# Tyrannosaurus

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

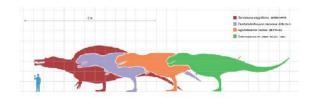
Tyrannosaurus (/tɨ rænəˈsɔːrəs/ or /tai rænəˈsɔːrəs/, meaning "tyrant lizard", from the Ancient Greek tyrannos (τύραννος), "tyrant", and sauros (σαῦρος), "lizard"[1]) is a genus of coelurosaurian theropod dinosaur. The species Tyrannosaurus rex (rex meaning "king" in Latin), commonly abbreviated to T.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

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

More than 50 specimens of *Tyrannosaurus rex* have been identified, some of which are nearly complete skeletons. Soft tissue and proteins have been reported in at least one of these specimens. The abundance of fossil material has allowed significant research into many aspects of its biology, including its life history and biomechanics. The feeding habits, physiology and potential speed of

Tyrannosaurus rex are a few subjects of debate. Its taxonomy is also controversial, as some scientists consider *Tarbosaurus bataar* from Asia to be a second *Tyrannosaurus* species while others maintain *Tarbosaurus* is a separate genus. Several other genera of North American tyrannosaurids have also been synonymized with *Tyrannosaurus*.

## 1 Description



Size (in green) compared with selected giant theropods

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

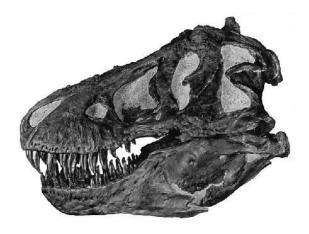
The neck of *Tyrannosaurus rex* formed a natural S-shaped curve like that of other theropods, but was short and muscular to support the massive head. The fore-limbs had only two clawed fingers, [21] along with an additional small metacarpal representing the remnant of a

2 1 DESCRIPTION



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

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



Profile view of a skull (AMNH 5027)

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

The teeth of *Tyrannosaurus rex* displayed marked heterodonty (differences in shape). [21][29] The premaxillary teeth at the front of the upper jaw

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

#### 1.1 Skin and feathers

Main article: Feathered dinosaur

While there is no direct evidence for Tyrannosaurus rex



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

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

The first evidence for feathers in tyrannosauroids came from the small species *Dilong paradoxus*, found in the Yixian Formation of China, and reported in the journal *Nature* in 2004. As with many other theropods discovered in the Yixian, the fossil skeleton was preserved with a coat of filamentous structures which are commonly recognized as the precursors of feathers. [33] Because all known skin impressions from larger tyrannosauroids known at the time showed evidence of scales, the researchers who studied *Dilong* speculated that feathers may correlate negatively with body size—that juveniles may have been feathered, then shed the feathers and expressed only scales as the animal became larger and no longer needed insulation to stay warm. [33] However, subsequent discoveries showed that even some gigantic tyrannosauroids had feathers covering much of their bodies, casting doubt on the hypothesis that they were a size-related feature. [34]

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

## 2 Classification

Tyrannosaurus is the type genus of the superfamily Tyrannosauroidea, the family Tyrannosauridae, and the subfamily Tyrannosaurinae; in other words it is the standard by which paleontologists decide whether to include other species in the same group. Other members of the tyrannosaurine subfamily include the North American *Daspletosaurus* and the Asian *Tarbosaurus*,[37][38] both of which have occasionally been synonymized with *Tyrannosaurus*.<sup>[28]</sup> 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.<sup>[27]</sup>

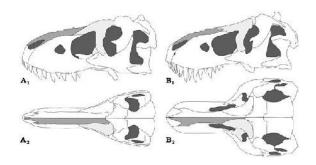


Diagram showing the differences between a generalized Tarbosaurus (A) and Tyrannosaurus (B) skull

In 1955, Soviet paleontologist Evgeny Maleev named a new species, *Tyrannosaurus bataar*, from Mongolia. [39] By 1965, this species had been renamed *Tarbosaurus bataar*. [40] Despite the renaming, many phylogenetic analyses have found *Tarbosaurus bataar* to be the sister taxon of *Tyrannosaurus rex*, [38] and it has often been considered an Asian species of *Tyrannosaurus*. [27][41][42] A recent redescription of the skull of *Tarbosaurus bataar* has shown that it was much narrower than that of *Tyrannosaurus rex* and that during a bite, the distribution of stress in the skull would have been very different, closer to that of *Alioramus*, another Asian tyrannosaur. [43] A re-



Nanotyrannus lancensis holotype, possibly a juvenile Tyrannosaurus

lated cladistic analysis found that *Alioramus*, not *Tyran-nosaurus*, was the sister taxon of *Tarbosaurus*, which, if true, would suggest that *Tarbosaurus* and *Tyrannosaurus* should remain separate.<sup>[37]</sup>

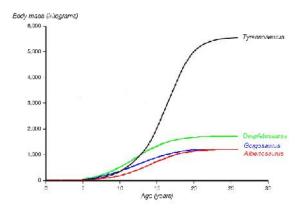
Other tyrannosaurid fossils found in the same formations as Tyrannosaurus rex were originally classified as separate taxa, including Aublysodon and Albertosaurus megagracilis, [28] the latter being named Dinotyrannus megagracilis in 1995.<sup>[44]</sup> However, these fossils are now universally considered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

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

## 3 Paleobiology

#### 3.1 Life history

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



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

to the maximum for the species.<sup>[6]</sup>



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

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

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

## 3.2 Sexual dimorphism



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

3.4 Arms 5

As the number of known specimens increased, scientists began to analyze the variation between individuals and discovered what appeared to be two distinct body types, or *morphs*, similar to some other theropod species. As one of these morphs was more solidly built, it was termed the 'robust' morph while the other was termed 'gracile'. Several morphological differences associated with the two morphs were used to analyze sexual dimorphism in Tyrannosaurus rex, with the 'robust' morph usually suggested to be female. For example, the pelvis of several 'robust' specimens seemed to be wider, perhaps to allow the passage of eggs.<sup>[57]</sup> 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.<sup>[58]</sup>

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

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

## 3.3 Posture

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

Like many bipedal dinosaurs, *Tyrannosaurus rex* was historically depicted as a 'living tripod', with the body at



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

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

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

#### **3.4** Arms



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

When Tyrannosaurus rex was first discovered, the humerus was the only element of the forelimb known. [66] For the initial mounted skeleton as seen by the public in 1915, Osborn substituted longer, three-fingered forelimbs like those of *Allosaurus*. [67] However, a year earlier, Lawrence Lambe described the short, two-fingered forelimbs of the closely related *Gorgosaurus*. <sup>[68]</sup> This strongly suggested that Tyrannosaurus rex had similar forelimbs, but this hypothesis was not confirmed until the first complete Tyrannosaurus rex forelimbs were identified in 1989, belonging to MOR 555 (the "Wankel rex"). [69] The remains of Sue also include complete forelimbs.<sup>[21]</sup> Tyrannosaurus 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. However, 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.<sup>[70]</sup> It has also been suggested that the forelimbs were used to assist the animal in rising from a prone position. [63]

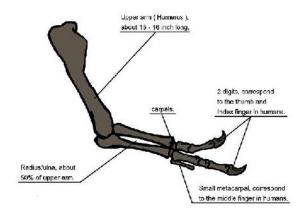


Diagram illustrating arm anatomy

Another possibility is that the forelimbs held struggling prey while it was killed by the tyrannosaur's enor-This hypothesis may be supported by mous jaws. biomechanical analysis. Tyrannosaurus rex forelimb bones exhibit extremely thick cortical bone, which have been interpreted as evidence that they were developed to withstand heavy loads. The biceps brachii muscle of a full-grown Tyrannosaurus 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 Tyrannosaurus 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 *Tyrannosaurus rex* was an obligate scavenger.<sup>[71]</sup>

#### 3.5 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 Tyrannosaurus 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.<sup>[72]</sup> 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. [73] 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. [72] Research on some of the tissues involved has suggested that birds are closer relatives to tyrannosaurs than other modern animals.<sup>[74]</sup>

In studies reported in Science in April 2007, Asara and colleagues concluded that seven traces of collagen proteins detected in purified Tyrannosaurus 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".[75]

Subsequent studies in April 2008 confirmed the close connection of *Tyrannosaurus rex* to modern birds. Post-doctoral biology researcher Chris Organ at Harvard University announced, "With more data, they would probably



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

be able to place *T. rex* on the evolutionary tree between alligators and chickens and ostriches." Co-author John M. Asara added, "We also show that it groups better with birds than modern reptiles, such as alligators and green anole lizards."<sup>[76]</sup>

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.<sup>[77]</sup> 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.<sup>[78]</sup> However, Schweitzer has strongly criticized Kaye's claims and argues that there's no reported evidence that biofilms can produce branching, hollow tubes like those noted in her study. [79] 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.<sup>[80]</sup> Other research challenges the identification of soft tissue as biofilm and confirms finding "branching, vessel-like structures" from within fossilized bone.[81]

### 3.6 Thermoregulation

Main article: Physiology of dinosaurs

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. [82][83] Tyrannosaurus rex itself was claimed to have been endothermic ("warm-blooded"), implying a very active lifestyle.[13] 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 Tyrannosaurus 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, Tyrannosaurus rex growth was limited mostly to immature animals, rather than the indeterminate growth seen in most other vertebrates.[51]

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 Tyrannosaurus rex maintained a constant internal body temperature (homeothermy) and that it enjoyed a metabolism somewhere between ectothermic reptiles and endothermic mammals.<sup>[84]</sup> 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).[85] 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). [86] Ornithischian dinosaurs also showed evidence of homeothermy, while varanid lizards from the same formation did not.[87] Even if Tyrannosaurus 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. [88][89]

#### 3.7 Footprints

Two isolated fossilized footprints have been tentatively assigned to *Tyrannosaurus rex*. The first was discovered at Philmont Scout Ranch, New Mexico, in 1983



Probable footprint from New Mexico

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 *Tyrannosaurus rex*, which would make it the first known footprint from this species. The track was made in what was once a vegetated wetland mud flat. It measures 83 centimeters (33 in) long by 71 centimeters (28 in) wide. [90]

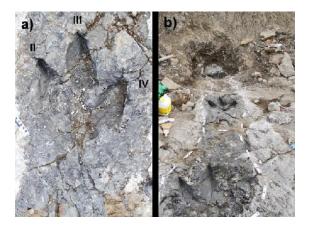
A second footprint that may have been made by a *Tyran-nosaurus* was first reported in 2007 by British paleon-tologist Phil Manning, from the Hell Creek Formation of Montana. This second track measures 72 centimeters (28 in) long, shorter than the track described by Lockley and Hunt. Whether or not the track was made by *Tyrannosaurus* is unclear, though *Tyrannosaurus* and *Nanotyrannus* are the only large theropods known to have existed in the Hell Creek Formation. [91][92]

A set of footprints in Glenrock, Wyoming dating to the Maastrichtian stage of the late cretaceous and hailing from the Lance Formation were recently described by Scott Persons, Phil Currie et al. in January 2016, and are believed to belong to either a juvenile Tyrannosaurus rex or the dubious tyrannosaurid genus 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). The discovery was described in the journal *Cretaceous Research*. [93][94][95][96]

#### 3.8 Locomotion

There are two main issues concerning the locomotory abilities of *Tyrannosaurus*: how well it could turn; and what its maximum straight-line speed was likely to have been. Both are relevant to the debate about whether it was a hunter or a scavenger.

Tyrannosaurus may have been slow to turn, possibly taking one to two seconds to turn only 45°—an amount that humans, being vertically oriented and tailless, can spin in a fraction of a second. [97] The cause of the difficulty is rotational inertia, since much of Tyrannosaurus' mass was some distance from its center of gravity, like a human carrying a heavy timber—although it might have reduced the average distance by arching its back and tail and pulling its head and forelimbs close to its body, rather like the way ice skaters pull their arms closer in order to spin faster. [98]



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

Scientists have produced a wide range of maximum speed estimates, mostly around 11 meters per second (40 km/h; 25 mph), but a few as low as 5–11 meters per second (18– 40 km/h; 11-25 mph), and a few as high as 20 meters per second (72 km/h; 45 mph). Researchers have to rely on various estimating techniques because, while there are many tracks of very large theropods walking, so far none have been found of very large theropods running-and this absence may indicate that they did not run. [99] 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 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. Additionally, some have argued that Tyrannosaurus had relatively larger leg muscles than any animal alive today, which could have enabled fast running at 40-70 kilometers per hour (25–43 mph).[100]



Femur (thigh bone)
Tibia (shin bone)
Metatarsals (foot bones)
Dewclaw
Phalanges (toe bones)
Skeletal anatomy of a *T. rex* right leg

Jack Horner and Don Lessem argued in 1993 that Tyrannosaurus was slow and probably could not run (no airborne phase in mid-stride), because its ratio of femur (thigh bone) to tibia (shin bone) length was greater than 1, as in most large theropods and like a modern elephant. [69] However, Holtz (1998) 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 that more effectively transmitted locomotory forces from the foot to the lower leg than in earlier theropods ("metatarsus" means the foot bones, which function as part of the leg in digitigrade animals). He therefore concluded that tyrannosaurids and their close relatives were the fastest large theropods. [101] Thomas Holtz Jr. would echo these sentiments in his 2013 lecture, stating that the giant allosaurs had shorter feet for the same body size than Tyrannosaurus, whereas Tyrannosaurus had longer, skinnier and more interlocked feet for the same body size; attributes of faster moving animals.[55]



T. rex foot showing the compressed arctometatarsalian condition of the middle metatarsal, compared to that of Allosaurus

A study by Eric Snively and Anthony P. Russel pub-

lished in 2003 would also find that the tyrannosaurid arctometatarsals and elastic ligaments worked together in what he called a 'tensile keystone model' to strengthen the feet of Tyrannosaurus, increase the animal's stability and add greater resistance to dissociation over that of other theropod families; while still allowing resiliency that is otherwise reduced in ratites, horses, giraffids and other animals with metapodia to a single element. The study would also point out that elastic ligaments in larger vertebrates could store and return relatively more elastic strain energy, which could have improved locomotor efficiency and decrease the strain energy transferred to the bones. The study would suggest that this mechanism could have worked efficiently in tyrannosaurids as well. Hence, the study involved identifying the type of ligaments attached to the metatarsals, then how they functioned together and comparing it to those of other theropods and modern day analogs. The scientists would find that arctometatarsals may have enabled tyrannosaurid feet to absorb forces such as linear deceleration, lateral acceleration and torsion more effectively than those of other theropods. It is also stated in their study that this may imply, though not demonstrate, that tyrannosaurids such as Tyrannosaurus had greater agility than other large theropods without an arctometatarsus.[102]

Christiansen (1998) estimated that the leg bones of *Tyrannosaurus* were not significantly stronger than those of elephants, which are relatively limited in their top speed and never actually run (there is no airborne phase), and hence proposed that the dinosaur's maximum speed would have been about 11 meters per second (40 km/h; 25 mph), which is about the speed of a human sprinter. But he also noted that such estimates depend on many dubious assumptions. [103]

