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Patterns of maximum body size evolution in Cenozoic land mammals: eco-evolutionary processes and abiotic forcing

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There is accumulating evidence that macroevolutionary patterns of mammal evolution during the Cenozoic follow similar trajectories on different continents. This would suggest that such patterns are strongly determined by global abiotic factors, such as climate, or by basic eco-evolutionary processes such as filling of niches by specialization. The similarity of pattern would be expected to extend to the history of individual clades. Here, we investigate the temporal distribution of maximum size observed within individual orders globally and on separate continents. While the maximum size of individual orders of large land mammals show differences and comprise several families, the times at which orders reach their maximum size over time show strong congruence, peaking in the Middle Eocene, the Oligocene and the Plio-Pleistocene. The Eocene peak occurs when global temperature and land mammal diversity are high and is best explained as a result of niche expansion rather than abiotic forcing. Since the Eocene, there is a significant correlation between maximum size frequency and global temperature proxy. The Oligocene peak is not statistically significant and may in part be due to sampling issues. The peak in the Plio-Pleistocene occurs when global temperature and land mammal diversity are low, it is statistically the most robust one and it is best explained by global cooling. We conclude that the macroevolutionary patterns observed are a result of the interplay between eco-evolutionary processes and abiotic forcing.

1. Introduction

The ecological opportunity provided by the end Cretaceous extinction, which eliminated dinosaurs and other large-bodied taxa, led to a rapid increase in mammal body size [1–4]. Within 30 Myr, mammals ranged in size from 2 g to over 10 tons, filling a variety of ecological niches [2]. This pattern of rapid exponential growth, followed by a plateau as physiological, ecological and life-history factors imposed constraints on large-bodied mammals, is found on all continents during the Cenozoic. This led to the suggestion that physical drivers such as

temperature and land mass may have affected maximum size fluctuations through time [2], even if eco-evolutionary processes such as filling of niches by specialization and competition have most probably driven the early phase of rapid body size increase [5]. There is currently little agreement as to which is the dominant effect as opposite conclusions have been reached by studies using different approaches [2,3,6–8].

Two main hypotheses encapsulate the major factors most widely thought to underlie the evolution of mammal body size, Cope's rule and Bergmann's rule. Cope's rule refers to the tendency of mammal clades to increase in size throughout their evolutionary history, an observation widely attributed to Cope [3,9–12]. Alroy [1] provided evidence supporting Cope's rule showing that, based on body mass estimates, North American fossil mammal species are on average 9.1% larger than older species in the same genera. Raia *et al.* [3] suggest that Cope's rule is explained by increasing clade-level niche expansion during the Cenozoic because of ecological specialization of species rather than active selection for larger size.

Bergmann's rule refers to the tendency of the body size of species within a taxonomic group to be larger in colder environments, both across time and space. It is often considered to imply that evolution of larger size is driven by factors associated with climate, based on the physiological benefits of large body volume under cold conditions [13]. Not only cold, but also dry and seasonally harsh climatic conditions can favour large body size through benefits in increased fasting endurance, increased ability to migrate following favourable conditions and decreased loss of water [13,14]. Other hypotheses of abiotic, environmental factors affecting body size evolution have concentrated on the possible effects of atmospheric oxygen percentage and land area on maximum body size [6,7,15,16].

Janis [17] and later Smith *et al.* [2] already noted similar evolutionary trends among mammals across the continents and related them causally to global climatic and vegetation changes as well as dispersal events during the Cenozoic. Jernvall *et al.* [18] also showed highly congruent trends between three continents in the Cenozoic history of mammal diversity and disparity of dental morphology based on data compiled by Savage & Russel [19]. The observation of congruent evolutionary patterns on separate continents is thus well established and deserves attention. To explore the patterns in more detail, we therefore investigated the patterns of maximum size evolution in terrestrial mammal orders and analysed them in relation to proxy data for global temperature, atmospheric oxygen content and taxonomic diversity. In addition to analysing the maximum size evolution for each order, we analysed the frequency at which orders reached their maximum size in successive time intervals at the subepoch level. This approach allowed us to separate between the patterns of maximum size evolution of the orders and the timing at which maximum size typically occurs in mammals. Any congruence in the timing of maximum size can then be evaluated against the hypotheses of how eco-evolutionary processes and abiotic forcing have affected mammal body size evolution during the Cenozoic.

