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The rise of carnivoran mammals in Europe through the lens of body mass

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Carnivoran mammals (cats, dogs, bears, seals, etc.) and their kin radiated during the Palaeogene, among other carnivorous clades (hyaenodonts, mesonychians, and oxyaenodonts). This radiation has often been framed as a competition ultimately won by carnivorans, but the data supporting this hypothesis largely originate from North America. We derive body mass (BM) from dental measurements in European hyaenodonts, mesonychians, oxyaenodonts, and carnivoramorphans ranging from the latest Palaeocene to the end of the Oligocene (MP 6–30; 57.2–23.3 Ma) and compare those with North American data. We show that European assemblages tell a different story, with a marked increase of the disparity of carnivoramorphan BMs at and after the Middle Eocene Climatic Optimum (MECO; 40 Ma), with no clear effect on hyaenodonts. The '*Grande Coupure*' (Eocene–Oligocene transition, approx. 34–33.5 Ma) marks the onset of a progressive decrease in the mean BM of hyaenodonts, while carnivoramorphans continue their rise initiated around the MECO. The observed BM patterns therefore do not follow the expected double-wedge pattern of competitive replacement and are possibly best explained by climate change-induced biodiversity dynamics.

1. Introduction

Fifty million years ago, during the early Eocene, several clades of sympatric placental mammals (hyaenodonts, oxyaenodonts, mesonychians, and carnivoramorphans (carnivorans and their stem-relatives)) occupied predator niches in North America and Europe [1–3], sharing a series of convergent adaptations for such a lifestyle (e.g. carnassial teeth, claws) [4–6]. Among this diversity, Carnivora (cats, dogs, bears, and kin) is the only clade that eventually prevailed [7], and previous studies framed this rise as a case of ecological competition won by carnivorans during the Eocene [1,2,8,9]. Their success has been postulated to notably result from increased dental plasticity, being able to evolve a wider variety of post-carnassial molar shapes and functions than other clades,

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which exclusively possess carnassialized molars [1]. However, this hypothesis has emerged from studies mainly focused on the North American fossil record, not addressing the biodiversity dynamics in other regions (but e.g. [10]). The rise of carnivoramorphans, and thus ultimately carnivorans, as the most diverse clade of predatory mammals occurs 16 My later in Europe than in North America, even though these groups entered the fossil record roughly at the same time (around the Palaeocene–Eocene transition) on both continents [3]. In this article, we analyse the evolution of Palaeogene carnivorous mammals from Europe through the lens of body mass (BM). Body mass is a crucial predictor of ecology (e.g. [11,12]), and mammals with similar diets tend to have similar BM (e.g. [13]). We find that carnivoramorphans markedly increased their BM range long before the Eocene–Oligocene transition (EOT), with no discernible effect on hyaenodonts. We then use this opportunity to question the main drivers of the radiation of carnivorans.

2. Material and methods

(a) Sampling

Our European dataset encompasses 155 species of carnivoramorphs (stem + crown Carnivora), hyaenodonts, oxyaenodonts, and mesonychians from the Palaeogene of Europe (see supplementary material). Reliable spatiotemporal data are available for all sampled taxa, including the locality and the assignment to an MP (a reference level of the mammalian biochronological scale for the European Palaeogene) [14,15]. We treated specimens with cf. and aff. specific determination as a valid occurrence of a species if this species is already recorded in this MP and locality. We also used Lazarus ranges to populate the time bins and reduce the influence of sampling biases [16]. A large part of the dataset is composed of the records from the Quercy Phosphorites Formation in France, but our dataset also includes many other localities from France, Germany, Belgium, Spain, Switzerland, Hungary, and England (see metadata in supplementary material). For North American data, we used the dataset of Juhn *et al.* [17], containing BM and biostratigraphic (North American Land Mammal Ages, NALMA) data for carnivorous mammals.

