Tyrannosaurus

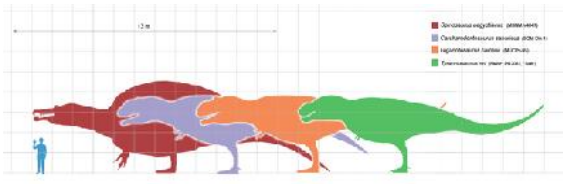
"T. rex" redirects here. For the Marc Bolan fronted rock band, see T. Rex (band). For other uses, see T. Rex (disambiguation).

Tyrannosaurus (/tɪˌrænəˈsɔːrəs/ or /taɪˌrænəˈsɔːrəs/, meaning "tyrant lizard", from the Ancient Greek *tyrannos* (τύραννος), "tyrant", and *sauros* (σαῦρος), "lizard"[1]) is a genus of coelurosaurian theropod dinosaur. The species ***Tyrannosaurus rex*** (*rex* meaning "king" in Latin), commonly abbreviated to *T. rex*, is one of the most well-represented of the large theropods. *Tyrannosaurus* lived throughout what is now western North America, on what was then an island continent known as Laramidia. *Tyrannosaurus* had a much wider range than other tyrannosaurids. Fossils are found in a variety of rock formations dating to the Maastrichtian age of the upper Cretaceous Period, 68 to 66 million years ago.[2] It was the last known member of the tyrannosaurids,[3] and among the last non-avian dinosaurs to exist before the Cretaceous–Paleogene extinction event.

Like other tyrannosaurids, *Tyrannosaurus* was a bipedal carnivore with a massive skull balanced by a long, heavy tail. Relative to its large and powerful hind limbs, *Tyrannosaurus* fore limbs were short but unusually powerful for their size and had two clawed digits. The most complete specimen measures up to 12.3 m (40 ft) in length,[4] up to 4 meters (13 ft) tall at the hips,[5] and up to 6.8 metric tons (7.5 short tons) in weight.[6] Although other theropods rivaled or exceeded *Tyrannosaurus rex* in size, it is still among the largest known land predators and is estimated to have exerted the largest bite force among all terrestrial animals.[7][8] By far the largest carnivore in its environment, *Tyrannosaurus rex* was most likely an apex predator, preying upon hadrosaurs, ceratopsians, and possibly sauropods.[9] Some experts, however, have suggested the dinosaur was primarily a scavenger. The question of whether *Tyrannosaurus* was an apex predator or a pure scavenger was among the longest ongoing debates in paleontology.[10] It is accepted now that *Tyrannosaurus rex* acted as a predator, and scavenged as modern mammalian and avian predators do.

More than 50 specimens of *Tyrannosaurus rex* have been identified, some of which are nearly complete skeletons. Soft tissue and proteins have been reported in at least one of these specimens. The abundance of fossil material has allowed significant research into many aspects of its biology, including its life history and biomechanics. The feeding habits, physiology and potential speed of *Tyrannosaurus rex* are a few subjects of debate. Its taxonomy is also controversial, as some scientists consider *Tarbosaurus bataar* from Asia to be a second *Tyrannosaurus* species while others maintain *Tarbosaurus* is a separate genus. Several other genera of North American tyrannosaurids have also been synonymized with *Tyrannosaurus*.

1 Description



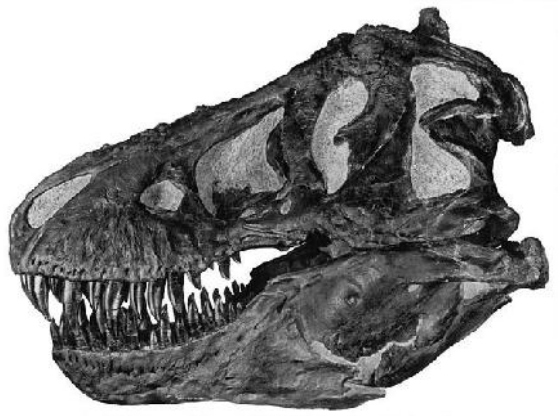
Size (in green) compared with selected giant theropods

