= Tyrannosauroidea =

Tyrannosauroidea (meaning ' tyrant lizard forms ') is a superfamily (or clade) of coelurosaurian theropod dinosaurs that includes the family Tyrannosauridae as well as more basal relatives . Tyrannosauroids lived on the Laurasian supercontinent beginning in the Jurassic Period . By the end of the Cretaceous Period , tyrannosauroids were the dominant large predators in the Northern Hemisphere , culminating in the gigantic Tyrannosaurus itself . Fossils of tyrannosauroids have been recovered on what are now the continents of North America , Europe , Asia , South America and Australia .

Tyrannosauroids were bipedal carnivores , as were most theropods , and were characterized by numerous skeletal features , especially of the skull and pelvis . Early in their existence , tyrannosauroids were small predators with long , three @-@ fingered forelimbs . Late Cretaceous genera became much larger , including some of the largest land @-@ based predators ever to exist , but most of these later genera had proportionately small forelimbs with only two digits . Primitive feathers have been identified in fossils of two species , and may have been present in other tyrannosauroids as well . Prominent bony crests in a variety of shapes and sizes on the skulls of many tyrannosauroids may have served display functions .

= = Description = =

Tyrannosauroids varied widely in size , although there was a general trend towards increasing size over time . Early tyrannosauroids were small animals . One specimen of Dilong , almost fully grown , measured 1 @.@ 6 meters (5 @.@ 3 ft) in length , and a fully @-@ grown Guanlong measured 3 meters (10 ft long) . Teeth from lower Lower Cretaceous rocks (140 to 136 million years old) of Hyogo , Japan , appear to have come from an approximately 5 metres (16 ft) long animal , possibly indicating an early size increase in the lineage . An immature Eotyrannus was over 4 meters (13 ft) in length , and a subadult Appalachiosaurus was estimated at more than 6 meters (20 ft) long , indicating that both genera reached larger sizes . The Late Cretaceous tyrannosaurids ranged from the 9 meter (30 ft) Albertosaurus and Gorgosaurus to Tyrannosaurus , which exceeded 12 meters (39 ft) in length and may have weighed more than 6400 kilograms (7 short tons) . A 2010 review of the literature concluded that tyrannosaurs were " small- to mid @-@ sized " for their first 80 million years but were " some of the largest terrestrial carnivores to ever live " in their last 20 million years .

Skulls of early tyrannosauroids were long , low and lightly constructed , similar to other coelurosaurs , while later forms had taller and more massive skulls . Despite the differences in form , certain skull features are found in all known tyrannosauroids . The premaxillary bone is very tall , blunting the front of the snout , a feature which evolved convergently in abelisaurids . The nasal bones are characteristically fused together , arched slightly upwards and often very roughly textured on their upper surface . The premaxillary teeth at the front of the upper jaw are shaped differently from the rest of the teeth , smaller in size and with a D @-@ shaped cross section . In the lower jaw , a prominent ridge on the surangular bone extends sideways from just below the jaw joint , except in the basal Guanlong .

Tyrannosauroids had S @-@ shaped necks and long tails , as did most other theropods . Early genera had long forelimbs , about 60 % the length of the hindlimb in Guanlong , with the typical three digits of coelurosaurs . The long forelimb persisted at least through the Early Cretaceous Eotyrannus , but is unknown in Appalachiosaurus . Derived tyrannosaurids have forelimbs strongly reduced in size , the most extreme example being Tarbosaurus from Mongolia , where the humerus was only one @-@ quarter the length of the femur . The third digit of the forelimb was also reduced over time . This digit was unreduced in the basal Guanlong , while in Dilong it was more slender than the other two digits . Eotyrannus also had three functional digits on each hand . Tyrannosaurids had only two , although the vestigial metacarpal of the third are preserved in some well @-@ preserved specimens . As in most coelurosaurs , the second digit of the hand is the largest , even when the third digit is not present .

