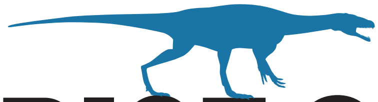

RISE OF THE TITANS

The sauropods were the biggest creatures ever to walk the planet. But the keys to their success emerged in their tiny ancestors.

BY FREDRIC HEEREN

From tail to snout, they stretched as long as four London double-decker buses parked end-to-end. The largest grew from 10-kilogram hatchlings to 100,000-kilogram adults. Their legs alone weighed several tonnes. No land creatures before or since have ever attained the size of the sauropod dinosaurs.

Those four-legged titans of the Jurassic and Cretaceous periods, 200 million–65 million years ago, had a suite of specializations that enabled them to reach such immense proportions. With long necks, wide-opening jaws and rake-like teeth, *Diplodocus*, *Brachiosaurus* and their ilk swept their heads through the treetops, consuming vast amounts of foliage without expending a lot of energy moving their massive legs. Adaptations of the pelvis and limbs created a frame sturdy enough to support their heft, and hollowed-out vertebrae and relatively small heads lightened the load. Their specialized bone development made it possible for juvenile sauropods to grow quickly, putting on several tonnes per year.

Palaeontologists have long thought that these anatomical novelties arose with the large sauropods — that a burst of evolutionary specializations coincided with the explosion in size. But a slew of discoveries in recent years reveals that many important changes first showed up long before, among the relatively puny forerunners of sauropods known as the early sauropodomorphs. Paul Barrett, a palaeontologist at the Natural History Museum in London, calls this group “the unsung members of the dino community”.

Walking upright on two legs, the early sauropodomorphs looked nothing like the lumbering beasts that came to dominate later. But these small creatures and their descendants gradually acquired adaptations that changed how they ate, moved and breathed — in ways that would later enable sauropods to achieve their size (see ‘How to build a giant’).

“It is not that sauropods have these characters because they were gigantic,” says Diego Pol, a palaeontologist at the Egidio Feruglio Palaeontological Museum in Trelew, Argentina. “Instead, they achieved their gigantic size because they evolved from small-bodied ancestors that already had these features.”

STAGE 1: STARTING SMALL

The discoveries have not come easily. Many of the relevant fossils were found in remote sites in the Southern Hemisphere, including Argentina and South Africa.

In 2006, palaeontologist Ricardo Martinez discovered a promising set of bones in the desert of northwestern Argentina. They emerged from rock that dated to the late Triassic Period, about 230 million years ago — a time when the first dinosaurs were starting to appear. He hauled the prize back to the Natural Sciences Museum in San Juan, then spent months freeing a lower jaw from the surrounding rock. Martinez found that the teeth had coarse serrations along their edges, an adaptation for cutting through fibrous plant material. Other early dinosaurs had fine serrations, more suitable for slicing through flesh. This told Martinez that he had found a tiny predecessor of the great sauropods, one with a relatively big skull like its carnivorous ancestors, but teeth more like those of an omnivore.

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In 2009, Martinez and Oscar Alcober, also at the San Juan museum, described[1] the partial skeleton as the earliest and most primitive sauropodomorph yet found. Moving on two legs, the 1.6-metre-long animal had a body the size of a turkey, and a long tail. It weighed only 7–8 kilograms. Martinez called it *Panphagia protos*, meaning ‘first eater of everything’, to celebrate its step on the road from carnivory to herbivory.

Barrett lists “the greater reliance on vegetation rather than animal food” as one of the factors that “kick-started the increase in body size”. The advantage of herbivory is in the logistics of gathering food. Giant sauropods would never have been able to find and catch enough prey to fill their daily nutritional quota — which might have neared a tonne’s worth for the largest.

Traditional grazing could not have done the job either, says Martin Sander, a palaeontologist at the University of Bonn in Germany. Instead of continuously shifting locations, burning through energy as they hoisted their colossal legs, sauropods swung their heads back and forth, mowing efficiently through the foliage.