Farlow and colleagues (1995) have argued that a *Tyrannosaurus* weighing 5.4 metric tons (6.0 short tons) to 7.3 metric tons (8.0 short tons) would have been critically or even fatally injured if it had fallen while moving quickly, since its torso would have slammed into the ground at a deceleration of 6 g (six times the acceleration due to gravity, or about 60 meters/s²) and its tiny arms could not have reduced the impact.<sup>[14]</sup> However, giraffes have been known to gallop at 50 kilometers per hour (31 mph), despite the risk that they might break a leg or worse, which can be fatal even in a "safe" environment such as a zoo.<sup>[104][105]</sup> Thus it is possible that *Tyrannosaurus* also moved fast when necessary and had to accept such risks.<sup>[106][107]</sup>

In a study published by Gregory S. Paul in the journal *Gaia*, he would point out that the flexed kneed and digitigrade adult *Tyrannosaurus* were much better designed for running than elephants or humans, pointing out that *Tyrannosaurus* had a large ilium bone and cnemial crest that would have supported large muscles needed for running. He would also mention that Alexander's (1989) formula to calculate speed by bone strength was only partly reliable. He suggests that the formula is overly



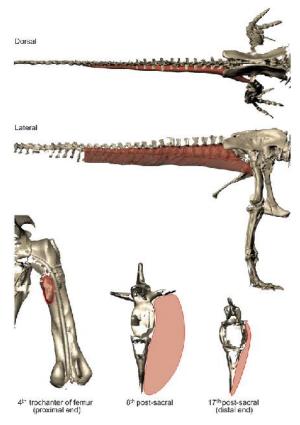
Leg mass of T. rex and a chicken compared, by Luis Rey

sensitive to bone length; making long bones artificially weak. He would also point out that the lowered risk of being wounded in combat may have been worth the risk of *Tyrannosaurus* falling while running.<sup>[108]</sup>

Most recent research on Tyrannosaurus locomotion does not support speeds faster than 40 kilometers per hour (25 mph), i.e. moderate-speed running. For example, a 2002 paper in *Nature* used a mathematical model (validated by applying it to three living animals, alligators, chickens, and humans; later eight more species including emus and ostriches<sup>[99]</sup>) to gauge the leg muscle mass needed for fast running (over 40 km/h or 25 mph).[100] They found that proposed top speeds in excess of 40 kilometers per hour (25 mph) were infeasible, because they would require very large leg muscles (more than approximately 40–86% of total body mass). Even moderately fast speeds would have required large leg muscles. This discussion is difficult to resolve, as it is unknown how large the leg muscles actually were in Tyrannosaurus. If they were smaller, only 18 kilometers per hour (11 mph) walking or jogging might have been possible.[100]

A study in 2007 used computer models to estimate running speeds, based on data taken directly from fossils, and claimed that *Tyrannosaurus rex* had a top running speed of 8 meters per second (29 km/h; 18 mph). An average professional football (soccer) player would be slightly slower, while a human sprinter can reach 12 meters per second (43 km/h; 27 mph). These computer models predict a top speed of 17.8 meters per second (64 km/h; 40 mph) for a 3-kilogram (6.6 lb) *Compsognathus*<sup>[109][110]</sup> (probably a juvenile individual).

However, in 2010, Scott Persons, a graduate student from the University of Alberta proposed that *Tyrannosaurus's* 



Muscle mass reconstruction of M. caudofemoralis longus

speed may have been enhanced by strong tail muscles. [112] He found that theropods such as T rex had certain muscle arrangements that are different from modern day birds and mammals but with some similarities to modern reptiles.<sup>[113]</sup> He concluded that the caudofemoralis muscles which link the tail bones and the upper leg bones could have assisted Tyrannosaurus in leg retraction and enhanced its running ability, agility and balance. The caudofemoralis muscle would have been a key muscle in femoral retraction; pulling back the leg at the femur. [112] The study also found that theropod skeletons such as those of Tyrannosaurus had adaptations (such as elevated transverse processes in the tail vertebrae) to enable the growth of larger tail muscles and that Tyrannosaurus's tail muscle mass may have been underestimated by over 25 percent and perhaps as much as 45 percent. The caudofemoralis muscle was found to comprise 58 percent of the muscle mass in the tail of Tyrannosaurus. Tyrannosaurus also had the largest absolute and relative caudofemoralis muscle mass out of the three extinct organisms in the study. This is because Tyrannosaurus also had additional adaptations to enable large tail muscles; the elongation of its tail's hemal arches. According to Persons, the increase in tail muscle mass would have moved the center of mass closer to the hindquarters and hips which would have lessened the strain on the leg muscles to support its weight; improving its overall balance and agility. This would also have made the animal less front-heavy, thus reducing rotational inertia. Persons also notes that the tail is also rich in tendons and septa which could have been stores of elastic energy, and thereby improved locomotive efficiency. Persons adds that this means non-avian theropods actually had broader tails than previously depicted, as broad or broader laterally than dorsoventrally near the base. [112][113]

Heinrich Mallison from Berlin's Museum of Natural History would also present a theory in 2011, suggesting that Tyrannosaurus and many other dinosaurs may have achieved relatively high speeds through short rapid strides instead of the long strides employed by modern birds and mammals when running, likening their movement to power-walking. This, according to Mallison, would have been achievable irrespective of joint strength and lessened the need for additional muscle mass in the legs, particularly at the ankles. To support his theory, Mallison assessed the limbs of various dinosaurs and found that they were different from those of modern mammals and birds; having their stride length greatly limited by their skeletons, but also having relatively large muscles at the hindquarters. He would however find a few similarities between the muscles in dinosaurs and race-walkers; having less muscle mass in the ankles but more at the hindquarters. Mallison suggests that the differences between dinosaurs, extant mammals, and birds would also have made equations to calculate speed from stride length inapplicable to dinosaurs. John Hutchinson however advised caution regarding this theory, suggesting that they must first look into dinosaur muscles to see how frequently they could have contracted. [114][115]

Those who argue that Tyrannosaurus was incapable of running estimate the top speed of Tyrannosaurus at about 17 kilometers per hour (11 mph). This is still faster than its most likely prey species, hadrosaurids and ceratopsians.[100] In addition, some advocates of the idea that Tyrannosaurus was a predator claim that tyrannosaur running speed is not important, since it may have been slow but still faster than its probable prey.[116] Thomas Holtz would also note that Tyrannosaurus had proportionately longer feet than the animals it hunted: duckbilled dinosaurs and horned dinosaurs.<sup>[55]</sup> However, Paul and Christiansen (2000) argued that at least the later ceratopsians had upright forelimbs and the larger species may have been as fast as rhinos.[117] Healed Tyrannosaurus bite wounds on ceratopsian fossils are interpreted as evidence of attacks on living ceratopsians (see below). If the ceratopsians that lived alongside Tyrannosaurus were fast, that casts doubt on the argument that Tyrannosaurus did not have to be fast to catch its prey.[107]

## 3.9 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 coordi-



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

nated eye and head movements, as well as an enhanced ability to sense low frequency sounds that would allow tyrannosaurs to track prey movements from long distances and an enhanced sense of smell.[118] A study published by Kent Stevens of the University of Oregon concluded that Tyrannosaurus had keen vision. 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, and had 13 times the visual acuity of a human, thereby surpassing the visual acuity of an eagle which is only 3.6 times that of a person. This would have allowed Tyrannosaurus to discern objects as far as 6 km (3.7 mi) away, which is greater than the 1.6 km (1 mi) that a human can see. [24][25][119][120]

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 may have had 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*. [55]

Tyrannosaurus had very large olfactory bulbs and



Cast of the braincase at the Australian Museum, Sydney.

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 *Tyrannosaurus rex* had the most highly developed sense of smell of 21 sampled nonavian dinosaur species.<sup>[121]</sup>

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 *Tyrannosaurus rex* heard best in the low-frequency range, and that low-frequency sounds were an important part of tyrannosaur behavior. [118]

A study by Grant R. Hurlburt, Ryan C. Ridgely and Lawrence Witmer would obtain estimates for Encephalization Quotients (EQs), based on reptiles and birds, as well as estimates for the ratio of cerebrum to brain mass. The study would conclude that Tyrannosaurus had the relatively largest brain of all adult nonavian dinosaurs with the exception of certain small maniraptoriforms (Bambiraptor, Troodon and Ornithomimus). The study would however find 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. [122]

## 3.10 Feeding strategies

#### Main article: Feeding behaviour of Tyrannosaurus

A 2012 study by scientists Karl Bates and Peter Falkingham suggested that the bite force of *Tyrannosaurus* could have been the strongest of any terrestrial animal that has ever lived. The calculations suggested that adult *T. rex* 



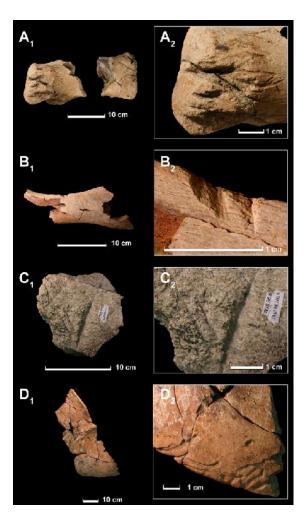
Head reconstruction in the Natural History Museum of Vienna

could have generated from 35,000 to 57,000 Newtons of force in the back teeth. [123][124][125] However, even higher estimates were made by professor Mason B. Meers of the University of Tampa in 2003. In his study, Meers estimated a possible bite force of around 183,000 to 235,000 Newtons or 18.3 to 23.5 metric tons (20.2 to 25.9 short tons). [8] Research done by Stephan Lautenschlager et al. of the University of Bristol, also reveals Tyrannosaurus was also capable of a maximum jaw gape of around 63 degrees, a necessary adaptation for a wide range of jaw angles in order to power the creature's strong bite. [126][127]

The debate about whether *Tyrannosaurus* was a predator or a pure scavenger is as old as the debate about its locomotion. Lambe (1917) described a good skeleton of *Tyrannosaurus* close relative *Gorgosaurus* and concluded that it and therefore also *Tyrannosaurus* was a pure scavenger, because the *Gorgosaurus* teeth showed hardly any wear. This argument is no longer taken seriously, because 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. [129]

Paleontologist Jack Horner has been a major advocate of the idea that *Tyrannosaurus* was exclusively a scavenger and did not engage in active hunting at all, [69][130][131] though Horner himself has claimed that he never published this idea in the peer-reviewed scientific literature and used it mainly as a tool to teach a popular audience, particularly children, the dangers of making assumptions in science (such as assuming *T. rex* was a hunter) without using evidence. [132] Nevertheless, Horner presented several 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. [133]
- Tyrannosaurs had large olfactory bulbs and olfactory nerves (relative to their brain size). These sug-



Tyrannosaurus tooth marks on bones of various herbivores

gest 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. [134] Opponents of the pure scavenger hypothesis have used the example of vultures in the opposite way, arguing that the scavenger hypothesis is implausible because the only modern pure scavengers are large gliding birds, which use their keen senses and energy-efficient gliding to cover vast areas economically.<sup>[135]</sup> However, researchers from Glasgow concluded that an ecosystem as productive as the current Serengeti would provide sufficient carrion for a large theropod scavenger, although the theropod might have had to be cold-blooded in order to get more calories from carrion than it spent on foraging (see Metabolism of dinosaurs). They also suggested that modern ecosystems like the Serengeti have no large terrestrial scavengers because gliding birds now do the job much more efficiently, while large theropods did not face competition for the scavenger ecological niche from gliding birds. [136]

• 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.<sup>[137]</sup>

• 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. [130][138] 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. [100][116]

Other evidence suggests hunting behavior in *Tyran-nosaurus*. 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. Horner also pointed out that the tyrannosaur lineage had a history of steadily improving binocular vision. 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. [24][25] In modern animals, binocular vision is found mainly in predators.



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. 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. [140] Since the *Triceratops* wounds healed, it is most likely that the *Triceratops* survived the encounter and managed to overcome the *Tyrannosaurus*. Paleontologist Peter Dodson estimates that in a battle against a bull *Triceratops*, the *Triceratops* had the upper hand and would successfully defend itself by inflicting fatal wounds to the *Tyrannosaurus* using its sharp horns. [141]

When examining Sue, paleontologist Pete Larson found a broken and healed fibula and tail vertebrae, scarred facial bones and a tooth from another Tyrannosaurus embedded in a neck vertebra. If correct, these might be strong evidence for aggressive behavior between tyrannosaurs but whether it would have been competition for food and mates or active cannibalism is unclear. [142] However, further recent investigation of these purported wounds has shown that most are infections rather than injuries (or simply damage to the fossil after death) and the few injuries are too general to be indicative of intraspecific conflict.<sup>[130]</sup> Some researchers argue that if Tyrannosaurus were a scavenger, another dinosaur had to be the top predator in the Amerasian Upper Cretaceous. Top prey were the larger marginocephalians and ornithopods. The other tyrannosaurids share so many characteristics that only small dromaeosaurs and troodontids remain as feasible top predators. In this light, scavenger hypothesis adherents have suggested that the size and power of tyrannosaurs allowed them to steal kills from smaller predators, [138] although they may have had a hard time finding enough meat to scavenge, being outnumbered by smaller theropods.<sup>[143]</sup> Most paleontologists accept that Tyrannosaurus was both an active predator and a scavenger like most large carnivores.



Two teeth from the lower jaw of specimen MOR 1125, "B-rex", showing the variation in tooth size within an individual

Tyrannosaurus may have had infectious saliva used to kill its prey. This theory was first proposed by William Abler. [144] Abler examined the teeth of tyrannosaurids between each tooth serration; the serrations may have held pieces of carcass with bacteria, giving Tyrannosaurus a deadly, infectious bite much like the Komodo dragon was thought to have. However, Jack Horner regards Tyrannosaurus tooth serrations as more like cubes in shape than the serrations on a Komodo monitor's teeth, which are rounded. [145] All forms of saliva contain possibly hazardous bacteria, so the prospect of it being used

as a method of predation is disputable.

