

Triceratops

Triceratops was a genus of herbivorous chasmosaurine ceratopsid dinosaur that first appeared during the late Maastrichtian stage of the Late Cretaceous period, about 68 million years ago in what is now North America. It is one of the last-known non-avian dinosaur genera, and became extinct in the Cretaceous–Paleogene extinction event 66 million years ago. The name *Triceratops*, which literally means 'three-horned face', is derived from the Greek words *trí-* (τρί-) meaning 'three', *kéras* (κέρας) meaning 'horn', and *ṓps* (ῥψ) meaning 'face'.

Bearing a large bony frill, three horns on the skull, and a large four-legged body, exhibiting convergent evolution with rhinoceroses and bovines, *Triceratops* is one of the most recognizable of all dinosaurs and the most well-known ceratopsid. It was also one of the largest, up to 8 meters (26.2 ft) long and 9 metric tons (9.9 short tons) in body mass. It shared the landscape with and was most likely preyed upon by *Tyrannosaurus*, though it is less certain that two adults did battle in the fanciful manner often depicted in museum displays and popular images. The functions of the frills and three distinctive facial horns on its head have long inspired debate. Traditionally, these have been viewed as defensive weapons against predators. More recent interpretations find it probable that these features were primarily used in species identification, courtship, and dominance display, much like the antlers and horns of modern ungulates.

Triceratops was traditionally placed within the "short-frilled" ceratopsids, but modern cladistic studies show it to be a member of the Chasmosaurinae which usually have long frills. Two species, ***T. horridus*** and ***T. prorsus***, are considered valid today, from the seventeen species that have ever been named. Research published in 2010 concluded that the contemporaneous *Torosaurus*, a ceratopsid long regarded as a separate genus, represents *Triceratops* in its mature form. This view has been disputed; further data is needed to settle the debate.

Triceratops has been documented by numerous remains collected since the genus was first described in 1889 by American paleontologist Othniel Charles Marsh. Specimens representing life stages from hatchling to adult have been found. As the archetypal ceratopsid, *Triceratops* is one of the most popular dinosaurs, and has been featured in film, postal stamps, and many other types of media.^[1]

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<div><div></div><div>Skeletal mount of a <i>T. prorsus</i> specimen at the <u>Natural History Museum of Los Angeles</u></div></div>																		
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Discovery and identification

The first named fossil specimen now attributed to *Triceratops* is a pair of brow horns attached to a skull roof, found by George Lyman Cannon near Denver, Colorado, in the spring of 1887.^[2] This specimen was sent to Marsh, who believed that the formation from which it came dated from the Pliocene, and that the bones belonged to a particularly large and unusual bison, which he named *Bison alticornis*.^{[2][3]} He realized that there were horned dinosaurs by the next year, which saw his publication of the genus *Ceratops* from fragmentary remains,^[4] but he still believed *B. alticornis* to be a Pliocene mammal. It took a third and much more complete skull to change his mind.

Although not confidentially assignable, fossils possibly belonging to *Triceratops* were described as two taxa, *Agathaumas sylvestris* and *Polygonax mortuarius* in 1872 and 1874 respectively, by Marsh's rival Edward Drinker Cope.^{[5][6]} *Agathaumas* was named based on a pelvis, several vertebrae, and some ribs collected by Fielding Bradford Meek and Henry Martyn Bannister near the Green River of southeastern Wyoming from layers coming from the Maastrichtian Lance Formation.^[7] Due to the fragmentary nature of the remains, it can only confidently be assigned to Ceratopsidae.^{[8][9]} *Polygonax mortuarius* was collected by Cope himself in 1873 from northeastern Colorado, possibly coming from the Maastrichtian Denver Formation.^{[10][6]} The



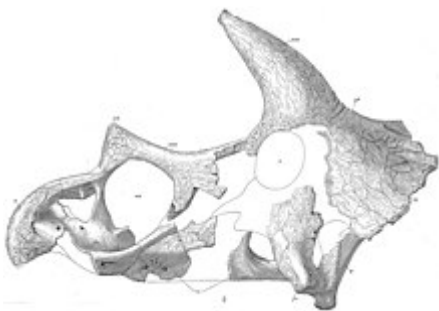
Illustration of specimen YPM 1871E, the horn cores that were erroneously attributed to *Bison alticornis*, the first named specimen of *Triceratops*

fossils only consisted of fragmentary horn cores, 3 dorsal vertebrae, and fragmentary limb elements.^[6] *Polyonax* has the same issue as *Agathaumas*, with the fragmentary remains non-assignable beyond Ceratopsidae.^{[11][8]}

The *Triceratops* holotype (YPM 1820) was collected in 1888 from the Lance Formation of Wyoming, USA, by fossil hunter John Bell Hatcher, yet Marsh initially described this specimen as another species of *Ceratops*.^[12] Cowboy Edmund B. Wilson had been startled by the sight of a monstrous skull poking out of the side of a ravine. He tried to recover it by throwing a lasso around one of the horns. When it broke off, the skull tumbling to the bottom of the cleft, Wilson brought the horn to his boss, the rancher and avid fossil collector Charles Arthur Guernsey, who happened to show it to Hatcher. Marsh subsequently ordered Hatcher to locate and salvage the skull.^[8] The holotype was first named *Ceratops horridus*. When further preparation uncovered the third nose horn, Marsh changed his mind and gave the piece the generic name *Triceratops* (lit. 'three horn face'), accepting his *Bison alticornis* as another species of *Ceratops*.^[13] (It would later be added to *Triceratops*.)^[14] The sturdy nature of the animal's skull has ensured that many examples have been preserved as fossils, allowing variations between species and individuals to be studied. *Triceratops* remains have subsequently been found in the American states of Montana and South Dakota (and more in Colorado and Wyoming), as well as the Canadian provinces of Saskatchewan and Alberta.