We retrieved phylogenetic relationships (posterior distribution of 1000 trees) from Faurby *et al*. [18] and added taxa for which BM data were available by manually grafting species within their genera if present in the phylogeny [18], or as sister lineage to closely related genera (see supplementary material for all details). We followed Spaulding *et al.* [19] by placing Mesonychia as the sister clade to Carnivoramorpha + Hyaenodonta + Oxyaenodonta. These 1000 trees were time-scaled after a randomized resolution of zero-length branches, using the minimum branch length algorithm (mbl = 1 My) and the Extended Hedman algorithm, which uses the sequence of outgroup ages to date nodes [20]. We selected the K/Pg (66 Ma) boundary as the maximum possible age of the root, as well as the following outgroups: *Eoconodon* (63.4 Ma minimum age), *Goniacodon* (57.5 Ma minimum age) [21]. The root age will not be of crucial importance for subsequent analyses. Both dating methods drop all tips for which no BM data are present; the following packages were used in the *R* statistical environment [22]: ape v5.8-1 [23], phytools v2.5-2 [24], strap v1.6-1 [25], and paleotree v3.4.7 [26] (supplementary material, figures S1 and S2).

(b) Imputation of body mass

We imputed the BM (expressed in kg) using clade-wide equation based on dental measurements. Dental measurements of each specimen were taken first-hand with a calliper or from pictures in the literature using ImageJ [27,28]. We used the equation of Van Valkenburgh [29] for carnivoramorphans:

$$\log10\,(\mathrm{BM}) = [2.97 \bullet \log10\,(\mathrm{Lm1})] - 2.27$$

where Lm1 = the length of the first lower molar mm^{-1}.

For mesonychians, we used the equation provided by Zhou [30] (see also [31]), which we modified to provide a $\log_{10}$ of BM:

$$\log10\,(\mathrm{BM}) = (1.327 \bullet x - 3.355)/\ln\,(10)$$

where x = ln(Length of m2 • Width of m2 mm^{-2}).

For hyaenodonts and oxyaenodonts, we used the equation provided by Morlo [32]:

$$\log10\,(\mathrm{BM}) = (3.5104 \bullet \log10)\,(\mathrm{MmL}) - 2.6469$$

where MmL = mean molar length mm^{-1}.

Body mass is considered uniform over time for each species because the resolution of the data makes it difficult to unambiguously identify intraspecific changes. We also removed any taxa whose imputed BM was <100 g; these unrealistic values are resulting from the possible bias of the equations we used for very small taxa.

(c) Evolution of body mass through time and phylogeny

In the R statistical environment, we computed the evolution of minimum, maximum, mean, median and the variance of BM through time (i.e. within each MP or NALMA bin), for the entire dataset and per larger clade of interest (Carnivoramorpha, Hyaenodonta, Oxyaenodontae, etc.) for both European and North American data (supplementary material, table S1a–m).

Regression of BM variance among European predatory mammals against their sampled diversity showed no correlation (supplementary material, figure S3), with or without generalized differencing (using a custom function made available by G. T. Lloyd [33]) (supplementary material, table S1n), suggesting that the BM data we gathered are not directly driven by sampling intensity. We used Hartigans' dip test of multimodality [34] to test whether assemblages pre- and post-Middle Eocene Climatic Optimum (MECO) and pre- and post-EOT were multimodal (supplementary material, table S1p).

We used two approaches to analyse temporal trends. First, we associated BM information to all tips in a sample of 100 mbl−time-scaled trees and 100 Extended Hedman−time-scaled trees. Besides producing phenograms with these data (supplementary material, figures S4 and S5), we fitted six evolutionary models and compared their Akaike Information Criterion (corrected for small sample size, AICc) scores: Brownian motion (using the geiger package v2.0.11 [35]), uniform trend (also using geiger), multiple trends with one, two, or three node shifts (using code provided by Benson *et al.* [36]), and Ornstein−Uhlenbeck in the form of a modified version of the *surface* algorithm that uses the phylogenetic Bayesian information criterion to reduce the rate of false positives (using code provided by Benson *et al.* [36]). The best model for each sampled tree can be visualized in supplementary material, figures S6–S8, and is reported in table S1o of the supplementary material. The second approach uses the full dataset, that is, with multiple temporal occurrences of taxa and their BMs, and without a phylogenetic framework. This better captures the evolution of early carnivorous mammalian communities through MPs and also eludes recurrent issues in the phylogeny of carnivorans (e.g. the position of ursoids [37,38]). To analyse this dataset, we serialized the non-parametric test of Kolmogorov–Smirnov (the D statistic) to identify a potential temporal shift in the evolution of BMs. This protocol functions like a running mean, identifying the MP for which all the BMs before (older) and all the BMs after (younger) are most different from one another, thus where the maximum of the absolute value of Kolmogorov & Smirnov's D is located [39] (supplementary material, table S1q–r). Because this method suffers from evident boundary effects, the very beginnings and endings of these curves should be discarded, as just a couple of bins are compared with a much larger sample. Thus, in this kind of analysis, the timing of mid-curve maxima, if any, is the signal of interest. All data and R scripts are available as supplementary material [40].