Characteristic features of the tyrannosauroid pelvis include a concave notch at the upper front end

of the ilium , a sharply defined vertical ridge on the outside surface of the ilium , extending upwards from the acetabulum (hip socket) , and a huge " boot " on the end of the pubis , more than half as long as the shaft of the pubis itself . These features are found in all known tyrannosauroids , including basal members Guanlong and Dilong . The pubis is not known in Aviatyrannis or Stokesosaurus but both show typical tyrannosauroid characters in the ilium . The hindlimbs of all tyrannosauroids , like most theropods , had four toes , although the first toe (the hallux) did not contact the ground . Tyrannosauroid hindlimbs are longer relative to body size than almost any other theropods , and show proportions characteristic of fast @-@ running animals , including elongated tibiae and metatarsals . These proportions persist even in the largest adult Tyrannosaurus , despite its probable inability to run . The third metatarsal of tyrannosaurids was pinched at the top between the second and fourth , forming a structure known as the arctometatarsus . The arctometatarsus was also present in Appalachiosaurus but it is unclear whether it was found in Eotyrannus or Dryptosaurus . This structure was shared by derived ornithomimids , troodontids and caenagnathids , but was not present in basal tyrannosauroids like Dilong , indicating convergent evolution .

= = Classification = =

Tyrannosaurus was named by Henry Fairfield Osborn in 1905 , along with the family Tyrannosauridae . The name is derived from the Ancient Greek words ???????? / tyrannos (' tyrant ') and ?????? / sauros (' lizard ') . The superfamily name Tyrannosauroidea was first published in a 1964 paper by the British paleontologist Alick Walker . The suffix -oidea , commonly used in the name of animal superfamilies , is derived from the Greek ????? / eidos (' form ') .

Scientists have commonly understood Tyrannosauroidea to include the tyrannosaurids and their immediate ancestors . With the advent of phylogenetic taxonomy in vertebrate paleontology , however , the clade has received several more explicit definitions . The first was by Paul Sereno in 1998 , where Tyrannosauroidea was defined as a stem @-@ based taxon including all species sharing a more recent common ancestor with Tyrannosaurus rex than with neornithean birds . To make the family more exclusive , Thomas Holtz redefined it in 2004 to include all species more closely related to Tyrannosaurus rex than to Ornithomimus velox , Deinonychus antirrhopus or Allosaurus fragilis . Sereno published a new definition in 2005 , using Ornithomimus edmontonicus , Velociraptor mongoliensis and Troodon formosus as external specifiers . The Sereno definition was adopted in a 2010 review .

Some studies have suggested that the clade Megaraptora , usually considered to be allosauroids , are basal tyrannosauroids . However , other authors disputed the placement of megaraptorans within Tyrannosauroidea , and a study of megaraptoran hand anatomy published in 2016 caused even the original scientists suggesting their tyrannosauroid relationships to at least partly reject their prior conclusion .

= = = Species = = =

The following taxa are classified based on the latest studies of these animals .
Superfamily Tyrannosauroidea
Appalachiosaurus montgomeriensis (Late Cretaceous , eastern North America)
Aviatyrannis jurassica (Late Jurassic , Portugal)
Dryptosaurus aquilunguis (Late Cretaceous , New Jersey , United States)
Eotyrannus lengi (Early Cretaceous , southern England)
Labocania anomala (Late Cretaceous , western Mexico)
Timurlengia euotica (Middle Cretaceous , Uzbekistan)
Xiongguanlong baimoensis (Early Cretaceous , central China)
Family Coeluridae ?
Family Proceratosauridae
Family Tyrannosauridae
Uncertain placement

Bagaraatan ostromi (Late Cretaceous , Mongolia ; might be a maniraptoran instead)
Chingkankousaurus fragilis (Late Cretaceous , China)
Diplotomodon horrificus (Late Cretaceous , New Jersey , United States ; may be synonymous with either Dryptosaurus species)
Dryptosaurus macropus (Late Cretaceous , eastern North America ; too fragmentary , may belong to another kind of theropod)
Raptorex kriegsteini (Late Cretaceous ? , Mongolia ? ; might represent a juvenile specimen of Tarbosaurus bataar instead .)

