WIKIPEDIA

Tyrannosaurus

Tyrannosaurus[nb 1] is a genus of large theropod dinosaur. The species ***Tyrannosaurus rex*** (*rex* meaning "king" in Latin), often called ***T. rex*** or colloquially ***T-Rex***, is one of the best represented 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. It was the last known member of the tyrannosaurids 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, the forelimbs of *Tyrannosaurus* were short but unusually powerful for their size, and they had two clawed digits. The most complete specimen measures up to 12.3–12.4 m (40.4–40.7 ft) in length, though *T. rex* could grow to lengths of over 12.4 m (40.7 ft), up to 3.66–3.96 m (12–13 ft) tall at the hips, and according to most modern estimates 8.4 metric tons (9.3 short tons) to 14 metric tons (15.4 short tons) in weight. 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 strongest bite force among all terrestrial animals. By far the largest carnivore in its environment, *Tyrannosaurus rex* was most likely an apex predator, preying upon hadrosaurs, juvenile armored herbivores like ceratopsians and ankylosaurs, and possibly sauropods. Some experts 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 debates in paleontology. Most paleontologists today accept that *Tyrannosaurus* was both an active predator and a scavenger.

Specimens of *Tyrannosaurus rex* include some that 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

Tyrannosaurus

Temporal range: Late Cretaceous (Maastrichtian),

Reconstruction of the *T. rex* type specimen (CM 9380) at the Carnegie Museum of Natural History

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Clade:	Dinosauria
Clade:	Saurischia
Clade:	Theropoda
Family:	†Tyrannosauridae
Subfamily:	†Tyrannosaurinae
Genus:	†*Tyrannosaurus* Osborn, 1905

Type species

†***Tyrannosaurus rex***

Osborn, 1905

Other species

See text

Synonyms

Genus synonymy

others maintain *Tarbosaurus* is a separate genus. Several other genera of North American tyrannosaurids have also been synonymized with *Tyrannosaurus*.

As the archetypal theropod, *Tyrannosaurus* has been one of the best-known dinosaurs since the early 20th century and has been featured in film, advertising, postal stamps, and many other media.

Contents

- *Dinotyrannus*
  Olshevsky & Ford, 1995
- *Dynamosaurus*
  Osborn, 1905
- *Manospondylus*
  Cope, 1892
- *Nanotyrannus*
  Bakker, Williams & Currie, 1988
- *Stygivenator*
  Olshevsky, 1995
- *Tarbosaurus*?
  Maleev, 1955

Species synonymy

- *Aublysodon amplus*?
  Marsh, 1892
- *Deinodon amplus*?
  (Marsh, 1892)
- *Manospondylus amplus*?
  (Marsh, 1892)
- *Stygivenator amplus*?
  (Marsh, 1892)
- *Tyrannosaurus amplus*?
  (Marsh, 1892)
- *Aublysodon cristatus*?
  Marsh, 1892
- *Deinodon cristatus*?
  (Marsh, 1892)
- *Stygivenator cristatus*?
  (Marsh, 1892)
- *Manospondylus gigas*
  Cope, 1892
- *Ornithomimus grandis*
  (Marsh, 1897)
- *Dynamosaurus imperiosus*
  Osborn, 1905
- *Tyrannosaurus imperiosus*
  (Osborn, 1905)

- *Albertosaurus lancensis* (Gilmore, 1946)
- *Aublysodon lancensis* (Gilmore, 1946)
- *Deinodon lancensis* (Gilmore, 1946)
- *Gorgosaurus lancensis* Gilmore, 1946
- *Nanotyrannus lancensis* (Gilmore, 1946)
- *Dinotyrannus megagracilis* Olshevsky & Ford, 1995
- *Stygivenator molnari* (Paul, 1988)

History of research

Earliest finds

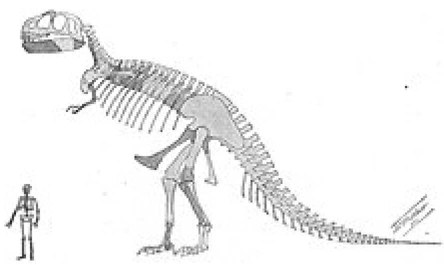
Type specimen (AMNH 3982) of *Manospondylus gigas*

Teeth from what is now documented as a *Tyrannosaurus rex* were found in 1874 by Arthur Lakes near Golden, Colorado. In the early 1890s, John Bell Hatcher collected postcranial elements in eastern Wyoming. The fossils were believed to be from the large species *Ornithomimus grandis* (now *Deinodon*) but are now considered *T. rex* remains.[2]

In 1892, Edward Drinker Cope found two vertebral fragments of a large dinosaur. Cope believed the fragments belonged to an "agathaumid" (ceratopsid) dinosaur, and named them *Manospondylus gigas*, meaning "giant porous vertebra", in reference to the numerous openings for blood vessels he found in the bone.[2] The *M. gigas* remains were, in 1907, identified by Hatcher as those of a theropod rather than a ceratopsid.[3]

Henry Fairfield Osborn recognized the similarity between *Manospondylus gigas* and *T. rex* as early as 1917, by which time the second vertebra had been lost. Owing to the fragmentary nature of the *Manospondylus* vertebrae, Osborn did not synonymize the two genera, instead considering the older genus indeterminate.[4] In June 2000, the Black Hills Institute found around 10% of a *Tyrannosaurus* skeleton (BHI 6248) at a site that might have been the original *M. gigas* locality.[5]

Skeleton discovery and naming



Skeletal restoration by William D. Matthew from 1905, published alongside Osborn's description paper

Barnum Brown, assistant curator of the American Museum of Natural History, found the first partial skeleton of *T. rex* in eastern Wyoming in 1900. Brown found another partial skeleton in the Hell Creek Formation in Montana in 1902, comprising approximately 34 fossilized bones.[6] Writing at the time Brown said "Quarry No. 1 contains the femur, pubes, humerus, three vertebrae and two undetermined bones of a large Carnivorous Dinosaur not described by Marsh.... I have never seen anything like it from the Cretaceous".[7] Henry Fairfield Osborn, president of the American Museum of Natural History, named the second skeleton *T. rex* in 1905. The generic name is derived from the Greek words *τύραννος* (*tyrannos*, meaning "tyrant") and *σαῦρος* (*sauros*, meaning "lizard"). Osborn used the Latin word *rex*, meaning "king", for the specific name. The full binomial therefore translates to "tyrant lizard the king" or "King Tyrant Lizard", emphasizing the animal's size and perceived dominance over other species of the time.[6]

Dynamosaurus imperiosus holotype, Natural History Museum

Osborn named the other specimen *Dynamosaurus imperiosus* in a paper in 1905.[6] In 1906, Osborn recognized that the two skeletons were from the same species and selected *Tyrannosaurus* as the preferred name.[8] The original *Dynamosaurus* material resides in the collections of the Natural History Museum, London.[9] In 1941, the *T. rex* type specimen was sold to the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania, for $7,000.[7] *Dynamosaurus* would later be honored by the 2018 description of another species of tyrannosaurid by Andrew McDonald and colleagues, *Dynamoterror dynastes*, whose name was chosen in reference to the 1905 name, as it had been a "childhood favorite" of McDonald's.[10]

From the 1910s through the end of the 1950s, Barnum's discoveries remained the only specimens of *Tyrannosaurus*, as the Great Depression and wars kept many paleontologists out of the field.[5]

Resurgent interest

Specimen "Sue", Field Museum of Natural History, Chicago

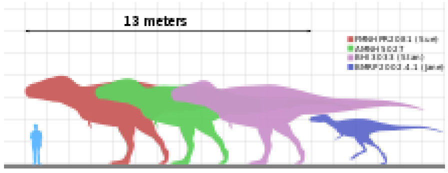
Beginning in the 1960s, there was renewed interest in *Tyrannosaurus*, resulting in the recovery of 42 skeletons (5–80% complete by bone count) from Western North America.[5] In 1967, Dr. William MacMannis located and recovered the skeleton named "MOR 008", which is 15% complete by bone count and has a reconstructed skull displayed at the Museum of the Rockies. The 1990s saw numerous discoveries, with nearly twice as many finds as in all previous years, including two of the most complete skeletons found to date: Sue and Stan.[5]

Sue Hendrickson, an amateur paleontologist, discovered the most complete (approximately 85%) and largest *Tyrannosaurus* skeleton in the Hell Creek Formation on August 12, 1990. The specimen Sue, named after the discoverer, was the object of a legal battle over its ownership. In 1997, the litigation was settled in favor of Maurice Williams, the original land owner. The fossil collection was purchased by the Field Museum of Natural History at auction for $7.6 million, making it the most expensive dinosaur skeleton until the sale of Stan for $31.8 million in 2020.[11] From 1998 to 1999, Field Museum of Natural History staff spent over 25,000 hours taking the rock off the bones.[12] The bones were then shipped to New Jersey where the mount was constructed, then shipped back to Chicago for the final assembly. The mounted skeleton opened to the public on May 17, 2000, in the Field Museum of Natural History. A study of this specimen's fossilized bones showed that Sue reached full size at age 19 and died at the age of 28, the longest estimated life of any tyrannosaur known.[13]

Another *Tyrannosaurus*, nicknamed Stan (BHI 3033), in honor of amateur paleontologist Stan Sacrison, was recovered from the Hell Creek Formation in 1992. Stan is the second most complete skeleton found, with 199 bones recovered representing 70% of the total.[14] This tyrannosaur also had many bone pathologies, including broken and healed ribs, a broken (and healed) neck, and a substantial hole in the back of its head, about the size of a *Tyrannosaurus* tooth.[15]

"Scotty", the largest known specimen, exhibited in Japan

In 1998, Bucky Derflinger noticed a *T. rex* toe exposed above ground, making Derflinger, who was 20 years old at the time, the youngest person to discover a *Tyrannosaurus*. The specimen, dubbed Bucky in honor of its discoverer, was a young adult, 3.0 metres (10 ft) tall and 11 metres (35 ft) long. Bucky is the first *Tyrannosaurus* to be found that preserved a furcula (wishbone). Bucky is permanently displayed at The Children's Museum of Indianapolis.[16]



The specimens "Sue", AMNH 5027, "Stan", and "Jane", to scale with a human.

In the summer of 2000, crews organized by Jack Horner discovered five *Tyrannosaurus* skeletons near the Fort Peck Reservoir.[17] In 2001, a 50% complete skeleton of a juvenile *Tyrannosaurus* was discovered in the Hell Creek Formation by a crew from the Burpee Museum of Natural History. Dubbed Jane (BMRP 2002.4.1), the find was thought to be the first known skeleton of a pygmy tyrannosaurid, *Nanotyrannus*, but subsequent research revealed that it is more likely a juvenile *Tyrannosaurus*, and the most complete juvenile example known;[18] Jane is exhibited at the Burpee Museum of Natural History.[19] In 2002, a skeleton named Wyrex, discovered by amateur collectors Dan Wells and Don Wyrick, had 114 bones and was 38% complete. The dig was concluded over 3 weeks in 2004 by the Black Hills Institute with the first live online *Tyrannosaurus* excavation providing daily reports, photos, and video.[5]

In 2006, Montana State University revealed that it possessed the largest *Tyrannosaurus* skull yet discovered (from a specimen named MOR 008), measuring 5 feet (152 cm) long.[20] Subsequent comparisons indicated that the longest head was 136.5 centimetres (53.7 in) (from specimen LACM 23844) and the widest head was 90.2 centimetres (35.5 in) (from Sue).[21]

Footprints

Probable footprint from New Mexico

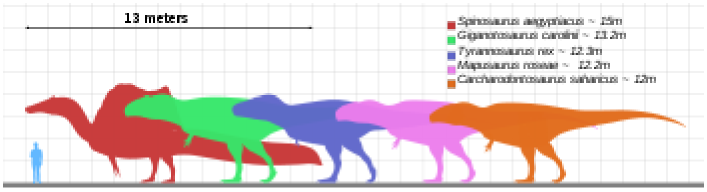
Two isolated fossilized footprints have been tentatively assigned to *T. rex*. The first was discovered at Philmont Scout Ranch, New Mexico, in 1983 by American geologist Charles Pillmore. Originally thought to belong to a hadrosaurid, examination of the footprint revealed a large 'heel' unknown in ornithopod dinosaur tracks, and traces of what may have been a hallux, the dewclaw-like fourth digit of the tyrannosaur foot. The footprint was published as the ichnogenus *Tyrannosauripus pillmorei* in 1994, by Martin Lockley and Adrian Hunt. Lockley and Hunt suggested that it was very likely the track was made by a *T. rex*, which would make it the first known footprint from this species. The track was made in what was once a vegetated wetland mudflat. It measures 83 centimeters (33 in) long by 71 centimeters (28 in) wide.[22]

A second footprint that may have been made by a *Tyrannosaurus* was first reported in 2007 by British paleontologist Phil Manning, from the Hell Creek Formation of Montana. This second track measures 72 centimeters (28 in) long, shorter than the track described by Lockley and Hunt. Whether or not the track was made by *Tyrannosaurus* is unclear, though *Tyrannosaurus* is the only large theropod known to have existed in the Hell Creek Formation.[23][24]

A set of footprints in Glenrock, Wyoming dating to the Maastrichtian stage of the Late Cretaceous and hailing from the Lance Formation were described by Scott Persons, Phil Currie and colleagues in 2016, and are believed to belong to either a juvenile *T. rex* or the dubious tyrannosaurid *Nanotyrannus lancensis*. From measurements and based on the positions of the footprints, the animal was believed to be traveling at a walking speed of around 2.8 to 5 miles per hour and was estimated to have a hip height of 1.56 m (5.1 ft) to 2.06 m (6.8 ft).[25][26][27] A follow-up paper appeared in 2017, increasing the speed estimations by 50–80%.[28]

Description

Size

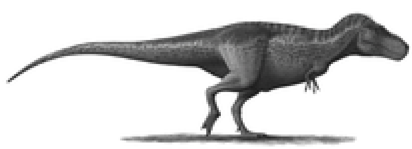


Size (in blue) compared with selected giant theropods and a human

T. rex was one of the largest land carnivores of all time. One of the largest and the most complete specimens, nicknamed Sue (FMNH PR2081), is located at the Field Museum of Natural History. Sue measured 12.3–12.4 m (40.4–40.7 ft) long,[29][30] was 3.66–3.96 meters (12–13 ft) tall at the hips,[31][32][33] and according to the most recent studies, using a variety of techniques, estimated to have weighed between 8.4 metric tons (9.3 short tons) to 14 metric tons (15.4 short tons).[29][34][35] A specimen nicknamed Scotty (RSM P2523.8), located at the Royal Saskatchewan Museum, is reported to measure 13 m (43 ft) in length. Using a mass estimation technique that extrapolates from the circumference of the femur, Scotty was estimated as the largest known specimen at 8.8 metric tons (9.7 short tons) in weight.[36][37]

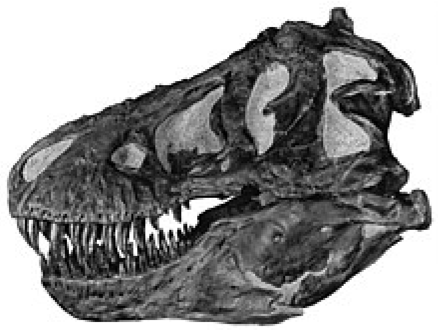
Not every adult *Tyrannosaurus* specimen recovered is as big. Historically average adult mass estimates have varied widely over the years, from as low as 4.5 metric tons (5.0 short tons),[38][39] to more than 7.2 metric tons (7.9 short tons),[40] with most modern estimates ranging between 5.4 metric tons (6.0 short tons) and 8.0 metric tons (8.8 short tons).[29][41][42][43][44]

Skeleton


Restoration showing scaly skin with sparse feathering, and lipped jaws

The largest known *T. rex* skulls measure up to 1.52 meters (5 ft) in length.[20][31] Large fenestrae (openings) in the skull reduced weight, as in all carnivorous theropods. In other respects *Tyrannosaurus*'s skull was significantly different from those of large non-tyrannosaurid theropods. It was extremely wide at the rear but had a narrow snout, allowing unusually good binocular vision.[45][46] 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) and thus 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.[47][48][49] 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.[50]

The teeth of *T. rex* displayed marked heterodonty (differences in shape).[51][52] The premaxillary teeth, four per side 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.[53] Those in the upper jaw, twelve per side in mature individuals,[51] were larger than their counterparts of the lower jaw, except at the rear. The largest found so far is estimated to have been 30.5 centimeters (12 in) long including the root when the animal was alive, making it the largest tooth of any carnivorous dinosaur yet found.[54] The lower jaw was robust. Its front dentary bone bore thirteen teeth. Behind the tooth row, the lower jaw became notably taller.[51] The upper and lower jaws of *Tyrannosaurus*, like those of many dinosaurs, possessed numerous foramina, or small holes in the bone. Various functions have been proposed for these foramina, such as a crocodile-like sensory system[55] or evidence of extra-oral structures such as scales or potentially lips.[56][57][58]



Profile view of a skull (AMNH 5027)

The vertebral column of *Tyrannosaurus* consisted of ten neck vertebrae, thirteen back vertebrae and five sacral vertebrae. The number of tail vertebrae is unknown and could well have varied between individuals but probably numbered at least forty. Sue was mounted with forty-seven of such caudal vertebrae.[51] The neck of *T. rex* formed a natural S-shaped curve like that of other theropods. Compared to these, it was exceptionally short, deep and muscular to support the massive head. The second vertebra, the axis, was especially short. The remaining neck vertebrae were weakly opisthocoelous, i.e. with a convex front of the vertebral body and a concave rear. The vertebral bodies had single pleurocoels, pneumatic depressions created by air sacs, on their sides.[51] The vertebral bodies of the torso were robust but with a narrow waist. Their undersides were keeled. The front sides were concave with a deep vertical trough. They had large pleurocoels. Their neural spines had very rough front and rear sides for the attachment of strong tendons. The sacral vertebrae were fused to each other, both in their vertebral bodies and neural spines. They were pneumatized. They were connected to the pelvis by transverse processes and sacral ribs. The tail was heavy and moderately long, in order to balance the massive head and torso and to provide space for massive locomotor muscles that attached to the thighbones. The thirteenth tail vertebra formed the transition point between the deep tail base and the middle tail that was stiffened by a rather long front articulation processes. The underside of the trunk was covered by eighteen or nineteen pairs of segmented belly ribs.[51]

The shoulder girdle was longer than the entire forelimb. The shoulder blade had a narrow shaft but was exceptionally expanded at its upper end. It connected via a long forward protrusion to the coracoid, which was rounded. Both shoulder blades were connected by a small furcula. The paired breast bones possibly were made of cartilage only.[51]

Furcula of specimen "Sue"

The forelimb or arm was very short. The upper arm bone, the humerus, was short but robust. It had a narrow upper end with an exceptionally rounded head. The lower arm bones, the ulna and radius, were straight elements, much shorter than the humerus. The second metacarpal was longer and wider than the first, whereas normally in theropods the opposite is true. The forelimbs had only two clawed fingers,[51] along with an additional splint-like small third metacarpal representing the remnant of a third digit.[59]


Right forelimb of *Tyrannosaurus*

The pelvis was a large structure. Its upper bone, the ilium, was both very long and high, providing an extensive attachment area for hindlimb muscles. The front pubic bone ended in an enormous pubic boot, longer than the entire shaft of the element. The rear ischium was slender and straight, pointing obliquely to behind and below.[51]

In contrast to the arms, the hindlimbs were among the longest in proportion to body size of any theropod. In the foot, the metatarsus was "arctometatarsalian", meaning that the part of the third metatarsal near the ankle was pinched. The third metatarsal was also exceptionally sinuous.[51] Compensating for the immense bulk of the animal, many bones throughout the skeleton were hollowed, reducing its weight without significant loss of strength.[51]

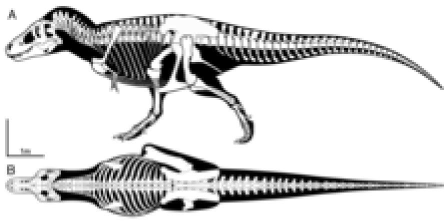
Classification


Skull casts of different *Tyrannosaurus* specimens

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*,[18][60] both of which have occasionally been synonymized with *Tyrannosaurus*.[61] 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.[50]

Many phylogenetic analyses have found *Tarbosaurus bataar* to be the sister taxon of *T. rex*.[60] The discovery of the tyrannosaurid *Lythronax* further indicates that *Tarbosaurus* and *Tyrannosaurus* are closely related, forming a clade with fellow Asian tyrannosaurid *Zhuchengtyrannus*, with *Lythronax* being their sister taxon.[62][63] A further study from 2016 by Steve Brusatte, Thomas Carr and colleagues, also indicates that *Tyrannosaurus* may have been an immigrant from Asia, as well as a possible descendant of *Tarbosaurus*.[64]

