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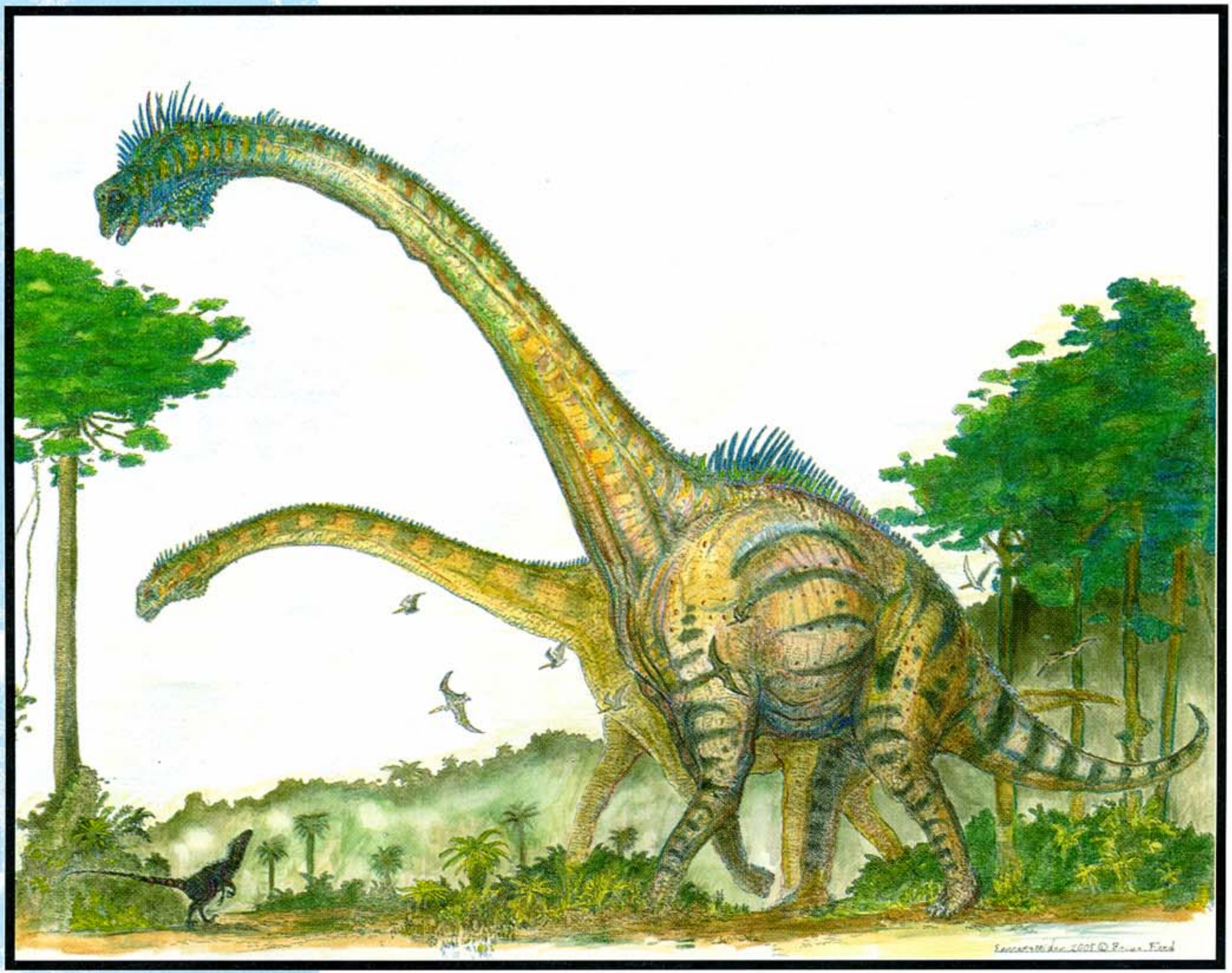

Featuring: • ***Sauroposeidon*: Oklahoma's native giant**

on the cover

A Little Local Color: The Giant Dinosaur *Sauroposeidon*

Paleontologists are very often asked "How do you know what extinct animals looked like?" Once in a while we get lucky: A cave painting or a perfectly preserved specimen can show us details about the form and color of an animal that we would never have known otherwise, like the patch of dark hair on the shoulder hump of the extinct giant deer *Megaloceros*, or the long tail feathers in males of the primitive bird *Confuciusornis* (Fig. 1). Such cases are very rare. Most extinct vertebrates are known from only a few bones or teeth, and to reconstruct them we must rely on comparative anatomy. The giant dinosaur *Sauroposeidon* is a good example of how paleontologists use comparative methods to fill in the missing pieces.

Sauroposeidon is known only from a few vertebrae from Atoka County, Oklahoma. (See "*Sauroposeidon*: Oklahoma's Native Giant," page 40 of this issue.) The form of the vertebrae shows that they came from the neck of a sauropod dinosaur, one of the group that includes *Apatosaurus* and *Diplodocus*. The vertebrae are most like those of *Brachiosaurus*, which is known from nearly complete skeletons. An average adult *Brachiosaurus* was 22 m (72 ft) long and 14 m (46 ft) tall, and weighed perhaps 30 tons. The vertebrae of *Sauroposeidon* are about 15% larger than those of *Brachiosaurus*; they are also longer relative to their diameter, by about 33%. This indicates an animal 28 m (92 ft) long and 18 m (59 ft) tall, and weighing about 50 tons.

No brachiosaurids have ever been found with preserved skin impressions, so we must draw inferences about *Sauroposeidon*'s hide from other groups of sauropods. Diplodocids had spines running down their backs, like those of an iguana, and titanosaurids had armor plates. Skin impressions from dinosaurs other than sauropods show a variety of bumps, knobs, plates, spiky scales, and tufts of filaments—not to mention true feathers in many carnivorous dinosaurs. Considering the examples, it seems reasonable to assume some kind of skin ornamentation in the ancestral sauropod, and in *Sauroposeidon* as well.

What about colors? Most restorations of dinosaurs show them in dull earth tones, perhaps because large mammals like elephants and rhinos are not brightly colored. But mammals are unusual among vertebrates in having very poor color vision, possibly as a result of spending 160 million years living under the dinosaurs' feet (we primates are an exception to the general rule). Even so, gazelles, oryxes, zebras, and Malaysian tapirs all have stark patches of black and white. Birds and reptiles have good color vision, and in those groups we find bright colors and bold patterns even in large forms. Storks, cranes, swans, and turkeys often sport vivid hues and a variety of crests and wattles. Among reptiles, iguanas and river turtles show that big does not always mean dull. Ambush predators like crocodiles and Komodo dragons have an incentive to be low key, but *Sauroposeidon* did not share their need to be inconspicuous.

So what was *Sauroposeidon*—a reptilian giraffe? A four-legged bird? An anaconda draped over an antelope? Sauropods shared something with each of those animals—and everything with none of them. Walter Coombs (1975, p. 29) said it best in the conclusion of his classic paper ("Sauropod Habits and Habitats"): "Sauropods are basically alien animals . . . what can be said of the habits of an animal with the nose of a Macrauchenia [an extinct mammal with a trunk], the neck of a giraffe, the limbs of an elephant, the feet of a chalicothere, the lungs of a bird, and the tail of a lizard? With so many plausible but conflicting interpretations, it is unlikely there will be general agreement on sauropod habits as long as more than one paleontologist has an opinion on the matter."

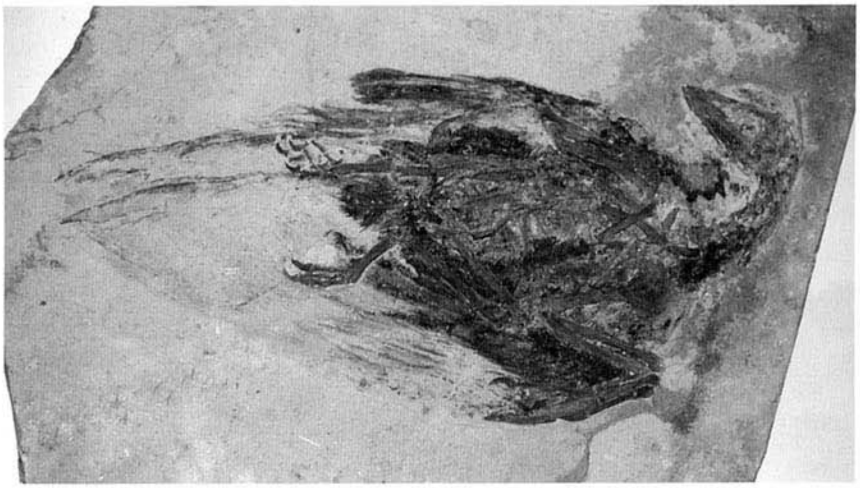

Figure 1. The primitive bird *Confuciusornis* from Liaoning, China. *Confuciusornis* lived at roughly the same time as *Sauroposeidon*. Similar birds probably lived in North America, but such delicate fossils are preserved only in exceptional circumstances, and none have been found in Oklahoma. Photo taken by R. Kent Sanders; used here by courtesy of the Museum of Ancient Life at Thanksgiving Point, Lehi, Utah.

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Coombs, W. P., 1975, Sauropod habits and habitats: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 17, p. 1–33.

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Cover illustration by Brian Ford

Sauroposeidon: Oklahoma's Native Giant

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ABSTRACT.—*Sauroposeidon*, the largest dinosaur ever discovered in Oklahoma, is one of the largest dinosaurs that ever lived. *Sauroposeidon* is represented by a series of neck vertebrae, which show that it is a sauropod dinosaur closely related to *Brachiosaurus*. Computed tomography (CT) scans of the vertebrae reveal a network of small internal chambers. In life, the chambers would have been filled with air, like similar chambers in the bones of living birds. These pneumatic spaces would have substantially lightened the neck, which was 12 meters (39 feet) long. An isolated vertebra from Montana and giant footprints in Texas may also pertain to *Sauroposeidon*.

INTRODUCTION

Sauropod dinosaurs, the "brontosaurs," are at once the most and least familiar dinosaurs. Immense and exotic, sauropods are practically the totem animals of the Mesozoic Era, from the pudgy green mascot of the Sinclair Corporation to the *Brachiosaurus* that greeted visitors to *Jurassic Park*. Although they are instantly recognizable to even small children, sauropods were until recently one of the least studied groups of dinosaurs. Their giant skeletons have been museum centerpieces for a century, but we are only beginning to understand how they lived. The last decade has seen the first modern study of sauropod relationships (Upchurch, 1995), the first discovery of sauropod nests and embryos (Chiappe and others, 1998), and the first attempt to investigate sauropod biomechanics using computer models (Stevens and Parrish, 1999).

The recent boom in the study of sauropods has been fueled in part by many new discoveries, from localities as farflung as Nigeria and Thailand and as close by as Arizona and Texas. Among the new discoveries, a remarkable contribution has come from Oklahoma. A locality in the southeastern quarter of the State has yielded remains of one of the largest animals that ever lived: *Sauroposeidon*. Formal description and taxonomy of this dinosaur have been presented elsewhere (Wedel and others, 2000a,b). Herein we describe the discovery and excavation of *Sauroposeidon*, trace its relationships to other sauropods, and discuss its size and probable habits.

THE FOSSIL RECORD OF SAUROPODS IN NORTH AMERICA

Sauropods were among the most diverse and successful groups of dinosaurs (see Fig. 1). They appeared early in the Mesozoic, at the very dawn of the Age of Dinosaurs, and persisted until the mass extinction at the end of the Cretaceous (Fig. 2). The earliest known sauropod is *Antetonitrus* from the Late Triassic of South Africa (Yates and Kitching, 2003). Like other early sauropods, *Antetonitrus* was relatively small and unspecialized. Nevertheless, it was the first representative of a group that includes the largest animals that ever walked on land. Sauropods diversified in the Jurassic Period (Day and others, 2004), and by Late Jurassic times they were the dominant herbivores in most dinosaur faunas worldwide (McIntosh, 1990). Remains of sauropods have been recovered on every continent, including Antarctica.

The evolutionary history and biogeography of North American sauropods are complicated. Sauropods migrated to North America from other continents at least four times. The migration events can be used to divide the fossil record of North American sauropods into four broad episodes: (1) the early appearance of sauropods in the Jurassic; (2) the "Golden Age" of the Late Jurassic, when sauropods hit a peak of abundance and diversity; (3) the persistence of brachiosaurids and the appearance of new lineages in the Early Cretaceous; and (4) the migration of derived titanosaurids in the Late Cretaceous. (Here "derived" means that the titanosaurids had evolved markedly from their ancestral condition.)

