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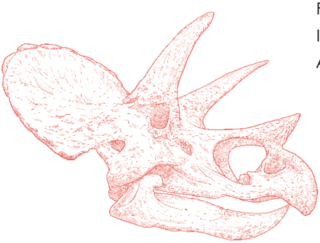

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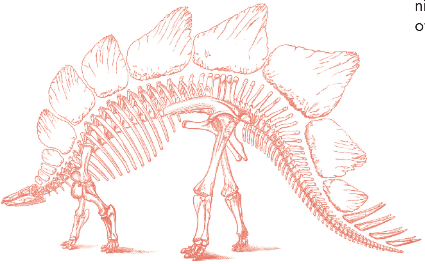
THE BONE WARS

One of the greatest periods of discovery in those early days of dinosaur paleontology owes itself to a scientific rivalry. In the late 1800s, dinosaur fossils were the new gold rush for North America, and two eminent scientists of the time led (and funded much of) the charge: Edward Drinker Cope (1840–97) and Othniel Charles Marsh (1831–99).

Immediately the challenge became for each to find more and grander dinosaurs than the other, by any means necessary. Public slander, bribery, theft of specimens, and even actively destroying each other's finds took place and became worryingly commonplace in paleontology for years. It was a war of science fueled by fragile egos. Their feud was bitter, the stories of sabotage and scandal leaving a permanent mark on the field, but its other legacy was the discovery of some of the most famed names in the dinosaur world, including *Triceratops*, *Diplodocus*, and *Stegosaurus*.

↓ Orniel Marsh's classic reconstruction of *Stegosaurus* may not be particularly accurate from a scientific point of view, but it acted as an iconic blueprint for how many people see dinosaurs some 150 years later.

→ *Allosaurus fragilis* was another famous dinosaur found during the Bone Wars. A top predator of the Morrison Formation of ancient North America, it would later gain the media nickname of the "lion of the Jurassic."



DINOSAUR CENTURY

The huge popularity of dinosaurs, both with the general public and in scientific research, only grew at the turn of the 20th century as even more discoveries revealed just how abundant and widespread they had been as a group.

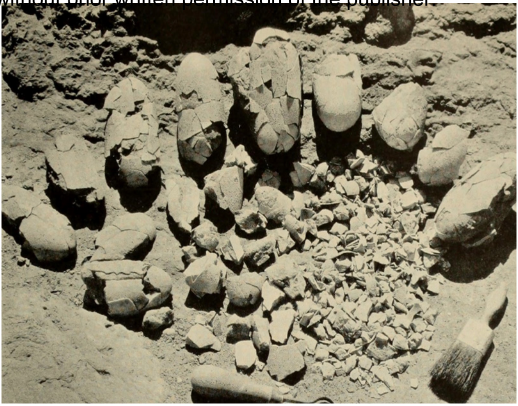
FAMED NAMES

One of the most prolific paleontologists of the early 1900s was the German Friedrich von Huene (1875–1969), who named around 30 dinosaur genera. Although many of these names were based on fragmentary evidence and have since been cast into doubt, some of his other work, such as being the first to recognize and name the "Sauropoda" as a group, has stood the test of time.

There is no shortage of interesting figures from this period of dinosaur science. They include American Barnum Brown (1875–1963), who discovered *Tyrannosaurus rex*, and the truly fascinating Hungarian Baron Franz Nopcsa (1877–1933), who pioneered work on dinosaur physiology (as well as formally nominating himself as King of Albania).

DESTROYED DINOSAURS

Despite being extinct for millions of years, dinosaurs were not untouched by the events of the 20th century. Small museum pieces were easy to move during the bombing raids of the Second World War, but this was not the case for the heavy rock remains of giant dinosaurs, many of which were left behind in the hope that they would not be hit. Unfortunately, many were unlucky. The most high profile of these were the remains of the huge theropod *Spinosaurus*, which were obliterated when Munich's *Paläontologishes* Museum was bombed in April 1944.



EGG EXPEDITIONS

One influential but controversial series of expeditions in dinosaur paleontology were those undertaken by the American Roy Chapman Andrews (1884–1960) in the 1920s. His group explored the vast bone fields of the Gobi Desert, making many remarkable discoveries, including the first verified fossils of dinosaur eggs (belonging to the beaked theropod, *Oviraptor*). However, one of these very eggs caused great controversy, as he put it up for auction upon returning to America. Andrews had assured the ruling government (China at the time) that the eggs had no monetary value, and they in turn accused him of conning them, plundering their precious finds for profit in the United States. As such, any further expeditions were banned for over a year.

THE DINOSAUR RENAISSANCE

Ever since the sensational discovery of dinosaurs and the huge sizes they could reach, it was generally assumed that any animal so large must have been a lumbering giant, slowly plodding its way across the primordial world. Surely it was impossible for such large creatures to move with any rapidity or grace.

TERRIBLE CLAW

The spark for the revolution in thinking was the discovery of a new dinosaur genus, *Deinonychus*, in 1963 (the first remains were discovered in the 1930s but never formally described). *Deinonychus* was an American raptor, a group known for many distinctly bird-like features, including the sickle claw on the toe for which the group is infamous (the genus name even means "Terrible Claw"). These features caused the paleontologists of the time to bring back a theory first proposed only a few years after the publication of Darwin's theory of evolution: that birds had evolved from dinosaurs. It's not fully known why this idea had fallen out of fashion, although some blame a popular work by Danish paleontologist Gerhard Heilmann, *The Origin of Birds* (1926), which dismissed the idea as fanciful. But now that it had been raised again it almost appeared too obvious, and with every specimen checked, more evidence mounted that the two groups were connected.