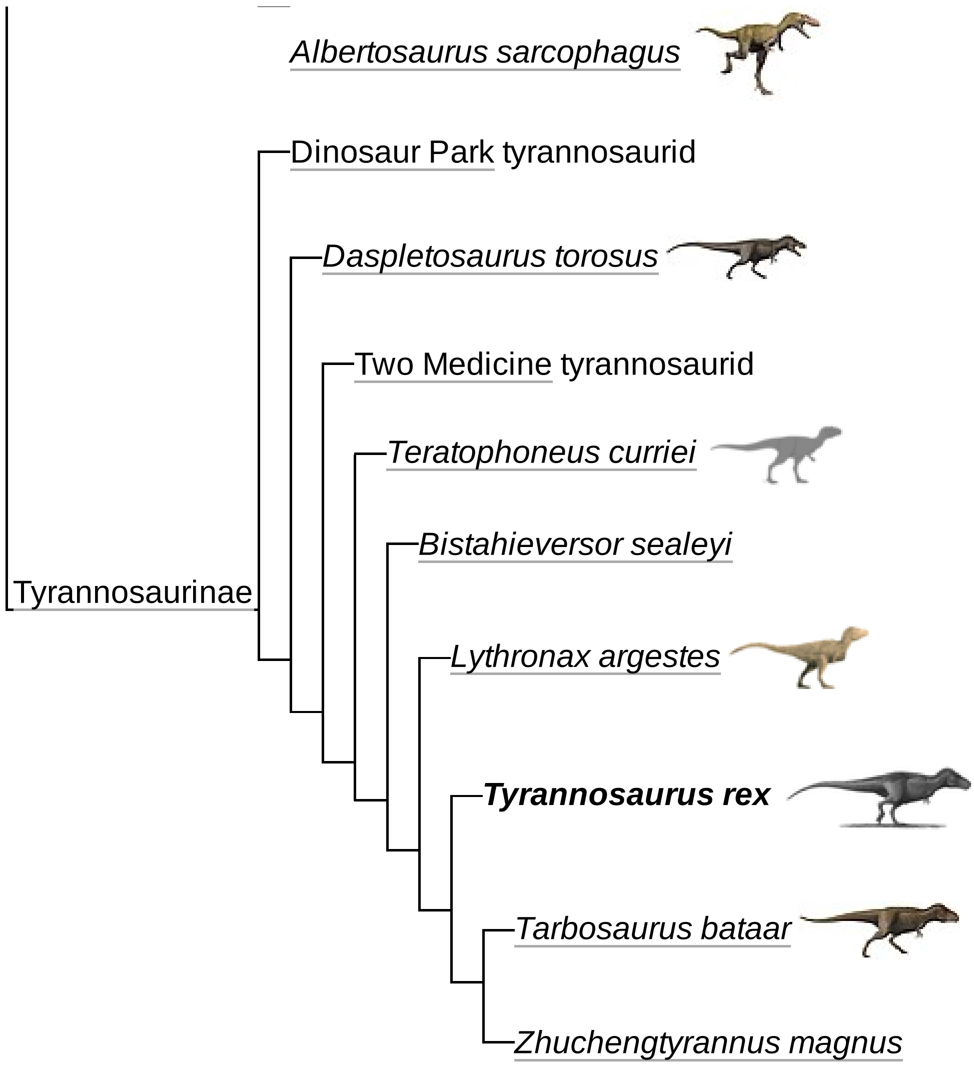
Below is the cladogram of Tyrannosauridae based on the phylogenetic analysis conducted by Loewen and colleagues in 2013.[62]



Skeletal reconstruction of "Sue"

Tyrannosauridae Albertosaurinae

Gorgosaurus libratus 



Additional species

In 1955, Soviet paleontologist Evgeny Maleev named a new species, *Tyrannosaurus bataar*, from Mongolia.[65] By 1965, this species was renamed as a distinct genus, *Tarbosaurus bataar*.[66] While most palaeontologists continue to maintain the two as distinct genera, some authors such as Thomas Holtz, Kenneth Carpenter, and Thomas Carr argue that the two species are similar enough to be considered members of the same genus, with the Mongolian taxon having the resulting binomial of *Tyrannosaurus bataar*.[50][67][55]

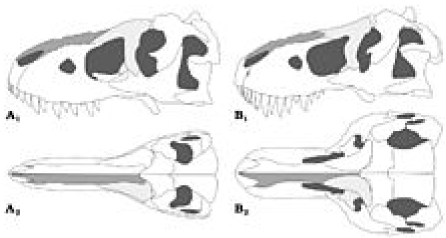


Diagram showing the differences between a generalized *Tarbosaurus* (A) and *Tyrannosaurus* (B) skull

In 2001, various tyrannosaurid teeth and a metatarsal unearthed in a quarry near Zhucheng, China were assigned by Chinese paleontologist Hu Chengzhi to the newly erected species *Tyrannosaurus zhuchengensis*. However, in a nearby site, a right maxilla and left jawbone were assigned to the newly erected tyrannosaurid genus *Zhuchengtyrannus* in 2011. It is possible that *T. zhuchengensis* is synonymous with *Zhuchengtyrannus*. In any case, *T. zhuchengensis* is considered to be a *nomen dubium* as the holotype lacks diagnostic features below the level Tyrannosaurinae.[68]

In a 2022 study, Gregory S. Paul and colleagues argued that *Tyrannosaurus rex*, as traditionally understood, actually represents three species: the type species *Tyrannosaurus rex*, and two new species: *T. imperator* (meaning "tyrant lizard emperor") and *T. regina* (meaning "tyrant lizard queen"). The holotype of the former (*T. imperator*) is the Sue specimen, and the holotype of the latter (*T. regina*) is Wankel rex. The division into multiple species was primarily based on the observation of a very high degree of variation in the proportions and robusticity of the femur across catalogued *T. rex* specimens, more so than that observed in other theropods recognized as one species. Differences of general body proportions representing robust and gracile morphotypes was also used as a line of evidence, in addition to the number of small, slender incisiform teeth in the dentary, as based on tooth sockets. Specifically, the paper's *T. rex* was distinguished by robust anatomy, a moderate ratio of femur length vs circumference, and the possession of a singular slender incisiform dentary tooth; *T. imperator* was considered to be robust with a small femur length to circumference ratio and two of the slender teeth; and *T. regina* was a gracile form with a high femur ratio and one of the slender teeth. It was observed that variation in proportions and robustness became more extreme higher up in the sample, stratigraphically. This was interpreted as a single earlier population, *T. imperator*, speciating into more than one taxon, *T. rex* and *T. regina*.[69]

However, several other leading paleontologists, including Stephen Brusatte, Thomas Carr, Thomas Holtz, David Hone, Jingmai O'Connor, and Lindsay Zanno, criticized the study or expressed skepticism of its conclusions when approached by various media outlets for comment.[70][71][72] Holtz and Zanno both remarked that it was plausible that more than one species of *Tyrannosaurus* existed, but felt the new study was insufficient to support the species it proposed. Holtz remarked that, even if *Tyrannosaurus imperator* represented a distinct species from *Tyrannosaurus rex*, it may represent the same species as *Nanotyrannus lancensis* and would need to be called *Tyrannosaurus lancensis*. O'Connor, a curator at the Field Museum, where the *T. imperator* holotype Sue is displayed, regarded the new species as too poorly-supported to justify modifying the exhibit signs. Brusatte, Carr, and O'Connor viewed the distinguishing features proposed between the species as reflecting natural variation within a species. Both Carr and O'Connor expressed concerns about the study's inability to determine which of the proposed species several well-preserved specimens belonged to. Another paleontologist, Philip J. Currie, originally co-authored the study but withdrew from it as he did not want to be involved in naming the new species.[70]

Nanotyrannus

Former holotype of *Nanotyrannus lancensis*, now interpreted as a juvenile *Tyrannosaurus*

Other tyrannosaurid fossils found in the same formations as *T. rex* were originally classified as separate taxa, including *Aublysodon* and *Albertosaurus megagracilis*,[61] the latter being named *Dinotyrannus megagracilis* in 1995.[73] These fossils are now universally considered to belong to juvenile *T. rex*.[74] A small but nearly complete skull from Montana, 60 centimeters (2.0 ft) long, might be an exception. This skull, CMNH 7541, was originally classified as a species of *Gorgosaurus* (*G. lancensis*) by Charles W. Gilmore in 1946.[75] In 1988, the specimen was re-described by Robert T. Bakker, Phil Currie, and Michael Williams, then the curator of paleontology at the Cleveland Museum of Natural History, where the original specimen was housed and is now on display. Their initial research indicated that the skull bones were fused, and that it therefore represented an adult specimen. In light of this, Bakker and colleagues assigned the skull to a new genus named *Nanotyrannus* (meaning "dwarf tyrant", for its apparently small adult size). The specimen is estimated to have been around 5.2 meters (17 ft) long when it died.[76] However, In 1999, a detailed analysis by Thomas Carr revealed the specimen to be a juvenile, leading Carr and many other paleontologists to consider it a juvenile *T. rex* individual.[77][78]

In 2001, a more complete juvenile tyrannosaur (nicknamed "Jane", catalog number BMRP 2002.4.1), belonging to the same species as the original *Nanotyrannus* specimen, was uncovered. This discovery prompted a conference on tyrannosaurs focused on the issues of *Nanotyrannus* validity at the Burpee Museum of Natural History in 2005. Several paleontologists who had previously published opinions that *N.*

Reconstructed skeleton of "Jane", Burpee Museum of Natural History

lancensis was a valid species, including Currie and Williams, saw the discovery of "Jane" as a confirmation that *Nanotyrannus* was, in fact, a juvenile *T. rex*.[79][80][81] Peter Larson continued to support the hypothesis that *N. lancensis* was a separate but closely related species, based on skull features such as two more teeth in both jaws than *T. rex*; as well as proportionately larger hands with phalanges on the third metacarpal and different wishbone anatomy in an undescribed specimen. He also argued that *Stygivenator*, generally considered to be a juvenile *T. rex*, may be a younger *Nanotyrannus* specimen.[82][83] Later research revealed that other tyrannosaurids such as *Gorgosaurus* also experienced reduction in tooth count during growth,[77] and given the disparity in tooth count between individuals of the same age group in this genus and *Tyrannosaurus*, this feature may also be due to individual variation.[78] In 2013, Carr noted that all of the differences claimed to support *Nanotyrannus* have turned out to be individually or ontogenetically variable features or products of distortion of the bones.[84]

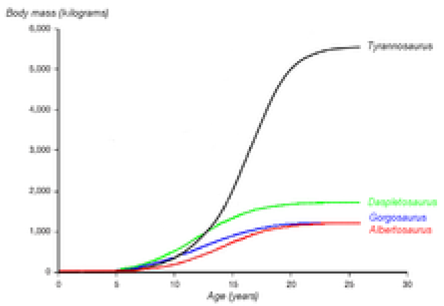
Adult *T. rex* skeleton (the specimen AMNH 5027) at American Museum of Natural History.

In 2016, analysis of limb proportions by Persons and Currie suggested *Nanotyrannus* specimens to have differing cursoriality levels, potentially separating it from *T. rex*.[85] However, paleontologist Manabu Sakomoto has commented that this conclusion may be impacted by low sample size, and the discrepancy does not necessarily reflect taxonomic distinction.[86] In 2016, Joshua Schmerge argued for *Nanotyrannus*' validity based on skull features, including a dentary groove in BMRP 2002.4.1's skull. According to Schmerge, as that feature is absent in *T. rex* and found only in *Dryptosaurus* and albertosaurines, this suggests *Nanotyrannus* is a distinct taxon within the Albertosaurinae.[87] The same year, Carr and colleagues noted that this was not sufficient enough to clarify *Nanotyrannus*' validity or classification, being a common and ontogenetically variable feature among tyrannosauroids.[88]

A 2020 study by Holly Woodward and colleagues showed the specimens referred to *Nanotyrannus* were all ontogenetically immature and found it probable that these specimens belonged to *T. rex*.[89] The same year, Carr published a paper on *T. rex*'s growth history, finding that CMNH 7541 fit within the expected ontogenetic variation of the taxon and displayed juvenile characteristics found in other specimens. It was classified as a juvenile, under 13 years old with a skull less than 80 cm (31 in). No significant sexual or phylogenetic variation was discernible among any of the 44 specimens studied, with Carr stating that characters of potential phylogenetic importance decrease throughout age at the same rate as growth occurs.[90] Discussing the paper's results, Carr described how all "*Nanotyrannus*" specimens formed a continual growth transition between the smallest juveniles and the subadults, unlike what would be expected if it were a distinct taxon where the specimens would group to the exclusion of *Tyrannosaurus*. Carr concluded that "the 'nanomorphs' are not all that similar to each other and instead form an important bridge in the growth series of *T. rex* that captures the beginnings of the profound change from the shallow skull of juveniles to the deep skull that is seen in fully-developed adults."[91]

Paleobiology

Life history



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

The identification of several specimens as juvenile *T. 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 about 5,650 kg (12,460 lb). Histologic analysis of *T. 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 to the maximum for the species.[41]

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 *T. 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 *T. 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).[41] A 2004 histological study performed by different workers corroborates these results, finding that rapid growth began to slow at around 16 years of age.[92]

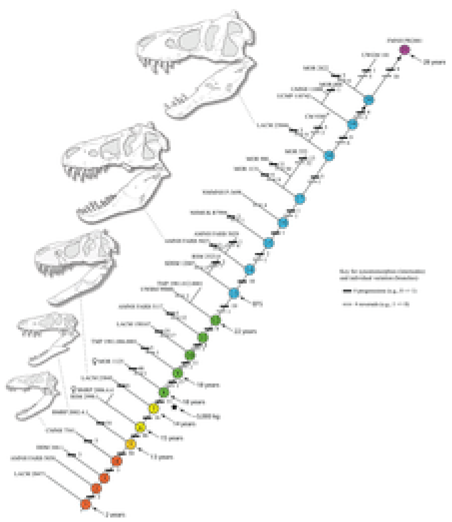


Diagram showing growth stages

A study by Hutchinson and colleagues in 2011 corroborated the previous estimation methods in general, but their estimation of peak growth rates is significantly higher; it found that the "maximum growth rates for T. rex during the exponential stage are 1790 kg/year".[29] 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.[29] 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 *T. 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.[93] Further study indicates an age of 18 for this specimen.[94] In 2016, it was finally confirmed by Mary Higby Schweitzer and Lindsay Zanno and colleagues that the soft tissue within the femur of MOR 1125 was medullary tissue. This also confirmed the identity of the specimen as a female. The discovery of medullary bone tissue within *Tyrannosaurus* may prove valuable in determining the sex of other dinosaur species in future examinations, as the chemical makeup of medullary tissue is unmistakable.[95] Other tyrannosaurids exhibit extremely similar growth curves, although with lower growth rates corresponding to their lower adult sizes.[96]

An additional study published in 2020 by Woodward and colleagues, for the journal *Science Advances* indicates that during their growth from juvenile to adult, *Tyrannosaurus* was capable of slowing down its growth to counter environmental factors such as lack of food. The study, focusing on two juvenile specimens between 13 and 15 years old housed at the Burpee Museum in Illinois, indicates that the rate of maturation for *Tyrannosaurus* was dependent on resource abundance. This study also indicates that in such changing environments, *Tyrannosaurus* was particularly well-suited to an environment that shifted yearly in regards to resource abundance, hinting that other midsize predators might have had difficulty surviving in such harsh conditions and explaining the niche partitioning between juvenile and adult tyrannosaurs. The study further indicates that *Tyrannosaurus* and the dubious genus *Nanotyrannus* are synonymous, due to analysis of the growth rings in the bones of the two specimens studied.[97][98]

Over half of the known *T. 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 *T. rex* fossils is due in part to low juvenile mortality rates; the animals were not dying in large numbers at these ages, and thus were not often fossilized. 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.[96] In a 2013 lecture, Thomas Holtz Jr. suggested that dinosaurs "lived fast and died young" because they reproduced quickly whereas mammals have long life spans because they take longer to reproduce.[99] Gregory S. Paul also writes that *Tyrannosaurus* reproduced quickly and died young, but attributes their short life spans to the dangerous lives they lived.[100]

Skin and possible filamentous feathering

Fossilized skin impressions from the tail region of a *Tyrannosaurus*, Houston Museum of Natural Science

The discovery of feathered dinosaurs led to debate regarding whether, and to what extent, *Tyrannosaurus* might have been feathered.[101][102] Filamentous structures, which are commonly recognized as the precursors of feathers, have been reported in the small-bodied, basal tyrannosauroid *Dilong paradoxus* from the Early Cretaceous Yixian Formation of China in 2004.[103] Because integumentary impressions of larger tyrannosauroids known at that time showed evidence of scales, the researchers who studied *Dilong* speculated that insulating feathers might have been lost by larger species due to their smaller surface-to-volume ratio.[103] The subsequent discovery of the giant species *Yutyrannus huali*, also from the Yixian, showed that even some large tyrannosauroids had feathers covering much of their bodies, casting doubt on the hypothesis that they were a size-related feature.[104] A 2017 study reviewed known skin impressions of tyrannosaurids, including those of a *Tyrannosaurus* specimen nicknamed "Wyrex" (BHI 6230) which preserves patches of mosaic scales on the tail, hip, and neck.[5] The study concluded that feather covering of large tyrannosaurids such as *Tyrannosaurus* was, if present, limited to the upper side of the trunk.[101]

A conference abstract published in 2016 posited that theropods such as *Tyrannosaurus* had their upper teeth covered in lips, instead of bare teeth as seen in crocodilians. This was based on the presence of enamel, which according to the study needs to remain hydrated, an issue not faced by aquatic animals like crocodilians.[57] A 2017 analytical study proposed that tyrannosaurids had large, flat scales on their snouts instead of lips.[55][105] However, there has been criticism where it favors the idea for lips. Crocodiles do not really have flat scales but rather cracked keratinized skin; by observing the hummocky rugosity of tyrannosaurids, and comparing it to extant lizards they found that tyrannosaurids had squamose scales rather than a crocodillian-like skin.[106][107]

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 *T. 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.[108] 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.[109]

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 *T. rex* sexes.[110] 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 *T. 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.[51]

Only a single *T. 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.[93] 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.[111]

Posture

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

Like many bipedal dinosaurs, *T. 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.[112] 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 *T. rex* skeleton arranged this way. It stood in an upright pose for 77 years, until it was dismantled in 1992.[113]

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.[114] 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)[115] until the 1990s, when films such as *Jurassic Park* introduced a more accurate posture to the general public.[116] Modern representations in museums, art, and film show *T. rex* with its body approximately parallel to the ground with the tail extended behind the body to balance the head.[117]

To sit down, *Tyrannosaurus* may have settled its weight backwards and rested its weight on a pubic boot, the wide expansion at the end of the pubis in some dinosaurs. With its weight rested on the pelvis, it may have been free to move the hindlimbs. Getting back up again might have involved some stabilization from the diminutive forelimbs.[118][114] The latter known as Newman's pushup theory has been debated. Nonetheless, *Tyrannosaurus* was probably able to get up if it fell, which only would have required placing the limbs below the center of gravity, with the tail as an effective counterbalance.[119]

Arms

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

When *T. rex* was first discovered, the humerus was the only element of the forelimb known.[6] For the initial mounted skeleton as seen by the public in 1915, Osborn substituted longer, three-fingered forelimbs like those of *Allosaurus*.[4] A year earlier, Lawrence Lambe described the short, two-fingered forelimbs of the closely related *Gorgosaurus*.[120] This strongly suggested that *T. rex* had similar forelimbs, but this hypothesis was not confirmed until the first complete *T. rex* forelimbs were identified in 1989, belonging to MOR 555 (the "Wankel rex").[121][122] The remains of Sue also include complete forelimbs.[51] *T. rex* arms are very small relative to overall body size, measuring only 1 meter (3.3 ft) long, and some scholars have labelled them as vestigial. The bones show large areas for muscle attachment, indicating considerable strength. This was recognized as early as 1906 by Osborn, who speculated that the forelimbs may have been used to grasp a mate during copulation.[8] It has also been suggested that the forelimbs were used to assist the animal in rising from a prone position.[114]

Another possibility is that the forelimbs held struggling prey while it was killed by the tyrannosaur's enormous jaws. This hypothesis may be supported by biomechanical analysis. *T. rex* forelimb bones exhibit extremely thick cortical bone, which has been interpreted as evidence that they were developed to withstand heavy loads. The biceps brachii muscle of an adult *T. rex* was capable of lifting 199 kilograms (439 lb) by itself; other muscles such as the brachialis would work along with the biceps to make elbow flexion even more powerful. The M. biceps muscle of *T. rex* was 3.5 times as powerful as the human equivalent. A *T. rex* forearm had a limited range of motion, with the shoulder and elbow joints allowing only 40 and 45 degrees of motion, respectively. In contrast, the same two joints in *Deinonychus* allow up to 88 and 130 degrees of motion, respectively, while a human arm can rotate 360 degrees at the shoulder and move through 165 degrees at the elbow. The heavy build of the arm bones, strength of the muscles, and limited range of motion may indicate a system evolved to hold fast despite the stresses of a struggling prey animal. In the first detailed scientific description of *Tyrannosaurus* forelimbs, paleontologists Kenneth Carpenter and Matt Smith dismissed notions that the forelimbs were useless or that *T. rex* was an obligate scavenger.[123]

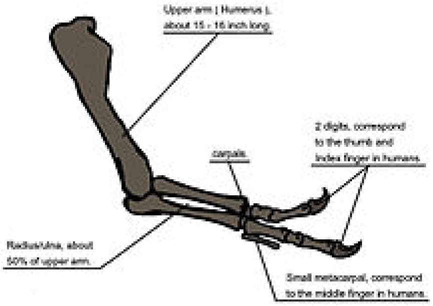


Diagram illustrating arm anatomy

According to paleontologist Steven M. Stanley, the 1 metre (3.3 ft) arms of *T. rex* were used for slashing prey, especially by using its claws to rapidly inflict long, deep gashes to its prey, although this concept is disputed by others believing the arms were used for grasping a sexual partner.[124] Padian (2022) argued that the reduction of the arms in tyrannosaurids did not serve a particular function but was a secondary adaptation; stating that as tyrannosaurid skulls and jaws developed to become larger and more powerful, the arms got smaller to avoid being bitten or torn by other individuals, particularly during group feedings.[125]

Thermoregulation


Restoration showing partial feathering

As of 2014, it is not clear if *Tyrannosaurus* was endothermic ("warm-blooded"). *Tyrannosaurus*, like most dinosaurs, was long thought to have an ectothermic ("cold-blooded") reptilian metabolism. The idea of dinosaur ectothermy was challenged by scientists like Robert T. Bakker and John Ostrom in the early years of the "Dinosaur Renaissance", beginning in the late 1960s.[126][127] *T. rex* itself was claimed to have been endothermic ("warm-blooded"), implying a very active lifestyle.[39] Since then, several paleontologists have sought to determine the ability of *Tyrannosaurus* to regulate its body temperature. Histological evidence of high growth rates in young *T. rex*, comparable to those of mammals and birds, may support the hypothesis of a high metabolism. Growth curves indicate that, as in mammals and birds, *T. rex* growth was limited mostly to immature animals, rather than the indeterminate growth seen in most other vertebrates.[92]