The earliest sauropod in North America is *Anchisaurus*, from the Early Jurassic of New England (Yates, 2004). *Anchisaurus* is positively tiny (for a sauropod); in life, it would have been less than 3 m (10 ft) long and weighed no more than a medium-size human. All the closest relatives of *Anchisaurus* are from other continents, and it does not seem to be closely related to any later North American sauropods. Thus we surmise that *Anchisaurus* (or its immediate ancestor) migrated to this continent from somewhere else, possibly South America or Europe, and became extinct without giving rise to any successors. The next sauropod known from

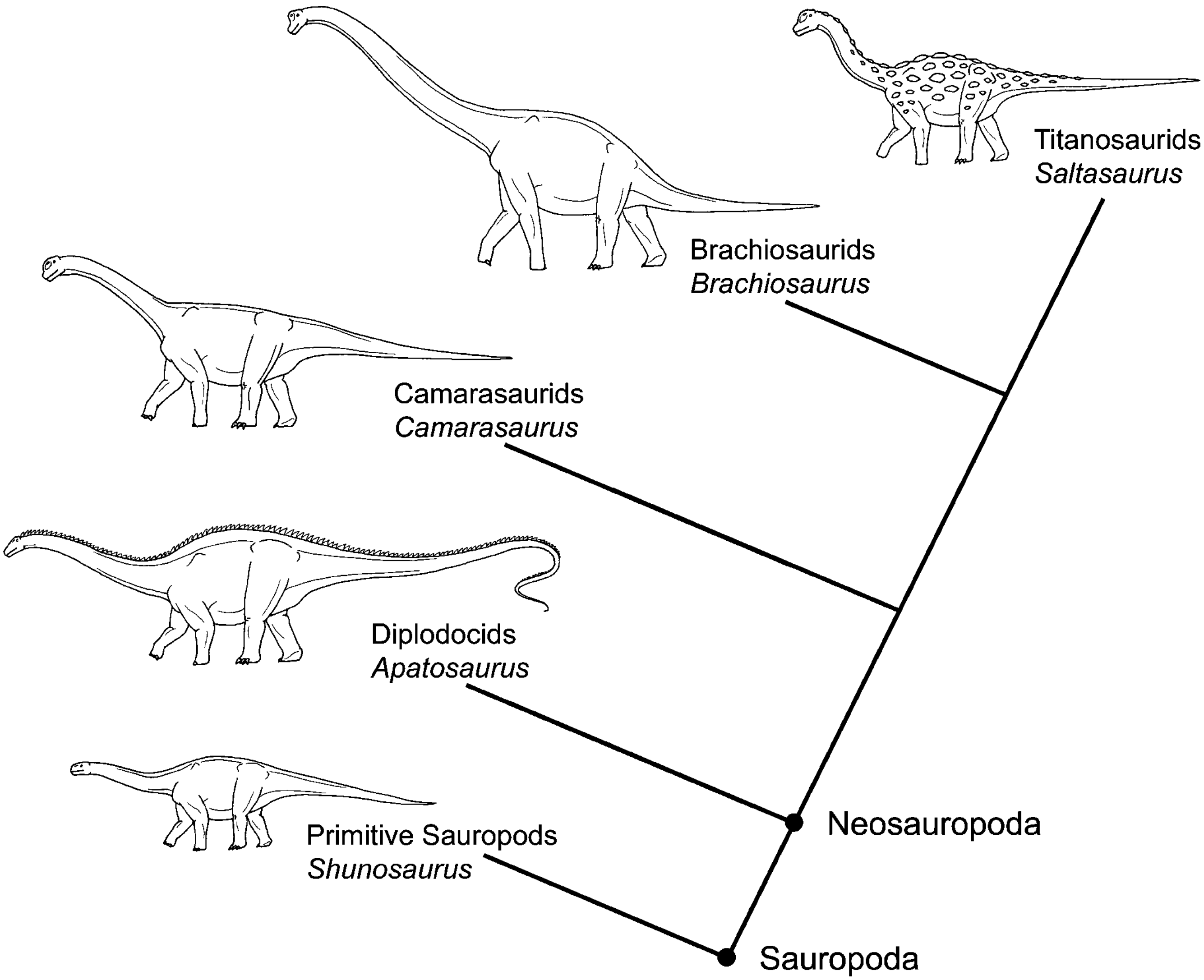


Figure 1. The evolutionary tree of sauropods. Initial radiation of primitive sauropods (e.g., *Shunosaurus*) during the Triassic and Early Jurassic was followed by the diversification of neosauropods in the Middle Jurassic or earlier. Diplodocids, camarasaurids, and brachiosaurids were all represented in North America in the Late Jurassic. Titanosaurids, the most derived group of sauropods—those most changed through evolution—also originated in the Jurassic, but did not spread to North America until the Cretaceous. *Sauroposeidon* was a member of the Brachiosauridae, which in North America ranged from the Late Jurassic to the end of the Early Cretaceous.

North America is *Dystrophaeus*, from the Middle or—more likely—Late Jurassic of Utah (Gillette, 1996). Unfortunately, the remains of *Dystrophaeus* are too incomplete to tell us much about its geographic origins or evolutionary relationships.

The scarcity of sauropods in North America during the Early and Middle Jurassic contrasts sharply with the abundance and diversity of the group in the Late Jurassic, about 150 million years ago (Mya). The sediments of the Morrison Formation were laid down during the Late Jurassic, and they now stretch from Montana and South Dakota south to New Mexico and Oklahoma's Panhandle. Sauropods are the most common and abundant dinosaurs in the Morrison (Turner and Peterson, 1999); the roster of sauropods from the Morrison includes some of the best known of all dinosaurs, such as *Apatosaurus*, *Brachiosaurus*, *Camarasaurus*, and *Diplodocus.* New sauropods are still being discovered in the Morrison: *Suuwassea*, a relative of *Apatosaurus* and *Diplodocus*, was described from Montana just last year (Harris and Dodson, 2004), and other new sauropods have been reported but not yet named (Vietti and Hartman, 2004).

The Morrison sauropods are closely related to African dinosaurs of the same age. *Brachiosaurus* and *Barosaurus* are found in the United States and also in Tanzania, and *Suuwassea* is a close relative of the African sauropod *Dicraeosaurus.* Right now it is difficult to tell whether these sauropods originated in North America and then spread to Africa, or vice versa. However, no Morrison sauropod is closely related to *Anchisaurus*, so they or their ancestors must have come to North America from elsewhere, possibly in the early part of the Jurassic Period.

After the end of the Jurassic, a gap appears in the North American fossil record. The next oldest dinosaur assemblages that are reasonably well represented are of Barremian age (perhaps 125 Mya; see Kirkland and others, 1998). Whereas sauropods were the most common dinosaurs in the Late

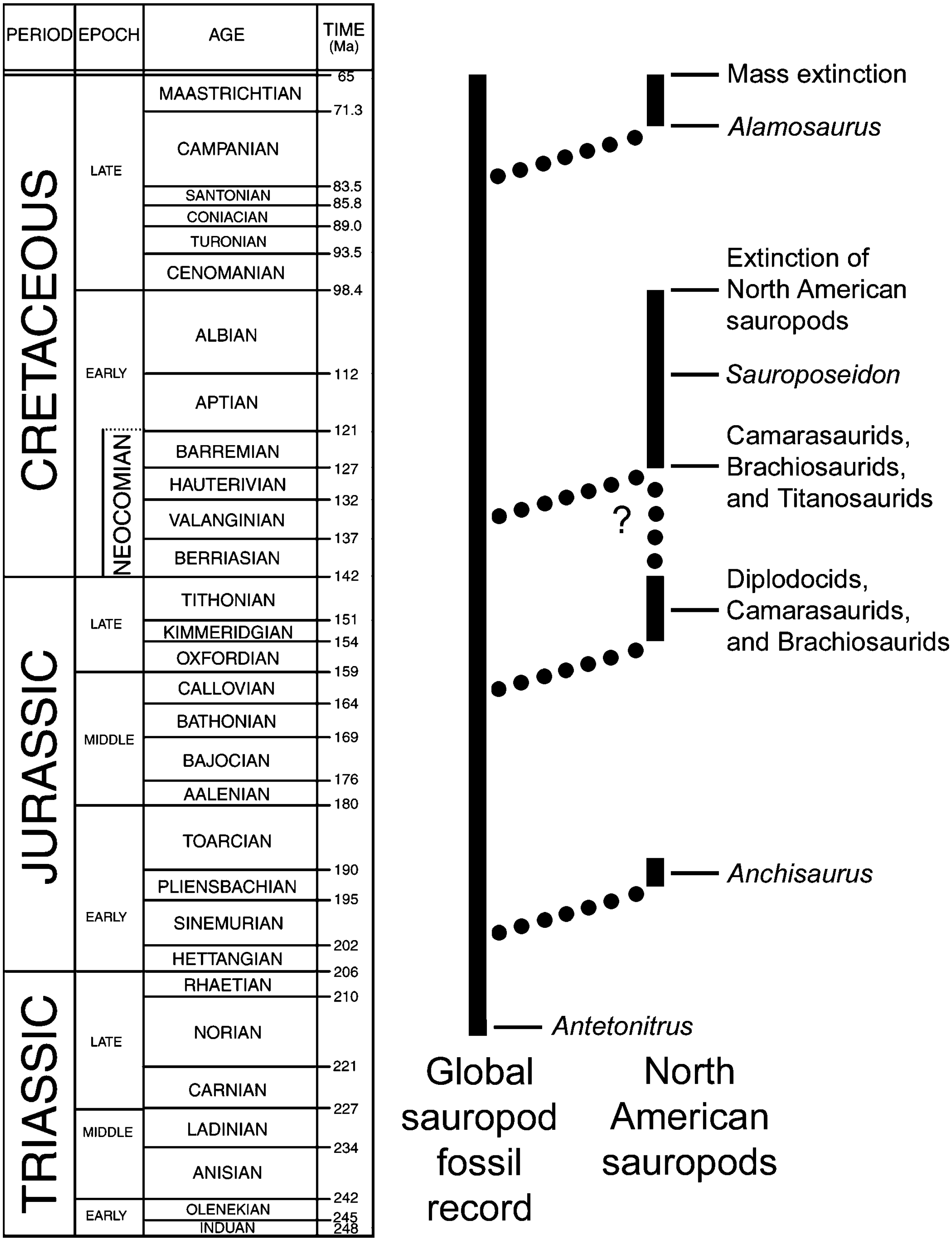


Figure 2. A timeline of the Mesozoic Era and the fossil record of sauropods. The solid vertical bar shows the extent of their fossil record worldwide. The earliest known sauropod is *Antetonitrus*, from the Late Triassic of South Africa. Sauropods eventually colonized every continent, and survived until the mass extinction at the end of the Cretaceous Period. The broken vertical bar shows the extent of the fossil record of sauropods in North America. Lines of heavy dots show gaps in the rock record and migration of sauropods from other continents. *Anchisaurus* arrived in North America in the Early Jurassic, but did not give rise to later groups. During the Late Jurassic, sauropods were the dominant herbivores on the continent. Despite a gap in the fossil record during much of the Neocomian (the initial part of the Early Cretaceous), about 142 to 125 Mya, sauropods probably still lived on the continent, for both camarasaurids and brachiosaurids are found in rock on each side of the gap. The first titanosaurids in North America may have arrived from Europe during the “missing time.” Sauropods appear to have died out in North America shortly after 98.4 Mya; *Sauroposeidon* was one of the last of its kind on the continent. Sauropods did not return until the arrival of *Alamosaurus*, which may have migrated from Asia or from South America. Time scale after Palmer and Geissman (1999).

Jurassic, they tend to be among the rarest elements in Early Cretaceous faunas. The most abundant North American dinosaur of the time was *Tenontosaurus*, a medium-size relative of *Iguanodon* and the duckbills. *Tenontosaurus* was similar to modern cattle in size, shape, and probable habits. The Early Cretaceous sauropod fauna differed very much from that of the Jurassic. Diplodocids, which were so common and diverse in the Jurassic, have not been found in the Early Cretaceous of North America; they disappeared sometime in the 20 million years for which we have no fossils. *Brachiosaurus* was one of the rarest sauropods of the Morrison, but most Early Cretaceous sauropods belonged in the brachiosaurid family.

