= Daspletosaurus =

Daspletosaurus (/ dæs?pli?t??s??r?s / das @-@ PLEET @-@ o @-@ SAWR @-@ ?s ; meaning " frightful lizard ") is a genus of tyrannosaurid theropod dinosaur that lived in western North America between 77 and 74 million years ago , during the Late Cretaceous Period . Fossils of the only named species (D. torosus) were found in Alberta , although other possible species from Alberta and Montana await description . Including these undescribed species makes Daspletosaurus the most species @-@ rich genus of tyrannosaur .

Daspletosaurus is closely related to the much larger and more recent Tyrannosaurus . Like most known tyrannosaurids , it was a multi @-@ tonne bipedal predator equipped with dozens of large , sharp teeth . Daspletosaurus had the small forelimbs typical of tyrannosaurids , although they were proportionately longer than in other genera .

As an apex predator , Daspletosaurus was at the top of the food chain , probably preying on large dinosaurs like the ceratopsid Centrosaurus and the hadrosaur Hypacrosaurus . In some areas , Daspletosaurus coexisted with another tyrannosaurid , Gorgosaurus , though there is some evidence of niche differentiation between the two . While Daspletosaurus fossils are rarer than other tyrannosaurids ' , the available specimens allow some analysis of the biology of these animals , including social behavior , diet and life history .

= = Description = =

While very large by the standard of modern predators , Daspletosaurus was not the largest tyrannosaurid . Adults could reach a length of 8 ? 9 meters (26 ? 30 ft) from snout to tail . Mass estimates have centered on 2 @.@ 5 tonnes (2 @.@ 75 short tons) but have ranged between 1 @.@ 8 and 3 @.@ 8 tonnes (2 @.@ 0 and 4 @.@ 1 short tons) .

Daspletosaurus had a massive skull that could reach more than 1 meter (3 @.@ 3 ft) in length . The bones were heavily constructed and some , including the nasal bones on top of the snout , were fused for strength . Large fenestrae (openings) in the skull reduced its weight . An adult Daspletosaurus was armed with about six dozen teeth that were very long but oval in cross section rather than blade @-@ like . Unlike its other teeth , those in the premaxilla at the end of the upper jaw had a D @-@ shaped cross section , an example of heterodonty always seen in tyrannosaurids . Unique skull features included the rough outer surface of the maxilla (upper jaw bone) and the pronounced crests around the eyes on the lacrimal , postorbital , and jugal bones . The orbit (eye socket) was a tall oval , somewhere in between the circular shape seen in Gorgosaurus and the ' keyhole ' shape of Tyrannosaurus . Split carinae have been found on Daspletosaurus teeth .

Daspletosaurus shared the same body form as other tyrannosaurids , with a short , S @-@ shaped neck supporting the massive skull . It walked on its two thick hindlimbs , which ended in four @-@ toed feet , although the first digit (the hallux) did not contact the ground . In contrast , the forelimbs were extremely small and bore only two digits , although Daspletosaurus had the longest forelimbs in proportion to body size of any tyrannosaurid . A long , heavy tail served as a counterweight to the head and torso , with the center of gravity over the hips .

= = Classification and systematics = =

Daspletosaurus belongs in the subfamily Tyrannosaurinae within the family Tyrannosauridae , along with Tarbosaurus , Tyrannosaurus and Alioramus . Animals in this subfamily are more closely related to Tyrannosaurus than to Albertosaurus and are known ? with the exception of Alioramus ? for their robust build with proportionally larger skulls and longer femora than in the other subfamily , the Albertosaurinae .

Daspletosaurus is usually considered to be closely related to Tyrannosaurus rex , or even a direct ancestor through anagenesis . Gregory Paul reassigned D. torosus to the genus Tyrannosaurus , creating the new combination Tyrannosaurus torosus , but this has not been generally accepted . Many researchers believe Tarbosaurus and Tyrannosaurus to be sister taxa or even to be the same

genus , with Daspletosaurus a more basal relative . On the other hand , Phil Currie and colleagues find Daspletosaurus to be more closely related to Tarbosaurus and other Asian tyrannosaurids like Alioramus than to the North American Tyrannosaurus . The systematics (evolutionary relationships) of Daspletosaurus may become clearer once all the species have been described .