= = = Phylogeny = = =

While paleontologists have long recognized the family Tyrannosauridae , its ancestry has been the subject of much debate . For most of the twentieth century , tyrannosaurids were commonly accepted as members of the Carnosauria , which included almost all large theropods . Within this group , the allosaurids were often considered to be ancestral to tyrannosaurids . In the early 1990s , cladistic analyses instead began to place tyrannosaurids into the Coelurosauria , echoing suggestions first published in the 1920s . Tyrannosaurids are now universally considered to be large coelurosaurs .
In 1994 , Holtz grouped tyrannosauroids with elmisaurids , ornithomimosaurs and troodonts into a coelurosaurian clade called Arctometatarsalia based on a common ankle structure where the second and fourth metatarsals meet near the tarsal bones , covering the third metatarsal when viewed from the front . Basal tyrannosauroids like Dilong , however , were found with non @-@ arctometatarsalian ankles , indicating that this feature evolved convergently . Arctometatarsalia has been dismantled and is no longer used by most paleontologists , with tyrannosauroids usually considered to be basal coelurosaurs outside Maniraptoriformes . One recent analysis found the family Coeluridae , including the Late Jurassic North American genera Coelurus and Tanycolagreus , to be the sister group of Tyrannosauroidea .
The most basal tyrannosauroid known from complete skeletal remains is Guanlong . Other early taxa include Stokesosaurus and Aviatyrannis , known from far less complete material . The better @-@ known Dilong is considered slightly more derived than Guanlong and Stokesosaurus . Dryptosaurus , long a difficult genus to classify , has turned up in several recent analyses as a basal tyrannosauroid as well , slightly more distantly related to Tyrannosauridae than Eotyrannus and Appalachiosaurus . Alectrosaurus , a poorly known genus from Mongolia , is definitely a tyrannosauroid but its exact relationships are unclear . Other taxa have been considered possible tyrannosauroids by various authors , including Bagaraatan and Labocania . Siamotyrannus from the Early Cretaceous of Thailand was originally described as an early tyrannosaurid , but is usually considered a carnosaur today . Iliosuchus has a vertical ridge on the ilium reminiscent of tyrannosauroids and may in fact be the earliest known member of the superfamily , but not enough material is known to be sure .
Below is a cladogram by Loewen et al. in 2013 that includes virtually all known tyrannosauroid species .

= = Distribution = =

The tyrannosauroids lived on the supercontinent Laurasia , which split from Gondwana in the Middle Jurassic , as well as on the northern continents , which separated from Laurasia later in the Mesozoic era . The earliest recognized tyrannosauroids lived in the Late Jurassic , including Guanlong from northwestern China , Stokesosaurus from the western United States and Aviatyrannis from Portugal . Some fossils currently referred to Stokesosaurus may instead belong to Aviatyrannis , given the great similarities in the dinosaur faunas of Portugal and North America during this time . If Iliosuchus from the Middle Jurassic of England is in fact a tyrannosauroid , it would be the earliest known genus and might suggest that the superfamily originated in Europe .
Early Cretaceous tyrannosauroids are also found on all three northern continents . Eotyrannus from

England and Dilong from northeastern China are the only two named genera of this age , while Early Cretaceous tyrannosauroid premaxillary teeth are known from the Cedar Mountain Formation in Utah and the Tetori Group of Japan .

By the middle of the Cretaceous , tyrannosauroid fossils are no longer found in Europe , suggesting a localized extinction on that continent . Tyrannosauroid teeth and possible body fossils are known from the North American Dakota Formation , as well as formations in Kazakhstan , Tajikistan and Uzbekistan , from the middle of the Cretaceous . The first unquestionable remains of tyrannosaurids occur in the Campanian stage of the Late Cretaceous in North America and Asia . Two subfamilies are recognized . The albertosaurines are only known from North America , while the tyrannosaurines are found on both continents . Tyrannosaurid fossils have been found in Alaska , which may have served as a land bridge allowing dispersal between the two continents . Non @-@ tyrannosaurid tyrannosauroids like Alectrosaurus and possibly Bagaraatan were contemporaneous with tyrannosaurids in Asia , while they are absent from western North America . Eastern North America was divided by the Western Interior Seaway in the middle of the Cretaceous and isolated from the western portion of the continent . The absence of tyrannosaurids from the eastern part of the continent suggests that the family evolved after the appearance of the seaway , allowing basal tyrannosauroids like Dryptosaurus and Appalachiosaurus to survive in the east as a relict population until the end of the Cretaceous .

