

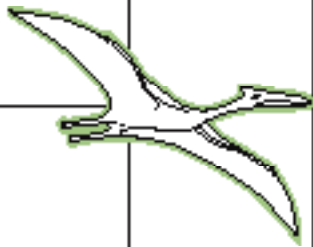
Look at the SIZE of those things!

They were the biggest land animals ever, but how did sauropods get so huge, asks James O'Donoghue

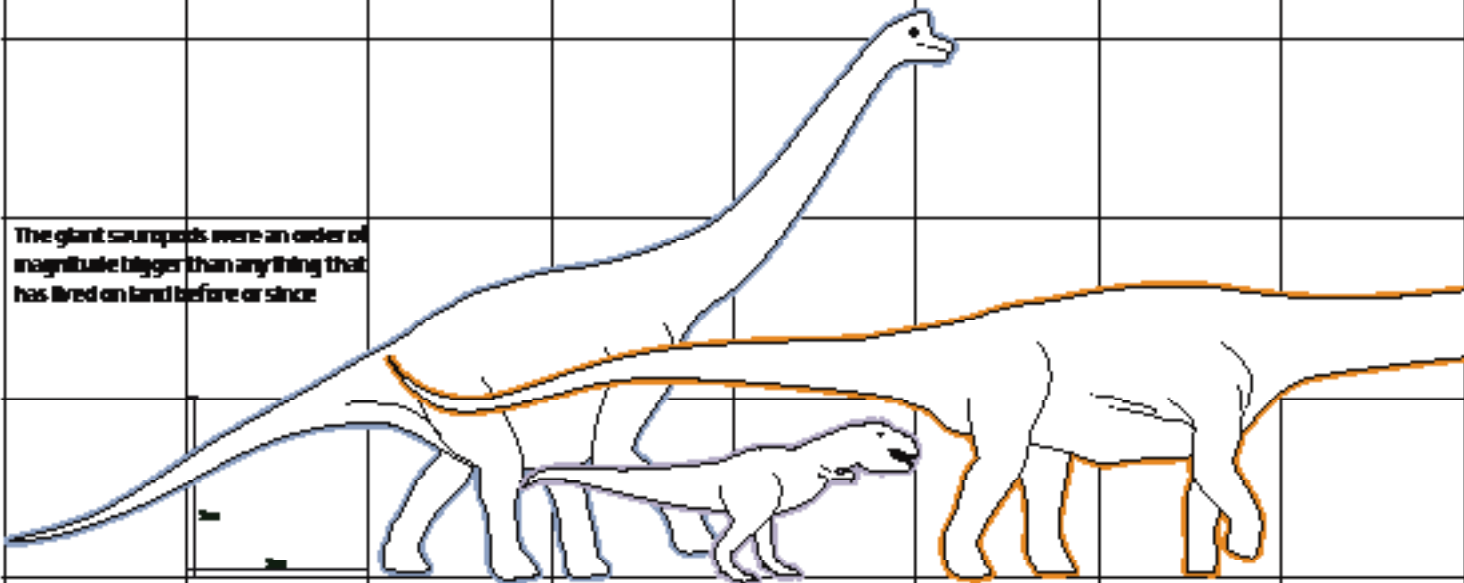
BEFORE my visit to Argentina, I had no real grasp of how large the very biggest dinosaurs could be. In the end, all it took was a glance at a single bone.

I was in the Argentine Museum of Natural Sciences in Buenos Aires when I came across a vertebra from a dinosaur's back. What to compare it with? A human vertebra would fit comfortably in the palm of your hand. An elephant's would take two hands. At 1.6 metres tall, the vertebra in front of me was on another scale entirely – it would need a forklift truck to shift it.

The vertebra belonged to argentinosauros, a 100-million-year-old dinosaur that, as far as we know, was the biggest land animal that ever lived. In life it was 35 metres long and weighed around 80 tonnes.



The giant sauropods were an order of magnitude bigger than anything that has lived on land before or since



Brachiosaurus
Not the longest sauropod, but probably the tallest, at 15 metres

Quetzalcoatlus
Biggest known pterosaur, with a wingspan of about 10 metres

Tyrannosaurus rex
One of the largest predatory dinosaurs, weighing around 7 tonnes

Argentinosaurus
Longest land animal ever. About 35 metres long and weighing in at 80 tonnes

Argentinosaurus is a member of the sauropods, an instantly recognisable group that includes diplodocus, brachiosaurus and apatosaurus. Sauropods had long necks, long tails, barrel-shaped torsos and trunk-like legs. They weren't all enormous, but the big ones were extraordinary.