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

= = Discovery and naming = =

The type specimen of Daspletosaurus torosus (CMN 8506) is a partial skeleton including the skull , the shoulder , a forelimb , the pelvis , a femur and all of the vertebrae from the neck , torso and hip , as well as the first eleven tail vertebrae . It was discovered in 1921 near Steveville , Alberta , by Charles Mortram Sternberg , who thought it was a new species of Gorgosaurus . It was not until 1970 that the specimen was fully described by Dale Russell , who made it the type of a new genus , Daspletosaurus , from the Greek ??????? (dasples , stem and connective vowel resulting in daspleto ~) (" frightful ") and ?????? / sauros (" lizard ") . The type species is Daspletosaurus torosus , the specific name torosus being Latin for ' muscular ' or ' brawny ' . Aside from the type , there is only one other well @-@ known specimen , RTMP 2001 @.@ 36 @.@ 1 , a relatively complete skeleton discovered in 2001 . Both specimens were recovered from the Oldman Formation in the Judith River Group of Alberta . The Oldman Formation was deposited during the middle Campanian stage of the Late Cretaceous , from about 77 to 76 Ma (million years ago) . A specimen from the younger Horseshoe Canyon Formation in Alberta has been reassigned to Albertosaurus sarcophagus .

= = = Unnamed species = = =

Two or three additional species have been assigned to the genus Daspletosaurus over the years , although as of 2007 none of these species have received a proper description or scientific name . In the meantime , all are designated as Daspletosaurus spp ; this does not imply that they all are the same species .

Along with the holotype , Russell designated a specimen collected by Barnum Brown in 1913 as the paratype of D. torosus . This specimen (AMNH 5438) consists of parts of the hindleg , the pelvis and some of its associated vertebrae . It was discovered in the Dinosaur Park Formation in Alberta . The Dinosaur Park Formation was formerly known as the Upper Oldman Formation and dates back to the middle Campanian , between 76 @.@ 5 and 74 @.@ 8 million years ago . Daspletosaurus fossils are known specifically from the middle to upper section of the formation , between 75 @.@ 6 and 75 @.@ 0 million years ago . In 1914 , Brown collected a nearly complete skeleton and skull ; forty years later his American Museum of Natural History sold this specimen to the Field Museum of Natural History in Chicago . It was mounted for display in Chicago and labeled as Albertosaurus libratus for many years , but after several skull features were later found to be modeled in plaster , including most of the teeth , the specimen (FMNH PR308) was reassigned to Daspletosaurus . A total of eight specimens have been collected from the Dinosaur Park Formation over the years since , most of them within the boundaries of Dinosaur Provincial Park . Phil Currie believes that the Dinosaur Park specimens represent a new species of Daspletosaurus , distinguished by certain features of the skull . Pictures of this new species have been published , but it still awaits a name and full description in print .

A new tyrannosaurid specimen (OMNH 10131) , including skull fragments , ribs and parts of the hindlimb , was reported from New Mexico in 1990 and assigned to the now @-@ defunct genus Aublysodon . Many later authors have reassigned this specimen , along with a few others from New Mexico , to yet another unnamed species of Daspletosaurus . However , research published in 2010 showed that this species , from the Hunter Wash Member of the Kirtland Formation , is actually a more primitive tyrannosauroid , and was classified in the genus Bistahieversor . There is currently disagreement over the age of the Kirtland Formation , with some workers claiming a late Campanian

age , while others suggest a younger age in the early Maastrichtian stage .

In 1992 , Jack Horner and colleagues published an extremely preliminary report of a tyrannosaurid from the upper parts of the Campanian Two Medicine Formation in Montana , which was interpreted as a transitional species between Daspletosaurus and the later Tyrannosaurus . Another partial skeleton was reported from the Upper Two Medicine in 2001 , preserving the remains of a juvenile hadrosaur in its abdominal cavity . This specimen was assigned to Daspletosaurus but not to any particular species . The remains of at least three more Daspletosaurus have also been described in a Two Medicine bonebed . These specimens have not been described in detail , but Currie believes all of the Two Medicine material represents an as @-@ yet @-@ unnamed third species of Daspletosaurus .

= = Paleobiology = =

= = = Coexistence with Gorgosaurus = = =

In the late Campanian of North America , Daspletosaurus was a contemporary of the albertosaurine tyrannosaurid Gorgosaurus . This is one of the few examples of two tyrannosaur genera coexisting . In modern predator guilds , similar @-@ sized predators are separated into different ecological niches by anatomical , behavioral or geographical differences that limit competition . Several studies have attempted to explain niche differentiation in Daspletosaurus and Gorgosaurus .