An earlier specimen, also recovered from the Lance Formation, was named *Agathaumas sylvestris* by Edward Drinker Cope in 1872. Originally identified as a hadrosaur, this specimen consists only of post-cranial remains and is only provisionally considered an example of *Triceratops*.^[15]

Species



Type specimen YPM 1820 of the type species, *T. horridus*

After *Triceratops* was described, between 1889 and 1891 Hatcher with great effort collected another thirty-one of its skulls. The first species had been named *T. horridus* by Marsh. Its specific name was derived from the Latin *horridus* ('rough, rugose'), perhaps referring to the type specimen's rough texture, later identified as an aged individual. The additional skulls varied to a lesser or greater degree from the original holotype. This variation is unsurprising, given that *Triceratops* skulls are large three-dimensional objects, coming from individuals of different ages and both sexes, and which were subjected to different amounts and directions of pressure during fossilization.^[8]

In the first attempt to understand the many species, Richard Swann Lull found two groups, although he did not say how he distinguished them: One composed of *T. horridus*, *T. prorsus*, and *T. brevicornus* ('the short-horned'); the other of *T. elatus* and *T. calicornis*. Two species (*T. serratus* and *T. flabellatus*) stood apart from these groups.^[14] By 1933 and his revision of the landmark 1907 Hatcher–Marsh–Lull monograph of all known ceratopsians, he retained his two groups and two unaffiliated species, with a third lineage of *T. obtusus* and *T. hatcheri* ('Hatcher's') that was characterized by a very small nasal horn.^[9] *T. horridus*–*T. prorsus*–*T. brevicornus* was now thought to be the most conservative lineage, with an increase in skull size and a decrease in nasal horn size, and *T. elatus*–*T. calicornis* was defined by large brow horns and small nasal horn.^{[9][16]} C. M. Sternberg made one modification, adding *T. eurycephalus* ('the wide-headed') and suggesting that it linked the second and third lineages closer together than they were to the *T. horridus* lineage.^[17]

With time, the idea that the differing skulls might be representative of individual variation within one (or two) species gained popularity. In 1986, John Ostrom and Peter Wellnhofer published a paper in which they proposed that there was only one species, *Triceratops horridus*.^[18] Part of their rationale was that

generally there are only one or two species of any large animal in a region. To their findings, Thomas Lehman added the old Lull–Sternberg lineages combined with maturity and sexual dimorphism, suggesting that the *T. horridus*–*T. prorsus*–*T. brevicornus* lineage was composed of females, the *T. calicornis*–*T. elatus* lineage was made up of males, and the *T. obtusus*–*T. hatcheri* lineage was of pathologic old males.^[19]



1896 skeletal restoration of *T. prorsus* by O. C. Marsh, based on the holotype skull YPM 1822 and referred elements

These findings were contested a few years later by Catherine Forster, who reanalyzed *Triceratops* material more comprehensively and concluded that the remains fell into two species, *T. horridus* and *T. prorsus*, although the distinctive skull of *T. ("Nedoceratops") hatcheri* differed enough to warrant a separate genus.^[20] She found that *T. horridus* and several other species belonged together, and *T. prorsus* and *T. brevicornus* stood alone. Since there were many more specimens in the first group, she suggested that this meant the two groups were two species. It is still possible to interpret the differences as representing a single species with sexual dimorphism.^{[8][21]}

In 2009, John Scannella and Denver Fowler supported the separation of *T. prorsus* and *T. horridus* and noted that the two species are also separated stratigraphically within the Hell Creek Formation, indicating that they did not live together at the same time.^[22]

Valid species

- *T. horridus* (Marsh, 1889) Marsh, 1889 (originally *Ceratops*) (type species)
- *T. prorsus* Marsh, 1890

Synonyms and doubtful species

Some of the following species are synonyms, as indicated in parentheses ("=*T. horridus*" or "=*T. prorsus*"). All the others are each considered a *nomen dubium* (lit. 'dubious name') because they are based on remains too poor or incomplete to be distinguished from pre-existing *Triceratops* species.



T. prorsus, Carnegie Museum of Natural History

- *T. albertensis* C. M. Sternberg, 1949
- *T. alticornis* (Marsh 1887) Hatcher, Marsh, and Lull, 1907 [originally *Bison alticornis*, Marsh 1887, and *Ceratops alticornis*, Marsh 1888]
- *T. brevicornus* Hatcher, 1905 (=*T. prorsus*)
- *T. calicornis* Marsh, 1898 (=*T. horridus*)
- *T. elatus* Marsh, 1891 (=*T. horridus*)
- *T. eurycephalus* Schlaikjer, 1935
- *T. flabellatus* Marsh, 1889 (= *Sterrhophus* Marsh, 1891) (=*T. horridus*)
- *T. galeus* Marsh, 1889
- *T. hatcheri* (Hatcher & Lull 1905) Lull, 1933 (contentious; see *Nedoceratops* below)
- *T. ingens* Marsh vide Lull, 1915



The skull (AMNH 5116) of this *T. horridus* composite specimen was formerly assigned to *T. elatus*

- *T. maximus* Brown, 1933
- *T. mortuarius* (Cope, 1874) Kuhn, 1936 (*nomen dubium*; originally *Polygonax mortuarius*)
- *T. obtusus* Marsh, 1898 (= *T. horridus*)
- *T. serratus* Marsh, 1890 (= *T. horridus*)
- *T. sulcatus* Marsh, 1890
- *T. sylvestris* (Cope, 1872) Olshevsky, 2000 (*nomen dubium*; originally *Agathaumas sylvestris*)

