

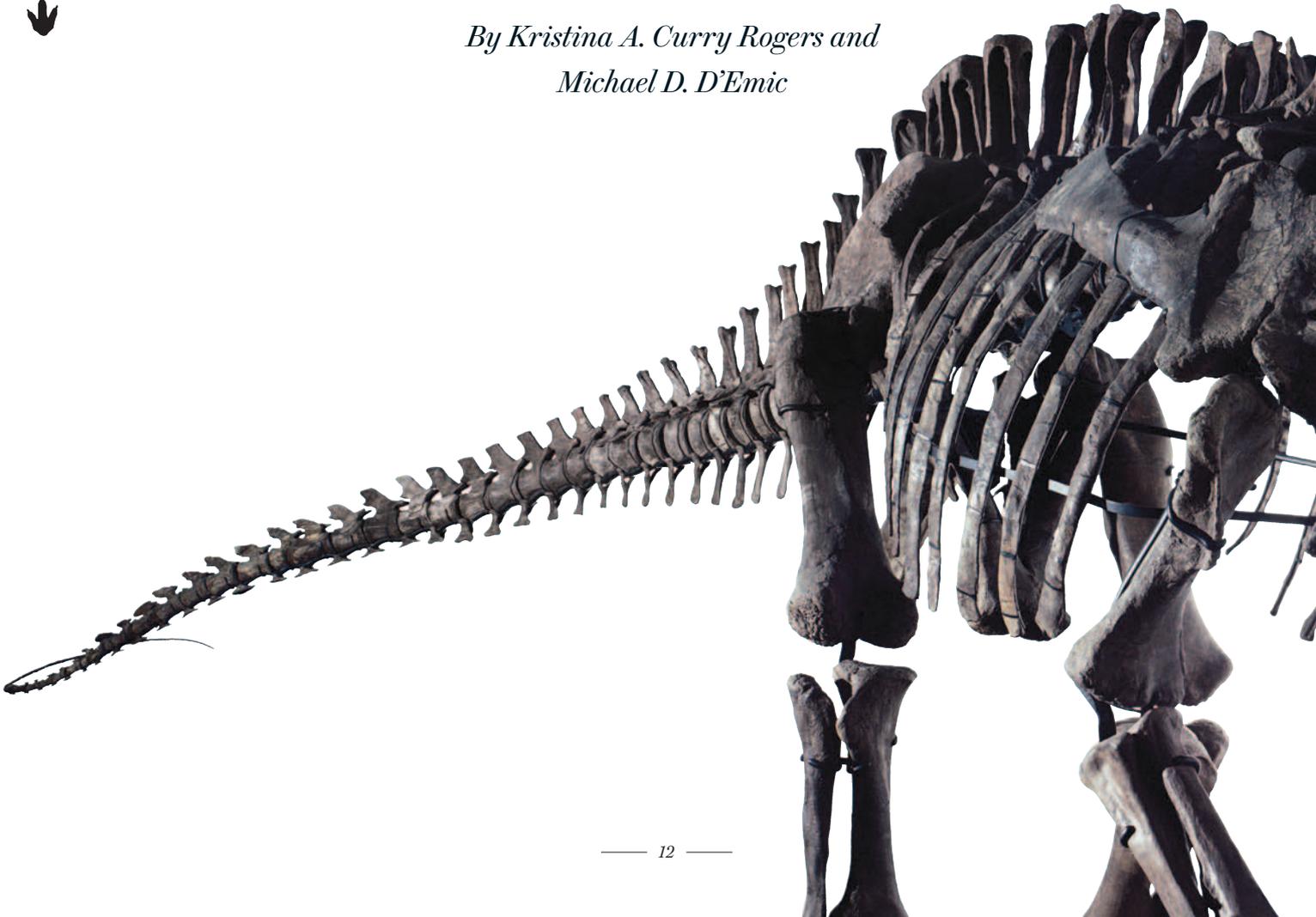
EVOLUTION

TRIUMPH OF THE TITANS

The long-necked dinosaurs known as sauropods, once seen as icons of extinction, thrived for millions of years all around the world

*By Kristina A. Curry Rogers and
Michael D. D'Emic*

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APATOSAURUS, the proper scientific name for the famous *Brontosaurus*, exhibits the classic sauropod silhouette: a long spinal column, tapered on both ends, topped with a small-brained skull and balanced on four pillarlike legs. Over the course of their long reign, sauropods evolved various body sizes and different teeth and snout shapes, but their basic architecture stayed the same.