*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. [146]

#### 3.10.1 Cannibalism

A study from Currie, Horner, Erickson and Longrich in 2010 has been put forward as evidence of cannibalism in the genus Tyrannosaurus. [147] 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 bite marks were made in a carcass. As the bite marks were made in body parts with relatively scanty amounts of flesh, it is suggested that the Tyrannosaurus was feeding on a carcass in which the more fleshy parts had already been consumed. They were also open to the possibility that other tyrannosaurids practiced cannibalism.[147] Other evidence for cannibalism has been unearthed. [148]

#### 3.10.2 Pack behavior



Mounted skeletons of different age groups, Los Angeles Natural History Museum

Philip J. Currie of the University of Alberta has suggested that *Tyrannosaurus* may have been pack animals. Currie compared *Tyrannosaurus rex* favorably to related species *Tarbosaurus bataar* and *Albertosaurus sarcophagus*, fossil evidence from which Currie had previously used to suggest that they lived in packs. [149] Currie pointed out that a find in South Dakota preserved three *Tyrannosaurus rex* skeletons in close proximity to each other. [150] After using CT scanning, Currie stated that *Tyrannosaurus* would have been capable of such complex behavior, because its brain size is three times greater than what would be expected for an animal of

its size. Currie elaborated that *Tyrannosaurus* had a larger brain-to-body-size proportion than crocodiles and three times more than plant eating dinosaurs such as *Triceratops* of the same size. Currie believed *Tyrannosaurus* to be six times smarter than most dinosaurs and other reptiles. [149][151] because the available prey, such as *Triceratops* and *Ankylosaurus*, were well-armored, and that others were fast-moving, it would have been necessary for *Tyrannosaurus* to hunt in groups. Currie speculated that juveniles and adults would have hunted together, with the faster juveniles chasing down the prey and the more powerful adults making the kill, by analogy to modern-day pack hunters where each member contributes a skill. [149]

However, Currie's pack-hunting hypothesis has been harshly criticized by other scientists. Brian Switek, writing for The Guardian in 2011,[152] noted that Currie's pack hypothesis has not been presented as research in a peer-reviewed scientific journal, but primarily in relation to a television special and tie-in book called Dino Gangs. Switek also noted that Currie's argument for pack hunting in Tyrannosaurus rex is primarily based on analogy to a different species, Tarbosaurus bataar, and that the supposed evidence for pack hunting in T. bataar itself has not yet been published and subjected to scientific scrutiny. According to Switek and other scientists who have participated in panel discussions about the *Dino* Gangs television program, the evidence for pack hunting in Tarbosaurus and Albertosaurus is weak, based primarily on the association of several skeletons, for which numerous alternative explanations have been proposed (e.g. drought or floods forcing numerous specimens together to die in one place). In fact, Switek notes that the Albertosaurus bonebed site, on which Currie has based most of the interpretations of supposed pack hunting in related species, preserves geological evidence of just such a flood. Switek said, "bones alone are not enough to reconstruct dinosaur behaviour. The geological context in which those bones are found – the intricate details of ancient environments and the pace of prehistoric time - are essential to investigating the lives and deaths of dinosaurs,"[152] and noted that Currie must first describe the geological evidence from other tyrannosaur bonebed sites before jumping to conclusions about social behavior. Switek described the sensational claims provided in press releases and news stories surrounding the Dino Gangs program as "nauseating hype" and noted that the production company responsible for the program, Atlantic Productions, has a poor record involving exaggerating claims about new fossil discoveries, most notably the controversial claim it published regarding the supposed early human ancestor Darwinius, which soon turned out to be a relative of lemurs instead.[152]

Lawrence Witmer pointed out that social behavior can't be determined by brain endocasts and the brains of solitary leopards are identical to those of a cooperatively hunting lion; estimated brain sizes only show that an animal *may* have hunted in groups. In his opinion, the brains of tyrannosaurs were large enough for what he dubs "communal hunting", a semi-organized behavior that falls between solitary and cooperative hunting. Witmer claims that communal hunting is a step towards the evolution of cooperative hunting. He found it hard to believe that tyrannosaurs wouldn't have exploited the opportunity to join others in making a kill, and thus decrease risk and increase their chances of success.<sup>[153]</sup>

On July 23, 2014, evidence, for the first time, in the form of fossilized trackways in Canada, showed that tyran-nosaurs may have hunted in groups. [154][155]

## 3.11 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.<sup>[156]</sup>

A 2009 study showed that holes in the skulls of several specimens that were previously explained by intraspecific

16 5 HISTORY

attacks might have been caused by *Trichomonas*-like parasites that commonly infect avians.<sup>[157]</sup> Further evidence of intraspecific attack would however be 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.<sup>[158]</sup> 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.<sup>[159]</sup>

## 4 Paleoecology



Tyrannosaurus and other animals of the Hell Creek Formation

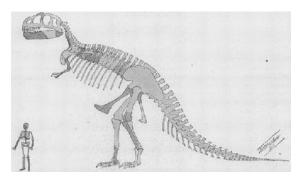
Tyrannosaurus lived during what is referred to as the Lancian faunal stage (Maastrichtian age) at the end of the Late Cretaceous. Tyrannosaurus ranged from Canada in the north to at least Texas and New Mexico in the south of Laramidia. During this time Triceratops was the major herbivore in the northern 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 Triceratops, related ceratopsians Nedoceratops, Tatankaceratops and Torosaurus, the harosaurid Edmontosaurus annectens and possibly a species of Parasaurolophus, the armored dinosaurs Denversaurus, Edmontonia, Ankylosaurus, Pachycephalosaurus, Stygimoloch, Sphaerotholus, and Dracorex, hypsilophodont Thescelosaurus, and the theropods Ornithomimus, Struthiomimus, Orcomimus ,Acheroraptor, Dakotaraptor, Richardoestesia, Paronychodon, Pectinodon and Troodon. [160]

Another formation with tyrannosaur 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. [161]

In its southern range *Tyrannosaurus* lived alongside the titanosaur *Alamosaurus*, the ceratopsians *Torosaurus*, *Bravoceratops* and *Ojoceratops*, a species of *Edmontosaurus*, the ankylosaur *Glyptodontopelta*, and the pterosaur *Quetzalcoatlus*.<sup>[162]</sup> 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.<sup>[163]</sup>

## 5 History

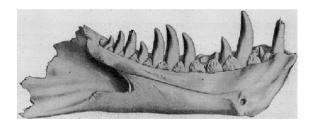


Skeletal restoration by William D. Matthew from 1905, the first reconstruction of this dinosaur ever published<sup>[164]</sup>

Henry Fairfield Osborn, president of the American Museum of Natural History, named  $Tyrannosaurus\ rex$  in 1905. The generic name is derived from the Greek words  $\tau v \rho \acute{a} v v o \varsigma$  (tyrannos, meaning "tyrant") and  $\sigma a \acute{v} \rho o \varsigma$  (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", [165] emphasizing the animal's size and perceived dominance over other species of the time. [66]

#### 5.1 Earliest finds

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 a large species of *Ornithomimus* (O. grandis) but are now considered *Tyrannosaurus* rex remains. Vertebral fragments found by Edward Drinker Cope in western South Dakota in 1892 and assigned to



Type specimen of Dynamosaurus imperiosus

*Manospondylus gigas* have also been recognized as belonging to *Tyrannosaurus rex*.<sup>[166]</sup>

Barnum Brown, assistant curator of the American Museum of Natural History, found the first partial skeleton of *Tyrannosaurus rex* in eastern Wyoming in 1900. H. F. Osborn originally named this skeleton *Dynamosaurus imperiosus* in a paper in 1905. Brown found another partial skeleton in the Hell Creek Formation in Montana in 1902. Osborn used this holotype to describe *Tyrannosaurus rex* in the same paper in which *D. imperiosus* was described. <sup>[66]</sup> In 1906, Osborn recognized the two as synonyms, and acted as first revisor by selecting *Tyrannosaurus* as the valid name. <sup>[70]</sup> The original *Dynamosaurus* material resides in the collections of the Natural History Museum, London. <sup>[167]</sup>

In total, Brown found five *Tyrannosaurus* partial skeletons. In 1941, Brown's 1902 find was sold to the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania. Brown's fourth and largest find, also from Hell Creek, is on display in the American Museum of Natural History in New York. [69]

#### 5.2 Manospondylus

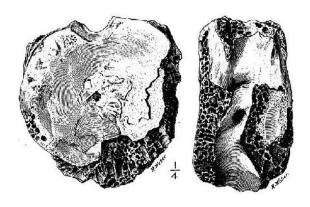


Illustration of the type specimen (AMNH 3982) of Manospondylus gigas

The first named fossil specimen which can be attributed to *Tyrannosaurus rex* consists of two partial vertebrae (one of which has been lost) found by Edward Drinker Cope in 1892. Cope believed that they 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.<sup>[166]</sup> The *M. gigas* remains were later identified as those of a theropod rather than a ceratopsid, and H.F. Osborn recognized the similarity between *M. gigas* and *Tyrannosaurus rex* as early as 1917. However, owing to the fragmentary nature of the *Manospondylus* vertebrae, Osborn did not synonymize the two genera.<sup>[67]</sup>

In June 2000, the Black Hills Institute located the type locality of M. gigas in South Dakota and unearthed more tyrannosaur bones there. These were judged to represent further remains of the same individual, and to be identical to those of Tyrannosaurus rex. [168] According to the rules of the International Code of Zoological Nomenclature (ICZN), the system that governs the scientific naming of animals, Manospondylus gigas should therefore have priority over Tyrannosaurus rex, because it was named first. However, the Fourth Edition of the ICZN, which took effect on January 1, 2000, states that "the prevailing usage must be maintained" when "the senior synonym or homonym has not been used as a valid name after 1899" and "the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years ..."[169] Tyrannosaurus rex may qualify as the valid name under these conditions and would most likely be considered a nomen protectum ("protected name") under the ICZN if it is ever formally published on, which it has not yet been. Manospondylus gigas could then be deemed a *nomen oblitum* ("forgotten name").<sup>[170]</sup>

## 5.3 Notable specimens

Main article: Specimens of Tyrannosaurus Sue Hendrickson, amateur paleontologist, discovered the



Sue specimen, Field Museum of Natural History, Chicago

most complete (approximately 85%) and largest *Tyran-nosaurus* fossil skeleton known in the Hell Creek Formation near Faith, South Dakota, on August 12, 1990. This *Tyrannosaurus*, nicknamed Sue in her honor, was the object of a legal battle over its ownership. In 1997 this 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

18 8 REFERENCES

to date. From 1998 to 1999 Field Museum of Natural History preparators spent over 25,000 man-hours taking the rock off each of the bones.<sup>[171]</sup> The bones were then shipped off to New Jersey where the mount was made. The finished mount was then taken apart, and along with the bones, shipped back to Chicago for the final assembly. The mounted skeleton opened to the public on May 17, 2000 in the great hall (Stanley Field Hall) at 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 age 28, the longest any tyrannosaur is known to have lived.[172] Early speculation that Sue may have died from a bite to the back of the head was not confirmed. Though subsequent study showed many pathologies in the skeleton, no bite marks were found.[21][173] Damage to the back of the skull may have been caused by post-mortem trampling. Recent speculation indicates that Sue may have died of starvation after contracting a parasitic infection from eating diseased meat; the resulting infection would have caused inflammation in the throat, ultimately leading Sue to starve because she could no longer swallow food. This hypothesis is substantiated by smooth-edged holes in her skull which are similar to those caused in modern-day birds that contract the same parasite.[174]



Skeleton of Bucky and cast of Stan, at the Children's Museum of Indianapolis

Another *Tyrannosaurus*, nicknamed Stan, in honor of amateur paleontologist Stan Sacrison, was found in the Hell Creek Formation near Buffalo, South Dakota, in the spring of 1987. It was not collected until 1992, as it was mistakenly thought to be a *Triceratops* skeleton. Stan is 63% complete and is on display in the Black Hills Institute of Geological Research in Hill City, South Dakota, after an extensive world tour during 1995 and 1996. [35] This tyrannosaur, too, was found to have many bone pathologies, including broken and healed ribs, a broken (and healed) neck and a spectacular hole in the back of its head, about the size of a *Tyrannosaurus* tooth. [175]

In the summer of 2000, Jack Horner discovered five *Tyrannosaurus* skeletons near the Fort Peck Reservoir in Montana. One of the specimens was reported to be perhaps the largest *Tyrannosaurus* ever found.<sup>[176]</sup>

In 2001, a 50% complete skeleton of a juvenile Tyran-

nosaurus was discovered in the Hell Creek Formation in Montana, by a crew from the Burpee Museum of Natural History of Rockford, Illinois. Dubbed Jane, the find was initially considered the first known skeleton of the pygmy tyrannosaurid Nanotyrannus but subsequent research has revealed that it is more likely a juvenile Tyrannosaurus. [177] It is the most complete and best preserved juvenile example known to date. Jane has been examined by Jack Horner, Pete Larson, Robert Bakker, Greg Erickson, and several other renowned paleontologists, because of the uniqueness of her age. Jane is currently on exhibit at the Burpee Museum of Natural History in Rockford, Illinois. [178][179]

In a press release on April 7, 2006, Bozeman Campus, Montana State University, USA revealed that it possessed the largest *Tyrannosaurus* skull yet discovered. Discovered in the 1960s and only recently reconstructed, the skull measures 59 inches (150 cm) long compared to the 55.4 inches (141 cm) of Sue's skull, a difference of 6.5%. [180][181]

## 6 In popular culture

Main article: Tyrannosaurus in popular culture

Since it was first described in 1905, *Tyrannosaurus 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) (*Tyrannosaurus rex*), and the scientific abbreviation *T. rex* has also come into wide usage.<sup>[21]</sup> Robert T. Bakker notes this in *The Dinosaur Heresies* and explains that a name like "*Tyrannosaurus rex* is just irresistible to the tongue."<sup>[13]</sup>

## 7 See also

• Timeline of tyrannosaur research

## 8 References

- [1] "Tyrannosaurus". Online Etymology Dictionary.
- [2] Hicks, J. F.; Johnson, K. R.; Obradovich, J. D.; Tauxe, L.; Clark, D. (2002). "Magnetostratigraphy and geochronology of the Hell Creek and basal Fort Union Formations of southwestern North Dakota and a recalibration of the Cretaceous-Tertiary Boundary" (PDF). Geological Society of America Special Papers 361: 35–55. doi:10.1130/0-8137-2361-2.35.
- [3] DiChristina, Mariette (Apr 14, 2015). "Rise of the Tyrants". ... was merely the last survivor of a startling variety of tyrannosaurs that lived across the globe right up until the asteroid impact 66 million years ago ...

- [4] 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". *PLoS ONE* 6 (10): e26037. doi:10.1371/journal.pone.0026037.
- [5] "Sue's vital statistics". Sue at the Field Museum. Field Museum of Natural History. Archived from the original on September 29, 2007. Retrieved September 15, 2007.
- [6] Erickson, Gregory M.; Makovicky, Peter J.; Currie, Philip J.; Norell, Mark A.; Yerby, Scott A.; Brochu, Christopher A. (2004). "Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs". *Nature* 430 (7001): 772–775. doi:10.1038/nature02699. PMID 15306807.
- [7] Snively, Eric; Henderson, Donald M.; Phillips, Doug S. (2006). "Fused and vaulted nasals of tyrannosaurid dinosaurs: Implications for cranial strength and feeding mechanics" (PDF). Acta Palaeontologica Polonica 51 (3): 435–454. Retrieved October 8, 2008.
- [8] Meers, Mason B. (August 2003). "Maximum bite force and prey size of *Tyrannosaurus rex* and their relationships to the inference of feeding behavior". *Historical Biology: A Journal of Paleobiology* 16 (1): 1–12. doi:10.1080/0891296021000050755.
- [9] Switeck, Brian (April 13, 2012). "When Tyrannosaurus Chomped Sauropods". Smithsonian Media. Retrieved August 24, 2013.
- [10] Hutchinson, John (July 15, 2013). "Tyrannosaurus rex: predator or media hype?". What's in John's Freezer?. Retrieved August 26, 2013.
- [11] Henderson, D. M. (January 1, 1999). "Estimating the masses and centers of mass of extinct animals by 3-D mathematical slicing". *Paleobiology* 25 (1): 88–106.
- [12] Anderson, J. F.; Hall-Martin, A. J.; Russell, Dale (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.
- [13] Bakker, Robert T. (1986). The Dinosaur Heresies. New York: Kensington Publishing. ISBN 0-688-04287-2. OCLC 13699558.
- [14] Farlow, J. O.; Smith, M. B.; Robinson, J. M. (1995). "Body mass, bone 'strength indicator', and cursorial potential of *Tyrannosaurus rex*". *Jour-nal of Vertebrate Paleontology* 15 (4): 713–725. doi:10.1080/02724634.1995.10011257.
- [15] Seebacher, Frank (2001). "A new method to calculate allometric length-mass relationships of dinosaurs". *Journal of Vertebrate Paleontology* 21 (1): 51–60. doi:10.1671/0272-4634(2001)021[0051:ANMTCA]2.0.CO;2.
- [16] Christiansen, Per; Fariña, Richard A. (2004). "Mass prediction in theropod dinosaurs". *Historical Biology* 16 (2–4): 85–92. doi:10.1080/08912960412331284313.