BIRD BLOOD

Unlike reptiles, birds are warm-blooded (endothermic), just like mammals. So if they evolved from dinosaurs, it is possible that some, if not all, dinosaurs were also warm-blooded, which would have enabled them to lead far more active lives. It would be some time before technology would advance enough to accurately report on these claims. Detailed studies of the bones of dinosaurs (and other prehistoric groups) using infrared spectroscopy showed the presence of tell-tale biomolecules indicative of a high metabolism, like that of birds. This suggests that endothermy may well have evolved at the base of the dinosaur tree, and the more active lifestyle proposed in the "Dinosaur Renaissance" can be applied to the whole group.

COLD-BLOODED COMPARISONS

The quick assignment of the dinosaur group to the Reptilia may well have had a hand in shaping our perception of them. After all, scientists at the time would have compared them directly to living reptiles, such as lizards and crocodiles. These groups are cold-blooded (ectothermic), meaning they are reliant on external heat sources to warm their bodies. As such, they spend much of their time basking in the sun and reserving energy by moving as little as possible until they have to, usually to feed. With dinosaurs being so closely compared to such reptiles, and because of the extra weight conferred by their enormous body sizes, an even more lethargic lifestyle was presumed for them.

INSPIRING IMAGES

What really boosted the new understanding of dinosaurs, however, was the famous image that accompanied the research. The paleontologist Robert Bakker (b.1945) reconstructed the animal as a fleet-footed and nimble hunter, drawn in the act of running and showing a lightweight and athletic build never before given to a dinosaur. This image would provide the blueprint for the way we picture dinosaurs to this day. Starting from a piece of artwork and exploding into a myriad of new paradigm-shifting research in the years that followed, this period of paleontology in the 1960s and early '70s is known as "Dinosaur Renaissance."

THE THEROPODA

The very first dinosaurs were likely all carnivorous; light and nimble hunters, they fed mostly on insects and other small reptiles, prey they were perfectly adapted to handle with their razor-sharp teeth. While some lineages went on to evolve herbivory and take advantage of the plentiful vegetation, one group stuck to their meaty diets and evolved into an amazing array of effective killers. These were the theropod dinosaurs.

MORPHOLOGY

Many of the features retained by the dinosaurs through the whole Mesozoic Era (252–66 Mya) can be seen in those Triassic pioneers. The theropods were saurischian dinosaurs (with the lizard-like arrangement of hip bones) and they were bipedal, leaving their arms free for use in catching prey, meaning that many evolved particularly sharp claws. The earliest members of the group possessed up to five digits on each hand, although this reduced to three in most later theropods.

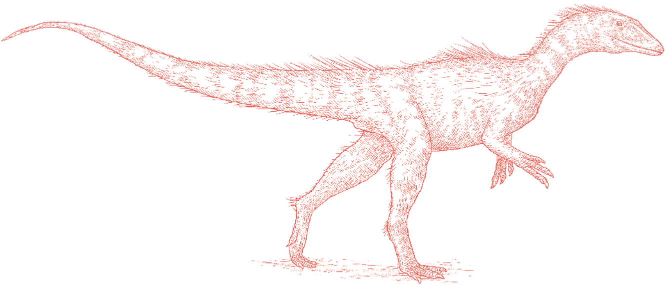
EXTINCTION SURVIVORS

We do know that despite the challenges, the theropods survived through the end-Triassic extinction. Finds from around this time are rare, but specimens from shortly after the extinction, such as *Dracoraptor* of Wales, give some clues as to how the group survived. The small serrated teeth and advanced sense of smell possessed by *Dracoraptor* hint that it was likely a specialist in small prey and had a scavenging lifestyle. The dinosaur was lean and nimble, with a body size a little over 6½ ft (2 m) in length. Being a fast opportunist during tough times helped the dinosaurs survive where the other top reptile carnivores failed.

GHOST RANCH

Much of what we know about the Triassic theropods comes from one location, Ghost Ranch in New Mexico, where it's estimated over a thousand individuals of *Coelophysis* have been discovered. These dinosaurs, a little over 3 ft (1 m) in height, had fairly narrow skulls atop relatively long, curved necks. Their lightweight jaws suggest that though they were diversifying, during the Triassic the theropods were sticking to small prey items. It was once thought that small bones in the body cavity of one *Coelophysis* were evidence that this dinosaur may have been involved in cannibalism, perhaps an extreme survival tactic during the harsh Triassic environment. However, we now know that the remains belonged to a different species of small reptile.

↘ Found in rocks from the earliest Jurassic of Penarth, Wales, *Dracoraptor hanigani* shows a fairly typical body plan for early theropods.



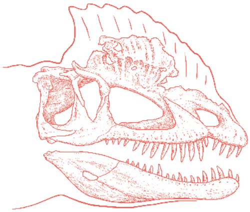
JURASSIC THEROPODS

By the Jurassic Period, herbivores were starting to reach those enormous sizes that we typically associate with dinosaurs. And as is to be expected, where large prey like herbivores is available, large and skillful predators will inevitably appear to tackle them.

