= Ceratopsia =

Ceratopsia or Ceratopia (/ ?s?r??t?psi? / or / ?s?r??to?pi? / ; Greek : " horned faces ") is a group of herbivorous , beaked dinosaurs that thrived in what are now North America , Europe , and Asia , during the Cretaceous Period , although ancestral forms lived earlier , in the Jurassic . The earliest known ceratopsian , Yinlong downsi , lived between 161 @.@ 2 and 155 @.@ 7 million years ago . The last ceratopsian species , Triceratops prorsus , became extinct during the Cretaceous ? Paleogene extinction event , 66 million years ago .

Early members of the ceratopsian group , such as Psittacosaurus , were small bipedal animals . Later members , including ceratopsids like Centrosaurus and Triceratops , became very large quadrupeds and developed elaborate facial horns and frills extending over the neck . While these frills might have served to protect the vulnerable neck from predators , they may also have been used for display , thermoregulation , the attachment of large neck and chewing muscles or some combination of the above . Ceratopsians ranged in size from 1 meter (3 ft) and 23 kilograms (50 lb) to over 9 meters (30 ft) and 5 @,@ 400 kg (12 @,@ 000 lb) .

Triceratops is by far the best @-@ known ceratopsian to the general public . It is traditional for ceratopsian genus names to end in " -ceratops " , although this is not always the case . One of the first named genera was Ceratops itself , which lent its name to the group , although it is considered a nomen dubium today as its fossil remains have no distinguishing characteristics that are not also found in other ceratopsians .

= = Anatomy = =

Ceratopsians are easily recognized by features of the skull . On the tip of a ceratopsian upper jaw is the rostral bone , an edentulous (toothless) ossification , unique to ceratopsians . Othniel Charles Marsh recognized and named this bone , which acts as a mirror image of the predentary bone on the lower jaw . This ossification evolved to morphologically aid the mastication of plant matter . Along with the predentary bone , which forms the tip of the lower jaw in all ornithischians , the rostral forms a superficially parrot @-@ like beak . Also , the jugal bones below the eye are very tall and flare out sideways , making the skull appear somewhat triangular when viewed from above . This triangular appearance is accentuated in later ceratopsians by the rearwards extension of the parietal and squamosal bones of the skull roof , to form the neck frill .

The epoccipital is a distinctive bones found lining the frills of ceratopsians . The name is a misnomer , as they are not associated with the occipital bone . Epoccipitals begin as separate bones that fuse during the animal 's growth to either the squamosal or parietal bones that make up the base of the frill . These bones were ornamental instead of functional , and may have helped differentiate species . Epoccipitals probably were present in all known ceratopsids with the possible exception of Zuniceratops . They appear to have been broadly different between short @-@ frilled ceratopsids (centrosaurines) and long @-@ frilled ceratopsids (chasmosaurines) , being elliptical with constricted bases in the former group , and triangular with wide bases in the latter group . Within these broad definitions , different species would have somewhat different shapes and numbers . In centrosaurines especially , like Centrosaurus , Pachyrhinosaurus , and Styracosaurus , these bones become long and spike- or hook @-@ like . A well @-@ known example is the coarse sawtooth fringe of broad triangular epoccipitals on the frill of Triceratops . When regarding the ossification 's morphogenetic traits , it can be described as dermal . The term epoccipital was coined by famous paleontologist Othniel Charles Marsh in 1889 .

= = History of study = =

The first ceratopsian remains known to science were discovered during the U.S. Geological and Geographical Survey of the Territories led by the American geologist F.V. Hayden . Teeth discovered during an 1855 expedition to Montana were first assigned to hadrosaurids and included within the genus Trachodon . It was not until the early 20th century that some of these were

recognized as ceratopsian teeth . During another of Hayden 's expeditions in 1872 , Fielding Bradford Meek found several giant bones protruding from a hillside in southwestern Wyoming . He alerted paleontologist Edward Drinker Cope , who led a dig to recover the partial skeleton . Cope recognized the remains as a dinosaur , but noted that even though the fossil lacked a skull , it was different from any type of dinosaur then known . He named the new species Agathaumas sylvestris , meaning " marvellous forest @-@ dweller " . Soon after , Cope named two more dinosaurs that would eventually come to be recognized as ceratopsids : Polyonax and Monoclonius . Monoclonius was notable for the number of disassociated remains found , including the first evidence of ceratopsid horns and frills . Several Monoclonius fossils were found by Cope , assisted by Charles Hazelius Sternberg , in the summer of 1876 near the Judith River in Chouteau County , Montana . Since the ceratopsians had not been recognised yet as a distinctive group , Cope was uncertain about much of the fossil material , not recognizing the nasal horn core , nor the brow horns , as part of a fossil horn . The frill bone was interpreted as a part of the breastbone .