2. Material and methods

Our analyses used a database of the largest mammalian species in each order for each subepoch of the Cenozoic on each different continent (Mammoth v1.0) [2]. The mass estimates provided in Mammoth were obtained in a variety of ways. For some mammal species, estimates were directly available from the primary or the secondary literature or from online databases (Paleobiology Database (PaleoBD), http://paleobiodb.org/cgi-bin/bridge.pl); New and Old Worlds Database of Fossil Mammals (NOW), University of Helsinki, Mikael Fortelius (coordinator), http://www.helsinki.fi/science/now/). Primary literature was preferentially used as the source. For other species, body mass was estimated using either molar or limb measurements obtained from the literature, unpublished compilations provided by authorities, extracted from online databases or measured directly from museum specimens. Molars, in particular, provide a robust basis for estimating mass for both fossil and modern mammals [20]. Mass was estimated from skeletal or dental measurements using ordinal or family specific allometric regressions based on extant taxa. Fossil ages were standardized using the midpoint for each Cenozoic subepoch on the geological time scale [21].

We plotted maximum size for long-duration orders globally and on continents separately, and analysed whether these patterns are correlated with any abiotic variable (atmospheric oxygen percentage [15], global land area [22], or $\delta^{18}O$ fraction in global marine isotope record [23]). For the present purposes, the analysis was restricted to terrestrial habitats and well sampled, terrestrial placental mammal orders with long durations in the fossil record. We used data for North America, Eurasia, Africa and South America. Australia and Antarctica were excluded because of lack of extensive Cenozoic mammal fossil records. The South American record is incomplete and results are only shown for the maximum size trends of the orders.

We analysed the frequency of the largest maximum body size occurrence in terrestrial placental mammal orders on each subepoch of the Cenozoic in order to examine whether they typically follow a specific pattern of maximum size occurrence or whether there are times when multiple orders tend to reach maximum size simultaneously. This was done by counting the number of orders that reach their maximum size for a given subepoch, both globally and on continents separately, and then calculating the ratio of the number of orders reaching their maximum to the total number of orders present in a given subepoch. Hereafter, we refer to this metric as maximum size frequency (MxSF). We used a likelihood ratio (LR) test [3,24] to evaluate whether there are statistically significant peaks in the MxSF through time globally and on the major continents separately. For the LR test, an average MxSF was calculated by dividing the sum of the numbers of maximum size orders by the sum of the numbers of orders present over the whole time series, and this average MxSF value was used to calculate a predicted, unbiased number of maximum size orders for each time bin based on the number of orders present. Likelihood values for observed and predicted numbers of maximum size orders of the total numbers of orders present were then calculated for each time bin. The LRs were then calculated comparing the likelihoods of the observed number of maximum size orders against the likelihoods of the predicted number of maximum size orders for each time bin.

We examined the effect of evolutionary time on MxSF by plotting the number of orders that have their maximum size against the time from origination to maximum size in those orders both in absolute time (Myr = millions of years) and generations (Mgen = millions of generations; see [25] for the method of estimating generation times).

We did a multiple regression analysis in order to find out whether any of the abiotic factors (atmospheric oxygen percentage, global land area or $\delta^{18}O$ fraction in global marine isotope record), absolute time in Myr or number of orders (ordinal diversity) correlate with the temporal pattern of MxSF. The MxSF