CRESTED PREDATORS

Early in the Jurassic came one of the most unusual theropods, *Dilophosaurus*. This dinosaur shot to unexpected fame when it appeared in the 1993 movie *Jurassic Park*—although, unfortunately, this rise in popularity was accompanied by a host of very persistent misconceptions. *Dilophosaurus* had neither an expanding neck frill, nor the ability to spit venom. It did, however, possess that bizarre double-crest on top of its head. Analysis of the bone shows the crest of *Dilophosaurus* was highly pneumatized, suggesting that its primary function was for display. It was certainly too fragile to have been of any combative use. The crest was also much larger than it is depicted in the movie. Standing up to about 8 ft (2.5 m) in height, *Dilophosaurus* was one of the first truly large theropod dinosaurs, but through the Jurassic it was followed by many more.

Another predator of the Jurassic Period, *Ceratosaurus*, also had distinctive head features—two large bone ridges just in front of the eyes and a large central ridge, which would, in life, have supported a keratinous horn structure.



← The skull of the theropod *Dilophosaurus wetherilli*, showing the impressive vascular crest. The gap between the bones around the nostril indicates that this dinosaur did not have a particularly powerful bite.

ALLOSAURUS

The best known of the Late Jurassic theropods is surely *Allosaurus*, the 30-ft (9-m) long hunter with a narrow snout, those *Ceratosaurus*-style eye ridges, and three particularly vicious-looking claws on the end of each hand. Fossils of this North American apex predator are common in the Morrison Formation (a hotbed of dinosaur discovery across several northern states in the United States), making it one of the most well-studied theropods of all.

Recent analysis of the jaw structure of *Allosaurus* has suggested that it could have opened its jaws to an extreme gaping angle of 92 degrees, and used this in combination with a strong neck action to effectively hack at its prey. This theory remains controversial, though, as the detrimental effects this action may have had on the head of the animal remain unknown.

THE SMALL THEROPODS

While the larger species typically attract all the attention, the true innovators of the Jurassic Period were the small theropods. It was they who made the biggest evolutionary leap by far, which would change the ecosystems of the world forever, but we will discuss these small theropods later in Chapter 7.

GLOBAL DOMINANCE

Thanks to an abundance of fossils, the theropod predators of Jurassic North America may be the best known, but plenty of others have been discovered elsewhere. They include the nimble hunter *Megalosaurus* of Europe, and the aptly named, 23-ft (7-m) long *Afrovenator* of Africa. We even find theropods from Antarctica in the Jurassic. Well before the continent was locked in ice, the single-crested *Cryolophosaurus* hunted here, although due to difficulty accessing fossil sites, so far only the fossils of one individual have been found. Oddly, very few remains of theropods from the Jurassic have been discovered in Australasia, whether due to a lack of fossils found or an absence of theropods we can't be certain (a saying in paleontology being "absence of evidence is not evidence of absence").

THE CHASERS

If ambush fails, hunters may have to run to catch their prey, and some dinosaurs evolved especially for this strategy. Perhaps the most dedicated were the abelisaurids, a group of theropods found across South America, Africa, and India through the Jurassic and Cretaceous.

Abelisaurids had massively reduced arms, to the point where from a distance you probably wouldn't even notice they were there. Their heads were fairly stout compared to the elongate shape of other theropods, and overall their sizes were modest. Most were comparable to an adult human in height, with the exception of some like *Carnotaurus sastrei*, at nearly 10 ft (3 m) tall, which is also known for the distinctive protruding horns of its skull. Abelisaurids probably specialized in chasing small prey, their powerful legs and spring-loaded feet giving them effective bursts of speed—equally useful for scarpering when scavenging the kills of other, larger predators, should they return to reclaim them.

↙ The hugely reduced arms of abelisaurids would have seemed almost entirely useless compared to the arms of other theropods.

↙ The skull of the theropod *Carnotaurus sastrei* shows two large bone protrusions above the eyes. In life, these protrusions would likely have been covered by a keratin sheath.

→ *Carnotaurus sastrei* was one of the largest known abelisaurid dinosaurs and would have been a top predator in Argentina 70 Mya ago. Thanksto exceptional skin preservation, it is known that *Carnotaurus* lacked the feathers seen in many other theropods, and had scaly skin and randomly distributed large "feature scales."

FISHING

When it came to hunting prey, theropods did not restrict themselves purely to what they could find on land. There was no need to stick to that when there were plenty of fish in the waters. Catching fish requires a completely different skillset to that needed for tackling dinosaur prey, and no group evolved to specialize more for this than the spinosaurids. First evolving in the early Cretaceous, this group was hugely successful, with representatives on every continent.

CONVERGING TACTICS

The most distinctive features of the spinosaurids were their skulls, which were very elongate, with long, thin snouts lined with rounded, narrow teeth. This head and tooth shape combination was ideal for snapping up fish and preventing them wriggling free. It's a familiar look, with spinosaurid skulls looking quite like those of crocodiles. The reason for this is called convergent evolution. Essentially, both groups were evolving to solve the same problem and came up with the same solution.

