

Correspondence

The evolution of maximum terrestrial body mass in sauropod dinosaurs

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The long-necked dinosaurs, sauropods, are famous for their extreme body sizes, evolving body masses several times greater than the next-heaviest terrestrial animals, elephant-like and rhinoceros-like mammals and 'duck-billed' dinosaurs. The pace of sauropod discovery has been exponential in recent decades, resulting in the recognition of sauropods as a global, ecologically diverse group of herbivorous dinosaurs comprising over 250 known species¹. However, limitations due to missing data from their patchy fossil record have so far limited studies of sauropod body-size evolution to less than half their known diversity¹. Here, I present models to confidently predict unknown limb-bone measurements in sauropods, resulting in a dataset 50% larger than previously assembled. Leveraging the emerging consilience among body mass estimation methods for fossil tetrapods, I then map sauropod body mass evolution through time in a phylogenetic context. Likelihood-based ancestral state reconstruction reveals that sauropods convergently surpassed maximum terrestrial mammalian body mass at least three dozen times over the course of 100 million years, on at least six landmasses and in at least five ecomorphologically disparate clades. Sauropod maximum body mass rapidly increased early in their evolutionary history from under 5,000 kg before levelling off around 40,000 kg (with notable exceptions)², in a pattern similar to that observed in terrestrial mammals³.

I reconstruct that the median sauropod body mass was just 11.7 ± 2.9 metric tons, or less than half

the mass of the largest known fossil mammals^{3,4}, three-quarters the mass of the largest hadrosaurid dinosaur, about the same as the largest ceratopsian dinosaur², and less than a sixth the mass of the heaviest known sauropod, *Argentinosaurus*. The sauropod body mass distribution is only slightly negatively skewed (Figure S1A in Supplemental information; skewness = -0.44 ; Shapiro-Wilk $W = 0.98$, $p = 0.008$).

Over the course of 100 million years, a remarkable 36 sauropod lineages independently surpassed the body masses evolved by other terrestrial clades, before or since, including two non-neosauropod lineages, two lineages within Turiasauria, seven within Diplodocoidea, and 25 within Macronaria, including three within Brachiosauridae and 15 within Titanosauria (Figures 1 and S2), based on current knowledge

of sauropod evolution. These numbers would decrease if fossils of many purportedly fully grown sauropods are instead from immature individuals, but histological evidence suggests that this is not the case⁵. Uncertainty in body mass estimation does not affect this result: even more lineages would surpass more conservative body mass estimates for the largest mammals (Figure 1). Sauropod lineages that surpassed the mammalian threshold have been found on all landmasses except India and Antarctica, each of which is relatively underexplored², suggesting that larger species await discovery in those areas. Each of the surpassing lineages' ancestral body mass was at or below ca. 15 metric tons (Figure 1), less than the mass of the largest hadrosaurids or mammals^{3,4} and similar to the optimum sauropod body mass reconstructed from a macroevolutionary analysis of

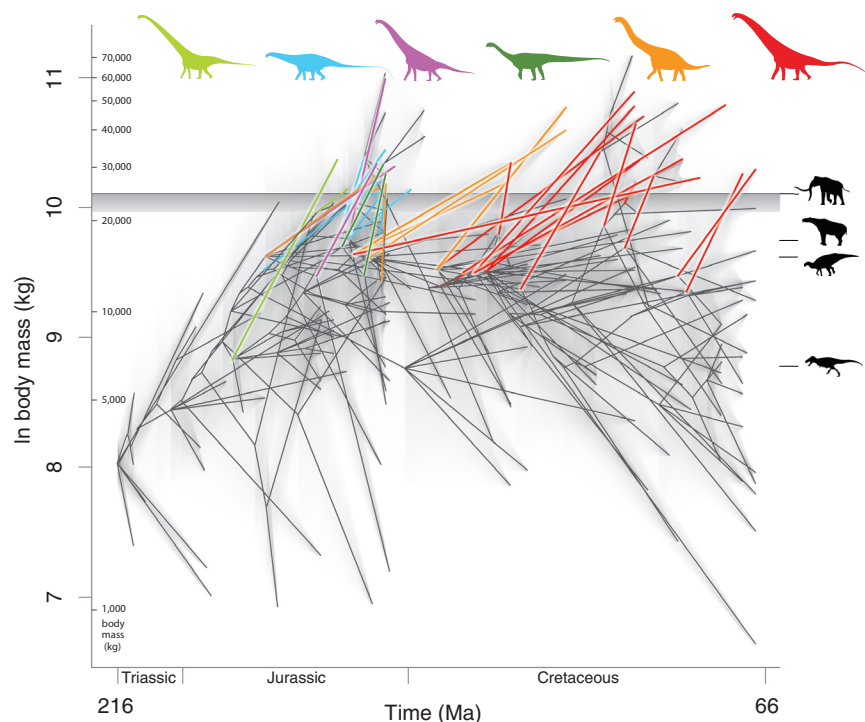


Figure 1. Phenogram of sauropod body mass through geologic time.