Oxygen isotope ratios in fossilized bone are sometimes used to determine the temperature at which the bone was deposited, as the ratio between certain isotopes correlates with temperature. In one specimen, the isotope ratios in bones from different parts of the body indicated a temperature difference of no more than 4 to 5 °C (7 to 9 °F) between the vertebrae of the torso and the tibia of the lower leg. This small temperature range between the body core and the extremities was claimed by paleontologist Reese Barrick and geochemist William Showers to indicate that *T. rex* maintained a constant internal body temperature (homeothermy) and that it enjoyed a metabolism somewhere between ectothermic reptiles and endothermic mammals.[128] Other scientists have pointed out that the ratio of oxygen isotopes in the fossils today does not necessarily represent the same ratio in the distant past, and may have been altered during or after fossilization (diagenesis).[129] Barrick and Showers have defended their conclusions in subsequent papers, finding similar results in another theropod dinosaur from a different continent and tens of millions of years earlier in time (*Giganotosaurus*).[130] Ornithischian dinosaurs also showed evidence of homeothermy, while varanid lizards from the same formation did not.[131] Even if *T. rex* does exhibit evidence of homeothermy, it does not necessarily mean that it was endothermic. Such thermoregulation may also be explained by gigantothermy, as in some living sea turtles.[132][133][134] Similar to contemporary alligators, dorsotemporal fenestra in Tyrannosaurus's skull may have aided thermoregulation.[135]

Soft tissue

In the March 2005 issue of *Science*, Mary Higby Schweitzer of North Carolina State University and colleagues announced the recovery of soft tissue from the marrow cavity of a fossilized leg bone from a *T. rex*. The bone had been intentionally, though reluctantly, broken for shipping and then not preserved in the normal manner, specifically because Schweitzer was hoping to test it for soft tissue.[136] Designated as the Museum of the Rockies specimen 1125, or MOR 1125, the dinosaur was previously excavated from the Hell Creek Formation. Flexible, bifurcating blood vessels and fibrous but elastic bone matrix tissue were recognized. In addition, microstructures resembling blood cells were found inside the matrix and vessels. The structures bear resemblance to ostrich blood cells and vessels. Whether an unknown process, distinct from normal fossilization, preserved the material, or the material is original, the researchers do not know, and they are careful not to make any claims about preservation.[137] If it is found to be original material, any surviving proteins may be used as a means of indirectly guessing some of the DNA content of the dinosaurs involved, because each protein is typically created by a specific gene. The absence of previous finds may be the result of people assuming preserved tissue was impossible, therefore not looking. Since the first, two more tyrannosaurs and a hadrosaur have also been found to have such tissue-like structures.[136] Research on some of the tissues involved has suggested that birds are closer relatives to tyrannosaurs than other modern animals.[138]

T. rex femur (MOR 1125) from which demineralized matrix and peptides (insets) were obtained

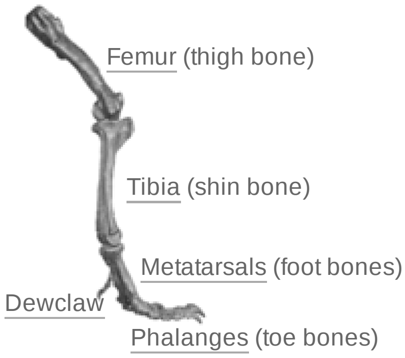
In studies reported in *Science* in April 2007, Asara and colleagues concluded that seven traces of collagen proteins detected in purified *T. rex* bone most closely match those reported in chickens, followed by frogs and newts. The discovery of proteins from a creature tens of millions of years old, along with similar traces the team found in a mastodon bone at least 160,000 years old, upends the conventional view of fossils and may shift paleontologists' focus from bone hunting to biochemistry. Until these finds, most scientists presumed that fossilization replaced all living tissue with inert minerals. Paleontologist Hans Larsson of McGill University in Montreal, who was not part of the studies, called the finds "a milestone", and suggested that dinosaurs could "enter the field of molecular biology and really slingshot paleontology into the modern world".[139]

The presumed soft tissue was called into question by Thomas Kaye of the University of Washington and his co-authors in 2008. They contend that what was really inside the tyrannosaur bone was slimy biofilm created by bacteria that coated the voids once occupied by blood vessels and cells.[140] The researchers found that what previously had been identified as remnants of blood cells, because of the presence of iron, were actually framboids, microscopic mineral spheres bearing iron. They found similar spheres in a variety of other fossils from various periods, including an ammonite. In the ammonite, they found the spheres in a place where the iron they contain could not have had any relationship to the presence of blood.[141] Schweitzer has strongly criticized Kaye's claims and argues that there is no reported evidence that biofilms can produce branching, hollow tubes like those noted in her study.[142] San Antonio, Schweitzer and colleagues published an analysis in 2011 of what parts of the collagen had been recovered, finding that it was the inner parts of the collagen coil that had been preserved, as would have been expected from a long period of protein degradation.[143] Other research challenges the identification of soft tissue as biofilm and confirms finding "branching, vessel-like structures" from within fossilized bone.[144]

Speed

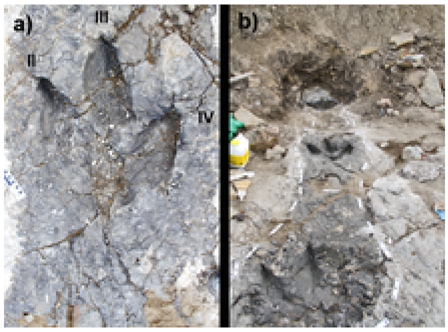
Scientists have produced a wide range of possible maximum running speeds for *Tyrannosaurus*: mostly around 9 meters per second (32 km/h; 20 mph), but as low as 4.5–6.8 meters per second (16–24 km/h; 10–15 mph) and as high as 20 meters per second (72 km/h; 45 mph), though it running this speed is very unlikely. *Tyrannosaurus* was a bulky and heavy carnivore so it is unlikely to run very fast at all compared to other theropods like *Carnotaurus* or *Giganotosaurus*.[145] Researchers have relied on various estimating techniques because, while there are many tracks of large theropods walking, none showed evidence of running.[146]

A 2002 report used a mathematical model (validated by applying it to three living animals: alligators, chickens, and humans; and eight more species, including emus and ostriches[146]) to gauge the leg muscle mass needed for fast running (over 40 km/h or 25 mph).[145] Scientists who think that *Tyrannosaurus* was able to run point out that hollow bones and other features that would have lightened its body may have kept



Skeletal anatomy of a *T. rex* right leg

adult weight to a mere 4.5 metric tons (5.0 short tons) or so, or that other animals like ostriches and horses with long, flexible legs are able to achieve high speeds through slower but longer strides.[146] Proposed top speeds exceeded 40 kilometers per hour (25 mph) for *Tyrannosaurus*, but were deemed infeasible because they would require exceptional leg muscles of approximately 40–86% of total body mass. Even moderately fast speeds would have required large leg muscles. If the muscle mass was less, only 18 kilometers per hour (11 mph) for walking or jogging would have been possible.[145] Holtz noted that tyrannosaurids and some closely related groups had significantly longer distal hindlimb components (shin plus foot plus toes) relative to the femur length than most other theropods, and that tyrannosaurids and their close relatives had a tightly interlocked metatarsus (foot bones).[147] The third metatarsal was squeezed between the second and fourth metatarsals to form a single unit called an arctometatarsus. This ankle feature may have helped the animal to run more efficiently.[148] Together, these leg features allowed *Tyrannosaurus* to transmit locomotory forces from the foot to the lower leg more effectively than in earlier theropods.[147]



Only known tyrannosaurid trackway (*Bellatoripes fredlundi*), from the Wapiti Formation, British Columbia

Additionally, a 2020 study indicates that *Tyrannosaurus* and other tyrannosaurids were exceptionally efficient walkers. Studies by Dececchi *et al.*, compared the leg proportions, body mass, and the gaits of more than 70 species of theropod dinosaurs including *Tyrannosaurus* and its relatives. The research team then applied a variety of methods to estimate each dinosaur's top speed when running as well as how much energy each dinosaur expended while moving at more relaxed speeds such as when walking. Among smaller to medium-sized species such as dromaeosaurids, longer legs appear to be an adaptation for faster running, in line with previous results by other researchers. But for theropods weighing over 1,000 kg (2,200 lb), top running speed is limited by body size, so longer legs instead were found to have correlated with low-energy walking. The results further indicate that smaller theropods evolved long legs as a means to both aid in hunting and escape from larger predators while larger theropods that evolved long legs did so to reduce the energy costs and increase foraging efficiency, as they were freed from the demands of predation pressure due to their role as apex predators. Compared to more basal groups of theropods in the study, tyrannosaurs like *Tyrannosaurus* itself showed a marked increase in foraging efficiency due to reduced energy expenditures during hunting or scavenging. This in turn likely resulted in tyrannosaurs having a reduced need for hunting forays and requiring less food to sustain themselves as a result. Additionally, the research, in conjunction with studies that show tyrannosaurs were more agile than other large-bodied theropods, indicates they were quite well-adapted to a long-distance stalking approach followed by a quick burst of speed to go for the kill. Analogies can be noted between tyrannosaurids and modern wolves as a result, supported by evidence that at least some tyrannosaurids were hunting in group settings.[149][150]

A study published in 2021 by Pasha van Bijlert *et al.*, calculated the preferred walking speed of *Tyrannosaurus*, reporting a speed of 1.28 meters per second (4.6 km/h; 2.9 mph). While walking, animals reduce their energy expenditure by choosing certain step rhythms at which their body parts resonate. The same would have been true for dinosaurs, but previous studies did not fully account for the impact the tail had on their walking speeds. According to the authors, when a dinosaur walked, its tail would slightly sway up and down with each step as a result of the interspinous ligaments suspending the tail. Like rubber bands, these ligaments stored energy when they are stretched due to the swaying of the tail. Using a 3-D model of *Tyrannosaurus* specimen Trix, muscles and ligaments were reconstructed to simulate the tail movements. This results in a rhythmic, energy-efficient walking speed for *Tyrannosaurus* similar to that seen in living animals such as humans, ostriches and giraffes.[151]

A 2017 study estimated the top running speed of *Tyrannosaurus* as 17 mph (27 km/h), speculating that *Tyrannosaurus* exhausted its energy reserves long before reaching top speed, resulting in a parabola-like relationship between size and speed.[152][153] Another 2017 study hypothesized that an adult *Tyrannosaurus* was incapable of running due to high skeletal loads. Using a calculated weight estimate of 7 tons, the model showed that speeds above 11 mph (18 km/h) would have probably shattered the leg bones of *Tyrannosaurus*. The finding may mean that running was also not possible for other giant theropod dinosaurs like *Giganotosaurus*, *Mapusaurus* and *Acrocanthosaurus*.[154] However, studies by Eric Snively and colleagues, published in 2019 indicate that *Tyrannosaurus* and other tyrannosaurids were more maneuverable than allosauroids and other theropods of comparable size due to low rotational inertia compared to their body mass combined with large leg muscles. As a result, it is hypothesized that *Tyrannosaurus* was capable of making relatively quick turns and could likely pivot its body more quickly when close to its prey, or that while turning, the theropod could "pirouette" on a single planted foot while the alternating leg was held out in a suspended swing during a pursuit. The results of this study potentially could shed light on how agility could have contributed to the success of tyrannosaurid evolution.[155]

Possible footprints

Depiction of *Tyrannosaurus* rising from the ground, based on fossil tracks described in 2021.

Rare fossil footprints and trackways found in New Mexico and Wyoming that are assigned to the ichnogenus *Tyrannosauripus* have been attributed to being made by *Tyrannosaurus*, based on the stratigraphic age of the rocks they are preserved in. The first specimen, found in 1994 was described by Lockley and Hunt and consists of a single, large footprint. Another pair of ichnofossils, described in 2021, show a large tyrannosaurid rising from a prone position by rising up using its elbows in conjunction with the pads on their feet to stand. These two unique sets of fossils were found in Ludlow, Colorado and Cimarron, New Mexico.[156] Another ichnofossil described in 2018, perhaps belonging to a juvenile *Tyrannosaurus* or the dubious genus *Nanotyrannus* was uncovered in the Lance Formation of Wyoming. The trackway itself offers a rare glimpse into the walking speed of tyrannosaurids, and the trackmaker is estimated to have been moving at a speed of 4.5–8.0 kilometers per hour (2.8–5.0 mph), significantly faster than previously assumed for estimations of walking speed in tyrannosaurids.[157][158]

Brain and senses

A study conducted by Lawrence Witmer and Ryan Ridgely of Ohio University found that *Tyrannosaurus* shared the heightened sensory abilities of other coelurosaurs, highlighting relatively rapid and coordinated eye and head movements; an enhanced ability to sense low frequency sounds, which would allow tyrannosaurs to track prey movements from long distances; and an enhanced sense of smell.[159] A study published by Kent Stevens concluded that *Tyrannosaurus* had keen vision. By applying modified perimetry to facial reconstructions of several dinosaurs including *Tyrannosaurus*, the study found that *Tyrannosaurus* had a binocular range of 55 degrees, surpassing that of modern hawks. Stevens estimated that *Tyrannosaurus* had 13 times the visual acuity of a human and surpassed the visual acuity of an eagle, which is 3.6 times that of a person. Stevens estimated a limiting far point (that is, the distance at which an object can be seen as separate from the horizon) as far as 6 km (3.7 mi) away, which is greater than the 1.6 km (1 mi) that a human can see.[45][46][160]

The eye-sockets faced mainly forwards, giving it good binocular vision (Sue specimen).

Thomas Holtz Jr. would note that high depth perception of *Tyrannosaurus* may have been due to the prey it had to hunt, noting that it had to hunt horned dinosaurs such as *Triceratops*, armored dinosaurs such as *Ankylosaurus*, and the duck-billed dinosaurs and their possibly complex social behaviors. He would suggest that this made precision more crucial for *Tyrannosaurus* enabling it to, "get in, get that blow in and take it down." In contrast, *Acrocanthosaurus* had limited depth perception because they hunted large sauropods, which were relatively rare during the time of *Tyrannosaurus*.[99]

Tyrannosaurus had very large olfactory bulbs and olfactory nerves relative to their brain size, the organs responsible for a heightened sense of smell. This suggests that the sense of smell was highly developed, and implies that tyrannosaurs could detect carcasses by scent alone across great distances. The sense of smell in tyrannosaurs may have been comparable to modern vultures, which use scent to track carcasses for scavenging. Research on the olfactory bulbs has shown that *T. rex* had the most highly developed sense of smell of 21 sampled non-avian dinosaur species.[161]

Cast of the braincase at the Australian Museum, Sydney.

Somewhat unusually among theropods, *T. rex* had a very long cochlea. The length of the cochlea is often related to hearing acuity, or at least the importance of hearing in behavior, implying that hearing was a particularly important sense to tyrannosaurs. Specifically, data suggests that *T. rex* heard best in the low-frequency range, and that low-frequency sounds were an important part of tyrannosaur behavior.[159] A 2017 study by Thomas Carr and colleagues found that the snout of tyrannosaurids was highly sensitive, based on a high number of small openings in the facial bones of the related *Daspletosaurus* that contained sensory neurons. The study speculated that tyrannosaurs might have used their sensitive snouts to measure the temperature of their nests and to gently pick up eggs and hatchlings, as seen in modern crocodylians.[55] Another study published in 2021 further suggests that *Tyrannosaurus* had an acute sense of touch, based on neurovascular canals in the front of its jaws, which it could utilize to better detect and consume prey. The study, published by Kawabe and Hittori *et al.*, suggests that *Tyrannosaurus* could also accurately sense slight differences in material and movement, allowing it to utilize different feeding strategies on different parts of its prey's carcasses depending on the situation. The sensitive neurovascular canals of *Tyrannosaurus* also likely were adapted to performing fine movements and behaviors such as nest building, parental care, and other social behavior such as intraspecific communication. The results of this study also align with results made in studying the related tyrannosaurid *Daspletosaurus horneri* and the allosauroid *Neovenator*, which have similar neurovascular adaptations, suggesting that the faces of theropods were highly sensitive to pressure and touch.[162][163] However, a more recent study reviewing the evolution of the trigeminal canals among sauropsids notes that a much denser network of neurovascular canals in the snout and lower jaw is more commonly encountered in aquatic or semiaquatic taxa (e.g., *Spinosaurus*, *Halszkaraptor*, *Plesiosaurus*), and taxa that developed a rhamphotheca (e.g., *Caenagnathasia*), while the network of canals in *Tyrannosaurus* appears simpler, though still more derived than in most ornithischians, and overall terrestrial taxa such as tyrannosaurids and *Neovenator* may have had average facial sensitivity for non-edentulous terrestrial theropods, although further research is needed. The neurovascular canals in *Tyrannosaurus* may instead have supported soft tissue structures for thermoregulation or social signaling, the latter of which could be confirmed by the fact that the neurovascular network of canals may have changed during ontogeny.[164]

A study by Grant R. Hurlburt, Ryan C. Ridgely and Lawrence Witmer obtained estimates for Encephalization Quotients (EQs), based on reptiles and birds, as well as estimates for the ratio of cerebrum to brain mass. The study concluded that *Tyrannosaurus* had the relatively largest brain of all adult non-avian dinosaurs with the exception of certain small maniraptoriforms (*Bambiraptor*, *Troodon* and *Ornithomimus*). The study found that *Tyrannosaurus*'s relative brain size was still within the range of modern reptiles, being at most 2 standard deviations above the mean of non-avian reptile EQs. The estimates for the ratio of cerebrum mass to brain mass would range from 47.5 to 49.53 percent. According to the study, this is more than the lowest estimates for extant birds (44.6 percent), but still close to the typical ratios of the smallest sexually mature alligators which range from 45.9–47.9 percent.[165] Other studies, such as those by Steve Brusatte, indicate the encephalization quotient of *Tyrannosaurus* was similar in range (2.0–2.4) to a chimpanzee (2.2–2.5), though this may be debatable as reptilian and mammalian encephalization quotients are not equivalent.[166]

Social behavior

Mounted skeletons of different age groups (skeleton in lower left based on the juvenile formerly named *Stygivenator*), Natural History Museum of Los Angeles County

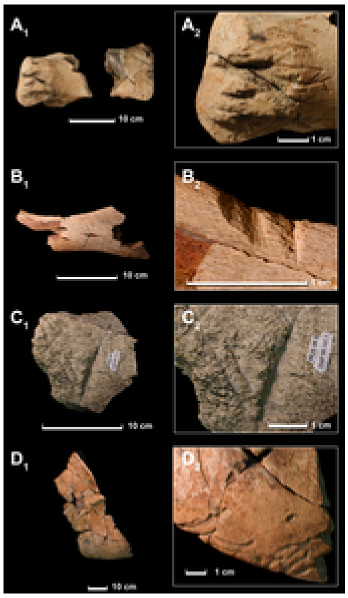
Philip J. Currie suggested that Tyrannosaurus may have been pack hunters, comparing *T. rex* to related species *Tarbosaurus bataar* and *Albertosaurus sarcophagus*, citing fossil evidence that may indicate gregarious (describing animals that travel in herds or packs) behavior.[167] A find in South Dakota where three *T. rex* skeletons were in close proximity may suggest the formation of a pack.[168][169] Cooperative pack hunting may have been an effective strategy for subduing prey with advanced anti-predator adaptations which pose potential lethality such as *Triceratops* and *Ankylosaurus*.[167]

Currie's pack-hunting *T. rex* hypothesis has been criticized for not having been peer-reviewed, but rather was discussed in a television interview and book called *Dino Gangs*.[170] The Currie theory for pack hunting by *T. rex* is based mainly by analogy to a different species, *Tarbosaurus bataar*. Evidence of gregariousness in *T. bataar* itself has not been peer-reviewed, and to Currie's own admission, can only be interpreted with reference to evidence in other closely related species. According to Currie gregariousness in *Albertosaurus sarcophagus* is supported by the discovery of 26 individuals with varied ages in the Dry Island bonebed. He ruled out the possibility of a predator trap due to the similar preservation state of individuals and the near absence of herbivores.[170][171]

Additional support of Tyrannosaurid gregariousness can be found in fossilized trackways from the Upper Cretaceous Wapiti Formation of northeastern British Columbia, Canada, left by three tyrannosaurids traveling in the same direction.[172][173] According to scientists assessing the Dino Gangs program, the evidence for pack hunting in *Tarbosaurus* and *Albertosaurus* is weak and based on group skeletal remains for which alternate explanations may apply (such as drought or a flood forcing dinosaurs to die together in one place).[170] Others researchers have speculated that instead of large theropod social groups, some of these finds represent behavior more akin to Komodo dragon-like mobbing of carcasses, even going as far as to say true pack-hunting behavior may not exist in any non-avian dinosaurs due to its rarity in modern predators.[174]

Evidence of intraspecific attack was found by Joseph Peterson and his colleagues in the juvenile *Tyrannosaurus* nicknamed Jane. Peterson and his team found that Jane's skull showed healed puncture wounds on the upper jaw and snout which they believe came from another juvenile *Tyrannosaurus*. Subsequent CT scans of Jane's skull would further confirm the team's hypothesis, showing that the puncture wounds came from a traumatic injury and that there was subsequent healing.[175] The team would also state that Jane's injuries were structurally different from the parasite-induced lesions found in Sue and that Jane's injuries were on her face whereas the parasite that infected Sue caused lesions to the lower jaw.[176]

Feeding strategies



Tyrannosaurus tooth marks on bones of various herbivorous dinosaurs

Most paleontologists accept that *Tyrannosaurus* was both an active predator and a scavenger like most large carnivores.[177] By far the largest carnivore in its environment, *T. rex* was most likely an apex predator, preying upon hadrosaurs, armored herbivores like ceratopsians and ankylosaurs, and possibly sauropods.[178] A study in 2012 by Karl Bates and Peter Falkingham found that *Tyrannosaurus* had the most powerful bite of any terrestrial animal that has ever lived, finding an adult *Tyrannosaurus* could have exerted 35,000 to 57,000 N (7,868 to 12,814 lbf) of force in the back teeth.[179][180][181] Even higher estimates were made by Mason B. Meers in 2003.[48] This allowed it to crush bones during repetitive biting and fully consume the carcasses of large dinosaurs.[21] Stephan Lautenschlager and colleagues calculated that *Tyrannosaurus* was capable of a maximum jaw gape of around 80 degrees, a necessary adaptation for a wide range of jaw angles to power the creature's strong bite.[182][183]

A debate exists, however, about whether *Tyrannosaurus* was primarily a predator or a pure scavenger. The debate originated in a 1917 study by Lambe which argued that large theropods were pure scavengers because *Gorgosaurus* teeth showed hardly any wear.[184] This argument disregarded the fact that theropods replaced their teeth quite rapidly. Ever since the first discovery of *Tyrannosaurus* most scientists have speculated that it was a predator; like modern large predators it would readily scavenge or steal another predator's kill if it had the opportunity.[185]


A *Tyrannosaurus* mounted next to a *Triceratops* at the Los Angeles Natural History Museum

Paleontologist Jack Horner has been a major proponent of the view that *Tyrannosaurus* was not a predator at all but instead was exclusively a scavenger.[121][186][187] He has put forward arguments in the popular literature to support the pure scavenger hypothesis:

- Tyrannosaur arms are short when compared to other known predators. Horner argues that the arms were too short to make the necessary gripping force to hold on to prey.[188] Other paleontologists such as Thomas Holtz Jr. argued that there are plenty of modern-day predators that do not use their forelimbs to hunt such as wolves, hyenas, and secretary birds as well as other extinct animals thought to be predators that would not have used their forelimbs such as Phorusrhacids.[189][190]
- Tyrannosaurs had large olfactory bulbs and olfactory nerves (relative to their brain size). These suggest a highly developed sense of smell which could sniff out carcasses over great distances, as modern vultures do. Research on the olfactory bulbs of dinosaurs has shown that *Tyrannosaurus* had the most highly developed sense of smell of 21 sampled dinosaurs.[161]

- Tyrannosaur teeth could crush bone, and therefore could extract as much food (bone marrow) as possible from carcass remnants, usually the least nutritious parts. Karen Chin and colleagues have found bone fragments in coprolites (fossilized feces) that they attribute to tyrannosaurs, but point out that a tyrannosaur's teeth were not well adapted to systematically chewing bone like hyenas do to extract marrow.[191]
- Since at least some of *Tyrannosaurus*'s potential prey could move quickly, evidence that it walked instead of ran could indicate that it was a scavenger.[186] On the other hand, recent analyses suggest that *Tyrannosaurus*, while slower than large modern terrestrial predators, may well have been fast enough to prey on large hadrosaurs and ceratopsians.[145][24]

Other evidence suggests hunting behavior in *Tyrannosaurus*. The eye sockets of tyrannosaurs are positioned so that the eyes would point forward, giving them binocular vision slightly better than that of modern hawks. It is not obvious why natural selection would have favored this long-term trend if tyrannosaurs had been pure scavengers, which would not have needed the advanced depth perception that stereoscopic vision provides.[45][46] In modern animals, binocular vision is found mainly in predators.