HEAVY CLAW

Converging with our own fishing inventions, some spinosaurids even evolved fish hooks. *Baryonyx* was a dinosaur from the United Kingdom dubbed "Heavy Claw" due to the 12-in (30-cm) sickle claw on each "hand," which was used to snare fish from rivers. A diet of fish is nothing to be sneered at either, for it sustained the largest terrestrial carnivore currently known to science. At 46 ft (14 m) in length, *Spinosaurus*, the dinosaur that gave this group its name, was 6½ ft (2 m) longer than a *Tyrannosaurus rex*.

THE LIFE AQUATIC?

Instantly recognizable from the 5-ft (1.5-m) high sail running along its back, *Spinosaurus* also holds the unfortunate crown of being perhaps the most controversial dinosaur among paleontologists, simply because nobody seems able to agree on how best to reconstruct it. Evidence from the high bone density of its ribs and femur, along with the flattened, paddle-like structure of its tail, have led some scientists to suggest that *Spinosaurus* was an aquatic dinosaur, more comfortable actively swimming in rivers than standing or wading around the banks. It seems that every year more papers are published reassessing the look and lifestyle of *Spinosaurus*, but maybe one day more fossils and study will help reveal the true nature of this enigmatic beast.

← The Brazilian *Irritator challengeri* shows many dinosaurian fishing adaptations—the slender, crocodile-like snout and large clawed arms—athough it lacks the sail of the famous *Spinosaurus*.

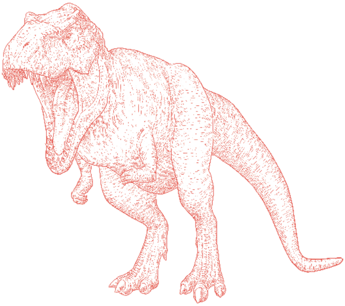
THE TYRANTS

There can be no question that the most famous dinosaur of all is *Tyrannosaurus rex*. When this dinosaur was first described in 1910 it was an instant sensation. A combination of early 20th-century American performance and the staggering features of the great predator captured the imagination like no other dinosaur has before or since.

POWERFUL BITERS

Tyrannosaurus rex is just one species from a whole group of dinosaurs, the tyrannosaurids, many of which shared one major trait: an extremely large and powerful set of jaws. Uniquely, the nasal bones of tyrannosaurids were fused, giving their skulls increased resistance to pressure and allowing for a higher bite force. Using evidence of injury in other dinosaurs, and mechanical analysis of the skull, *T. rex* likely had a bite force of over 40,000 Newton, strong enough to break bones. Their teeth were enormous, conical, and had serrations along the reverse edge. They were specifically evolved to take on large dinosaurs.

It has been proposed in the past that *T. rex* was a scavenger, not a hunter. However, we do have evidence of healed wounds made by *T. rex* in other dinosaurs, suggesting that they were attacked while still alive. It seems likely therefore that the animal was an active hunter.



← The 5-ft (1.5-m) long skull of *Tyrannosaurus rex* evolved specifically to have a strong bite force. The extreme stresses involved in biting were dissipated by the shape of the skull.

TINY ARMS

It is the impressive skull that was the reason for the tyrannosaurids' other famous feature, their tiny arms. If they'd had arms the size seen in other theropods, they would have been too front-heavy to balance effectively, and so evolved smaller arms in order to maximize their head strength. Whether these arms had any function whatsoever is still a matter of some scientific debate.

FEATHERED REX?

Whether *Tyrannosaurus rex* had feathers is a hard question to answer conclusively. However, fossils have been found with preserved *Tyrannosaurus* skin, and from this we can deduce that at least some sections, including the legs and head, were covered in scales and not feathers. While evidence for *T. rex* leans toward a mostly scaled appearance, we know some tyrannosaurids did have feathers. An early member of the group, *Yutyrannus*, from northeast China, shows direct evidence of a feathered body from fossilized imprints, which makes this 30-ft (9-m) long theropod the largest animal with confirmed feathers yet described by science.

WORLDWIDE FAMILY

Tyrannosaur ancestry can be traced back through to the Jurassic, with species found across much of the Northern Hemisphere. The earliest group members, such as *Guanlong* of Late Jurassic Asia, look remarkably different to later members, even sporting a large head crest. But it is in the Late Cretaceous of western North America that the group truly flourished. The tyrannosaurids *Daspletosaurus* and *Gorgosaurus* are the top predators found in the fossil-rich Dinosaur Provincial Park of Canada. Another Canadian member, *Albertosaurus*, has the honor of being named the National Dinosaur of the country. And to the south, in what is now the United States, *T. rex* was king.

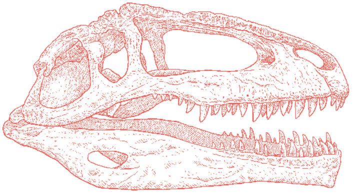
GIANT KILLERS

The tyrannosaurids were not the only giant dinosaur hunters. The Cretaceous was also a golden age for other terrifyingly large terrestrial predators. In South America, for example, even the sauropods were not safe from the 43-ft (13-m) long *Giganotosaurus*, while in northern Africa, *Carcharodontosaurus* ruled, taking their name from their thin, shark-like teeth. Neither had jaws quite as powerful as those of *Tyrannosaurus rex*, but both were larger, and they had more formidable clawed arms that could be used against prey.