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EVER SINCE FOSSILS OF THE BEHEMOTH, LONG-NECKED DINOSAURS KNOWN as sauropods surfaced in England more than 170 years ago, they have awed and confused scientists. Even when the great English anatomist Sir Richard Owen recognized in 1842 that dinosaurs constituted a group of their own, apart from reptiles, he excluded the gigantic bones later classified as sauropods. Instead he interpreted them as belonging to a type of aquatic crocodile, which he had named *Cetiosaurus*, or “whale lizard,” for the enormous size of its bones. Nearly 30 years later, in 1871, University of Oxford geologist John Phillips would report the discovery of a *Cetiosaurus* skeleton sufficiently complete to reveal that, far from being an aquatic crocodile, the animal spent at least some of its time on land.

Phillips’s assessment caused considerable consternation among paleontologists for decades—they just could not conceive how such a massive animal could support its weight on land. Because sauropods were perceived as animals without a place, unsuited for land or sea, they came to be seen as unwieldy, overgrown, archaic herbivores fated for rapid extinction or, at least, marginalization by more “advanced” dinosaurs. As recently as 1991, scientists argued that sauropods were far from the apex of dinosaur success and only flourished in the absence of more specialized plant-eating dinosaurs. In this view, these giants of the Jurassic period, between about 200 million and 145 million years ago, gave way to bigger-brained, better-adapted herbivores in the Cretaceous, between some 145 million and 66 million years ago, such as the duckbilled hadrosaurs and horned ceratopsians, which outcompeted the sauropods and pushed them to the fringe.

Relegated to the Southern Hemisphere, so the story goes, only a handful of sauropod stragglers held out to the end of the Cretaceous, when an asteroid impact brought the dinosaur era to a close.

This view of maladapted sauropods plodding along to obscurity was itself destined for extinction. Recent discoveries of sauropods from locales around the world—more than 70 new species since 2002—have revealed an extraordinarily resilient group that flourished for millions of years at the observed limits of terrestrial body

size. Thanks to such finds and new analytical tools for evaluating them, scientists have begun to answer key questions about how sauropods reproduced, how they grew, what they ate and how they adapted to dramatic environmental change. These revelations have changed almost everything that we thought we knew about this iconic group.

BEYOND THE BIG FOUR

LIKE MOST PEOPLE, the two of us first encountered the long-necked giants of the dinosaur world amid the cacophony of kid-filled natural history museums. Towering above the din of excited field-trippers stood the stately sauropod: longer than two school buses, its neck and skull stretched far above the crowds and the other dinosaurs. Even in dust-covered silence, the bones inspired awe. Most of the classic sauropods—such as *Diplodocus*, *Camarasaurus* and *Apatosaurus*—made their debut in the late 1800s, and by the turn of the century every major natural history museum had to have one. Jurassic sauropod bones flowed into museums in such great numbers that it is still possible to find shelves of these fossils in the bowels of their collections, encased in plaster field jackets, waiting to be opened and studied.

But those classic sauropods represented only a small fraction of the diversity of this group. The story of how sauropods originated and how they evolved into so many forms over their 150-million-year evolutionary history begins even before their appearance—about 210 mil-

IN BRIEF

<p>Paleontologists traditionally viewed the long-necked, small-brained giant dinosaurs referred to as sauropods as</p>	<p>doomed creatures unfit for life on land or in the water. Recent discoveries have upended that</p>	<p>scenario, revealing that sauropods prospered for nearly 150 million years. The secrets of their success seem to</p>	<p>have been their mix of mammal-like and reptilelike traits, combined with an ability to adapt to a changing world.</p>
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PHOTOGRAPHED ON LOCATION AT CARNEGIE MUSEUM OF NATURAL HISTORY (preceding pages)

lion years ago in the late Triassic, a time when the world witnessed an extinction event of other reptile groups that cleared the path for dinosaurs and their subsequent dominance of terrestrial ecosystems.