A 2021 study focused on the vision and hearing of the small theropod *Shuvuuia*, to which *Tyrannosaurus* was compared suggests that *Tyrannosaurus* was diurnal and would have hunted predominantly during daylight hours, a feature it shared with *Dromaeosaurus*, a third dinosaur compared to *Shuvuuia* in the study.[192][193]


The damage to the tail vertebrae of this *Edmontosaurus annectens* skeleton (on display at the Denver Museum of Nature and Science) indicates that it may have been bitten by a *Tyrannosaurus*

A skeleton of the hadrosaurid *Edmontosaurus annectens* has been described from Montana with healed tyrannosaur-inflicted damage on its tail vertebrae. The fact that the damage seems to have healed suggests that the *Edmontosaurus* survived a tyrannosaur's attack on a living target, i.e. the tyrannosaur had attempted active predation.[194] Despite the consensus that the tail bites were caused by *Tyrannosaurus*, there has been some evidence to show that they might have been created by other factors. For example, a 2014 study suggested that the tail injuries might have been due to *Edmontosaurus* individuals stepping on each other,[195] while another study in 2020 backs up the hypothesis that biomechanical stress is the cause for the tail injuries.[196] There is also evidence for an aggressive interaction between a *Triceratops* and a *Tyrannosaurus* in the form of partially healed tyrannosaur tooth marks on a *Triceratops* brow horn and squamosal (a bone of the neck frill); the bitten horn is also broken, with new bone growth after the break. It is not known what the exact nature of the interaction was, though: either animal could have been the aggressor.[197] Since the *Triceratops* wounds healed, it is most likely that the *Triceratops* survived the encounter and managed to overcome the *Tyrannosaurus*. In a battle against a bull *Triceratops*, the *Triceratops* would likely defend itself by inflicting fatal wounds to the *Tyrannosaurus* using its sharp horns.[198] Studies of Sue found a broken and healed fibula and tail vertebrae, scarred facial bones and a tooth from another *Tyrannosaurus* embedded in a neck vertebra, providing evidence for aggressive behavior.[199] Studies on hadrosaur vertebrae from the Hell Creek Formation that were punctured by the teeth of what appears to be a late-stage juvenile *Tyrannosaurus* indicate that despite lacking the bone-crushing adaptations of the adults, young individuals were still capable of using the same bone-puncturing feeding technique as their adult counterparts.[200]

Tyrannosaurus may have had infectious saliva used to kill its prey, as proposed by William Abler in 1992. Abler observed that the serrations (tiny protuberances) on the cutting edges of the teeth are closely spaced, enclosing little chambers. These chambers might have trapped pieces of carcass with bacteria, giving *Tyrannosaurus* a deadly, infectious bite much like the Komodo dragon was thought to have.[201][202] Jack

Horner and Don Lessem, in a 1993 popular book, questioned Abler's hypothesis, arguing that *Tyrannosaurus*'s tooth serrations as more like cubes in shape than the serrations on a Komodo monitor's teeth, which are rounded.[121]:214–215

Tyrannosaurus, and most other theropods, probably primarily processed carcasses with lateral shakes of the head, like crocodilians. The head was not as maneuverable as the skulls of allosauroids, due to flat joints of the neck vertebrae.[203]

Cannibalism

Evidence also strongly suggests that tyrannosaurs were at least occasionally cannibalistic. *Tyrannosaurus* itself has strong evidence pointing towards it having been cannibalistic in at least a scavenging capacity based on tooth marks on the foot bones, humerus, and metatarsals of one specimen.[204] Fossils from the Fruitland Formation, Kirtland Formation (both Campanian in age) and the Maastichtian aged Ojo Alamo Formation suggest that cannibalism was present in various tyrannosaurid genera of the San Juan Basin. The evidence gathered from the specimens suggests opportunistic feeding behavior in tyrannosaurids that cannibalized members of their own species.[205] A study from Currie, Horner, Erickson and Longrich in 2010 has been put forward as evidence of cannibalism in the genus *Tyrannosaurus*.[204] They studied some *Tyrannosaurus* specimens with tooth marks in the bones, attributable to the same genus. The tooth marks were identified in the humerus, foot bones and metatarsals, and this was seen as evidence for opportunistic scavenging, rather than wounds caused by intraspecific combat. In a fight, they proposed it would be difficult to reach down to bite in the feet of a rival, making it more likely that the bitemarks were made in a carcass. As the bitemarks were made in body parts with relatively scantly amounts of flesh, it is suggested that the *Tyrannosaurus* was feeding on a cadaver in which the more fleshy parts already had been consumed. They were also open to the possibility that other tyrannosaurids practiced cannibalism.[204]

Parenting

While there is no direct evidence of *Tyrannosaurus* raising their young (the rarity of juvenile and nest Tyrannosaur fossils has left researchers guessing), it has been suggested by some that like its closest living relatives, modern archosaurs (birds and crocodiles) *Tyrannosaurus* may have protected and fed its young. Crocodilians and birds are often suggested by some paleontologists to be modern analogues for dinosaur parenting.[206] Direct evidence of parental behavior exists in other dinosaurs such as *Maiasaura peeblesorum*, the first dinosaur to have been discovered to raise its young, as well as more closely related Oviraptorids, the latter suggesting parental behavior in theropods.[207][208][209][210][211]

Pathology

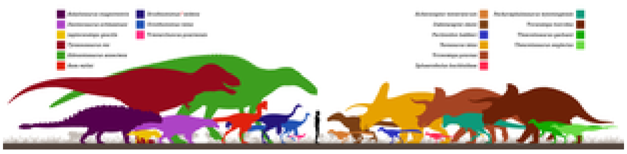

Restoration of an individual (based on MOR 980) with parasite infections

In 2001, Bruce Rothschild and others published a study examining evidence for stress fractures and tendon avulsions in theropod dinosaurs and the implications for their behavior. Since stress fractures are caused by repeated trauma rather than singular events they are more likely to be caused by regular behavior than other types of injuries. Of the 81 *Tyrannosaurus* foot bones examined in the study, one was found to have a stress fracture, while none of the 10 hand bones were found to have stress fractures. The researchers found tendon avulsions only among *Tyrannosaurus* and *Allosaurus*. An avulsion injury left a divot on the humerus of Sue the *T. rex*, apparently located at the origin of the deltoid or teres major muscles. The presence of avulsion injuries being limited to the forelimb and shoulder in both *Tyrannosaurus* and *Allosaurus* suggests that theropods may have had a musculature more complex than and functionally different from those of birds. The researchers concluded that Sue's tendon avulsion was probably obtained from struggling prey. The presence of stress fractures and tendon avulsions, in general, provides evidence for a "very active" predation-based diet rather than obligate scavenging.[212]

A 2009 study showed that smooth-edged holes in the skulls of several specimens might have been caused by *Trichomonas*-like parasites that commonly infect birds. According to the study, seriously infected individuals, including "Sue" and MOR 980 ("Peck's Rex"), might therefore have died from starvation after feeding became increasingly difficult. Previously, these holes had been explained by the bacterious bone infection Actinomycosis or by intraspecific attacks.[213] A subsequent study found that while trichomoniasis has many attributes of the model proposed (osteolytic, intra oral) several features make the assumption that it was the cause of death less supportable by evidence. For example, the observed sharp margins with little reactive bone shown by the radiographs of *Trichomonas*-infected birds are dissimilar to the reactive bone seen in the affected *T. rex* specimens. Also, trichomoniasis can be very rapidly fatal in birds (14 days or less) abeit in its milder form, and this suggests that if a *Trichomonas*-like protozoan is the culprit, trichomoniasis was less acute in its non-avian dinosaur form during the Late Cretaceous. Finally, the relative size of this type of lesions is much larger in small bird throats, and may not have been enough to choke a *T. rex*.[214]

One study of *Tyrannosaurus* specimens with tooth marks in the bones attributable to the same genus was presented as evidence of cannibalism.[204] Tooth marks in the humerus, foot bones and metatarsals, may indicate opportunistic scavenging, rather than wounds caused by combat with another *T. rex*.[204][215] Other tyrannosaurids may also have practiced cannibalism.[204]

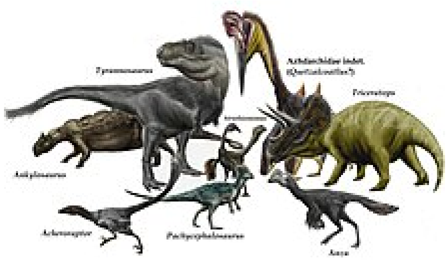
Paleoecology



Fauna of Hell Creek (*Tyrannosaurus* in **dark red**, left)

Tyrannosaurus lived during what is referred to as the Lancian faunal stage (Maastrichtian age) at the end of the Late Cretaceous. *Tyrannosaurus* ranged from Canada in the north to at least New Mexico in the south of Laramidia.[5] During this time *Triceratops* was the major herbivore in the northern portion of its range, while the titanosaurian sauropod *Alamosaurus* "dominated" its southern range. *Tyrannosaurus* remains have been discovered in different ecosystems, including inland and coastal subtropical, and semi-arid plains.

Several notable *Tyrannosaurus* remains have been found in the Hell Creek Formation. During the Maastrichtian this area was subtropical, with a warm and humid climate. The flora consisted mostly of angiosperms, but also included trees like dawn redwood (*Metasequoia*) and *Araucaria*. *Tyrannosaurus* shared this ecosystem with ceratopsians *Leptoceratops*, *Torosaurus*, and *Triceratops*, the hadrosaurid *Edmontosaurus annectens*, the parksosaurid *Thescelosaurus*, the ankylosaurs *Ankylosaurus* and *Denversaurus*, the pachycephalosaurs *Pachycephalosaurus* and *Sphaerotholus*, and the theropods *Ornithomimus*, *Struthiomimus*, *Acheroraptor*, *Dakotaraptor*, *Pectinodon* and *Anzu*.[216]



Tyrannosaurus and other animals of the Hell Creek Formation

Another formation with *Tyrannosaurus* remains is the Lance Formation of Wyoming. This has been interpreted as a bayou environment similar to today's Gulf Coast. The fauna was very similar to Hell Creek, but with *Struthiomimus* replacing its relative *Ornithomimus*. The small ceratopsian *Leptoceratops* also lived in the area.[217]

In its southern range *Tyrannosaurus* lived alongside the titanosaur *Alamosaurus*, the ceratopsians *Torosaurus*, *Bravoceratops* and *Ojoceratops*, hadrosaurs which consisted of a species of *Edmontosaurus*, *Kritosaurus* and a possible species of *Gryposaurus*, the nodosaur *Glyptodontopelta*, the oviraptorid *Ojoraptosaurus*, possible species of the theropods *Troodon* and *Richardoestesia*, and the pterosaur *Quetzalcoatlus*.[218] The region is thought to have been dominated by semi-arid inland plains, following the probable retreat of the Western Interior Seaway as global sea levels fell.[219]

Tyrannosaurus may have also inhabited Mexico's Lomas Coloradas formation in Sonora. Though skeletal evidence is lacking, six shed and broken teeth from the fossil bed have been thoroughly compared with other theropod genera and appear to be identical to those of *Tyrannosaurus*. If true, the evidence indicates the range of *Tyrannosaurus* was possibly more extensive than previously believed.[220] It is possible that tyrannosaurs were originally Asian species, migrating to North America before the end of the Cretaceous period.[221]

Population estimates

According to studies published in 2021 by Charles Marshall *et al.*, the total population of adult *Tyrannosaurus* at any given time was perhaps 20,000 individuals, with computer estimations also suggesting a total population no lower than 1,300 and no higher than 328,000. The authors themselves suggest that the estimate of 20,000 individuals is probably lower than what should be expected, especially when factoring in that disease pandemics could easily wipe out such a small population. Over the span of the genus' existence, it is estimated that there were about 127,000 generations and that this added up to a total of roughly 2.5 billion animals until their extinction.[222][223]

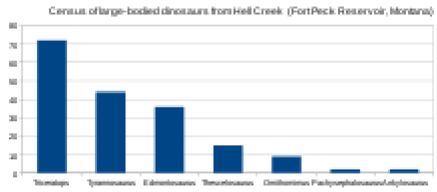


Chart of the time-averaged census for large-bodied dinosaurs from the entire Hell Creek Formation in the study area

In the same paper, it is suggested that in a population of *Tyrannosaurus* adults numbering 20,000, the amount of individuals living in an area the size of California could be as high as 3,800 animals, while an area the size of Washington D.C. could support a population of only two adult *Tyrannosaurus*. The study does not take into account the amount of juvenile animals in the genus present in this population estimate due to their occupation of a different niche than the adults, and thus it is likely the total population was much higher when accounting for this factor. Simultaneously, studies of living carnivores suggest that some predator populations are higher in density than others of similar weight (such as jaguars and hyenas, which are similar in weight but have vastly differing population densities). Lastly, the study suggests that in most cases, only one in 80 million *Tyrannosaurus* would become fossilized, while the chances were likely as high as one in every 16,000 of an individual becoming fossilized in areas that had more dense populations.[222][223]

Meiri (2022) questioned the reliability of the estimates, citing uncertainty in metabolic rate, body size, sex and age-specific survival rates, habitat requirements and range size variability as shortcomings Marshall *et al.* didn't take into account.[224] The authors of the original publication replied that while they agree that their reported uncertainties were probably too small, their framework is flexible enough to accommodate unceraintny in physiology, and that their calculations do not depend on short-term changes in population density and geographic range, but rather on their long-term averages. Finally, they remark that they did estimate the range of reasonable survivorship curves and that they did include uncertainty in the time of onset of sexual maturity and in the growth curve by incorporating the uncertainty in the maximum body mass.[225]

Cultural significance

A depiction of a *Tyrannosaurus* on a German postage stamp.

Since it was first described in 1905, *T. rex* has become the most widely recognized dinosaur species in popular culture. It is the only dinosaur that is commonly known to the general public by its full scientific name (binomial name) and the scientific abbreviation *T. rex* has also come into wide usage.[51] Robert T. Bakker notes this in *The Dinosaur Heresies* and explains that, "a name like '*T. rex*' is just irresistible to the tongue."[39]

See also

- History of paleontology
- Sue (dinosaur) (FMNH-PR-2081)
- Tyrannosauridae

Explanatory notes

1. Pronounced /tɪˌrænəˈsɔːrəs, taɪ-/; lit. 'tyrant lizard'; from Ancient Greek τύραννος *(túrannos)* 'tyrant', and σαῦρος *(saûros)* 'lizard'[1]

References

1. Harper, Douglas. "Tyrannosaurus" (https://www.etymonline.com/?term=Tyrannosaurus). *Online Etymology Dictionary*.
2. Breithaupt, B. H.; Southwell, E. H.; Matthews, N. A. (October 15, 2005). "In Celebration of 100 years of *Tyrannosaurus rex*: *Manospondylus gigas*, *Ornithomimus grandis*, and *Dynamosaurus imperiosus*, the Earliest Discoveries of *Tyrannosaurus rex* in the West" (https://archive.today/20120530024000/http://gsa.confex.com/gsa/2005AM/finalprogram/abstract_96150.htm). *Abstracts with Programs; 2005 Salt Lake City Annual Meeting*. Geological Society of America. **37** (7): 406. Archived from the original (http://gsa.confex.com/gsa/2005AM/finalprogram/abstract_96150.htm) on May 30, 2012. Retrieved October 8, 2008.
3. Hatcher, J. B. (1907). "The Ceratopsia" (https://archive.org/stream/TheCeratopsia/Musgs-1907-hatcherEtAl-theCeratopsiaLkUsaPart1Monograph#page/n111). *Monographs of the United States Geological Survey*. **49**: 113–114.
4. Osborn, H. F. (1917). "Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*". *Bulletin of the American Museum of Natural History*. **35** (43): 733–771. hdl:2246/1334 (https://hdl.handle.net/2246%2F1334).
5. Larson, N. L. (2008). "One hundred years of *Tyrannosaurus rex*: the skeletons". In Larson, P.; Carpenter, K. (eds.). Tyrannosaurus rex*, The Tyrant King* (https://archive.org/details/tyrannosaurusrex00plar). Bloomington, IN: Indiana University Press. pp. 1 (https://archive.org/details/tyrannosaurusrex00plar/page/n16)–55. ISBN 978-0-253-35087-9.
6. Osborn, H. F. (1905). "*Tyrannosaurus* and other Cretaceous carnivorous dinosaurs". *Bulletin of the AMNH*. **21** (14): 259–265. hdl:2246/1464 (https://hdl.handle.net/2246%2F1464). Retrieved October 6, 2008.

7. Dingus, L.; Norell, M. (May 3, 2010). *Barnum Brown: The Man Who Discovered* Tyrannosaurus rex (https://archive.org/details/barnumbrownmanwh00ding). University of California Press. pp. 90 (https://archive.org/details/barnumbrownmanwh00ding/page/n106), 124. ISBN 978-0-520-94552-4.
8. Osborn, H. F.; Brown, B. (1906). "*Tyrannosaurus*, Upper Cretaceous carnivorous dinosaur". *Bulletin of the AMNH*. **22** (16): 281–296. hdl:2246/1473 (https://hdl.handle.net/2246%2F1473).
9. Breithaupt, B. H.; Southwell, E. H.; Matthews, N. A. (2006). Lucas, S. G.; Sullivan, R. M. (eds.). "*Dynamosaurus imperiosus* and the earliest discoveries of *Tyrannosaurus rex* in Wyoming and the West" (http://econtent.unm.edu/utils/getdownloaditem/collection/bulletins/id/693/filename/694.pdf/mapsto/pdf) (PDF). *New Mexico Museum of Natural History and Science Bulletin*. **35**: 258. "The original skeleton of *Dynamosaurus imperiosus* (AMNH 5866/BM R7995), together with other *T. rex* material (including parts of AMNH 973, 5027, and 5881), were sold to the British Museum of Natural History (now The Natural History Museum) in 1960. This material was used in an interesting 'half-mount' display of this dinosaur in London. Currently the material resides in the research collections."
10. McDonald, A. T.; Wolfe, D. G.; Dooley Jr, A. C. (2018). "A new tyrannosaurid (Dinosauria: Theropoda) from the Upper Cretaceous Menefee Formation of New Mexico" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6183510). *PeerJ*. **6**: 6:e5749. doi:10.7717/peerj.5749 (https://doi.org/10.7717%2Fpeerj.5749). PMC 6183510 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6183510). PMID 30324024 (https://pubmed.ncbi.nlm.nih.gov/30324024).
11. Small, Zachary (October 7, 2020). "T. Rex Skeleton Brings $31.8 Million at Christie's Auction" (https://www.nytimes.com/2020/10/06/arts/design/t-rex-skeleton-brings-31-8-million-at-christies-auction.html). *New York Times*. Archived (https://web.archive.org/web/20201007175400/https://www.nytimes.com/2020/10/06/arts/design/t-rex-skeleton-brings-31-8-million-at-christies-auction.html) from the original on October 7, 2020. Retrieved May 5, 2021.
12. "Preparing Sue's bones" (http://archive.fieldmuseum.org/sue/?_ga=1.256723145.352611903.1414146341#preparing). *Sue at the Field Museum*. The Field Museum. 2007. Retrieved October 24, 2014.
13. Erickson, G.; Makovicky, P. J.; Currie, P. J.; Norell, M.; Yerby, S.; Brochu, C. A. (May 26, 2004). "Gigantism and life history parameters of tyrannosaurid dinosaurs". *Nature*. **430** (7001): 772–775. Bibcode:2004Natur.430..772E (https://ui.adsabs.harvard.edu/abs/2004Natur.430..772E). doi:10.1038/nature02699 (https://doi.org/10.1038%2Fnature02699). PMID 15306807 (https://pubmed.ncbi.nlm.nih.gov/15306807). S2CID 4404887 (https://api.semanticscholar.org/CorpusID:4404887).
14. "Stan" (https://web.archive.org/web/20100918104233/http://www.museum.manchester.ac.uk/yourvisit/galleries/stan/). *The University of Manchester*. September 18, 2010. Archived from the original (http://www.museum.manchester.ac.uk/yourvisit/galleries/stan/) on September 18, 2010.
15. Fiffer, S. (2000). "Jurassic Farce". Tyrannosaurus *Sue* (https://archive.org/details/tyrannosaurussue00fiff_672). W. H. Freeman and Company, New York. pp. 121 (https://archive.org/details/tyrannosaurussue00fiff_672/page/n139)–122. ISBN 978-0-7167-4017-9.
16. "Meet Bucky The Teenage T. Rex" (https://www.childrensmuseum.org/blog/meet-bucky-the-teenage-t-rex-v2). *Children's Museum of Indianapolis*. July 7, 2014. Archived (https://web.archive.org/web/20141227210245/http://www.childrensmuseum.org/blog/meet-bucky-the-teenage-t-rex-v2) from the original on December 27, 2014. Retrieved December 2, 2019.
17. "Dig pulls up five T. rex specimens" (http://news.bbc.co.uk/2/hi/science/nature/965609.stm). *BBC News*. October 10, 2000. Retrieved December 13, 2008.
18. Currie, P. J.; Hurum, J. H.; Sabath, K. (2003). "Skull structure and evolution in tyrannosaurid dinosaurs" (http://www.app.pan.pl/archive/published/app48/app48-227.pdf) (PDF). *Acta Palaeontologica Polonica*. **48** (2): 227–234. Retrieved October 8, 2008.