Both *Giganotosaurus* and *Carcharodontosaurus* were part of the Allosauroidea family, which had dominated the Jurassic. We know this because of the ridge structure on each side of their heads, running from the nostrils to the eyes. This bumpy bone structure, known as rugose texture, suggests the presence of keratin on the surface, extending the crests to more exaggerated display structures. They possibly used these to attract mates, providing a glimpse into a more intimate side of the lives of these huge predators.

↓ *Giganotosaurus carolinii* had a skull measuring over 5 ft (1.5 m) in length. It is the largest known theropod from South America. The top surface of the skull shows the bumpy rugose texture, which helps distinguish itfrom that of other large theropods such as the tyrannosaurids.

→ *Carcharodontosaurus saharicus* was one of the largest terrestrial predators ever to have existed. Although its skull and teeth are relatively well known, there are not many known remains of the rest of its body, with much material having been lost in the Second World War.



HUMBLE BEGINNINGS

The sauropod dinosaurs (often referred to as the "long necks") were the largest dinosaurs of all, the giants of the ancient world. However, tracking back through their family tree, it can be seen that even these huge creatures started off small.

BASAL DEBATE

Sauropodomorphs are saurischian dinosaurs, meaning that despite drastic differences in appearance, they are more closely related to the theropods than any other major herbivorous group. The similarities are more evident in the group's earliest members.

One particularly controversial potential relative is *Eoraptor*, 230 Mya, a small bipedal omnivore among the earliest dinosaurs. The exact placement of this dinosaur is debated—was it a basal theropod or sauropodomorph? This confusion shows just how similar the first sauropod relatives were to early theropods.

By the end of the Triassic, the early sauropodomorphs were clearly on their own evolutionary path. Studies of the teeth of *Thecodontosaurus*, an early sauropodomorph from the United Kingdom, show a transition from carnivore to herbivore, although it was still a cursorial biped.

Elsewhere in Europe the sauropodomorphs started to become larger, as evidenced by the nearly 33-ft (10-m) long *Plateosaurus*. The neck of *Plateosaurus* was longer than in most contemporary dinosaurs of the time, although still short by sauropod standards. And, as with all the Triassic sauropods, it was a biped.

FORELIMB USE

With their forelimbs free, several of the early sauropodomorphs had evolved large claws for feeding. It's been suggested that these arms would have been used to rip foliage from trees but may also have served in defense.

TREE CONFUSION

As evidenced by *Eoraptor*, the base of the sauropodomorph family tree is unclear. The problem reaches beyond this and has resulted in many examples of "wastebasket taxa." This is when many different species are accidentally lumped into one. *Plateosaurus* is one of the largest offenders here, with no agreement on which of the many assigned specimens are legitimately in the same genus. Surprisingly, the reverse can also be true, when two species that should be the same are classed as different. This has been argued for *Thecodontosaurus* and the Welsh *Pantydraco*. It stems from a lack of consensus on what the true defining characteristics of each should be.

← *Plateosaurus* is known from many specimens across Europe, making it probably the most extensively studied of all Triassic sauropods.

ON ALL FOURS

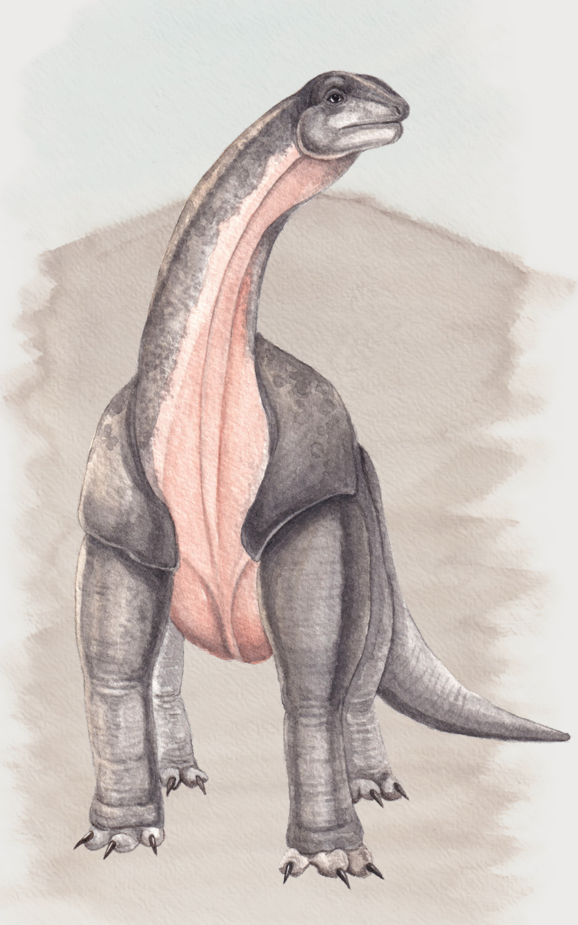
As sauropodomorphs evolved to reach larger sizes, there came a point when they could no longer balance effectively on just two legs and needed to transfer to a fully quadrupedal posture. There is, however, some debate over when exactly this transition took place. The traditional view held that the first quadrupedal sauropodomorphs evolved in the middle of the Jurassic. But more recent fossil evidence suggests an earlier evolution.

Ledumahadi, the largest known animal from South Africa, is thought to have weighed 13 US tons (11,800 kg) and walked as a full quadruped during the earliest stages of the Jurassic. Footprints from Greenland hint at an even earlier origin of quadrupedality, into the Late Triassic, although no skeletal evidence is confirmed as associated with these tracks. Some of the sauropodomorphs that came after *Ledumahadi* show bipedal stances, suggesting that the evolution of quadrupedality may have occurred multiple times in the sauropod family tree. Essentially, the group was exploring different ways of achieving massive body sizes.