Description

Size



Size comparison with *T. horridus* in blue and *T. prorsus* in red

Triceratops is estimated to have reached about 7.9 to 9 meters (25.9 to 29.5 ft) in length, 2.9 to 3.0 meters (9.5 to 9.8 ft) in height,^{[23][24]} and 6.1 to 12.0 metric tons (6.7 to 13.2 short tons) in weight.^[25] The most distinctive feature is their large skull, among the largest of all land animals. The largest-known skull (specimen MWC 7584, formerly BYU 12183) is estimated to have been 2.5 meters (8.2 ft) in length when complete,^[26] and could reach almost a third of the length of the entire animal.^[27] A specimen of *T. horridus* named Kelsey measured 7.3 meters (24 ft) long with a 2-meter (6.5 ft) skull, stood about 2.3 meters (7.5 ft) tall, and was estimated by the Black Hills institute to weight nearly 6 metric tons (6.6 short tons).^[28] A *Triceratops* 8 meters (26.2 ft) long has been estimated by Gregory S. Paul to have massed 9 metric tons (9.9 short tons).^[29]

Skull

Like all chasmosaurines, *Triceratops* had a large skull relative to its body size. The front of the head was equipped with a large beak in front of the teeth. The core of the top beak was formed by a special rostral bone.^[30] Behind it, the premaxillae bones were located, embayed from behind by very large circular nostrils. In chasmosaurines, the premaxillae met on their midline in a complex bone plate, the rear edge of which was reinforced by the "narial strut". From the base of this strut, a triangular process jutted out into the nostril. *Triceratops* differs from most relatives in that this process was hollowed out on the outer side.^[30] Behind the toothless premaxilla, the maxilla bore thirty-six to forty tooth positions, in which three to five teeth per position were vertically stacked. The teeth were closely appressed, forming a "dental battery" curving to the inside. The skull bore a single horn on the snout, above the nostrils. In *Triceratops*, the nose horn is sometimes recognisable as a separate ossification, the epinasal.^[30]



Skull of *Triceratops horridus* from the Houston Museum of Natural Science

The skull also featured a pair of "brow" or supraorbital horns approximately 1 meter (3.3 ft) long, with one above each eye.^{[31][32]} The jugal bones pointed to below at the rear sides of the skull and were capped by separate epijugals. With *Triceratops* these were not particularly large and sometimes touched the quadratojugals. The bones of the skull roof were fused. By a folding of the frontal bones, a "double" skull roof was created.^[30] In *Triceratops*, some specimens show a fontanelle, an opening in the upper roof layer.^[30] The cavity between the layers invaded the bone cores of the brow horns.^[30]

At the rear of the skull, the outer squamosal bones and the inner parietal bones grew into a relatively short, bony frill, adorned with epoccipitals in young specimens. These were low triangular processes on the frill edge, representing separate skin ossifications or osteoderms. Typically, with *Triceratops* specimens there are two epoccipitals present on each parietal bone, with an additional central process on their border. Each squamosal bone had five processes. Most other ceratopsids had large parietal fenestrae, openings, in their frills, but those of *Triceratops* were noticeably solid,^[33] unless the genus *Torosaurus* represents mature *Triceratops* individuals. Under the frill, at the rear of the skull, a huge occipital condyle, up to 106 millimeters (4.2 in) in diameter, connected the head to the neck.^[30]

The lower jaws were elongated and met at their tips in a shared epidentary bone, the core of the toothless lower beak. In the dentary bone, the tooth battery curved to the outside to meet the battery of the upper jaw. At the rear of the lower jaw, the articular bone was exceptionally wide, matching the general width of the jaw joint.^[30] *T. horridus* can be distinguished from *T. prorsus* by having a shallower snout.^[29]

The largest *Triceratops* skull ever found was discovered in 1992 and excavated in 2003 in Dawson County, Montana, in the Hell Creek Formation. It is a 65-million-year-old male *Triceratops* skull, 9.2 feet (2.8 m) long, 5.2 feet (1.6 m) high and 4.6 feet (1.4 m) wide and weighing over 1,300 lb (600 kg). It has been dubbed 'Dragon King' and is understood to be the most expensive skull to ever trade privately.^{[34][35]}

Postcranial skeleton

Chasmosaurines showed little variation in their postcranial skeleton.^[30] The skeleton of *Triceratops* is markedly robust. Both *Triceratops* species possessed a sturdy build, with strong limbs, short hands with three hooves each, and short feet with four hooves each.^[36] The vertebral column consisted of ten neck, twelve back, ten sacral and about forty-five tail vertebrae. The front neck vertebrae were fused into a syncervical. Traditionally, this was assumed to have incorporated the first three vertebrae which would imply that the frontmost atlas was very large and sported a neural spine. Later interpretations revived an old hypothesis by John Bell Hatcher that at the very front a vestige of the real atlas can be observed, the syncervical then consisting of four vertebrae. The vertebral count mentioned, is adjusted to this view. In *Triceratops* the neural spines of the neck are constant in height, instead of gradually sloping upwards. Another peculiarity is that the neck ribs only begin to lengthen with the ninth cervical vertebra.^[30]