Tyrannosaurus rex was one of the largest land carnivores of all time; the largest complete specimen, located at the Field Museum of Natural History under the name FMNH PR2081 and nicknamed Sue, measured 12.3 meters (40 ft) long,[4] and was 4 meters (13 ft) tall at the hips.[5] Mass estimates have varied widely over the years, from more than 7.2 metric tons (7.9 short tons),[11] to less than 4.5 metric tons (5.0 short tons),[12][13] with most modern estimates ranging between 5.4 metric tons (6.0 short tons) and 6.8 metric tons (7.5 short tons).[6][14][15][16] One study in 2011 found that the maximum weight of Sue, the largest *Tyrannosaurus*, was between 9.5 and 18.5 metric tons (9.3–18.2 long tons; 10.5–20.4 short tons), though the authors stated that their upper and lower estimates were based on models with wide error bars and that they "consider [them] to be too skinny, too fat, or too disproportionate".[4] Packard *et al.* (2009) tested dinosaur mass estimation procedures on elephants and concluded that those of dinosaurs are flawed and produce over-estimations; thus, the weight of *Tyrannosaurus* could have been much less than previously thought.[17] Other estimations have concluded that the largest known *Tyrannosaurus* specimens had masses approaching[18] or exceeding 9 tonnes.[4][19][20]

The neck of *Tyrannosaurus rex* formed a natural S-shaped curve like that of other theropods, but was short and muscular to support the massive head. The forelimbs had only two clawed fingers,[21] along with an additional small metacarpal representing the remnant of a

Life restoration of an adult T. rex *with feathers (a trait that can be inferred by phylogenetic bracketing)*

third digit.[22] In contrast the hind limbs were among the longest in proportion to body size of any theropod. The tail was heavy and long, sometimes containing over forty vertebrae, in order to balance the massive head and torso. To compensate for the immense bulk of the animal, many bones throughout the skeleton were hollow, reducing its weight without significant loss of strength.[21]



Profile view of a skull (AMNH 5027)

The largest known *Tyrannosaurus rex* skulls measure up to 1.5 meters (4.9 ft) in length.[23] Large fenestrae (openings) in the skull reduced weight and provided areas for muscle attachment, as in all carnivorous theropods. But in other respects *Tyrannosaurus*'s skull was significantly different from those of large non-tyrannosauroid theropods. It was extremely wide at the rear but had a narrow snout, allowing unusually good binocular vision.[24][25] The skull bones were massive and the nasals and some other bones were fused, preventing movement between them; but many were pneumatized (contained a "honeycomb" of tiny air spaces) which may have made the bones more flexible as well as lighter. These and other skull-strengthening features are part of the tyrannosaurid trend towards an increasingly powerful bite, which easily surpassed that of all non-tyrannosaurids.[7][8][26] The tip of the upper jaw was U-shaped (most non-tyrannosauroid carnivores had V-shaped upper jaws), which increased the amount of tissue and bone a tyrannosaur could rip out with one bite, although it also increased the stresses on the front teeth.[27][28]

The teeth of *Tyrannosaurus rex* displayed marked heterodonty (differences in shape).[21][29] The premaxillary teeth at the front of the upper jaw were closely packed, *D*-shaped in cross-section, had reinforcing ridges on the rear surface, were incisiform (their tips were chisel-like blades) and curved backwards. The *D*-shaped cross-section, reinforcing ridges and backwards curve reduced the risk that the teeth would snap when *Tyrannosaurus* bit and pulled. The remaining teeth were robust, like "lethal bananas" rather than daggers, more widely spaced and also had reinforcing ridges.[30] Those in the upper jaw were larger than those in all but the rear of the lower jaw. The largest found so far is estimated to have been 30 centimeters (12 in) long including the root when the animal was alive, making it the largest tooth of any carnivorous dinosaur yet found.[5]

1.1 Skin and feathers

Main article: Feathered dinosaur

While there is no direct evidence for *Tyrannosaurus rex*

Full size model in Poland, depicting Tyrannosaurus *with both feathers and scales*

having had feathers, many scientists now consider it likely that *T. rex* had feathers on at least parts of its body,[31] due to their presence in related species of similar size. Mark Norell of the American Museum of Natural History summarized the balance of evidence by stating that: "we have as much evidence that *T. rex* was feathered, at least during some stage of its life, as we do that australopithecines like Lucy had hair."[32]