3. Results

(a) Body mass evolution

The earliest carnivorous mammalian communities of the Eocene of Europe are characterized by small carnivoramorphans and hyaenodonts, all weighing less than 2 kg (figures 1*c*,*d*; supplementary material, figures S4, S5, S9; supplementary material, table S1). Oxyaenodonts and especially mesonychians occupy the niches of large carnivorous mammals at that time, with masses usually ranging between 10 and 100 kg (supplementary material, figures S4, S5, S9; supplementary material, table S1). Hyaenodonts show a BM increase through the Ypresian–Lutetian interval, but this increase is modest: their mean BM is approximately 2 kg, while that of carnivoramorphans reaches approximately 1 kg at the end of the Lutetian. These modest increases do not compensate for the disappearance of the oxyaenodonts and mesonychians after the Early Eocene Climatic Optimum (EECO, approx. 53–49 Ma), resulting in a marked drop in maximal BMs of carnivorous mammals (supplementary material, table S1). Both hyaenodonts and carnivoramorphans are more massive right after the MECO (40.75–40.00 Ma) [41], and both groups show an increase in BMs throughout the middle Bartonian−Priabonian interval (figure 1*b*–*j*). The mean BM of hyaenodonts is approximately 21 kg and that of carnivoramorphans under 6 kg just prior (MP19) to the EOT (MP19). But the most important change right after the MECO is a marked increase in the range and disparity of carnivoramorphans' BMs, ranging from 300 g to 28 kg and with a variance markedly higher than that of hyaenodonts (figure 2*b*). At the end of the Eocene, European stem carnivoramorphans are larger than carnivorans. The EOT is another breakpoint: the progressive disappearance of endemic European hyaenodonts (which started by the middle Eocene and sharpened at the EOT [3]) results in a decrease in BMs during the early Oligocene (Rupelian), while carnivoramorphans maintain the increasing trend initiated by after the MECO. The largest European carnivorans outweigh the largest coeval hyaenodonts by MP22 (middle Rupelian), reaching masses close to 100 kg, like early Eocene mesonychians and Priabonian hyaenodonts. The distribution of BM of Eocene–Oligocene European carnivorous mammals appears consistently multimodal before or after the MECO (Hartigan's dip test for multimodality p-values before and after MECO = 0.046 and 0.0005, respectively); carnivoramorphan and hyaenodont assemblages are multimodal pre-MECO and pre-GC, but not after these events (figure 1*g*–*j*; supplementary material, table S1p). No matter the distributions, mode(s) shift towards higher BMs over time for individual clades as well as the entire dataset (figure 1*e*–*j*; supplementary material, table S1p).

North American carnivorous mammals exhibit tempos and modes in their BM evolution throughout the Eocene−Oligocene that are distinct from those detected in Europe (figures 2; supplementary material, figures S10 and S11). In North America, BM variances are maximal during the first half of the Eocene, with a peak by the middle Lutetian. The specific diversity of carnivoramorphans sampled by Juhn *et al.* [17] is higher than that of hyaenodonts for nearly all NALMA of Eocene−Oligocene interval; the variance of carnivoramorphan BMs over this interval is also mostly constant (figure 2*c*,*d*). In North America, the MECO is not associated with a marked increase of the disparity of carnivoramorphan BM, unlike in Europe, but the late Bartonian is the first time when the variance of carnivoramorphan BMs surpasses that of hyaenodonts since the late Ypresian, on both regions. The variance of carnivoramorphan BMs increases towards the EOT, then stabilizes in North America, while it decreases and re-rises in Europe across the middle Priabonian-middle Rupelian interval (figures 2; supplementary material, figures S10 and S11).