Life reconstruction of a subadult
Triceratops horridus

The rather short and high vertebrae of the back were in its middle region reinforced by ossified tendons running along the tops of the neural arches. The straight sacrum was long and adult individuals show a fusion of all sacral vertebrae. In *Triceratops* the first four and last two sacrals had transverse processes, connecting the vertebral column to the pelvis, that were fused at their distal ends. Sacrals seven and eight had longer processes, causing the sacrum to have an oval profile in top view. On top of the sacrum a neural plate was present formed by a fusion of the neural spines of the second through fifth vertebrae. *Triceratops* had a large pelvis with a long ilium. The ischium was curved downwards. The foot was short with four functional toes. The phalangeal formula of the foot is 2-3-4-5-0.^[30]

Although certainly quadrupedal, the posture of horned dinosaurs has long been the subject of some debate. Originally, it was believed that the front legs of the animal had to be sprawling at a considerable angle from the thorax in order to better bear the weight of the head.^[8] This stance can be seen in paintings by Charles Knight and Rudolph Zallinger. Ichnological evidence in the form of trackways from horned dinosaurs and recent reconstructions of skeletons (both physical and digital) seem to show that *Triceratops* and other

ceratopsids maintained an upright stance during normal locomotion, with the elbows flexed to behind and slightly bowed out, in an intermediate state between fully upright and fully sprawling, comparable to the modern rhinoceros.^{[36][37][38][39]}



Closeup of pelvis of *Triceratops* specimen at the [Oxford University Museum of Natural History](#)

The hands and forearms of *Triceratops* retained a fairly primitive structure compared to other quadrupedal dinosaurs such as thyreophorans and many sauropods. In those two groups, the forelimbs of quadrupedal species were usually rotated so that the hands faced forward with palms backward ("pronated") as the animals walked. *Triceratops*, like other ceratopsians and the related quadrupedal ornithomorphs, together forming the Ceratopsia, walked with most of their fingers pointing out and away from the body, the original condition for dinosaurs, also retained by bipedal forms like the theropods. In *Triceratops*, the weight of the body was carried by only the first three fingers of the hand, while digits 4 and 5 were vestigial and lacked claws or hooves.^[36] The phalangeal formula of the hand is 2-3-4-3-1, meaning that the first or innermost finger of the forelimb has two bones, the next has three, etc.^[40]

Skin

Preserved skin of *Triceratops* is known from a specimen found in Wyoming, though it has not been formally published in the scientific literature. These consist of large ~50–60 millimetres (2.0–2.4 in) across hexagonal tubercles, along with larger ~ 100 millimetres (3.9 in) across tubercles with conical projections.^[41]

Classification



Specimen nicknamed "Lane", was the most complete known specimen until 2014

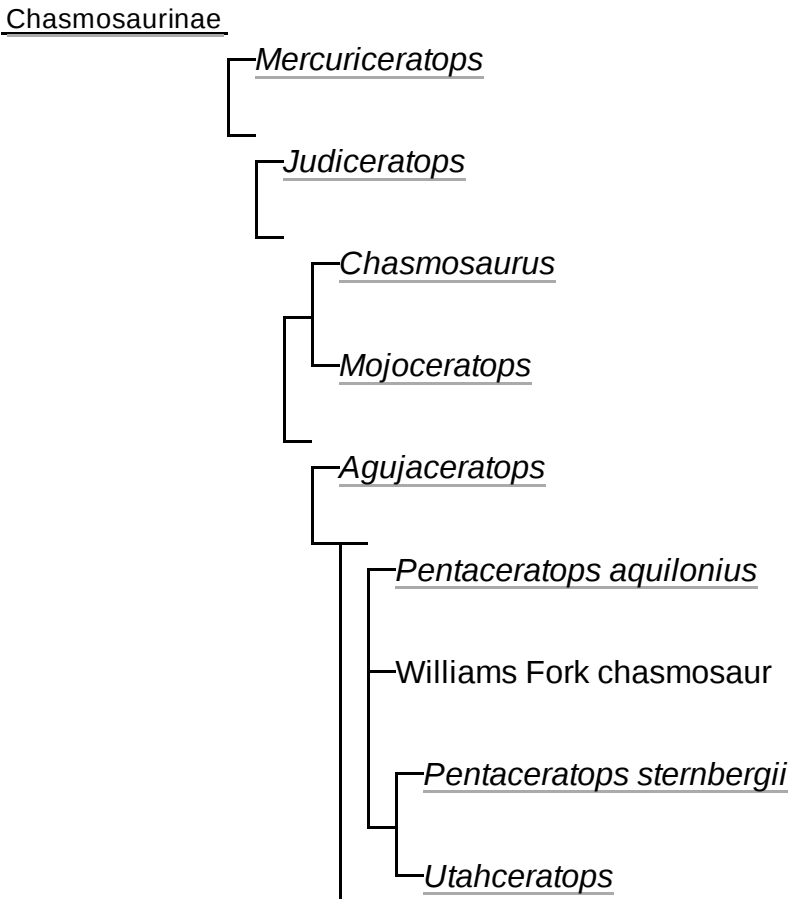
Triceratops is the best-known genus of the Ceratopsidae, a family of large, mostly North American horned dinosaurs. The exact relationship of *Triceratops* among the ceratopsids has been debated over the years. Confusion stemmed mainly from the combination of a short, solid frill (similar to that of Centrosaurinae), with long brow horns (more akin to Chasmosaurinae).^[42] In the first overview of horned dinosaurs, R. S. Lull hypothesized the existence of two lineages, one of Monoclonius and Centrosaurus leading to *Triceratops*, the other with Ceratops and Torosaurus, making *Triceratops* a centrosaurine as the group is understood today.^[14] Later revisions supported this view, Lawrence Lambe in 1915 formally describing the first, short-frilled group as the Centrosaurinae (including *Triceratops*), and the second, long-frilled

group as the Chasmosaurinae.^{[9][43]}

In 1949, Charles M. Sternberg was the first to question this position, proposing instead that *Triceratops* was more closely related to Arrhinoceratops and Chasmosaurus based on skull and horn features, making *Triceratops* a chasmosaurine ("ceratopsine" in his usage) genus.^[17] He was largely ignored, with John Ostrom^[44] and later David Norman placing *Triceratops* within the Centrosaurinae.^[45]