- [17] Boardman, T. J.; Packard, G. C.; Birchard, G. F. (2009). "Allometric equations for predicting body mass of dinosaurs". *Journal of Zoology* 279 (1): 102–110. doi:10.1111/j.1469-7998.2009.00594.x.
- [18] Hartman, Scott (July 7, 2013). "Mass estimates: North vs South redux". Scott Hartman's Skeletal Drawing.com. Retrieved August 24, 2013.
- [19] Francois Therrien; Donald M. Henderson (2007). "MY THEROPOD IS BIGGER THAN YOURS ... OR NOT: ESTIMATING BODY SIZE FROM SKULL LENGTH IN THEROPODS" (PDF). Journal of Vertebrate Paleontology 27: 108–115.
- [20] Therrien, F.; Henderson, D. M. (2007). "My theropod is bigger than yours ... or not: estimating body size from skull length in theropods". *Journal of Verte-brate Paleontology* 27 (1): 108–115. doi:10.1671/0272-4634(2007)27[108:MTIBTY]2.0.CO;2. ISSN 0272-4634.
- [21] 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. JSTOR 3889334.
- [22] Lipkin, Christine; Carpenter, Kenneth (2008). "Looking again at the forelimb of *Tyrannosaurus rex*". In Carpenter, Kenneth; Larson, Peter E. *Tyrannosaurus rex, the Tyrant King (Life of the Past)*. Bloomington: Indiana University Press. pp. 167–190. ISBN 0-253-35087-5.
- [23] "Museum unveils world's largest T-rex skull" (Press release). Montana State University. April 7, 2006. Retrieved September 13, 2008.
- [24] 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.
- [25] Jaffe, Eric (July 1, 2006). "Sight for 'Saur Eyes: *T. rex* vision was among nature's best". *Science News* **170** (1): 3–4. doi:10.2307/4017288. JSTOR 4017288. Retrieved October 6, 2008.
- [26] 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". *Nature* 382 (6593): 706–708. doi:10.1038/382706a0.
- [27] Holtz, Thomas R. (1994). "The Phylogenetic Position of the Tyrannosauridae: Implications for Theropod Systematics". *Journal of Palaeontology* **68** (5): 1100–1117. JSTOR 1306180.
- [28] Paul, Gregory S. (1988). *Predatory dinosaurs of the world: a complete illustrated guide*. New York: Simon and Schuster. ISBN 0-671-61946-2. OCLC 18350868.
- [29] Smith, J. B. (December 2005). "Heterodonty in *Tyran-nosaurus 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.

20 8 REFERENCES

[30] Douglas, K.; Young, S. (1998). "The dinosaur detectives". New Scientist. Retrieved October 16, 2008. One palaeontologist memorably described the huge, curved teeth of T. rex as 'lethal bananas'

- [31] Hone, D. (2012) "Did Tyrannosaurus rex have feathers?" *The Guardian*, October 17, 2012. Accessed online August 8, 2013.
- [32] Keim, B. (2012). "Giant Feathered Tyrannosaur Found in China." Wired, April 4, 2012. Accessed online August 8, 2013.
- [33] Xing Xu; Norell, Mark A.; Xuewen Kuang; Xiaolin Wang; Qi Zhao; Chengkai Jia (October 7, 2004). "Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids". *Nature* **431** (7009): 680–684. doi:10.1038/nature02855. PMID 15470426.
- [34] Xing Xu; Wang, Kebai; Ke Zhang; Qingyu Ma; Xing, Lida; Sullivan, Corwin; Dongyu Hu; Shuqing Cheng; Shuo Wang (5 April 2012). "A gigantic feathered dinosaur from the Lower Cretaceous of China" (PDF). *Nature* 484: 92–95. doi:10.1038/nature10906. PMID 22481363.
- [35] Larson, Neal L. (2008). "One hundred years of *Tyran-nosaurus rex*: the skeletons". In Larson, Peter; and Carpenter, Kenneth, editors. *Tyrannosaurus Rex, The Tyrant King*. Bloomington, IN: Indiana University Press. pp. 1–55. ISBN 978-0-253-35087-9.
- [36] Paul, Gregory S. (2008). "The extreme lifestyles and habits of the gigantic tyrannosaurid superpredators of the Late Cretaceous of North America and Asia". In Carpenter, Kenneth; Larson, Peter E. *Tyrannosaurus rex, the Tyrant King (Life of the Past)*. Bloomington: Indiana University Press. p. 316. ISBN 0-253-35087-5.
- [37] Currie, Philip J.; Hurum, Jørn H.; Sabath, Karol (2003). "Skull structure and evolution in tyrannosaurid dinosaurs" (PDF). Acta Palaeontologica Polonica 48 (2): 227–234. Retrieved October 8, 2008.
- [38] Holtz, Thomas R., Jr. (2004). "Tyrannosauroidea". In Weishampel, David B.; Dodson, Peter; Osmólska, Halszka. *The dinosauria*. Berkeley: University of California Press. pp. 111–136. ISBN 0-520-24209-2.
- [39] Maleev, E. A. (1955). translated by F. J. Alcock. "(title in Russian)" [Gigantic carnivorous dinosaurs of Mongolia] (PDF). *Doklady Akademii Nauk SSSR* (in Russian) 104 (4): 634–637.
- [40] Rozhdestvensky, AK (1965). "Growth changes in Asian dinosaurs and some problems of their taxonomy". *Pale-ontological Journal* **3**: 95–109.
- [41] Carpenter, Kenneth (1992). "Tyrannosaurids (Dinosauria) of Asia and North America". In Mateer, Niall J.; Pei-ji Chen. Aspects of nonmarine Cretaceous geology. Beijing: China Ocean Press. ISBN 978-7-5027-1463-5. OCLC 28260578.
- [42] Carr, Thomas D.; Williamson, Thomas E.; Schwimmer, David R. (March 2005). "A New Genus and Species of Tyrannosauroid from the Late

- Cretaceous (Middle Campanian) Demopolis Formation of Alabama". *Journal of Vertebrate Paleontology* **25** (1): 119–143. doi:10.1671/0272-4634(2005)025[0119:ANGASO]2.0.CO;2.
- [43] Hurum, Jørn H.; Sabath, Karol (2003). "Giant theropod dinosaurs from Asia and North America: Skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared" (PDF). *Acta Palaeontologica Polonica* 48 (2): 161–190. Retrieved October 8, 2008.
- [44] Olshevsky, George (1995). "The origin and evolution of the tyrannosaurids". *Kyoryugaku Saizensen* [Dino Frontline] **9–10**: 92–119.
- [45] Carr, T. D.; Williamson, T. E. (2004). "Diversity of late Maastrichtian Tyrannosauridae (Dinosauria: Theropoda) from western North America". *Zoological Journal of the Linnean Society* 142 (4): 479–523. doi:10.1111/j.1096-3642.2004.00130.x.
- [46] Gilmore, C. W. (1946). "A new carnivorous dinosaur from the Lance Formation of Montana". Smithsonian Miscellaneous Collections 106: 1–19.
- [47] Bakker, R. T.; Williams, M.; Currie, P. J. (1988). "*Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana". *Hunteria* **1** (5): 1–30.
- [48] Carr, TD (1999). "Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Theropoda)". *Journal of Vertebrate Paleontology* **19** (3): 497–520. doi:10.1080/02724634.1999.10011161.
- [49] Currie, Philip J. (2003). "Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada" (PDF). *Acta Palaeontologica Polonica* 42 (2): 191–226. Retrieved October 9, 2008.
- [50] Loewen, M.A.; Irmis, R.B.; Sertich, J.J.W.; Currie, P. J.; Sampson, S. D. (2013). Evans, David C, ed. "Tyrant Dinosaur Evolution Tracks the Rise and Fall of Late Cretaceous Oceans". *PLoS ONE* 8 (11): e79420. doi:10.1371/journal.pone.0079420.
- [51] Horner, J. R.; Padian, K. (September 2004). "Age and growth dynamics of Tyrannosaurus rex". *Proceedings. Biological sciences / the Royal Society* 271 (1551): 1875–80. doi:10.1098/rspb.2004.2829. PMC 1691809. PMID 15347508. Retrieved October 5, 2008.
- [52] Schweitzer MH, Wittmeyer JL, Horner JR (June 2005).

  "Gender-specific reproductive tissue in ratites and Tyrannosaurus rex". Science 308 (5727): 1456–60. doi:10.1126/science.1112158.

  Retrieved October 5, 2008.
- [53] Lee, Andrew H.; Werning, Sarah (2008). "Sexual maturity in growing dinosaurs does not fit reptilian growth models". *Proceedings of the National Academy of Sciences* 105 (2): 582–587. doi:10.1073/pnas.0708903105. PMC 2206579. PMID 18195356.
- [54] Erickson GM, Currie PJ, Inouye BD, Winn AA (July 2006). "Tyrannosaur life tables: an example of nonavian dinosaur population biology". *Science* 313 (5784): 213–7. doi:10.1126/science.1125721. PMID 16840697.

- [55] Holtz, Thomas R Jr. (March 19, 2013) [Lecture was held March 8, 2013]. The Life and Times of Tyrannosaurus rex, with Dr. Thomas Holtz (Lecture). Kane Hall Room 130 University of Washington Seattle, WA 98195: Burke Museum of Natural History and Culture. Retrieved October 12, 2013.
- [56] Paul, Gregory S. (2008). "Chapter 18: The Extreme Life Style and Habits of the Gigantic Tyrannosaurid Superpredators of the Cretaceous North America and Asia". In Larson, Peter L.; Carpenter, Kenneth. *Tyrannosaurus*, *The Tyrant King*. Indiana University Press. pp. 307– 345. ISBN 978-0-253-35087-9. Retrieved September 14, 2013.
- [57] Carpenter, Kenneth (1992). "Variation in *Tyrannosaurus rex*". In Kenneth Carpenter and Philip J. Currie. *Dinosaur Systematics: Approaches and Perspectives*. Cambridge: Cambridge University Press. pp. 141–145. ISBN 0-521-43810-1.
- [58] Larson, P.L. (1994). "Tyrannosaurus sex. In: Rosenberg, G.D. & Wolberg, D.L. Dino Fest". The Paleontological Society Special Publications 7: 139–155.
- [59] Erickson GM, Kristopher Lappin 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. PMID 16351976. Retrieved October 8, 2008.
- [60] Schweitzer MH, Elsey RM, Dacke CG, Horner JR, Lamm ET (April 2007). "Do egg-laying crocodilian (Alligator mississippiensis) archosaurs form medullary bone?". *Bone* 40 (4): 1152–8. doi:10.1016/j.bone.2006.10.029. PMID 17223615. Retrieved October 8, 2008.
- [61] Leidy, J (1865). "Memoir on the extinct reptiles of the Cretaceous formations of the United States". *Smithsonian Contributions to Knowledge* **14**: 1–135.
- [62] "Tyrannosaurus". American Museum of Natural History. Retrieved October 16, 2008.
- [63] Newman, BH (1970). "Stance and gait in the flesh-eating *Tyrannosaurus*". *Biological Journal of the Linnean Society* **2** (2): 119–123. doi:10.1111/j.1095-8312.1970.tb01707.x.
- [64] "The Age of Reptiles Mural". Yale University. 2008. Retrieved October 16, 2008.
- [65] 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: 145–160. Bibcode:2013JGeEd..61..145R. doi:10.5408/11-259.1.
- [66] Osborn, H. F. (1905). "Tyrannosaurus and other Cretaceous carnivorous dinosaurs". Bulletin of the AMNH (New York City: American Museum of Natural History) 21 (14): 259–265. hdl:2246/1464. Retrieved October 6, 2008.

- [67] Osborn, H. F. (1917). "Skeletal adaptations of Ornit-holestes, Struthiomimus, Tyrannosaurus". Bulletin of the American Museum of Natural History (New York City: American Museum of Natural History) 35 (43): 733–771. hdl:2246/1334. Retrieved October 8, 2008.
- [68] 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.
- [69] Horner, John R.; Lessem, Don (1993). The complete T. rex. New York City: Simon & Schuster. ISBN 0-671-74185-3.
- [70] Osborn, Henry Fairfield; Brown, Barnum (1906). "Tyrannosaurus, Upper Cretaceous carnivorous dinosaur". Bulletin of the AMNH (New York City: American Museum of Natural History) 22 (16): 281–296. hdl:2246/1473. Retrieved October 6, 2008.
- [71] Carpenter, Kenneth; Smith, Matt (2001). "Forelimb Osteology and Biomechanics of *Tyrannosaurus rex*". In Tanke, Darren; Carpenter, Kenneth. *Mesozoic vertebrate life*. Bloomington: Indiana University Press. pp. 90–116. ISBN 0-253-33907-3.
- [72] Fields, Helen (May 2006). "Dinosaur Shocker". Smithsonian Magazine. Retrieved October 2, 2008.
- [73] Schweitzer, Mary H.; Wittmeyer, Jennifer L.; Horner, John R.; Toporski, Jan K. (March 2005). "Soft-tissue vessels and cellular preservation in *Tyrannosaurus rex*". Science 307 (5717): 1952–5. Bibcode:2005Sci...307.1952S. doi:10.1126/science.1108397. PMID 15790853. Retrieved October 2, 2008.
- [74] Rincon, Paul (April 12, 2007). "Protein links T. rex to chickens". *BBC News*. Retrieved October 2, 2008.
- [75] Vergano, Dan (April 13, 2007). "Yesterday's T. Rex is today's chicken". USA Today. Retrieved October 8, 2008.
- [76] Schmid, Randolph E.; Associated Press (April 24, 2008).
  "Scientists study evidence modern birds came from dinosaurs". Newsvine. Retrieved October 8, 2008.
- [77] Kaye, Thomas G.; Gaugler, Gary; Sawlowicz, Zbigniew (July 2008). Stepanova, Anna, ed. "Dinosaurian Soft Tissues Interpreted as Bacterial Biofilms". *PLoS ONE* 3 (7): e2808. doi:10.1371/journal.pone.0002808. PMC 2483347. PMID 18665236.
- [78] "New Research Challenges Notion That Dinosaur Soft Tissues Still Survive" (Press release). Newswise. July 24, 2008. Retrieved October 8, 2008.
- [79] "Researchers Debate: Is It Preserved Dinosaur Tissue, or Bacterial Slime?" (Press release). Discover. July 30, 2008. Retrieved September 4, 2008.
- [80] San Antonio, James D.; Schweitzer, Mary H.; Jensen, Shane T.; Kalluri, Raghu; Buckley, Michael; Orgel, Joseph P. R. O. (2011). Van Veen, Hendrik W., ed. "Dinosaur Peptides Suggest Mechanisms

22 REFERENCES

of Protein Survival". PLoS ONE 6 (6): e20381. doi:10.1371/journal.pone.0020381. PMC 3110760. PMID 21687667.