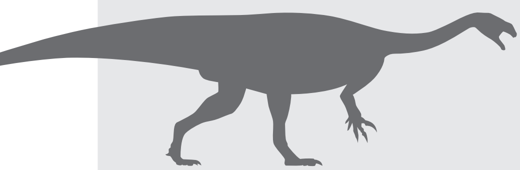
That kind of feeding required long necks, which would have been impossibly heavy if they were built with solid vertebrae. But large sauropods had vertebrae riddled with holes. These air-filled, or pneumatic, bones weighed only about 35% as much as solid ones, which helped the sauropods to carry necks up to 15 metres long, says Mathew Wedel, a palaeontologist at the Western University of Health Sciences in Pomona, California. Hollow areas within the pneumatic bones may have connected to air sacs in the body cavity that helped to blow air through the lungs and improved the breathing

HOW TO BUILD A GIANT

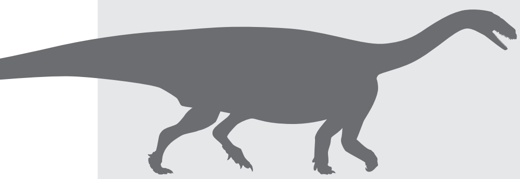
The evolution of sauropods can be split into four stages, starting with tiny dinosaurs in the late Triassic (about 230 million years ago).

STAGE 1: EARLY SAUROPODOMORPHS
Small, fleet, bipedal animals just 1–2.5 metres long that are among the oldest known dinosaurs.

STAGE 2: PROSAUROPODS
Bipedal creatures that reached up to 10 metres long. Some had specializations for rapid bone growth.



STAGE 3: NEAR SAUROPODS
Specialized prosauropods with adaptations that made their limbs and backbones sturdier.



STAGE 4: SAUROPODS
Biggest land animals ever. *Brachiosaurus* (shown right), reached about 25 metres long, and fragmentary fossils hint at much larger species.

efficiency of the giants — features seen in modern birds. Without the extra volume provided by such air sacs, it would have been impossible for the sauropods to clear the stale air that filled their necks after each breath; their lungs were simply too small to do the job alone.

Pneumatic vertebrae would seem to be an adaptation related to giant size. But Wedel has found potential precursors in a small, early sauropodomorph named *Pantydraco*. Its neck vertebrae have pits that match the positions of the holes in the sauropod vertebrae[2].

So how could the precursors of air sacs and pneumatic bones aid tiny dinosaurs? Researchers suspect that they increased the efficiency of oxygen exchange, possibly helping the ancestors of dinosaurs to out-compete their contemporaries during the late Permian and early Triassic periods (260 million–240 million years ago), when atmospheric oxygen concentrations were much lower than they are today[3].

STAGE 2: ADDING TONNES PER YEAR

The earliest sauropodomorphs were small, fast, and mostly moved on two legs. They could rely on speed to evade predators. But the next stage in evolution took the creatures a step up in size, to between 2 and 10 metres long.

The oldest known fossils of these 'core prosauropods' date from the start of the Jurassic period, about 200 million years ago. These creatures had longer necks and torsos, with larger bodies and relatively shorter legs than their predecessors. That made prosauropods less nimble, but their size helped to keep them safe.

That defence took its most extreme form with the later sauropods. "Adult sauropods presumably were almost immune from predation because of their body mass being an order of magnitude greater than that of the largest predators," says Sander. "Their sheer volume made it difficult for an attacker to place an effective bite."

If sauropods grew slowly like most reptiles, each one could have taken more than one hundred years to reach full size. But that would have left the smaller juveniles vulnerable for decades. Instead, evidence is emerging that these dinosaurs grew much faster than modern reptiles.

