HOW TO BUILD A GIANT

Figure 1. Mounted skeleton of *Argentionsaurus huinculensis*, a giant Titanosaurid sauropod unearthed in Patagonia, Argentina. Fernbank Museum of Natural History, Atlanta, Georgia.

Biomechanics of Sauropod Dinosaurs

By Fernando Racimo

Picture yourself transported back in time to the Mesozoic Era: the Age of Dinosaurs. Your time machine drops you off in a coniferous forest, surrounded by lush vegetation. You hear a low-pitched rumbling sound in the distance and feel the earth trembling beneath your feet. You look up and see a giant: ten times heavier than a modern elephant, as tall as a six-story building. Barely recovering from the goosebumps on your skin, you see five others like it, their long necks reaching up into the canopy. But these are gentle giants - slow-walking four-footed plant-eaters, looking for the next tree to devour. They are sauropod dinosaurs - the largest creatures ever to have walked on land.

Living Large

Sauropods arose in the early Jurassic period, about 200 million years ago, and went extinct at the end of the Cretaceous, 65 million years ago. They were all quadrupedal herbivores, though some may have been able to stand on their hind feet to reach tall trees. There were three major clades of sauropod dinosaurs: diplodocids, brachiosaurids, and titanosaurids. Diplodocids had long, whip-like tails and were relatively slender. Brachiosaurids had upright necks, long forelegs and were heavier than diplodocids. Titanosaurids were close relatives to brachiosaurids, but had smaller heads, shorter necks, and lived mostly in the Southern hemisphere.

The most famous sauropods are *Diplodocus carnegii* (2) and *Brachiosaurus altithorax* (1), from which their respective families got their names. But perhaps the largest sauropod was a Titanosaurid. Discovered in Argentina in 1993, *Argentinosaurus huinculensis* measured up to 30 meters in length and weighed 90 tons (3). A professional basketball player would not have been able to reach up to its knees.

Permissive Environment or Permissive Body Plan?

So how did sauropods evolve to be so large? Some have argued for an environmental cause (4). A sauropod body would need large amounts of oxygen distributed throughout its body. If oxygen were more abundant in the atmosphere, large animals would not have a problem acquiring enough quantities to fuel their metabolism. However, the Jurassic atmosphere had less or as much oxygen as our current atmosphere (5). Yet no living terrestrial animal even approaches the size reached by sauropods.

The key lies not in the Mesozoic environment, but in the sauropod body plan. Sauropods did not masticate what they ate. Food was mainly processed within their enormous guts. Their jaws did not need to be big or strong, and thus their heads were small relative to the rest of their bodies. Small heads permitted long necks to evolve, so as to reach food that other dinosaurs could not (6).

Vertebral pneumaticity was another favorable condition for gigantic bodies. Sauropod vertebrae had interconnected, air-filled compartments that penetrated into the bone and could have allowed them to efficiently distribute their daunting body mass. The theory that pneumaticity enabled gigantism comes from a mathematical technique called Finite Element Analysis (FEA), which allows engineers to determine where the points of greatest stress occur in a particular 3D structure. Paleobiologists have applied FEA to diplodocid and brachiosaurid neck vertebrae to investigate the weight distribution on the bone (7). FEA results show that the air-filled vertebrae distributed weight evenly along the neck and dissipated it to the external bone surfaces. This biomechanical configuration made vertebrae especially light, and may have allowed sauropods to grow massive long necks. Pneumatic cavities also ran along the rest of the body, which suggests that these structures must have been essential to support extreme body weights (7).

Metabolism and Circulation

Perhaps the greatest challenge sauropods faced was their own metabolism. Large bodies are bad at dissipating heat, because their surface areas are very small relative to their total volumes. Heat can only escape very slowly under these conditions. To solve this problem, sauropods may have possessed a complex air-sac respiratory system, similar to that of modern birds (8). Birds are better than mammals at extracting oxygen from the atmosphere because their sac system has a low surface-to-volume ratio, which makes it cheap to inflate. Dinosaurs are the ancestors of birds, so it is probable that they too possessed this system, which would have allowed them to get more bang for their breath. Without needing to breath in and circulate so much oxygen, sauropods may have been able to keep their metabolisms low, thereby preventing over-heating (8).