Subsequent discoveries and analyses, however, proved the correctness of Sternberg's view on the position of *Triceratops*, with Thomas Lehman defining both subfamilies in 1990 and diagnosing *Triceratops* as "ceratopsine" on the basis of several morphological features. Apart from the one feature of a shortened frill, *Triceratops* shares no derived traits with centrosaurines.^[19] Further research by Peter Dodson, including a 1990 cladistic analysis and a 1993 study using RFTRA (resistant-fit theta-rho analysis), a morphometric technique which systematically measures similarities in skull shape, reinforces *Triceratops*' placement in the chasmosaurines.^{[46][47]}

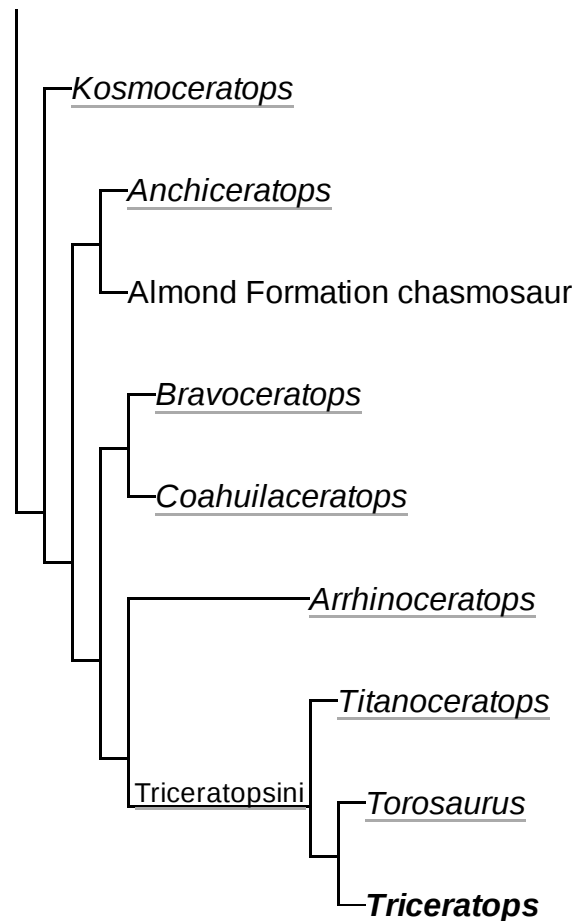
The cladogram below follows Longrich (2014), who named a new species of *Pentaceratops*, and included nearly all species of chasmosaurine.^[48]



First mounted *T. horridus* skeleton (the holotype of *T. "obtusus"*), nicknamed "Hatcher", Smithsonian Museum



Yoshi's Trike, an immature specimen with 115 cm horn cores, on display in the Museum of the Rockies in Montana, USA



Skull of specimen DMNH 48617 from the Laramie Formation of eastern Colorado. Based on the age of the formation, it may be the oldest *Triceratops* known.

For many years after its discovery, the deeper evolutionary origins of *Triceratops* and its close relatives remained largely obscure. In 1922, the newly discovered *Protoceratops* was seen as its ancestor by Henry Fairfield Osborn,^[8] but many decades passed before additional findings came to light. Recent years have been fruitful for the discovery of several antecedents of *Triceratops*. *Zuniceratops*, the earliest-known ceratopsian with brow horns, was described in the late 1990s, and *Yinlong*, the first known Jurassic ceratopsian, in 2005.

These new finds have been vital in illustrating the origins of horned dinosaurs in general, suggesting an

Asian origin in the Jurassic, and the appearance of truly horned ceratopsians by the beginning of the Late Cretaceous in North America.^[30]

In phylogenetic taxonomy, the genus *Triceratops* has been used as a reference point in the definition of Dinosauria; dinosaurs have been designated as all descendants of the most recent common ancestor of *Triceratops* and modern birds.^[49] Furthermore, the bird-hipped dinosaurs have been defined as those dinosaurs more closely related to *Triceratops* than to modern birds.^[50]



'Horridus', the most complete *Triceratops* fossil known, on display at the Melbourne Museum.

Paleobiology

Although *Triceratops* are commonly portrayed as herding animals, there is currently little evidence that they lived in herds. While several other genera of horned dinosaurs are known from bone beds preserving bones from two to hundreds or thousands of individuals, to date there is only one documented bonebed dominated by *Triceratops* bones: a site in southeastern Montana with the remains of three juveniles. It may be significant that only juveniles were present.^[51] In 2012, a group of three *Triceratops* in relatively complete condition, each of varying sizes from a full-grown adult to a small juvenile, were found near Newcastle, Wyoming. The remains are currently under excavation by paleontologist Peter Larson and a team from the Black Hills Institute. It is believed that the animals were traveling as a family unit, but it remains unknown if the group consists of a mated pair and their offspring, or two females and a juvenile they were caring for. The remains also show signs of predation or scavenging from *Tyrannosaurus*, particularly on the largest specimen, with the bones of the front limbs showing breakage and puncture wounds from *Tyrannosaurus* teeth.^[52] New evidence presented in 2020 by Illies and Fowler *et al.* suggests that *Triceratops* lived in small groups of perhaps between five and ten individuals based on fossils collected in the previous decade.^[53]



