects the Europe-wide disappearance of the highly diverse Nimravidae (Feliformia) (see also Rémy *et al.*, 1987), and a few of aeluroids (Fig. 2C, Fig. 5). A decrease in diversity around MP25-MP26 has been observed for other groups of mammals, notably the rodents (Vianey-Liaud & Schmid, 2009). The disappearance of Nimravidae in Europe renders feliformians less diverse than caniformians for the first time, losing their position as the dominant predators in Europe (Peigné, 2000). The extinction of Nimravidae in Europe (Fig. 5) might be associated with increased aridity in Europe. In North America nimravids inhabited closed forest habitats and their decline in the late Oligocene correlates with the spread of grassland ecosystems, the result of increased aridity (Bryant, 1996).

Chattian

The end of the Oligocene in Europe is marked by increased seasonality, which is characterized by a dry season and a more open environment with fewer forests (Mennecart,

2012; Weidmann *et al.*, 2014). Watinne *et al.* (2018) described the end of the Chattian (MP29-MP30) as a period of general aridity, which is associated with a cooler climate. Based on cenogram analysis, Escarguel *et al.* (2008) suggested that middle to latest Chattian (MP26-MP29) climate was rather temperate and humid and that the Quercy area was predominated by temperate deciduous forests. In contrast, from 24.5 Ma (MP29-MP30) to the end of the Oligocene, closed environments and warm and humid conditions prevailed in Europe (Escarguel *et al.*, 2008), indicating a return to the more temperate to subtropical (but probably less humid) conditions of the Priabonian (see also De Man & Van Simaey, 2004). The ecology of the ruminants suggests that these mammals characterized wooded environments before the *Microbunodon* Event – an event of generalized dispersals across Eurasia around MP28 (Fig. 5). After the *Microbunodon* Event these ruminants lived in more open habitats (Mennecart, 2015). The results of Mennecart (2015) and Escarguel *et al.* (2008) clearly support ecosystems change during the Chattian, but the findings of these studies seem to contradict each other (open environments with fewer forests *versus* closed environments and warm, subtropical conditions). We think that this contradiction indicates the existence of a mosaic of ecosystems across Europe. The *Microbunodon* Event might be related to the Alpine orogeny and the Late Oligocene Warming that occurred around 26–23 Ma (Fig. 5) (Mennecart, 2015). The Late Oligocene Warming corresponds to a global marine temperature increase of 2 to 4°C, a terrestrial temperature increase of nearly 10°C, and the collapse of the Antarctic ice sheet (Zachos *et al.*, 2001).

Similar to what has been observed for the ruminants, the diversity of carnivorous mammals' rebounds in MP27 to MP29 (Figs. 1A, 3, 5, Supplementary Texts 1-2), largely the result of the appearances of numerous caniformians at the end of the Chattian (Fig. 2A-B). MP28 records the first occurrence of mustelids and ailurids in Europe (Bonis, 1976). All these appearances may be the result of dispersals from Asia into Europe, but the lack of data concerning the phylogenetic relationships of caniformians from the latest Chattian makes it difficult to test. The taxa that arrive during this interval are clearly part of the *Microbunodon* Event; the taxa correspond to “the late travelers of the big Stampian migration” of Viret (1929; see also Bonis, 2011). After this bioevent, the caniformians became the dominant predators of Europe during the Chattian (Fig. 5). Finally, large amphicyonid carnivorans appear at MP28 and MP29 (Ginsburg, 1966). Their occurrence supports the hypothesis that terrestrial environments are becoming more open.

COMPARISON WITH NORTH AMERICA

The rise of carnivoran mammals during the Paleogene is an iconic case of competition between mammal clades (Savage, 1977; Radinsky, 1982; Van Valkenburgh, 1999; Friscia & Van Valkenburgh, 2010). According to Radinsky (1982, p.192), feliformians and caniformians “radiated to fill niches vacated by the extinction of many groups of Eocene carnivorous mammals during the climatic deterioration at the end of the Eocene”. Van Valkenburgh (1999) considered that, in North America, the transition from a guild composed of mesonychids, oxyaenids, hyaenodonts, viverravids, and early carnivoraforms to one largely composed of carnivorans and hyaenodontines represents a double-wedge turnover (i.e., one taxon rises in diversity, but then declines alongside an increase in the diversity of a second group), resulting from an active, competitive replacement of one group by another (Benton,

1987, 1996). However, the possibility that climatic events might have also affected the evolution of the carnivorous mammals cannot be ruled out, prompting Van Valkenburgh (1999, p.473) to conclude “that the cause of the decline of the first dynasty of carnivorous mammals remains a mystery”. Friscia & Van Valkenburgh (2010) further developed this view by investigating the hypothesis of a competitive replacement of oxyaenids and hyaenodonts by carnivoramorphans. They suggested that carnivoramorphans increase in size throughout the Eocene, and that the dietary diversity of carnivoramorphans increased throughout the Eocene, while that of the hyaenodonts decreased. In North America, carnivoramorphans clearly outnumbered other groups by the early Lutetian (= Uintan North American land mammal age; see Speijer *et al.*, 2020). Friscia & Van Valkenburgh (2010) concluded that the replacement of ‘creodonts’ (i.e., Oxyaenidae and Hyaenodonta) by Carnivoraformes corresponds to a competitive replacement that might have been driven by the anterior position of the carnassial teeth in Carnivoraformes compared to the posterior position of carnassial teeth in oxyaenids and hyaenodontoids. The anterior position of the carnassial teeth may have allowed the distal molars to evolve different morphologies, resulting in a broader range of dental adaptations and thus a broader range of diets.