No land animal has come close to the size of argentinosaurus and its ilk (marine animals are a different story – see “The whales’ tale”, page 40). The biggest land animal today is the African elephant, with a large male weighing in at around 6 tonnes. The largest land mammal ever was a 6-metre-tall hornless rhino known as *Paraceratherium*, which lived 30 million years ago and would have tipped the scales at 15 tonnes. Even among the dinosaurs, sauropods were in a class of their own. A mature *Tyrannosaurus rex* would have weighed just 7 tonnes, while the largest non-sauropod was a duck-billed dinosaur from China called shantungosaurus, which weighed in at 16 tonnes.

Sauropods’ unprecedented bulk has long posed a thorny problem for biologists. How did they get to be so big? Why have no other land animals reached such

massive proportions before or since? There have not been convincing answers to these questions. Until now.

“We now have a coherent theory on how dinosaur gigantism evolved,” says Martin Sander, a palaeontologist at the University of Bonn in Germany. For six years, Sander has headed an international team of scientists put together to tackle the gigantism conundrum. It turns out that sauropods had a unique set of biological features that combined to propel them to unrivalled sizes.

Bigger is better

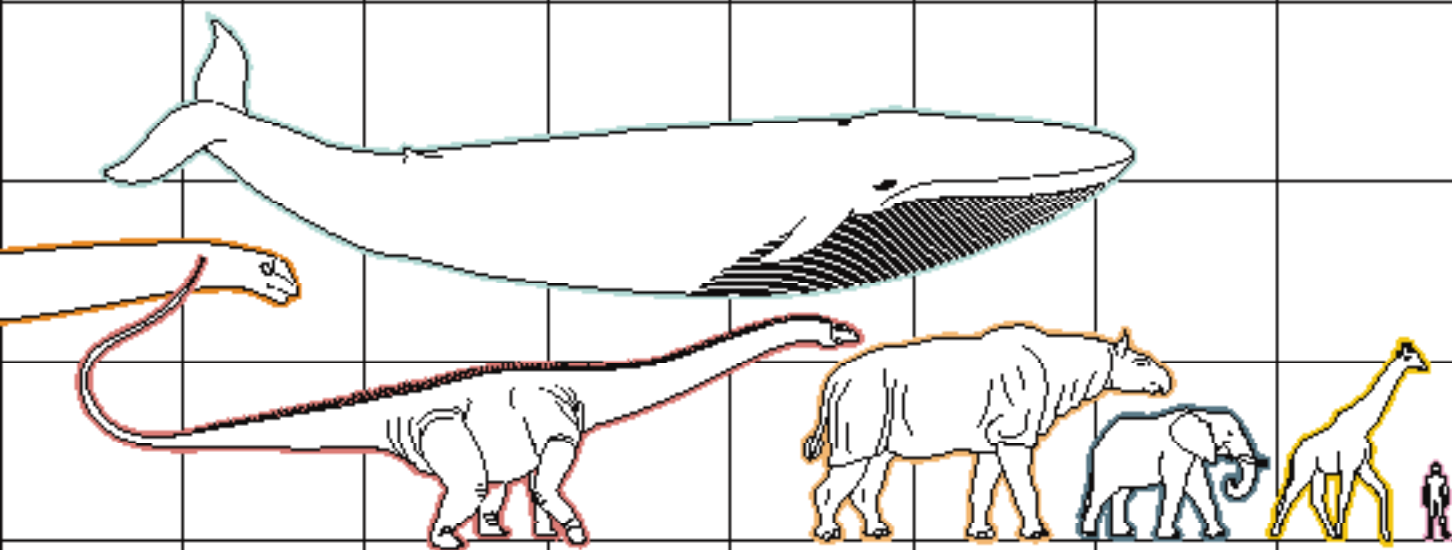
Sander’s starting point was observations made by the 19th-century palaeontologist Edward Drinker Cope, who noticed that animal lineages tend to get bigger over evolutionary time, starting out small and leaving ever bigger descendants. This process came to be known as Cope’s rule.

Getting bigger has evolutionary advantages, explains David Hone, an expert on Cope’s rule at the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, China. “You are harder to predate and it is easier

for you to fight off competitors for food or for mates.” But eventually it catches up with you. “We also know that big animals are generally more vulnerable to extinction,” he says. Larger animals eat more and breed more slowly than smaller ones, so their problems are greater when times are tough and food is scarce. “Many of the very large mammals, such as *Paraceratherium*, had a short tenure in the fossil record, while smaller species often tend to be more persistent,” says mammal palaeobiologist Christine Janis of Brown University in Providence, Rhode Island. So on one hand natural selection encourages animals to grow larger, but on the other it eventually punishes them for doing so. This equilibrium between opposing forces has prevented most land animals from exceeding about 10 tonnes.

Large size poses other problems too. How do you support your massive bulk? How do you cram enough food and oxygen into your body? How do you prevent yourself from overheating? Somehow the sauropods overcame all of these challenges.