In 1888 and 1889 , Othniel Charles Marsh described the first well preserved horned dinosaurs , Ceratops and Triceratops . In 1890 Marsh classified them together in the family Ceratopsidae and the order Ceratopsia . This prompted Cope to reexamine his own specimens and to realized that Triceratops , Monoclonius , and Agathaumas all represented a single group of similar dinosaurs , which he named Agathaumidae in 1891 . Cope redescribed Monoclonius as a horned dinosaur , with a large nasal horn and two smaller horns over the eyes , and a large frill .

= = Classification = =

Ceratopsia was coined by Othniel Charles Marsh in 1890 to include dinosaurs possessing certain characteristic features , including horns , a rostral bone , teeth with two roots , fused neck vertebrae , and a forward @-@ oriented pubis . Marsh considered the group distinct enough to warrant its own suborder within Ornithischia . The name is derived from the Greek ????? / keras meaning ' horn ' and ???? / opsis meaning ' face ' . As early as the 1960s , it was noted that the name Ceratopsia is actually incorrect linguistically and that it should be Ceratopia . However , this spelling , while technically correct , has been used only rarely in the scientific literature , and the vast majority of paleontologists continue to use Ceratopsia . As the ICZN does not govern taxa above the level of superfamily , this is unlikely to change .

= = = Taxonomy = = =

Following Marsh , Ceratopsia has usually been classified as a suborder within the order Ornithischia . While ranked taxonomy has largely fallen out of favor among dinosaur paleontologists , some researchers have continued to employ such a classification , though sources have differed on what its rank should be . Most who still employ the use of ranks have retained its traditional ranking of suborder , though some have reduced to the level of infraorder .

This list of ceratopsian genera by classification and location follows a review by Thomas R. Holtz , Jr. in 2010 .

Ceratopsia
Albalophosaurus - (Japan)
Micropachycephalosaurus - (Shandong , eastern China)
Stenopelix - (Germany)
Yinlong - (Xinjiang , western China)
Family Chaoyangsauridae
Chaoyangsaurus - (Liaoning , northeastern China)
Xuanhuaceratops - (Hebei , China)
Family Psittacosauridae
Psittacosaurus - (China & Mongolia)
Neoceratopsia
Archaeoceratops - (Gansu , northwestern China)

Auroraceratops - (Gansu , northwestern China)
Helioceratops - (Jilin , northwestern China)
Koreaceratops - (South Korea)
Kulceratops - (Uzbekistan)
Liaoceratops - (Liaoning , northeastern China)
Microceratus - (Mongolia)
Mosaiceratops - (central China)
Yamaceratops - (Mongolia)
Family Leptoceratopsidae
Asiaceratops - (China , Mongolia , Uzbekistan)
Cerasinops - (Montana , US)
Gryphoceratops - (Alberta , Canada)
Ischioceratops - (China)
Leptoceratops - (Alberta , Canada & Wyoming , US)
Montanoceratops - (Montana , US)
Prenoceratops - (Montana , US)
Udanoceratops - (Mongolia)
Unescoceratops - (Alberta , Canada)
Zhuchengceratops - (Zhucheng , China)
Family Bagaceratopidae
Ajkaceratops - (Hungary)
Bagaceratops - (Mongolia)
Bainoceratops - (Mongolia)
Gobiceratops - (Mongolia)
Lamaceratops - (Mongolia)
Family Protoceratopsidae
Breviceratops - (Mongolia)
Graciliceratops - (Mongolia)
Magnirostris - (Inner Mongolia , China)
Protoceratops - (Mongolia)
Superfamily Ceratopsoidea
Turanoceratops - (Uzbekistan)
Zuniceratops - (New Mexico , US)
Family Ceratopsidae
Subfamily Centrosaurinae
Albertaceratops - (Alberta , Canada & ? Montana , USA)
Avaceratops - (Montana , USA)
Brachyceratops - (Montana , USA & Alberta , Canada)
Centrosaurus - (Alberta , Canada)
Coronosaurus - (Alberta , Canada)
Diabloceratops - (Utah , USA)
Monoclonius - (Montana , USA & Alberta , Canada)
Nasutoceratops - (Utah , USA)
Rubeosaurus - (Montana , USA)
Spinops - (Alberta , Canada)
Styracosaurus - (Alberta , Canada & Montana , USA)
Xenoceratops - (Alberta , Canada)
Tribe Pachyrhinosaurini
Achelousaurus - (Montana , USA)
Einiosaurus - (Montana , USA)
Pachyrhinosaurus- (Alberta , Canada & Alaska , USA)
Sinoceratops - (Shandong , China)
Subfamily Ceratopsinae