↓ This trackway in Greenland appears to show a dinosaur moving quadrupedally in the Late Triassic, but the maker is a mystery.

→ Although smaller than its later relatives, it is thought that when *Ledumahadi* existed, 200 Mya, it may have been the largest animal ever to have lived.

Shortly after, other African sauropods, like *Vulcanodon*, are seen to have evolved quadrupedality with fully columnar legs.



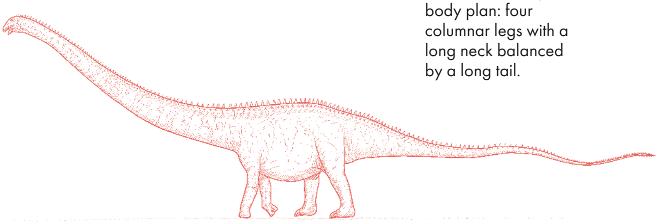
SAUROPOD MORPHOLOGY

By the Late Jurassic, the sauropods had evolved to become the largest animals ever to have walked the Earth. How they accomplished this is a marvel of biological engineering, but they largely achieved it by making themselves as light as possible.

LIGHT BODIES, LONG NECKS

Some sauropod dinosaurs weighed more than 50 US tons (45,000 kg), but this is actually lighter than they should have been. This was made possible due to huge air sacs throughout their bodies. It's estimated that internally some of these giants may have been up to 10 percent air. Having these pneumatic structures made it easier for the sauropods to move because their muscles did not have to expend as much energy for simple movements.

Classically, sauropods were reconstructed with a "swan-neck" pose, a high, curving "S" shape thought to have allowed them to reach the tops of trees. Reaching leaves that no other herbivore could was certainly part of the neck's function, but the positioning is more debated. Going for the greatest verticality required necks to be heavily muscular, as is seen in *Giraffatitan* and *Brachiosaurus*. These dinosaurs both had much larger forelimbs in comparison to their hind limbs, allowing an even greater reach.



↙ *Supersaurus* shows the classic sauropod body plan: four columnar legs with a long neck balanced by a long tail.

SKULLS AND FEEDING

Sauropod skulls were very small compared to the rest of their bodies, which is likely related to how they fed. Their peg-like teeth were not adapted for chewing food, so they did not need heavy jaw musculature.

Diplodocus-like sauropods have narrow skulls, which are relatively flattened compared to the stout skulls of the macronarian sauropods, like *Brachiosaurus*. The rounded high-tops of macronarian skulls were formed by arching nasal bones, creating a huge skull cavity (although the nostrils themselves remained at the front of the snout, as expected). This large cavity may have helped the animals communicate through sound, or been part of a modified respiratory system suitable for their size. The answer isn't definitively known.

Tooth analysis suggests that different sauropods specialized in feeding on different foliage. This niche partitioning allowed multiple species of giant herbivores to survive together in one environment.

TAIL FUNCTION

Some *Diplodocus* have been reported as having 80 caudal vertebrae, giving them exceptionally long tails. Possible functions of this tail have been suggested, beyond just their use in balancing the animal. Early theories suggested the tail may have been used as a weapon, although its very thin end couldn't have transmitted much impactful force. An exception to this may have been *Shunosaurus*, whose tail ended in a club-like collection of spiked osteoderms (essentially armored scales within and on the skin). Another theory suggests that the tails were used for visual display and may have had patterning along them.

RECONSTRUCTION MYTHS

All scientists agree that the old notion that sauropods were in some way aquatic, needing water to support their body weight and using their necks as snorkels, is false. They could support their weight on land and the pressure differences and difficulties in staying submerged would have made life underwater impossible. Another extreme theory asked whether sauropod tails could be flicked to generate a "whipcrack" sound for signaling. But any modeling of the negative effects this would have had on the soft tissue around the tail would refute that as a plausible function.

THE TITANS

During the Cretaceous, the largest dinosaurs were the perfectly named titanosaurs. Included in this group and time were the biggest terrestrial animals the planet has ever seen. Due to the patchy fossil record for certain rarely preserved parts of their bodies, paleontologists have had to rely on specimens of their embryos, still preserved within the eggs, to fill in the blanks.

ARMORED SKIN

Titanosaurs are the only sauropod group seen to have osteoderms—nodules of bone set within the skin of the dinosaur, usually located across the back. In the small (relatively) titanosaur *Saltasaurus*, some of these osteoderms could reach 4¾ in (12 cm) across. It has been assumed that these were used for defense, raising the possibility that even such leviathans were not safe from large theropods, although with so little evidence to go on, this is still uncertain and it's possible they served another unknown function.