Sauropod-like dinosaurs first appeared about 220 million years ago and quickly



Diplodocus
A typical sauropod, about 25 metres long

Blue whale
Largest animal ever. Up to 30 metres long and about 150 tonnes

Paraceratherium
Largest known land mammal, 5.5 metres tall at the shoulder

African elephant
At around 6 tonnes, this is the largest living land animal

Giraffe
Tallest living land mammal, at 5.5 metres

grew very large. The earliest known true sauropod is the 210-million-year-old, 15-tonne isanosaurus (*Comptes Rendus Palevol*, vol 1, p 103). From there, they just kept on getting bigger. Massive sauropods evolved time and time again, in different lineages all over the world.

How did this come about? In the 1990s, Janis suggested that one important factor was the sauropods' method of reproduction. Like all dinosaurs they laid eggs, while nearly all mammals give birth to live young.

"The larger a mammal is, the fewer offspring it has, and the further apart they are born," explains Janis. "Yet big dinosaurs could carry on having large clutches of eggs and lots of young. As dinosaurs increase in size you don't see any reduction in the number of young." Elephants only give birth every four years. In the same period, a big dinosaur could have laid hundreds of eggs.

This would have allowed sauropods to sidestep one of the hazards that large size usually brings. Faced with a crisis, the population would have had the potential to rebound much more quickly than large mammals can (*Annales Zoologici Fennici*,

vol 28, p 201). Support for Janis's hypothesis has come from studies of fossilised eggs. Sauropods left behind an astonishingly detailed record of eggs and nests, sometimes with well-preserved embryos inside. The eggs were the size of ostrich eggs or smaller and the clutches contained up to eight eggs, although larger clutches have been found in Argentina.

Small fry

What struck Sander was the size imbalance between adult sauropods and their small eggs and clutch sizes. "A huge part of an individual's energy usually goes into reproduction," he says, "and yet a sauropod mother, who probably weighed at least 5 tonnes, produces at most 24 kilograms of eggs at a time. So she must have laid several clutches a year, otherwise her reproductive effort would have been too low." The nest sites also reveal no sign of parental care, further increasing the adults' ability to produce lots of offspring.

Egg laying and a lack of parental care, however, cannot be the whole story as all dinosaurs laid eggs and few cared for their young. So Sander looked elsewhere in search

of further pieces of the puzzle.

It seems obvious, but in order to get very big, it helps to grow fast. To understand dinosaur growth rates, thin sections of their bones are examined under microscopes. Most dinosaurs have growth lines – akin to tree rings – in their bones, indicating the fitful growth typical of animals with a sluggish metabolism. Sauropod bones, in contrast, have a pattern of continuous growth similar to that seen in mammals and birds. Sander concludes that sauropods had a fast metabolism, which enabled them to attain immense sizes relatively quickly. "No other dinosaur has such high growth rates as sauropods," he says.

Research by his team on a 30-tonne Asian sauropod called mamenchisaurus shows how this rapid growth translated into astonishing weight gains. At its peak, it grew up to 2 tonnes a year. In comparison, an African elephant gains at most 200 kilograms in a year.

Fast growth is all well and good, but once an animal reaches an immense size, how does it deal with the demands of its body and its lifestyle? Sauropods all conformed to the same basic body plan: a long neck terminating with a small head, a huge barrel-like body and, inevitably, thick sturdy legs. Sander and others now argue that the creatures' unique anatomical combination – inside and out – was key to its sizeable success.

In the 1980s, Jyrki Hokkanen of the University of Helsinki in Finland tackled one part of this problem – how to support and move a massive body. By analysing bone and muscle strength in large animals, he concluded that even the largest sauropods were nowhere near the theoretical upper limit for body size. "Brachiosaurus could have been at least a couple of times bigger and still have walked on land," he concluded (*Journal of Theoretical Biology*, vol 118, p 491). So, while a large sauropod would have been cumbersome, that in itself did not inhibit its size.

A related problem is how to get enough oxygen. In 2003, Mathew Wedel of the Sam Noble Oklahoma Museum of Natural History solved this by showing that sauropods had bird-like lungs.

Birds breathe in a far more efficient way than mammals. When they inhale, air fills their lungs and also air sacs further inside their body. Upon exhaling, fresh air from the air sacs flows out and replaces the air that was in the lungs. This means that the lungs contain a constant stream of fresh air and can extract up to two-and-a-half times as much oxygen per breath as a mammal. "Sauropods had an

Reign of the sauropods

- **220 million years ago (late Triassic)** Discernible sauropod ancestors appear in the fossil record.
- **210 million years ago (late Triassic)** First true sauropod – the 15-tonne isanosaurus
- **155 million years ago (late Jurassic)** Sauropod heyday. Colossi such as mamenchisaurus and the brachiosaurus appear, along with children's favourites diplodocus and apatosaurus.