Ceratops - (Montana , USA & Alberta , Canada)
Subfamily Chasmosaurinae
Agathaumas - (Wyoming , USA)
Agujaceratops - (Texas , USA)
Anchiceratops - (Alberta , Canada)
Arrhinoceratops - (Alberta , Canada)
Chasmosaurus - (Alberta , Canada)
Coahuilaceratops - (Coahuila , Mexico)
? Dysganus - (Montana , USA)
Judiceratops - (Montana , USA)
Kosmoceratops - (Utah , USA)
Medusaceratops - (Montana , USA)
Mojoceratops - (Alberta & Saskatchewan , Canada)
Pentaceratops - (New Mexico , USA)
? Polyonax - (Colorado , USA)
Utahceratops - (Utah , USA)
Vagaceratops - (Alberta , Canada)
Tribe Triceratopsini
Eotriceratops - (Alberta , Canada)
Nedoceratops - (Wyoming , USA)
Ojoceratops - (New Mexico , USA)
Regaliceratops - (Alberta , Canada)
Tatankaceratops - (South Dakota , USA)
Titanoceratops - (New Mexico , USA)
Torosaurus - (Wyoming , Montana , South Dakota , North Dakota , & Utah , USA & Saskatchewan , Canada)
Triceratops - (Montana & Wyoming , USA & Saskatchewan & Alberta , Canada)

Possible ceratopsians from the Southern Hemisphere include the Australian Serendipaceratops , known from an ulna , and Notoceratops from Argentina is known from a single toothless jaw (which has been lost) . Craspedodon from the Late Cretaceous (Santonian) of Belgium may also be a ceratopsian , specifically a neoceratopsian closer to ceratopsoidea than protoceratopsidae . Possible leptoceratopsid remains have also been described from the early Campanian of Sweden .

= = = Phylogeny = = =

Paleontologists today agree on the overall structure of the ceratopsian family tree , although there are differences on individual taxa . There have been several cladistic studies performed on basal ceratopsians since 2000 . None have used every taxon listed above and many of the differences between the studies are still unresolved .

In clade @-@ based phylogenetic taxonomy , Ceratopsia is often defined to include all marginocephalians more closely related to Triceratops than to Pachycephalosaurus . Under this definition , the most basal known ceratopsians are Yinlong , from the Late Jurassic Period , along with Chaoyangsaurus and the family Psittacosauridae , from the Early Cretaceous Period , all of which were discovered in northern China or Mongolia . The rostral bone and flared jugals are already present in all of these forms , indicating that even earlier ceratopsians remain to be discovered .

The clade Neoceratopsia includes all ceratopsians more derived than psittacosaurids . Another subset of neoceratopsians is called Coronosauria , which currently includes all ceratopsians more derived than Auroraceratops . Coronosaurs show the first development of the neck frill and the fusion of the first several neck vertebrae to support the increasingly heavy head . Within Coronosauria , three groups are generally recognized , although the membership of these groups varies somewhat from study to study and some animals may not fit in any of them . One group can be called Protoceratopsidae and includes Protoceratops and its closest relatives , all Asian . Another

group , Leptoceratopsidae , includes mostly North American animals that are more closely related to Leptoceratops . The Ceratopsoidea includes animals like Zuniceratops , which are more closely related to the family Ceratopsidae . This last family includes Triceratops and all the large North American ceratopsians and is further divided into the subfamilies Centrosaurinae and Ceratopsinae (also known as Chasmosaurinae) .

= = = = Farke phylogeny = = = =

Andrew Farke and his colleagues in 2014 published a description of a new neoceratopsian , Aquilops americanus , through the peer @-@ reviewed science journal PLOS ONE . They analysed their taxa as well as most other primitive ceratopsians to get a consensus cladogram . They created their own data matrix and through it found that many groups of ceratopsians could be supported , and that Aquilops was a basal neoceratopsian that could potentially be a protoceratopsid , leptoceratopsid , or ceratopsid , although any one of these groups would have a large ghost lineage with Aquilops .

Their study also found an equal consensus cladogram finding Ajkaceratops not as a neoceratopsian but a protoceratopsid . Nothing else about the cladograms changed .

= = = = Xu / Makovicky / Chinnery Phylogeny = = = =

Xu Xing of the Chinese Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing , along with Peter Makovicky , formerly of the American Museum of Natural History (AMNH) in New York City and others , published a cladistic analysis in the 2002 description of Liaoceratops . This analysis is very similar to one published by Makovicky in 2001 . Makovicky , who currently works at the Field Museum of Natural History in Chicago , also included this analysis in his 2002 doctoral thesis . Xu and other colleagues added Yinlong to this analysis in 2006 .

Brenda Chinnery , formerly of the Museum of the Rockies in Bozeman , Montana , independently described Prenoceratops in 2005 and published a new phylogeny . In 2006 , Makovicky and Mark Norell of the AMNH incorporated Chinnery 's analysis into their own and also added Yamaceratops , although they were not able to include Yinlong . The cladogram presented below is a combination of Xu , Makovicky , and their colleagues ' most recent work .

