The Evolution of Maximum Body Size of Terrestrial Mammals

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The Evolution of Maximum Body Size of Terrestrial Mammals

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The extinction of dinosaurs at the Cretaceous/Paleogene (K/Pg) boundary was the seminal event that opened the door for the subsequent diversification of terrestrial mammals. Our compilation of maximum body size at the ordinal level by sub-epoch shows a near-exponential increase after the K/Pg. On each continent, the maximum size of mammals leveled off after 40 million years ago and thereafter remained approximately constant. There was remarkable congruence in the rate, trajectory, and upper limit across continents, orders, and trophic guilds, despite differences in geological and climatic history, turnover of lineages, and ecological variation. Our analysis suggests that although the primary driver for the evolution of giant mammals was diversification to fill ecological niches, environmental temperature and land area may have ultimately constrained the maximum size achieved.

For the first 140 million years of their evolutionary history, mammals were small and occupied a fairly narrow range of body sizes and niches (*1*, *2*). Although diverse feeding adaptations evolved by the middle Mesozoic, and larger mammals may have preyed on small dinosaurs (*3*, *4*), their body size range extended only from ~3 to 5 g to ~10 to 15 kg (*4*, *5*). This restricted range almost certainly constrained the ecological roles of early mammals in paleocommunities. For example, herbivory was probably limited; allometric, anatomical, and physiological constraints set a lower threshold of ~5 kg for ruminant herbivores (*6*). The Cretaceous/Paleogene (K/Pg) mass extinction, which eliminated nonavian dinosaurs as well as many vertebrate, plant, and invertebrate taxa, was followed by a wholesale reorganization of ecological communities (*7*). It marked the onset of rapid morphological, ecological, and phylogenetic diversification in terrestrial mammals that led to an expansion in mass by four orders of magnitude and the occupation of a full range of ecological roles (*8*).

Here we analyze maximum size of terrestrial mammals across different continents, taxonomic groups, phylogenetic lineages, and feeding guilds. We compiled and analyzed data on the maximum body size of each taxonomic order in each sub-epoch on each continent over their entire evolutionary history (*9*). Information about body mass was obtained for fossil taxa from primary sources or estimated directly from taxon-specific allometric regressions based on measurements of teeth or limbs (table S1). Because of taphonomic considerations, we focused on the maximum size achieved by each order; it tends to be reported in the literature and is robustly related to the overall body size distribution and hence to the mean and median body size (*10*). Fossil ages were standardized using the midpoint for each Cenozoic sub-epoch on the Gradstein geological time scale (*11*). Diversity estimates were extracted from the Paleobiology Database (*12*), using the range-through option for each interval of time. We conducted simulations to assess the potential effect of sampling on the probability of detecting the largest mammal; including as few as 10% of fossil sites yielded nearly 100% probability of recovering the largest mammal on a continent (fig. S1).

The data show that the pattern of body size evolution was similar across continents, lineages, and trophic groups. Globally, and on each continent, maximum body mass increased rapidly during the early Cenozoic (Fig. 1). By the late Eocene [42.9 million years ago (Ma)], maximum body mass was three orders of magnitude larger than at the beginning of the Cenozoic. Our results are consistent with a previous analysis of North American mammals (*5*, *8*). The upper limit of ~17 tons was reached in the early Oligocene of Eurasia, with the evolution of *Indricotherium transouralicum* (Perissodactyla) and again in the Miocene by several *Deinotherium* species (Proboscidea) in Eurasia and Africa (Fig. 1B; fig. S2); North America never supported a mammal of this size. Strikingly, the overall pattern was not driven by a single taxon or an individual continent. At one time or another, six different orders and three of the four continents contained the largest mammal. Because of the current paucity of data for South America, body mass values for this continent should be considered an underestimate; nonetheless, results illustrate the same general trends. Contrary to earlier suggestions (*13*–*15*), increases in body mass were not driven by increasing generic or ordinal diversity: Mammals were not consistently larger when they were more diverse (*9*) (fig. S3).