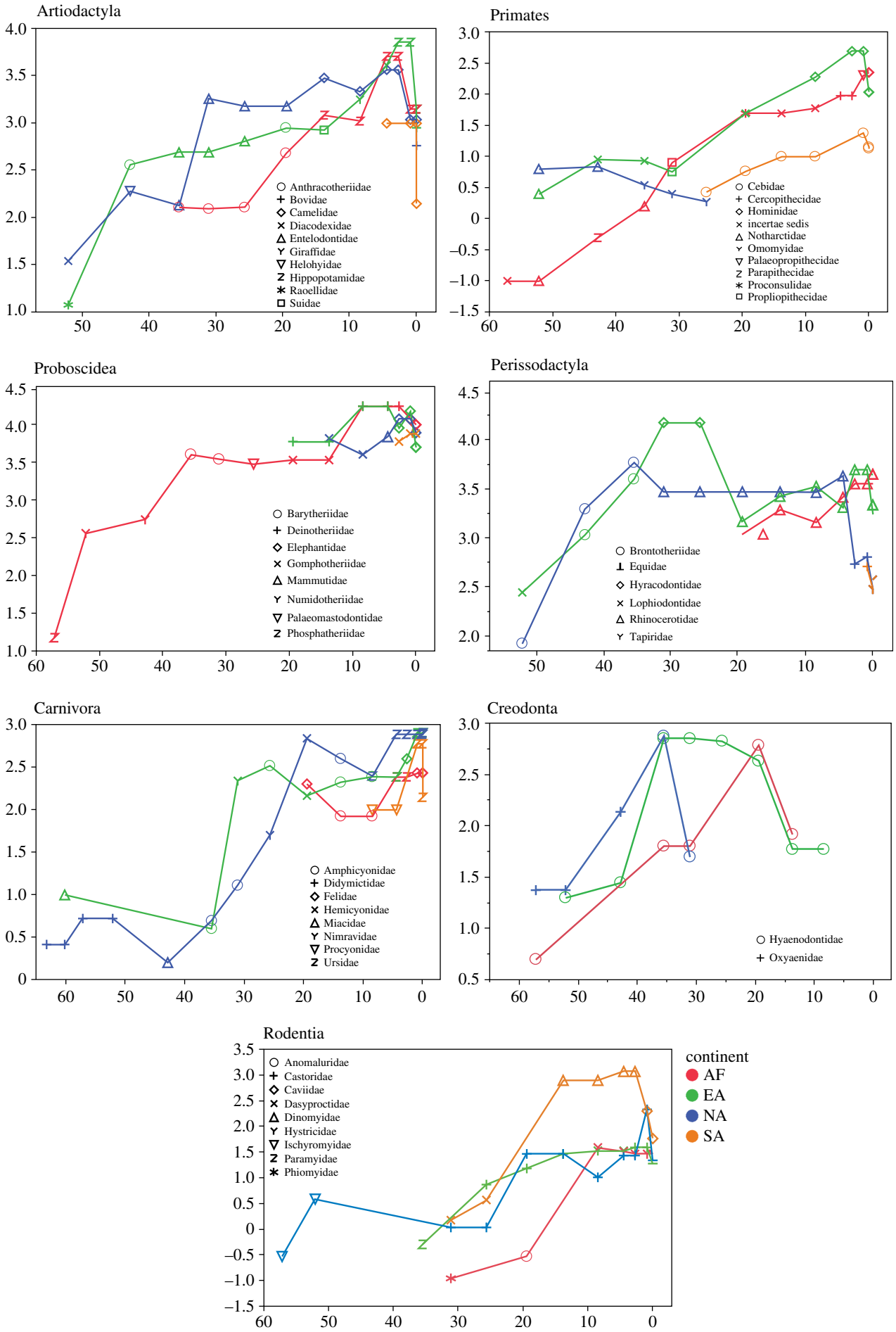

Figure 1. Maximum body size in major terrestrial mammal orders on continents throughout the Cenozoic. *x*-axis = time in Myr, *y*-axis = maximum body mass (log-transformed).

