= Edmontosaurus =

Edmontosaurus (/ ?d?m?nt??s??r?s / ed @-@ MON @-@ t? @-@ SAWR @-@ ?s) is a genus of hadrosaurid (duck @-@ billed) dinosaur . It contains two known species : Edmontosaurus regalis and Edmontosaurus annectens . Fossils of E. regalis have been found in rocks of western North America that date from the late Campanian stage of the Cretaceous Period 73 million years ago , while those of E. annectens were found in the same geographic region but in rocks dated to the end of the Maastrichtian stage of the Cretaceous , 66 million years ago . Edmontosaurus was one of the last non @-@ avian dinosaurs , and lived alongside dinosaurs like Triceratops and Tyrannosaurus shortly before the Cretaceous ? Paleogene extinction event .

Edmontosaurus included some of the largest hadrosaurid species , measuring up to 12 metres (39 ft) long and weighing around 4 @.@ 0 metric tons (4 @.@ 4 short tons). Evidence does exist in the form of two fossilized specimens housed at the Museum of the Rockies for an even greater maximum size of 15 m (49 ft) and weighing 9 @.@ 07 metric tons (10 @.@ 00 short tons) for Edmontosaurus annectens. Several well @-@ preserved specimens are known that include not only bones, but in some cases extensive skin impressions and possible gut contents. It is classified as a genus of saurolophine (or hadrosaurine) hadrosaurid, a member of the group of hadrosaurids which lacked large, hollow crests, instead having smaller solid crests or fleshy combs.

The first fossils named Edmontosaurus were discovered in southern Alberta (named after Edmonton , the capital city) , in the Horseshoe Canyon Formation (formerly called the lower Edmonton Formation) . The type species , E. regalis , was named by Lawrence Lambe in 1917 , although several other species that are now classified in Edmontosaurus were named earlier . The best known of these is E. annectens , named by Othniel Charles Marsh in 1892 ; originally as a species of Claosaurus , known for many years as a species of Trachodon , and later as Anatosaurus annectens . Anatosaurus and Anatotitan are now generally regarded as synonyms of Edmontosaurus .

Edmontosaurus was widely distributed across western North America . The distribution of Edmontosaurus fossils suggests that it preferred coasts and coastal plains . It was a herbivore that could move on both two legs and four . Because it is known from several bone beds , Edmontosaurus is thought to have lived in groups , and may have been migratory as well . The wealth of fossils has allowed researchers to study its paleobiology in detail , including its brain , how it may have fed , and its injuries and pathologies , such as evidence for tyrannosaur attacks on a few edmontosaur specimens .

= = Description = =

Edmontosaurus has been described in detail from numerous specimens. Like other hadrosaurids, it was a bulky animal with a long, laterally flattened tail and a head with an expanded, duck @-@ like beak. The skull had no bony crest, unlike many other hadrosaurids, but bore a comb @-@ like crest of skin and scales. The fore legs were not as heavily built as the hind legs, but were long enough to be used in standing or movement. Edmontosaurus was among the largest hadrosaurids: depending on the species, a fully grown adult could have been 9 metres (30 ft) long, and some of the larger specimens reached the range of 12 metres (39 ft) to 13 metres (43 ft) long. Its weight was on the order of 4 @.@ 0 metric tons (4 @.@ 4 short tons). Traditionally, E. regalis has been regarded as the largest species, though this was challenged by the hypothesis that the larger hadrosaurid Anatotitan copei is a synonym of Edmontosaurus annectens, as put forward by Jack Horner and colleagues in 2004, and supported in studies by Campione and Evens in 2009 and 2011 . The type specimen of E. regalis , NMC 2288 , is estimated as 9 to 12 metres (30 to 39 ft) long . E. annectens is often seen as smaller . Two mounted skeletons , USNM 2414 and YPM 2182 , measure 8 @.@ 00 metres (26 @.@ 25 ft) long and 8 @.@ 92 metres (29 @.@ 3 ft) long , respectively. However, these are probably subadult individuals, and there is at least one report of a much larger potential E. annectens specimen , almost 12 metres (39 ft) long . Two specimens still under study in the collection of the Museum of the Rockies; a 7 @.@ 6 m (25 ft) tail labelled

as MOR 1142 and another labelled as MOR 1609 , indicate that Edmontosaurus annectens could have been even larger , possibly rivaling Shantungosaurus in size . The specimens of these individuals indicate a length of up to 15 m ($49\ \text{ft}$) , as confirmed by paleontologists and the development team of the scientifically accurate simulation game Saurian (video game) . Such large individuals of Edmontosaurus would likely have been very rare due to such factors as environmental stress , disease , and predation .