The first evidence for feathers in tyrannosauroids came from the small species *Dilong paradoxus*, found in the Yixian Formation of China, and reported in the journal *Nature* in 2004. As with many other theropods discovered in the Yixian, the fossil skeleton was preserved with a coat of filamentous structures which are commonly recognized as the precursors of feathers.[33] Because all known skin impressions from larger tyrannosauroids known at the time showed evidence of scales, the researchers who studied *Dilong* speculated that feathers may correlate negatively with body size—that juveniles may have been feathered, then shed the feathers and expressed only scales as the animal became larger and no longer needed insulation to stay warm.[33] However, subsequent discoveries showed that even some gigantic tyrannosauroids had feathers covering much of their bod-

ies, casting doubt on the hypothesis that they were a size-related feature.[34]

While skin impressions from a *Tyrannosaurus rex* specimen nicknamed "Wyrex" (BHI 6230) discovered in Montana in 2002,[35] as well as some other giant tyrannosauroid specimens, show at least small patches of mosaic scales,[36] others, such as *Yutyrannus huali* (which was up to 9 meters (30 ft) long and weighed about 1,400 kilograms (3,100 lb)), preserve feathers on various sections of the body, strongly suggesting that its whole body was covered in feathers.[34] It is possible that the extent and nature of feather covering in tyrannosauroids may have changed over time in response to body size, a warmer climate, or other factors.[34]

2 Classification

Tyrannosaurus is the type genus of the superfamily Tyrannosauroidea, the family Tyrannosauridae, and the subfamily Tyrannosaurinae; in other words it is the standard by which paleontologists decide whether to include other species in the same group. Other members of the tyrannosaurine subfamily include the North American *Daspletosaurus* and the Asian *Tarbosaurus*,[37][38] both of which have occasionally been synonymized with *Tyrannosaurus*.[28] Tyrannosaurids were once commonly thought to be descendants of earlier large theropods such as megalosaurs and carnosaurs, although more recently they were reclassified with the generally smaller coelurosaurs.[27]

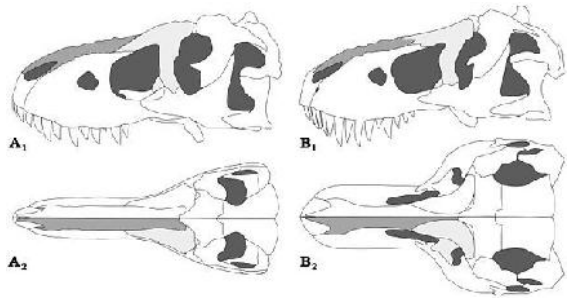


Diagram showing the differences between a generalized Tarbosaurus *(A) and* Tyrannosaurus *(B) skull*

In 1955, Soviet paleontologist Evgeny Maleev named a new species, *Tyrannosaurus bataar*, from Mongolia.[39] By 1965, this species had been renamed *Tarbosaurus bataar*.[40] Despite the renaming, many phylogenetic analyses have found *Tarbosaurus bataar* to be the sister taxon of *Tyrannosaurus rex*,[38] and it has often been considered an Asian species of *Tyrannosaurus*.[27][41][42] A recent redescription of the skull of *Tarbosaurus bataar* has shown that it was much narrower than that of *Tyrannosaurus rex* and that during a bite, the distribution of stress in the skull would have been very different, closer to that of *Alioramus*, another Asian tyrannosaur.[43] A related cladistic analysis found that *Alioramus*, not *Tyrannosaurus*, was the sister taxon of *Tarbosaurus*, which, if true, would suggest that *Tarbosaurus* and *Tyrannosaurus* should remain separate.[37]