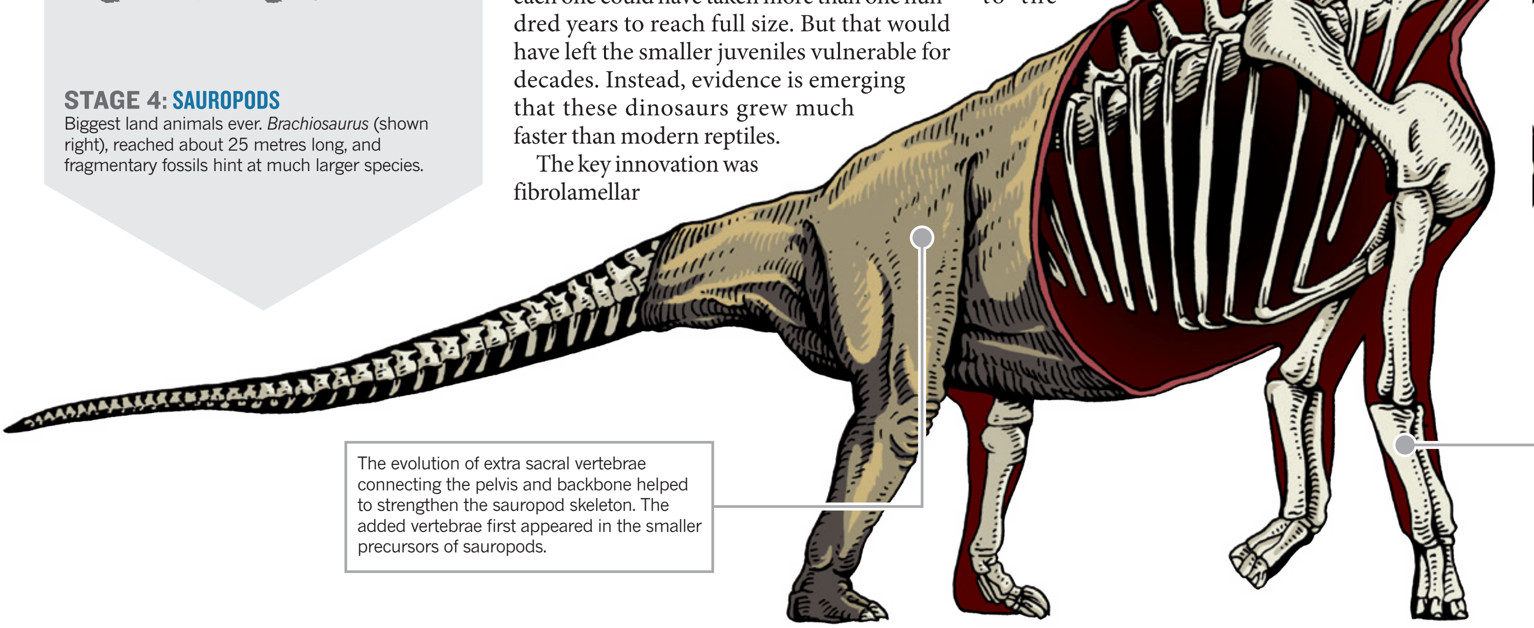
The key innovation was fibrolamellar bone, which develops in two stages, says Sander. "A scaffold of bone is thrown up very quickly, making the bone grow in thickness by about one tenth of a millimetre per day, which then is filled in more gradually." Over the past decade, Sander and other researchers have analysed the structure of fossilized bone and documented the presence of fibrolamellar bone in sauropods. He estimates that the animals could grown by a few tonnes per year.

But the origins of this trait appeared long before the giant sauropods. In 2005, Sander and one of his graduate students, Nicole Klein, reported[4] signs of fibrolamellar bone in *Plateosaurus,* a core prosauropod that lived during the late Triassic and reached only about 10 metres long. By studying bones from more than 40 *Plateosaurus* individuals in Germany, Klein and Sander found that some reached full size in as little as 12 years.

Growth that fast is more characteristic of a warm-blooded animal than a cold-blooded one, and some dinosaurs might have had elevated body temperatures. Robert Eagle, a geochemist at the California Institute of Technology in Pasadena, and his colleagues reported[5] last month that two giant sauropods, *Brachiosaurus* and *Camarasaurus*, had body temperatures 5–12 °C higher than those of modern alligators.

Plateosaurus and other prosauropods showed further anatomical developments that later helped their descendants to achieve massive size. For example, they had a beefed-up sacrum — the structural link between the backbone and rear legs. Early sauropodomorphs had two sacral vertebrae, but prosauropods had three, which would have given more support[6].