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

For many years, *Triceratops* finds were known only from solitary individuals.^[51] These remains are very common; for example, Bruce Erickson, a paleontologist of the Science Museum of Minnesota, has reported having seen 200 specimens of *T. prorsus* in the Hell Creek Formation of Montana.^[54] Similarly, Barnum Brown claimed to have seen over 500 skulls in the field.^{[8]:79} Because *Triceratops* teeth, horn fragments, frill fragments, and other skull fragments are such abundant fossils in the Lancian faunal stage of the late Maastrichtian (Late Cretaceous, 66 mya) Period of western North America, it is regarded as among the dominant herbivores of the time, if not the most dominant herbivore. In 1986, Robert Bakker estimated it as making up five sixths of the large dinosaur fauna at the end of the Cretaceous.^[55] Unlike most animals, skull fossils are far more common than postcranial bones for *Triceratops*, suggesting that the skull had an unusually high preservation potential.^[56]

Analysis of the endocranial anatomy of *Triceratops* suggest its sense of smell was poor compared to that of other dinosaurs. Its ears were attuned to low frequency sounds given the short cochlear lengths recorded in an analysis by Sakagami *et al.*. This same study also suggests that *Triceratops* held its head about 45 degrees to the ground; an angle which would showcase the horns and frill most effectively while simultaneously allowing the animal to take advantage of food through grazing.^[57]

Dentition and diet

Triceratops were herbivorous, and because of their low slung head, their primary food was probably low growing vegetation, although they may have been able to knock down taller plants with their horns, beak, and bulk.^{[30][58]} The jaws were tipped with a deep, narrow beak, believed to have been better at grasping and plucking than biting.^[44]

Triceratops teeth were arranged in groups called batteries, of 36 to 40 tooth columns in each side of each jaw, with 3 to 5 stacked teeth per column, depending on the size of the animal.^[30] This gives a range of 432 to 800 teeth, of which only a fraction were in use at any given time (Tooth replacement was continuous throughout the life of the animal).^[30] They functioned



Close up of the jaws and teeth

by shearing in a vertical to near-vertical orientation.^[30] The great size and numerous teeth of *Triceratops* suggests that they ate large volumes of fibrous plant material, with some researchers suggesting palms and cycads,^{[59][60]} and others suggesting ferns, which then grew in prairies.^[61]

Functions of the horns and frill



Front view of skull with a prominent epoccipital fringe, Houston Museum of Natural Science

There has been much speculation over the functions of *Triceratops*' head adornments. The two main theories have revolved around use in combat and in courtship display, with the latter now thought to be the most likely primary function.^[30]

Early on, Lull postulated that the frills may have served as anchor points for the jaw muscles to aid chewing by allowing increased size and thus power for the muscles.^[62] This has been put forward by other authors over the years, but later studies do not find evidence of large muscle attachments on the frill bones.^[63]

Triceratops were long thought to have used their horns and frills in combat with predators such as *Tyrannosaurus*, the idea being discussed first by Charles H. Sternberg in 1917 and 70 years later by Robert Bakker.^{[55][64]}

There is evidence that *Tyrannosaurus* did have aggressive head-on encounters with *Triceratops*, based on partially healed tyrannosaur tooth marks on a *Triceratops* brow horn and squamosal; the bitten horn is also

broken, with new bone growth after the break. Which animal was the aggressor is not known.^[65] Since the *Triceratops* wounds healed, it is most likely that the *Triceratops* survived the encounter. 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. *Tyrannosaurus* is also known to have fed on *Triceratops*, as shown by a heavily tooth-scored *Triceratops* ilium and sacrum.^[66]

In addition to combat with predators using horns, *Triceratops* are popularly shown engaging each other in combat with horns locked. While studies show that such activity would be feasible, if unlike that of present-day horned animals,^[67] there is disagreement about whether they did so. Although pitting, holes, lesions, and other damage on *Triceratops* skulls (and the skulls of other ceratopsids) are often attributed to horn damage in combat, a 2006 study finds no evidence for horn thrust injuries causing these forms of damage (for example, there is no evidence of infection or healing). Instead, non-pathological bone resorption, or unknown bone diseases, are suggested as causes.^[68] A newer study compared incidence rates of skull lesions and periosteal reaction in *Triceratops* and *Centrosaurus* and showed that these were consistent with *Triceratops* using its horns in combat and the frill being adapted as a protective structure, while lower pathology rates in *Centrosaurus* may indicate visual rather than physical use of cranial ornamentation, or a form of combat focused on the body rather than the head.^[69] The frequency of injury was found to be 14% in *Triceratops*.^[70] The researchers also concluded that the damage found on the specimens in the study was often too localized to be caused by bone disease.^[71] Histological examination reveals that the frill of *Triceratops* is composed of fibrolamellar bone^[72] which contains fibroblasts that play a critical role in wound healing, and are capable of rapidly depositing bone during remodeling.^{[73][74]}



Examples of periosteal reactive bone in selected specimens of *Triceratops*



Juvenile and adult skulls—the juvenile skull is about the size of an adult human head

One skull was found with a hole in the jugal bone, apparently a puncture wound sustained while the animal was alive, as indicated by signs of healing. The hole has a diameter close to that of the distal end of a *Triceratops* horn. This, and other apparent healed wounds in the skulls of ceratopsians, has been cited as evidence of non-fatal intraspecific competition in these dinosaurs.^{[75][76]} Another specimen, referred to as "Big John" has a similar fenestra to the squamosal caused by what appears to be another *Triceratops* horn, and the squamosal bone shows signs of significant healing, further vindicating the hypothesis that this ceratopsian used its horns for intra-specific combat.^[77]