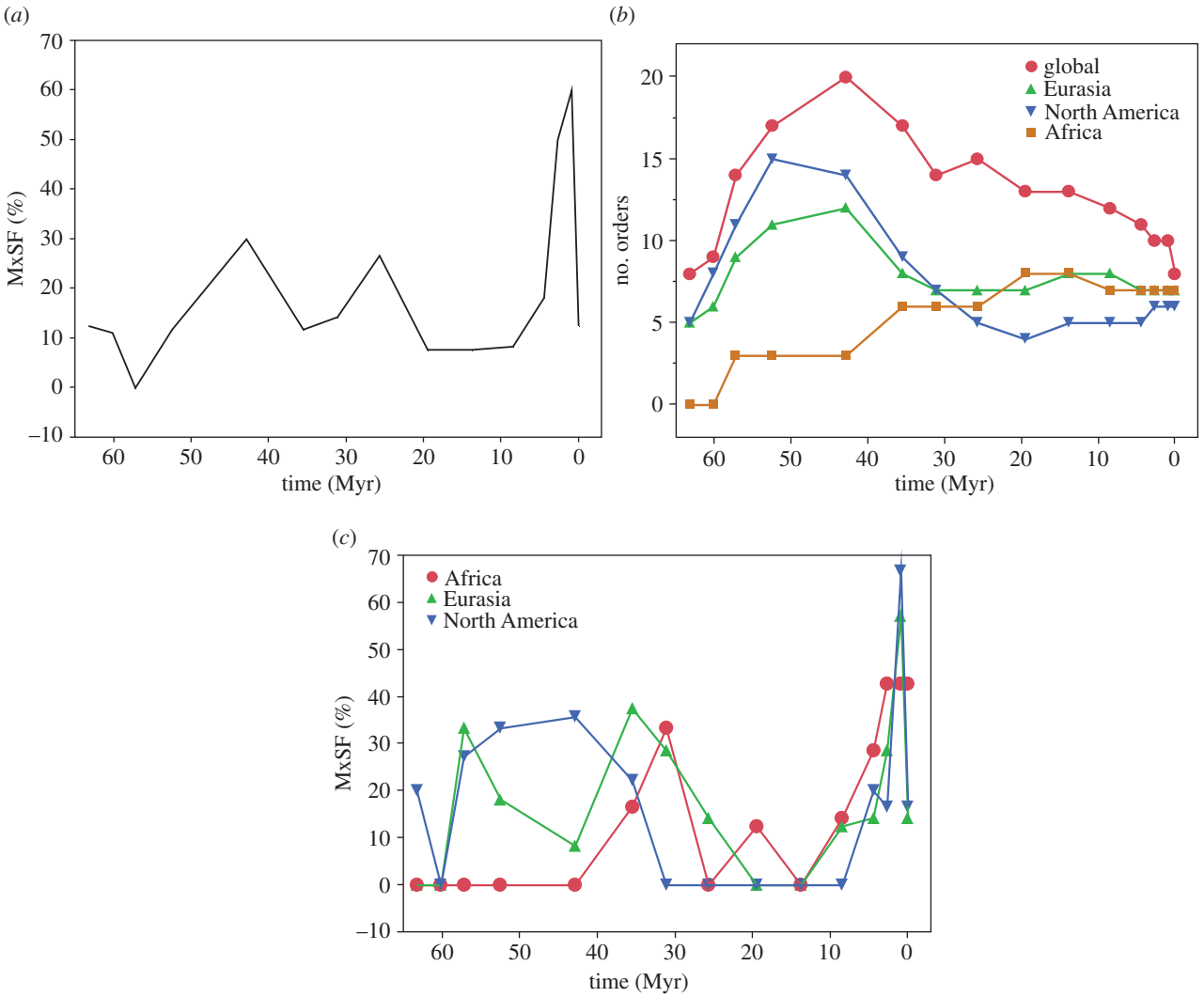

Figure 2. MxSF through time. (*a*) Global MxSF as percentage of terrestrial mammal orders. (*b*) Ordinal diversity as number of mammal orders included in this study. (*c*) MxSF in Africa, Eurasia and North America.

values were not log-transformed for this analysis. The multiple correlation analysis of MxSF and the predicting variables were done separately for the early phase of exponential maximum body size evolution (from the beginning of the Cenozoic 65.5 Ma to the Late Eocene 33.9 Ma) and for the time since the saturation of maximum size evolution (from Late Eocene 33.9 Ma to present), based on the results by Smith *et al.* [2]. By doing this, we seek to answer the question of whether the timing of maximum size occurrence in mammal orders is driven by abiotic factors or only by basic eco-evolutionary patterns. If there are significant temporal peaks of ordinal MxSF, and if these peaks correlate with time, ordinal diversity or abiotic factors (climate, land area or atmospheric oxygen), we can conclude that those factors have played a significant role in the maximum size evolution of mammals.

3. Results

The major orders of large terrestrial mammals show mostly relatively similar patterns of maximum size evolution throughout the Cenozoic across the major continents (figure 1), and their maximum size is in most cases significantly correlated with the global $\delta^{18}O$ data and land area estimates through the Cenozoic (electronic supplementary material, table S1). This result is consistent with the overall global pattern of maximum size evolution in mammals [2]. Within the orders, there is typically no single clade which would dominate the maximum size range, but instead there are multiple clades which present the maximum size at different times. Repeated replacements of clades having maximum size within the orders throughout their Cenozoic evolution are evident in Perissodactyla (Lophiodontidae—Brontotheriidae—Hyracodontidae—Rhinocerotidae), in Proboscidea (Phosphatheriidae—Numidotheriidae—Barytheriidae—Deinotheriidae—Elephantidae), in Artiodactyla (Diacodexidae—Anthracotheriidae—Entelodontidae—Camelidae/Hippopotamidae), in Carnivora (Miacidae—Amphicyonidae—Ursidae), in Creodonta (Oxyaenidae—Hyaenodontidae), in Rodentia (Ischyromyidae—Castoridae—Dinomyidae) and in Old World Primates (Notharctidae—Parapithecidae/Propliopithecidae—Hominidae).

The MxSF shows three global peaks during the Cenozoic: Middle Eocene, Late Oligocene and Late Pliocene–Pleistocene (figure 2*a*; electronic supplementary material table S2). The Middle Eocene and the Late Pliocene–Pleistocene peaks are statistically significant based on the LR test (table 1), whereas the Late Oligocene peak is not quite significant. The global MxSF peaks are reflected on the Eurasian and North American continents, but not in Africa, which lacks extensive Palaeogene mammal record (figure 2). The Pleistocene peak is statistically significant and very prominent in Eurasia and North America,

Table 1. Likelihood ratio values for MxSF through the Cenozoic. (LR = Likelihood ratio. Significant LR values are given in bold.)