- [81] Peterson, Joseph E.; Lenczewski, Melissa E.; Scherer, Reed P. (October 12, 2010). "Influence of Microbial Biofilms on the Preservation of Primary Soft Tissue in Fossil and Extant Archosaurs". PLoS ONE **5** (10): e13334. Bibcode:2010PLoSO...513334P. doi:10.1371/journal.pone.0013334. Retrieved March 30, 2012. [T]he interpretation of preserved organic remains as microbial biofilm [is] highly unlikely
- [82] Bakker, Robert T. (1968). "The superiority of dinosaurs" (PDF). Discovery 3 (2): 11-12. Archived from the original (PDF) on September 9, 2006. Retrieved October 7, 2008.
- [83] Bakker, Robert T. (1972). "Anatomical and ecological evidence of endothermy in dinosaurs" (PDF). Nature **238** (5359): 81–85. Bibcode:1972Natur.238...81B. doi:10.1038/238081a0. Archived from the original (PDF) on September 9, 2006. Retrieved October 7, 2008.
- [84] Barrick, Reese E.; Showers, William J. (July 1994). "Thermophysiology of Tyrannosaurus rex: Evidence from Oxygen Isotopes". Science (New York City) 265 (5169): 222-224. doi:10.1126/science.265.5169.222. PMID 17750663. Retrieved October 7, 2008.
- [85] Trueman, Clive; Chenery, Carolyn; Eberth, David A.; Spiro, Baruch (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. doi:10.1144/0016-764903-019.
- [86] Barrick, Reese E.; Showers, William J. (October 1999). "Thermophysiology and biology of Giganotosaurus: comparison with Tyrannosaurus". Palaeontologia Electronica [100] Hutchinson JR, Garcia M (February 2002). "Tyran-2 (2). Retrieved October 7, 2008.
- [87] Barrick, Reese E.; Stoskopf, Michael K.; Showers, William J. (1999). "Oxygen isotopes in dinosaur bones". [101] Holtz, Thomas R. (May 1, 1996). "Phylogenetic tax-In James O. Farlow and M. K. Brett-Surman. The Complete Dinosaur. Bloomington: Indiana University Press. pp. 474-490. ISBN 0-253-21313-4.
- [88] Paladino, Frank V.; Spotila, James R.; Dodson, Peter (1999). "A blueprint for giants: modeling the physiology of large dinosaurs". In James O. Farlow and M. K. Brett-Surman. The Complete Dinosaur. Bloomington: Indiana University Press. pp. 491-504. ISBN 0-253-21313-4.
- iology of nonavian dinosaurs". In David B. Weishampel, Peter Dodson and Halszka Osmólska. The dinosauria. Berkeley: University of California Press. pp. 643-659. ISBN 0-520-24209-2.
- [90] Lockley, MG; Hunt, AP (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.
- [91] "A PROBABLE TYRANNOSAURID TRACK FROM THE HELL CREEK FORMATION(UPPER CRETA-CEOUS), MONTANA, UNITED STATES". 2008.

- [92] 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: 645–647. doi:10.2110/palo.2008.p08-030r.
- [93] http://www.sciencedaily.com/releases/2016/01/ 160116214746.htm
- [94] http://www.sciencemag.org/news/2016/01/ you-could-probably-have-outrun-t-rex
- [95] http://www.dailymail.co.uk/ sciencetech/article-3419984/ Could-outrun-T-rex-Researchers-reveal-dinosaur-s-walk-slower-human-rur
- [96] http://www.usatoday.com/story/news/2016/01/27/ tyrannosaurs-faster-than-velociraptors/79423372/
- [97] Hutchinson JR, Ng-Thow-Hing V, Anderson FC (June "A 3D interactive method for estimating body segmental parameters in animals: application to the turning and running performance of Tyrannosaurus rex". Journal of Theoretical Biology 246 (4): 660-80. doi:10.1016/j.jtbi.2007.01.023. PMID 17363001.
- [98] Carrier, David R.; Walter, Rebecca M.; Lee, David V. (November 15, 2001). "Influence of rotational inertia on turning performance of theropod dinosaurs: clues from humans with increased rotational inertia". Journal of Experimental Biology (Company of Biologists) 204 (22): 3917-3926. PMID 11807109.
- [99] Hutchinson, J.R. (2004). "Biomechanical Modeling and Sensitivity Analysis of Bipedal Running Ability. II. Extinct Taxa" (PDF). Journal of Morphology 262 (1): 441-461. doi:10.1002/jmor.10240. PMID 15352202.
- nosaurus was not a fast runner". Nature 415 (6875): 1018-21. doi:10.1038/4151018a. PMID 11875567.
- onomy of the Coelurosauria (Dinosauria; Theropoda)". Journal of Paleontology 70 (3): 536-538. Retrieved October 3, 2008.
- [102] , Snively, Eric, Russell, Anthony P. (2003) "Kinematic Model of Tyrannosaurid (Dinosauria: Theropoda) Arctometatarsus Function" Journal of Morphology255(2)215-227. doi:10.1002/jmor.10059
- [89] Chinsamy, Anusuya; Hillenius, Willem J. (2004). "Phys- [103] Christiansen, P. (1998). "Strength indicator values of theropod long bones, with comments on limb proportions and cursorial potential" (PDF). Gaia 15: 241-255. ISSN 0871-5424.
  - [104] "Giraffe". WildlifeSafari.info. Retrieved April 29, 2006.
  - [105] "Chronological History of Woodland Park Zoo Chapter 4". Retrieved October 24, 2014.
  - [106] Alexander, R.M. (August 7, 2006). "Dinosaur biomechanics". Proc Biol Sci. (The Royal Society) 273 (1596): 1849-1855. doi:10.1098/rspb.2006.3532. PMC 1634776. PMID 16822743.

- tion in a sub-adult theropod dinosaur (Allosaurus fragilis) with comparisons to allosaur pathology in the Cleveland-Lloyd dinosaur quarry collection". Journal of Verte- [120], Stevens, Kent A. (April 1, 2011) The Binocular Vision brate Paleontology 22 (1): 76-90. doi:10.1671/0272-4634(2002)022[0076:MIAIIA]2.0.CO;2. ISSN 0272-4634. catalogs the injuries of the Allosaurus known as [121] "T. Rex brain study reveals a refined 'nose'". Calgary Her-"Big Al" – at least one was attributed to a fall.
- running performance in ostrich-mimics and tyrannosaurs" (PDF). Gaia 15: 257-270. Retrieved 2013.
- [109] Sellers, W.I., and Manning, P.L. (July 2007). "Estimating dinosaur maximum running speeds using evolutionary robotics". Proc. R. Soc. B (The Royal Society) 274 (1626): 2711-6. doi:10.1098/rspb.2007.0846. PMC 2279215. PMID 17711833.
- [110] Seward, L (August 21, 2007). "T. rex 'would outrun footballer". BBCNews. Retrieved October 16, 2008.
- [111] Callison, G.; Quimby, H. M. (1984). "Tiny dinosaurs: Are they fully grown?". Vertebrate Paleontology 3 (4): 200-209. doi:10.1080/02724634.1984.10011975.
- [112] Persons, Scott W.; Currie, Philip J. (January 2011) [Article first published online November 12, 2010]. "The Tail of Tyrannosaurus: Reassessing the Size and Locomotive Importance of the M. caudofemoralis in Non-Avian Theropods". The Anatomical Record 294 (1): 119-131,. [125] Crispian Scully, (2002) Oxford Handbook of Applied Dendoi:10.1002/ar.21290. Retrieved 2013.
- [113] "Guest Post: Bulking-Up the Back End Why Tyrannosaurus Tail Mass Matters | Dave Hone's Archosaur [126] "Estimating Musings". Archosaurmusings.wordpress.com. Retrieved 2015-12-23.
- [114] Kaplan, Matt (November 7, 2011). "Tyrannosaurs were power-walkers". Nature. doi:10.1038/news.2011.631. [127] Archived November 4, 2015 at the Wayback Machine Retrieved August 23, 2013.
- [115] Daily Mail Reporter (November 15, 2011). "T Rex 'power walked' to hunt down prey thanks to superior muscles in his posterior". Associated Newspapers Ltd. Retrieved August 23, 2013.
- [116] Manning P (2008). "T. rex speed trap". In Carpenter, Kenneth; Larson, Peter E. Tyrannosaurus rex, the Tyrant King (Life of the Past). Bloomington: Indiana University Press. pp. 205-228. ISBN 0-253-35087-5.
- [117] Paul, G.S., and Christiansen, P. (September 2000). "Forelimb posture in neoceratopsian dinosaurs: implications for gait and locomotion". Paleobiology **26** (3): 450-465. doi:10.1666/0094-8373(2000)026<0450:FPINDI>2.0.CO;2. **ISSN** 0094-8373.
- [118] Witmer, Lawrence M.; Ridgely, Ryan C. (September 2009). "New Insights Into the Brain, Braincase, and [133] Amos, Jonathan (2003-07-31). "Science/Nature | T. rex Ear Region of Tyrannosaurs (Dinosauria, Theropoda), with Implications for Sensory Organization and Behavdoi:10.1002/ar.20983.

- [107] Hanna, Rebecca R. (2002). "Multiple injury and infec- [119], Emily, John (July 3, 2006). Supersight for a Dino King. Retrieved July 7, 2006.
  - of Theropod Dinosaurs. Retrieved July 29, 2013.
  - ald. October 28, 2008. Retrieved October 29, 2008.
- [108] Paul, Gregory S. (2000). "Limb design, function and [122] Hurlburt, Grant S.; Ridgely, Ryan C.; Witmer, Lawrence M. (July 5, 2013) [This volume originated in a conference held on September 16-18, 2005, titled 'The Origin, Systematics, and Paleobiology of Tyrannosauridae,' and sponsored by the Burpee Museum of Natural History and Northern Illinois University]. "Chapter 6: Relative size of brain and cerebrum in Tyrannosaurid dinosaurs: an analysis using brain-endocast quantitative relationships in extant alligators". In Parrish, Michael J.; Molnar, Ralph E.; Currie, Philip J.; Koppelhus, Eva B. Tyrannosaurid Paleobiology (Life of the Past). Indiana University Press. pp. 134-154. ISBN 978-0-253-00947-0. Retrieved October 20, 2013.
  - Journal [123] Switek, Brian (October 2012). "The Tyrannosaurus Rex's Dangerous and Deadly Bite". Smithsonian.com.
    - [124] , Bates, K.T & Falkingham P.L. (2012). mating maximum bite performance in Tyrannosaurus rex using multi-body dynamics. Biological Letters. doi:10.1098/rsbl.2012.0056
    - tal Sciences, Oxford University Press -ISBN 978-0-19-851096-3 P156
    - cranial musculoskeletal constraints in theropod dinosaurs | Open Science". Rsos.royalsocietypublishing.org. 2015-11-04. Retrieved 2015-12-23.

    - [128] Lambe, L. B. (1917). "The Cretaceous theropodous dinosaur Gorgosaurus". Memoirs of the Geological Survey of Canada 100: 1-84. doi:10.4095/101672.
    - [129] Farlow, J. O. and Holtz, T. R. (2002). "The fossil record of predation in dinosaurs" (pdf). In Kowalewski, M. and Kelley, P.H. The Fossil Record of Predation. The Paleontological Society Papers 8. pp. 251-266.
    - [130] 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.
    - [131] Amos, J. (July 31, 2003). "T. rex goes on trial". BBC.
    - [132] "Sound file" (MP3). Media.libsyn.com. Retrieved 2015-12-23.
    - goes on trial". BBC News. Retrieved 2015-12-23.
  - ior". The Anatomical Record 292 (9): 1266-1296. [134] "T. Rex brain study reveals a refined 'nose'". Calgary Herald. October 28, 2008. Retrieved October 29, 2008.

24 REFERENCES

[135] Paul, G. S. (1988). Predatory Dinosaurs of the World. [148] Perkins, Sid (29 October 2015). "Tyrannosaurs were Simon and Schuster. ISBN 0-671-61946-2. OCLC 18350868.

- [136] Ruxton, GD; Houston, DC (April 2003). "Could Tyran- [149] Archived January 19, 2012 at the Wayback Machine nosaurus rex have been a scavenger rather than a predator? An energetics approach". Proceedings. Biolog- [150] Collins, Nick (June 22, 2011). ical sciences / the Royal Society 270 (1516): 731-3. doi:10.1098/rspb.2002.2279. PMC 1691292. PMID 12713747. Retrieved October 5, 2008.
- [137] Chin, Karen; Tokaryk, Timothy T.; Erickson, Gregory M.; Calk, Lewis C. (June 18, 1998). "A kingsized theropod coprolite". Nature 393 (6686): 680-682. doi:10.1038/31461. Summary at Monastersky, R. [152] Switek, Brian (July 25, 2011). "A bunch of bones (June 20, 1998). "Getting the scoop from the poop of T. rex". Science News 153 (25): 391. doi:10.2307/4010364. JSTOR 4010364. Archived from the original on May 11, [153] Witmer, Lawrence (July 13, 2011). "Dino Gangs: soli-2013.
- [138] Walters, Martin (1995). Bloomsbury Illustrated Dictionary of Prehistoric Life (Bloomsbury Illustrated Dictionaries). Godfrey Cave Associates Ltd. ISBN 1-85471-648-4.
- [139] Carpenter, K. (1998). "Evidence of predatory behavior by theropod dinosaurs". Gaia 15: 135-144. Archived from the original on November 17, 2007. Retrieved December 5, 2007.
- [140] Happ, John; Carpenter, Kenneth (2008). "An analysis of predator-prey behavior in a head-to-head encounter between Tyrannosaurus rex and Triceratops". In Carpenter, Kenneth; and Larson, Peter E. (editors). Tyrannosaurus rex, the Tyrant King (Life of the Past). Bloomington: Indiana University Press. pp. 355-368. ISBN 0-253-35087-
- [141] Dodson, Peter, The Horned Dinosaurs, Princeton Press. p.19
- [142] Tanke, Darren H.; Currie, Philip J. (1998). "Head-biting behavior in theropod dinosaurs: paleopathological evidence" (PDF). Gaia (15): 167-184. ISSN 0871-5424.
- [143] Carbone, Chris; Turvey, Samuel T.; Bielby, Jon (January 26, 2011). "Intra-guild Competition and its Implications for One of the Biggest Terrestrial Predators, Tyrannosaurus rex". Proceedings of the Royal Society B: Biological Sciences 278: 2682-2690. doi:10.1098/rspb.2010.2497.
- [144] 1999. The teeth of the Tyrannosaurus. Scientific American 281: 40-41.
- [145] The Complete T. Rex: How Stunning New Discoveries are Changing our Understanding of the World's Most Famous Dinosaur copyright 1993 by John R. Horner: pp 214-215
- [146] Snively, Eric.; Cotton, John R.; Ridgely, Ryan; Witmer, Lawrence M. (2013). "Multibody dynamics model of head and neck function in Allosaurus (Dinosauria, Theropoda)". Palaeontologica Electronica 16 (2).
- [147] Longrich N R., Horner J.R., Erickson G.M. & Currie P.J. (2010), "Cannibalism in Tyrannosaurus rex", Public Library of Science.