Nanotyrannus lancensis *holotype, possibly a juvenile* Tyrannosaurus

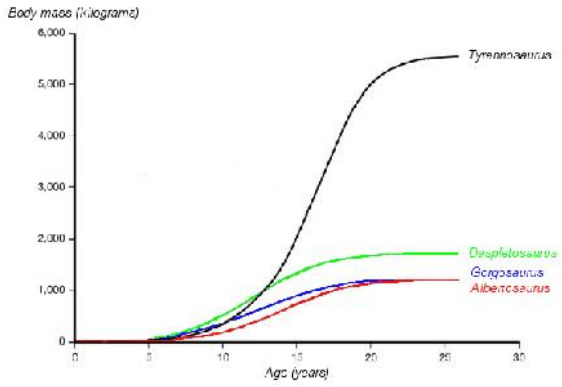
Other tyrannosaurid fossils found in the same formations as *Tyrannosaurus rex* were originally classified as separate taxa, including *Aublysodon* and *Albertosaurus megagracilis*,[28] the latter being named *Dinotyrannus megagracilis* in 1995.[44] However, these fossils are now universally considered to belong to juvenile *Tyrannosaurus rex*.[45] A small but nearly complete skull from Montana, 60 centimeters (2.0 ft) long, may be an exception. This skull was originally classified as a species of *Gorgosaurus* (*G. lancensis*) by Charles W. Gilmore in 1946,[46] but was later referred to a new genus, *Nanotyrannus*.[47] Opinions remain divided on the validity of *N. lancensis*. Many paleontologists consider the skull to belong to a juvenile *Tyrannosaurus rex*.[48] There are minor differences between the two species, including the higher number of teeth in *N. lancensis*, which lead some scientists to recommend keeping the two genera separate until further research or discoveries clarify the situation.[38][49]

Below is the cladogram of Tyrannosauridae based on the phylogenetic analysis conducted by Loewen *et al.* in 2013.[50]

3 Paleobiology

3.1 Life history

The identification of several specimens as juvenile *Tyrannosaurus rex* has allowed scientists to document ontogenetic changes in the species, estimate the lifespan, and determine how quickly the animals would have grown. The smallest known individual (LACM 28471, the "Jordan theropod") is estimated to have weighed only 30 kg (66 lb), while the largest, such as FMNH PR2081 (Sue) most likely weighed over 5,400 kg (11,900 lb). Histologic analysis of *Tyrannosaurus rex* bones showed LACM 28471 had aged only 2 years when it died, while Sue was 28 years old, an age which may have been close



A graph showing the hypothesized growth curve, body mass versus age (drawn in black, with other tyrannosaurids for comparison). Based on Erickson et al. 2004

to the maximum for the species.[6]

11-year-old juvenile (Jane) specimen, with adult in the background, Burpee Museum of Natural History

Histology has also allowed the age of other specimens to be determined. Growth curves can be developed when the ages of different specimens are plotted on a graph along with their mass. A *Tyrannosaurus rex* growth curve is S-shaped, with juveniles remaining under 1,800 kg (4,000 lb) until approximately 14 years of age, when body size began to increase dramatically. During this rapid growth phase, a young *Tyrannosaurus rex* would gain an average of 600 kg (1,300 lb) a year for the next four years. At 18 years of age, the curve plateaus again, indicating that growth slowed dramatically. For example, only 600 kg (1,300 lb) separated the 28-year-old Sue from a 22-year-old Canadian specimen (RTMP 81.12.1).[6] A 2004 histological study performed by different workers corroborates these results, finding that rapid growth began to slow at around 16 years of age.[51] Another study corroborated the latter study's results but found the growth rate to be much faster, finding it to be around 1800 kilograms (4000 lbs). Although these results were much higher than previous estimations, the authors noted that these results significantly lowered the great difference between its actual growth rate and the one which would be expected of an animal of its size.[4] The sudden change in growth rate at the end of the growth spurt may indicate physical maturity, a hypothesis which is supported by the discovery of medullary tissue in the femur of a 16 to 20-year-old *Tyrannosaurus rex* from Montana (MOR 1125, also known as B-rex). Medullary tissue is found only in female birds during ovulation, indicating that B-rex was of reproductive age.[52] Further study indicates an age of 18 for this specimen.[53] Other tyrannosaurids exhibit extremely similar growth curves, although with lower growth rates corresponding to their lower adult sizes.[54]