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Coupled to mechanical challenges was the problem of fueling a brain several meters away from the heart. The head of *Brachiosaurus*, for example, was 9 meters above the heart. For blood to reach such heights, the mean arterial pressure would have had to reach 750 mmHg, 7 times higher than the mean human blood pressure! The sheer force required to achieve this pressure has induced several scientists to propose that sauropods may have had an auxiliary

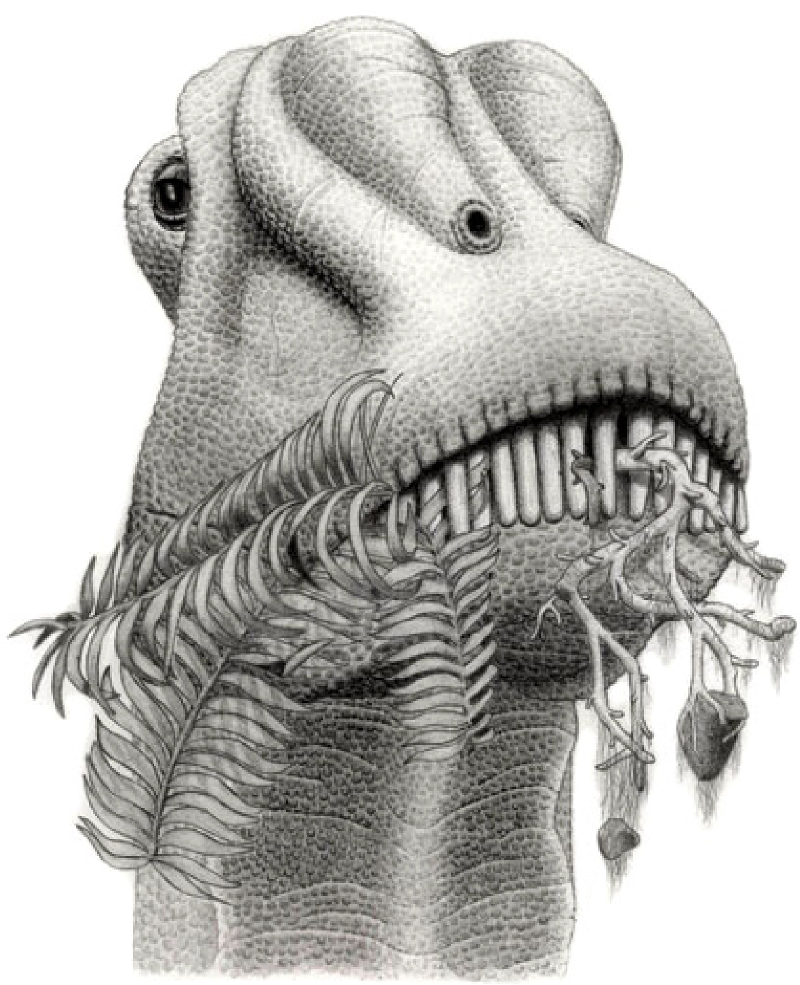

Figure 2. Sketch of a diplodocid feeding. Sauropods did not masticate their food, which allowed their heads to remain small.