Brachiosaurids from the Early Cretaceous of North America include *Cedarosaurus* (Tidwell and others, 1999), *Sonorasaurus* (Ratkevitch, 1998), and undescribed forms from Montana (Wedel, 2000), Texas (Winkler and others, 1997a; Rose, 2004), and Utah (Coulson and others, 2004). Another undescribed sauropod from Utah seems to be related to the Late Jurassic *Camarasaurus* (Britt and Stadtman, 1997). The most intriguing sauropods of the Early Cretaceous are titanosaurids, which have been reported from Montana (Ostrom, 1970) and Utah (Britt and Stadtman, 1997). By the Middle Jurassic, titanosaurids had appeared on other continents (Day and others, 2004), but no titanosaurs have been found in the Morrison Formation. The Early Cretaceous titanosaurs must have come to North America from elsewhere, possibly Europe (Kirkland and others, 1998).

In general, the North American sauropods were smaller and less abundant during the Early Cretaceous than during the Jurassic. Sauropods persisted in North America until the beginning of the Cenomanian epoch, about 98.4 Mya. The last of the "early" sauropods in North America appears to have been a dwarf brachiosaurid—smaller than a horse—which left its tiny teeth in the Cedar Mountain Formation of central Utah (Maxwell and Cifelli, 2000). Above the Albian–Cenomanian boundary, sauropods are absent from North America until the late Campanian, a gap of 25 million years. Cenomanian–Campanian strata are plentiful and rich in fossils that record the diversification of the horned ceratopsians, duck-billed hadrosaurs, and tyrannosaurs. The absence of sauropod material from the well-sampled Two Medicine and Judith River Formations may indicate a continent-specific extinction of the group (Lucas and Hunt, 1989), but the cause of the extinction remains mysterious, especially because sauropods on other continents—notably the southern landmasses—continued to flourish. When sauropods reappeared in North America in the late Campanian, it was in the form of *Alamosaurus* (Sullivan and Lucas, 2000). Although *Alamosaurus* was a titanosaur, it was probably not descended from the Early Cretaceous titanosaurs mentioned above. *Alamosaurus* was most closely related to sauropods from South America and Asia, and it or its ancestors probably migrated to North America from one of those continents (Lucas and Hunt, 1989; Wilson and Sereno, 1998).

In Oklahoma, Mesozoic rocks are found at opposite corners of the State. The Morrison Formation is exposed near Black Mesa in the Panhandle. There J. Willis Stovall, who founded what would become the Oklahoma Museum of Natural History (OMNH), excavated the Morrison quarries in the 1930s using crews from the Works Project Administration. Stovall's crews found bones of the sauropods *Apatosaurus*, *Brachiosaurus*, *Camarasaurus*, *Diplodocus*, and—possibly—*Barosaurus* (*Barosaurus* is similar to *Diplodocus* and their bones are sometimes confused; no one has determined for certain whether *Barosaurus* occurs in Oklahoma). The crews also found non-sauropod dinosaurs including *Allosaurus*, the armored-plated *Stegosaurus*, and the giant predator *Saurophaganax*, Oklahoma's state fossil (Stovall, 1938; Czaplewski and others, 1994; Chure, 1995; Bonnan and Wedel, 2004).

Oklahoma's other dinosaur-bearing rock unit is the Antlers Formation, which lies in the southeast quarter of the State and is home to the largest—and last—dinosaur of Oklahoma.

THE ANTLERS FORMATION AND ITS DINOSAURS

The Antlers Formation consists of sandstones and claystones laid down in the Early Cretaceous, about 110 Mya (Fig. 3). It extends across north-central Texas, southeast Oklahoma, and southwest Arkansas in a pattern marking the edge of what was then the Gulf Coast (Fig. 4). The paleoenvironment of the Antlers Formation was probably similar to that of modern-day Louisiana, with forests, deltas, bayous, and lagoons (Fig. 5). Along the ancient coastline lived dinosaurs. As in most Early Cretaceous deposits of western North America, the most common dinosaur in the Antlers is the ubiquitous *Tenontosaurus*. Over the last decade, crews from the OMNH have recovered the remains of nearly two dozen individuals of *Tenontosaurus*, ranging from isolated toe bones to complete, articulated skeletons. All the recently worked sites are in Atoka County, although *Tenontosaurus* is

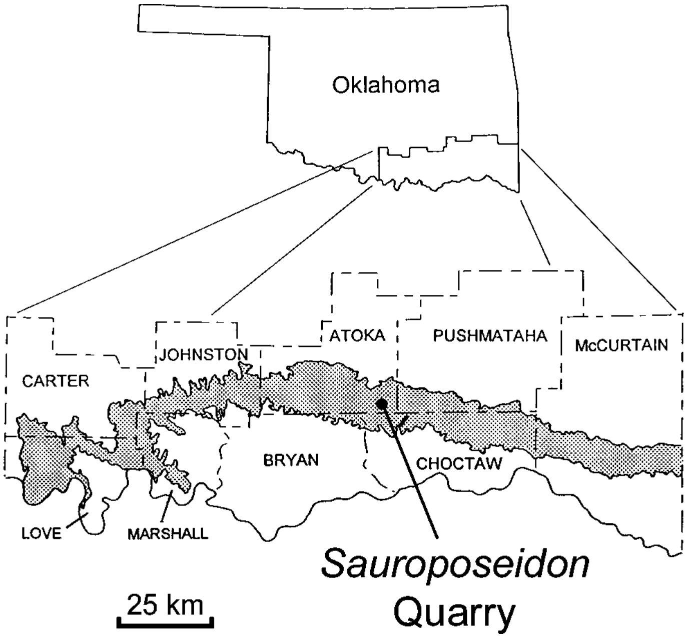


Figure 3. Distribution of the Antlers Formation in Oklahoma, and the location of the *Sauroposeidon* quarry in Atoka County. Modified from Hart and Davis (1981).

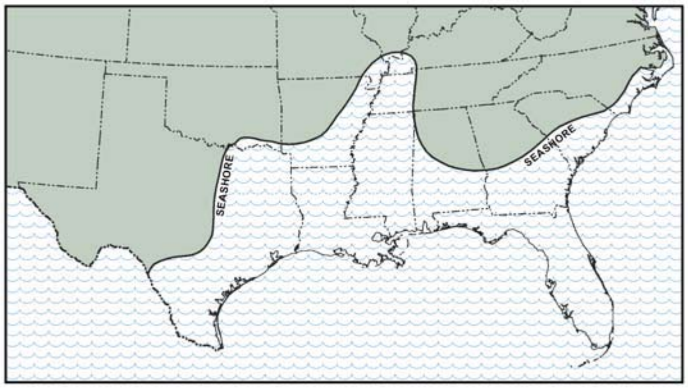


Figure 4. Beachfront property in Oklahoma. During the time of *Sauroposeidon*, the sea level was much higher than today, and the modern Gulf Coast lay under water. Sediments of the Antlers Formation were laid down in coastal swamps and on floodplains.

known from elsewhere in Oklahoma and in the Trinity Group—which includes the Antlers—of Texas (Langston, 1974; Jacobs, 1995; Winkler and others, 1997b).

Tenontosaurus was first discovered in the Cloverly Formation of Montana, where at least one specimen was found in association with the remains of a small carnivore, *Deinonychus* (Ostrom, 1970). *Deinonychus*, a North American cousin of the now-famous *Velociraptor*, had a long, rigid tail, large grasping hands, and a sickle-shaped killing claw on each foot. At one fossil site, the association of several *Deinonychus* skeletons with a single adult *Tenontosaurus* suggests that these raptorial predators hunted in packs. Evidently a group of 50-kg theropods succeeded in bringing down their 1-ton prey, but several *Deinonychus* died in the fray (Maxwell and Ostrom, 1995). The association of *Deinonychus* and *Tenontosaurus*, first discovered in Montana, is now known in Oklahoma as well. It is a rare *Tenontosaurus* that emerges from an OMNH quarry without a few *Deinonychus* teeth mixed in among its bones, and a juvenile *Deinonychus* from Atoka County includes certain parts of the skeleton that had never been described before (Brinkman and others, 1998).

As fantastic and frightening as *Deinonychus* undoubtedly was, it was not the only carnivore to stalk the Oklahoma coastline during the Early Cretaceous. *Acrocanthosaurus*, a 12-m, 4-ton theropod comparable in size to *Tyrannosaurus*, was first discovered in Atoka County (Stovall and Langston, 1950), only a few kilometers from quarries that have recently yielded *Tenontosaurus* and *Deinonychus*. Subsequent discoveries in Texas and Oklahoma have made *Acrocanthosaurus* one of the best-known large theropods (Harris, 1998; Currie and Carpenter, 2000). Like *Deinonychus*, it left behind more teeth than bones: their serrated blades, several centimeters long, are occasionally found in *Tenontosaurus* quarries.

In fact, most of the species of vertebrates known from the Antlers Formation are represented by teeth (Cifelli and oth-

ers, 1997). Teeth are more durable than bone, and most vertebrates shed their teeth throughout their lives, greatly increasing the number of specimens to be found. Primitive mammals, crocodiles, lizards, turtles, and fish left behind their teeth and scutes or scales. Together, the remains enable us to reconstruct a vanished ecosystem, one that included much more than just dinosaurs. In terms of sheer numbers, the most common fossils in the Antlers are undoubtedly the scales of *Lepisosteus*, a garfish. *Lepisosteus* is still cruising Oklahoma waterways today, a living relic of the Age of Dinosaurs.

Sauropods also occur in the Antlers. An isolated coracoid (a part of the shoulder girdle) of indeterminate affinities represents the first Early Cretaceous sauropod discovered west of the Mississippi (Larkin, 1910). Tiny teeth, less than 1 cm long, also demonstrate sauropods in the Antlers (Cifelli and others, 1997). Sauropods from the Antlers of Oklahoma remained unidentified until 1994, when a discovery on the grounds of an Oklahoma prison unveiled one of the largest animals that ever lived.

DISCOVERY AND DESCRIPTION OF *SAUROPOSEIDON*

The story of *Sauroposeidon* begins with two remarkable Oklahomans: Harvey Arnold and Bobby Cross. Both men live in Atoka County, in the southeast quarter of the State. Harvey Arnold, now retired, has been a veterinarian and an attorney, in addition to running a farm. His family has owned and worked their land for generations. Of the three dinosaurs with type localities in Oklahoma, two—*Acrocanthosaurus* and *Sauroposeidon*—were discovered on Arnold land (the third, *Saurophaganax*, is from the Panhandle). In 1950, J. Willis Stovall and Wann Langston, Jr., described *Acrocanthosaurus* from fossils found on Herman Arnold's farm (Stovall and Langston, 1950). Herman probably didn't expect that almost half a century later, his son, Harvey, would also have a new dinosaur turn up in his backyard.

The Arnold farm sits right next to the Howard McLeod Correctional Center, which is where Bobby Cross comes into the story (Fig. 6). Cross has probably discovered more dinosaurs than any other Oklahoman in history. He is now retired, but until recently he was an officer at the McLeod facility, where he trained hounds for the prison's K-9 unit. In the course of training the dogs, he regularly traversed the entire prison grounds on foot. When he saw new fossils eroding out of the ground, he called the museum and a crew would go investigate. From isolated teeth of *Acrocanthosaurus* to complete skeletons of *Tenontosaurus*, Bobby Cross has found practically every dinosaur specimen collected in Oklahoma in the last 15 years, including the type material of *Sauroposeidon*.