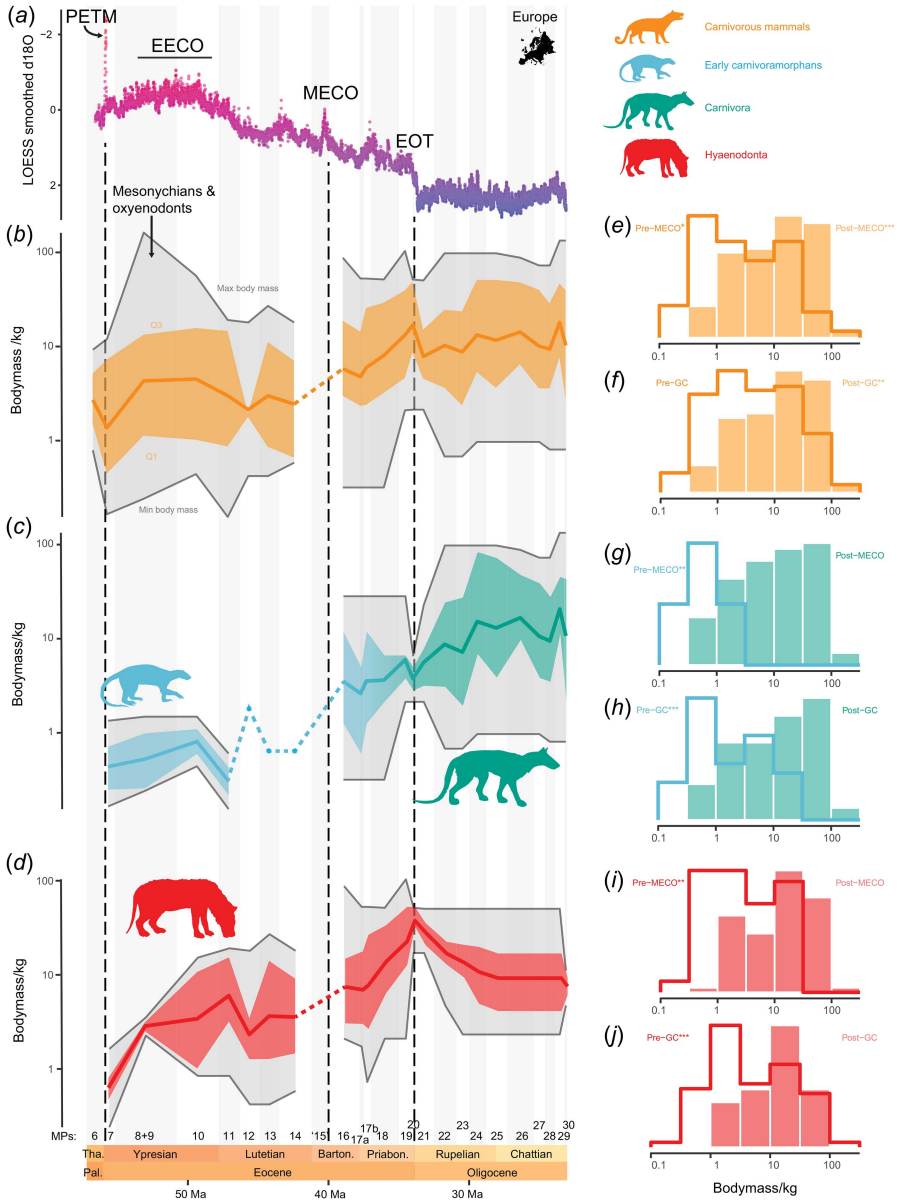

Figure 1. (*a*) Evolution of Palaeogene sea surface temperatures ($\partial^{18}O$, scale inverted) using a 10 pts LOESS smoothed data from Westerhold *et al.* [42]. (*b–d*) Evolution of the minimum, maximum, 1st and 3rd quartile, and mean BM (in kg, logarithmic scale) for European carnivorous mammals (*b*), European carnivoramorphans (*c*), and European hyaenodonts (*d*) during the Palaeogene (MP6 to MP30). (*e–j*) Comparison of BM distributions (log-scale) before (solid line) and after (bars) the MECO (MP15, early Bartonian) (*e*, *g*, and *i*) and before (solid line) and after (bars) the Eocene—Oligocene boundary (MP20) (*f*, *h*, *j*) for European carnivorous mammals (*e* and *f*), European carnivoramorphans (*g* and *h*), and European hyaenodonts (*i* and *j*), asterisks indicate significant multimodality (Hartigans' dip test). Abbreviations: EECO: Early Eocene Climatic Optimum; EOT: Eocene-Oligocene Transition; MECO: Middle Eocene Climatic Optimum; PETM: Palaeocene–Eocene Thermal Maximum. Silhouettes from Phylopic: *Mesonyx* by Zimices, *Vulpavus* by Steven Traver, *Daphoenodon* by Robert Bruce Horsfall, T. Michael Keesey, *Hyaenodon* by Robert Bruce Horsfall, Andrew Farke.