The large frill also may have helped to increase body area to regulate body temperature.^[78] A similar theory has been proposed regarding the plates of *Stegosaurus*,^[79] although this use alone would not account for the bizarre and extravagant variation seen in different members of the Ceratopsidae, which would rather support the sexual display theory.^[30]

The theory that frills functioned as a sexual display was first proposed by Davitashvili in 1961 and has gained increasing acceptance since.^{[19][63][80]} Evidence that visual display was important, either in courtship or other social behavior, can be seen in the horned dinosaurs differing markedly in their adornments, making each species highly distinctive. Also, modern living creatures with such displays of horns and adornments use them similarly.^[81] A 2006 study of the smallest *Triceratops* skull, ascertained to be a juvenile, shows the frill and horns developed at a very early age, predating sexual development and thus probably important for visual communication and species recognition in general.^[82] The use of the exaggerated structures to enable dinosaurs to recognize their own species has been questioned, as no such function exists for such structures in modern species.^[83]

Growth and ontogeny

In 2006, the first extensive ontogenetic study of *Triceratops* was published in the journal *Proceedings of the Royal Society*. The study, by John R. Horner and Mark Goodwin, found that individuals of *Triceratops* could be divided into four general ontogenetic groups: babies, juveniles, subadults, and adults. With a total number of 28 skulls studied, the youngest was only 38 centimeters (15 in) long. Ten of the 28 skulls could be placed in order in a growth series with one representing each age. Each of the four growth stages were found to have identifying features. Multiple ontogenetic trends were discovered, including the size reduction of the epoccipitals, development and reorientation of postorbital horns, and hollowing out of the horns.^[84]



Skull growth series

Torosaurus as growth stage of *Triceratops*

Torosaurus is a ceratopsid genus first identified from a pair of skulls in 1891, two years after the identification of *Triceratops* by Charles Marsh. The genus *Torosaurus* resembles *Triceratops* in geological age, distribution, anatomy and size and it has been recognised as a close relative.^[85] Its distinguishing features are an elongated skull and the presence of two fenestrae, or holes, in the frill. Paleontologists investigating dinosaur ontogeny (growth and development of individuals over the life span) in Montana's Hell Creek Formation have recently presented evidence that the two represent a single genus.

John Scannella, in a paper presented in Bristol at the conference of the Society of Vertebrate Paleontology (September 25, 2009), reclassified *Torosaurus* as especially mature *Triceratops* individuals, perhaps representing a single sex. Horner, Scannella's mentor at Bozeman Campus, Montana State University, noted that ceratopsian skulls consist of metaplastic bone. A characteristic of metaplastic bone is that it lengthens and shortens over time, extending and resorbing to form new shapes. Significant variety is seen even in those skulls already identified as *Triceratops*, Horner said, "where the horn orientation is backwards in juveniles and forward in adults". Approximately 50% of all subadult *Triceratops* skulls have two thin areas in the frill that correspond with the placement of "holes" in *Torosaurus* skulls, suggesting that holes developed to offset the weight that would otherwise have been added as maturing *Triceratops* individuals grew longer frills.^[86] A paper describing these findings in detail was published in July 2010 by Scannella and Horner. It formally argues that *Torosaurus* and the similar contemporary *Nedoceratops* are synonymous with *Triceratops*.^[26]



A, *Triceratops prorsus* holotype YPM 1822 and B, *Torosaurus latus* ANSP 15192

The assertion ignited debate. Andrew Farke had in 2006 stressed that, apart from the frill, no systematic differences could be found between *Torosaurus* and *Triceratops*.^[85] He nevertheless disputed Scannella's conclusion by arguing in 2011 that the proposed morphological changes required to "age" a *Triceratops* into a *Torosaurus* would be without precedent among ceratopsids. Such changes would include the growth of additional epoccipitals, reversion of bone texture from an adult to immature type and back to adult again, and growth of frill holes at a later stage than usual.^[87] A study by Nicholas Longrich and Daniel Field analyzed 35 specimens of both *Triceratops* and *Torosaurus*. The authors concluded that *Triceratops* individuals too old to be considered immature forms are represented in the fossil record, as are *Torosaurus* individuals too young to be considered fully mature adults. The synonymy of *Triceratops* and *Torosaurus* cannot be supported, they said, without more convincing intermediate forms than Scannella and Horner initially produced. Scannella's *Triceratops* specimen with a hole on its frill, they argued, could represent a diseased or malformed individual rather than a transitional stage between an immature *Triceratops* and mature *Torosaurus* form.^{[88][89]}

Other genera as growth stages of *Triceratops*

Opinion has varied on the validity of a separate genus for *Nedoceratops*. Scannella and Horner regarded it as an intermediate growth stage between *Triceratops* and *Torosaurus*.^{[26][90]} Farke, in his 2011 redescription of the only known skull, concluded that it was an aged individual of its own valid taxon, *Nedoceratops hatcheri*.^[87] Longrich and Fields also did not consider it a transition between *Torosaurus* and *Triceratops*, suggesting that the frill holes were pathological.^[89]

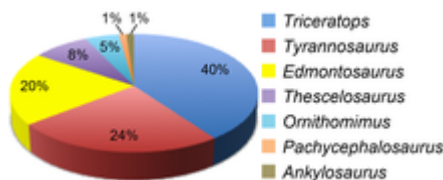


Comparisons between the skulls of *Triceratops* and *Nedoceratops*

As described above, Scannella had argued in 2010 that *Nedoceratops* should be considered a synonym of *Triceratops*.^[26] Farke (2011) maintained that it represents a valid distinct genus.^[87] Longrich agreed with Scannella about *Nedoceratops* and made a further suggestion: that the recently described *Ojoceratops* was likewise a synonym. The fossils, he argued, are indistinguishable from the *Triceratops horridus* specimens that were previously attributed to the defunct species *Triceratops serratus*.