We tested two hypotheses for the evolution of maximum body size. The first is a simple growth model, in which maximum body size (M) evolves following a geometric Brownian motion, that is, an unconstrained random walk on the logarithmic scale. This model implicitly assumes that niche space is uniformly distributed. Under a random walk, M is predicted to increase as a power law of the form $\log M = M_0 t^{\gamma}$, where M_0 is initial maximum body size, t is time, and $\gamma = 1/2$, so that maximum body size increases as the square root of time (*15*).

The second model has growth saturating over time, reflecting limits of resources or physiological, allometric, biomechanical, or ecological constraints, such as the slower life histories of larger mammals. Thus, the initial change in body mass M with time is proportional to body mass (that is, $\frac{dM}{dt} \propto M$) and increases at some intrinsic rate α. However, as maximum body size evolves, the evolutionary possibilities for increasing size are progressively exhausted. Consequently, the rate of change is also proportional to the availability of open niche space, which is captured by the difference between asymptotic (K) and current log body mass [that is, $\log(K) - \log(M)$], or $\log\left(\frac{K}{M}\right)$. Combining these ecological and evolutionary growth dynamics yields the Gompertz equation $\frac{dM}{dt} = \alpha M \log\left(\frac{K}{M}\right)$, a sigmoidal growth model often used in time series analyses. The integrated form is $\log M = \log K - \log\left(\frac{K}{M_0}\right)e^{-\alpha t}$, where M_0 is initial maximum body size. The Gompertz model is more biologically plausible than the random walk model, because it captures both the multiplicative nature of body size evolution and the saturating effects of exponentially decreasing niche space availability at larger body sizes.

We compared model fits using corrected Akaike information criteria (AICc). The results suggested that the random walk was not an appropriate model (Table 1). Although a power function provided a reasonable fit to the data, the fitted exponent γ was 0.25, significantly less than the predicted value of 0.50. Moreover, after the initial growth phase, the residuals were not normally distributed. This was probably because maximum

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body size approaches a plateau as opposed to increasing monotonically. The Gompertz model provided a much better fit to the data throughout the time series and yielded the lowest AICc (Table 1 and fig. S2). The inflection point between the growth phase and the saturating phase occurred during the late Eocene at 42.9 Ma, at a body mass of 4850 kg.