The oldest known dinosaurs in the fossil record are small-bodied, bipedal animals whose remains were found in roughly 230-million-year-old sediments in the Southern Hemisphere; these animals would eventually evolve into the more familiar sauropods and theropods (such as *Tyrannosaurus rex*). Paleontologists have found characteristic trackways of true sauropods—with their quadrupedal posture and elephantine feet—dating to around 225 million years ago in North America and in Argentina. The oldest hints of their massive skeletons are just a little younger, represented by creatures such as *Isanosaurus* from Thailand, *Gongxianosaurus* from China and *Vulcanodon* from Zimbabwe. These early species already bear the signature sauropod stamps: they were walking backbones (many sauropod species have more than 100 vertebrae), with long, tapering necks and tails, tiny skulls, and pillarlike limbs made for bearing serious weight. That basic architectural plan would persist in sauropods for their entire evolutionary duration, making them among the most recognizable of any dinosaur group.

Sauropods did not stagnate, however. Their body plan got more elaborate as time played on, with plate tectonics helping to drive the global diversification of their lineages. Sauropod diversity waxed and waned throughout the evolutionary history of the group—right up to the end of the dinosaur era. These recurrent spikes in diversity contradict the long-standing view that sauropods hit their short-lived prime in the Jurassic and limped along to their nadir in the Cretaceous. Instead we see important sauropod groups, such as the stocky titanosaurs and the shovel-faced rebbachisaurids, flourishing long after this presumed Jurassic heyday. Even in the twilight of dinosaur times during the Late Cretaceous, sauropods were diverse and still living large.

SIZING UP SAUROPODS

NEW DISCOVERIES HAVE SHOWN that sauropods were successful in terms of geographic range, diversity and the longevity of lineages. But what exactly were their strategies for getting by in the world? The answer seems to be that they made use of a special mix of reptilelike and mammal-like characteristics, which merged to create unique organisms. Although Sir Owen was wrong in thinking that sauropods were lizards, in this respect his “whale lizard” name turned out to be fairly apt after all.

In their reproductive habits, sauropods, like all dinosaurs and most reptiles, hatched from eggs. The first concrete evidence for sauropod reproductive biology came from roughly 80-million-year-old deposits at Auca Mahuevo in Argentina, where in 1997 Luis Chiappe of the Natural History Museum of Los Angeles County and his colleagues found a sauropod nesting ground containing thousands of eggs. Inside some of the eggs, the researchers found the first known embryos of sauropods, some of which preserve fossilized skin and egg membranes.

These nesting traces provide clear evidence that titanosaur sauropods laid 20 to 40 spherical eggs per clutch in excavated depressions. The eggs are relatively small, averaging 13 to 15 centimeters in diameter, about the size of a grapefruit. The abundance of nests in the same layers at Auca Mahuevo suggests that the titanosaurs there associated in large groups and nested at the same area at least six

times. Still, no convincing evidence exists that they sat on the eggs or cared for the young once they hatched. In fact, the proximity of the nesting structures to one another suggests that these titanosaurs were hands-off parents. Unlike other large-bodied vertebrates, such as elephants and whales, in which parents invest heavily in raising a single offspring, sauropods apparently stuck with the typical reptilian pattern of producing many offspring that were then left to fend for themselves.

Although sauropod parental investment hewed to the reptilian norm, the growth rates of these animals did not. Sauropods had the furthest to grow from newborn to adult of any animal ever to live. Baby sauropods were less than half a meter long and weighed less than 10 kilograms. As adults, the largest sauropods attained body lengths of 30 meters and body masses between 25,000 and 40,000 kilograms or more. For comparison, the average baby African elephant weighs around 120 kilograms at birth and reaches an adult weight of 2,268 to 6,350 kilograms.

Most early dinosaur researchers simply extrapolated reptilian growth rates to estimate sauropod growth history. In this model, even smaller sauropods would have taken until age 60 to experience their first growth plateau and more than a century to reach adult size. That would mean waiting until age 60 to reproduce—risky business for any animal that stays relatively small and predator-prone for a big part of life.

A different perspective on sauropod development began to emerge in the 1960s, when Armand de Ricqlès, now emeritus at the Collège de France in Paris, began to study the internal microstructure, or histology, of bone for insights into the life history of dinosaurs and other extinct animals. The patterns of bone mineral, the density and architecture of the cavities left behind by blood vessels, and the degree of bone resorption are all preserved in fossil bones. These features indicate that sauropod growth rates soared through most of life and that they were generally faster than the growth rates of reptiles and on par with those of living large-bodied mammals, many of which mature within decades. Therefore, sauropods did not have to live for centuries to become giants.