Chaoyangsaurus is recovered in a more basal position than Psittacosauridae , although Chinnery 's original analysis finds it within Neoceratopsia . Protoceratopsidae is considered to be the sister group of Ceratopsoidea . The fragmentary Asiaceratops was included in these studies and is found to have a variable position , either as a basal neoceratopsian or as a leptoceratopsid , most likely due to the amount of missing information . Removal of Asiaceratops stabilizes the entire cladogram .

Makovicky 's latest analysis includes IVPP V12722 (" Xuanhuasaurus ") , a Late Jurassic ceratopsian from China that , at the time , was awaiting publication , but has since been published as Xuanhuaceratops . Kulceratops and Turanoceratops are considered nomina dubia in this study . Makovicky believes Lamaceratops , Magnirostris , and Platyceratops to be junior synonyms of Bagaceratops , and Bainoceratops to be synonymous with Protoceratops .

= = = = You / Dodson Phylogeny = = = =

You Hailu of Beijing 's Chinese Academy of Geological Sciences , was a co @-@ author with Xu and Makovicky in 2002 but , in 2003 , he and Peter Dodson from the University of Pennsylvania published a separate analysis . The two presented this analysis again in 2004 . In 2005 , You and three others , including Dodson , published on Auroraceratops and inserted this new dinosaur into their phylogeny .

In contrast to the previous analysis , You and Dodson find Chaoyangsaurus to be the most basal neoceratopsian , more derived than Psittacosaurus , while Leptoceratopsidae , not Protoceratopsidae , is recovered as the sister group of Ceratopsidae . This study includes

Auroraceratops , but lacks seven taxa found in Xu and Makovicky 's work , so it is unclear how comparable the two studies are . Asiaceratops and Turanoceratops are each considered nomina dubia and not included . Along with Dong Zhiming , You described Magnirostris in 2003 , but to date has not included it in any of his cladograms .

= = Paleobiology = =

= = = Biogeography = = =

Ceratopsia appears to have originated in Asia , as all of the earliest members are found there . Fragmentary remains , including teeth , which appear to be neoceratopsian , are found in North America from the Albian stage (112 to 100 million years ago) , indicating that the group had dispersed across what is now the Bering Strait by the middle of the Cretaceous Period . Almost all leptoceratopsids are North American , aside from Udanoceratops , which may represent a separate dispersal event , back into Asia . Ceratopsids and their immediate ancestors , such as Zuniceratops , were unknown outside of western North America , and were presumed endemic to that continent . The traditional view that ceratopsoids originated in North America was called into question by the 2009 discovery of better specimens of the dubious Asian form Turanoceratops , which confirmed it as a ceratopsid . It is unknown whether this indicates ceratopsids actually originated in Asia , or if the Turanoceratops immigrated from North America .

= = = Individual variation = = =

Unlike almost all other dinosaur groups , skulls are the most commonly preserved elements of ceratopsian skeletons and many species are known only from skulls . There is a great deal of variation between and even within ceratopsian species . Complete growth series from embryo to adult are known for Psittacosaurus and Protoceratops , allowing the study of ontogenetic variation in these species . Significant sexual dimorphism has been noted in Protoceratops and several ceratopsids .

= = = Ecological role = = =

Psittacosaurus and Protoceratops are the most common dinosaurs in the different Mongolian sediments where they are found . Triceratops fossils are far and away the most common dinosaur remains found in the latest Cretaceous rocks in the western United States , making up as much as 5 / 6ths of the large dinosaur fauna in some areas . These facts indicate that some ceratopsians were the dominant herbivores in their environments .

Some species of ceratopsians , especially Centrosaurus and its relatives , appear to have been gregarious , living in herds . This is suggested by bonebed finds with the remains of many individuals of different ages . Like modern migratory herds , they would have had a significant effect on their environment , as well as serving as a major food source for predators .

Although ceratopsians are generally considered herbivorous , a few paleontologists , such as Darren Naish and Mark Witton , have speculated online that at least some ceratopsians may have been opportunistically omnivorous .

= = = Posture and locomotion = = =

Most restorations of ceratopsians show them with erect hindlimbs but semi @-@ sprawling forelimbs , which suggest that they were not fast movers . But 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 , which can run at up to 56 km or 35 miles per hour .

= = = Daily activity patterns = = =

A nocturnal lifestyle has been suggested for the primitive ceratopsian Protoceratops . However , comparisons between the scleral rings of Protoceratops and Psittacosaurus and modern birds and reptiles indicate that they may have been cathemeral , active throughout the day at short intervals .

= = = Paleopathology = = =

Activity @-@ related bone fractures have been documented in ceratopsians . Periostitis has also been documented in the shoulder blade of a ceratopsian .

= = Timeline of genera = =