- probably cannibals". sciencemag.org. November 2015.
- "Tvrannosaurus Rex 'hunted in packs'". The Telegraph. Retrieved March 23, 2014.
- [151] Wallis, Paul (2012-06-11). "Op-Ed: T. Rex pack hunters? Scary, but likely to be true". Digitaljournal.com. Retrieved 2015-12-23.
- doesn't make a gang of bloodthirsty tyrannosaurs". The Guardian. Retrieved June 21, 2015.
- tary, communal, or cooperative hunting in tyrannosaurs". Pick & Scalpel WitmerLab at Ohio University. Retrieved October 12, 2013.
- [154] Sample, Ian (July 23, 2014). "Researchers find first sign that tyrannosaurs hunted in packs". The Guardian. Retrieved July 28, 2014.
- [155] McCrea, R. T. (2014). "A 'Terror of Tyran-The First Trackways of Tyrannosaurids nosaurs': and Evidence of Gregariousness and Pathology in *PLoS ONE* **9** (7): Tyrannosauridae". e103613. doi:10.1371/journal.pone.0103613.
- [156] Rothschild, B., Tanke, D. H., and Ford, T. L., 2001, Theropod stress fractures and tendon avulsions as a clue to activity: In: Mesozoic Vertebrate Life, edited by Tanke, D. H., and Carpenter, K., Indiana University Press, p. 331-336.
- [157] Wolff EDS, Salisbury SW, Horner JR, Varricchi DJ (2009). Hansen, Dennis Marinus, ed. "Common Avian Infection Plagued the Tyrant Dinosaurs". PLoS ONE 4 (9): e7288. doi:10.1371/journal.pone.0007288. PMC 2748709. PMID 19789646. Retrieved November 1, 2009.
- Peterson, Joseph E.; Henderson, Michael D.; Sherer, Reed P.; Vittore, Christopher P. (November 2009). "Face Biting On A Juvenile Tyrannosaurid And Behavioral Implications". PALAIOS 24 (11): 780-784. doi:10.2110/palo.2009.p09-056r.
- [159] Parisi, Tom (November 2, 2009). "The terrible teens of T. rex NIU scientists: Young tyrannosaurs did serious battle against each other". Northern Illinois University. Retrieved August 10, 2013.
- [160] Estes, R., and P. Berberian. 1970. Paleoecology of a late Cretaceous vertebrate community from Montana. Breviora volume 343, 35 pages
- [161] Derstler, Kraig (1994). "Dinosaurs of the Lance Formation in eastern Wyoming". In Nelson, Gerald E. (ed.). The Dinosaurs of Wyoming. Wyoming Geological Association Guidebook, 44th Annual Field Conference. Wyoming Geological Association. pp. 127–146.

- [162] Weishampel, David B.; Barrett, Paul M.; Coria, Rodolfo [173] Brochu, C. A. (December 2003). "Lessons From A A.; Loeuff, Jean Le; Xu Xing; Zhao Xijin; Sahni, Ashok; Gomani, Elizabeth M. P.; Noto, Christopher R. (2004). "Dinosaur Distribution". In Weishampel, David B.; Dodson, Peter; Osmólska, Halszka. The Dinosauria (2nd ed.). Berkeley: University of California Press. pp. 574–588. ISBN 0-520-24209-2.
- [163] 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. [175] Fiffer, Steve (2000). "Jurassic Farce". Tyrannosaurus Bulletin, 53, 216-271.
- [164] "The First Tyrannosaurus Skeleton, 1905". Linda Hall Library of Science, Engineering and Technology. [176] Archived from the original on September 28, 2006. Retrieved August 3, 2008.
- [165] Compare Oedipus rex, translated as Oedipus the King or King Oedipus, as the second part of the species name is syntactically an apposition to the genus name.
- [166] Breithaupt, Brent H.; Southwell, Elizabeth H.; Matthews, [178] Neffra A. (October 18, 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". Abstracts with Programs. 2005 Salt Lake City Annual Meeting. Geological Society of America. p. 406. Retrieved October 8, 2008.
- [167] Breithaupt, Brent H.; Southwell, Elizabeth H.; Matthews, Neffra A. (2006). Lucas, S. G.; Sullivan, R. M., eds. "Dynamosaurus imperiosus and the earliest discoveries of Tyrannosaurus rex in Wyoming and the West" (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.
- [168] Anonymous, 2000. "New discovery may endanger T-Rex's name" The Associated Press. June 13, 2000.
- [169] Ride, W. D. L. (1999). "Article 23.9 Reversal of Precedence". International code of zoological nomenclature. London: International Commission on Zoological Nomenclature. ISBN 0-85301-006-4. OCLC 183090345. Retrieved October 8, 2008.
- [170] Taylor, Mike (August 27, 2002). "So why hasn't Tyrannosaurus been renamed Manospondylus?". The Dinosaur FAQ. Retrieved October 8, 2008.
- [171] "Preparing Sue's bones". Sue at the Field Museum. The Field Museum. 2007. Retrieved October 24, 2014.
- [172] 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. doi:10.1038/nature02699. PMID 15306807.

- Tyrannosaur: The Ambassadorial Role Of Paleontology". PALAIOS 18 (6): 475-476. doi:10.1669/0883-1351(2003)018<0475:LFATTA>2.0.CO;2. ISSN 0883-1351.
- [174] Devitt, Terry (September 30, 2009). University of Wisconsin-Madison, ed. "Was Mighty T. Rex 'Sue' Felled By A Lowly Parasite?". ScienceDaily. Retrieved June 27, 2015.
- Sue. W. H. Freeman and Company, New York. pp. 121-122. ISBN 0-7167-4017-6.
- "Dig pulls up five T. rex specimens". BBC News. October 10, 2000. Retrieved December 13, 2008.
- [177] Currie, PJ; Huru, JH; Sabath, K (2003). "Skull structure and evolution in tyrannosaurid dinosaurs" (PDF). Acta Palaeontologica Polonica 48 (2): 227-234. Retrieved October 16, 2008.
- Henderson, M (2005). "Nano No More: The death of the pygmy tyrant". In Henderson, M. The origin, systematics, and paleobiology of Tyrannosauridae. Dekalb, Illinois: Northern Illinois University Press.
- [179] "Visit Jane the Dinosaur at the Burpee Museum, Rockford, Illinois". Archived from the original on May 25, 2008. Retrieved October 16, 2008.
- [180] "Museum unveils world's largest *T-rex* skull.". Retrieved April 7, 2006.
- [181] Ryan, M. J. "New Biggest *T-rex* Skull.". Retrieved April 12, 2006.

## **Further reading**

• Farlow, J. O.; Gatesy, S. M.; Holtz, T. R., Jr.; Hutchinson, J. R.; Robinson, J. M. (2000). "Theropod Locomotion". American Zoologist (The Society for Integrative and Comparative Biology) 40 (4): 640-663. doi:10.1093/icb/40.4.640.

#### **External links** 10

• The University of Edinburgh Lecture Dr Stephen Brusatte - Tyrannosaur Discoveries Feb 20, 2015

## 11 Text and image sources, contributors, and licenses

#### 11.1 Text

• Tyrannosaurus Source: https://en.wikipedia.org/wiki/Tyrannosaurus?oldid=705668618 Contributors: Eloquence, Mav, Bryan Derksen, Timo Honkasalo, Stephen Gilbert, Jeronimo, Clasqm, Sjc, Eclecticology, Danny, William Avery, Azhyd, Richhill, Daniel C. Boyer, Quercusrobur, Olivier, Rickyrab, Kchishol1970, Ixfd64, Zanimum, Arpingstone, Pcb21, Ahoerstemeier, Snoyes, Jeandré du Toit, Evercat, GCarty, Rl, Rogor, Tarosan~enwiki, Doradus, Tjunier, DJ Clayworth, Tpbradbury, Motor, Thechoipolloi, Furrykef, Saltine, Nv8200pa, Philopp, Samsara, EikwaR, Bevo, Shizhao, Prisonblues, AnonMoos, Wetman, Francs2000, 80.255, Phil Boswell, Ke4roh, TomPhil, Fredrik, RedWolf, Modulatum, Smallweed, Postdlf, Sverdrup, Academic Challenger, Bkell, Hadal, UtherSRG, Ruakh, David Gerard, Ancheta Wis, Giftlite, DocWatson42, MPF, Fudoreaper, Abigail-II, MathKnight, Mark Richards, Everyking, Lefty, Bkonrad, Michael Devore, Henry Flower, Rick Block, Duncharris, Yekrats, Jason Quinn, Solipsist, Apv, Chameleon, Gwydion~enwiki, Gadfium, Alexf, Gazibara, Gdr, Yath, Quadell, Antandrus, The Singing Badger, Williamb, Fredcondo, Evertype, MisfitToys, Rdsmith4, SAMAS, Kuralyov, Icairns, Sam Hocevar, Figure, Tyrannosaurus roll, Aramgutang, Marcus2, Jcw69, Neale Monks, Robin klein, Intrigue, Lacrimosus, CALR, DanielCD, Discospinster, Rich Farmbrough, Lejean2000, Vsmith, Florian Blaschke, Solkoll~enwiki, Xezbeth, Antaeus Feldspar, Michael Zimmermann, SpookyMulder, Corvun, Bender235, ESkog, Kbh3rd, Kjoonlee, BookWorm, Kwamikagami, Shanes, Spearhead, RoyBoy, Triona, Bobo192, Circeus, Adraeus, Wisdom89, Elipongo, Angie Y., Nicke Lilltroll~enwiki, Jag123, Cunningham, DCEdwards1966, Nsaa, Orangemarlin, Davidweman, Stephen G. Brown, Alansohn, Gary, Anthony Appleyard, Kswiston, Arthena, Ricky81682, Lectonar, Axl, Water Bottle, Fritzpoll, Alex '05, Mysdaao, Snowolf, Schapel, XB-70, Saga City, Danaman5, Suruena, Dinoguy2, Oghmoir, BlastO-Butter42, Versageek, Gene Nygaard, Redvers, Kazvorpal, Larry Dunn, Feezo, Stemonitis, Nuno Tavares, Angr, Bacteria, Firsfron, OwenX, Woohookitty, TigerShark, SpaceCaptain, BillC, Madchester, Kzollman, Scjessey, Commander Keane, XtremeGamer99, Kelisi, Sengkang, GregorB, BlaiseFEgan, Eras-mus, DemetriosMVital, Casius, Wdanwatts, Wayward, MechBrowman, Cedrus-Libani, Mtloweman, Phlebas, Palica, Pfalstad, Gerbrant, Mandarax, Ashmoo, Graham87, WBardwin, Magister Mathematicae, BD2412, FreplySpang, Keyzersoze, Jelemens, Reisio, Mendaliv, Icey, Ketiltrout, Drbogdan, Sjakkalle, Rjwilmsi, Est Xplosif, Koavf, Vary, JoshuacUK, MZMcBride, ErikHaugen, Kazrak, HappyCamper, The wub, Bhadani, Monger, Ucucha, Yamamoto Ichiro, MWAK, Fish and karate, SLi, Scorpionman, FlaBot, Naraht, RobertG, Doc glasgow, Nihiltres, RexNL, Gurch, Tegsirat, TheDJ, TeaDrinker, ChrisMD123, CJLL Wright, Typhin, Chobot, Bornhj, DVdm, Gdrbot, Bgwhite, Debivort, Philihp, UkPaolo, The Rambling Man, YurikBot, Wavelength, Crotalus horridus, Neitherday, Rtkat3, Jimp, Jlittlet, Pip2andahalf, Bryant.cutler, Briguy109, Red Slash, Pigman, Ramallite, Chris Capoccia, Stalmannen, SluggoOne, Hydrargyrum, Akamad, Stephenb, Manop, Gaius Cornelius, Lusanaherandraton, NawlinWiki, Swollib, SEWilcoBot, Dysmorodrepanis~enwiki, Wiki alf, Aeusoes1, Dtrebbien, Joelr31, Lexicon, Cleared as filed, Apokryltaros, Irishguy, Aaron Brenneman, Moe Epsilon, Rick lay95, Killdevil, Mad Max, Zelphics, Alex43223, Dbfirs, Olleicua, DeadEyeArrow, T-rex, Blowdart, Jkelly, Richardcavell, WAS 4.250, FF2010, NorsemanII, Ecksem Diem, 21655, ChrisGriswold, Closedmouth, Spawn Man, Reyk, Banana04131, Dspradau, BorgQueen, JuJube, Petri Krohn, Spliffy, DoriSmith, Vahid83, Kungfuadam, Paul Erik, Greece666, Gslide, DVD R W, WesleyDodds, That Guy, From That Show!, Attilios, SmackBot, Drizzt Do'Urden~enwiki, Unschool, Haymaker, Rose Garden, KnowledgeOfSelf, Hydrogen Iodide, Grazon, Bolesey, Phaldo, Thunderboltz, Piccadilly, Majts, Frymaster, HalfShadow, Master Deusoma, Aksi great, Gilliam, Ohnoitsjamie, ERcheck, Durova, Wigren, Yami Takashi, Persian Poet Gal, 32X, Jprg1966, Predator, Bignole, MalafayaBot, SchfiftyThree, The Rogue Penguin, ERobson, J. Spencer, DHN-bot~enwiki, Gruzd, Konstable, Darth Panda, StealthsneakII, Royboycrashfan, Philc 0780, King of the Dancehall, Kazeku, Can't sleep, clown will eat me, White Wolf, Abyssal, Onorem, KaiserbBot, MJCdetroit, Benjamin Mako Hill, XQ fan, Darwin's Bulldog, Addshore, Celarnor, Madman 2001, Stevenmitchell, Jerkov, Khoikhoi, PiMaster 3, Ritchie 333, Flyguy 649, Qilinmon, PopiethePopester, Johaen, Wirewad, Nakon, EVula, Iblardi, RandomP, Derek R Bullamore, ProjectShadow, PatrickA, Adrigon, John.Conway, Cephal-odd, Ligulembot, Evlekis, Alan G. Archer, Richard0612, Captainbeefart, Samuel Sol, Wikipedical, Ricky540, Esrever, CFLeon, Rory096, Quendus, MrSharp, O.Stainton, AlanD, Soap, Kuru, Carnby, Zapptastic, Writtenonsand, Mitternacht90, Mrlopez2681, Kevmin, A.b.s, Secretaria, Chodorkovskiy, JorisvS, Hemmingsen, Tim Q. Wells, Minna Sora no Shita, Mgiganteus1, Goodnightmush, Majorclanger, Aleenf 1, Mr. Lefty, Joshua Scott, Marblewonder, RomanSpa, A. Parrot, Volkan Yuksel, Loadmaster, Smith609, Siobhan30, Werdan7, Xunex, Mathewignash, Mr Stephen, Bendzh, Macellarius, Podiggady, SandyGeorgia, Geologyguy, Ryulong, Big Smooth, Tapatio, MTSbot~enwiki, Sasata, Caiaffa, Nicolharper, Sheep81, Jrhutch, Ginkgo100, PaulGS, Vlad788, BranStark, Iridescent, Judgesurreal777, Erik Peterson, Hipporoo, Samson1986, Recomposer, Blehfu, Greygirlbeast, Anger22, Tawkerbot2, Nyarpy, IronChris, Will Pittenger, J Milburn, JForget, MoneyMantra, Robincard, Traitorfish, Americasroof, Andrew amezcua2, CmdrObot, Tanthalas39, Bridesmill, SupaStarGirl, Eric, Rawling, Shuuvuia, DeLarge, CWY2190, CBWolf, DinoDam, Icedragon9559, Thursday Postal, NickW557, Controller of planet x, Spinosaur, El aprendelenguas, FlyingToaster, K00bine, Ballista, Rain74, Deibid, Casper2k3, Coronis, Andy king50, Hobohob, Cydebot, Expletivization, Mutedfaith169, DAntirrhopus, Kanags, Ax0l0tl, Johnny Arrombador 01, Gogo Dodo, Ahawowow, ST47, Derazzaboy, Odie5533, Tawkerbot4, Vallam, DumbBOT, Narayanese, Omicronpersei8, Gazzster, Zalgo, Gimmetrow, Lithuanian~enwiki, Centuriono, Casliber, Altaileopard, Thijs!bot, Epbr123, Wraithe, Jobba, Wikid77, Fneep, SonicBlue, Qwyrxian, Isaac-Sapphire, InSpace~enwiki, Cclennon26, Mojo Hand, Headbomb, Marek69, John254, Alientraveller, Dragon Helm, Triple-Quadruple, Dfrg.msc, Pcbene, CharlotteWebb, Chavando, Mandyjb, MichaelMaggs, Natalie Erin, Noclevername, Escarbot, Mentifisto, Porqin, KrakatoaKatie, AntiVandalBot, MewShaVinBasUra, Addydo1, Majorly, Luna Santin, Mark t young, Seaphoto, Turlo Lomon, QuiteUnusual, Dr. Blofeld, Doc Tropics, Teen Tyrant, RapidR, Mdotley, Oraroht, Whiteowl32, Kevin Nelson, Davegrupp, Rugz, Myanw, DCincarnate, DOS-Guy, JAnDbot, Thylacinus cynocephalus, Deflective, Husond, MER-C, Sonicsuns, Lawofmetal, Honette, Sophie means wisdom, Justin The Claw, Roleplayer, Dricherby, Makron In, Mirk Meister, Kirrages, Some-Guy-w-Problem, Wolfman SF, Aaron CBurke, Bongwarrior, VoABot II, Shotput king, JNW, Meleh, Xkcd, Think outside the box, Jim Douglas, Becksguy, Nyttend, Paul Haymon, SparrowsWing, Majestic Lizard, Sam Medany, Bubba hotep, Animum, Macadotios, ArthurWeasley, Adrian J. Hunter, Allstarecho, Schumi555, Glen, Talon Artaine, Chris G, JaGa, Edward321, PieCam, Paliku, Joepimps, Undead1, Greenguy1090, Grook Da Oger, Gofastfast, Thecarp, Coozick21, Cliff smith, Mkpowers, Conquerist, 47.46.45, Hdt83, MartinBot, Strinbop, Coreyrobinson, Randies on a Plane, Iheartrobojesus, Ngun, Znicker, Neekolas, Tuganax-enwiki, Azalea pomp, Sport woman, Burnedthru, CommonsDelinker, AlexiusHoratius, LightningPower, EdBever, Jsmith86, Artaxiad, RockMFR, Manticore, Huzzlet the bot, J.delanoy, Captain panda, Pharaoh of the Wizards, Nev1, DrKay, Mwbrooks, Danielw46, Philcha, Geopavl, Uncle Dick, Dwarf King, Cuddly Panda, Sandwichbob, Rufous-crowned Sparrow, Brazo622, Bot-Schafter, Pyrospirit, DjScrawl, NewEnglandYankee, Cadwaladr, SJP, Ferahgo the Assassin, Touch Of Light, Tad102, Mustafa Al Habib, Juliancolton, Steveoc 86, Limetolime, Jacob Fitzgerald, Prot D, Treisijs, Dice1561, Mike V, Schnelle86, Theavatar3, Useight, Gosho940204, Rexparry sydney, Rexregum, Idioma-bot, Funandtrvl, Spellcast, Crass conversationalist, Black Kite, Tatoute, UnicornTapestry, Deor, Benjicharlton, Evangelos Giakoumatos, VolkovBot, ABF, Leopold B. Stotch, Benosaurus, Indubitably, Thomas Kassa, Rutherfordjigsaw, Soliloquial, Philip Trueman, Slut.i.huvudet, Servalo, Malinaccier, Clammeh Hands, A4bot, Bermax~enwiki, Beef yum, Anonymous Dissident, Twin rex, Qxz, Transfat, Sintaku, FogDevil, Dendodge, Claidheamohmor, JhsBot, Sanfranman59, Mardhil, LeaveSleaves, Guldenat, MarshallKe, Luuva, Lombar2, Kcatena, Colin stuart, MearsMan, Doug, Plazak, KabbalistPhysicist, Enigma11.2 Images 27