With such rapid growth rates and enormous adult body sizes, sauropods must have had prodigious appetites. Indeed, one of the most perplexing mysteries of sauropod biology is how these giants gathered enough plant matter to survive, much less thrive, for so long. Studies of sauropod feeding have focused on tooth shape, microscopic wear marks, jaw muscle reconstructions, and analyses of the biomechanics involved in opening and closing the jaw. This research has revealed that different sauropods employed distinctive feeding methods—some bit off tough vegetation, whereas others cropped or clipped softer plants.

Researchers generally agree that sauropods did not do a lot of chewing and thus most likely required some “postmouth” processing to break down plant food into usable energy. The most commonly cited solution to this need for extra processing is the use of gastroliths—or stomach stones, as they are popularly known. Polished stones often turn up in sauropod-bearing rock formations in western North America, and scientists have long hypothesized that these stones are analogous to the gastroliths that some modern vertebrates, such as certain birds, ingest to help grind up food and aid in digestion. In 2007, however, Oliver Wings, now at the Niedersächsischen Landesmuseums Hannover in Germany, and Martin Sander of the University of

EVEN IN THE TWILIGHT OF DINOSAUR TIMES, SAUROPODS WERE DIVERSE AND STILL LIVING LARGE.

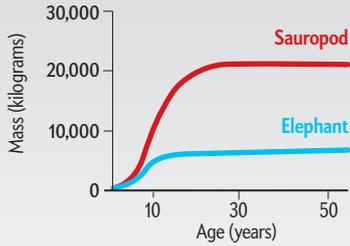
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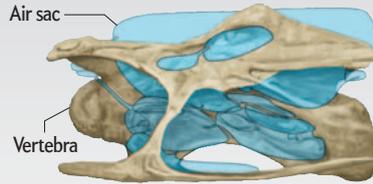
Survival Tricks

Sauropods benefited from a host of adaptations to living large on land, thus allowing them to reach sizes unequalled by any terrestrial animal since.

Unlike most reptiles, sauropods grew fast—akin to modern terrestrial giants, such as elephants—and would have reached adult size in a few decades.



Hollow vertebrae would have lightened sauropod bodies and may have permitted the expansion of air sacs from the lungs that could have allowed them to take in more oxygen with each breath.