(b) Detection of evolutionary dynamics shifts

Among the evolutionary models tested on European data (Brownian motion, uniform trend, trends with node shifts, and OU), AICc favours a trend model with three node shifts 84% of the time for mbl trees and 66% of the time for Extended Hedman trees (supplementary material, table S1o). Brownian motion is recovered as the worst model, while OU or a trend model with two node shifts are the second best (supplementary material, figure S6). Yet the difference in AICc values among the best models is minimal (supplementary material, table S1o and figure S6). Many non-uniform trend models, including the two best ones (supplementary material, figures S7 and S8), recover a single trend regime for (most) carnivoramorphans and hyaenodonts (together or separately), with oxyenodonts and mesonychians often evolving under a different regime. Trend models with multiple node shifts and the OU models usually favour local changes in small clades only (e.g. *Dissacus*, *Eusmilus*, *Eofelis*). Therefore, our best models fail to recover long-lasting changes in the trend or the body size optimum of carnivoramorphans and hyaenodonts, despite ranges in BMs spanning two orders of magnitude after the MECO. We interpret this as resulting from the fluctuating BM ranges, with relatively stable mean values; evolutionary models will therefore fail to detect shifts in optima or trends within these clades.

The serialized Kolmogorov–Smirnov tests (figure 2*e–g*; supplementary material, table S1q–r) identify moment(s) at which the older and younger communities are most distinct from one another. For European taxa, such a point occurs just after the MECO