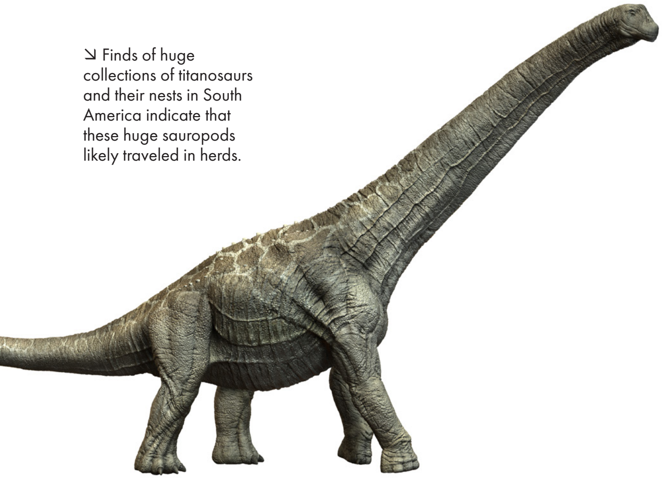
TOE LOSS

A more subtle difference can be seen in the front limbs, with later titanosaurs appearing to lack any kind of claws. It is thought that these were lost as vestigial organs (they no longer served any function). This loss was not universal across titanosaurs, however, with some species maintaining front toe claws. It's likely that there wasn't a particularly high selective pressure on this feature, and so evolution acted slowly. Trackways from Australia show the presence of front claws, whereas their counterparts in South America are lacking, hinting at different rates of evolution of this feature across the globe. All titanosaurs do, however, maintain the claws on their back feet.

WHO'S THE BIGGEST?

Whenever dinosaurs are discussed, it is inevitable that the question should be asked: Which species of dinosaur was the biggest of all? It's a surprisingly tricky question because, although it can be said with some certainty that it was a titanosaur of some kind, if you try to narrow it down any further, things get murky. Estimations of body weight are precisely that, estimations. There's plenty of room for error, as well as the human temptation to exaggerate finds to maximize media coverage. The current best estimates would place *Argentinosaurus* on top of the podium, weighing in at an impressive 83 US tons (75,300 kg). However, it's always sensible to take such statements with a pinch of salt.

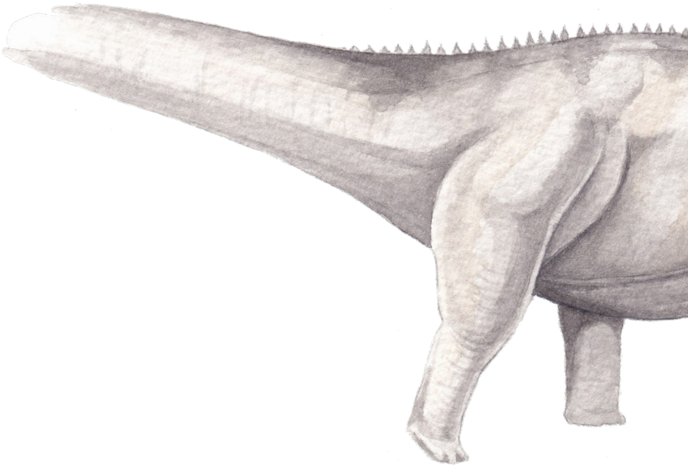
↘ Finds of huge collections of titanosaurs and their nests in South America indicate that these huge sauropods likely traveled in herds.

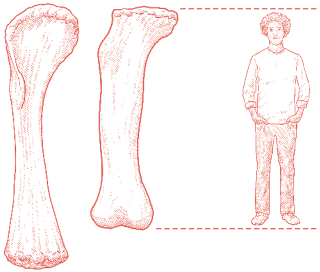


POOR PRESERVATION

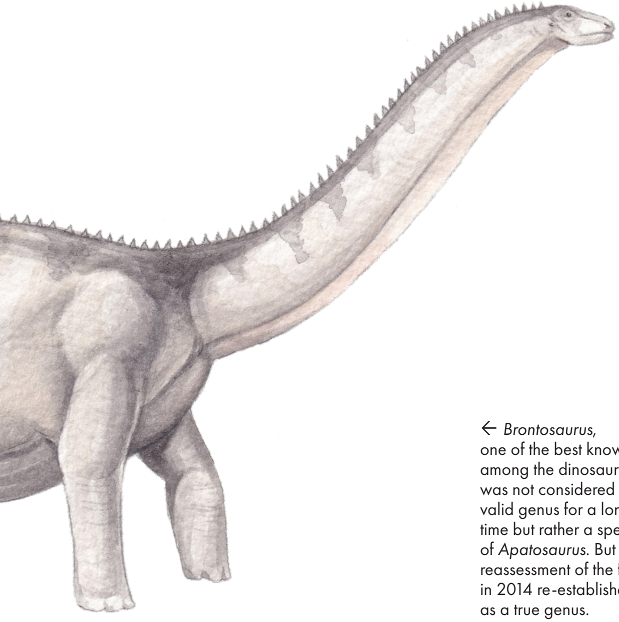
Despite some sauropods having individual bones larger than an adult human, they have a relatively bad fossil record compared to other dinosaur groups, and their size is part of the problem. This is because one of the factors determining good fossil preservation is the speed of burial of the remains. For small organisms this is relatively easy, but a huge amount of sediment displacement is required for sauropods. Instead of being quickly covered, sauropod remains were regularly left on the surface for scavengers to break apart. The air sacs that kept sauropod bones light also made them fragile when exposed and liable to be crushed and destroyed by the pressures of the fossilization process

Finally, a surprising reason for their rarity is due to us as extractors. Small fossils are easily removed for study, whereas giant sauropod bones can require heavy machinery and days of excavation for just a single specimen. In some ways, there is an unfortunate bias against their study in paleontology.