man, Ubervochina, Juangarcia1982, Falcon8765, Enviroboy, Drutt, Thanatos666, Brianga, Legoktm, Vsst, Ertgf, Klettanator, Yhnbgt, Tczuel, Ponyo, SieBot, Éiginnte, Beffan, ShuttleBird, Tresiden, YonaBot, Eeeasterbunny, Azazyel, Gerakibot, Lauri Hirvisalo~enwiki, IH81107, Buteofalcon, Roflworthy, Rubble pile, FunkMonk, Tiptoety, Radon210, Exert, Darth Chyrsaor, Oda Mari, Robster1983, Jc-SOCO, Whytock88, JSpung, Antonio Lopez, Faradayplank, Ih8spino, Bagatelle, Lightmouse, Tombomp, Techman224, Wlegro, Hobartimus, Alex.muller, Deejaye6, Nancy, Kumioko (renamed), Rosiestep, Maelgwnbot, Jkellymc, Cyfal, Tarb, SuperSaiyaMan, Hamiltondaniel, WikiLaurent, Saule sauliite, Diesel 10, Spotty11222, Yair rand, Pinkadelica, Bamboozlingbert, Nergaal, Vishalsh521, Hermione is a dude, Troy 07, Explicit, SallyForth123, Rat at WikiFur, Mcelite, ClueBot, SubZeroSilver, PipepBot, The Thing That Should Not Be, Eumys, Bamboozlingbert21, Blizzardofshmoz, Czarkoff, Drmies, Cp111, Tiptopper, TBustah, CounterVandalismBot, Iratissimus9, Xenon54, Auntof6, Mspraveen, DragonBot, Excirial, Aslan10000, -Midorihana-, The Winged Yoshi, Ontopofthewall, Eeekster, G.I Bob, Sun Creator, Mechagio, NuclearWarfare, J.Gowers, Millionsandbillions, Cenarium, Arjayay, Exilian, Razorflame, Dinosauria10198, Gundersen53, MedicRoo, Tor722, The Red, Banime, Muro Bot, Thehelpfulone, La Pianista, Probe24gt, Wabeka, Elasmosaurus, Yoda227, Thingg, Aitias, Horselover Frost, Aarom, jordanisgay, Footballfan190, StingRayWhore, Wcp07, Ottoxgam, Mr.Heizman, Versus22, Dana boomer, Lonephenylring, Johnuniq, Jayfern7, Sebas678, SoxBot III, Modem12345, ENDWW, Apparition11, Vigilius, Vanished User 1004, DumZiBoT, Finalnight, DeltaSquad5, BendersGame, Wikiswitcher, Alienanus, XLinkBot, Fastily, Anydam, Spitfire, Antiboboy, Rror, Kintaro, Glopal, J2theimmy, Badgernet, WikiDao, Juiceebabee17, Blackhsif, Johnny6000, Lemmey, 11achitturi, Gggh, Surtsicna, Kbdankbot, HexaChord, LikeHolyWater, Addbot, Rex550, Jimbo1995, Pitchingfever10, Yousou, Denali134, Rosschudasama, DOI bot, Bigboylovin22, Theleftorium, M.nelson, Swearer77, SunDragon34, Fladrif, Kevin hipwell, Fieldday-sunday, Creativefates, Luke's Mall, Januarian Winter, Vishnava, CanadianLinuxUser, Leszek Jańczuk, Cst17, Freemasonx, Download, Funky Fantom, Clover08, The Shadow-Fighter, Virus worm3000, 61x62x61, Glass Sword, AndersBot, Ruralbadly999, Matt G, Koliri, Tide rolls, JohnGolberg, Ranaldo, Gail, Thatoneguy89, Raghuvarv, SuperYou~enwiki, Woome, Hilscher, Luckas-bot, Munkel Davidson, Yobot, 2D, Now05ster, Senator Palpatine, Joshinatorg, II MusLiM HyBRiD II, Washburnmav, THEN WHO WAS PHONE?, Wazzup1223, Worm That Turned, Mrburntorange, Johnpigg, IW.HG, Callowaywarbird, Iroony, Eric-Wester, Szajci, AnomieBOT, Andrewrp, Rubinbot, Rjanag, Merton81, IRP, Dwayne, Royote, Piano non troppo, Toddfergason, Littlepils, Kingpin13, Dr. Günter Bechly, DaffySchmoo, Ulric1313, CityFeedback, Flewis, Dandan5, Giants27, Materialscientist, Robun, The High Fin Sperm Whale, Citation bot, StormDaebak, Williamstrother, Dr. Xodar, Derp234, B. Fairbairn, LovesMacs, GrimmjowJabberjack, LilHelpa, JSW15, Crob14, Andrewmc123, Xqbot, TinucherianBot II, Mariomassone, Luuvabot, FanCollector, Mr. Prez, Capricorn42, Termininja, Wapondaponda, Horde08, Hush101, Pontificalibus, DSisyphBot, Aaaaaaahh, JRLivesey, Gilo1969, Happyfunrun, SachiniCK, H1024d11908, Fatchair27, Tyrol5, Almabot, Abce2, Tofer is cool, Poohbear54321, Frankie0607, Evanphoto, Mark Schierbecker, Venatico, RibotBOT, Steve.altus, TimTech, Conty~enwiki, WaynePacelle, Doulos Christos, Cheese moron, Ifailedmyphysicsexam, Natural Cut, Rodkimble, PM800, Erik9, Mompants, EZ4U2OMG, GaryNuman52, Samantha1961, FrescoBot, Zolee82, Yautja GD1, LucienBOT, Huh102, Bkamoua, RodgeyPPPPP, Sky Attacker, Oldlaptop321, Gooner-bill, VdBOT, Aran 0098, Endofskull, Wikidude9302, Tarascosaurus, Chris Amundson, Cannolis, Citation bot 1, 1Anthony90, Javert, OreL.D, Legoman978, Pshent, ScottRobertAnselmo, NoahHenkle, Pinethicket, Forescore68, Tori1998, HRoestBot, Fredrostar, Abductive, Chessboy123, Scoundr31, Supreme Deliciousness, Wikitanvir, HMallison, Paleo Kid, Todd bowles, Word113, FoxBot, Trappist the monk, Animalparty, Fama Clamosa, Reaper Eternal, AStrangerintheAlps, Linguisticgeek, Tbhotch, Minimac, El Mayimbe, DARTH SIDIOUS 2, Danó534661, RjwilmsiBot, Albertonykus, Bento00, DASHBot, J03Ltheone, EmausBot, Ornitholestes, WikitanvirBot, GoingBatty, Pahazzard, Stupefyduo, Wesley J M, Tommy2010, Anirudh Emani, Komododragonfan16, ZéroBot, Dinolover45, Troodon58, AvicAWB, Geno the Great, H3llBot, Wiooiw, Rexprimoris, DeinonychusDinosaur999, Wayne Slam, HammerFilmFan, EricWesBrown, Brandmeister, ScoBrit, Meeee21, L Kensington, Peter M. Brown, Bandit96, Stefan Milosevski, Cougarfan13, Dromaeosaur Dude, Arnolfosaur, Orange Suede Sofa, Michczu, Spunkylover6, Pro.Shark, ChuispastonBot, Ihardlythinkso, Thetyranasaurous rex roaaaaaaaaar, Emperor grant johnny, Peter Karlsen, Basel kamoua, Crimsonraptor, Nonfictions, DASHBotAV, Budz333, Barbie911, Blessed Frog, Twbxxx, Kleopatra, E. Fokker, Metamorphosed Fossil, Sk84lyfe99, ClueBot NG, Ohthreeohnine, Taylorsazombie, Matthiaspaul, CocuBot, LittleJerry, Pale-CloudedWhite, Movses-bot, Snotbot, Mozzyepic24, Meeeeeoo, Anupmehra, Gfrsdgerr, Megalobingosaurus, Helpful Pixie Bot, Paulmec, Beelzebubbles101, SaberToothedWhale, Dotname2469, Rextron, Kndimov, King Goth, Baily'sMacomb, Cyberpower678, AvocatoBot, Chris the Paleontologist, Dkspartan1, Yowanvista, Cadiomals, Vcohen, NotWith, Mike BRZ, Moldovan0731, Duxwing, BattyBot, Cyberbot II, ChrisGualtieri, MathKnight-at-TAU, Gilborrego, TylerDurden8823, Obtund, Dexbot, Aliafroz1901, Mogism, Ifgoofy, Uneedk, CuriousMind01, Akdulj, Dromeosaur34, عميد طاهر, Dinoexpert, Saberrex, SHFW70, FamAD123, Biomedicinal, Raptormimus456, IJReid, Tomopteryx, Serpinium, Lindenhurst Liberty, Elliot Teong, BigCat82, Ycooldog, Георгий Суворов, Ashorocetus, Marigold100, Levi bernardo, Paleocemoski, Nagging Prawn, Elitre (WMF), JeanLucMargot, DinopediaR, Crbzzj, Stamptrader, Dennonychus, Crb1972, Azertopius, Jinfengopteryx, Grammarian 79, Twirlypen, Monkbot, Jordan L 462, Large Andre, Ewriter 600, Burklemore 1, Tyrannosaurus rex, Theshanerocks, YeOldeGentleman, Christina1969, Beauty94, Alistairgray42, Veppex, Srednuas Lenoroc, Caftaric, Garlap, JohannSnow, Eclips57, DerpderpX, Spinofan0731, T.rex777 and Anonymous: 1197

