PALEONTOLOGY

Sauropod Gigantism

How did sauropod dinosaurs reach body sizes that remain unsurpassed in land-living animals?

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Sauropod dinosaurs were the largest animals ever to inhabit the land (see the figure). At estimated maximum body masses of 50 to 80 metric tons, they surpassed the largest terrestrial mammals and nonsauropod dinosaurs by an order of magnitude. With body lengths of more than 40 m and heights of more than 17 m, their linear dimensions also remain unique in the animal kingdom. From their beginnings in the Late Triassic (about 210 million years ago), sauropods diversified into about 120 known genera. They dominated ecosystems for more than 100 million years from the Middle Jurassic to the end of the Cretaceous, setting a record that mammalian herbivores will only match if they can double their current geological survival time. Thus, sauropods were not only gigantic but also, in evolutionary terms, very successful. Recent advances bring us closer to understanding the enigma of their gigantism (*1*–*3*).

Extrinsic causes have repeatedly been advanced to explain the success of sauropod dinosaurs and the gigantism seen in the dinosaur era. However, physical and chemical conditions in the Mesozoic (250 to 65 million years ago) were probably less favorable for plant and animal life than they are today; for example, atmospheric O_2 concentrations were much lower (*4*). The variation of other factors (such as land mass size, ambient temperature, and atmospheric CO_2 concentrations) through time is not tracked by variations in sauropod body size (*2*, *5*). Thus, the clue to sauropod gigantism must lie in their unusual biology (see the figure).

Sauropods had an elephantine body supported by four columnar legs and ending in a long tail. From the body arose a long neck bearing a small skull. Sauropods exhibit diverse oral, dental, and neck designs, indicating dietary niche differentiation; this variety makes reliance on any particular food source (*6*) as the reason for gigantism unlikely. However, one evolutionarily primitive character truly sets sauropods apart: In contrast to mammals and advanced bird-hipped dinosaurs (duck-billed and horned dinosaurs), they did not masticate their food; nor did they grind it in a gastric mill, as did some other herbivorous dinosaurs (*7*). Because gut capacity increases with body mass (*8*), the enormous gut capacity of sauropods would have guaranteed the long digestion times (*6*) necessary for degrading unchewed plant parts, even at a relatively high food intake.

The lack of a masticatory apparatus allowed sauropod heads to remain small and was one prerequisite for their long neck to

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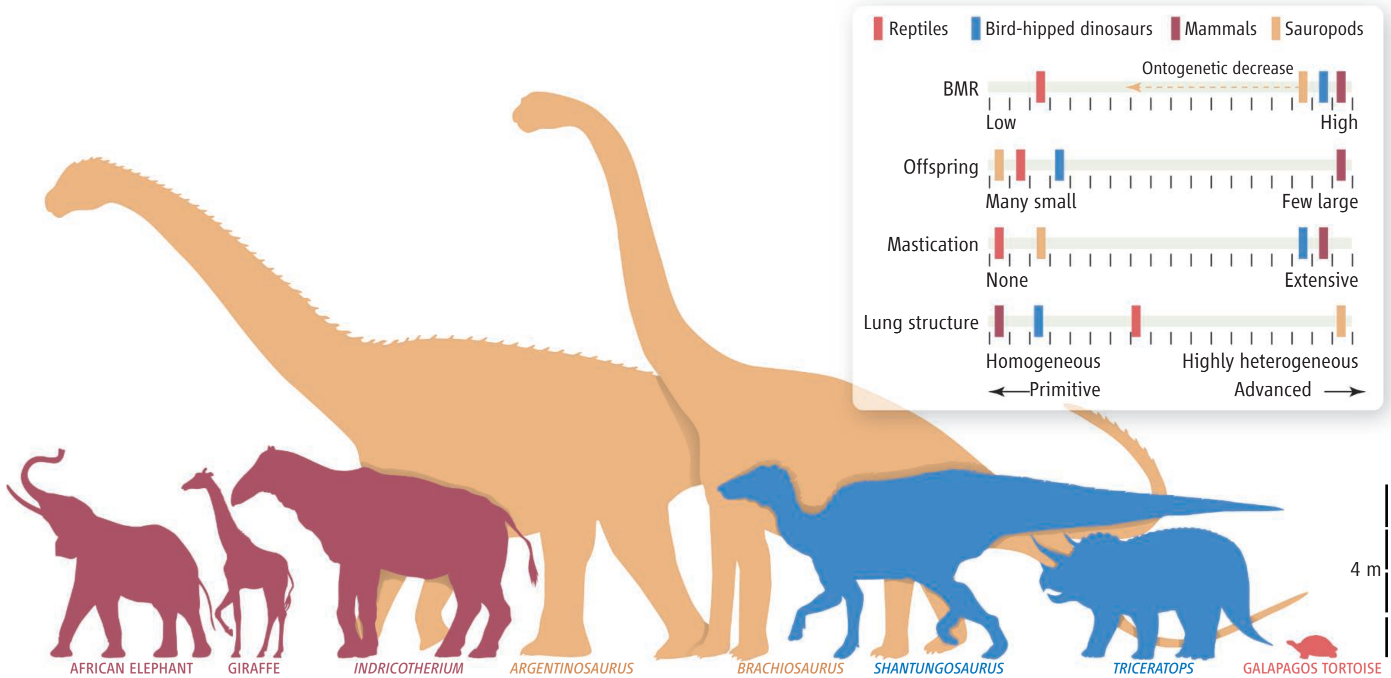

Toward understanding sauropod dinosaur gigantism. The sauropod dinosaurs *Brachiosaurus* and *Argentinosaurus* were much larger than the largest bird-hipped dinosaurs *Shantungosaurus* and *Triceratops*, the fossil rhinoceros *Indricotherium* (the largest known land mammal), the African elephant, the giraffe, and the Galapagos tortoise (the largest living herbivorous reptile). (**Inset**) The main biological properties that control the upper limits of body size in terrestrial herbivores—sauropod dinosaurs, bird-hipped dinosaurs, mammals, and ectothermic herbivorous reptiles—are visualized as sliders, with the evolutionarily primitive state to the left and the advanced state to the right. The slider position for each herbivore group (color-coded to match the images) indicates the specific combination of primitive and advanced states that led to the maximal body size of this group. The unique gigantism of sauropod dinosaurs was made possible by a high basal metabolic rate (BMR, advanced), many small offspring (primitive), no mastication (primitive), and a highly heterogeneous lung (advanced). We hypothesize that ontogenetic flexibility of BMR was also important.