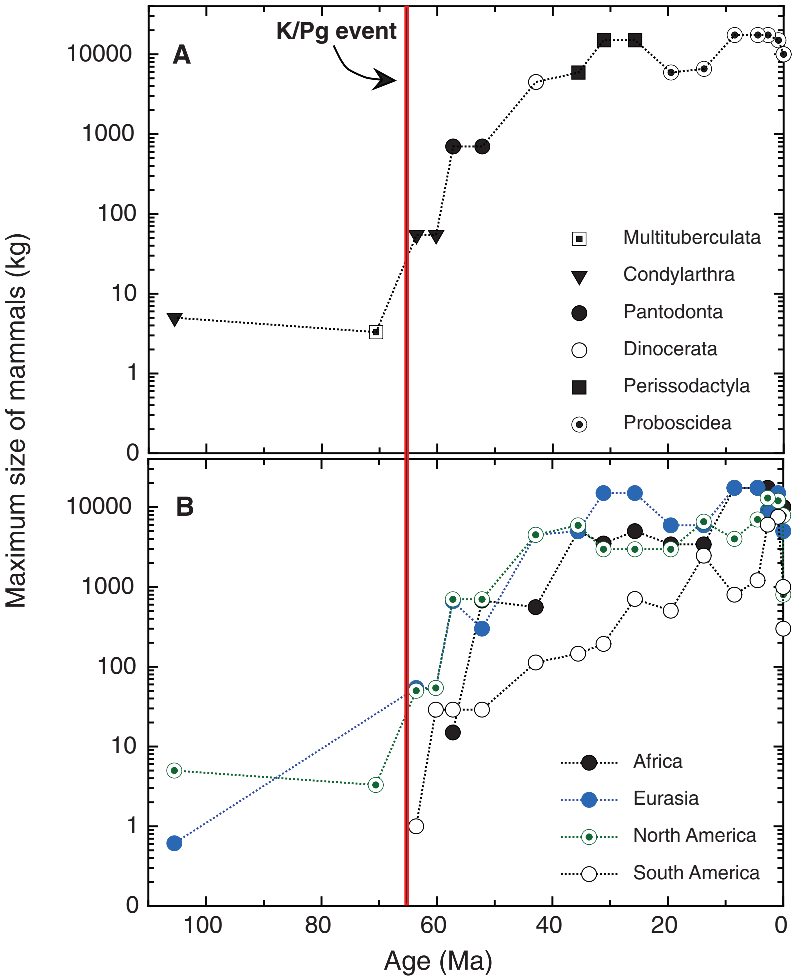

Fig. 1. Maximum body mass of terrestrial mammals over time and space. (**A**) Maximum body mass over time examined globally at the sub-epoch level over the past 110 million years. (**B**) Maximum body mass for the largest continents (South America, North America, Africa, and Eurasia) over the same time interval. The overall trend is not driven by a single taxonomic order or an individual continent; six different orders and three of the four continents depicted have at one time or another housed the largest mammal. Data for Australia (not shown) and South America were particularly difficult to obtain because of limited material and/or collecting; thus, estimates for these continents should be considered underestimates. Data are binned at the resolution of sub-epochs using the Gradstein time scale (*12*).

Table 1. Model fits for global, continental and trophic level body size trajectories. The power law is of the form $\log M = c_0 t^{\gamma}$ and the Gompertz equation $\log M = \log K - \log(\frac{K}{M_0})e^{-\alpha t}$.

Model	Parameters	AICc	R^2 value	*P* value
All data				
Power law	$c_0 = 1.504, \gamma = 0.25$	9.3	0.92	<0.001
Gompertz	$K = 13182.57, M_0 = 6.92, \alpha = 0.08$	8.2	0.94	<0.001
Eurasia				
Gompertz	$K = 15977.18, M_0 = 25.14, \alpha = 0.05$	—	0.83	<0.001
Africa				
Gompertz	$K = 12900.31, M_0 = 0.44, \alpha = 0.06$	—	0.86	<0.001
North America				
Gompertz	$K = 6675.75, M_0 = 8.78, \alpha = 0.07$	—	0.85	<0.001
Carnivores				
Gompertz	$K = 710.56, M_0 = 14.62, \alpha = 0.10$	—	0.76	<0.001

The Gompertz model also provided good fits for the trajectories of maximum body size on each continent (Table 1 and fig. S2). Fifteen different lineages, representative of different archaic and modern orders (such as Proboscidea, Perissodactyla, Artiodactyla, Dinocerata, Pantodonta, Condylarthra, Xenarthra, etc.) evolved similar maximum size at different times and on different continents. These results show that the sigmoidal or saturating trajectory of maximal size evolution for Cenozoic mammals in North America (*5*, *8*) occurred independently in multiple lineages on all the large continents. These results support the interpretation that similar niches were available to and filled by comparably sized giant mammals on each continent after 35 to 40 Ma. Because these niches were occupied by multiple different lineages at different times and on different continents, the patterns suggest that large mammals convergently evolved to fill similar ecological roles. Consistent with this idea, the largest mammals after the beginning of the Cenozoic were always herbivores. These patterns are also congruent with arguments relating the maximum body size of contemporary herbivorous mammals to constraints of diet and digestive physiology (*16*).

Carnivorous mammals showed similar saturating trajectories but attained smaller maximum sizes than coexisting megaherbivores (Fig. 2). Large mammal-eating mammals were effectively absent in the early Paleocene; instead, birds, terrestrial crocodiles, snakes, and large lizards were the dominant carnivores (*17*). Once carnivorous mammal guilds began to diversify, however, they showed a similar trajectory to that of the herbivores—also well fit by a Gompertz function (Table 1). Although carnivores and herbivores started from a similar size immediately after the K/Pg, after ~30 million years the largest carnivores approached an asymptotic maximum about one order of magnitude smaller than that of the largest herbivores (Fig. 2). As with herbivores (Fig. 1A), the carnivores convergently evolved similar maximum sizes in different lineages: the archaic orders Creodonta and Mesonychia, and the modern order Carnivora. Although the duration of these clades overlapped, there was turnover in the ordinal affiliation of the largest carnivore, with each sequentially evolving to a maximum body mass of ~1000 kg (Fig. 2). After the initial size increase, the ratio of body masses of coexisting carnivorous and herbivorous mammals remained similar across the entire Cenozoic (Pearson correlation = 0.819, $P < 0.000$; fig. S4). This suggests at least an indirect relation in which the maximal sizes of carnivores followed the overall size distribution of mammals, but not necessarily a direct causal relation between the largest carnivores and herbivores. Indeed, the largest carnivores probably did not prey on the largest herbivores. The disparity in maximum size between carnivores and herbivores persists in contemporary mammals: Lions, tigers, and bears are about an order of magnitude smaller than elephants and rhinos. The asymptotic maximum size of carnivores of