Longrich observed that another newly described genus, *Tatankaceratops*, displayed a strange mix of characteristics already found in adult and juvenile *Triceratops*. Rather than representing a distinct genus, *Tatankaceratops* could as easily represent a dwarf *Triceratops* or a *Triceratops* individual with a developmental disorder that caused it to stop growing prematurely.^[91]

Paleoecology



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

Triceratops lived during the Late Cretaceous of North America, its fossils coming from the Evanston Formation, Scollard Formation, Laramie Formation, Lance Formation, Denver Formation, and Hell Creek Formation.^[92] These fossil formations date back to the time of the Cretaceous–Paleogene extinction event, which has been dated to 66 ± 0.07 million years ago.^[93] Many animals and plants have been found in these formations, but mostly from the Lance Formation and Hell Creek Formation.^[92] *Triceratops* was one of the last ceratopsian genera to appear before the end of the Mesozoic. The related *Torosaurus*, and the more distantly related diminutive *Leptoceratops*, were also present, though their remains

have been rarely encountered.^[8]

Theropods from these formations include genera of dromaeosaurids, tyrannosaurids, ornithomimids, troodontids,^[92] avialans,^[94] and caenagnathids,^[95] Dromaeosaurids from the Hell Creek Formation are *Acheroraptor* and *Dakotaraptor*. Indeterminate dromaeosaurs are known from other fossil formations. Common teeth previously referred to *Dromaeosaurus* and *Saurornitholestes* later were considered to be *Acheroraptor*.^[96] The tyrannosaurids from the formation are *Nanotyrannus* and *Tyrannosaurus*, although the former might be a junior synonym of the latter. Among ornithomimids are the genera *Struthiomimus* as well as *Ornithomimus*,^[92] an undescribed animal named "Orcomimus" could be from the formation.^[97] Troodontids are only represented by *Pectinodon* and *Paronychodon* in the Hell Creek Formation; with a possible species of *Troodon* from the Lance Formation. One species of coelurosaur is known from Hell Creek and similar formations by a single species, *Richardoestesia*. Only three oviraptorosaurs are from the Hell Creek Formation: *Anzu*, *Leptorhynchus*,^[95] and a giant species of caenagnathid, very similar to *Gigantoraptor*, from South Dakota. However, only fossilized foot prints were discovered.^[98] The avialans known from the formation are *Avisaurus*,^[92] multiple species of *Brodavis*,^[99] and several other species of hesperornithoforms, as well as several species of true birds, including *Cimolopteryx*.^[94]



Restoration of *Triceratops* and smaller *Leptoceratops* in the Hell Creek environments

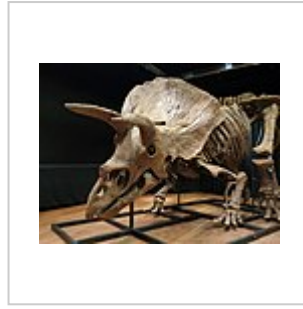
Ornithischians are abundant in the Scollard, Laramie, Lance, Denver, and Hell Creek Formation. The main groups of ornithischians are ankylosaurians, ornithopods, ceratopsians, and pachycephalosaurians. Three ankylosaurians are known: *Ankylosaurus*, *Denversaurus*, and possibly a species of *Edmontonia* or an undescribed genus. Multiple genera of ceratopsians are known from the formation other than *Triceratops*, the leptoceratopsid *Leptoceratops*, and the chasmosaurine ceratopsids *Torosaurus*,^[92] *Nedoceratops* and *Tatankaceratops*.^[100] Ornithopods are common in the Hell Creek Formation, and are known from several species of the ornithopod *Thescelosaurus* and the hadrosaurid *Edmontosaurus*.^{[92][101]} Several



A *Tyrannosaurus* skull next to a *Triceratops* skull.



Triceratops horridus



The Big John *Triceratops* in Paris being auctioned.



A side view of *Triceratops*.



Torosaurus (a possible species of the *Triceratops* genus).

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- LiveScience: Facts about *Triceratops* (<http://www.livescience.com/24011-triceratops-facts.html>) at LiveScience.com
- Clash of the Dinosaurs: The Defenders – The Triceratops Threat (<https://www.youtube.com/watch?v=jjwhEx4LwIE>) on YouTube
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- Smithsonian Exhibit (<https://web.archive.org/web/20030202134913/http://www.mnh.si.edu/exhibits/triceratops/index.html>)
- *Triceratops* at the Internet Archive (https://archive.org/details/en.wikipedia.org_wiki_Triceratops_2007_March_19)
- *Triceratops* in the Dino Directory (<http://www.nhm.ac.uk/nature-online/life/dinosaurs-other-extinct-creatures/dino-directory/triceratops.html>)
- *Triceratops* (<https://web.archive.org/web/20090226220159/http://www.cbv.ns.ca/marigold/history/dinosaurs/datafiles/triceratops.html>) (short summary and good color illustration)
- *Triceratops* For Kids (<http://www.enchantedlearning.com/subjects/dinosaurs/dinos/Triceratops.shtml>) (a fact sheet about the *Triceratops* with activities for kids)
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