That and other developments helped to fuel an evolutionary jump during the late Triassic, from 7-kilogram early sauropodomorphs such as *Panphagia* to the



The evolution of extra sacral vertebrae connecting the pelvis and backbone helped to strengthen the sauropod skeleton. The added vertebrae first appeared in the smaller precursors of sauropods.

4,000-kilogram *Plateosaurus*. “The dramatic size increase observed along the first 25 million years of sauropodomorph history was the fastest one in the history of life,” says Martin Ezcurra, a palaeontologist at the Bernardino Rivadavia Argentinian Museum of Natural Sciences in Buenos Aires.

STAGE 3: EDGE OF GREATNESS

Some of the most recent fossil discoveries fall into a third chapter of sauropodomorph evolution: creatures that could be called near-sauropods. Adam Yates, a palaeontologist at the University of Witwatersrand in Johannesburg, came to South Africa hoping to find fossils from this stage that could reveal how sauropodomorphs became quadrupedal.

He and a student hit the jackpot on a hill called Spion Kop. “Bone was piled upon bone,” says Yates. “Given that we were finding so much of the skeleton, including parts of the small, fragile skull, we knew this was a major find.”

Last year, Yates and his colleagues named the new species *Aardonyx celestae*[7]. From the lower jaw of *Aardonyx*, Yates could tell that it did not have fleshy cheeks that limited how far the jaw could gape open. Instead of taking small bites and chewing as its older relatives did, *Aardonyx* could have opened its jaws wider and grabbed big mouthfuls, gulping them down whole.

That adaptation enabled the development of extremely long necks among sauropods, because it did away with the need for big jaw muscles and massive heads. “The long neck was only possible because they did not chew,” says Sander.

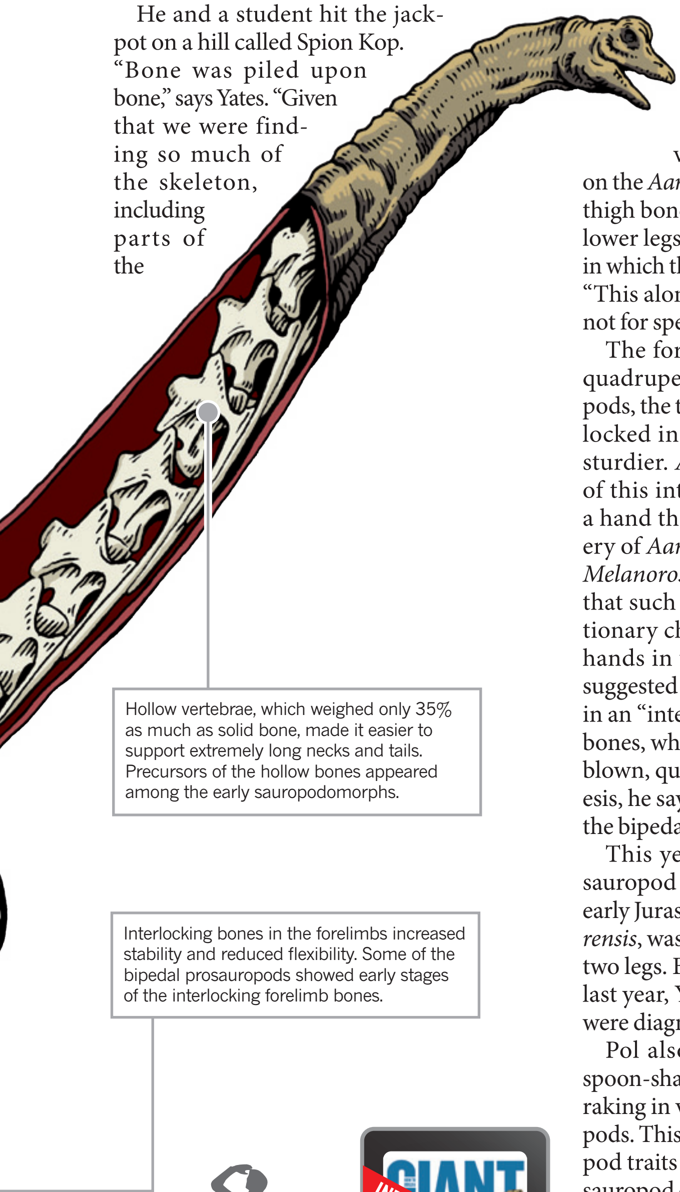
Aardonyx was bipedal, but it had acquired some leg features that show up in quadrupedal sauropods, with their lumbering gait. Matthew Bonnan, a palaeobiologist at Western Illinois University in Macomb and a co-author on the *Aardonyx* paper, says that the creature’s thigh bones were longer than the bones of its lower legs, unlike earlier sauropodomorphs, in which these bones were about the same size. “This alone suggests animals that were built not for speed but for support,” says Bonnan.