Dale Russell hypothesized that the more lightly built and more common Gorgosaurus may have preyed on the abundant hadrosaurs of the time , while the more robust and less common Daspletosaurus may have specialized on the less prevalent but better @-@ defended ceratopsids , which may have been more difficult to hunt . However , a specimen of Daspletosaurus (OTM 200) from the Two Medicine Formation preserves the digested remains of a juvenile hadrosaur in its gut region . The higher and broader muzzles of tyrannosaurines like Daspletosaurus are mechanically stronger than the lower snouts of albertosaurines like Gorgosaurus , although tooth strengths are similar between the two groups . This may indicate a difference in feeding mechanics or diet .

Other authors have suggested that competition was limited by geographical separation . Unlike some other groups of dinosaurs , there appears to be no correlation with distance from the sea . Neither Daspletosaurus nor Gorgosaurus was more common at higher or lower elevations than the other . However , while there is some overlap , Gorgosaurus appears to be more common at northern latitudes , with species of Daspletosaurus more abundant to the south . The same pattern is seen in other groups of dinosaurs . Chasmosaurine ceratopsians and hadrosaurine hadrosaurs are also more common in the Two Medicine Formation and in southwestern North America during the Campanian . Thomas Holtz has suggested that this pattern indicates shared ecological preferences between tyrannosaurines , chasmosaurines and hadrosaurines . Holtz notes that , at the end of the later Maastrichtian stage , tyrannosaurines like Tyrannosaurus rex , hadrosaurines and chasmosaurines like Triceratops were widespread throughout western North America , while albertosaurines and centrosaurines became extinct , and lambeosaurines were very rare .

= = = Social behavior = = =

A young specimen of the Dinosaur Park Daspletosaurus species (TMP 94 @.@ 143 @.@ 1) shows bite marks on the face that were inflicted by another tyrannosaur . The bite marks are healed over , indicating that the animal survived the bite . A full @-@ grown Dinosaur Park Daspletosaurus (TMP 85 @.@ 62 @.@ 1) also exhibits tyrannosaur bite marks , showing that attacks to the face were not limited to younger animals . While it is possible that the bites were attributable to other species , intraspecific aggression , including facial biting , is very common among predators . Facial bites are seen in other tyrannosaurs like Gorgosaurus and Tyrannosaurus , as well as in other theropod genera like Sinraptor and Saurornitholestes . Darren Tanke and Phil Currie hypothesize that the bites are due to intraspecific competition for territory or resources , or for dominance within a

social group .

Evidence that Daspletosaurus lived in social groups comes from a bonebed found in the Two Medicine Formation of Montana . The bonebed includes the remains of three Daspletosaurus , including a large adult , a small juvenile , and another individual of intermediate size . At least five hadrosaurs are preserved at the same location . Geologic evidence indicates that the remains were not brought together by river currents but that all of the animals were buried simultaneously at the same location . The hadrosaur remains are scattered and bear numerous marks from tyrannosaur teeth , indicating that the Daspletosaurus were feeding on the hadrosaurs at the time of death . The cause of death is unknown . Currie speculates that the daspletosaurs formed a pack , although this cannot be stated with certainty . Other scientists are skeptical of the evidence for social groups in Daspletosaurus and other large theropods ;

Brian Roach and Daniel Brinkman have suggested that Daspletosaurus social interaction would have more closely resembled the modern Komodo dragon , where non @-@ cooperative individuals mob carcasses , frequently attacking and even cannibalizing each other in the process . Evidence of cannibalism in Daspletosaurus was published in 2015 .

= = = Life history = = =

Paleontologist Gregory Erickson and colleagues have studied the growth and life history of tyrannosaurids . Analysis of bone histology can determine the age of a specimen when it died . Growth rates can be examined when the age of various individuals are plotted against their size on a graph . Erickson has shown that after a long time as juveniles , tyrannosaurs underwent tremendous growth spurts for about four years midway through their lives . After the rapid growth phase ended with sexual maturity , growth slowed down considerably in adult animals . Erickson only examined Daspletosaurus from the Dinosaur Park Formation , but these specimens show the same pattern . Compared to albertosaurines , Daspletosaurus showed a faster growth rate during the rapid growth period due to its higher adult weight . The maximum growth rate in Daspletosaurus was 180 kilograms (400 lb) per year , based on a mass estimate of 1800 kilograms (2 tons) in adults . Other authors have suggested higher adult weights for Daspletosaurus ; this would change the magnitude of the growth rate but not the overall pattern .