continent	subepoch	time (Myr)	no. orders present	no. orders with max. size	MxSF (%)	LRT
global	Early Palaeocene	63.3	8	1	13	0.498
	Middle Palaeocene	60.2	9	1	11	0.379
	Late Palaeocene	57.25	14	0	0	0.022
	Early Eocene	52.5	17	2	12	0.189
	Middle Eocene	42.9	20	6	30	**32.779**
	Late Eocene	35.55	17	2	12	0.189
	Early Oligocene	31.15	14	2	14	0.43
	Late Oligocene	25.715	15	4	27	6.489
	Early Miocene	19.5	13	1	8	0.127
	Middle Miocene	13.79	13	1	8	0.127
	Late Miocene	8.47	12	1	8	0.167
	Early Pliocene	4.465	11	2	18	0.977
	Late Pliocene	2.703	10	5	50	**113.74**
	Pleistocene	0.9035	10	6	60	**506.954**
	Holocene	0.005	8	1	13	0.498
	summary		191	35	18.3	
Eurasia	Early Palaeocene	63.3	5	0	0	0.255
	Middle Palaeocene	60.2	6	0	0	0.194
	Late Palaeocene	57.25	9	3	33	7.916
	Early Eocene	52.5	11	2	18	1.013
	Middle Eocene	42.9	12	1	8	0.170
	Late Eocene	35.55	8	3	38	**10.403**
	Early Oligocene	31.15	7	2	29	3.022
	Late Oligocene	25.715	7	1	14	0.668
	Early Miocene	19.5	7	0	0	0.148
	Middle Miocene	13.79	8	0	0	0.112
	Late Miocene	8.47	8	1	13	0.508
	Early Pliocene	4.465	7	1	14	0.668
	Late Pliocene	2.703	7	2	29	3.022
	Pleistocene	0.9035	7	4	57	**61.849**
	Holocene	0.005	7	1	14	0.668
	summary		116	21	18.1	
North America	Early Palaeocene	63.3	5	1	20	0.953
	Middle Palaeocene	60.2	8	0	0	0.108
	Late Palaeocene	57.25	11	3	27	2.630
	Early Eocene	52.5	15	5	33	**12.662**
	Middle Eocene	42.9	14	5	36	**16.721**
	Late Eocene	35.55	9	2	22	1.199
	Early Oligocene	31.15	7	0	0	0.143
	Late Oligocene	25.715	5	0	0	0.249
	Early Miocene	19.5	4	0	0	0.329
	Middle Miocene	13.79	5	0	0	0.249
	Late Miocene	8.47	5	0	0	0.249
	Early Pliocene	4.465	5	1	20	0.953
	Late Pliocene	2.703	6	1	17	0.722

(*Continued.*)

Table 1. (*Continued.*)

continent	subepoch	time (Myr)	no. orders present	no. orders with max. size	MxSF (%)	LRT
	Pleistocene	0.9035	6	4	67	**40.412**
	Holocene	0.005	6	1	17	0.722
	summary		111	23	20.7	
Africa	Early Palaeocene	63.3	0	0	0	1.000
	Middle Palaeocene	60.2	0	0	0	1.000
	Late Palaeocene	57.25	3	0	0	0.218
	Early Eocene	52.5	3	0	0	0.218
	Middle Eocene	42.9	3	0	0	0.218
	Late Eocene	35.55	6	1	17	0.232
	Early Oligocene	31.15	6	2	33	1.132
	Late Oligocene	25.715	6	0	0	0.048
	Early Miocene	19.5	8	1	13	0.084
	Middle Miocene	13.79	8	0	0	0.017
	Late Miocene	8.47	7	1	14	0.140
	Early Pliocene	4.465	7	2	29	0.681
	Late Pliocene	2.703	7	3	43	3.321
	Pleistocene	0.9035	7	3	43	3.321
	Holocene	0.005	7	3	43	3.321
	summary		78	16	20.5	

whereas the significant Eocene peak appears somewhat earlier in North America (in the Early–Middle Eocene) than in Eurasia (in the Late Eocene) (table 1). LR values of greater than or equal to 8 indicate significant peaks [24].

The Eocene peak of MxSF parallels the particularly high ordinal diversity during this period, even if MxSF is in general not significantly correlated with diversity, and is most prominent in North America, which has a good Palaeogene mammal record. This peak comprises archaic orders which originated early and became extinct after the Eocene ('Condylarthra', Dinocerata, Mesonychia, Plesiadapiformes, Taeniodonta and Tillodontia). The Oligocene peak is barely significant and it does not coincide with any peak in diversity but follows climatic deterioration after the Eocene. The statistically most robust peak in the MxSF in mammals is that of the Late Pliocene–Pleistocene, where 50% of the orders have their maximum size. It comprises some of the most diverse extant large terrestrial mammal orders (Carnivora, Primates and Artiodactyla), but also some endemic South American orders (Xenarthra, Litopterna and Notoungulata). Also Proboscidea, Perissodactyla and Rodentia include notably large sized species in the Late Pliocene and especially Pleistocene, but their maximum size peaks occur earlier. The Late Pliocene–Pleistocene peak does not correspond with high ordinal diversity (figure 2*b*).