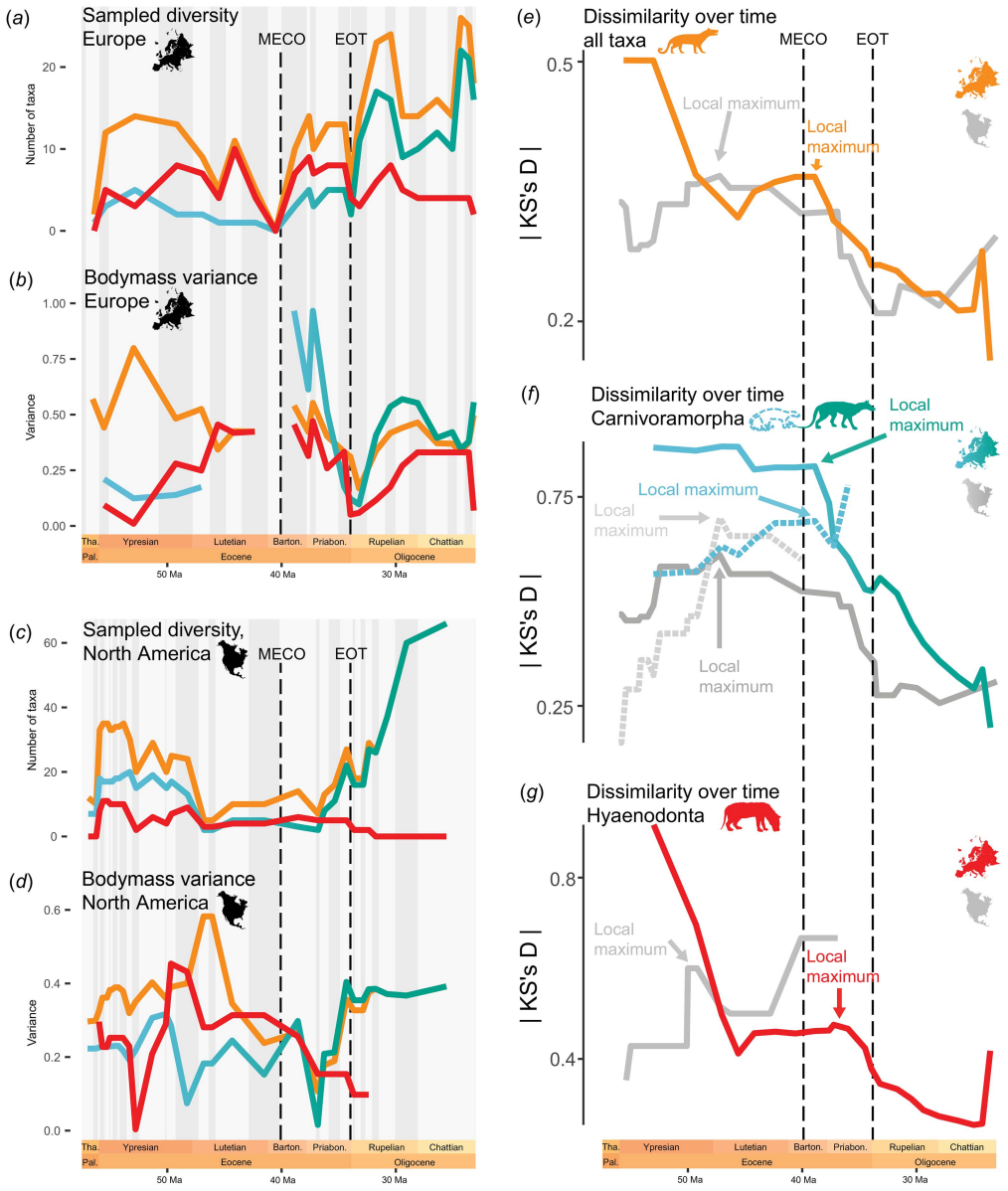

Figure 2. (*a*–*d*) Temporal evolution of the sampled diversity (*a* and *c*) and BM variances (*b* and *d*) of Palaeogene carnivorous mammals in Europe (*a* and *b*) and North America (*c* and *d*). (*e*–*g*) Visualization of the serialized two-sample Kolmogorov–Smirnov tests (dissimilarity of assemblages) for the entire European and North American datasets (*e*), carnivoramorphans (*f*), and hyaenodonts (*g*). The timing of local maxima is the signal of interest, indicating the moment when assemblages before and after are maximally distinct.

(middle-late Bartonian) when considering all taxa combined as well as hyaenodonts separately and is particularly evident among early carnivoramorphans (supplementary material, figure S4). The strength of BM change (i.e. the absolute value of Kolmogorov & Smirnov's D) before and after MECO is always larger than across the EOT, for any clade or for the whole dataset. This indicates that the early Bartonian is a breakpoint of primary importance for the evolution of BMs among the European carnivorous mammals. For North American taxa, the local maxima in the absolute value of Kolmogorov and Smirnov's D are found earlier: by the late Ypresian for hyaenodonts and by the early Lutetian for carnivoramorphans and the entire dataset. Yet, as is the case in Europe, the strength of BM change across MECO is larger than across the EOT.

4. Discussion

(a) The importance of the Middle Eocene Climatic Optimum

A series of taxonomic turnovers profoundly altered European carnivorous mammal assemblages over the course of the Palaeogene; the most important being the mid-late Ypresian (disappearance of the oxyaenodonts and mesonychians), the Bartonian-early Priabonian (appearance of Hyainailourinae, Hyaenodontinae, and Amphicyonidae), the EOT (the '*Grande Coupure*'; disappearance of endemic hyaenodonts and appearance of numerous carnivoran groups), and the Chattian (diversity drop) [3,43]. These events did not, however, result in pervasive changes in BM among the European carnivorous assemblages. Instead, our data reveal the early Bartonian (approx. 40 Ma) as the most important turning point, with the arrival of large carnivorous mammal

lineages in Europe (*Simamphicyon* and amphicyonids among carnivoramorphans, *Hyaenodon* probably immigrating from Asia, and hyainailourines probably immigrating from Africa) [3,44–46], mixing with endemic fauna [3,47]. This early Bartonian turnover has been linked to a 500 to 750 kyr long warming interval known as the MECO [48,49], which forced a drier, seasonal climate with more open habitats in Europe [50,51].