The prison land and Harvey Arnold's farm meet in a complicated patchwork of forest, swamp, and pasture. Because roads and fences do not always follow the most direct paths,

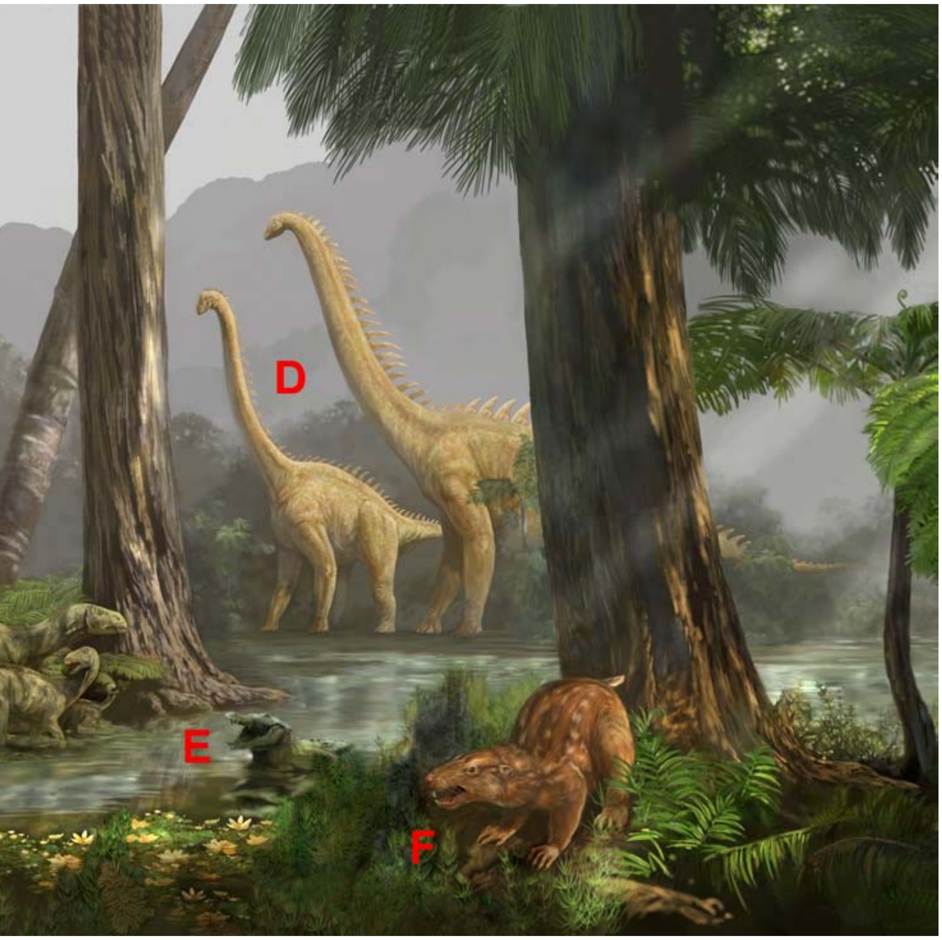


Figure 5. Southeast Oklahoma in the Early Cretaceous. The mural, "Cretaceous Coastal Environment," painted by Karen Carr, forms the backdrop of the Early Cretaceous display at the Sam Noble Oklahoma Museum of Natural History, in Norman. (A) is *Deinonychus*, (B) pterosaurs, *Istiodactylus*, (C) a herd of plant-eating *Tenontosaurus*, (D) *Sauroposeidon*, (E) a crocodile, *Goniopholis*, and (F) an opossum-size mammal, *Gobiconodon*. Fossils of *Deinonychus*, *Tenontosaurus*, *Goniopholis*, and *Sauroposeidon* have all been found in Atoka County. Pterosaurs have not yet been found in Oklahoma, probably because their bones are extremely fragile and are rarely preserved as fossils. *Istiodactylus* is from the Early Cretaceous of England, where sauropods related to *Sauroposeidon* are known to have existed. Although *Gobiconodon* has not been found in Oklahoma, its relatives have been, and it coexisted with *Sauroposeidon*-like brachiosaurids in Montana. During the same time, flowering plants, such as the magnolia-like flowers in the foreground, were radiating throughout North America.

Figure 6. The *Sauroposeidon* quarry in August 1994. From left to right: Bobby Cross, who found the specimen; Herman Arnold, whose son, Harvey Arnold, owns the site; Rich Cifelli, who led the excavation. At right is a plaster jacket enclosing part of *Sauroposeidon*. In the 1940s, the giant predator *Acrocanthosaurus* was discovered on Herman Arnold's land, just a few miles away.

some parts of the prison are accessible only from Arnold's land, and vice versa. Bobby Cross kept his eye out for fossils when he crossed the farmland, and he'd already found *Tenontosaurus* there. Then, on a hot, muggy day in May 1994, Cross found another patch of bone weathering out of a low bluff at what the museum crews had come to call "Arnold's Farm locality." The OMNH sent a crew down to Atoka County to follow up on the discovery. As the workers cleared off a column of bone 4 m (13 ft) long, it soon became clear that it was not just another *Tenontosaurus*. It was something out of place and out of time, part of the neck of a giant sauropod.

In two digs during May and August of 1994, the specimen was uncovered, wrapped in protective plaster jackets (Fig. 7), and cut into three pieces for transport (the cuts proved useful later, too, because the internal structure of the vertebrae was revealed at the broken faces—discussed in text to follow). The largest block weighed almost 3 tons, and heavy equipment was required to lift the plaster jackets out of the quarry and onto a trailer (Fig. 8). Once the specimen was back at the museum, the long process of preparation began. In all, OMNH

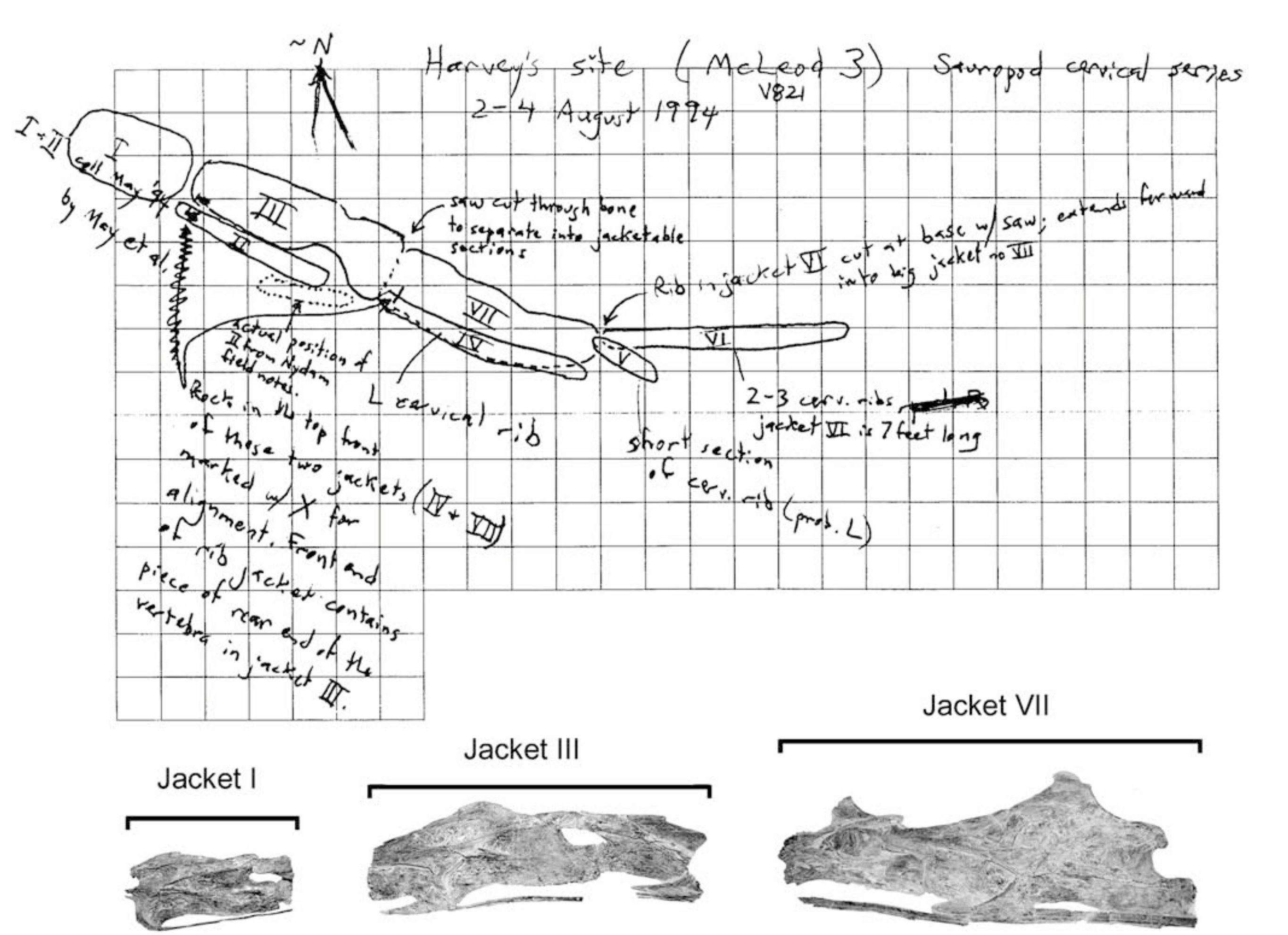


Figure 7. OMNH 53062, the type specimen of *Sauroposeidon*, as it was found in the quarry. At the top is the original field sketch by Nick Czaplewski, showing the plaster jackets in the ground. At bottom are the articulated vertebrae divided into three pieces (compare Fig. 9). The anterior part of cervical vertebra 5 and the neural spine of vertebra 7 were missing when the specimen was discovered. Cervical vertebra 6 and 7 were sawed apart to divide the specimen into manageable units. The photos are of the right sides of the vertebra, here reversed (left to right) to match the orientation of the enclosing jackets in the field sketch. The vertebrae were found lying on their right sides; the left sides, nearer the surface, had been damaged by erosion.

Figure 8. Getting *Sauroposeidon* out of the quarry. The tractor is lifting a plaster jacket that held all of cervical vertebra 8 and the back half of cervical vertebra 7; it weighed almost 3 tons.

staff and volunteers would spend 3 years removing the sandstone that enclosed the vertebrae, using tiny chisels, brushes, and dental picks.

The specimen—OMNH 53062—consists of four vertebrae from the middle of the neck of a very large sauropod (Fig. 9). The largest vertebra is 1.4 m (4 ft, 7 in.) long, the longest vertebra ever discovered for any animal, living or extinct. But even given its spectacular size, how much can we really learn about an animal from only four vertebrae? Because OMNH 53062 belonged to a sauropod, the answer is "a surprising amount." For most animals, vertebrae are conservative—they evolve slowly—and thus are fairly useless for determining a precise identification. For example, the horned and frilled ceratopsians are recognized primarily by their impressive headgear, and we mammals are differentiated mainly by our complex teeth. Sauropods are unusual in that their vertebrae are often the most distinctive parts of the skeleton (McIntosh, 1990).

Among the broad diversity of known sauropods, OMNH 53062 bears striking resemblances to cervical (neck) vertebrae of *Brachiosaurus* (Fig. 10), a giant long-necked form from the Late Jurassic. The osteology of *Brachiosaurus* is reasonably well known because the genus is represented by several incomplete skeletons from quarries in Colorado and Tanzania. Complete skeletons of *Brachiosaurus*, cobbled together from the remains of several individuals, are on display at the Field Museum in Chicago, Illinois, and the Humboldt Museum in Berlin, Germany. They are impressive: each stretches more than 22 m (72 ft) from nose to tail, and even conservative estimates suggest that in life *Brachiosaurus* weighed more than 30 metric tons (Anderson and others, 1985). All sauropods are characterized by long necks. Even so, the neck of *Brachiosaurus* is remarkable: the aforementioned mounted skeletons stand almost 14 m (46 ft) tall, with necks 9 m (30 ft) long.

OMNH 53062 resembles *Brachiosaurus* in more than size; the proportions of the vertebrae are also distinctive. Other groups of sauropods evolved long necks, but generally by adding more vertebrae (Wilson and Sereno, 1998). Brachiosaurids retained a fairly primitive count of 13 vertebrae in the neck, but the vertebrae themselves are longer, relative to diameter, than those of other dinosaurs. OMNH 53062 and *Brachiosaurus* are further distinctive in having unusually long cervical ribs. Those ribs are probably ossified tendons that supported large muscle groups; similar cervical ribs are found in the necks of modern birds. Perhaps the most convincing character linking OMNH 53062 to *Brachiosaurus* is a transition point midway along the neck, where the neural spines of the vertebrae change abruptly from very low to very high (Fig. 10). The transition may have been related to the posture of the neck, and—most significantly—it has been identified only in *Brachiosaurus* and OMNH 53062 (Wedel and others, 2000b).

On the other hand, the sauropod represented by OMNH 53062 is in many ways more derived than *Brachiosaurus*—it has evolved many new characters—relative to their common ancestor. Its vertebrae are even longer, both in proportions and also in absolute size, and they are more lightly built than those of *Brachiosaurus*. The impressions of air sacs on the bones are larger, and the internal structure is more finely divided. Those characters and others, such as details of where and how the cervical ribs are attached, helped us to distinguish OMNH 53062 from *Brachiosaurus* and to define it as a separate genus and species.

Together with our colleague R. Kent Sanders, a radiologist who helped us interpret the anatomy of the specimen, we designated OMNH 53062 the type specimen of *Sauroposeidon proteles* (Wedel and others, 2000a). Poseidon was the Greek god of earthquakes, and *Sauroposeidon* means "lizard earthquake god," which seems appropriate for such an earth-shaker. *Sauroposeidon* is the most derived brachiosaurid discovered to date, and it was one of the last sauropods in the Early Cretaceous of North America. That explains the species name, *proteles*, a Greek idiomatic construction meaning "perfected before the end" (Brown, 1954). A colleague in Poland has informed us that *proteles* can also mean "a sacrifice to the gods," which is equally appropriate for an animal named after a mythological deity (Z. Kielan-Jaworowska, personal communication in 2000).