Basal tyrannosauroids may have also been present in what is now southeastern Australia during the Aptian of the Early Cretaceous . NMV P186069 , a partial pubis (a hip bone) with a distinctive tyrannosauroid @-@ like form , was discovered in Dinosaur Cove in Victoria , indicating that tyrannosauroids were not limited to the northern continents as previously thought .

An as yet undescribed and unnamed tyrannosauroid from the Zuni Basin of New Mexico has been found .

= = Paleobiology = =

= = = Feathers = = =

Long filamentous structures have been preserved along with skeletal remains of numerous coelurosaurs from the Early Cretaceous Yixian Formation and other nearby geological formations from Liaoning , China . These filaments have usually been interpreted as " protofeathers , " homologous with the branched feathers found in birds and some non @-@ avian theropods , although other hypotheses have been proposed . A skeleton of Dilong was described in 2004 that included the first example of feathers in a tyrannosauroid . Similarly to down feathers of modern birds , the feathers found in Dilong were branched but not pennaceous , and may have been used for insulation . Even large tyrannosauroids have been found with evidence of feathers . Yutyrannus huali , also from the Yixian Formation , is known from three specimens , each preserving traces of feathers on various parts of the body . While not all areas of the body preserve impressions across all three specimens , these fossils demonstrate that even in this medium @-@ sized species , most of the body was covered in feathers .

The presence of feathers in basal tyrannosauroids is not surprising , since they are now known to be characteristic of coelurosaurs , found in other basal genera like Sinosauropteryx , as well as all more derived groups . Rare fossilized skin impressions of some Late Cretaceous tyrannosaurids lack feathers , however , instead showing skin covered in fine , non @-@ overlapping scales . It is possible that feathers were present on areas of the body not preserved with skin impressions (which are very small and come primarily from the legs , pelvic region and underside of the tail) . Alternatively , secondary loss of feathers in large tyrannosaurids may be analogous with the similar loss of hair in the largest modern mammals like elephants , where a low surface area @-@ to @-@ volume ratio slows down heat transfer , making insulation by a coat of hair unnecessary . A precedent can be seen in other dinosaur groups such as ornithischians , in which filamentous structures were lost , and scales reappeared .

= = = Head crests = = =

Bony crests are found on the skulls of many theropods , including numerous tyrannosauroids . The most elaborate is found in Guanlong , where the nasal bones support a single , large crest which runs along the midline of the skull from front to back . This crest was penetrated by several large foramina (openings) which reduced its weight . A less prominent crest is found in Dilong , where low , parallel ridges run along each side of the skull , supported by the nasal and lacrimal bones . This ridges curve inwards and meet just behind the nostrils , making the crest Y @-@ shaped . The fused nasals of tyrannosaurid are often very rough @-@ textured . Alioramus , a possible tyrannosaurid from Mongolia , bears a single row of five prominent bony bumps on the nasal bones ; a similar row of much lower bumps is present on the skull of Appalachiosaurus , as well as some specimens of Daspletosaurus , Albertosaurus , and Tarbosaurus . In Albertosaurus , Gorgosaurus and Daspletosaurus , there is a prominent horn in front of each eye on the lacrimal bone . The lacrimal horn is absent in Tarbosaurus and Tyrannosaurus , which instead have a crescent @-@ shaped crest behind each eye on the postorbital bone .

These head crests may have been used for display , perhaps for species recognition or courtship behavior . An example of the handicap principle may be the case of Guanlong , where the large , delicate crest may have been a hindrance to hunting in what was presumably an active predator . If an individual was healthy and successful at hunting despite the fragile crest , it would indicate the superior quality of the individual over others with smaller crests . Similarly to the unwieldy tail of a male peacock or the outsized antlers of an Irish elk , the crest of Guanlong may have evolved via sexual selection , providing an advantage in courtship that outweighed any decrease in hunting ability .

= = = Reproduction = = =

Neonate sized tyrannosaur fossils have been documented in the scientific literature .