The number of orders with their time of maximum size evolution is shown in both absolute time (Myr) and generations (Mgen) in figure 3 (see the electronic supplementary material table S3 for the data). The strong peak in the orders which evolved their maximum size relatively fast in 0–10 Mgen comprises mostly the orders which have their maximum size in the Eocene. However, the orders which have their maximum size in the Plio-Pleistocene include ones which evolved their maximum size in 5–10 Mgen, 10–20 Mgen and 20–30 Mgen (figure 3). This suggests that although the 0–10 Mgen peak in the evolutionary time in generations parallels the Middle Eocene peak in MxSF, evolutionary time in generations fails to explain the Plio-Pleistocene peak in MxSF conclusively.

The variable that explains most of the variation in MxSF in the period after the saturation point of the maximum size evolution [2] (33.9 Ma–present) is the global $\delta^{18}O$ fractions from the ocean isotope record (table 2). No other variable shows significant correlation with the MxSF. In the early phase (65.5–33.9 Myr ago), none of the variables (time, ordinal diversity or the abiotic variables) show significant correlation with the MxSF. The timing of the MxSF peaks clearly shows that the Middle Eocene peak corresponds with rapid diversification of mammal orders (Cope's rule), whereas the Oligocene and the Pliocene–Pleistocene peaks occur at times of low diversity and correspond instead with harsh climatic conditions (Bergmann's rule).

4. Discussion

Maximum body size in major terrestrial land mammal orders shows coarsely similar global and regional trajectories with strong increase in maximum size especially in the early phase and peaking of maximum size in the Pleistocene. Perissodactyla, Proboscidea and Rodentia are different in that their global maximum size peak occurs much earlier than the Plio-Pleistocene (for Perissodactyla in Oligocene, for Proboscidea in Late Miocene and for Rodentia in Pliocene). Primates have an almost continuously increasing maximum size trend until the Pleistocene except in North America.

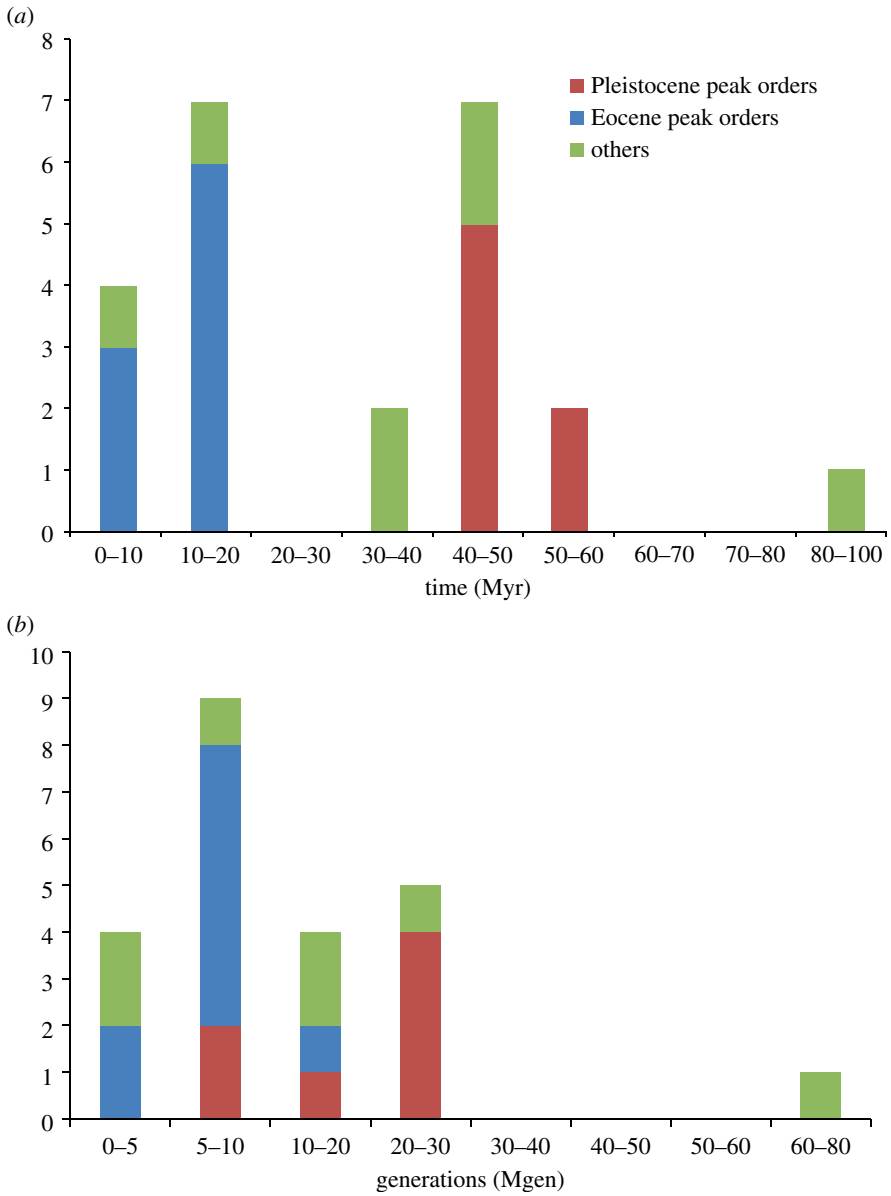

Figure 3. Occurrence of maximum size in mammal orders since time of origination in (*a*) absolute time and (*b*) in Mgen. *y*-axis = number of orders.