Recently, Naish and others (2004) described a cervical vertebra of a large sauropod from England. The vertebra resembles those of *Brachiosaurus* and *Sauroposeidon* in size and form, and clearly belongs to a brachiosaurid. In fact, it is intermediate between *Brachiosaurus* and *Sauroposeidon* in many respects, including its internal structure and the size of its pneumatic fossae (the air sac impressions). The specimen adds information important to our understanding of *Sauroposeidon.* Because it is intermediate in form, the British giant shows how *Sauroposeidon* may have evolved from *Brachio-*

saurus. Also, the occurrence of a close relative of *Sauroposeidon* in Europe emphasizes the complicated biogeographic history of Early Cretaceous sauropods.

One lasting mystery about *Sauroposeidon* concerns what happened to the rest of the skeleton. The entire animal must have been about 28 m (92 ft) long and probably weighed 50 metric tons (discussed in text to follow). More than a decade has passed since the original discovery, and OMNH workers have found and excavated many more fossils from the Arnold farm, but none belongs to *Sauroposeidon*. Where is the rest of the body? Surely 50 tons of dead dinosaur didn't just float away. It seems more likely that the body stayed where it fell, and the neck floated away and came to rest where it was found. But the scenario is hard to square with the facts. Bones transported by water tend to get rolled and broken. The vertebrae of *Sauroposeidon* are very delicately constructed, and could not have survived a long trip downriver. Furthermore, the cervical ribs of the specimen are all in

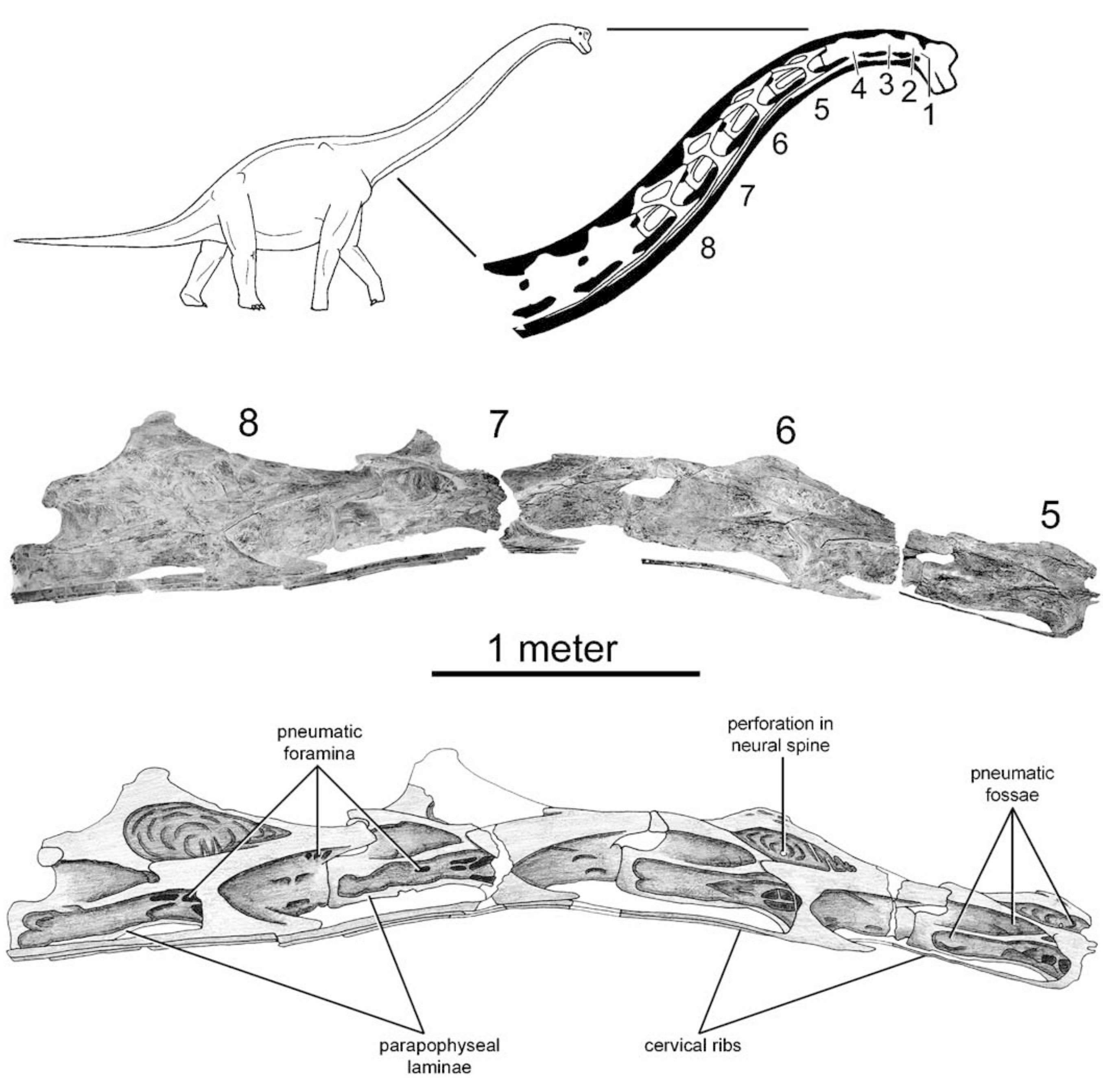


Figure 9. OMNH 53062, the type specimen of *Sauroposeidon*, in right view (parts of the cervical ribs were temporarily removed for conservation and study). The specimen probably represents cervical vertebrae 5 through 8, judging by comparison with *Brachiosaurus*. The pneumatic fossae are hollows that in life were filled with air sacs. In vertebrae 5 and 6, the pneumatic fossae on each side are so deep that they meet in the middle and make small perforations through the neural spines. The air sacs entered the bones through the pneumatic foramina.

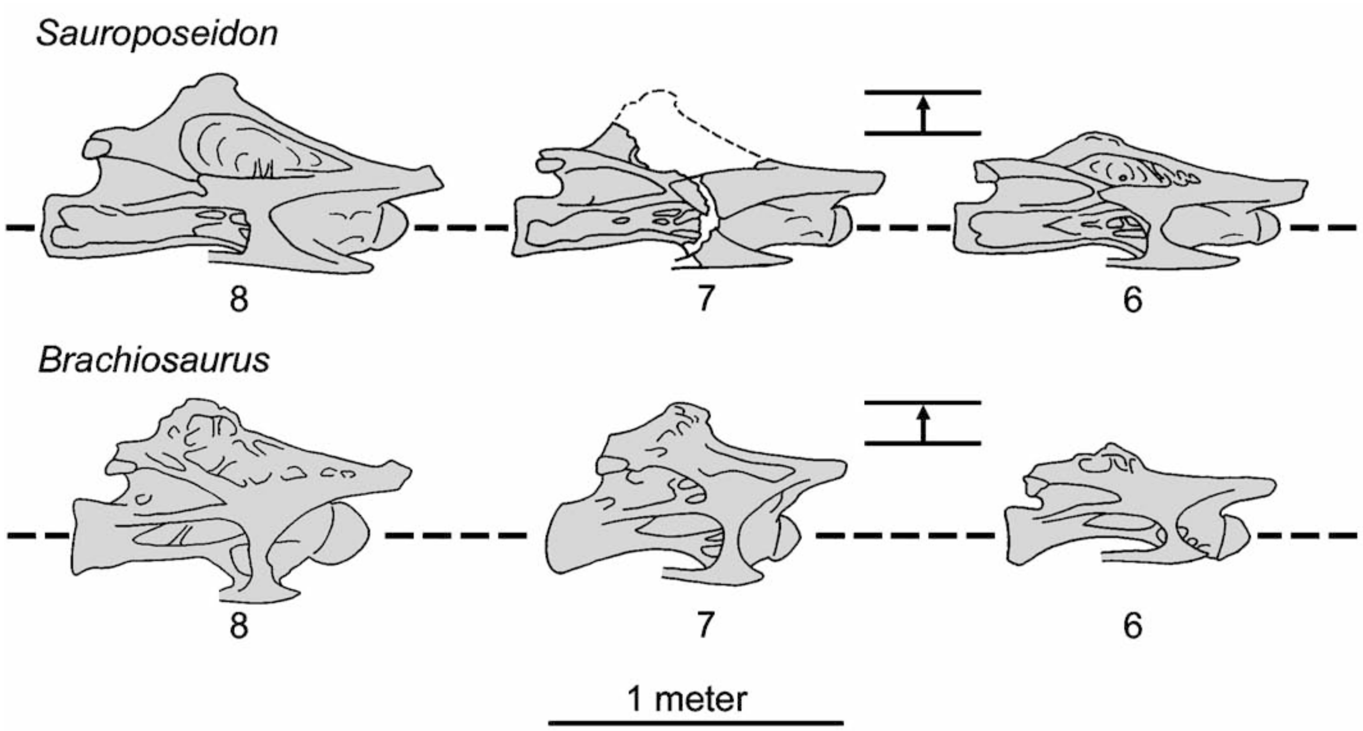


Figure 10. Vertebrae of *Brachiosaurus* and *Sauroposeidon* compared. Cervical vertebrae 6–8 are shown in right lateral view. In both sauropods the neural spine of vertebra 7 is markedly higher than that of vertebra 6. Even though vertebra 7 of *Sauroposeidon* is incomplete, enough of the spine remains to demonstrate the abrupt change. The transition point is unique to *Brachiosaurus* and *Sauroposeidon*.

place, so it was probably buried with the flesh intact. The carcass was pulled apart by something strong enough to dismember a giant dinosaur, but gentle enough to leave the fragile vertebrae and cervical ribs intact. There is always a chance that future discoveries will reveal what happened to *Sauroposeidon*'s body, but for now the trail has gone cold.

GETTING INSIDE *SAUROPOSEIDON*

An unusual feature of sauropods has attracted attention since the first discoveries in the 19th century: their vertebrae are hollow. One of the first sauropods discovered in England was named *Ornithopsis*, meaning "bird-like," because its vertebrae were filled with chambers and thus resembled the vertebrae of birds (Seeley, 1870). In 1877, Edward Drinker Cope named *Camarasaurus*—"chambered lizard"—for its hollow vertebrae (Cope, 1877). The hollow construction of sauropod vertebrae probably reduced their mass, a feature particularly important for a sauropod with a very long neck, such as *Sauroposeidon*.

To investigate the internal structure of the vertebrae of *Sauroposeidon* we used computed tomography (CT) scans. The work was made possible by the generous assistance of the Department of Radiology at University Hospital in Oklahoma City. Beginning in January 1998, we transported vertebrae of *Sauroposeidon* and other sauropods to the hospital for scanning, and there we met R. Kent Sanders, who directed the scanning and went on to help us describe *Sauroposeidon*.

Scanning such large specimens posed special challenges. First, the bed of the CT scanner was designed to support human patients, not fossilized bones weighing hundreds of pounds, so the size of specimens we could scan was limited. Second, the aperture of the scanner was 48 cm in diameter. At 69 cm by 140 cm, the largest vertebra of *Sauroposeidon* would not fit through the scanner. Finally, medical CT machines lack the energy to punch X-rays through large fossils. In large and dense specimens, X-rays tend to scatter, and the scatter shows up as dark radial streaks in the CT images. Even so, scanning yielded a wealth of information.

As revealed by the CT scans, vertebrae of *Sauroposeidon* have extremely delicate construction. In cross section, the vertebrae look like stick figures (Fig. 11). The "head" of the figure is the neural spine, which is supported by a narrow septum. The "arms" are the diapophyses, which extend out at each side and support the cervical ribs from above. The "legs" are the parapophyseal laminae, which also are attached to the cervical ribs. The vertebrae articulate with each other by means of ball-and-socket joints, so they must have a round cross-section at each end. But in between, the centrum narrows down to a thin, vertically oriented plate. The plate is the median septum, which forms the "body" of the stick figure. The vertebrae of *Sauroposeidon* were not only reduced in overall construction; they were also filled with air cells. The internal structure of the vertebrae consists entirely of small chambers separated by thin walls of bone (Fig. 12). Except for the cervical ribs, which are solid, no part of the bone is thicker than 4 mm, and in most places the bone is 1 mm or less in thickness—eggshell thin.