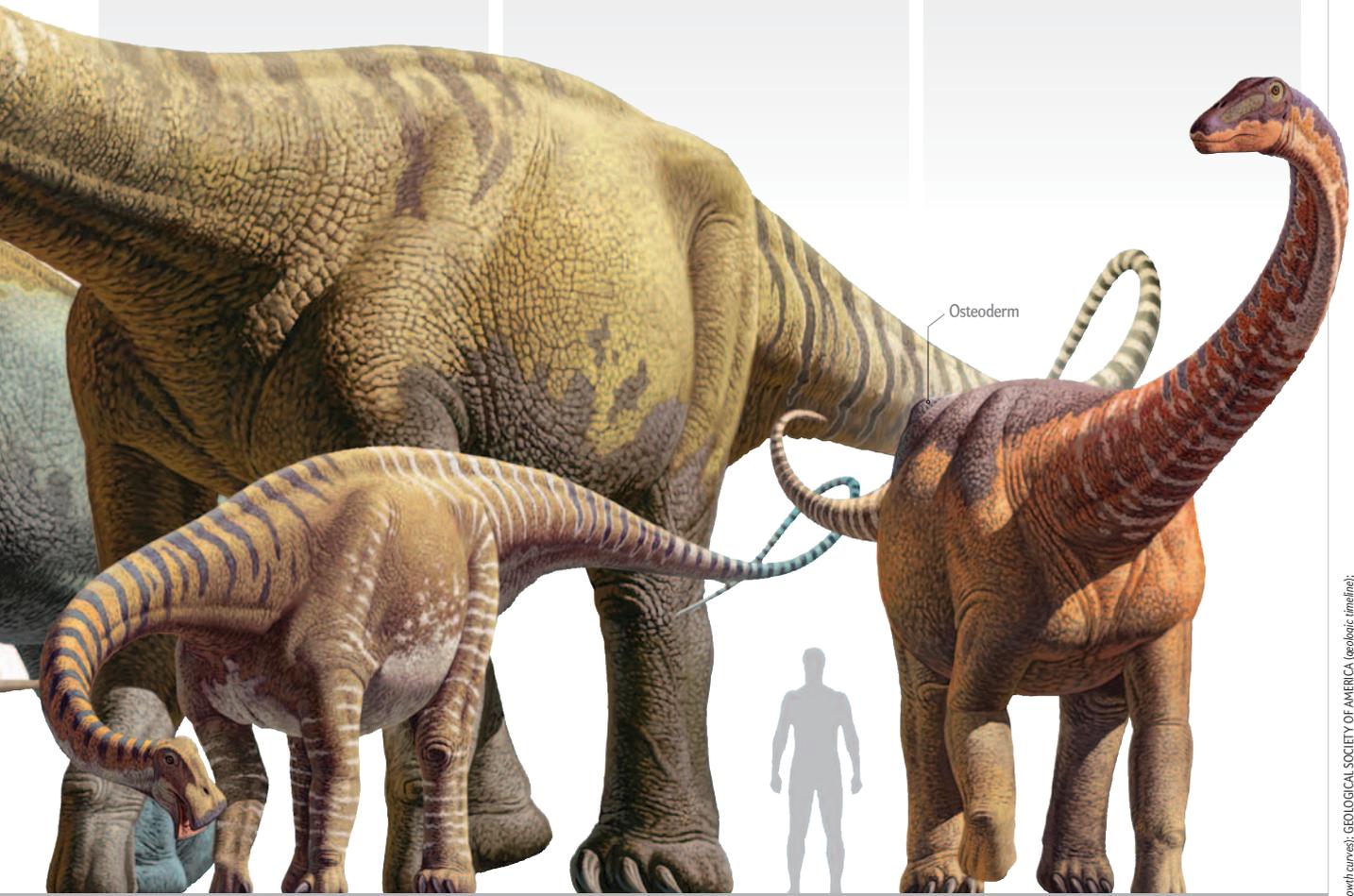


Bony plates called osteoderms, which were embedded in the skin of some sauropods, may have served as mineral reserves in hard times. As an animal aged, its osteoderms grew hollow from donating their calcium to the blood.

Osteoderm cross section



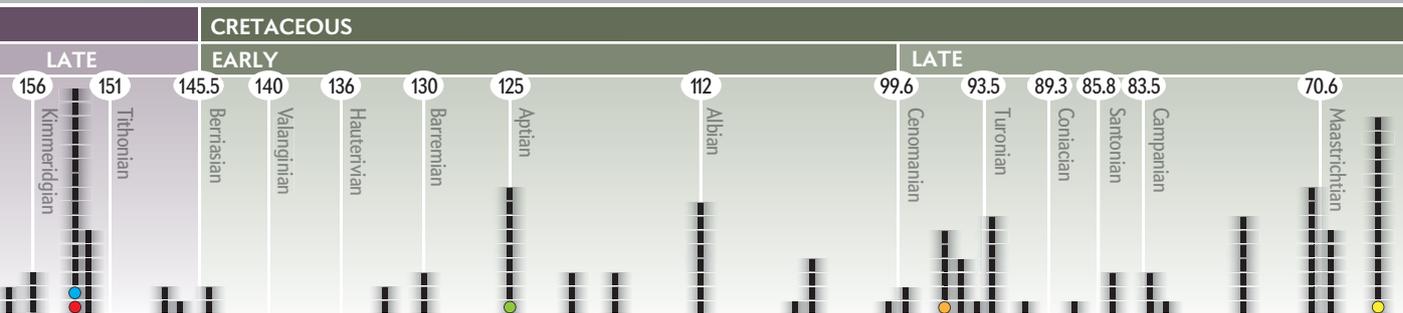
57 cm



● Nigersaurus

● Argentinosaurus

● Rapetosaurus



SOURCES: KRISTINA A. CURRY ROGERS AND MICHAEL D. D'EMIC (growth curves); GEOLOGICAL SOCIETY OF AMERICA (geologic timeline); DANIELA SCHWARZ-WINGS (Museum of Natural History, Berlin (vertebra detail))

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SNACK-SIZE SAUROPODS: Sauropods may have been untouchable as adults, but as babies they were highly susceptible to predators large and small. In 2010 Jeffrey Wilson of the University of Michigan and his colleagues described a clutch of sauropod eggs from India that includes a fossilized 12-foot-long snake coiled around and crushing one of them, alongside a tiny sauropod hatchling—as shown in the artist's reconstruction above. Several such examples from their field area of snakes associated with dinosaur eggs support the idea that these snakes frequented sauropod nesting grounds and feasted on eggs and hatchlings.