- Sauropods are found on all continents except Antarctica.
- **100 million years ago (late Cretaceous)** Argentinosaurus, the largest known sauropod, lived in what is now Patagonia. It is considered unlikely that a significantly bigger one remains undiscovered.
- **65 million years ago** Sauropods go extinct along with all the other non-avian dinosaurs.

The whales' tale

While 80-tonne argentinosaurus is the largest land animal we know of, it is not the largest animal of all time. That honour (further discoveries notwithstanding) goes to the blue whale, which typically weighs between 100 and 150 tonnes, but has been known to reach 190 tonnes. How do whales manage to outgrow even the biggest dinosaurs?

One factor is the buoyancy provided by seawater, which largely frees them from the constraints of gravity. They also benefit from having enormous quantities of protein-rich krill to eat, a high-quality food resource that is unparalleled on land. During the feeding season, a blue whale can swallow as much as 3.5 tonnes of krill daily.



“A large sauropod probably needed to eat a tonne of grass, leaves and branches every day”

air sac system that was, as far as we can tell, just as complex as that of birds,” says Wedel (*Paleobiology*, vol 29, p 243).

Bird-like breathing would have helped to support a large size in a variety of ways. First, it solves the problem of getting enough oxygen. Secondly, the air sacs were located in and around the vertebrae, greatly reducing their weight. Giant vertebrae, such as the one I saw in Argentina, would have been full of air sac cavities, like a Swiss cheese, keeping the overall body weight down.

Finally, breathing like a bird would solve another problem: how the sauropods stopped themselves from overheating. A high metabolism coupled with a huge body, with its low surface area-to-volume ratio, would normally spell trouble. “Big sauropods could probably pant to cool themselves off, like ostriches,” says Wedel.

Anatomy also explains how an 80-tonne animal could obtain enough to eat. The largest land animals today are all vegetarians that survive by eating huge amounts of plant material of poor nutritional quality. This

is because there is not enough higher-quality food such as fruits and seeds to sustain a large animal, but grasses, leaves and branches are much more abundant. It is assumed that this is true for the extinct giants too.

But subsisting on poor quality forage means eating a lot. An elephant spends as much as 18 hours a day feeding, eating up to 200 kilograms of vegetation a day, and the ability to eat enough in the time available is one limiting factor on their size.

Large sauropods probably needed to eat a tonne of vegetation a day, so how did they manage it? Sander sees the crane-like neck and small head as being the key.

The lightweight vertebrae allowed their necks to grow longer, which would have increased their feeding range, both side to side and up and down. This would have allowed them to stand still while their necks did all the work, helping to conserve energy.

What is more, instead of chewing their food, sauropods used their simple peg-like teeth to pluck leaves and branches from plants before swallowing them whole. This allowed them to

Biomechanics suggest that sauropods could have grown even bigger, so why didn't they?

cram in much more food per day than if they had spent time chewing. It also meant they had no need of heavy grinding teeth and the elaborate musculature that goes with them, reducing the mass of their heads and allowing their necks to grow even longer.

The nutrients from this huge unchewed meal would have been extracted by lengthy microbial fermentation inside their huge torsos. That, however, posed yet another problem. As flowering plants did not evolve until late in the sauropods' reign, their diet was limited to plants such as monkey puzzles, ginkgos and horsetails. According to animal nutritionist Jürgen Hummel at the University of Bonn, it is commonly believed that such fodder is of exceptionally low nutritional quality. How did the sauropods manage to survive on this restricted diet?

Hummel set about trying to find out. In 2008, he simulated dinosaur digestion by placing samples of these primitive plants among the gut microbes of sheep. It turns out that many of the plants were more nutritious than they had been given credit for. “When you give the ancient plants enough time, they are digested quite reasonably. A long retention time in the digestive tract of a sauropod would have been the solution,” he says (*Proceedings of the Royal Society B*, vol 275, p 1015).

With their unique combination of reproduction, growth and anatomy, sauropods were able to overcome the limits on body size that have constrained all other land animals, and it was a hugely successful design. The giant sauropods were a fixture of the dinosaur age, persisting for 145 million years. Yet it is 65 million years since they became extinct. Could Earth ever see their like again?

Sander believes there is no reason why not – but you would need another extraordinary set of biological attributes to come together. “Sauropods did a number of things right, but I don't think they are the only way to reach gigantic sizes,” he says. “However, you would need a mass extinction to reset the whole system to zero, plus evolutionary runs of 30 to 40 million years to give a different design a chance to see how far it can take body size.” *Argentinosaurus*, it seems, will hold the crown for a long time to come. ■

James O'Donoghue is a writer based in Essex, UK