~1000 kg is consistent with the recent prediction that this represents an upper limit for flesh-eating terrestrial mammals because of physiological and ecological constraints (*18*).

We compared the overall global trajectory of maximum body mass with time series of three major abiotic factors: global temperature (*19*), atmospheric oxygen levels (*20*), and terrestrial land area (*21*) (Fig. 3 and table S1). Each of these variables has been hypothesized theoretically and sometimes shown empirically to affect body size evolution in mammals: temperature by affecting how mammals dissipate heat through Bergmann's rule (*22*–*24*); greater land area by allowing larger populations and reducing extinction probabilities for the largest mammals (*25*, *26*); and higher atmospheric oxygen concentrations by allowing higher rates of metabolism and biomass production (*27*–*29*). We averaged the abiotic values, which were generally reported at a finer scale, using the durations for each geological sub-epoch so we could compare against the trajectory of global body mass over the Cenozoic (table S1). Binned values are superimposed over the finer-scale data shown in Fig. 3. Our analyses were not based on specific values and slopes of these curves at specific times. We varied bin widths and averaging techniques; results were robust with regard to the binning technique employed (*9*). These abiotic records are based on proxies (*19*, *21*) or on modeling of carbon isotopic records (*20*); hence, they contain significant unresolved uncertainties, which complicate interpretations of the patterns.

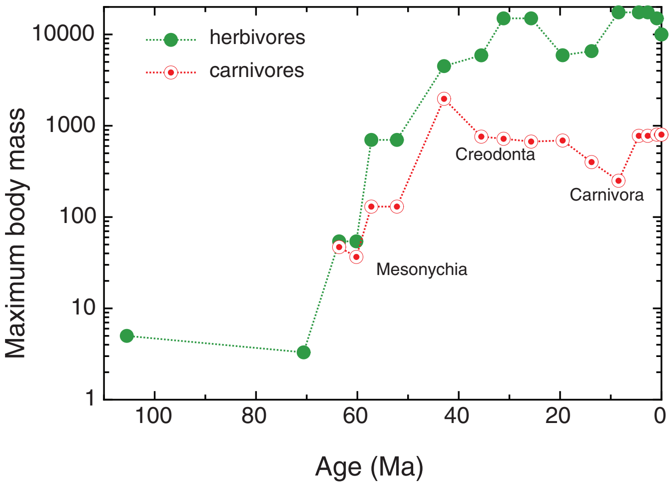

Fig. 2. The trajectory of body mass evolution of selected trophic guilds over the Cenozoic. Green solid circles, herbivores; red open circles with dots, carnivores. Carnivore maximum body mass closely tracks that of herbivores (fig. S4). The ceiling for maximum size is different for herbivores and carnivores (~10 to 15 tons versus ~1 ton) but consistent over time within a trophic group, irrespective of taxonomic affiliation. The largest mammals before the K/Pg may have been omnivorous rather than strict herbivores; our interpretations are based solely on patterns for the Cenozoic.