Bonn in Germany took the notion of sauropod gastroliths to task in an experimental analysis of how gizzard stones in living birds are processed and degraded. Their study showed that purported sauropod gastroliths lack the surface texture expected when compared with the true gastroliths of birds. Moreover, evidence of gastroliths discovered inside sauropod body cavities was scarce and equivocal. They thus concluded that, like modern big herbivorous animals such as rhinos, sauro pods relied on microbial fermentation in their incredibly elongated digestive systems, not gastroliths, to extract energy from plants.

Additional insights into sauropod feeding strategies have come from studies of their most distinctive trait: that trademark long neck. Conventional wisdom held that the animals used their necks to dine in the treetops, reaching leaves unattainable by other dinosaurs. New research has challenged this view. John Whitlock, now at the University of British Columbia, reconstructed feeding strategies among diplodocoids, a group of sauro pods that includes the familiar *Apatosaurus* and *Diplodocus* that persisted from the Late Jurassic to the Late Cretaceous. Variation in snout shape and microscopic wear patterns on teeth indicate that some sauro pods specialized in particular kinds of plants and others were generalists; whereas some grazed on ground-height plants, others fed from the trees. Different research groups have drawn similar conclusions from analyses of sauropod neck postures, which show that sauropod feeding

was additionally constrained by vertebral flexibility: sauro pods varied in their ability to crane their necks to reach plants up high and down low. This diversity of dining habits helps to explain how so many giants shared the same ecosystems.

Sauropod dietary adaptations flourished in the Cretaceous, concurrent with the rise of flowering plants. An old-school hypothesis held that other dinosaurian vegetarians better suited to dining on these new plants pushed sauro pods to the evolutionary sidelines in the Cretaceous. In this view, sauro pods, with their weak teeth, small heads and giant bodies, were no match for the more efficient duckbills and horned dinosaurs, which possessed conveyor belts of teeth packed together to form formidable dental batteries that acted as one giant, ever growing powerful tooth.

What we now know is that the Cretaceous was actually the most diverse interval of sauropod evolution and arguably the most interesting. Far from being outcompeted by newcomers, sauro pods diversified in form and function, evolving novel means of exploiting a wide variety of plants. Take, for example, *Nigersaurus*: a 115-million-year-old species discovered in Niger in the mid-1990s by Paul Sereno of the University of Chicago and his colleagues. The creature evolved broad dental batteries with extremely fast tooth replacement rates (one new tooth in each position every month, which is up to twice as fast as those of duckbills and horned dinosaurs), keeping teeth sharp

TYLER KEILLOR

for efficient clipping of vegetation. The orientation of the semicircular canals of the inner ear—the organs of balance—in *Nigersaurus* suggests that this animal usually held its head with its muzzle pointing directly downward, rotated 70 degrees from the usual horizontal pose inferred for other sauropods. This position suggests that it specialized in feeding on plants near the ground.

As the Cretaceous progressed and flowering plants diversified, sauropods found themselves with more options on the table. Microscopic analysis of fossilized feces, or coprolites, from titanosaurs has revealed silicified plant tissues called phytoliths that document at least five different types of grass in addition to such flowering plants as magnolias, conifers and palms. This discovery, reported by Vandana Prasad of the Birbal Sahni Institute of Paleobotany in India and her colleagues in 2005, pushed the origin and diversification of modern grasses back by some 30 million years and supports the notion that some sauropods fed fairly indiscriminately. As is true for any respectable fast-growing vertebrate herbivore, it paid for sauropods to not be picky. Far from being pushed out of these emergent ecosystems, they seem to have taken full advantage of the new resources, eating everything from the tops of trees to the forage at their feet.

Enhanced oxygen intake may have further fueled sauropod growth. In living birds, air sacs connected to outpocketings of the lungs invade their hollowed-out vertebrae, allowing the birds to suck more oxygen out of each breath than mammals can. Air sacs in birds allow for a unidirectional airflow through the lungs, which increases the oxygen content extracted from each breath. (In mammals, airflow is bidirectional: each new breath mixes in our lungs with old air, resulting in a relatively inefficient method of oxygen extraction.) Sauropod vertebrae resemble those of modern birds in having nearly identical internal cavities and a complex pattern of external hollows bounded by struts. The greatest hollowness, or pneumaticity, is found in neck and trunk vertebrae, but in some sauropod species it can extend to parts of the shoulders, hips and tail. The primary effect of pneumatization is overall reduction in the weight of the vertebral column, and estimates indicate that it may have significantly reduced sauropod body mass. For example, the North American colossus *Sauroposeidon* had a neck that was more than 75 percent air. It is also possible that, as in birds, the pneumatized vertebrae of sauropods housed an extensive air sac system with flow-through ventilation of the lungs that aided respiration and would have allowed them to maintain stable, high metabolic rates and increased activity levels consistent with their rapid growth rate and massive adult body size.