Maximum size occurs in several clades within an order rather than in a single clade during the evolution of the orders. This is evident in Perissodactyla, Proboscidea, Artiodactyla, Carnivora and in Old World Primates. This finding suggests that maximum size evolution is not clade-specific, and would further indicate that there are universal driving forces behind the maximum size evolution of mammals which have affected maximum size evolution similarly within the orders despite taxonomic diversity. These driving forces are either eco-evolutionary processes (filling of niches by specialization and competition) or abiotic changes (climatic forcing).

The peaks in MxSF reflect patterns of body size evolution at high taxonomic levels. Globally, there are two statistically significant MxSF peaks, in the Middle Eocene and in the Late Pliocene–Pleistocene. The Middle Eocene peak is caused by archaic mammal orders ('Condylarthra', Mesonychia, Pantodonta, Plesiadapiformes, Tillodonta, Taeniodonta and Dinocerata). The Middle Eocene peak is most prominent in North America, possibly because of more complete and better sampled fossil record, especially compared to the mostly lacking record in Africa. This sampling bias may also explain why there is no peak in MxSF (or in diversity of mammal orders) in the Eocene of Africa. A significant Eocene peak in MxSF occurs in Eurasia as well but is somewhat later than the one in North America (Late Eocene). The peaking of the MxSF in the Middle Eocene is consistent with the other recent findings [2,4], which indicate a rapid initial burst in body size evolution in mammals after the Late Cretaceous mass extinction through ecological specialization before reaching a 'cut-off point' in the Middle Eocene. The peak in MxSF in the Late Oligocene is not statistically significant and it is driven by Eurasian and African data. It is probably caused by the decrease in ordinal diversity after the Eocene maximum and the appearance of some very large forms in a few mammal orders. Perissodactyla is perhaps the most notable case because their ultimate maximum size peak is clearly in the Oligocene with the giant indricotheres. The Oligocene peak in MxSF may be a sampling artefact, but it may also be connected to the climatic cooling from the Late Eocene to Oligocene [26,27].

The Late Pliocene–Pleistocene peak in MxSF is very prominent and statistically robust based on the LR test, and it involves large land mammal orders representing all the trophic groups. This peak is too strong to be explained merely by filling of larger body size niches in the orders which have survived

Table 2. Multiple regressions analysis of MxSF with time, number of orders and the abiotic variables ($\delta^{18}O$, global land area and atmospheric oxygen %) in the early phase of exponential growth (65.5–33.9 Myr ago) and after the global maximum size saturation (33.9 Ma to present). (Note that for Africa there are data only for the period from 33.9 Ma to present. AIC = Akaike information criterion. Significant positive correlations are given in bold.)

continent	time period	parameter	*p*-value	R^2	AIC
Eurasia	33.9 Myr to present	time (Myr)	0.39	0.12	79.42
		no. orders present	0.28	0.19	78.81
		$\delta^{18}O$	**0.02**	**0.62**	**72.71**
		land area	0.56	0.06	80
		atmospheric oxygen %	0.57	0.06	80
	65.5–33.9 Myr ago	time (Myr)	0.23	0.33	65.07
		no. orders present	0.53	0.1	66.81
		$\delta^{18}O$	0.46	0.14	66.54
		land area	0.19	0.38	64.6
		atmospheric oxygen %	0.44	0.16	66.46
North America	33.9 Myr to present	time (Myr)	0.08	0.42	79.61
		no. orders present	0.47	0.09	83.23
		maximum body size (kg)	0.05	0.39	92.96
		$\delta^{18}O$	**0.006**	**0.75**	**72.95**
		land area	0.14	0.33	80.8
		atmospheric oxygen %	0.2	0.26	81.58
	65.5–33.9 Myr ago	time (Myr)	0.39	0.19	63.33
		no. orders present	0.13	0.48	60.63
		$\delta^{18}O$	0.9	0.004	64.55
		land area	0.9	0.005	64.54
		atmospheric oxygen %	0.47	0.14	63.69
Africa	33.9 Myr to present	time (Myr)	0.24	0.19	83.85
		no. orders present	0.69	0.02	85.53
		$\delta^{18}O$	**0.02**	**0.57**	**78.2**
		land area	0.41	0.1	84.81
		atmospheric oxygen %	0.27	0.17	84.09
global	33.9 Myr to present	time (Myr)	0.18	0.28	79.16
		no. orders present	0.1	0.39	77.86
		$\delta^{18}O$	**0.01**	**0.66**	**73.11**
		land area	0.25	0.22	79.85
		atmospheric oxygen %	0.41	0.12	80.8
	65.5–33.9 Myr ago	time (Myr)	0.39	0.19	59.88
		no. orders present	0.35	0.22	59.67
		$\delta^{18}O$	0.67	0.05	60.81
		land area	0.89	0.006	61.09
		atmospheric oxygen %	0.23	0.34	58.67