By tabulating the number of specimens of each age group , Erickson and his colleagues were able to draw conclusions about life history in a population of Albertosaurus . Their analysis showed that while juveniles were rare in the fossil record , subadults in the rapid growth phase and adults were far more common . While this could be due to preservation or collection biases , Erickson hypothesized that the difference was due to low mortality among juveniles over a certain size , which is also seen in some modern large mammals like elephants . This low mortality may have resulted from a lack of predation , since tyrannosaurs surpassed all contemporaneous predators in size by the age of two . Paleontologists have not found enough Daspletosaurus remains for a similar analysis , but Erickson notes that the same general trend seems to apply .

A 2009 study found evidence of Trichomonas gallinae @-@ like infection in the jaws of various specimens of Daspletosaurus .

= = Paleoecology = =

All known Daspletosaurus fossils have been found in formations dating to the middle to late Campanian stage of the Late Cretaceous Period , between 77 and 74 million years ago . Since the middle of the Cretaceous , North America had been divided in half by the Western Interior Seaway , with much of Montana and Alberta below the surface . However , the uplift of the Rocky Mountains in the Laramide Orogeny to the west , which began during the time of Daspletosaurus , forced the seaway to retreat eastwards and southwards . Rivers flowed down from the mountains and drained into the seaway , carrying sediment along with them that formed the Two Medicine Formation , the Judith River Group , and other sedimentary formations in the region . About 73 million years ago , the seaway began to advance westwards and northwards again , and the entire region was covered

by the Bearpaw Sea , represented throughout the western United States and Canada by the massive Bearpaw Shale .

Daspletosaurus lived in a vast floodplain along the western shore of the interior seaway . Large rivers watered the land , occasionally flooding and blanketing the region with new sediment . When water was plentiful , the region could support a great deal of plant and animal life , but periodic droughts also struck the region , resulting in mass mortality as preserved in the many bonebed deposits found in Two Medicine and Judith River sediments , including the Daspletosaurus bonebed . Similar conditions exist today in East Africa . Volcanic eruptions from the west periodically blanketed the region with ash , also resulting in large @-@ scale mortality , while simultaneously enriching the soil for future plant growth . It is these ash beds that allow precise radiometric dating as well . Fluctuating sea levels also resulted in a variety of other environments at different times and places within the Judith River Group , including offshore and nearshore marine habitats , coastal wetlands , deltas and lagoons , in addition to the inland floodplains . The Two Medicine Formation was deposited at higher elevations farther inland than the other two formations .

The excellent vertebrate fossil record of Two Medicine and Judith River rocks resulted from a combination of abundant animal life , periodic natural disasters , and the deposition of large amounts of sediment . Many types of freshwater and estuarine fish are represented , including sharks , rays , sturgeons , gars and others . The Judith River Group preserves the remains of many aquatic amphibians and reptiles , including frogs , salamanders , turtles , Champsosaurus and crocodilians . Terrestrial lizards , including whiptails , skinks , monitors and alligator lizards have also been discovered . Azhdarchid pterosaurs , and birds like Apatornis and Avisaurus flew overhead , while several varieties of mammals coexisted with Daspletosaurus and other types of dinosaurs in the various formations that make up the Judith River wedge .

In the Oldman Formation (the geological equivalent of the Judith River formation) , Daspletosaurus torosus could have preyed upon the hadrosaur species Brachylophosaurus canadensis , the ceratopsians Coronosaurus brinkmani and Albertaceratops nesmoi , pachycephalosaurs , ornithomimids , therizinosaurs and possibly ankylosaurs . Other predators included troodontids , oviraptorosaurs , the dromaeosaurid Saurornitholestes and possibly an albertosaurine tyrannosaur (genus currently unknown) . The younger Dinosaur Park and Two Medicine Formations had faunas similar to the Oldman , with the Dinosaur Park in particular preserving an unrivaled array of dinosaurs . The albertosaurine Gorgosaurus lived alongside unnamed species of Daspletosaurus in the Dinosaur Park and Upper Two Medicine environments . Young tyrannosaurs may have filled the niches in between adult tyrannosaurs and smaller theropods , which were separated by two orders of magnitude in mass . A Saurornitholestes dentary has been discovered in the Dinosaur Park Formation that bore tooth marks left by the bite of a young tyrannosaur , possibly Daspletosaurus .