← Sauropods had some of the largest individual bones of any animal. Single limb bones, such as the femur and humerus, could be longer than the height of an adult human.



← *Brontosaurus*, one of the best known among the dinosaurs, was not considered a valid genus for a long time but rather a species of *Apatosaurus*. But a reassessment of the fossils in 2014 re-established it as a true genus.

OTHER GIANTS

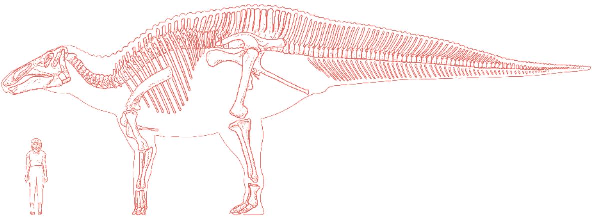
The sauropods were the largest of all dinosaurs, but they were by no means the only group to achieve such huge sizes. Gigantism is seen to have evolved repeatedly in the dinosaurs, across many of the disparate groups.

ORNITHOPODS

Other herbivores became large enough that they were comparable to the sauropods. For example, weighing an approximate 14 US tons (12,700 kg) and with a body length of 50 ft (15 m), the ornithopod *Shantungosaurus* was the largest known dinosaur outside the Sauropoda. Part of the hadrosaur family, this dinosaur was similar to the better-known *Edmontosaurus*.

Shantungosaurus was not alone among the hadrosaurs either, as other genera, like *Saurolophus* and *Magnapaulia*, reached similarly enormous sizes. Hadrosaurs have a relatively good record of fossil skin and so we know they had a scaly appearance. Feathers first evolved to provide insulation in dinosaurs, but it would seem the larger bodied dinosaurs had less use for them and may have secondarily lost them.

It is thought that hadrosaurs were able to achieve such large sizes through continuous growth, as opposed to the bursts of seasonal growth seen in most other dinosaurs. They likely lived quite long lives by dinosaur standards, much the same as large mammals are seen to have relatively long life spans today.



OTHER HERBIVORES

The largest of the horned dinosaurs may not have been *Triceratops*, but a close relative, as evidenced by the similar name: *Eotriceratops*. The skull alone of this dinosaur was almost 10 ft (3 m) in length, from the tip of the beak to the back of the frill. Likewise, *Stegosaurus* could potentially have reached 26 ft (8 m). It is unlikely that these herbivores attained the length or height of a double-decker bus (as is often suggested), but this does not detract from just how massive they were.

CARNIVORES

As we have seen, the largest known carnivorous dinosaur was the 46-ft (14-m) long *Spinosaurus*. Just among the theropods, examples of gigantism are seen to have evolved independently multiple times. This includes the tyrannosaurids and several other members of the Coelurosauria. What is especially important, however, is their stance, as these huge theropods were the largest ever known fully bipedal animals. For the most part, evolution to large sizes was likely a response to prey animals doing the same. Predators and prey are invariably linked to evolve together, and size is just one factor in the evolutionary arms race.

MESOZOIC GIGANTISM

It wasn't just the dinosaurs that achieved massive sizes during the Mesozoic Era. Other reptile groups did too. Notable among these were the ichthyosaurs, the largest of which was *Shonisaurus*—estimated to have reached up to 50 ft (15 m) in length. That's about the same as a modern Sperm Whale (*Physeter macrocephalus*), and the presence of very small teeth in its long jaws suggests it may have fulfilled a similar niche in its environment. Although the ichthyosaurs have since been "overtaken" by whales as the largest creatures in the oceans, the dinosaurs still hold the record for the largest terrestrial animals ever and azhdarchid pterosaurs the largest animals to have flown.

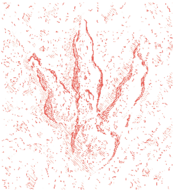
← At about the size of a double-decker bus, *Shantungosaurus* showed that sauropods weren't the only giant herbivorous dinosaurs.

SAFETY IN NUMBERS

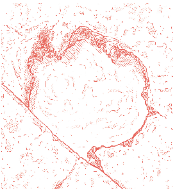
Perhaps the simplest form of defense is to go by the adage of safety in numbers. The principle is simple: If you are surrounded by many other animals, the odds of you being the one singled out by a predator are substantially reduced. As such, we see herding behavior in animals the world over today. But was the same true of dinosaurs? In short, yes. Evidence for herds of dinosaurs can be found throughout their reign. The most direct evidence comes from trackways, such as in Denali National Park, in Alaska. Here we find many matching sets of footprints, clearly from the same dinosaur species (in this case, hadrosaurs) and all moving in the same direction.

Mass assemblages of dinosaurs caught in storm surges, like the centrosaurs of the Hilda Mega-Bonebed, in Canada, suggest they may have been migrating together. From a distance, some Mesozoic scenes may have looked much like those seen on the open grasslands of today.

↓ The classic three-toed shape makes theropod footprints instantly recognizable. They strongly resemble the imprints of modern birds.



↓ Large sauropod footprints are rounder, the toe imprints showing the direction of travel. These footprints indicate that the sauropods were traveling in herds, nearly all in the same direction.



→Lacking any specialized weaponry, dinosaurs such as hadrosaurs would have relied on herding behavior for defense. Fossilized trackways and the remains of nests from this dinosaur group have been found across the world.

(continued...)

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