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evolve. This neck would have provided access to food out of reach of other animals (*9*) with little foraging movement of the whole body, while probably also functioning as a display organ and hence being subject to runaway sexual selection (*10*). In herbivorous mammals and evolutionarily advanced bird-hipped dinosaurs, in contrast, a disproportionate evolutionary increase in the size of the head and the masticatory apparatus relative to the rest of the body set a mechanical limit to the evolution of very long necks. In addition, the vulnerability of a long neck (*10*) makes its evolution unlikely without protection from predation by superior body size.

The long neck and large body size pose particular physiological problems. Large body size in endothermic animals is associated with a major problem of dissipating excess body heat. A long neck also means that a large volume of air must be moved in the windpipe during ventilation before fresh air reaches the lung. These problems appear to have been solved by an evolutionary innovation shared by sauropods and theropods (meat-eating dinosaurs) and their descendants, the birds: a highly heterogeneous avian-style respiratory system (*11*) with cross-current gas exchange in the lung and air sacs that pneumatized the vertebrae of the neck and the trunk and filled large parts of the body cavity. Compared to mammalian or reptilian lungs, this system overcame the problem of the long windpipe of sauropods (*11*) and also probably helped to dissipate excess body heat via the visceral air sac surfaces (*11, 12*).

For selective advantages conferred by large body size to be effective (*13*), this large body size must be reached quickly by the individual. Uniquely among amniotes, sauropods grew through five orders of magnitude from a 10-kg hatchling to a 100,000-kg fully grown individual. Bone histological evidence indicates that this growth took place at rates comparable to those of large terrestrial mammals (*14*, *15*); reproductive maturity was reached in the second decade of life and full size in the third decade of life (*15*), as predicted from demographic models that show higher ages at first reproduction to be incompatible with long-term population persistence (*16*). Such high growth rates are seen only in animals with a basal metabolic rate (BMR) of mammals and birds (*17*). For sauropods, rather than assuming a constant metabolic rate throughout the animals' life, an ontogenetic decrease in BMR has been suggested (*12*, *18*). Such a decrease would reconcile rapid growth rates in juveniles with problems resulting from gigantic body size (such as overheating and high food requirements) in adults. Considering the costs of a high BMR, it may have evolved early on in sauropods, as an adaptation for the high growth rates necessary for reaching very large body size.

At the population level, egg-laying and the associated production of many small offspring (*19*), in contrast to the one-offspring strategy of mammalian megaherbivores, is a key characteristic of sauropod reproductive biology and of the dinosaur ecosystem (*20*, *21*). This strategy may have guaranteed long-term survival of gigantic species (*20*). In mammals, large body size increases the risk of chance extinction by reducing population density and increasing population recovery time: With increasing body size, fewer offspring are produced, and these take longer to mature. The retention of the primitive feature of egg-laying might have alleviated this constraint through much higher population recovery rates than in large mammals (*21*).

Thus, we suggest that the unique gigantism of sauropods was made possible by a combination of phylogenetic heritage (lack of mastication, egg-laying) and a cascade of evolutionary innovations (high growth rate, avian-style respiratory system, and a flexible metabolic rate). Although modern mammals evolved a high growth rate independently, the comparison with sauropods identifies the mastication of food (inherited from small insectivorous ancestors), overheating caused by an inadequate cooling mechanism, and giving birth to live offspring as the major factors limiting the potential body size of mammalian herbivores (see the figure).

Recent modeling studies found a high metabolic rate to be incompatible with gigantic body size because of the problem of heat dissipation (*22*, *23*); however, these models assumed metabolic rate to have remained constant throughout life. In addition, one of the studies (*23*) suffers from poor bone histologic constraints on sauropod growth rates, as does a study (*24*) arguing against fast growth in sauropods. Compared to other dinosaurs, the long bones of sauropods rarely preserve growth marks, probably because bone tissue was deposited too rapidly to record them (*15*). Histologic growth rate studies using skeletal elements other than long bones may provide more reliable estimates.

Theropod dinosaurs such as *Tyrannosaurus rex* are similarly outsized compared to mammalian carnivores (*1*) as sauropods are compared to mammalian herbivores. Thus, there may be links between sauropod gigantism and meat-eating dinosaur gigantism. One such link may be the mode of reproduction. Egg-laying of sauropods must have made large amounts of food available to predators in the form of many small, little-protected young sauropods. In contrast, mammalian megaherbivores withhold this food source from carnivores by rearing very few, well-protected offspring. This greatly decreased resource base may limit maximum body size of carnivores today (*21*).

Further progress in understanding dinosaur gigantism will come from a conservation biology approach that models the carrying capacity of Mesozoic ecosystems based on the juvenile-biased population structure of dinosaurs (*19*, *20*). Such an approach, which goes beyond the reconstruction of an individual's metabolism (*14*, *15*, *22*, *23*), will be much more informative regarding resource limitations, population growth potential, and body size evolution of dinosaurs.

References and Notes

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