19. Black, Riley (October 28, 2015). "Tiny terror: Controversial dinosaur species is just an awkward tween *Tyrannosaurus*" (https://www.smithsonianmag.com/science-nature/tiny-terror-controversial-dinosaur-species-just-awkward-tween-tyrannosaurus-180957084/). *Smithsonian Magazine*. Retrieved December 10, 2018.
20. "Museum unveils world's largest *T-rex* skull" (https://web.archive.org/web/20060414021235/http://www.montana.edu/cpa/news/nwview.php?article=3607). 2006. Archived from the original (http://www.montana.edu/cpa/news/nwview.php?article=3607) on April 14, 2006. Retrieved April 7, 2006.
21. Gignac, P. M.; Erickson, G. M. (2017). "The biomechanics behind extreme osteophagy in *Tyrannosaurus rex*" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5435714). *Scientific Reports*. **7** (1): 2012. Bibcode:2017NatSR...7.2012G (https://ui.adsabs.harvard.edu/abs/2017NatSR...7.2012G). doi:10.1038/s41598-017-02161-w (https://doi.org/10.1038%2Fs41598-017-02161-w). PMC 5435714 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5435714). PMID 28515439 (https://pubmed.ncbi.nlm.nih.gov/28515439).
22. Lockley, M. G.; Hunt, A. P. (1994). "A track of the giant theropod dinosaur *Tyrannosaurus* from close to the Cretaceous/Tertiary boundary, northern New Mexico". *Ichnos*. **3** (3): 213–218. doi:10.1080/10420949409386390 (https://doi.org/10.1080%2F10420949409386390).
23. "A Probable Tyrannosaurid Track From the Hell Creek Formation (Upper Cretaceous), Montana, United States" (https://web.archive.org/web/20071214014855/http://www.nhm.ac.uk/about-us/news/2007/october/news_12515.html). *National Museum of History News*. 2007. Archived from the original (http://www.nhm.ac.uk/about-us/news/2007/october/news_12515.html) on December 14, 2007. Retrieved December 18, 2007.
24. Manning, P. L.; Ott, C.; Falkingham, P. L. (2009). "The first tyrannosaurid track from the Hell Creek Formation (Late Cretaceous), Montana, U.S.A". *PALAIOS*. **23** (10): 645–647. Bibcode:2008Palai..23..645M (https://ui.adsabs.harvard.edu/abs/2008Palai..23..645M). doi:10.2110/palo.2008.p08-030r (https://doi.org/10.2110%2Fpalo.2008.p08-030r). S2CID 129985735 (https://api.semanticscholar.org/CorpusID:129985735).
25. Smith, S. D.; Persons, W. S.; Xing, L. (2016). "A "Tyrannosaur" trackway at Glenrock, Lance Formation (Maastrichtian), Wyoming" (https://www.sciencedaily.com/releases/2016/01/160116214746.htm). *Cretaceous Research*. **61** (1): 1–4. doi:10.1016/j.cretres.2015.12.020 (https://doi.org/10.1016%2Fj.cretres.2015.12.020).
26. Perkins, S. (2016). "You could probably have outrun a *T. rex*" (http://www.sciencemag.org/news/2016/01/you-could-probably-have-outrun-t-rex). *Palaeontology*. doi:10.1126/science.aae0270 (https://doi.org/10.1126%2Fscience.aae0270).
27. Walton, T. (2016). "Forget all you know from Jurassic Park: For speed, *T. rex* beats *velociraptor*s" (https://www.usatoday.com/story/news/2016/01/27/tyrannosaurs-faster-than-velociraptors/79423372/). *USA Today*. Retrieved March 13, 2016.
28. Ruiz, J. (2017). "Comments on "A tyrannosaur trackway at Glenrock, Lance Formation (Maastrichtian), Wyoming" (Smith *et al.*, *Cretaceous Research*, v. 61, pp. 1–4, 2016)". *Cretaceous Research*. **82**: 81–82. doi:10.1016/j.cretres.2017.05.033 (https://doi.org/10.1016%2Fj.cretres.2017.05.033).
29. Hutchinson, J. R.; Bates, K. T.; Molnar, J.; Allen, V.; Makovicky, P. J. (2011). "A Computational Analysis of Limb and Body Dimensions in Tyrannosaurus rex with Implications for Locomotion, Ontogeny, and Growth" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3192160). *PLOS ONE*. **6** (10): e26037. Bibcode:2011PLoSO...626037H (https://ui.adsabs.harvard.edu/abs/2011PLoSO...626037H). doi:10.1371/journal.pone.0026037 (https://doi.org/10.1371%2Fjournal.pone.0026037). PMC 3192160 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3192160). PMID 22022500 (https://pubmed.ncbi.nlm.nih.gov/22022500).
30. Holtz, T. R. (2011). "Dinosaurs: The Most Complete, Up-to-Date Encyclopedia for Dinosaur Lovers of All Ages, Winter 2011 Appendix" (http://www.geol.umd.edu/~tholtz/dinoappendix/HoltzappendixWinter2011.pdf) (PDF). Retrieved January 13, 2012.

31. "Sue Fact Sheet" (https://web.archive.org/web/20160818213556/https://www.fieldmuseum.org/sites/default/files/Sue%20Fact%20Sheet.pdf) (PDF). *Sue at the Field Museum*. Field Museum of Natural History. Archived from the original (https://www.fieldmuseum.org/sites/default/files/Sue%20Fact%20Sheet.pdf) (PDF) on August 18, 2016.
32. "How well do you know SUE?" (https://www.fieldmuseum.org/blog/how-well-do-you-know-sue). Field Museum of Natural History. August 11, 2016. Retrieved December 31, 2018.
33. "Sue the T. Rex" (https://www.fieldmuseum.org/blog/sue-t-rex). *Field Museum*. February 5, 2018. Retrieved July 20, 2018.
34. Therrien, F.; Henderson, D. M. (March 12, 2007). "My theropod is bigger than yours ... or not: estimating body size from skull length in theropods". *Journal of Vertebrate Paleontology*. **27** (1): 108–115. doi:10.1671/0272-4634(2007)27[108:MTIBTY]2.0.CO;2 (https://doi.org/10.1671%2F0272-4634%282007%2927%5B108%3AMTIBTY%5D2.0.CO%3B2). ISSN 0272-4634 (https://www.worldcat.org/issn/0272-4634).
35. Hartman, Scott (July 7, 2013). "Mass estimates: North vs South redux" (http://www.skeletaldrawing.com/home/mass-estimates-north-vs-south-redux772013). Scott Hartman's Skeletal Drawing.com. Archived (https://web.archive.org/web/20131012065922/http://www.skeletaldrawing.com/home/mass-estimates-north-vs-south-redux772013) from the original on October 12, 2013. Retrieved August 24, 2013.
36. Persons, S. W.; Currie, P. J.; Erickson, G. M. (2020). "An Older and Exceptionally Large Adult Specimen of *Tyrannosaurus rex*" (https://doi.org/10.1002%2Far.24118). *The Anatomical Record*. **303** (4): 656–672. doi:10.1002/ar.24118 (https://doi.org/10.1002%2Far.24118). ISSN 1932-8486 (https://www.worldcat.org/issn/1932-8486). PMID 30897281 (https://pubmed.ncbi.nlm.nih.gov/30897281).
37. Lyle, A. (March 22, 2019). "Paleontologists identify biggest *Tyrannosaurus rex* ever discovered" (https://www.folio.ca/paleontologists-identify-biggest-tyrannosaurus-rex-ever-discovered/). Folio, University of Alberta. Retrieved March 25, 2019.
38. Anderson, J. F.; Hall-Martin, A. J.; Russell, D. (1985). "Long bone circumference and weight in mammals, birds and dinosaurs". *Journal of Zoology*. **207** (1): 53–61. doi:10.1111/j.1469-7998.1985.tb04915.x (https://doi.org/10.1111%2Fj.1469-7998.1985.tb04915.x).
39. Bakker, R. T. (1986). *The Dinosaur Heresies* (https://archive.org/details/dinosaurheresies00robe/page/241). New York: Kensington Publishing. p. 241 (https://archive.org/details/dinosaurheresies00robe/page/241). ISBN 978-0-688-04287-5. OCLC 13699558 (https://www.worldcat.org/oclc/13699558).
40. Henderson, D. M. (January 1, 1999). "Estimating the masses and centers of mass of extinct animals by 3-D mathematical slicing" (http://paleobiol.geoscienceworld.org/cgi/content/abstract/25/1/88). *Paleobiology*. **25** (1): 88–106.
41. Erickson, G. M.; Makovicky, P. J.; Currie, P. J.; Norell, M. A.; Yerby, S. A.; Brochu, C. A. (2004). "Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs". *Nature*. **430** (7001): 772–775. Bibcode:2004Natur.430..772E (https://ui.adsabs.harvard.edu/abs/2004Natur.430..772E). doi:10.1038/nature02699 (https://doi.org/10.1038%2Fnature02699). PMID 15306807 (https://pubmed.ncbi.nlm.nih.gov/15306807). S2CID 4404887 (https://api.semanticscholar.org/CorpusID:4404887).
42. Farlow, J. O.; Smith, M. B.; Robinson, J. M. (1995). "Body mass, bone 'strength indicator', and cursorial potential of *Tyrannosaurus rex*" (https://web.archive.org/web/20081023063102/http://www.vertpaleo.org/publications/jvp/15-713-725.cfm). *Journal of Vertebrate Paleontology*. **15** (4): 713–725. doi:10.1080/02724634.1995.10011257 (https://doi.org/10.1080%2F02724634.1995.10011257). Archived from the original (http://www.vertpaleo.org/publications/jvp/15-713-725.cfm) on October 23, 2008.

43. Seebacher, F. (2001). "A new method to calculate allometric length–mass relationships of dinosaurs" (http://dinoweb.ucoz.ru/_fr/4/A_new_method_to.pdf) (PDF). *Journal of Vertebrate Paleontology*. **21** (1): 51–60. CiteSeerX 10.1.1.462.255 (https://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.462.255). doi:10.1671/0272-4634(2001)021[0051:ANMTCA]2.0.CO;2 (https://doi.org/10.1671%2F0272-4634%282001%29021%5B0051%3AANMTCA%5D2.0.CO%3B2).
44. Christiansen, P.; Fariña, R. A. (2004). "Mass prediction in theropod dinosaurs". *Historical Biology*. **16** (2–4): 85–92. doi:10.1080/08912960412331284313 (https://doi.org/10.1080%2F08912960412331284313). S2CID 84322349 (https://api.semanticscholar.org/CorpusID:84322349).
45. Stevens, Kent A. (June 2006). "Binocular vision in theropod dinosaurs". *Journal of Vertebrate Paleontology*. **26** (2): 321–330. doi:10.1671/0272-4634(2006)26[321:BVITD]2.0.CO;2 (https://doi.org/10.1671%2F0272-4634%282006%2926%5B321%3ABVITD%5D2.0.CO%3B2).
46. Jaffe, E. (July 1, 2006). "Sight for 'Saur Eyes: *T. rex* vision was among nature's best" (http://www.sciencenews.org/view/generic/id/7500/title/Sight_for_Saur_Eyes_%3Ci%3ET._rex%3Ci%3E_vision_was_among_natures_best). *Science News*. **170** (1): 3–4. doi:10.2307/4017288 (https://doi.org/10.2307%2F4017288). JSTOR 4017288 (https://www.jstor.org/stable/4017288). Retrieved October 6, 2008.
47. Snively, E.; Henderson, D. M.; Phillips, D. S. (2006). "Fused and vaulted nasals of tyrannosaurid dinosaurs: Implications for cranial strength and feeding mechanics" (http://www.app.pan.pl/archive/published/app51/app51-435.pdf) (PDF). *Acta Palaeontologica Polonica*. **51** (3): 435–454. Retrieved October 8, 2008.
48. Meers, M. B. (August 2003). "Maximum bite force and prey size of *Tyrannosaurus rex* and their relationships to the inference of feeding behavior". *Historical Biology*. **16** (1): 1–12. doi:10.1080/0891296021000050755 (https://doi.org/10.1080%2F0891296021000050755). S2CID 86782853 (https://api.semanticscholar.org/CorpusID:86782853).
49. Erickson, G. M.; Van Kirk, S. D.; Su, J.; Levenston, M. E.; Caler, W. E.; Carter, D. R. (1996). "Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones" (https://zenodo.org/record/3730962). *Nature*. **382** (6593): 706–708. Bibcode:1996Natur.382..706E (https://ui.adsabs.harvard.edu/abs/1996Natur.382..706E). doi:10.1038/382706a0 (https://doi.org/10.1038%2F382706a0). S2CID 4325859 (https://api.semanticscholar.org/CorpusID:4325859).
50. Holtz, T. R. (1994). "The Phylogenetic Position of the Tyrannosauridae: Implications for Theropod Systematics". *Journal of Paleontology*. **68** (5): 1100–1117. doi:10.1017/S0022336000026706 (https://doi.org/10.1017%2FS0022336000026706). JSTOR 1306180 (https://www.jstor.org/stable/1306180).
51. Brochu, C. R. (2003). "Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull". *Society of Vertebrate Paleontology Memoirs*. **7**: 1–138. doi:10.2307/3889334 (https://doi.org/10.2307%2F3889334). JSTOR 3889334 (https://www.jstor.org/stable/3889334).
52. Smith, J. B. (December 1, 2005). "Heterodonty in *Tyrannosaurus rex*: implications for the taxonomic and systematic utility of theropod dentitions". *Journal of Vertebrate Paleontology*. **25** (4): 865–887. doi:10.1671/0272-4634(2005)025[0865:HITRIF]2.0.CO;2 (https://doi.org/10.1671%2F0272-4634%282005%29025%5B0865%3AHITRIF%5D2.0.CO%3B2).
53. Douglas, K.; Young, S. (1998). "The dinosaur detectives" (https://www.newscientist.com/channel/life/dinosaurs/mg15821305.300). *New Scientist*. Retrieved October 16, 2008. "One palaeontologist memorably described the huge, curved teeth of T. rex as 'lethal bananas'"
54. "Sue's vital statistics" (https://web.archive.org/web/20070929090231/http://www.fieldmuseum.org/SUE/about_vital.asp). *Sue at the Field Museum*. Field Museum of Natural History. Archived from the original (http://www.fieldmuseum.org/sue/about_vital.asp) on September 29, 2007. Retrieved September 15, 2007.

55. Carr, T. D.; Varricchio, D. J.; Sedlmayr, J. C.; Roberts, E. M.; Moore, J. R. (March 30, 2017). "A new tyrannosaur with evidence for anagenesis and crocodile-like facial sensory system" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5372470). *Scientific Reports*. **7**: 44942. Bibcode:2017NatSR...744942C (https://ui.adsabs.harvard.edu/abs/2017NatSR...744942C). doi:10.1038/srep44942 (https://doi.org/10.1038%2Fsrep44942). ISSN 2045-2322 (https://www.worldcat.org/issn/2045-2322). PMC 5372470 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5372470). PMID 28358353 (https://pubmed.ncbi.nlm.nih.gov/28358353).
56. Morhardt, Ashley (2009). *Dinosaur smiles: Do the texture and morphology of the premaxilla, maxilla, and dentary bones of sauropsids provide osteological correlates for inferring extra-oral structures reliably in dinosaurs?* (https://www.academia.edu/3871353) (MSc thesis). Western Illinois University.
57. Reisz, R. R.; Larson, D. (2016). "Dental anatomy and skull length to tooth size ratios support the hypothesis that theropod dinosaurs had lips" (https://ejournals.library.ualberta.ca/index.php/VAMP/article/download/28196/20702). *4th Annual Meeting, 2016, Canadian Society of Vertebrate Palaeontology*. ISSN 2292-1389 (https://www.worldcat.org/issn/2292-1389).
58. *MORPHOLOGY, TAXONOMY, AND PHYLOGENETIC RELATIONSHIPS OF THE MONTEVIALE CROCODYLIANS (OLIGOCENE, ITALY)* (https://scholar.google.com/scholar?hl=en&as_sdt=0%2C14&as_ylo=2018&as_yhi=2018&q=MORPHOLOGY%2C+TAXONOMY%2C+AND+PHYLOGENETIC+RELATIONSHIPS+OF+THE+MONTEVIALE+CROCODYLIANS+%28OLIGOCENE%2C+ITALY%29.&btnG=). 2018. p. 67. Retrieved October 9, 2020.
59. Lipkin, C.; Carpenter, K. (2008). "Looking again at the forelimb of *Tyrannosaurus rex*". In Carpenter, K.; Larson, P. E. (eds.). Tyrannosaurus rex*, the Tyrant King* (https://archive.org/details/tyrannosaurusrex00plar). Bloomington: Indiana University Press. pp. 167 (https://archive.org/details/tyrannosaurusrex00plar/page/n182)–190. ISBN 978-0-253-35087-9.
60. Holtz, T. R., Jr. (2004). "Tyrannosauroidea". In Weishampel, D. B.; Dodson, P.; Osmólska, H. (eds.). *The dinosauria* (https://archive.org/details/dinosauriandedit00weis). Berkeley: University of California Press. pp. 111 (https://archive.org/details/dinosauriandedit00weis/page/n129)–136. ISBN 978-0-520-24209-8.
61. Paul, Gregory S. (1988). *Predatory dinosaurs of the world: a complete illustrated guide* (https://archive.org/details/predatorydinosau00paul/page/228). New York: Simon and Schuster. p. 228 (https://archive.org/details/predatorydinosau00paul/page/228). ISBN 978-0-671-61946-6. OCLC 18350868 (https://www.worldcat.org/oclc/18350868).
62. Loewen, M. A.; Irmis, R. B.; Sertich, J. J. W.; Currie, P. J.; Sampson, S. D. (2013). Evans, D. C (ed.). "Tyrant Dinosaur Evolution Tracks the Rise and Fall of Late Cretaceous Oceans" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3819173). *PLoS ONE*. **8** (11): e79420. Bibcode:2013PLoSO...879420L (https://ui.adsabs.harvard.edu/abs/2013PLoSO...879420L). doi:10.1371/journal.pone.0079420 (https://doi.org/10.1371%2Fjournal.pone.0079420). PMC 3819173 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3819173). PMID 24223179 (https://pubmed.ncbi.nlm.nih.gov/24223179).
63. Vergano, D. (November 7, 2013). "Newfound "King of Gore" Dinosaur Ruled Before T. Rex" (https://news.nationalgeographic.com/news/2013/11/131106-king-gore-tyrannosaurus-dinosaur/). *National Geographic*. Retrieved November 10, 2017.
64. Geggel, L. (February 29, 2016). "*T. Rex* Was Likely an Invasive Species" (http://www.livescience.com/53877-t-rex-was-invasive-species.html). *Live Science*. Retrieved November 10, 2017.
65. Maleev, E. A. (1955). translated by F. J. Alcock. "(title in Russian)" (http://paleoglot.org/files/Maleev_55a.pdf) [Gigantic carnivorous dinosaurs of Mongolia] (PDF). *Doklady Akademii Nauk SSSR* (in Russian). **104** (4): 634–637.
66. Rozhdestvensky, A. K. (1965). "Growth changes in Asian dinosaurs and some problems of their taxonomy". *Paleontological Journal*. **3**: 95–109.