We had begun the CT project not only to find out more about *Sauroposeidon* but also to compare the vertebrae of many sauropods and learn more about the evolution of the

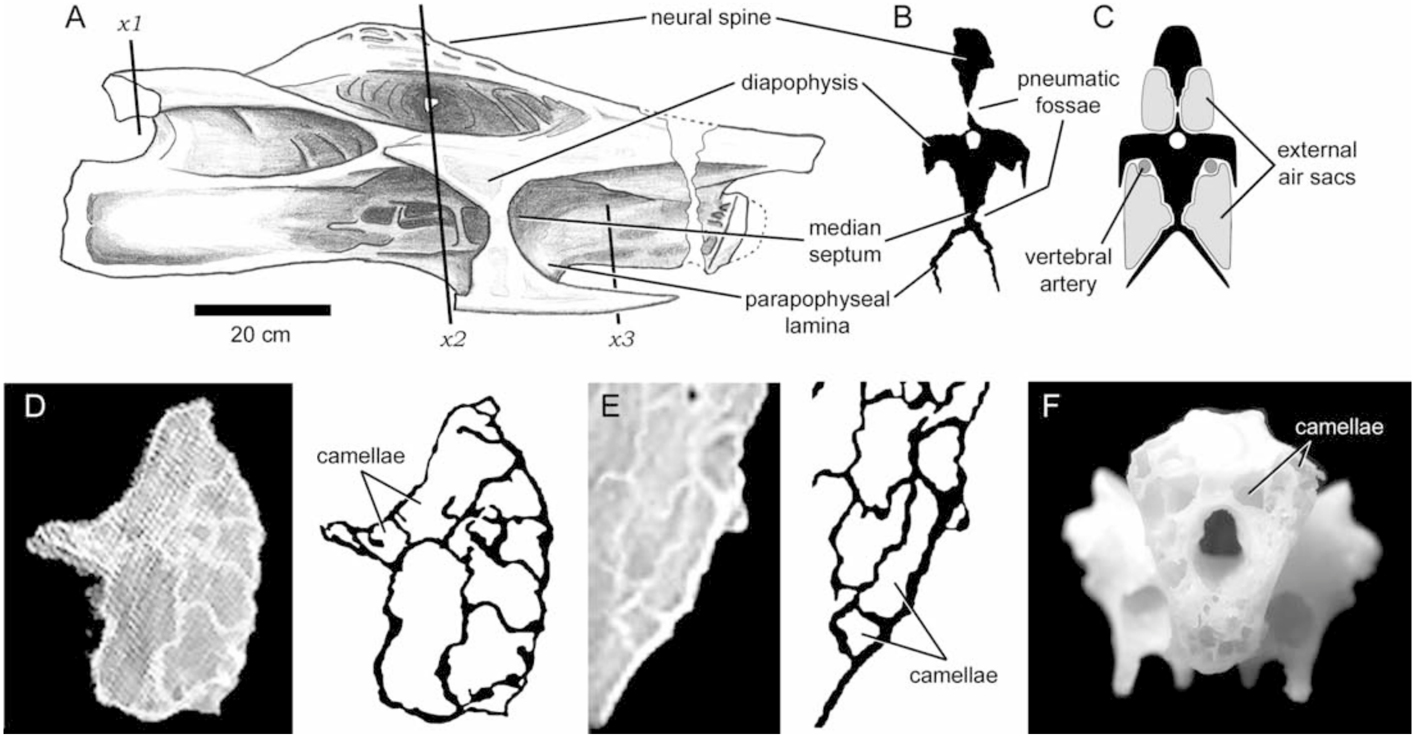
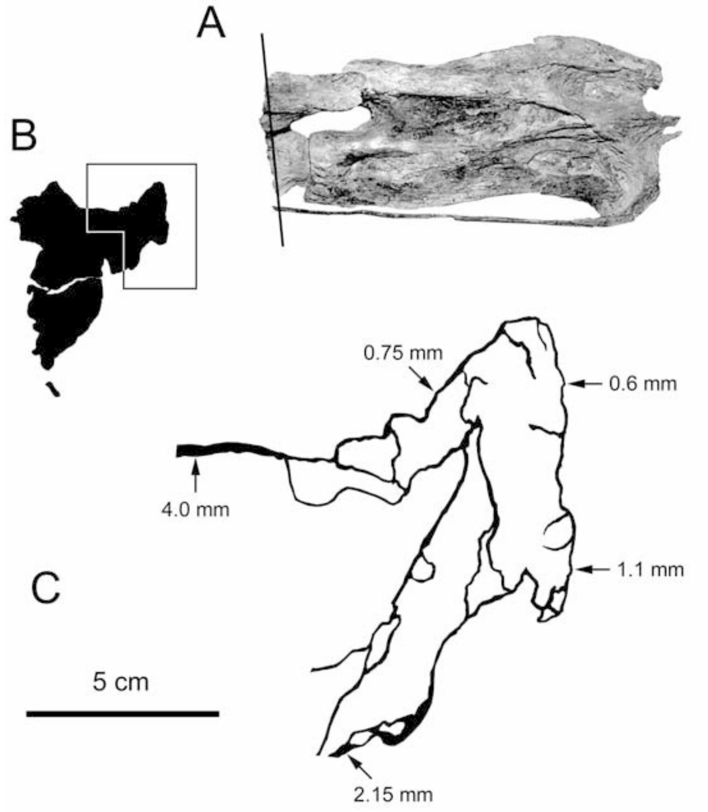


Figure 11. Cross-section of a *Sauroposeidon* vertebra. (A) depicts cervical vertebra 6 in right lateral view. (B), a CT cross section through the middle of the vertebra (along line ×2) resembles a stick figure. The "head" is the neural spine, and the "arms" and "legs" are the diapophyses and parapophyseal laminae. The spaces constricting the "neck" and "body" are pneumatic fossae. The hole in the stick figure's chest is the neural canal, which in life enclosed the spinal cord. (C) is the same section as it may have appeared in life. The pneumatic fossae contained large air sacs like those of birds. (D) and (E) show CT sections through other parts of the vertebra (lines ×1 and ×3). The internal structure is entirely filled with small pneumatic chambers called camellae. (F) The bones of living birds have similar camellae: this vertebra is from the senior author's Christmas turkey, cut in half to reveal the internal structure.

group. In addition to scanning *Sauroposeidon*, we scanned vertebrae from the sauropods *Apatosaurus, Diplodocus, Haplocanthosaurus, Camarasaurus, Brachiosaurus,* and *Malawisaurus*. The results reveal an interesting trend in the evolution of sauropods (Fig. 13).

Sauropods on the evolutionary line leading to *Sauroposeidon* include *Haplocanthosaurus, Camarasaurus,* and *Brachiosaurus*. Primitive sauropods, such as *Haplocanthosau-*

Figure 12 *(right)*. Internal structure of a *Sauroposeidon* vertebra. (A) shows cervical vertebra 5 and the front part of vertebra 6. The internal structure is exposed along the break in vertebra 6. The near-vertical line indicates the axis of the cross section shown in B. (B) shows a CT cross section from immediately in front of the break. In the field, the left side of the vertebra was facing up and was not as well preserved as the right side. The jagged white line running across the middle of the vertebra is a large crack. The box contains the area shown in (C), which is a part of the internal structure of the vertebra. This is a tracing of the bone exposed at the break, drawn from a photograph of the specimen and not from a CT scan. The black lines are bone, both the external surface of the vertebra and the bony septa that bound the internal chambers (white spaces). In the preserved specimen, these chambers are filled with sandstone; in life they were filled with air, as are the pneumatic bones of birds. We used digital calipers to measure the thickness of the bone at points marked by arrows. Although the vertebrae are immense, in life most of their volume was occupied by air and so they would have weighed surprisingly little.



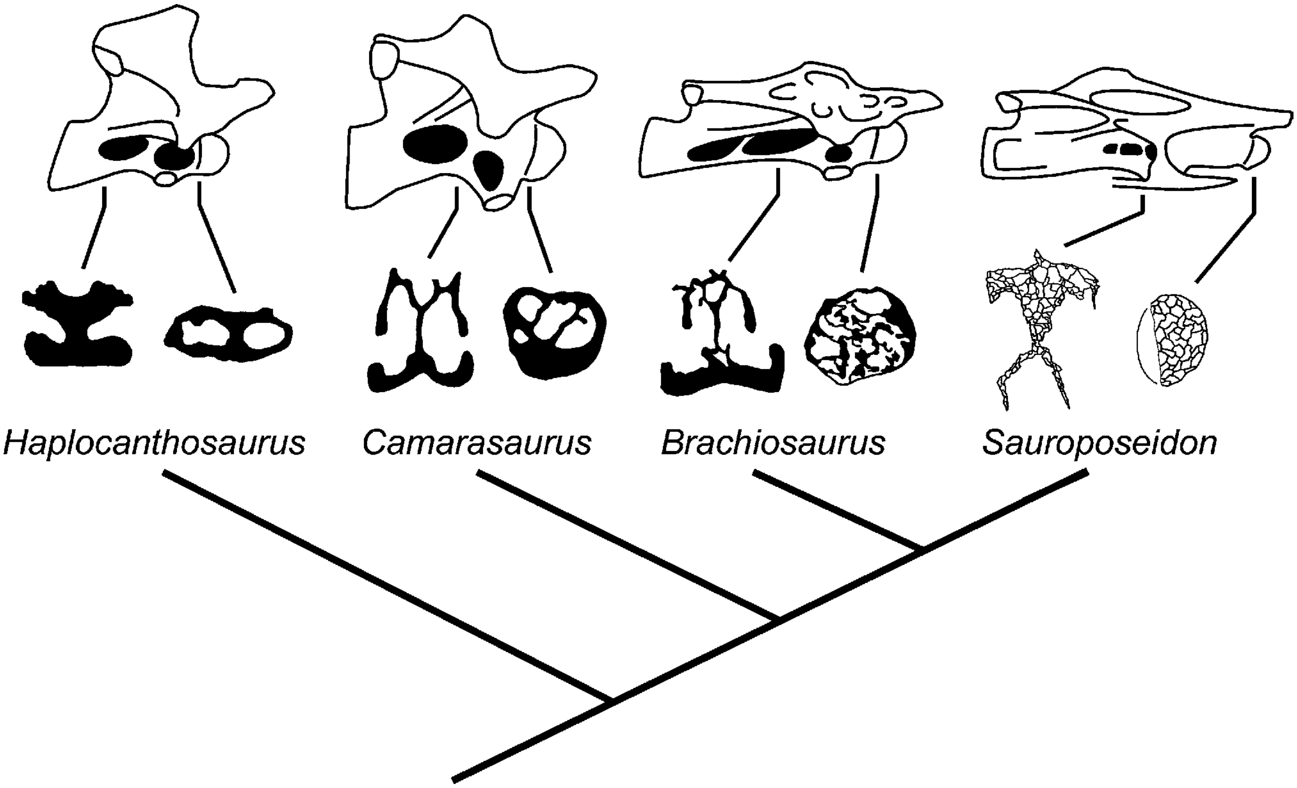


Figure 13. Evolution of vertebral internal structure in the lineage leading to *Sauroposeidon.* At top are diagrams (not to scale) of the vertebral structure of the various taxa; below, hypothetical relationships. Primitive sauropods such as *Haplocanthosaurus* have simple depressions on each side of the centrum, and small chambers toward the front. *Camarasaurus* and *Brachiosaurus* have large enclosed spaces called camerae. *Brachiosaurus* also has tiny, honeycomb-like spaces called camellae, which are mostly restricted to the ends of the vertebrae. The vertebrae of *Sauroposeidon* are the most lightly built, compared to those of the other sauropods in the figure. The bony walls enclosing the lateral air sacs have been reduced, turning the camerae into fossae, and the internal structure is entirely filled with camellae. The precise arrangement of the camellae in the vertebrae of *Sauroposeidon* is unknown because of problems associated with imaging a specimen so large and dense. The pattern shown here is speculative, but it is based on well-resolved camellae from other parts of the vertebra (see Figs. 11 and 12). The evolutionary tree is not the result of a cladistic analysis, but it is based on the cladistic analysis of Wilson and Sereno (1998) and the Hennigian tree of Wedel and others (2000a, fig. 3).

rus, lack internal chambers in their vertebrae. Instead, a simple depression or fossa is present on each side of the vertebra. In *Camarasaurus* the vertebrae are more lightly constructed, and contain several large, enclosed chambers called camerae. The vertebrae of these sauropods resemble I-beams in cross section. I-beam construction is a good way to combine strength with lightness. For some kinds of stress an even stronger design is the honeycomb, and the beginnings of honeycomb construction appear in *Brachiosaurus.* The vertebrae still have large camerae and I-beam cross sections, but the ends of the vertebrae are filled with a honeycomb of tiny, thin-walled chambers called camellae. Finally, in *Sauroposeidon,* the heavy bars of bone that formed the walls and floors of the vertebrae in *Brachiosaurus* are gone. Instead, the parapophyseal laminae meet the median septum at an obtuse angle to form the legs of a stick figure, and the internal structure consists entirely of camellae.