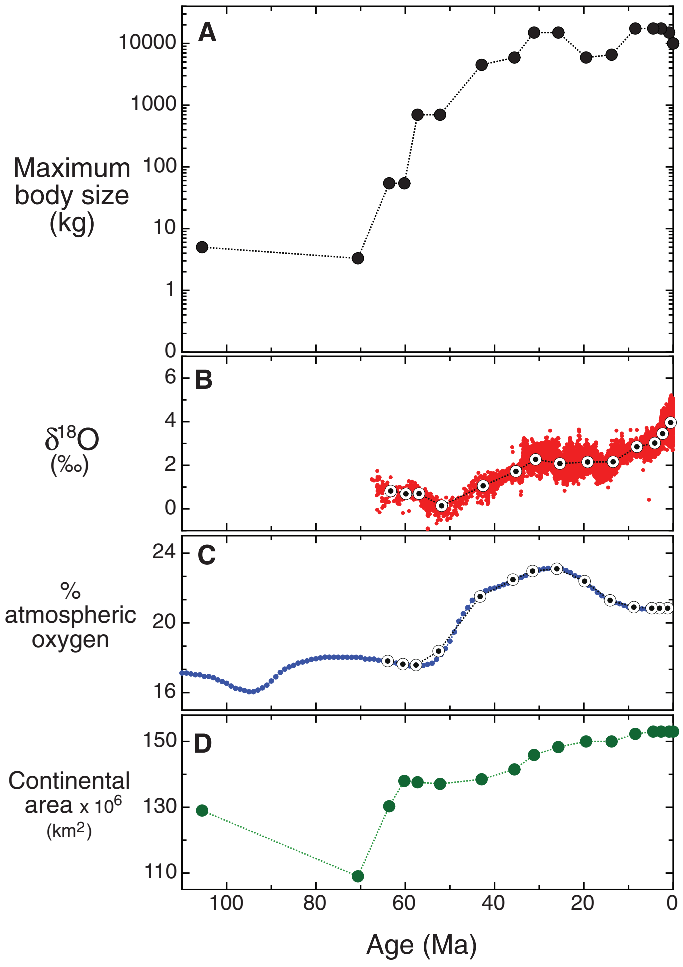

Fig. 3. Global fluctuations in maximum body size and various abiotic factors over the Cenozoic. (**A**) Maximum body mass (this study). (**B**) δ^{18}O adjusted in parts per thousand (*19*). (**C**) Percent atmospheric oxygen concentration (*20*). (**D**) Variations in terrestrial land area in square kilometers (*21*). Abiotic factors chosen were those that have been demonstrated or postulated to influence the body mass of mammals. Linear regression yields highly significant fits between all factors and global mammalian body mass over the Cenozoic; all but atmospheric oxygen concentration remain significant when data are restricted to the past 42.9 million years (table S3). Values for the Mesozoic were excluded because data are fairly scarce; data were truncated at the terminal Pleistocene to yield roughly comparable sub-epoch durations. Data vary in the fineness of their resolution; abiotic variables were binned to obtain values representing the averages of the temporal span represented by each body mass estimate. These binned values are superimposed on the finer-scale data.

All abiotic factors were significantly related to mammalian body mass over the Cenozoic (Fig. 3 and table S3). To determine whether significance was driven by the initial exponential phase, we also ran analyses using the temporal interval from the late Eocene through the Pleistocene (42.9 to 0.9 Ma; results were similar when early or middle Eocene values were chosen). Both global temperature and terrestrial land area remained highly significant: The largest mammals evolved when Earth was cooler and terrestrial land area was greater (table S3), but atmospheric oxygen level dropped out (table S3). However, as might be expected, temperature and land area were significantly related (Pearson correlation = 0.904, $P < 0.001$, df = 13): Lower global environmental temperatures (indexed by ^{18}O) corresponded to more water stored in ice caps, lower sea levels, and increased land areas, and probably to changes in vegetation cover and primary productivity.

That temperature and/or land area may have influenced the evolution of body mass in mammals is consistent with several well-established biogeographic principles. The influence of temperature is consistent with Bergmann's rule, a well-known ecogeographic trend of larger body mass in cooler habitats across space (*24*), and in a few instances, across time (*30*). Bergmann's rule probably reflects physiological adaptations to prevent heat loss, because larger animals have a reduced surface-to-volume ratio; or alternatively, to promote heat dissipation at smaller body masses (*24*). Our results are also consistent with the hypothesis that available land area constrains the upper body mass limit of mammals by limiting population through the size or number of home ranges that can be "packed in" or by reducing energy acquisition (*25*, *26*). Among contemporary mammals, maximum body mass is strongly influenced by terrestrial land area, with larger-bodied mammals being found in larger insular or continental "islands" (fig. S5). Thus, constraints on maximum body size potentially imposed by both abiotic factors ultimately may be traced to physiological processes related to endothermy.