67. Carpenter, K. (1992). "Tyrannosaurids (Dinosauria) of Asia and North America". In Mateer, N. J.; Chen, P.-j. (eds.). *Aspects of nonmarine Cretaceous geology*. Beijing: China Ocean Press. pp. 250–268. ISBN 978-7-5027-1463-5. OCLC 28260578 (https://www.worldcat.org/oclc/28260578).
68. Hone, D. W. E.; Wang, K.; Sullivan, C.; Zhao, X.; Chen, S.; Li, D.; Ji, S.; Ji, Q.; Xu, X. (2011). "A new, large tyrannosaurine theropod from the Upper Cretaceous of China". *Cretaceous Research*. **32** (4): 495–503. doi:10.1016/j.cretres.2011.03.005 (https://doi.org/10.1016%2Fj.cretres.2011.03.005).
69. Paul, Gregory S.; Persons IV, W. Scott; van Raalte, Jay (2022). "The Tyrant Lizard King, Queen and Emperor: Multiple Lines of Morphological and Stratigraphic Evidence Support Subtle Evolution and Probable Speciation Within the North American Genus Tyrannosaurus" (https://link.springer.com/article/10.1007/s11692-022-09561-5#Sec12). *Evolutionary Biology*. doi:10.1007/s11692-022-09561-5 (https://doi.org/10.1007%2Fs11692-022-09561-5).
70. Elbein, Asher (February 28, 2022). "They Want to Break T. Rex Into 3 Species. Other Paleontologists Aren't Pleased" (https://www.nytimes.com/2022/02/28/science/tyrannosaurus-rex-species.html?). *The New York Times*. Archived (https://web.archive.org/web/20220301014637/https://www.nytimes.com/2022/02/28/science/tyrannosaurus-rex-species.html) from the original on March 1, 2022. Retrieved March 1, 2022.
71. Hunt, Katie (March 1, 2022). "Tyrannosaurus rex may have been misunderstood" (https://edition.cnn.com/2022/02/28/world/t-rex-three-different-dinosaurs-scn/index.html). *CNN*.
72. Greshko, Michael (March 1, 2022). "Call to split T. rex into 3 species sparks fierce debate" (https://www.nationalgeographic.com/science/article/call-to-split-tyrannosaurus-rex-into-3-species-sparks-fierce-debate). *National Geographic*.
73. Olshevsky, G. (1995). "The origin and evolution of the tyrannosaurids". *Kyoryugaku Saizensen [Dino Frontline]*. **9–10**: 92–119.
74. Carr, T. D.; Williamson, T. E. (2004). "Diversity of late Maastrichtian Tyrannosauridae (Dinosauria: Theropoda) from western North America" (https://doi.org/10.1111%2Fj.1096-3642.2004.00130.x). *Zoological Journal of the Linnean Society*. **142** (4): 479–523. doi:10.1111/j.1096-3642.2004.00130.x (https://doi.org/10.1111%2Fj.1096-3642.2004.00130.x).
75. Gilmore, C. W. (1946). "A new carnivorous dinosaur from the Lance Formation of Montana". *Smithsonian Miscellaneous Collections*. **106**: 1–19.
76. Bakker, R.T.; Williams, M.; Currie, P.J. (1988). "*Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana". *Hunteria*. **1**: 1–30.
77. Carr, T.D. (1999). "Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria)" (https://zenodo.org/record/3371479). *Journal of Vertebrate Paleontology*. **19** (3): 497–520. doi:10.1080/02724634.1999.10011161 (https://doi.org/10.1080%2F02724634.1999.10011161).
78. Tsuihiji, T.; Watabe, M.; Tsogtbaatar, K.; Tsubamoto, T.; Barsbold, R.; Suzuki, S.; Lee, A.H.; Ridgely, R.C.; Kawahara, Y.; Witmer, L.M. (2011). "Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia". *Journal of Vertebrate Paleontology*. **31** (3): 497–517. doi:10.1080/02724634.2011.557116 (https://doi.org/10.1080%2F02724634.2011.557116). S2CID 15369707 (https://api.semanticscholar.org/CorpusID:15369707).
79. Currie, P.J. (2003a). "Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada". *Acta Palaeontologica Polonica*. **48**: 191–226.

80. Currie, Henderson, Horner and Williams (2005). "On tyrannosaur teeth, tooth positions and the taxonomic status of *Nanotyrannus lancensis*." In "The origin, systematics, and paleobiology of Tyrannosauridae", a symposium hosted jointly by Burpee Museum of Natural History and Northern Illinois University.
81. Henderson (2005). "Nano No More: The death of the pygmy tyrant." In "The origin, systematics, and paleobiology of Tyrannosauridae", a symposium hosted jointly by Burpee Museum of Natural History and Northern Illinois University.
82. Larson (2005). "A case for *Nanotyrannus*." In "The origin, systematics, and paleobiology of Tyrannosauridae", a symposium hosted jointly by Burpee Museum of Natural History and Northern Illinois University.
83. Larson P (2013), "The validity of Nanotyrannus Lancensis (Theropoda, Lancian – Upper Maastrichtian of North America", Society of Vertebrate Paleontology: 73rd annual meeting, *Abstracts with Programs*, p. 159.
84. D. Carr, Thomas (September 15, 2013). " "NANOTYRANNUS ISN'T REAL, REALLY" " (http://tyrannosauroideacentral.blogspot.com/2013/09/nanotyrannus-isnt-real-really.html?showComment=1447368882738#c6395910030969665299). *Tyrannosauroidea Central*. Retrieved May 28, 2019.
85. Persons, W. S.; Currie, P. J. (2016). "An approach to scoring cursorial limb proportions in carnivorous dinosaurs and an attempt to account for allometry" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4728391). *Scientific Reports*. **6**. 19828. Bibcode:2016NatSR...619828P (https://ui.adsabs.harvard.edu/abs/2016NatSR...619828P). doi:10.1038/srep19828 (https://doi.org/10.1038%2Fsrep19828). PMC 4728391 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4728391). PMID 26813782 (https://pubmed.ncbi.nlm.nih.gov/26813782).
86. "Hind limb proportions do not support the validity of Nanotyrannus" (http://mambobob-raptorsnest.blogspot.com/2016/03/hind-limb-proportions-cast-doubt-on.html). *mambobob-raptorsnest.blogspot.com*.
87. Schmerge, Joshua D.; Rothschild, Bruce M. (2016). "Distribution of the dentary groove of theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus Nanotyrannus Bakker et al., 1988". *Cretaceous Research*. **61**: 26–33. doi:10.1016/J.CRETRES.2015.12.016 (https://doi.org/10.1016%2FJ.CRETRES.2015.12.016). S2CID 85736236 (https://api.semanticscholar.org/CorpusID:85736236).
88. Brusatte, Stephen L.; Carr, Thomas D.; Williamson, Thomas E.; Holtz, Thomas R.; Hone, David W.E.; Williams, Scott A. (2016). "Dentary groove morphology does not distinguish 'Nanotyrannus' as a valid taxon of tyrannosauroid dinosaur. Comment on: "Distribution of the dentary groove of theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus Nanotyrannus Bakker et al., 1988" " (https://www.pure.ed.ac.uk/ws/files/23714255/23714179._AAM._BrusatteetalNanotyrannusResponseMSRevision.pdf) (PDF). *Cretaceous Research*. **65**: 232–237. doi:10.1016/J.CRETRES.2016.02.007 (https://doi.org/10.1016%2FJ.CRETRES.2016.02.007). hdl:20.500.11820/f1e76074-47eb-4c25-b4c1-a3782551fd5a (https://hdl.handle.net/20.500.11820%2Ff1e76074-47eb-4c25-b4c1-a3782551fd5a). S2CID 56090258 (https://api.semanticscholar.org/CorpusID:56090258).
89. Woodward, Holly N.; Tremaine, Katie; Williams, Scott A.; Zanno, Lindsay E.; Horner, John R.; Myhrvold, Nathan (2020). "Growing up Tyrannosaurus rex: Osteohistology refutes the pygmy "Nanotyrannus" and supports ontogenetic niche partitioning in juvenile *Tyrannosaurus*" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6938697). *Science Advances*. **6** (1): eaax6250. Bibcode:2020SciA....6.6250W (https://ui.adsabs.harvard.edu/abs/2020SciA....6.6250W). doi:10.1126/sciadv.aax6250 (https://doi.org/10.1126%2Fsciadv.aax6250). ISSN 2375-2548 (https://www.worldcat.org/issn/2375-2548). PMC 6938697 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6938697). PMID 31911944 (https://pubmed.ncbi.nlm.nih.gov/31911944).

90. Carr, T.D. (2020). "A high-resolution growth series of *Tyrannosaurus rex* obtained from multiple lines of evidence" (https://doi.org/10.7717%2Fpeerj.9192). *PeerJ*. **8**: e9192. doi:10.7717/peerj.9192 (https://doi.org/10.7717%2Fpeerj.9192).
91. Carr, T.D. (June 5, 2020). "A high-resolution growth series of Tyrannosaurus rex obtained from multiple lines of evidence–Author Dr. Thomas D. Carr discusses his new study" (https://peerj.com/blog/post/115284882629/a-high-resolution-growth-series-of-tyrannosaurus-rex-obtained-from-multiple-lines-of-evidence-author-dr-thomas-d-carr-discusses-his-new-study/). PeerJblog. Retrieved June 10, 2020.
92. Horner, J. R.; Padian, K. (2004). "Age and growth dynamics of Tyrannosaurus rex" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1691809). *Proceedings: Biological Sciences*. **271** (1551): 1875–80. doi:10.1098/rspb.2004.2829 (https://doi.org/10.1098%2Frspb.2004.2829). PMC 1691809 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1691809). PMID 15347508 (https://pubmed.ncbi.nlm.nih.gov/15347508).
93. Schweitzer, M. H.; Wittmeyer, J. L.; Horner, J. R. (2005). "Gender-specific reproductive tissue in ratites and *Tyrannosaurus rex*". *Science*. **308** (5727): 1456–60. Bibcode:2005Sci...308.1456S (https://ui.adsabs.harvard.edu/abs/2005Sci...308.1456S). doi:10.1126/science.1112158 (https://doi.org/10.1126%2Fscience.1112158). PMID 15933198 (https://pubmed.ncbi.nlm.nih.gov/15933198). S2CID 30264554 (https://api.semanticscholar.org/CorpusID:30264554).
94. Lee, A. H.; Werning, S. (2008). "Sexual maturity in growing dinosaurs does not fit reptilian growth models" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2206579). *Proceedings of the National Academy of Sciences*. **105** (2): 582–587. Bibcode:2008PNAS..105..582L (https://ui.adsabs.harvard.edu/abs/2008PNAS..105..582L). doi:10.1073/pnas.0708903105 (https://doi.org/10.1073%2Fpnas.0708903105). PMC 2206579 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2206579). PMID 18195356 (https://pubmed.ncbi.nlm.nih.gov/18195356).
95. Schweitzer, M. H.; Zheng, W.; Zanno, L.; Werning, S.; Sugiyama, T. (2016). "Chemistry supports the identification of gender-specific reproductive tissue in Tyrannosaurus rex" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4791554). *Scientific Reports*. **6** (23099): 23099. Bibcode:2016NatSR...623099S (https://ui.adsabs.harvard.edu/abs/2016NatSR...623099S). doi:10.1038/srep23099 (https://doi.org/10.1038%2Fsrep23099). PMC 4791554 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4791554). PMID 26975806 (https://pubmed.ncbi.nlm.nih.gov/26975806).
96. Erickson, G. M.; Currie, P. J.; Inouye, B. D.; Winn, A. A. (2006). "Tyrannosaur life tables: an example of nonavian dinosaur population biology". *Science*. **313** (5784): 213–7. Bibcode:2006Sci...313..213E (https://ui.adsabs.harvard.edu/abs/2006Sci...313..213E). doi:10.1126/science.1125721 (https://doi.org/10.1126%2Fscience.1125721). PMID 16840697 (https://pubmed.ncbi.nlm.nih.gov/16840697). S2CID 34191607 (https://api.semanticscholar.org/CorpusID:34191607).
97. Woodward, Holly N; Tremaine, Katie; Williams, Scott A; Zanno, Lindsay E; Horner, John R; Myhrvold, Nathan (January 1, 2020). "Growing up Tyrannosaurus rex: Osteohistology refutes the pygmy "Nanotyrannus" and supports ontogenetic niche partitioning in juvenile Tyrannosaurus" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6938697). *Science Advances*. **6** (1): eaax6250. Bibcode:2020SciA....6.6250W (https://ui.adsabs.harvard.edu/abs/2020SciA....6.6250W). doi:10.1126/sciadv.aax6250 (https://doi.org/10.1126%2Fsciadv.aax6250). PMC 6938697 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6938697). PMID 31911944 (https://pubmed.ncbi.nlm.nih.gov/31911944).
98. Greshko, Michael (January 1, 2020). "These sleek predatory dinosaurs really are teenage T. rex" (https://www.nationalgeographic.com/science/2020/01/nanotyrannus-fossils-really-are-teenage-t-rex-dinosaur-growth-rates/). *National Geographic*. Retrieved January 2, 2020.

99. Holtz, T. R., Jr (March 19, 2013) [Lecture held March 8, 2013]. *The Life and Times of Tyrannosaurus rex, with Dr. Thomas Holtz* (https://www.youtube.com/watch?v=sqkqkxYGNZc) (Lecture). Seattle, WA: Burke Museum of Natural History and Culture. Archived (https://ghostarchive.org/varchive/youtube/20211211/sqkqkxYGNZc) from the original on December 11, 2021. Retrieved October 12, 2013.
100. Paul, G. S. (2008). "Chapter 18: The Extreme Life Style and Habits of the Gigantic Tyrannosaurid Superpredators of the Cretaceous North America and Asia" (https://books.google.com/books?id=5WH9RnfKco4C&pg=PA307). In Larson, P. L.; Carpenter, K. (eds.). Tyrannosaurus*, The Tyrant King*. Indiana University Press. pp. 307–345. ISBN 978-0-253-35087-9. Retrieved September 14, 2013.
101. Bell, P. R.; Campione, N. E.; Persons IV, W. S.; Currie, P. J.; Larson, P. L.; Tanke, D. H.; Bakker, R. T. (2017). "Tyrannosauroid integument reveals conflicting patterns of gigantism and feather evolution" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5493735). *Biology Letters*. **13** (6): 20170092. doi:10.1098/rsbl.2017.0092 (https://doi.org/10.1098%2Frsbl.2017.0092). PMC 5493735 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5493735). PMID 28592520 (https://pubmed.ncbi.nlm.nih.gov/28592520).
102. Farago, J. (March 7, 2019). "T. Rex Like You Haven't Seen Him: With Feathers" (https://www.nytimes.com/2019/03/07/arts/design/t-rex-exhibition-american-museum-of-natural-history.html). *The New York Times*. Archived (https://web.archive.org/web/20190308002505/https://www.nytimes.com/2019/03/07/arts/design/t-rex-exhibition-american-museum-of-natural-history.html) from the original on March 8, 2019. Retrieved March 7, 2019.
103. Xing, X.; Norell, M. A.; Kuang, X.; Wang, X.; Zhao, Q.; Jia, C. (October 7, 2004). "Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids". *Nature*. **431** (7009): 680–684. Bibcode:2004Natur.431..680X (https://ui.adsabs.harvard.edu/abs/2004Natur.431..680X). doi:10.1038/nature02855 (https://doi.org/10.1038%2Fnature02855). PMID 15470426 (https://pubmed.ncbi.nlm.nih.gov/15470426). S2CID 4381777 (https://api.semanticscholar.org/CorpusID:4381777).
104. Xing, X.; Wang, K.; Zhang; Ma, Q.; Xing, L.; Sullivan, C.; Hu, D.; Cheng, S.; Wang, S. (April 5, 2012). "A gigantic feathered dinosaur from the Lower Cretaceous of China" (https://web.archive.org/web/20120417134949/http://www.xinglida.net/pdf/Xu_et_al_2012_Yutyrannus.pdf) (PDF). *Nature*. **484** (7392): 92–95. Bibcode:2012Natur.484...92X (https://ui.adsabs.harvard.edu/abs/2012Natur.484...92X). doi:10.1038/nature10906 (https://doi.org/10.1038%2Fnature10906). PMID 22481363 (https://pubmed.ncbi.nlm.nih.gov/22481363). S2CID 29689629 (https://api.semanticscholar.org/CorpusID:29689629). Archived from the original (http://www.xinglida.net/pdf/Xu_et_al_2012_Yutyrannus.pdf) (PDF) on April 17, 2012.
105. Naish, D. "The Sensitive Face of a Big Predatory Dinosaur" (https://blogs.scientificamerican.com/tetrapod-zoology/the-sensitive-face-of-a-big-predatory-dinosaur/). *Tetrapod Zoology*. Scientific American Blog Network. Retrieved December 5, 2018.
106. "MORPHOLOGY, TAXONOMY, AND PHYLOGENETIC RELATIONSHIPS OF THE MONTEVIALE CROCODYLIANS (OLIGOCENE, ITALY). p. 67" (https://scholar.google.com/scholar?hl=en&as_sdt=0%2C14&q=MORPHOLOGY%2C+TAXONOMY%2C+AND+PHYLOGENETIC+RELATIONSHIPS+OF+THE+MONTEVIALE+CROCODYLIANS+%28OLIGOCENE%2C+ITALY%29.&btnG=). *The Annual Symposium of Vertebrate Palaeontology and Comparative Anatomy*. Retrieved October 9, 2020.

107. Milinkovitch, Michel; Manukyan, Liana; Debry, Adrien; Di-Poi, Nicolas; Martin, Samuel; Singh, Daljit; Lambert, Dominique; Zwicker, Matthias (January 4, 2013). "Crocodile Head Scales Are Not Developmental Units But Emerge from Physical Cracking" (https://science.sciencemag.org/content/339/6115/78.abstract). *Science*. **339** (6115): 78–81. Bibcode:2013Sci...339...78M (https://ui.adsabs.harvard.edu/abs/2013Sci...339...78M). doi:10.1126/science.1226265 (https://doi.org/10.1126%2Fscience.1226265). PMID 23196908 (https://pubmed.ncbi.nlm.nih.gov/23196908). S2CID 6859452 (https://api.semanticscholar.org/CorpusID:6859452). Retrieved October 9, 2020.
108. Carpenter, K. (1992). "Variation in *Tyrannosaurus rex*". In Carpenter, K.; Currie, P. J. (eds.). *Dinosaur Systematics: Approaches and Perspectives*. Cambridge: Cambridge University Press. pp. 141–145. ISBN 978-0-521-43810-0.
109. Larson, P. L. (1994). "*Tyrannosaurus* sex". In Rosenberg, G. D.; Wolberg, D. L. (eds.). *Dino Fest*. Vol. 7. The Paleontological Society Special Publications. pp. 139–155.
110. Erickson, G. M.; Kristopher, L. A.; Larson, P. (2005). "Androgynous rex – the utility of chevrons for determining the sex of crocodilians and non-avian dinosaurs". *Zoology (Jena, Germany)*. **108** (4): 277–86. doi:10.1016/j.zool.2005.08.001 (https://doi.org/10.1016%2Fj.zool.2005.08.001). PMID 16351976 (https://pubmed.ncbi.nlm.nih.gov/16351976).
111. Schweitzer, M. H.; Elsey, R. M.; Dacke, C. G.; Horner, J. R.; Lamm, E. T. (2007). "Do egg-laying crocodilian (*Alligator mississippiensis*) archosaurs form medullary bone?". *Bone*. **40** (4): 1152–8. doi:10.1016/j.bone.2006.10.029 (https://doi.org/10.1016%2Fj.bone.2006.10.029). PMID 17223615 (https://pubmed.ncbi.nlm.nih.gov/17223615).
112. Leidy, J. (1865). "Memoir on the extinct reptiles of the Cretaceous formations of the United States". *Smithsonian Contributions to Knowledge*. **14**: 1–135.
113. "*Tyrannosaurus*" (https://web.archive.org/web/20081208143829/http://www.amnh.org/exhibitions/expeditions/treasure_fossil/Treasures/Tyrannosaurus/tyrannos.html?dinos). American Museum of Natural History. Archived from the original (http://www.amnh.org/exhibitions/expeditions/treasure_fossil/Treasures/Tyrannosaurus/tyrannos.html?dinos) on December 8, 2008. Retrieved October 16, 2008.
114. Newman, B. H. (1970). "Stance and gait in the flesh-eating *Tyrannosaurus*" (https://zenodo.org/record/3674749). *Biological Journal of the Linnean Society*. **2** (2): 119–123. doi:10.1111/j.1095-8312.1970.tb01707.x (https://doi.org/10.1111%2Fj.1095-8312.1970.tb01707.x).
115. "The Age of Reptiles Mural" (http://peabody.yale.edu/exhibits/age-reptiles-mural). Yale University. 2008. Retrieved October 16, 2008.
116. Ross, R. M.; Duggan-Haas, D.; Allmon, W. D. (2013). "The Posture of *Tyrannosaurus rex*: Why Do Student Views Lag Behind the Science?". *Journal of Geoscience Education*. **61** (1): 145–160. Bibcode:2013JGeEd..61..145R (https://ui.adsabs.harvard.edu/abs/2013JGeEd..61..145R). doi:10.5408/11-259.1 (https://doi.org/10.5408%2F11-259.1). S2CID 162343784 (https://api.semanticscholar.org/CorpusID:162343784).
117. "*Tyrannosaurus Rex*: Not a tripod anymore" (https://www.aaas.org/tyrannosaurus-rex-not-tripod-anymore). *American Association for the Advancement of Science*.
118. Stevens, Kent A. (2011). "Tyrannosaurus rex – "Rex, sit" " (http://ix.cs.uoregon.edu/~kent/paleontology/Tyrannosaurus/index.html). *ix.cs.uoregon.edu*. Retrieved July 26, 2020.
119. "If T. rex fell, how did it get up, given its tiny arms and low center of gravity?" (https://www.scientificamerican.com/article/if-t-rex-fell-how-did-it/). *Scientific American*. Retrieved July 26, 2020.
120. Lambe, L. M. (1914). "On a new genus and species of carnivorous dinosaur from the Belly River Formation of Alberta, with a description of the skull of *Stephanosaurus marginatus* from the same horizon". *Ottawa Naturalist*. **27**: 129–135.