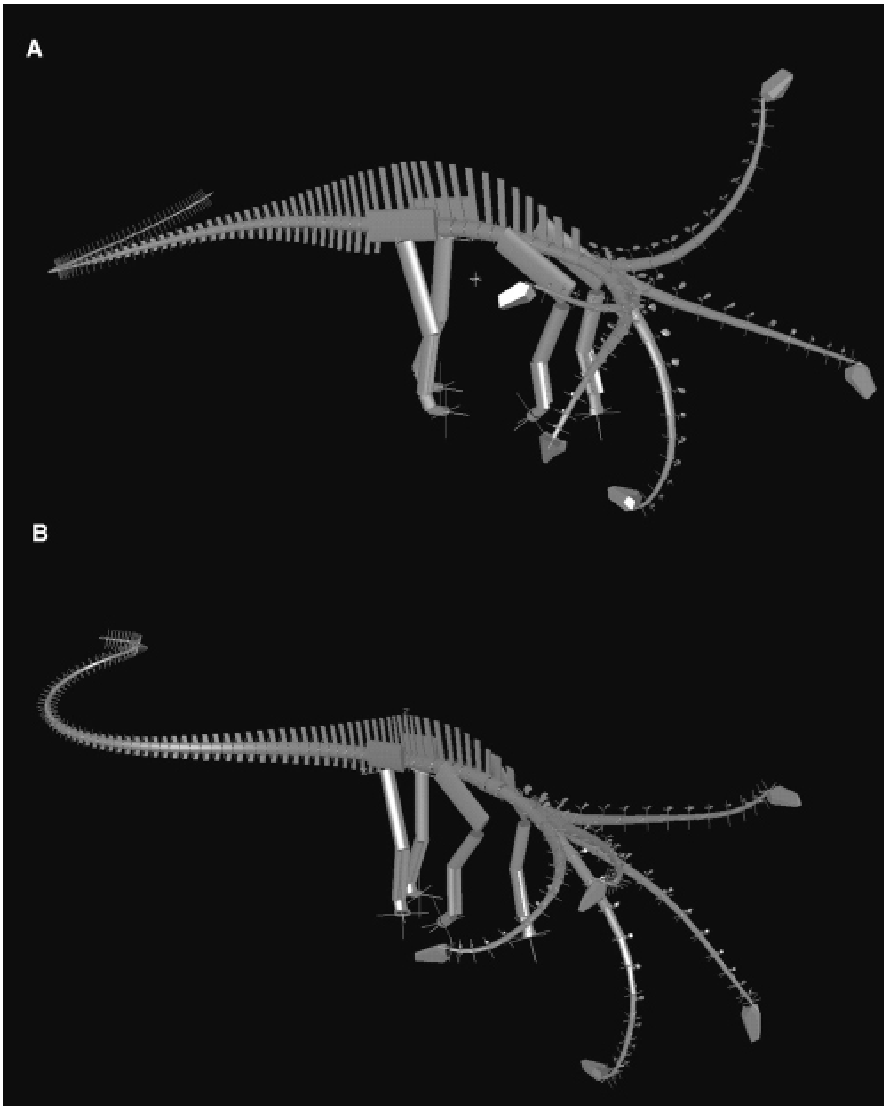

Figure 3. Computer-generated images of (A) *Apatosaurus louisae* with fully extendable neck and (B) *Diplodocus carnegii* in osteological neutral pose (ONP).

heart (9). Evidence supporting this claim is lacking and may never be found, since hearts are not preserved in the fossil record. A more credible solution comes from Roger Seymour (10), who suggests an almost horizontal neck posture to pump the blood to the brain without the added pull of gravity.

A Millstone Around the Neck

A horizontal or semi-horizontal neck is also supported by other studies. The now prevailing model for neck posture is called the "osteological neutral pose" (ONP), and was proposed by Stevens and Parrish in 1999 (11). Using computer simulations, they inferred neck curvature based on the shape of sauropod vertebrae. They concluded that these dinosaurs held their neck low, which would imply that they were not foliage feeders. Instead, they may have browsed large areas of low plants by ventriflexion: curving the neck so that the head was positioned between the knees (11).

The ONP model has been recently contested. On the other side of the debate, Taylor, Wedel and Nash (12) believe that the neck was fully extended to the vertical position. They base their claims on comparisons with extant animal taxa. No living mammal or bird adopts the ONP posture. Instead, these animals bend their necks strongly upwards and forwards, in an S-shaped posture. Birds are descended from dinosaurs, so it is unlikely that sauropods ever adopted the ONP (12). In Stevens and Parrish's defense, the sauropod body plan is historically unique, so it would not be surprising that their particular way of moving the neck was also unique.

Support and Movement

To withstand the weight of a 90-ton body is no easy feat: sauropod legs were especially designed for the job. The femur (upper leg bone) of *Diplodocus* measured up to 1.5 meters in length. It was part of a long and sturdy pillar-like leg. Some scientists have suggested that diplodocids may have even been able to stand up on their hind feet to reach tall foliage. Their center of mass was slightly in front of their hips, so the back half of the body could have supported the weight of the front half (13). *Brachiosaurus* and its relatives had their center of mass much more anteriorly, at the center of the body. Consequently, standing on two legs would have been close to impossible for them (14).

Compared to brachiosaurids, the diplodocid leg bones were gracile. There were therefore some locomotor differences between these two clades (15). Modern three-dimensional simulations of sauropod trackways shed some light on how these dinosaurs walked on land (16). Donald Henderson reconstructed the most stable possible types of gaits for *Diplodocus* and *Brachiosaurus*. He used a known correspondence between the area of the hind-feet and fore-feet to body weight distribution in Asian elephants, so as to infer the weight distribution in sauropods. The simulations predicted that *Diplodocus* must have had a narrow gait, while *Brachiosaurus* should have produced a much wider trackway while moving (16).

Conclusion

Sauropod bodies are difficult objects to study, not only because they went extinct millions of years ago, but also because no other creature has ever re-evolved their unique body plan. For now, most predictions border on mere speculation. Nevertheless, the unprecedented growth of computational and biometrical techniques has allowed paleontologists to analyze these giants in ways unimaginable only 30 years ago. This power of analysis will continue to expand, and with it, our ability to understand how sauropods walked, fed, breathed and withstood the weight of their own bodies. We may one day decode the secrets behind these dinosaurs, but they will never cease to amaze us: gentle giants, unlike any other organism in the history of our planet. H

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Figure 4. Reconstruction of a herd of *Camarasaurus supremus*, a North American brachiosaurid from the Jurassic period. As most other brachiosaurids, *Camarasaurus* must have produced a wide trackway while moving its heavy body.