The vertebrae of these sauropods document an architectural trend in which air spaces became smaller and more numerous and bony elements became thinner and more delicate. *Haplocanthosaurus, Camarasaurus,* and *Brachiosaurus* also have successively longer necks, a trend that culminated in the 12-m (39-ft) neck of *Sauroposeidon.* By combining strength and lightness, the increasingly specialized internal structure of the vertebrae may have facilitated the continued evolution of increasingly longer necks in this lineage. However, the biomechanical properties of the various internal structure types have not been determined, and much work remains to be done.

The internal structure of sauropod vertebrae tells us about more than just neck elongation. The only living vertebrates with similar spaces in their vertebrae are birds (Fig. 11F). The hollow spaces in bird vertebrae are filled with air. The air reaches the vertebrae through tiny air tubes called diverticula that extend out from the air sacs in the thorax and abdomen. The primary function of the air sacs is to ventilate the lungs. Unlike mammals, which get fresh air only upon inhalation, birds have a sophisticated flow-through breathing system. The air sacs blow fresh air through the lungs during both inhalation and exhalation—enabling birds to extract a much higher proportion of oxygen from each breath than do mammals (Bernstein, 1976).

What are the implications for sauropods? The internal structure of sauropod vertebrae is practically identical to that of birds, and no other mechanism produces the same kind of spaces inside bones. Furthermore, the air spaces in side sauropod vertebrae are connected to the outside of the bones by holes called foramina (Fig. 9). In birds, similar foramina allow air-filled diverticula extending from the air sacs to enter the bones. The presence of foramina in sauropod vertebrae indicates that the air was taken in from an external source. Other lines of evidence, including the spread of internal chambers along the vertebral column during sauropod evolution, also indicate that sauropods had an air sac system similar to that of birds (Wedel, 2003; see Fig.14). Pterosaurs and meat-eating theropod dinosaurs also had pneumatic bones, and they probably had air sacs, too. Does that mean sauropods and other dinosaurs had high-efficiency lungs like those of birds? The possibility (discussed in text to follow) may be a key to understanding how *Sauroposeidon* and other sauropods grew so large.

FLESH ON THE BONES

Sauroposeidon was one of the largest dinosaurs that ever lived. How it compares to other sauropods in terms of size depends on the various ways in which size is measured. For example, *Sauroposeidon* was not the longest of all dinosaurs. Even the familiar *Diplodocus*, with its thin, whip-like tail, may have been longer. The longest dinosaur discovered to date is probably *Supersaurus*, a close relative of *Diplodocus* from the Late Jurassic of Colorado. *Supersaurus*, like *Sauroposeidon*, is incompletely known. The bones that have been recovered indicate a truly stupendous animal: whereas *Diplodocus* was as much as 27 m (89 ft) in length, *Supersaurus* may have reached more than 40 m (131 ft). But *Supersaurus*, like *Diplodocus*, was lightly built, and may have weighed no more than 50 metric tons (Paul, 1997).

If, on the other hand, we look for the tallest dinosaur, then *Sauroposeidon* seems made to order (Fig. 15). Its vertebrae are 25% to 33% longer than equivalent vertebrae from *Brachiosaurus. Brachiosaurus* had a 9-m (30-ft) neck, so even by conservative estimates the neck of *Sauroposeidon* would have been 11.25–12 m (37–39 ft)—as long as an entire skeleton of *Acrocanthosaurus* or *Tyrannosaurus.* Despite their great length, the vertebrae of *Sauroposeidon* are only slightly larger in diameter than those of *Brachiosaurus*, and we estimate that its body was only 10% to 15% larger than that of its Jurassic cousin. That would give *Sauroposeidon* an overall length of perhaps 28 m (92 ft). Starting at the shoulder, 6 or 7 m (20 or 23 ft) off the ground, *Sauroposeidon*'s neck would have given it a reach of 17 or 18 m (56 to 59 ft), making it tall enough to peer into a sixth-story window. Whereas *Brachiosaurus* is estimated to have weighed 30 metric tons, *Sauroposeidon* may have tipped the scales at 50 tons.

Even the 12-m (39-ft) neck of *Sauroposeidon* was not the longest among dinosaurs (despite Wedel and others, 2000a). The single available neck vertebra from *Supersaurus* is, at 1.35 m (4 ft, 5 in.), slightly shorter than the longest vertebra from *Sauroposeidon.* However, if *Supersaurus* was built like other diplodocids, it would have had 15 vertebrae in its neck, and even estimating conservatively (assuming that the 1.35-m vertebra was the longest) *Supersaurus* had a whopping 14 m (46 ft) of neck. But computer models suggest that diplodocids could not raise their necks vertically (Stevens and Parrish, 1999), so *Supersaurus* would have had to rear up on its hind legs to reach higher than *Sauroposeidon.*

These stupendous animals were not mutants or sports of nature. *Supersaurus* and *Sauroposeidon* have similar adaptations for lightening the neck vertebrae. Their specializations probably evolved in populations of similar-size individuals. They were functioning members of their ecosystems, and they must have been successful over millions of years to accumulate their specific adaptations. For all their size and strangeness, these giant animals were just that, animals. Like all other organisms, they had to make a living in the day-to-day world of feeding and mating, competition and predation.

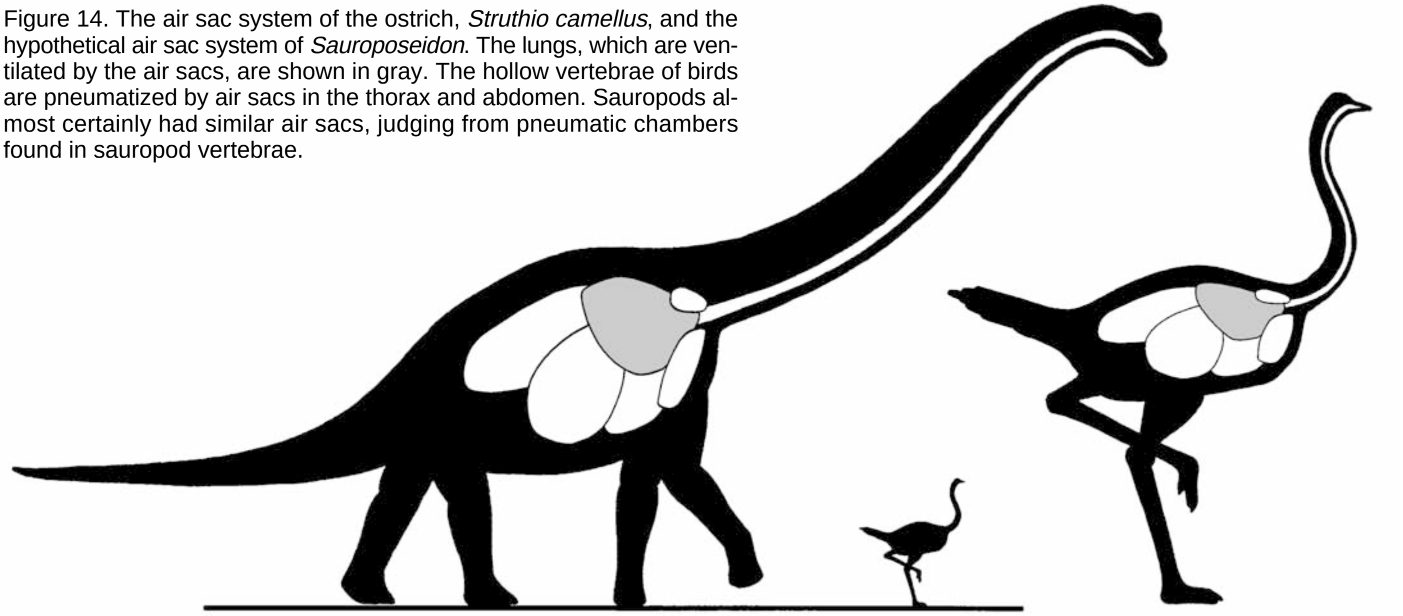


Figure 14. The air sac system of the ostrich, *Struthio camellus*, and the hypothetical air sac system of *Sauroposeidon*. The lungs, which are ventilated by the air sacs, are shown in gray. The hollow vertebrae of birds are pneumatized by air sacs in the thorax and abdomen. Sauropods almost certainly had similar air sacs, judging from pneumatic chambers found in sauropod vertebrae.

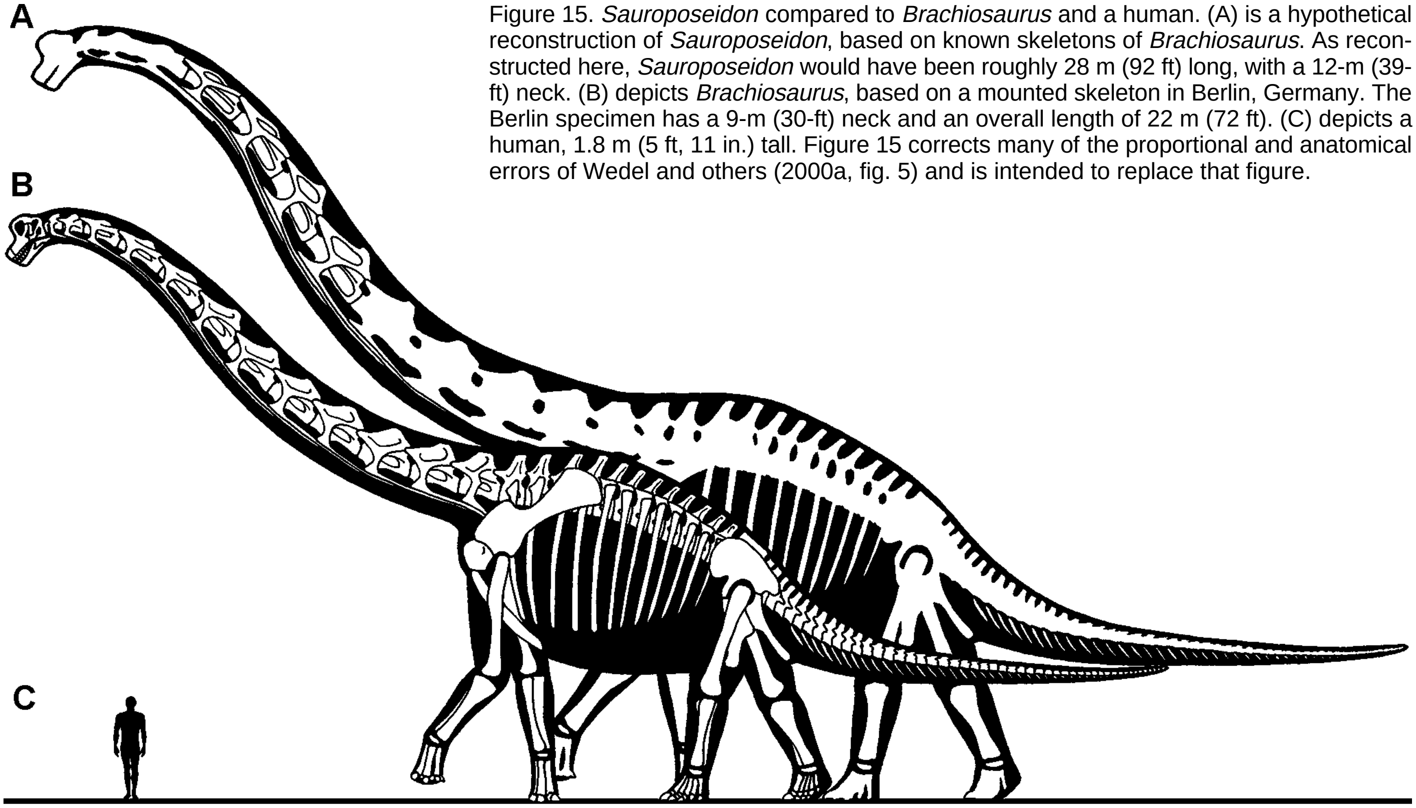


Figure 15. *Sauroposeidon* compared to *Brachiosaurus* and a human. (A) is a hypothetical reconstruction of *Sauroposeidon*, based on known skeletons of *Brachiosaurus*. As reconstructed here, *Sauroposeidon* would have been roughly 28 m (92 ft) long, with a 12-m (39-ft) neck. (B) depicts *Brachiosaurus*, based on a mounted skeleton in Berlin, Germany. The Berlin specimen has a 9-m (30-ft) neck and an overall length of 22 m (72 ft). (C) depicts a human, 1.8 m (5 ft, 11 in.) tall. Figure 15 corrects many of the proportional and anatomical errors of Wedel and others (2000a, fig. 5) and is intended to replace that figure.