121. Horner, J. R.; Lessem, D. (1993). *The complete T. rex* (https://archive.org/details/completetrexhows00horn). New York City: Simon & Schuster. ISBN 978-0-671-74185-3.
122. "A New View of T. Rex | Smithsonian National Museum of Natural History" (https://web.archive.org/web/20200413044033/https://naturalhistory.si.edu/education/teaching-resources/paleontology/new-view-t-rex). April 13, 2020. Archived from the original (https://naturalhistory.si.edu/education/teaching-resources/paleontology/new-view-t-rex) on April 13, 2020. Retrieved April 13, 2020.
123. Carpenter, K.; Smith, M. (2001). "Forelimb Osteology and Biomechanics of *Tyrannosaurus rex*" (https://archive.org/details/mesozoicvertebra0000unse/page/90). In Tanke, D. H.; Carpenter, K. (eds.). *Mesozoic vertebrate life*. Bloomington: Indiana University Press. pp. 90–116 (https://archive.org/details/mesozoicvertebra0000unse/page/90). ISBN 978-0-253-33907-2.
124. Pickrell, J. (November 2, 2017). "T. Rex's Tiny Arms May Have Been Vicious Weapons" (https://news.nationalgeographic.com/2017/11/tyrannosaurus-rex-arms-weapons-paleontology-science/). *National Geographic*. Retrieved December 10, 2018.
125. Padian, K. (2022). "Why tyrannosaurid forelimbs were so short: An integrative hypothesis". *Acta Palaeontologica Polonica*. **67** (1): 63–76. doi:10.4202/app.00921.2021 (https://doi.org/10.4202%2Fapp.00921.2021).
126. Bakker, R. T. (1968). "The superiority of dinosaurs" (https://web.archive.org/web/20060909131058/http://bio.fsu.edu/~amarquez/Evolutionary%20Morphology%20fall%202004/Bakker/Bakker%201968%20-%20Superiority%20of%20DInos.pdf) (PDF). *Discovery*. **3** (2): 11–12. Archived from the original (http://bio.fsu.edu/~amarquez/Evolutionary%20Morphology%20fall%202004/Bakker/Bakker%201968%20-%20Superiority%20of%20DInos.pdf) (PDF) on September 9, 2006. Retrieved October 7, 2008.
127. Bakker, R. T. (1972). "Anatomical and ecological evidence of endothermy in dinosaurs" (https://web.archive.org/web/20060909173036/http://bio.fsu.edu/~amarquez/Evolutionary%20Morphology%20fall%202004/Bakker/14-%20Bakker%201972%20-%20dino%20endothermy.pdf) (PDF). *Nature*. **238** (5359): 81–85. Bibcode:1972Natur.238...81B (https://ui.adsabs.harvard.edu/abs/1972Natur.238...81B). doi:10.1038/238081a0 (https://doi.org/10.1038%2F238081a0). S2CID 4176132 (https://api.semanticscholar.org/CorpusID:4176132). Archived from the original (http://bio.fsu.edu/~amarquez/Evolutionary%20Morphology%20fall%202004/Bakker/14-%20Bakker%201972%20-%20dino%20endothermy.pdf) (PDF) on September 9, 2006. Retrieved October 7, 2008.
128. Barrick, R. E.; Showers, W. J. (1994). "Thermophysiology of *Tyrannosaurus rex*: Evidence from Oxygen Isotopes". *Science*. **265** (5169): 222–224. Bibcode:1994Sci...265..222B (https://ui.adsabs.harvard.edu/abs/1994Sci...265..222B). doi:10.1126/science.265.5169.222 (https://doi.org/10.1126%2Fscience.265.5169.222). PMID 17750663 (https://pubmed.ncbi.nlm.nih.gov/17750663). S2CID 39392327 (https://api.semanticscholar.org/CorpusID:39392327).
129. Trueman, C.; Chenery, C.; Eberth, D. A.; Spiro, B. (2003). "Diagenetic effects on the oxygen isotope composition of bones of dinosaurs and other vertebrates recovered from terrestrial and marine sediments". *Journal of the Geological Society*. **160** (6): 895–901. Bibcode:2003JGSoc.160..895T (https://ui.adsabs.harvard.edu/abs/2003JGSoc.160..895T). doi:10.1144/0016-764903-019 (https://doi.org/10.1144%2F0016-764903-019). S2CID 130658189 (https://api.semanticscholar.org/CorpusID:130658189).
130. Barrick, R. E.; Showers, W. J. (1999). "Thermophysiology and biology of *Giganotosaurus*: comparison with *Tyrannosaurus*" (https://web.archive.org/web/20110517220816/http://palaeo-electronica.org/1999_2/gigan/issue2_99.htm). *Palaeontologia Electronica*. **2** (2). Archived from the original (http://palaeo-electronica.org/1999_2/gigan/issue2_99.htm) on May 17, 2011. Retrieved October 7, 2008.

131. Barrick, R. E.; Stoskopf, M. K.; Showers, W. J. (1999). "Oxygen isotopes in dinosaur bones". In Farlow, J. O.; Brett-Surman, M. K. (eds.). *The Complete Dinosaur*. Bloomington: Indiana University Press. pp. 474–490. ISBN 978-0-253-21313-6.
132. Paladino, F. V.; Spotila, J. R.; Dodson, P. (1999). "A blueprint for giants: modeling the physiology of large dinosaurs". In Farlow, J. O.; Brett-Surman, M. K. (eds.). *The Complete Dinosaur*. Bloomington: Indiana University Press. pp. 491–504. ISBN 978-0-253-21313-6.
133. Chinsamy, A.; Hillenius, W. J. (2004). "Physiology of nonavian dinosaurs". In Weishampel, D. B.; Dodson, P.; Osmólska, H. (eds.). *The dinosauria* (https://archive.org/details/dinosauriandedit00weis). Berkeley: University of California Press. pp. 643 (https://archive.org/details/dinosauriandedit00weis/page/n661)–659. ISBN 978-0-520-24209-8.
134. Seymour, R. S. (July 5, 2013). "Maximal Aerobic and Anaerobic Power Generation in Large Crocodiles versus Mammals: Implications for Dinosaur Gigantothermy" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3702618). *PLOS ONE*. **8** (7): e69361. Bibcode:2013PLoSO...869361S (https://ui.adsabs.harvard.edu/abs/2013PLoSO...869361S). doi:10.1371/journal.pone.0069361 (https://doi.org/10.1371%2Fjournal.pone.0069361). ISSN 1932-6203 (https://www.worldcat.org/issn/1932-6203). PMC 3702618 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3702618). PMID 23861968 (https://pubmed.ncbi.nlm.nih.gov/23861968).
135. "T. Rex had an air conditioner in its head, study suggests" (https://www.sciencedaily.com/releases/2019/09/190904125337.htm). *ScienceDaily*. Retrieved September 6, 2019.
136. Fields, H. (2006). "Dinosaur Shocker" (http://www.smithsonianmag.com/science-nature/10021606.html). *Smithsonian Magazine*. Retrieved October 2, 2008.
137. Schweitzer, M. H.; Wittmeyer, J. L.; Horner, J. R.; Toporski, J. K. (2005). "Soft-tissue vessels and cellular preservation in *Tyrannosaurus rex*". *Science*. **307** (5717): 1952–5. Bibcode:2005Sci...307.1952S (https://ui.adsabs.harvard.edu/abs/2005Sci...307.1952S). doi:10.1126/science.1108397 (https://doi.org/10.1126%2Fscience.1108397). PMID 15790853 (https://pubmed.ncbi.nlm.nih.gov/15790853). S2CID 30456613 (https://api.semanticscholar.org/CorpusID:30456613).
138. Rincon, P. (April 12, 2007). "Protein links T. rex to chickens" (http://news.bbc.co.uk/2/hi/science/nature/6548719.stm). *BBC News*. Retrieved October 2, 2008.
139. Vergano, D. (April 13, 2007). "Yesterday's T. Rex is today's chicken" (https://www.usatoday.com/tech/science/discoveries/2007-04-12-trex-protein_N.htm). *USA Today*. Retrieved October 8, 2008.
140. Kaye, T. G.; Gaugler, G.; Sawlowicz, Z. (2008). Stepanova, A. (ed.). "Dinosaurian Soft Tissues Interpreted as Bacterial Biofilms" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2483347). *PLOS ONE*. **3** (7): e2808. Bibcode:2008PLoSO...3.2808K (https://ui.adsabs.harvard.edu/abs/2008PLoSO...3.2808K). doi:10.1371/journal.pone.0002808 (https://doi.org/10.1371%2Fjournal.pone.0002808). PMC 2483347 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2483347). PMID 18665236 (https://pubmed.ncbi.nlm.nih.gov/18665236).
141. "New Research Challenges Notion That Dinosaur Soft Tissues Still Survive" (http://newswise.com/articles/view/542898/) (Press release). Newswise. July 24, 2008. Retrieved October 8, 2008.
142. "Researchers Debate: Is It Preserved Dinosaur Tissue, or Bacterial Slime?" (http://blogs.discovermagazine.com/80beats/2008/07/30/researchers-debate-is-it-preserved-dinosaur-tissue-or-bacterial-slime/) (Press release). Discover. July 30, 2008. Retrieved September 4, 2008.

143. San Antonio, J. D.; Schweitzer, M. H.; Jensen, S. T.; Kalluri, R.; Buckley, M.; Orgel, J. P. R. O. (2011). Van Veen, H. W. (ed.). "Dinosaur Peptides Suggest Mechanisms of Protein Survival" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3110760). *PLOS ONE*. **6** (6): e20381. Bibcode:2011PLoSO...620381S (https://ui.adsabs.harvard.edu/abs/2011PLoSO...620381S). doi:10.1371/journal.pone.0020381 (https://doi.org/10.1371%2Fjournal.pone.0020381). PMC 3110760 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3110760). PMID 21687667 (https://pubmed.ncbi.nlm.nih.gov/21687667).
144. Peterson, J. E.; Lenczewski, M. E.; Scherer, R. P. (October 12, 2010). "Influence of Microbial Biofilms on the Preservation of Primary Soft Tissue in Fossil and Extant Archosaurs" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2953520). *PLOS ONE*. **5** (10): e13334. Bibcode:2010PLoSO...513334P (https://ui.adsabs.harvard.edu/abs/2010PLoSO...513334P). doi:10.1371/journal.pone.0013334 (https://doi.org/10.1371%2Fjournal.pone.0013334). PMC 2953520 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2953520). PMID 20967227 (https://pubmed.ncbi.nlm.nih.gov/20967227). "[T]he interpretation of preserved organic remains as microbial biofilm [is] highly unlikely"
145. Hutchinson, J. R.; Garcia, M. (2002). "*Tyrannosaurus* was not a fast runner". *Nature*. **415** (6875): 1018–21. Bibcode:2002Natur.415.1018H (https://ui.adsabs.harvard.edu/abs/2002Natur.415.1018H). doi:10.1038/4151018a (https://doi.org/10.1038%2F4151018a). PMID 11875567 (https://pubmed.ncbi.nlm.nih.gov/11875567). S2CID 4389633 (https://api.semanticscholar.org/CorpusID:4389633).
146. Hutchinson, J. R. (2004). "Biomechanical Modeling and Sensitivity Analysis of Bipedal Running Ability. II. Extinct Taxa" (https://web.archive.org/web/20081031093050/http://www.rvc.ac.uk/AboutUs/Staff/jhutchinson/documents/JRH13.pdf) (PDF). *Journal of Morphology*. **262** (1): 441–461. doi:10.1002/jmor.10240 (https://doi.org/10.1002%2Fjmor.10240). PMID 15352202 (https://pubmed.ncbi.nlm.nih.gov/15352202). S2CID 15677774 (https://api.semanticscholar.org/CorpusID:15677774). Archived from the original (http://www.rvc.ac.uk/AboutUs/Staff/jhutchinson/documents/JRH13.pdf) (PDF) on October 31, 2008.
147. Holtz, T. R. (May 1, 1996). "Phylogenetic taxonomy of the Coelurosauria (Dinosauria; Theropoda)" (http://jpaleontol.geoscienceworld.org/cgi/content/abstract/70/3/536). *Journal of Paleontology*. **70** (3): 536–538. doi:10.1017/S0022336000038506 (https://doi.org/10.1017%2FS0022336000038506). Retrieved October 3, 2008.
148. Benton, M. (2014). *Vertebrate Palaeontology* (https://books.google.com/books?id=VThUUUtM8A4C&q=tyrannosaurus+metatarsals+squeezing&pg=PA193) (4th ed.). p. 193. ISBN 978-1118407554.
149. Dececchi, T. Alexander; Mloszewska, Aleksandra M.; Jr, Thomas R. Holtz; Habib, Michael B.; Larsson, Hans C. E. (May 13, 2020). "The fast and the frugal: Divergent locomotory strategies drive limb lengthening in theropod dinosaurs" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC7220109). *PLOS ONE*. **15** (5): e0223698. Bibcode:2020PLoSO..1523698D (https://ui.adsabs.harvard.edu/abs/2020PLoSO..1523698D). doi:10.1371/journal.pone.0223698 (https://doi.org/10.1371%2Fjournal.pone.0223698). PMC 7220109 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC7220109). PMID 32401793 (https://pubmed.ncbi.nlm.nih.gov/32401793).
150. "T. rex was a champion walker, super-efficient at lower speeds" (https://www.eurekalert.org/pub_releases/2020-05/p-trw051320.php). *EurekAlert!*.

151. van Bijlert, P. A.; van Soest, A. J. K.; Schulp, A. S. (2021). "Natural Frequency Method: estimating the preferred walking speed of *Tyrannosaurus rex* based on tail natural frequency" (https://phys.org/news/2021-04-dinosaur-biomechanical-tyrannosaurus-rex-gait.html). *Royal Society Open Science*. **8** (4): 201441. Bibcode:2021RSOS....801441V (https://ui.adsabs.harvard.edu/abs/2021RSOS....801441V). doi:10.1098/rsos.201441 (https://doi.org/10.1098%2Frsos.201441). PMC 8059583 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8059583). PMID 33996115 (https://pubmed.ncbi.nlm.nih.gov/33996115). S2CID 233312053 (https://api.semanticscholar.org/CorpusID:233312053).
152. "Why *Tyrannosaurus* was a slow runner and why the largest are not always the fastest" (https://www.sciencedaily.com/releases/2017/07/170717115657.htm). *ScienceDaily*. July 17, 2017. Retrieved November 10, 2017.
153. Hirt, M. R.; Jetz, W.; Rall, B. C.; Brose, U. (2017). "A general scaling law reveals why the largest animals are not the fastest". *Nature Ecology & Evolution*. **1** (8): 1116–1122. doi:10.1038/s41559-017-0241-4 (https://doi.org/10.1038%2Fs41559-017-0241-4). PMID 29046579 (https://pubmed.ncbi.nlm.nih.gov/29046579). S2CID 425473 (https://api.semanticscholar.org/CorpusID:425473).
154. Sellers, W. I.; Pond, S. B.; Brassey, C. A.; Manning, P. L.; Bates, K. T. (July 18, 2017). "Investigating the running abilities of *Tyrannosaurus rex* using stress-constrained multibody dynamic analysis" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5518979). *PeerJ*. **5**: e3420. doi:10.7717/peerj.3420 (https://doi.org/10.7717%2Fpeerj.3420). ISSN 2167-8359 (https://www.worldcat.org/issn/2167-8359). PMC 5518979 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5518979). PMID 28740745 (https://pubmed.ncbi.nlm.nih.gov/28740745).
155. Cotton, J. R.; Hartman, S. A.; Currie, P. J.; Witmer, L. M.; Russell, A. P.; Holtz, T. R. Jr; Burns, M. E.; Surring, L. A.; Mallison, H.; Henderson, D. M.; O'Brien, H.; Snively, E. (February 21, 2019). "Lower rotational inertia and larger leg muscles indicate more rapid turns in tyrannosaurids than in other large theropods" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6387760). *PeerJ*. **7**: e6432. doi:10.7717/peerj.6432 (https://doi.org/10.7717%2Fpeerj.6432). PMC 6387760 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6387760). PMID 30809441 (https://pubmed.ncbi.nlm.nih.gov/30809441).
156. Caneer, T.; Molkestad, T.; Lucas, S.G. (2021). "TRACKS IN THE UPPER CRETACEOUS OF THE RATON BASIN POSSIBLY SHOW TYRANNOSAURID RISING FROM A PRONE POSITION" (https://www.researchgate.net/publication/348002331). *New Mexico Museum of Natural History and Science*: 29–37.
157. Smith, S.D; Persons, W.S.; Xing, Lida (2016). "A tyrannosaur trackway at Glenrock, Lance Formation (Maastrichtian), Wyoming" (https://www.sciencedirect.com/science/article/abs/pii/S0195667115301452). *Cretaceous Research*. **61**: 1–4. doi:10.1016/j.cretres.2015.12.020 (https://doi.org/10.1016%2Fj.cretres.2015.12.020).
158. De Pastino, B. (2016). "Tyrannosaur Tracks Discovered in Wyoming Reveal Dinosaur's Speed" (http://westerndigs.org/tyrannosaur-tracks-discovered-in-wyoming-reveal-dinosaurs-speed/). *Western Digs*. **61**: 1–4. doi:10.1016/j.cretres.2015.12.020 (https://doi.org/10.1016%2Fj.cretres.2015.12.020).
159. Witmer, L. M.; Ridgely, R. C. (2009). "New Insights into the Brain, Braincase, and Ear Region of Tyrannosaurs (Dinosauria, Theropoda), with Implications for Sensory Organization and Behavior" (https://doi.org/10.1002%2Far.20983). *The Anatomical Record*. **292** (9): 1266–1296. doi:10.1002/ar.20983 (https://doi.org/10.1002%2Far.20983). PMID 19711459 (https://pubmed.ncbi.nlm.nih.gov/19711459). S2CID 17978731 (https://api.semanticscholar.org/CorpusID:17978731).
160. Stevens, K. A. (April 1, 2011). "The Binocular Vision of Theropod Dinosaurs" (http://ix.cs.uoregon.edu/~kent/paleontology/binocularVision/). Retrieved July 19, 2013.

161. "*T. Rex* brain study reveals a refined 'nose' " (http://www.canada.com/calgaryherald/story.html?id=3641f27e-ca2e-44e8-a56b-f9a0b4aef4b5). *Calgary Herald*. October 28, 2008. Retrieved October 29, 2008.
162. Kawabe, Soichiro; Hattori, Soki (2021). "Complex neurovascular system in the dentary of Tyrannosaurus" (https://doi.org/10.1080%2F08912963.2021.1965137). *Historical Biology*: 1–9. doi:10.1080/08912963.2021.1965137 (https://doi.org/10.1080%2F08912963.2021.1965137).
163. "T. rex's jaw had sensors that made it an even more fearsome predator" (https://phys.org/news/2021-08-rex-jaw-sensors-fearsome-predator.html). *phys.org*.
164. Benoit, Florian Bouabdellah, Emily Lessner, and Julien (January 20, 2022). "The rostral neurovascular system of Tyrannosaurus rex" (https://palaeo-electronica.org/content/2022/3518-t-rex-trigeminal-canals). *Palaeontologia Electronica*. **25** (1): 1–20. doi:10.26879/1178 (https://doi.org/10.26879%2F1178). ISSN 1094-8074 (https://www.worldcat.org/issn/1094-8074). S2CID 246204236 (https://api.semanticscholar.org/CorpusID:246204236).
165. Hurlburt, G. S.; Ridgely, R. C.; Witmer, L. M. (July 5, 2013). "Relative size of brain and cerebrum in Tyrannosaurid dinosaurs: an analysis using brain-endocast quantitative relationships in extant alligators" (https://www.researchgate.net/publication/256536375). In Parrish, M. J.; Molnar, R. E.; Currie, P. J.; Koppelhus, E. B. (eds.). *Tyrannosaurid Paleobiology*. Indiana University Press. pp. 134–154. ISBN 978-0-253-00947-0. Retrieved October 20, 2013.
166. Brusatten, Steve (2018). *The Rise and Fall of the Dinosaurs*. New York, New York: HarperCollins Publishers. p. 219. ISBN 9780062490438.
167. "Dino Gangs" (https://web.archive.org/web/20120119125039/http://www.discoveryuk.com/the-loop/dino-gangs/). *Discovery Channel*. June 22, 2011. Archived from the original (http://www.discoveryuk.com/the-loop/dino-gangs/) on January 19, 2012. Retrieved January 19, 2012.
168. Collins, N. (June 22, 2011). "Tyrannosaurus Rex 'hunted in packs' " (https://www.telegraph.co.uk/news/science/dinosaurs/8589113/Tyrannosaurus-Rex-hunted-in-packs.html). *The Telegraph*. Archived (https://ghostarchive.org/archive/20220110/https://www.telegraph.co.uk/news/science/dinosaurs/8589113/Tyrannosaurus-Rex-hunted-in-packs.html) from the original on January 10, 2022. Retrieved March 23, 2014.
169. Wallis, P. (June 11, 2012). "Op-Ed: T. Rex pack hunters? Scary, but likely to be true" (http://digitaljournal.com/article/326451). *Digitaljournal.com*. Retrieved December 23, 2015.
170. Switek, B. (July 25, 2011). "A bunch of bones doesn't make a gang of bloodthirsty tyrannosaurs" (https://www.theguardian.com/science/blog/2011/jul/25/bunch-bones-gang-bloodthirsty-tyrannosaurs). *The Guardian*. Retrieved June 21, 2015.
171. Currie, Philip J. (1998). "Possible evidence of gregarious behaviour in tyrannosaurids" (https://web.archive.org/web/20090326062833/http://www.mnhn.ul.pt/geologia/gaia/21.pdf) (PDF). *Gaia*. **15**: 271–277. Archived from the original (http://www.mnhn.ul.pt/geologia/gaia/21.pdf) (PDF) on March 26, 2009. Retrieved May 3, 2009. (not printed until 2000)
172. Sample, I. (July 23, 2014). "Researchers find first sign that tyrannosaurs hunted in packs" (https://www.theguardian.com/science/2014/jul/23/tyrannosaurs-hunted-packs-tracks-canada). *The Guardian*. Retrieved July 28, 2014.
173. McCrea, R. T. (2014). "A 'Terror of Tyrannosaurs': The First Trackways of Tyrannosaurids and Evidence of Gregariousness and Pathology in Tyrannosauridae" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4108409). *PLOS ONE*. **9** (7): e103613. Bibcode:2014PLoSO...9j3613M (https://ui.adsabs.harvard.edu/abs/2014PLoSO...9j3613M). doi:10.1371/journal.pone.0103613 (https://doi.org/10.1371%2Fjournal.pone.0103613). PMC 4108409 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4108409). PMID 25054328 (https://pubmed.ncbi.nlm.nih.gov/25054328).