The forelimbs of *Aardonyx* also showed quadruped-like adaptations. In true sauropods, the two long bones of the forearm interlocked in a way that made the front limbs sturdier. *Aardonyx* showed an earlier stage of this interlocking forearm, connected to a hand that could grasp. Before the discovery of *Aardonyx* and a related species called *Melanorosaurus*, Bonnan had hypothesized that such locking would produce an evolutionary chain reaction that also altered the hands in ways more suited to walking. He suggested that these adaptations would come in an “integrated functional suite” of shifting bones, which he expected to see first in a full-blown, quadrupedal sauropod. This hypothesis, he says, was “smashed” by the features of the bipedal *Aardonyx*.

This year, Pol described[8] another near-sauropod that demolished expectations. The early Jurassic dinosaur, *Leonerasaurus taquetrensis*, was just 2.5 metres long and walked on two legs. But it had four sacral vertebrae. Just last year, Yates had written[7] that four sacrals were diagnostic of the four-footed posture.

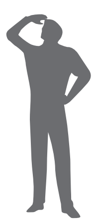
Pol also found that *Leonerasaurus* had spoon-shaped, forward-leaning front teeth for raking in vegetation — much like later sauropods. This 2.5-metre animal with many sauropod traits is helping to build a new picture of sauropod evolution that, Pol says, “has turned upside down the previous ideas”.

Researchers note that *Leonerasaurus* and other known sauropodomorphs were not the ancestors of sauropods. Because the fossil record is so spotty, it is usually impossible to identify direct ancestors. But the prosauropods and near-sauropods of the Jurassic preserve information about adaptations that appeared among the unknown ancestors of sauropods.



Hollow vertebrae, which weighed only 35% as much as solid bone, made it easier to support extremely long necks and tails. Precursors of the hollow bones appeared among the early sauropodomorphs.

Interlocking bones in the forelimbs increased stability and reduced flexibility. Some of the bipedal prosauropods showed early stages of the interlocking forelimb bones.



STAGE 4: ON ALL FOURS

Many late Triassic and early Jurassic sauropodomorphs could walk on two legs or four, as needed. But in 2008, Ronan Allain, a palaeontologist at the National Museum of Natural History in Paris, and Najat Aquesbi, a palaeontologist at Mohammed V University in Rabat, described an animal from the later part of the early Jurassic that seemed committed to four[9].

“*Tazoudasaurus* could be considered the oldest known ‘true sauropod’,” says Allain. Unlike its forebears, which had long fingers that could grasp, this 9-metre-long animal had a stubby hand suited to bearing weight. Allain placed *Tazoudasaurus* into a new group of sauropods that he named Gravisauria, or ‘heavy lizards’.

Heaviness is relative, and the most massive sauropods did not arise for another 90 million years. By the Cretaceous, fossils hint that some sauropods reached lengths of 40 metres and approached body masses of 100 tonnes. Yet in comparison with the changes that occurred during the early stages of sauropodomorph evolution, these later developments were relatively minor tweaks to a body plan that had emerged earlier.

The sauropod story shows the importance of pre-adaptations — traits that are neutral or serve some purpose but later become co-opted to fill a new function. Such traits constrain the future evolutionary pathways of a lineage, but with hindsight they can seem fortuitous for something that researchers consider an important attribute, such as gigantism. “The evolution of sauropods does look like kind of a crapshoot in which everything fell into place,” says Wedel. “Sauropods seem to have somehow gotten the evolutionary Wonka ticket of all the features that they needed to grow big.” ■ SEE BOOKS AND ARTS P.172

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