Although half a century ago it was a given that sauropods were sluggish swamp-dwellers, we can now be fairly certain that they lived on land. Aquatic and semi-aquatic animals, such as beavers or hippopotami, tend toward a barrel shape, with short legs and wide, spreading feet, the better to track across soft mud. The landmark studies of Bakker (1971) and Coombs (1975) brought to wide attention the obvious facts of sauropod anatomy: they were shaped more like giraffes than hippos. In fact, sauropod feet were so compact that the animals must have found soft ground treacherous. Fossils from Wyoming and Tanzania show that sauropods sometimes died on their feet, irretrievably mired in mudholes (Dodson and others, 1980; Russell and others, 1980).

Further evidence of the terrestrial habits of sauropods comes from their digestive tracts. A fossil of *Apatosaurus* shows evidence of conifer twigs and needles in the stomach (Stokes, 1964). Sauropods also swallowed cobbles: their stomach stones, or gastroliths, have been found in place among associated skeletons (Christiansen, 1996). Sauropods may have used gastroliths to help break down their food, just as modern chickens fill their gizzards with sharp grit to grind up grain, although not all paleontologists agree with this interpretation (Wings, 2003). Some gastroliths are distinctive enough to suggest sauropod migration patterns (Stokes, 1987; Ratkevitch, 1998); together with trackway evidence, they show that sauropods were as mobile as the large mammals of today (Dodson and others, 1980).

The tiny heads of sauropods look strange to us; how could such small mouths feed such enormous animals? Part of the problem is that we are mammals, and we're used to looking at other mammals, such as horses and cattle. Most mammals chew their food before they swallow it. That means they must have big teeth, and big heads. The head of a horse or a cow is a big grass-grinder with a brain and sense organs tacked on. Sauropods didn't chew their food. They couldn't; they lacked grinding teeth and muscular cheeks. Sauropods must have swallowed each bite whole, and the "chewing" was done in the gizzard or stomach. Because they didn't have to chew, sauropods could have eaten very quickly, one bite after another. Modern elephants spend up to half of each day just eating, although some of that time is given over to chewing. *Sauroposeidon* was many times the size of the largest elephant. Even without time off to chew, *Sauroposeidon* and other giant sauropods probably spent most of their waking hours eating. A 50-ton *Sauroposeidon* may have eaten a ton of plant material every day just to survive (based on calculations by Weaver, 1983).

In the 1980s it was briefly fashionable to imagine that the wide hips of sauropods served as birth canals for enormous babies that were born alive (Bakker, 1986; Morell, 1987). In fact, sauropods had wide hips because they themselves were wide. The recent discovery of sauropod nests in Patagonia demonstrates that sauropods—like all other dinosaurs including birds—laid eggs (Chiappe and others, 1998). The Patagonian nest sites stretch on for miles, indicating that sauropods gathered in vast numbers to lay their eggs. Two dozen eggs of grapefruit size filled each nest, and each egg contained an embryonic sauropod that upon hatching would have been about the size of a kitten. The Patagonian eggs came from small sauropods, but even the eggs of *Sauroposeidon* were probably no larger than soccer balls.

Recent studies show that young sauropods grew very rapidly. The growth rates of sauropods can be determined by counting growth lines in their bones, like counting rings in a tree. Independent studies of North American and African sauropods indicate that they reached reproductive maturity in 8 to 12 years and full adult size in less than two decades (Curry, 1999; Sander, 2000). Elephants take almost as long to mature, and they start out much larger and end up much smaller: hence, sauropods grew faster than elephants and almost as fast as modern birds. The best explanation for such rapid growth is that sauropods had high metabolic rates and that, in this respect at least, they were more like "warm-blooded" mammals and birds than "cold-blooded" amphibians and reptiles. Sauropods would have needed large amounts of oxygen to support the high metabolic rates required for fast growth. As already observed, the hollow vertebrae of sauropods suggest high-efficiency lungs like those of birds. The vertebral anatomy and the high growth rates both show that sauropods were physiologically much more like birds than like crocodiles, lizards, or snakes.

Pulling together those disparate facts gives us a better picture of *Sauroposeidon* and the world in which it lived (Fig. 5). We can imagine vast sauropods, singly or in herds, stripping twigs and needles from entire forests of conifers. They would have to eat almost constantly to stoke their metabolic fires. They might approach broad, slow-moving rivers with caution, afraid of bogging down because each meter-wide foot must support 10 tons or more. Gravid females may have congregated in vast rookeries to deposit their eggs. From each egg would come a tiny *Sauroposeidon* no bigger than a modern rabbit. The babies would grow at an astounding rate, several kilograms a day—if they evaded roving packs of *Deinonychus* and the terrible, meter-long jaws of *Acrocanthosaurus*. If they were lucky, the young sauropods would soon outstrip their hunters in size, and the theropods would turn back to the less imposing herds of *Tenontosaurus* to get their food, or die trying. Occasionally a flood would deposit a meter or more of sand and mud in a single event, entombing any carcasses—predator and prey alike—left on the river's floodplain. The dinosaurs were buried alongside their less spectacular neighbors: turtles, lizards, crocodiles, and the tiny, hairy mammals that would eventually inherit the Earth.

Most species persist for a few million years before going extinct (the conservative garfish, essentially unchanged since the Cretaceous, is an exception rather than the rule). *Sauroposeidon* must have existed for millennia at least, with thousands of individuals alive at any one time to maintain a healthy and stable population. So far we have discovered only one individual, and only about 5% of it, at that. Only future discoveries can tell us if our picture of *Sauroposeidon* is accurate.

IN THE FOOTSTEPS OF GIANTS

South of the Red River, the Antlers Formation thickens and becomes interbedded with marine sediments laid down on the bottom of a shallow sea—the ancient Gulf of Mexico. The terrestrial parts of the sedimentary sequence, known in central Texas as the Trinity Group, contain many of the same species as found in Oklahoma: the same turtles, the same crocodilians, even *Deinonychus*, *Tenontosaurus*, and *Acrocanthosaurus* (Jacobs, 1995; Winkler and others, 1997b; Brinkman and others, 1998; Harris, 1998). Sauropods are also known from the Trinity Group of Texas: the published record describes mainly small, fragmentary fossils (see Langston, 1974). A productive bone bed, now being investigated by researchers at Southern Methodist University, promises to dramatically increase our knowledge of sauropods from the Trinity Group (see Winkler and others, 1997a; Rose, 2004). Of greater interest in the context of this report are tracks left by sauropods near present-day Glen Rose, Texas. The celebrated dinosaur trackways of the Glen Rose Limestone have attracted widespread attention since their discovery early in the 20th century (Shuler, 1917). While working for the American Museum of Natural History, New York, Roland T. Bird collected a long sauropod trackway in the bed of the Paluxy River (Bird, 1985), and the tracks were named in his honor: *Brontopodus birdi*, "Bird's thunder foot" (Farlow and others, 1989).

Fossilized tracks receive their own names, independent of the presumed trackmakers, because it is usually impossible to match specific animals with specific trackways. However, in the case of *Brontopodus* we can offer informed speculation. Obviously, tracks of *Brontopodus* belong to a sauropod, but otherwise the most telling clue is size: the Paluxy footprints are truly enormous. A big footprint may be a meter (39 in.) in diameter, large enough for a child's bath (Fig. 16). Even the hind feet of *Brachiosaurus* are not large enough to have made such tracks. Skeletal remains of sauropods from the Trinity Group of Texas, although incomplete, do not suggest titans large enough to fit the footprints. However, the empty tracks are just about the right size to have been made

Figure 16. In the footsteps of giants. Giant sauropod tracks, such as this one, are common in Early Cretaceous strata of Texas. *Sauroposeidon* is the only dinosaur known from that time large enough to have made the tracks. (Negative number 319835, American Museum of Natural History Library, reprinted with permission.)

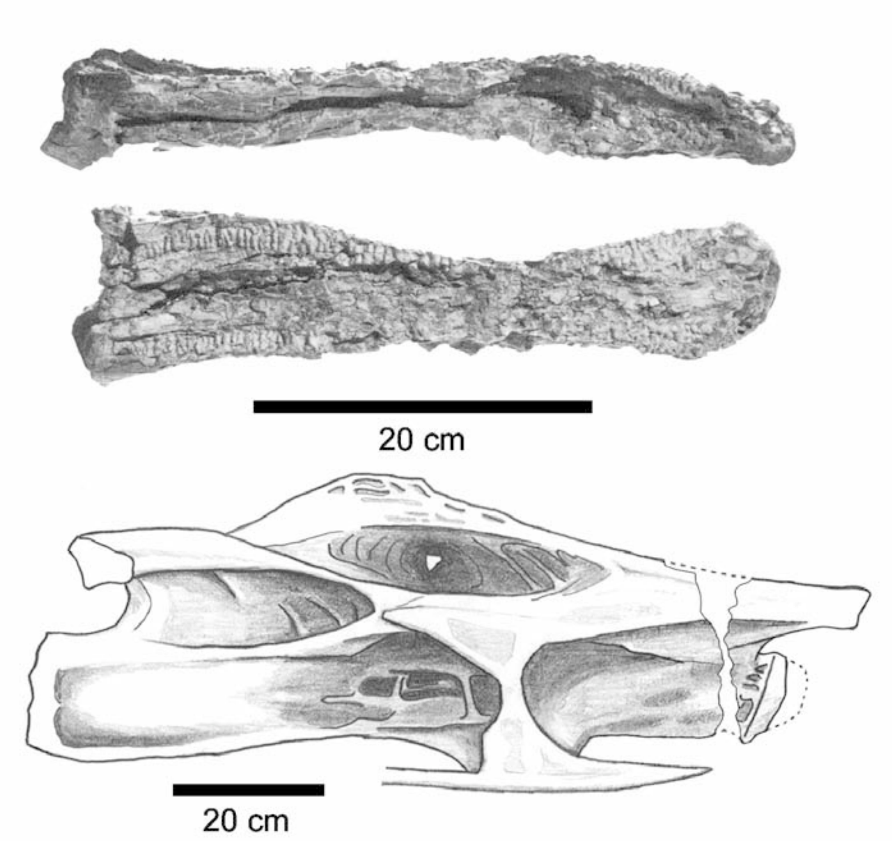


Figure 17. A sauropod from Montana, probably a juvenile, is represented here by YPM 5294 (side and top views, shown above). The specimen, a centrum from the Cloverly Formation, has most of the characteristics used to diagnose *Sauroposeidon*. The sauropod was either *Sauroposeidon* or a very close relative. After Ostrom (1970, pl. 15, reprinted with permission); reversed for comparison to cervical vertebra 6 of *Sauroposeidon*.

by *Sauroposeidon*. We may never know for certain, but so far *Sauroposeidon* is the only Early Cretaceous sauropod known from the entire North American continent large enough to have made the Paluxy tracks. The similarity of Oklahoma and Texas faunas at the time makes the possibility even more likely.

The first known specimens of two Early Cretaceous dinosaurs mentioned above, *Deinonychus* and *Tenontosaurus*, came from the Cloverly Formation of Montana and Wyoming. The Cloverly also yielded a few sauropod fossils. One specimen, Yale Peabody Museum (YPM) 5294, consists of a single neck vertebra from a juvenile sauropod (Ostrom, 1970; see Fig. 17). But what a juvenile: at 47 cm (18.5 in.) long, YPM 5294 is longer than the vertebrae of many adult sauropods. Although incomplete, it has most of the characteristics that set *Sauroposeidon* apart from all other sauropods (Wedel and others, 2000b). If it is not a vertebra from a juvenile *Sauroposeidon*, then it must represent a close relative of *Sauroposeidon*.

Footprints, an isolated vertebra: tantalizing bits, but to learn more about *Sauroposeidon* we need more fossils. The Antlers Formation stretches across nine counties in southeast Oklahoma. More remains of *Sauroposeidon* and other remarkable animals are out there, in bluffs and along creek beds, waiting to be found. Perhaps *Sauroposeidon* will not be the last of Oklahoma's giants, after all.

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