Over half of the known *Tyrannosaurus rex* specimens appear to have died within six years of reaching sexual maturity, a pattern which is also seen in other tyrannosaurs and in some large, long-lived birds and mammals today. These species are characterized by high infant mortality rates, followed by relatively low mortality among juveniles. Mortality increases again following sexual maturity, partly due to the stresses of reproduction. One study suggests that the rarity of juvenile *Tyrannosaurus rex* fossils is due in part to low juvenile mortality rates; the animals were not dying in large numbers at these ages, and so were not often fossilized. However, this rarity may also be due to the incompleteness of the fossil record or to the bias of fossil collectors towards larger, more spectacular specimens.[54] In a 2013 lecture, Thomas Holtz Jr. would suggest that dinosaurs "lived fast and died young" because they reproduced quickly whereas mammals have long life spans because they take longer to reproduce.[55] Gregory S. Paul also writes that *Tyrannosaurus* reproduced quickly and died young, but attributes their short life spans to the dangerous lives they lived.[56]

3.2 Sexual dimorphism

Skeleton casts mounted in a mating position, Jurassic Museum of Asturias

As the number of known specimens increased, scientists began to analyze the variation between individuals and discovered what appeared to be two distinct body types, or *morphs*, similar to some other theropod species. As one of these morphs was more solidly built, it was termed the 'robust' morph while the other was termed 'gracile'. Several morphological differences associated with the two morphs were used to analyze sexual dimorphism in *Tyrannosaurus rex*, with the 'robust' morph usually suggested to be female. For example, the pelvis of several 'robust' specimens seemed to be wider, perhaps to allow the passage of eggs.[57] It was also thought that the 'robust' morphology correlated with a reduced chevron on the first tail vertebra, also ostensibly to allow eggs to pass out of the reproductive tract, as had been erroneously reported for crocodiles.[58]

In recent years, evidence for sexual dimorphism has been weakened. A 2005 study reported that previous claims of sexual dimorphism in crocodile chevron anatomy were in error, casting doubt on the existence of similar dimorphism between *Tyrannosaurus rex* sexes.[59] A full-sized chevron was discovered on the first tail vertebra of Sue, an extremely robust individual, indicating that this feature could not be used to differentiate the two morphs anyway. As *Tyrannosaurus rex* specimens have been found from Saskatchewan to New Mexico, differences between individuals may be indicative of geographic variation rather than sexual dimorphism. The differences could also be age-related, with 'robust' individuals being older animals.[21]

Only a single *Tyrannosaurus rex* specimen has been conclusively shown to belong to a specific sex. Examination of B-rex demonstrated the preservation of soft tissue within several bones. Some of this tissue has been identified as a medullary tissue, a specialized tissue grown only in modern birds as a source of calcium for the production of eggshell during ovulation. As only female birds lay eggs, medullary tissue is only found naturally in females, although males are capable of producing it when injected with female reproductive hormones like estrogen. This strongly suggests that B-rex was female, and that she died during ovulation.[52] Recent research has shown that medullary tissue is never found in crocodiles, which are thought to be the closest living relatives of dinosaurs, aside from birds. The shared presence of medullary tissue in birds and theropod dinosaurs is further evidence of the close evolutionary relationship between the two.[60]

3.3 Posture

Modern representations in museums, art, and film show *Tyrannosaurus rex* with its body approximately parallel to the ground and tail extended behind the body to balance the head.[28]

Like many bipedal dinosaurs, *Tyrannosaurus rex* was historically depicted as a 'living tripod', with the body at 45 degrees or less from the vertical and the tail dragging along the ground, similar to a kangaroo. This concept dates from Joseph Leidy's 1865 reconstruction of *Hadrosaurus*, the first to depict a dinosaur in a bipedal posture.[61] In 1915, convinced that the creature stood upright, Henry Fairfield Osborn, former president of the American Museum of Natural History, further reinforced the notion in unveiling the first complete *Tyrannosaurus rex* skeleton arranged this way. It stood in an upright pose for 77 years, until it was dismantled in 1992.[62]

Outdated reconstruction (by Charles R. Knight), showing upright pose

By 1970, scientists realized this pose was incorrect and could not have been maintained by a living animal, as it would have resulted in the dislocation or weakening of several joints, including the hips and the articulation between the head and the spinal column.[63] The inaccurate AMNH mount inspired similar depictions in many films and paintings (such as Rudolph Zallinger's famous mural *The Age of Reptiles* in Yale University's Peabody Museum of Natural History)[64] until the 1990s, when films such as *Jurassic Park* introduced a more accurate posture to the general public.[65]

3.4 Arms

The forelimbs might have been used to help T. rex *rise from a resting pose, as seen in this cast (Bucky specimen)*