However, some caution should be used in the interpretation of our results. Quantitative analyses of these abiotic variables were complicated by a lack of resolution, potential collinearities, and a lack of statistical power that precluded the use of more-rigorous tests to fully explore the relationships between the predictor variables. Moreover, for some of these abiotic factors the uncertainties are not well characterized, and we currently have no way of knowing how these may interact to influence our results. For example, the oxygen isotope curve is confounded by changes in the terrestrial ice volume, atmospheric oxygen concentration is related to temperature through fluctuations in carbon dioxide and carbon sequestration (*19*) and potentially to global land area through changes in primary productivity, and global land area is clearly related to temperature and sea level. Moreover, other factors such as changes in seasonality and precipitation were not explicitly incorporated; the late Cenozoic saw a global trend toward cooler, drier, and more seasonal climates (*19*, *31*). Nevertheless, the potential role of abiotic factors in the overall trajectory of mammalian evolution cannot be ignored, and the available data suggest interesting and important trends, which should be explored further.

Our analysis implies that the increase in the maximum mass of mammals over the Cenozoic was neither a statistical inevitability driven by increasing species richness nor a random evolutionary walk from a small initial size, but rather reflected processes operating consistently across trophic and taxonomic groups, and independent of the physiographic history of each continent. We find no support for other hypotheses for the evolution of maximum body mass (*9*), including the expected increase in variance due to random divergence from a common ancestor or to increasing species richness (*13*–*15*); nor do terrestrial mammals ever approach sizes that might invoke biomechanical constraints (*32*). The K/Pg extinction provided the ecological opportunity for mammals to become larger. Terrestrial mammals did so in an exponentially decreasing fashion, reaching a more or less maximal size by 40 Ma as evolutionary possibilities for increasing body size were progressively exhausted and abiotic factors began constraining the upper limit.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/330/6008/1216/DC1
Materials and Methods
Figs. S1 to S5
Tables S1 to S3
References

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Modular Organic Structure-Directing Agents for the Synthesis of Zeolites

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Organic structure-directing agents (OSDAs) are used to guide the formation of particular types of pores and channels during the synthesis of zeolites. We report that the use of highly versatile OSDAs based on phosphazenes has been successfully introduced for the synthesis of zeolites. This approach has made possible the synthesis of the elusive boggsite zeolite, which is formed by 10- and 12-ring intersecting channels. This topology and these pore dimensions present interesting opportunities for catalysis in reactions of industrial relevance.

Zeolites are crystalline microporous and mesoporous materials (*1*–*4*) that offer a wide range of applications because of their well-defined structures, which are formed by channels with pore apertures of molecular dimensions. An important objective during the synthesis of zeolites is to achieve control of the pore dimensions and their connectivity through the use of organic structure-directing agents (OSDAs) that, at the limit, could act as template molecules. A large variety of quaternary organic ammonium salts have been successfully used as OSDAs (*2*, *4*–*6*) as well as analogous molecules, such as phosphonium-derived organic cations (*7*–*10*). However, rather than design new molecules for each zeolite target it could be more efficient to have a type of OSDA that could be easily built by blocks similar to Legos, with a large variety of substituents. Potential new structures could be simulated with molecular modeling techniques, and an OSDA that directs its synthesis by minimizing the energy of the zeolite-OSDA system could be predicted or at least can be selected from a limited number of candidates.

The described procedure requires having a tool box of OSDA molecules that are easy to prepare and adapt while having the adequate polarity and basicity. We present a type of OSDA molecule with a nearly unlimited synthesis flexibility that is based on building-block units. These molecules are based on phosphazenes that can mobilize silica, have the adequate polarity and stability, and offer more structural possibilities than quaternary ammonium or phosphonium cations. We used these OSDAs for the synthesis of new zeolite structures,

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