Although the MECO appears crucial for the BM evolution of carnivorans in Europe (figure 2), hyaenodonts remain taxonomically diverse [3,47] up until the '*Grande Coupure*.' The EOT is indeed marked by a drastic faunal [52] and floral shift, coeval with the large-scale Antarctic glaciation, global cooling, and changes in oceanic currents (e.g. [53,54]), which, through marine regressions, prompted (nearly) permanent connections between the former European archipelago and Asia [55]. This profoundly restructured European carnivorous fauna, as endemic hyaenodonts, early carnivoraforms, and hyainailourines went extinct, while nimravids, aeluroideans, and arctoideans dispersed and radiated [3,52]. In essence, the '*Grande Coupure*' resulted in replacing the typical, hyaenodont-dominated fauna in Europe by a carnivoran-dominated fauna through extinctions and migrations from Asia and Africa [3]. From the EOT onwards, hyaenodonts are mainly represented by the hypercarnivorous genus *Hyaenodon*. Thus, whereas the MECO at 40 Ma may have stimulated the radiation of European carnivoramorphans in terms of BMs, it took another 7 million years before carnivoramorphans replaced hyaenodonts as the dominant continental predators in both mass and diversity.

(b) Body mass dynamics challenges the competition hypothesis

The extraordinary diversity of carnivorans nowadays has its roots in the Palaeogene, when multiple clades of carnivorous mammals inhabited ecosystems of the Northern Hemisphere [1,5,6]. Multiple studies have singled out the versatility of the carnivoramorphan distal dental apparatus in driving their ultimate success [1,2,8,9]. However, it is now clear that the rise to dominance of carnivorans is diachronic, with long 'co-habitation' times in Europe between carnivoramorphans and diversified hyaenodonts [3], while such an overlap was much shorter in mainland North America [1,2]. Moreover, our results suggest a temporal decoupling between BM diversity and taxonomic diversity (figures 1,2). Because BM is a crucial ecological predictor in continental mammals (e.g. [11,56]), a strong increase in BM diversity within a clade will be linked to an increase in its ecological diversity. Therefore, our results suggest a decoupling between the ecological and the sampled taxic diversity in carnivoramorphans, the former starting to increase before the latter (figure 2), and within ecosystems hosting a wide diversity of hyaenodonts [3]. Contrary to what is seemingly found in North America [2], the BM of hyaenodonts did not decrease when that of carnivoramorphans increased in Europe, which suggests finer niche partitioning (figures 1,2). Finally, the long temporal gap between large mesonychians and oxyaenodonts and equally large carnivoramorphans (approx. 10.4 My for a BM of 20 kg, approx. 21.3 My for a BM of 100 kg) does not suggest a competitive replacement of the former by the latter (contra Jiangzuo *et al.* [57]), at least in Europe.

These spatiotemporal discrepancies in BM dynamics question the competition hypothesis as a universal mechanism behind the dominance of carnivorans and instead suggest that regional environmental factors were key. Indeed, the context within which North American and European carnivoramorphans radiated were markedly different, with the relatively larger diversity of hyaenodonts in Europe [2,3,58], as well as important differences in the structure, ecology, and evolution of prey [55,59]. Selonodont species became abundant in Europe during the Priabonian through the Second Intra-Eocene Mammal Turnover [60–62]. This transition happened earlier in North America, with the radiation of oreodonts [63], a clade fully absent from European ecosystems. Environmental changes between the two regions also appear diachronic: North America experienced aridification during the middle Eocene [63,64], while Europe became wetter between 40 and 38 Ma [65]. Although fully acknowledging that inferred BMs are just one facet through which the rise of carnivoramorphans should be studied, our results, combined with others [3,59,66], do not support intrinsic factors as the most likely hypothesis. Selective, climate-mediated turnovers rather than interclade competition appear to better fit the data presently at hand [59]. All things being equal, it might be possible that, akin to brachiopods and bivalves of much deeper times [67], carnivoramorphans and their 'competitors' were ships that pass in the night.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data, results, as well as the R script that generated all the analyses and figures are provided as electronic supplementary material and can be found in the online supplementary information on Figshare and on the Université de Liège institutional repository Orbi [68].

Supplementary material is available online [69].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. V.F.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, visualization, writing—original draft, writing—review and editing; F.S.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, writing—original draft; K.L.: data curation, investigation, methodology, writing—review and editing; B.M.: data curation, investigation, methodology, writing—review and editing; M.V.: data curation, investigation, methodology, writing—review and editing; N.C.: data curation, investigation, methodology, writing—review and editing; R.S.: conceptualization, writing—original draft, writing—review and editing; S.P.: data curation, investigation; T.S.: conceptualization, data curation, funding acquisition, project administration, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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