#### 11.2 Images

- File:Abyssal\_Brachiopod\_00148.jpg Source: https://upload.wikimedia.org/wikipedia/commons/5/5b/Abyssal\_Brachiopod\_00148.jpg License: Public domain Contributors: Own work Original artist: Myself
- File:Albertosaurus\_Clean.png Source: https://upload.wikimedia.org/wikipedia/commons/a/a3/Albertosaurus\_Clean.png License: CC BY-SA 3.0 Contributors: Own work Original artist: MCDinosaurhunter
- File:B-rex\_teeth.jpg Source: https://upload.wikimedia.org/wikipedia/commons/2/27/B-rex\_teeth.jpg License: CC BY 2.5 Contributors: http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0016574 Original artist: John R. Horner, Mark B. Goodwin, Nathan Myhrvold
- File:Commons-logo.svg Source: https://upload.wikimedia.org/wikipedia/en/4/4a/Commons-logo.svg License: CC-BY-SA-3.0 Contributors: ? Original artist: ?
- File:DMNS\_Edmontosaurus.png Source: https://upload.wikimedia.org/wikipedia/commons/6/6a/DMNS\_Edmontosaurus.png License: CC BY-SA 3.0 Contributors: Own work Original artist: Firsfron
- File:DSC02558\_Bucky\_(T.rex\_fossil),\_Kelsey\_(Triceratops\_fossil)\_and\_Stan\_(T.\_rex\_cast).jpg
   Source: https://upload.wikimedia.org/wikipedia/commons/6/65/DSC02558\_Bucky\_%28T.rex\_fossil%29%2C\_Kelsey\_%28Triceratops\_fossil%29\_and\_Stan\_%28T.\_rex\_cast%29.jpg License: CC BY-SA 3.0 Contributors: Own work Original artist: Volkan Yuksel
- File:Dynamosaurus.jpg Source: https://upload.wikimedia.org/wikipedia/commons/0/0c/Dynamosaurus.jpg License: Public domain Contributors: http://digitallibrary.amnh.org/dspace/handle/2246/1464 Original artist: Unknown<a href='//www.wikidata.org/</li>

- wiki/Q4233718' title='wikidata:Q4233718'><img alt='wikidata:Q4233718' src='https://upload.wikimedia.org/wikipedia/commons/thumb/f/ff/Wikidata-logo.svg/20px-Wikidata-logo.svg.png' width='20' height='11' srcset='https://upload.wikimedia.org/wikipedia/commons/thumb/f/ff/Wikidata-logo.svg/30px-Wikidata-logo.svg.png 1.5x, https://upload.wikimedia.org/wikipedia/commons/thumb/f/ff/Wikidata-logo.svg/40px-Wikidata-logo.svg.png 2x' data-file-width='1050' data-file-height='590' /></a>
- File:FMNH\_Daspletosaurus\_White\_Background.jpg Source: https://upload.wikimedia.org/wikipedia/commons/8/81/FMNH\_Daspletosaurus\_White\_Background.jpg License: CC BY-SA 3.0 Contributors: File:FMNH Daspletosaurus.jpg Original artist: ScottRobertAnselmo
- File:Feathered\_Tyrannosaurus\_model.jpg
   Tyrannosaurus\_model.jpg
   Source:
   https://upload.wikimedia.org/wikipedia/commons/6/6f/Feathered\_
   Tyrannosaurus\_model.jpg
   License:
   CC BY 2.0 Contributors:
   Tyranozaur Rex Original artist:
   Marcin Polak from Warszawa /
   Warsaw, Polska / Poland
- File:Gorgosaurus\_white\_background.jpg
   Source: https://upload.wikimedia.org/wikipedia/commons/0/05/Gorgosaurus\_white\_background.jpg
   License: CC BY-SA 2.0 Contributors: [1] Original artist: Sebastian Bergmann from Siegburg, Germany
- File:Largesttheropods.png Source: https://upload.wikimedia.org/wikipedia/commons/a/ae/Largesttheropods.png License: CC-BY-SA-3.0 Contributors: Own work Original artist: Matt Martyniuk
- File:Lebendrekonstruktion\_T.rex\_Schädel\_im\_NHM\_Wien.JPG Source: https://upload.wikimedia.org/wikipedia/commons/4/4d/
  Lebendrekonstruktion\_T.rex\_Sch%C3%A4del\_im\_NHM\_Wien.JPG License: CC BY-SA 3.0 de Contributors: Own work Original artist:
  Domser
- File:MUJA\_04.jpg Source: https://upload.wikimedia.org/wikipedia/commons/e/e1/MUJA\_04.jpg License: CC BY-SA 2.5 es Contributors: Tomada por Noemy García García usando una cámara Nikon E3200. Original artist: Usuario:NeGRa
- File:Manospondylus.jpg Source: https://upload.wikimedia.org/wikipedia/commons/3/31/Manospondylus.jpg License: Public domain Contributors: http://digitallibrary.amnh.org/dspace/handle/2246/1334 Original artist: R. Weber
- File:Nanotyrannus\_lancensis\_skull.jpg
   Source: https://upload.wikimedia.org/wikipedia/commons/3/3f/Nanotyrannus\_lancensis\_skull.jpg
   License: CC BY 2.0 Contributors: Nanotyrannus lancensis theropod dinosaur (Hell Creek Formation, Late Cretaceous; Carter County, southeastern Montana, USA)
   2 Original artist: James St. John
- File:Philmont\_Scout\_Ranch\_Tyrannosaurus\_footprint.jpg
   Source: <a href="https://upload.wikimedia.org/wikipedia/commons/a/af/">https://upload.wikimedia.org/wikipedia/commons/a/af/</a>
   Philmont\_Scout\_Ranch\_Tyrannosaurus\_footprint.jpg
   License: GFDL Contributors: Own work Original artist: Rufous-crowned Sparrow
- File:Portal-puzzle.svg Source: https://upload.wikimedia.org/wikipedia/en/f/fd/Portal-puzzle.svg License: Public domain Contributors: ? Original artist: ?
- File:Red\_Pencil\_Icon.png Source: https://upload.wikimedia.org/wikipedia/commons/7/74/Red\_Pencil\_Icon.png License: CC0 Contributors: Own work Original artist: Peter coxhead
- File:Sue\_TRex\_Skull\_Full\_Frontal.JPG Source: https://upload.wikimedia.org/wikipedia/commons/1/18/Sue\_TRex\_Skull\_Full\_Frontal.JPG License: CC BY-SA 3.0 Contributors: Own work Original artist: ScottRobertAnselmo
- File:Sues\_skeleton.jpg Source: https://upload.wikimedia.org/wikipedia/commons/f/fc/Sues\_skeleton.jpg License: CC BY-SA 2.0 Contributors: Sue, the world's largest and most complete dinosaur skeleton. Original artist: Connie Ma from Chicago, United States of America
- File:T-rex\_fossil\_Jane\_by\_Volkan\_Yuksel\_DSC08683g.JPG
   Source: https://upload.wikimedia.org/wikipedia/commons/9/96/
   T-rex\_fossil\_Jane\_by\_Volkan\_Yuksel\_DSC08683g.JPG License: CC BY-SA 3.0 Contributors: Own work Original artist: Volkan Yuksel
- File:T.\_rex\_infection.png Source: https://upload.wikimedia.org/wikipedia/commons/7/7e/T.\_rex\_infection.png License: CC BY 2.5 Contributors: Wolff EDS, Salisbury SW, Horner JR, Varricchio DJ (2009) Common Avian Infection Plagued the Tyrant Dinosaurs. PLoS ONE 4(9): e7288. doi:10.1371/journal.pone.0007288 Original artist: Chris Glen
- File:T.\_rex\_old\_posture.jpg Source: https://upload.wikimedia.org/wikipedia/commons/0/0c/T.\_rex\_old\_posture.jpg License: Public domain Contributors: National Geographic, United States http://research.amnh.org/paleontology/artwork/knight/index.html Original artist: Charles Robert Knight
- File:T.\_rex\_versus\_A.\_atrox\_feet.JPG Source: https://upload.wikimedia.org/wikipedia/commons/9/96/T.\_rex\_versus\_A.\_atrox\_feet. JPG License: CC BY-SA 2.0 Contributors: File:T. rex right hind foot (lat).JPG & File:Allosaurus atrox Cleveland-Lloyd Quarry.jpg Original artist: Ballista & James St. John
- File:T\_Rex\_Leg\_Bones.png Source: https://upload.wikimedia.org/wikipedia/commons/b/bc/T\_Rex\_Leg\_Bones.png License: Public domain Contributors: Transferred from en.wikipedia Originally from: http://digitallibrary.amnh.org/dspace/handle/2246/1334 Original artist: Original uploader was Philcha at en.wikipedia Based on image published by Osborn, Henry Fairfield, 1857-1935.
- File:Tarbosaurus\_and\_Tyrannosaurus.jpg Source: https://upload.wikimedia.org/wikipedia/commons/9/96/Tarbosaurus\_and\_ Tyrannosaurus.jpg License: CC BY 2.0 Contributors: http://app.pan.pl/article/item/app48-161.html Original artist: Jørn H. Hurum and Karol Sabath
- File:Tyrannosaur\_arm\_104.JPG Source: https://upload.wikimedia.org/wikipedia/commons/2/2c/Tyrannosaur\_arm\_104.JPG License: Public domain Contributors: Own work Original artist: Conty
- File:Tyrannosaurid\_trackway.png Source: https://upload.wikimedia.org/wikipedia/commons/0/0e/Tyrannosaurid\_trackway.png License: CC BY 2.5 Contributors: http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0103613 Original artist: Richard T. McCrea, Lisa G. Buckley, James O. Farlow, Martin G. Lockley, Philip J. Currie, Neffra A. Matthews, S. George Pemberton
- File:Tyrannosaurus\_AMNH\_5027\_(white\_background).jpg Source: https://upload.wikimedia.org/wikipedia/commons/7/78/
   Tyrannosaurus\_AMNH\_5027\_%28white\_background%29.jpg License: CC BY-SA 2.5 nl Contributors: File:T-Rex.jpg Original artist: J.M. Luiit

11.3 Content license 29

File:Tyrannosaurus\_Rex\_Growth\_Series.jpg Source: https://upload.wikimedia.org/wikipedia/commons/c/c8/Tyrannosaurus\_Rex\_Growth\_Series.jpg License: CC BY 2.0 Contributors: Tyrannosaurus Rex Growth Series Original artist: Maarten Heerlien from The Hague, The Netherlands

- File:Tyrannosaurus\_Rex\_Holotype.jpg Source: https://upload.wikimedia.org/wikipedia/commons/9/94/Tyrannosaurus\_Rex\_Holotype.jpg License: CC BY-SA 3.0 Contributors: Own work Original artist: ScottRobertAnselmo
- File:Tyrannosaurus\_Rey.jpg Source: https://upload.wikimedia.org/wikipedia/commons/5/55/Tyrannosaurus\_Rey.jpg License: CC BY 2.5 Contributors: Benton MJ (2010) Studying Function and Behavior in the Fossil Record. PLoS Biol 8(3): e1000321. doi:10.1371/journal. pbio.1000321 Original artist: Painting courtesy of Luis Rey.
- File:Tyrannosaurus\_brain\_aus.jpg Source: https://upload.wikimedia.org/wikipedia/commons/b/be/Tyrannosaurus\_brain\_aus.jpg License: GFDL Contributors: Own work Original artist: Matt Martyniuk (Dinoguy2)
- File:Tyrannosaurus\_muscle\_mass.png Source: https://upload.wikimedia.org/wikipedia/commons/8/86/Tyrannosaurus\_muscle\_mass.png License: CC BY 2.5 Contributors: http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0026037 Original artist: John R. Hutchinson, Karl T. Bates, Julia Molnar, Vivian Allen, Peter J. Makovicky
- File:Tyrannosaurus\_peptides.jpg Source: https://upload.wikimedia.org/wikipedia/commons/a/a2/Tyrannosaurus\_peptides.jpg License: CC BY 2.5 Contributors: http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0020381 Original artist: James D. San Antonio1\*, Mary H. Schweitzer2,3,4, Shane T. Jensen5, Raghu Kalluri6,7, Michael Buckley8,9, Joseph P. R. O. Orgel10\*
- File:Tyrannosaurus\_resting\_pose.jpg Source: https://upload.wikimedia.org/wikipedia/commons/a/ac/Tyrannosaurus\_resting\_pose.jpg License: CC BY-SA 2.0 Contributors: Tyrannosaurus ????????? Original artist: ssr ist4u from Ibaraki, Japan
- File:Tyrannosaurus\_rex\_mmartyniuk.png Source: https://upload.wikimedia.org/wikipedia/commons/8/87/Tyrannosaurus\_rex\_mmartyniuk.png License: CC BY-SA 3.0 Contributors: Own work Original artist: Matt Martyniuk
- File:Tyrannosaurus\_skeleton.jpg Source: https://upload.wikimedia.org/wikipedia/commons/9/9f/Tyrannosaurus\_skeleton.jpg License: Public domain Contributors: http://digitallibrary.amnh.org/dspace/bitstream/2246/1464/1/B021a14.pdf Original artist: William D. Matthew
- File:Tyrannosaurus\_tooth\_marks.png Source: https://upload.wikimedia.org/wikipedia/commons/2/25/Tyrannosaurus\_tooth\_marks.png License: CC BY 2.5 Contributors: http://www.ploscollections.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0013419; jsessionid=A98501981DFE173B51C4610B2E971013 Original artist: Nicholas R. Longrich, John R. Horner, Gregory M. Erickson, Philip I. Currie
- File:Tyrannoskull.jpg Source: https://upload.wikimedia.org/wikipedia/commons/e/e4/Tyrannoskull.jpg License: Public domain Contributors: https://digitallibrary.amnh.org/dspace/handle/2246/49 Original artist: A.E. Anderson
- File:Tyrantgraph.png Source: https://upload.wikimedia.org/wikipedia/commons/6/63/Tyrantgraph.png License: Public domain Contributors: ? Original artist: ?
- File:Wikibooks-logo.svg Source: https://upload.wikimedia.org/wikipedia/commons/f/fa/Wikibooks-logo.svg License: CC BY-SA 3.0 Contributors: Own work Original artist: User:Bastique. User:Ramac et al.
- File:Wikiquote-logo.svg Source: https://upload.wikimedia.org/wikipedia/commons/f/fa/Wikiquote-logo.svg License: Public domain Contributors: ? Original artist: ?
- File:Wikisource-logo.svg Source: https://upload.wikimedia.org/wikipedia/commons/4/4c/Wikisource-logo.svg License: CC BY-SA 3.0
  Contributors: Rei-artur Original artist: Nicholas Moreau
- File:Wikispecies-logo.svg Source: https://upload.wikimedia.org/wikipedia/commons/d/df/Wikispecies-logo.svg License: CC BY-SA 3.0 Contributors: Image:Wikispecies-logo.jpg Original artist: (of code) cs:User:-xfi-

### 11.3 Content license

• Creative Commons Attribution-Share Alike 3.0