de Vries *et al.* (2021) recently examined the Eocene-Oligocene boundary in Africa. They noted a crash in hyaenodont diversity in Africa (no carnivoran was present in Africa at that time). The African hyaenodonts, however, did recover in the Oligocene and Miocene. This observation is interesting because it suggests that diversity reduction, as well as recovery, in carnivorous faunas can be climate-induced rather than competition-induced. Alternatively, some studies focused on the evolution of the African carnivorous mammals around the Paleogene-Neogene boundary indicate that carnivorans displaced hyaenodonts after dispersal into Africa (Borths & Stevens, 2017c; Friscia *et al.*, 2020). This competitive replacement scenario recalls the one hypothesized for North American carnivorous mammal assemblages.

A competitive replacement scenario is not recorded in Europe. Our results demonstrate that hyaenodonts are more diverse than carnivoramorphans through the Eocene until the ‘Grande Coupure’ (Fig. 1B, Fig. 5; Supplementary Figure 1). This discrepancy between the European and North American records is rather surprising because the Ypresian (MP7-MP10) carnivorous mammal faunas of both regions were largely similar at the generic level, following the early Eocene MDE (e.g., Smith & Smith, 2001, 2010; Hooker, 2010; Solé *et al.*, 2013a,b) (Fig. 5). The Ypresian of Europe differs from North America because several groups disappear from Europe (i.e., mesonychids, oxyaenids, and viverravids) that continued to thrive in North America until the late Eocene. Moreover, while hyaenodonts were identical at the genus level on both sides of the North Atlantic during the earliest Eocene (MP7), the similarity decreased rapidly by MP8+9, as the hyaenodont genera went extinct earlier in Europe than in North America (Solé *et al.*, 2013a). Consequently, the composition of the European fauna changed during the Ypresian (Intra-Ypresian Mammal Turnover and Ypresian-Lutetian Mammal Turnover; Fig. 5). These extinctions probably had important consequences on European carnivorous mammal faunas because oxyaenids and mesonychids were the largest carnivorous mammals present in Europe at that time. Their disappearance possibly encouraged the diversification of hyaenodonts in Europe around the Ypresian-Lutetian transition (see above). By the Bartonian and early Priabonian, new endemic hyaenodonts and recently arrived taxa (Hyainailourinae, Hyaenodontinae) compose a newly

diverse hyaenodont fauna. In contrast, carnivoraformes were limited to three genera present at a given interval during the Eocene (Supplementary Figure 1; Supplementary Table 2). The marked differences between the North American and European records allow us to interrogate the drivers of the success or failure of the distinct groups of carnivorous mammals (e.g., ecomorphological replacement, climatic changes, dispersals).

CONCLUSIONS

The European record of fossil carnivorous mammals is rich and documents a series of turnovers that profoundly altered carnivorous mammal assemblages over the course of the Paleogene. Four main episodes stand out: the mid-late Ypresian, the Bartonian-early Priabonian, the Eocene-Oligocene boundary, and the Chattian. The Eocene/Oligocene boundary, the so-called ‘Grande Coupure’, represents a drastic faunal transition, involving a major extinction of the endemic European fauna and the rising dominance of carnivorans. However, this important faunal restructuring was a long (ca. 8 Myr) and complex transition, which can be split into several extinction and origination waves that started in the Bartonian (MP16) and ended in the early Rupelian (MP21). Several turnovers in carnivorous mammal evolution can be linked with bioevents identified in other European clades such as ruminants and rodents, as well as with regional to global environmental changes. This suggests that several levels of continental trophic chains were affected simultaneously during these episodes.

Our results reveal marked differences in the evolution of carnivorans on both sides of the North Atlantic. While carnivorans are present in Europe from at least the latest Thanetian, their diversification and dominance appear delayed in Europe, occurring abruptly at the Eocene-Oligocene boundary, *i.e.* 16 million years later than in North America.

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SUPPORTING INFORMATION

Supplementary Table 1. List of taxa and their stratigraphic distribution

Supplementary Table 2. Evolution of species-level and genus-level diversity of carnivorous mammals.

Supplementary Table 3. Evolution of the First Appearance Datum and Last Appearance Datum at the species level.

Supplementary Table 4. Evolution of the Percentage of Renewal.

Supplementary Table 5. Values for the analyses of the bias.

Supplementary Table 6. Calculation of the Poly-Cohort analysis.

Supplementary Text 1. Description of the evolution of the First Appearance Datum and Last Appearance Datum.

Supplementary Text 2. Description of the evolution of the Percentage of Renewal.

Supplementary Figure 1. Evolution of genus-level diversity of carnivorous mammals during the Paleogene in Europe.

Supplementary Figure 2. Evolution of the First Appearance Datum and Last Appearance Datum at the species level.

Supplementary Figure 3. Evolution of the Percentage of Renewal.

Supplementary Figure 4. Assessment of the bias.

DATA AVAILABILITY

The data underlying this work are available in the Supporting Information.

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Figures captions