WHEN THE GOING GOT TOUGH

BEING BIG had a real advantage for sauropods, as it does for modern behemoths. Even before they were halfway grown, many sauropod species exceeded the size of adult elephants, which have essentially no predators (apart from humans). Once they reached adult size, they were probably fairly immune to serious predators, such as *Allosaurus*. Large body size also left sauropods extra vulnerable in cases of food and water shortage. Yet some may have evolved solutions to even that problem: a handful of titanosaur species bore bizarre bony plates in their skin called osteoderms. A number of modern animals have osteoderms—they make up the armorlike covering of crocodilians, lizards and armadillos, and they formed the distinctive bony plates and spikes in dinosaurs such as *Stegosaurus*. Where on the sauropod body osteoderms resided has been impossible to determine, however, making it hard for scientists to discern their function.

New findings may resolve this question. In 2011 we described two

osteoderms that were found in Madagascar alongside one juvenile skeleton and one adult skeleton of a titanosaur called *Rapetosaurus*. At 57 centimeters long and more than 27 centimeters thick, with a volume of nearly 10 liters, the adult specimen is the most massive osteoderm ever discovered from any backboned animal. CT scans and drill cores indicate that the osteoderms of *Rapetosaurus* hollowed out during the course of the animal's life, and at very large sizes about five liters' worth of internal bone was replaced, probably with soft tissue. Instead of the pavementlike covering of osteoderms found in living animals, *Rapetosaurus* (and probably some other titanosaurs) had only a few large plates.

These features of the *Rapetosaurus* osteoderms helped us rule out several competing ideas about the function of osteoderms in titanosaurs. Such internally hollow elements would offer little in the way of protection because they would shatter under the force of a predator's jaws. Similarly, the low surface area to volume ratio of the elements and their sparse distribution in the skin would have rendered them useless for thermoregulation. We argue that titanosaur osteoderms instead served as an invaluable mineral reserve that may have helped sustain growth rates and egg-laying ability even through the harshest times, just as they do in some modern animals. In all living vertebrates, including humans, bone mineral is sacrificed to help maintain blood calcium levels. This resorption often increases seasonally, when resources are rare, during egg laying and with increasing age—which in humans leads to osteoporosis. Osteoderms have rich blood supplies that serve as the perfect conduits for the cells that do the resorbing and for the mineral resources that are unlocked from deep inside bones. This idea makes a lot of sense for a massive sauropod in Late Cretaceous Madagascar. Back then, the island was a harsh place to live—regular, severe droughts forced meat-eating dinosaurs such as *Majungasaurus* to cannibalize members of its own species and brought about the demise of innumerable animals, from frogs and birds to sauropods. Osteoderms may have helped sauropods in Madagascar and elsewhere survive environmental perturbations, including frequent, intense droughts.

Sauropods seem to test the laws of biological possibility in how fast they grew and how large they became. These breaches could have painted them into an evolutionary corner, yet our growing knowledge of the fossil record suggests the opposite. Indeed, they went extinct, but before that inescapable disaster struck, sauropods had a spectacular 150-million-year run as one of the most remarkable extravagances that evolution has ever invented. ■

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Michael D. D'Emic is a vertebrate paleontologist at Stony Brook University. His fieldwork focuses on early Cretaceous sauropods from Montana and Wyoming. He is particularly interested in a group of sauropods known as the titanosaurs.

MORE TO EXPLORE

The Sauropods: Evolution and Paleobiology. Kristina A. Curry Rogers and Jeffrey A. Wilson. University of California Press, 2005.

Inferences of Diplodocoid (Sauropoda: Dinosauria) Feeding Behavior from Snout Shape and Microwear Analyses. John A. Whitlock in *PLoS ONE*, Vol. 6, No. 4; April 6, 2011.

Sauropod Dinosaur Osteoderms from the Late Cretaceous of Madagascar. Kristina Curry Rogers et al. in *Nature Communications*, Vol. 2, Article No. 564. Published online November 29, 2011.

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