Lineages that surpassed maximum mammalian body mass within six derived sauropod groups are highlighted: non-neosauropods (light green), diplodocoids (blue), brachiosaurids (purple), turiasaurians (dark green), non-titanosaur and non-brachiosaurid macronarians (orange), and titanosaurs (red). Each lineage is represented by a solid line surrounded by 95% confidence intervals shown in grey. Horizontal grey rectangle indicates maximum known mammalian body mass with lower error range; horizontal tick marks with silhouettes indicate maximum known proboscidean, perissodactyl, ornithomimid, and theropod dinosaur body mass. Silhouettes from phylopic.org; licenses are cited in the Supplemental information.



a smaller dataset². Similarly, the ancestral body mass of every major sauropod clade but one (Lognkosauria) is reconstructed below the mammalian body mass threshold (Table S1). Only a handful of sauropod speciation events occurred above the mammalian threshold, and only a few lineages crossed the threshold in the reverse direction (Figure 1).

Sauropods first surpassed maximum terrestrial mammal body mass during the Middle Jurassic, a time characterized by the breakup of Pangaea into discrete landmasses. These first sauropods and the other lineages that later surpassed mammalian body mass differed markedly from one another in body proportions and associated locomotory biomechanics⁶, craniodental anatomy and inferred diet⁷, life history and growth rates⁵, the development of postcranial pneumaticity⁸, and inferred habitats¹. Sauropods show no overall trends in average body mass through time ($r = 0.13$; $p = 0.07$), but certain clades therein exhibit decreasing temporal trends, including Diplodocoidea ($r = -0.42$; $p = 0.02$), Titanosauriformes ($r = -0.26$; $p = 0.02$), and Titanosauria ($r = -0.29$; $p = 0.01$), culminating in repeated evolutionary dwarfing events⁹. There is no relationship between mean global temperature and body mass in sauropods (Supplemental experimental procedures, Figure S1B, $r = -0.25$, $p = 0.36$), suggesting that climate was not a significant driver of sauropod body mass evolution.

Both the fossil record and modern biodiversity attest to the rampancy of convergent evolution, and in myriad clades body size is no exception. For example, while hadrosaurid ('duck-billed') dinosaurs and perissodactyl (rhinoceros-like) and proboscidean (elephant-like) mammals independently evolved similar maximum body masses of ca. 15–24 metric tons^{3,4}, no terrestrial lineage has approached the scale of sauropods' bulk, despite several hallmark features of the sauropod *bauplan* evolving convergently in other reptiles. These include a relatively diminutive cranium set on a hyperelongate neck⁹, graviportal

limbs¹⁰ and extensive postcranial pneumaticity⁸.

Sauropod gigantism has been explained by an 'evolutionary cascade' of anatomical and physiological innovations facilitated by a nested array of historical prerequisites⁹. While this model explains the potential for sauropods to exceed the terrestrial body masses achieved by other lineages, there is no unifying feature or set of features that allowed sauropods to realize this potential dozens of times. In contrast, the potential for size increase seems to have been repeatedly realized upon their general *bauplan* in only a fraction of lineages, owing to a combination of ecological and life-history factors that played out against various historical contingencies.

The pattern of sauropod maximum body mass through time can be fit to a variety of models, as has been done for terrestrial mammals³, with the caveat that maxima are prone to be influenced by sampling bias or outliers. Comparing the fit of various models using Akaike's Information Criterion shows that, as in mammals, sauropod body mass evolution is well explained by saturating trajectories such as the Gompertz model (Figure S1C and Table S2), consistent with model-based investigations of sauropod body mass evolution². Sauropods plateaued in maximum body mass by the latter two-thirds of their evolutionary history, with the plateau sustained by the aforementioned 36 instances of exceptional body mass evolution (Supplemental information; Figure S1C). A saturating trajectory sustained by disparate clades through time has been ascribed to convergent niche-filling in mammals³ (Figure S1D). This explains the pattern in sauropods as well, evidenced by the great phenotypic disparity of the three dozen sauropod lineages that evolved to sizes unrivaled on land.

SUPPLEMENTAL INFORMATION

Supplemental information includes methods, figures and tables and can be found with this article online at <https://doi.org/10.1016/j.cub.2023.02.067>.

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AUTHOR CONTRIBUTIONS

M.D.D'E. designed the study, gathered and analyzed the data, and wrote and edited the paper.

DECLARATIONS OF INTERESTS

The author declares no competing interests.

INCLUSION AND DIVERSITY

The author supports inclusive, diverse, and equitable conduct of research.

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