174. Roach, Brian T.; Brinkman, Daniel T. (2007). "A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs". *Bulletin of the Peabody Museum of Natural History*. **48** (1): 103–138. doi:10.3374/0079-032X(2007)48[103:AROCPH]2.0.CO;2 (https://doi.org/10.3374%2F0079-032X%282007%2948%5B103%3AAROCPH%5D2.0.CO%3B2).
175. Peterson, J. E.; Henderson, M. D.; Sherer, R. P.; Vittore, C. P. (2009). "Face Biting On A Juvenile Tyrannosaurid And Behavioral Implications" (https://archive.today/20130811100341/http://palaios.sepmonline.org/content/24/11/780). *PALAIOS*. **24** (11): 780–784. Bibcode:2009Palai..24..780P (https://ui.adsabs.harvard.edu/abs/2009Palai..24..780P). doi:10.2110/palo.2009.p09-056r (https://doi.org/10.2110%2Fpalo.2009.p09-056r). S2CID 85602478 (https://api.semanticscholar.org/CorpusID:85602478). Archived from the original (http://palaios.sepmonline.org/content/24/11/780) on August 11, 2013.
176. Parisi, T. (November 2, 2009). "The terrible teens of T. rex NIU scientists: Young tyrannosaurs did serious battle against each other" (https://web.archive.org/web/20130814164927/http://www.niu.edu/PubAffairs/RELEASES/2009/nov/testytrex.shtml). Northern Illinois University. Archived from the original (http://www.niu.edu/PubAffairs/RELEASES/2009/nov/testytrex.shtml) on August 14, 2013. Retrieved August 10, 2013.
177. "Time to Slay the *T. rex* Scavenger "Debate" " (https://web.archive.org/web/20180712030717/https://www.nationalgeographic.com/science/phenomena/2013/07/16/time-to-slay-the-t-rex-scavenger-debate/). *National Geographic*. July 16, 2013. Archived from the original (https://www.nationalgeographic.com/science/phenomena/2013/07/16/time-to-slay-the-t-rex-scavenger-debate/) on July 12, 2018.
178. Black, Riley (April 13, 2012). "When *Tyrannosaurus* Chomped Sauropods" (https://www.smithsonianmag.com/science-nature/when-tyrannosaurus-chomped-sauropods-67170161/). *Smithsonian Magazine*. Smithsonian Media. **25**: 469. doi:10.1671/0272-4634(2005)025[0469:TRFTUC]2.0.CO;2 (https://doi.org/10.1671%2F0272-4634%282005%29025%5B0469%3ATRFTUC%5D2.0.CO%3B2). Retrieved August 24, 2013.
179. Black, Riley (2012). "The *Tyrannosaurus rex*s Dangerous and Deadly Bite" (https://www.smithsonianmag.com/science-nature/the-tyrannosaurus-rexs-dangerous-and-deadly-bite-37252918/). *Smithsonian Magazine*. Smithsonian Institution.
180. Bates, K. T.; Falkingham, P. L. (February 29, 2012). "Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3391458). *Biological Letters*. **8** (4): 660–664. doi:10.1098/rsbl.2012.0056 (https://doi.org/10.1098%2Frsbl.2012.0056). PMC 3391458 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3391458). PMID 22378742 (https://pubmed.ncbi.nlm.nih.gov/22378742).
181. Scully, C. (2002). *Oxford Handbook of Applied Dental Sciences* (https://archive.org/details/oxfordhandbookof00cris). Oxford University Press. p. 156 (https://archive.org/details/oxfordhandbookof00cris/page/156). ISBN 978-0-19-851096-3.
182. Lautenschlager, Stephan (November 4, 2015). "Estimating cranial musculoskeletal constraints in theropod dinosaurs" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4680622). *Royal Society Open Science*. **2** (11): 150495. Bibcode:2015RSOS....250495L (https://ui.adsabs.harvard.edu/abs/2015RSOS....250495L). doi:10.1098/rsos.150495 (https://doi.org/10.1098%2Frsos.150495). PMC 4680622 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4680622). PMID 26716007 (https://pubmed.ncbi.nlm.nih.gov/26716007).
183. "The better to eat you with? How dinosaurs' jaws influenced diet" (https://web.archive.org/web/20151104162130/https://www.sciencedaily.com/releases/2015/11/151103213705.htm). *Science Daily*. November 3, 2015. Archived from the original (https://www.sciencedaily.com/releases/2015/11/151103213705.htm) on November 4, 2015. Retrieved September 14, 2018.

184. Lambe, L. B. (1917). "The Cretaceous theropodous dinosaur *Gorgosaurus*" (https://www.biodiversitylibrary.org/item/252624). *Memoirs of the Geological Survey of Canada*. **100**: 1–84. doi:10.4095/101672 (https://doi.org/10.4095%2F101672).
185. Farlow, J. O.; Holtz (2002). "The fossil record of predation in dinosaurs" (https://web.archive.org/web/20081031093048/http://www.yale.edu/ypmip/predation/Chapter_09.pdf) (PDF). In Kowalewski, M.; Kelley, P. H. (eds.). *The Fossil Record of Predation*. The Paleontological Society Papers. Vol. 8. T. R. Jr. pp. 251–266. Archived from the original (http://www.yale.edu/ypmip/predation/Chapter_09.pdf) (PDF) on October 31, 2008.
186. Horner, J. R. (1994). "Steak knives, beady eyes, and tiny little arms (a portrait of *Tyrannosaurus* as a scavenger)". *The Paleontological Society Special Publication*. **7**: 157–164. doi:10.1017/S2475262200009497 (https://doi.org/10.1017%2FS2475262200009497).
187. Amos, J. (July 31, 2003). "Science/Nature: *T. rex* goes on trial" (http://news.bbc.co.uk/1/hi/sci/tech/3112527.stm). *BBC News*. Retrieved December 23, 2015.
188. Amos, J. (July 31, 2003). "Science/Nature: *T. rex* goes on trial" (http://news.bbc.co.uk/1/hi/sci/tech/3112527.stm). *BBC News*. Retrieved December 23, 2015.
189. Farlow, J. O.; Holtz, T.R. (2002). Kowalewski, M.; Kelley, P. H. (eds.). "The Fossil Record of Predation in Dinosaurs" (https://web.archive.org/web/20081031093048/http://www.yale.edu/ypmip/predation/Chapter_09.pdf) (PDF). *The Paleontological Society Papers*. **8**: 251–266. doi:10.1017/S108933260000111X (https://doi.org/10.1017%2FS108933260000111X). Archived from the original (http://www.yale.edu/ypmip/predation/Chapter_09.pdf) (PDF) on October 31, 2008.
190. Holtz, Thomas R. (2008). "Chapter 20: A critical re-appraisal of the obligate scavenging hypothesis for Tyrannosaurus rex and other tyrant dinosaurs" (https://www.academia.edu/293223). In Larson, Peter; Carpenter, Kenneth (eds.). *Tyrannosaurus rex: The Tyrant King*. Book Publishers. pp. 371–394. ISBN 978-0-253-35087-9.
191. Chin, K.; Tokaryk, T. T.; Erickson, G. M.; Calk, L. C. (June 18, 1998). "A king-sized theropod coprolite" (https://zenodo.org/record/3943146). *Nature*. **393** (6686): 680–682. Bibcode:1998Natur.393..680C (https://ui.adsabs.harvard.edu/abs/1998Natur.393..680C). doi:10.1038/31461 (https://doi.org/10.1038%2F31461). S2CID 4343329 (https://api.semanticscholar.org/CorpusID:4343329). Summary at Monastersky, R. (June 20, 1998). "Getting the scoop from the poop of *T. rex*" (https://web.archive.org/web/20130511121022/http://www.sciencenews.org/pages/sn_arc98/6_20_98/fob2.htm). *Science News*. **153** (25): 391. doi:10.2307/4010364 (https://doi.org/10.2307%2F4010364). JSTOR 4010364 (https://www.jstor.org/stable/4010364). Archived from the original (http://www.sciencenews.org/pages/sn_arc98/6_20_98/fob2.htm) on May 11, 2013.
192. Choiniere, Jonah N.; Neenan, James M.; Schmitz, Lars; Ford, David P.; Chapelle, Kimberley E. J.; Balanoff, Amy M.; Sipla, Justin S.; Georgi, Justin A.; Walsh, Stig A.; Norell, Mark A.; Xu, Xing; Clark, James M.; Benson, Roger B. J. (May 7, 2021). "Evolution of vision and hearing modalities in theropod dinosaurs" (https://science.sciencemag.org/content/372/6542/610). *Science*. **372** (6542): 610–613. Bibcode:2021Sci...372..610C (https://ui.adsabs.harvard.edu/abs/2021Sci...372..610C). doi:10.1126/science.abe7941 (https://doi.org/10.1126%2Fscience.abe7941). ISSN 0036-8075 (https://www.worldcat.org/issn/0036-8075). PMID 33958472 (https://pubmed.ncbi.nlm.nih.gov/33958472). S2CID 233872840 (https://api.semanticscholar.org/CorpusID:233872840).
193. "Shuvuuia: A dinosaur that hunted in the dark" (https://phys.org/news/2021-05-shuvuuia-dinosaur-dark.html). *phys.org*.
194. Carpenter, K. (1998). "Evidence of predatory behavior by theropod dinosaurs" (https://web.archive.org/web/20071117132451/http://vertpaleo.org/publications/jvp/15-576-591.cfm). *Gaia*. **15**: 135–144. Archived from the original (http://vertpaleo.org/publications/jvp/15-576-591.cfm) on November 17, 2007. Retrieved December 5, 2007.

195. Eberth, David A.; Evans, David C., eds. (2015). "Paleopathology in Late Cretaceous Hadrosauridae from Alberta, Canada". *Hadrosaurs*. Indiana University Press. pp. 540–571. ISBN 978-0-253-01390-3. preprint (https://www.researchgate.net/publication/290310286_Paleopathology_in_Late_Cretaceous_Hadrosauridae_from_Alberta_Canada)
196. Siviero, ART V.; Brand, Leonard R.; Cooper, Allen M.; Hayes, William K.; Rega, Elizabeth; Siviero, Bethania C.T. (2020). "Skeletal Trauma with Implications for Intratail Mobility in Edmontosaurus Annectens from a Monodominant Bonebed, Lance Formation (Maastrichtian), Wyoming USA" (https://pubs.geoscienceworld.org/sepm/palaios/article-abstract/35/4/201/584648/SKELETAL-TRAUMA-WITH-IMPLICATIONS-FOR-INTRATAIL?redirectedFrom=fulltext--). *PALAIOS*. **35** (4): 201–214. Bibcode:2020Palai..35..201S (https://ui.adsabs.harvard.edu/abs/2020Palai..35..201S). doi:10.2110/palo.2019.079 (https://doi.org/10.2110%2Fpalo.2019.079). S2CID 218503493 (https://api.semanticscholar.org/CorpusID:218503493).
197. Happ, J.; Carpenter, K. (2008). "An analysis of predator–prey behavior in a head-to-head encounter between *Tyrannosaurus rex* and *Triceratops*". In Carpenter, K.; Larson, P. E. (eds.). *Tyrannosaurus rex, the Tyrant King (Life of the Past)*. Bloomington: Indiana University Press. pp. 355–368. ISBN 978-0-253-35087-9.
198. Dodson, P. (1996). *The Horned Dinosaurs* (https://archive.org/details/horneddinosaursn00dods). Princeton University Press. p. 19 (https://archive.org/details/horneddinosaursn00dods/page/n32).
199. Tanke, D. H.; Currie, P. J. (1998). "Head-biting behavior in theropod dinosaurs: paleopathological evidence" (https://web.archive.org/web/20080227134632/http://www.mnhn.ul.pt/geologia/gaia/12.pdf) (PDF). *Gaia* (15): 167–184. ISSN 0871-5424 (https://www.worldcat.org/issn/0871-5424). Archived from the original (http://www.mnhn.ul.pt/geologia/gaia/12.pdf) (PDF) on February 27, 2008.
200. Peterson, J. E.; Daus, K. N. (March 4, 2019). "Feeding traces attributable to juvenile *Tyrannosaurus rex* offer insight into ontogenetic dietary trends" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6404657). *PeerJ*. **7**: e6573. doi:10.7717/peerj.6573 (https://doi.org/10.7717%2Fpeerj.6573). ISSN 2167-8359 (https://www.worldcat.org/issn/2167-8359). PMC 6404657 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6404657). PMID 30863686 (https://pubmed.ncbi.nlm.nih.gov/30863686).
201. Abler, W. L. (1992). "The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals". *Paleobiology*. **18** (2): 161–183. doi:10.1017/S0094837300013956 (https://doi.org/10.1017%2FS0094837300013956).
202. Goldstein, E. J. C.; Tyrrell, K. L.; Citron, D. M.; Cox, C. R.; Recchio, I. M.; Okimoto, B.; Bryja, J.; Fry, B. G. (June 1, 2013). "Anaerobic and aerobic bacteriology of the saliva and gingiva from 16 captive Komodo dragons (*Varanus komodoensis*): new implications for the "bacteria as venom" model". *Journal of Zoo and Wildlife Medicine*. **44** (2): 262–272. doi:10.1638/2012-0022R.1 (https://doi.org/10.1638%2F2012-0022R.1). ISSN 1042-7260 (https://www.worldcat.org/issn/1042-7260). PMID 23805543 (https://pubmed.ncbi.nlm.nih.gov/23805543). S2CID 9932073 (https://api.semanticscholar.org/CorpusID:9932073).
203. Snively, E.; Cotton, J. R.; Ridgely, R.; Witmer, L. M. (2013). "Multibody dynamics model of head and neck function in *Allosaurus* (Dinosauria, Theropoda)" (https://doi.org/10.26879%2F338). *Palaeontologia Electronica*. **16** (2). doi:10.26879/338 (https://doi.org/10.26879%2F338).
204. Longrich, N. R.; Horner, J. R.; Erickson, G. M.; Currie, P. J. (2010). "Cannibalism in *Tyrannosaurus rex*" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2955550). *PLOS ONE*. **5** (10): e13419. Bibcode:2010PLoSO...513419L (https://ui.adsabs.harvard.edu/abs/2010PLoSO...513419L). doi:10.1371/journal.pone.0013419 (https://doi.org/10.1371%2Fjournal.pone.0013419). PMC 2955550 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2955550). PMID 20976177 (https://pubmed.ncbi.nlm.nih.gov/20976177).

205. "NEW EVIDENCE FOR CANNIBALISM IN TYRANNOSAURID DINOSAURS FROM THE UPPER CRETACEOUS (CAMPANIAN/MAASTRICHTIAN) SAN JUAN BASIN OF NEW MEXICO" (https://www.researchgate.net/publication/348002335). *ResearchGate*.
206. Farlow, James Orville (1989). *Paleobiology of the Dinosaurs* (https://books.google.com/books?id=jXU6atz3RTYC&dq=dinosaur+parenting+behavior&pg=PA21). Geological Society of America. ISBN 978-0-8137-2238-2.
207. "Maiasaura," Dodson, et al. (1994); pages 116-117
208. Horner, J.R.; Makela, R. (1979). "Nest of juveniles provides evidence of family structure among dinosaurs". *Nature*. **282** (5736): 296–298. Bibcode:1979Natur.282..296H (https://ui.adsabs.harvard.edu/abs/1979Natur.282..296H). doi:10.1038/282296a0 (https://doi.org/10.1038%2F282296a0). S2CID 4370793 (https://api.semanticscholar.org/CorpusID:4370793).
209. " "The Best of all Mothers" Maiasaura peeblesorum" (http://bioweb.uwlax.edu/bio203/s2014/fischbac_sama/interactions.htm). *bioweb.uwlax.edu/*. University of Wisconsin-La Crosse. Retrieved March 22, 2021.
210. Norell, Mark A.; Clark, James M.; Chiappe, Luis M.; Dashzeveg, Demberelyin (1995). "A nesting dinosaur" (https://www.nature.com/articles/378774a0). *Nature*. **378** (6559): 774–776. Bibcode:1995Natur.378..774N (https://ui.adsabs.harvard.edu/abs/1995Natur.378..774N). doi:10.1038/378774a0 (https://doi.org/10.1038%2F378774a0). ISSN 1476-4687 (https://www.worldcat.org/issn/1476-4687). S2CID 4245228 (https://api.semanticscholar.org/CorpusID:4245228).
211. Watanabe, Myrna E. (March 1, 2009). "Evolving Ideas on the Origins of Parental Care" (https://doi.org/10.1525/bio.2009.59.3.17). *BioScience*. **59** (3): 272. doi:10.1525/bio.2009.59.3.17 (https://doi.org/10.1525%2Fbio.2009.59.3.17). ISSN 0006-3568 (https://www.worldcat.org/issn/0006-3568). S2CID 85066992 (https://api.semanticscholar.org/CorpusID:85066992).
212. Rothschild, B.; Tanke, D. H.; Ford, T. L. (2001). "Theropod stress fractures and tendon avulsions as a clue to activity". In Tanke, D. H.; Carpenter, K. (eds.). *Mesozoic Vertebrate Life*. Indiana University Press. pp. 331–336.
213. Wolff, E. D. S.; Salisbury, S. W.; Horner, J. R.; Varricchi, D. J. (2009). Hansen, D. M. (ed.). "Common Avian Infection Plagued the Tyrant Dinosaurs" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2748709). *PLOS ONE*. **4** (9): e7288. Bibcode:2009PLoSO...4.7288W (https://ui.adsabs.harvard.edu/abs/2009PLoSO...4.7288W). doi:10.1371/journal.pone.0007288 (https://doi.org/10.1371%2Fjournal.pone.0007288). PMC 2748709 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2748709). PMID 19789646 (https://pubmed.ncbi.nlm.nih.gov/19789646).
214. Rega, E. (2012). "Disease in Dinosaurs". In Brett-Surman, M.; Holtz, T.; Farlow, J. (eds.). *The Complete Dinosaur*. Bloomington: Indiana University Press.
215. Perkins, S. (October 29, 2015). "Tyrannosaurs were probably cannibals (Comment)" (http://news.sciencemag.org/paleontology/2015/10/tyrannosaurs-were-probably-cannibals). *Science*. Retrieved November 2, 2015.
216. Estes, R.; Berberian, P. (1970). "Paleoecology of a late Cretaceous vertebrate community from Montana". *Breviora*. **343**: 1–35.
217. Derstler, K. (1994). "Dinosaurs of the Lance Formation in eastern Wyoming". In Nelson, G. E. (ed.). *The Dinosaurs of Wyoming*. Wyoming Geological Association Guidebook, 44th Annual Field Conference. Wyoming Geological Association. pp. 127–146.
218. Weishampel, D. B.; Barrett, P. M.; Coria, R. A.; Loeuff, J. L.; Xu, X.; Zhao, X.; Sahni, A.; Gomani, E. M. P.; Noto, C. R. (2004). "Dinosaur Distribution". In Weishampel, D. B.; Dodson, P.; Osmólska, H. (eds.). *The Dinosauria* (https://archive.org/details/dinosauriandedit00weis) (2nd ed.). Berkeley: University of California Press. pp. 574 (https://archive.org/details/dinosauriandedit00weis/page/n592)–588. ISBN 978-0-520-24209-8.

219. Jasinski, S. E.; Sullivan, R. M.; Lucas, S. G. (2011). "Taxonomic composition of the Alamo Wash local fauna from the Upper Cretaceous Ojo Alamo Formation (Naashoibito Member) San Juan Basin, New Mexico". *Bulletin*. **53**: 216–271.
220. Serrano-Brañas, C. I.; Torres-Rodrígueza, E.; Luna, P. C. R.; González, I.; González-León, C. (2014). "Tyrannosaurid teeth from the Lomas Coloradas Formation, Cabullona Group (Upper Cretaceous) Sonora, México". *Cretaceous Research*. **49**: 163–171. doi:10.1016/j.cretres.2014.02.018 (https://doi.org/10.1016%2Fj.cretres.2014.02.018).
221. Brusatte, S. L.; Carr, T. D. (2016). "The phylogeny and evolutionary history of tyrannosauroid dinosaurs" (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4735739). *Scientific Reports*. **6**: 20252. Bibcode:2016NatSR...620252B (https://ui.adsabs.harvard.edu/abs/2016NatSR...620252B). doi:10.1038/srep20252 (https://doi.org/10.1038%2Fsrep20252). PMC 4735739 (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4735739). PMID 26830019 (https://pubmed.ncbi.nlm.nih.gov/26830019).
222. Chang, Kenneth (April 15, 2021). "How Many Tyrannosaurus Rexes Ever Lived on Earth? Here's a New Clue" (https://ghostarchive.org/archive/20211228/https://www.nytimes.com/2021/04/15/science/tyrannosaurus-rex-population.html). *The New York Times*. Archived from the original (https://www.nytimes.com/2021/04/15/science/tyrannosaurus-rex-population.html) on December 28, 2021.
223. Marshall, Charles R.; Latorre, Daniel V.; Wilson, Connor J.; Frank, Tanner M.; Magoulick, Katherine M.; Zimmt, Joshua B.; Poust, Ashley W. (April 16, 2021). "Absolute abundance and preservation rate of Tyrannosaurus rex" (https://doi.org/10.1126%2Fscience.abc8300). *Science*. **372** (6539): 284–287. Bibcode:2021Sci...372..284M (https://ui.adsabs.harvard.edu/abs/2021Sci...372..284M). doi:10.1126/science.abc8300 (https://doi.org/10.1126%2Fscience.abc8300). PMID 33859033 (https://pubmed.ncbi.nlm.nih.gov/33859033).
224. Meiri, Shai (2022). "Population sizes of T. rex cannot be precisely estimated" (https://escholarship.org/uc/item/8mj4015f). *Frontiers of Biogeography*. doi:10.21425/F5FBG53781 (https://doi.org/10.21425%2FF5FBG53781). S2CID 245288933 (https://api.semanticscholar.org/CorpusID:245288933).
225. Marshall, Charles R.; Latorre, Daniel V.; Wilson, Connor J.; Frank, Tanner M.; Magoulick, Katherine M.; Zimmt, Joshua P.; Poust, Ashley W. (2022). "With what precision can the population size of Tyrannosaurus rex be estimated? A reply to Meiri" (https://escholarship.org/uc/item/8vv2g57c). *Frontiers of Biogeography*. doi:10.21425/F5FBG55042 (https://doi.org/10.21425%2FF5FBG55042). S2CID 245314491 (https://api.semanticscholar.org/CorpusID:245314491). Text was copied from this source, which is available under a Creative Commons Attribution 4.0 International License (https://creativecommons.org/licenses/by/4.0/).

Further reading

- Farlow, J. O.; Gatesy, S. M.; Holtz, T. R., Jr.; Hutchinson, J. R.; Robinson, J. M. (2000). "Theropod Locomotion" (https://doi.org/10.1093%2Ficb%2F40.4.640). *American Zoologist*. **40** (4): 640–663. doi:10.1093/icb/40.4.640 (https://doi.org/10.1093%2Ficb%2F40.4.640). JSTOR 3884284 (https://www.jstor.org/stable/3884284).

External links

- The University of Edinburgh Lecture Dr Stephen Brusatte – Tyrannosaur Discoveries Feb 20, 2015 (https://www.youtube.com/watch?v=hVJmPmb_LWY)
- 28 species in the tyrannosaur family tree, when and where they lived (http://www.livescience.com/53877-t-rex-was-invasive-species.html) Stephen Brusatte Thomas Carr 2016

Exhibits

- American Museum of Natural History (http://www.amnh.org/exhibitions/permanent-exhibitions/fossil-halls/hall-of-saurischian-dinosaurs/tyrannosaurus-rex)