until Neogene and Quaternary times, especially because it does not coincide with any peak in diversity. Moreover, evolutionary time in generations does not conclusively explain the Plio-Pleistocene MxSF peak because it comprises orders which evolved their maximum size in 0–10 Mgen but also orders with much longer term maximum size evolution of 20–30 or 20–30 Mgen. Because evolutionary time alone does not explain the peaks in MxSF, it is more likely that abiotic (climatic) forcing rather than constant evolutionary increase in maximum size through time causes the pattern in MxSF.

Maximum body size of long-duration orders over the Cenozoic and the MxSF since the Eocene are significantly positively correlated with $\delta^{18}O$, and $\delta^{18}O$ alone explains most of the variation in the MxSF data since the saturation point of maximum body size evolution (33.9 Ma to present). These findings support the hypothesis that global climate has had an effect on maximum body size evolution of mammals through the Cenozoic, although the patterns of maximum size and MxSF are not parallel to each other. Global land area is significantly correlated with the

maximum size trajectories of long-duration mammal orders over the whole Cenozoic, but MxSF does not show any significant correlation with the land area. Atmospheric oxygen percentages do not show statistically significant correlations with MxSF, further supporting the conclusion of Smith *et al.* [2] that oxygen does not explain significantly the variation in global maximum mammalian body size.

We suggest that the strong seasonality and the dramatic glacial–interglacial shifts in the global temperatures [25] caused environmental conditions that favoured the evolution of particularly large body size in several modern orders of mammals in the Late Pliocene to Pleistocene. Note that the 'Late Pliocene' *sensu* [21] is partly considered to belong to the Early Pleistocene in the chronostratigraphic correlation table [28], and thus the Late Pliocene to Pleistocene maximum size peak could also be considered the 'Pleistocene peak' or the 'Ice Age peak' in a broader sense. The orders attaining their globally largest body size in the Late Pliocene or Pleistocene are Carnivora, Primates, Artiodactyla, Xenarthra, Litopterna and Notoungulata. In addition, the maximum body size of Proboscidea continues from the Late Miocene to Late Pliocene, and the Pleistocene forms were not much smaller. In fact, the proboscideans occupied maximum size niches in most continents (Africa, Eurasia and North America) for most of the Neogene, with some fluctuation in the maximum size. If the gigantic Oligocene indricotheriid perissodactyls, which can be seen as a very specialized clade among the Perissodactyla, are excluded, the rest of Perissodactyla had their largest body size in the Late Pliocene and Pleistocene in the form of the elasmotherine rhinoceroses of the genus *Elasmotherium*. The obvious dominance of this 'Ice Age peak' in the occurrence of the largest sized species in several terrestrial mammal orders contemporaneously indicates that the cold, dry and dramatically variable climatic conditions of the Pleistocene Ice Age have favoured large size.

After the Middle Eocene peak, the MxSF does not follow a continuously increasing trend. Instead, it shows a pattern of peaks consistent with the hypothesis of the effect of climatic cooling on gigantism in terrestrial mammal orders predicted by Bergmann's rule. Salient features of the pattern include the low values from the Early Miocene to the Late Pliocene, especially in times of relatively warm climate like the Early and Middle Miocene, the particularly strong peak of MxSF in the Late Pliocene to Pleistocene, and the significant correlation of relative maximum size occurrence with climatic proxy data.

The finding that climatic factors have had a prominent effect on maximum size after the evolutionary burst of mammal evolution is consistent with the results of Raia *et al.* [3], which show that the effects of Cope's rule and Bergmann's rule can be separated and shown to be independent factors contributing to mammal body size evolution. We reached the same conclusion by analysing the MxSF pattern. Moreover, Raia *et al.* [4] show that both taxonomic and phenotypic (i.e. body size) evolution were drastic and highly correlated in the Palaeogene but not in the Neogene. This is in concert with our interpretation that the adaptive radiation of the Palaeogene led to the high occurrence of the largest sized members in several orders in the Eocene, but that there was no such radiation behind the Pliocene–Pleistocene MxSF peak. Taken together, this study and [2] show that global changes in land area and temperature during the Cenozoic seem to have profoundly affected patterns of body size evolution both within and across higher taxa of mammals. It remains to be seen whether these factors were of similar importance in driving body size evolution in other endothermic and ectothermic clades.

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Data accessibility. All the data used in this study are publically available in the electronic supplementary material.

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