= = = Skull = = =

The skull of a fully grown Edmontosaurus could be over a metre long . One skull of E. annectens (formerly Anatotitan) measures 3 @.@ 87 feet (1 @.@ 18 m) long . The skull was roughly triangular in profile , with no bony cranial crest . Viewed from above , the front and rear of the skull were expanded , with the broad front forming a duck @-@ bill or spoon @-@ bill shape . The beak was toothless , and both the upper and lower beaks were extended by keratinous material . Substantial remains of the keratinous upper beak are known from the " mummy " kept at the Senckenberg Museum . In this specimen , the preserved nonbony part of the beak extended for at least 8 centimetres (3 @.@ 1 in) beyond the bone , projecting down vertically . The nasal openings of Edmontosaurus were elongate and housed in deep depressions surrounded by distinct bony rims above , behind , and below . In at least one case (the Senckenberg specimen) , rarely preserved sclerotic rings were preserved in the eye sockets . Another rarely seen bone , the stapes (the reptilian ear bone) , has also been seen in a specimen of Edmontosaurus .

Teeth were present only in the maxillae (upper cheeks) and dentaries (main bone of the lower jaw) . The teeth were continually replaced , taking about half a year to form . They were composed of six types of tissues , rivaling the complexity of mammal teeth . They grew in columns , with an observed maximum of six in each , and the number of columns varied based on the animal 's size . Known column counts for the two species are : 51 to 53 columns per maxilla and 48 to 49 per dentary (teeth of the upper jaw being slightly narrower than those in the lower jaw) for E. regalis ; and 52 columns per maxilla and 44 per dentary for E. annectens (an E. saskatchewanensis specimen) .

= = = Postcranial skeleton = = =

The number of vertebrae differs between specimens . E. regalis had thirteen neck vertebrae , eighteen back vertebrae , nine hip vertebrae , and an unknown number of tail vertebrae . A specimen once identified as belonging to Anatosaurus edmontoni (now considered to be the same as E. regalis) is reported as having an additional back vertebra and 85 tail vertebrae , with an undisclosed amount of restoration . Other hadrosaurids are only reported as having 50 to 70 tail vertebrae , so this appears to have been an overestimate . The anterior back was curved toward the ground , with the neck flexed upward and the rest of the back and tail held horizontally . Most of the back and tail were lined by ossified tendons arranged in a latticework along the neural spines of the vertebrae . This condition has been described as making the back and at least part of the tail " ramrod " straight . The ossified tendons are interpreted as having strengthened the vertebral column against gravitational stress , incurred through being a large animal with a horizontal vertebral column otherwise supported mostly by the hind legs and hips .

The shoulder blades were long flat blade @-@ like bones , held roughly parallel to the vertebral column . The hips were composed of three elements each : an elongate ilium above the articulation with the leg , an ischium below and behind with a long thin rod , and a pubis in front that flared into a plate @-@ like structure . The structure of the hip hindered the animal from standing with its back erect , because in such a position the thigh bone would have pushed against the joint of the ilium and pubis , instead of pushing only against the solid ilium . The nine fused hip vertebrae provided support for the hip .

The fore legs were shorter and less heavily built than the hind legs. The upper arm had a large deltopectoral crest for muscle attachment, while the ulna and radius were slim. The upper arm and

forearm were similar in length . The wrist was simple , with only two small bones . Each hand had four fingers , with no thumb (first finger) . The index second , third , and fourth fingers were approximately the same length and were united in life within a fleshy covering . Although the second and third finger had hoof @-@ like unguals , these bones were also within the skin and not apparent from the outside . The little finger diverged from the other three and was much shorter . The thigh bone was robust and straight , with a prominent flange about halfway down the posterior side . This ridge was for the attachment of powerful muscles attached to the hips and tail that pulled the thighs (and thus the hind legs) backward and helped maintain the use of the tail as a balancing organ . Each foot had three toes , with no big toe or little toe . The toes had hoof @-@ like tips .

= = = Skin = = = =

Multiple specimens of Edmontosaurus annectens have been found with preserved skin impressions . Several have been well @-@ publicized , such as the " Trachodon mummy " of the early 20th century , and the specimen nicknamed " Dakota " , the latter apparently including remnant organic compounds from the skin . Because of these finds , the scalation of Edmontosaurus annectens is known for most areas of the body . Skin impressions are less well known for E. regalis , but some well @-@ preserved examples have been studied , including one which preserves a soft tissue crest or wattle on the head . It is unknown whether such a crest was present on E. annectens , and whether it was an indicator of sexual dimorphism .

= = Classification = =

Edmontosaurus was a hadrosaurid (a duck @-@ billed dinosaur) , a member of a family of dinosaurs which to date are known only from the Late Cretaceous . It is classified within the Saurolophinae (alternately Hadrosaurinae) , a clade of hadrosaurids which lacked hollow crests . Other members of the group include Brachylophosaurus , Gryposaurus , Lophorhothon , Maiasaura , Naashoibitosaurus , Prosaurolophus , and Saurolophus . It was either closely related to or includes the species Anatosaurus annectens (alternately Edmontosaurus annectens) , a large hadrosaurid from various latest Cretaceous formations of western North America . The giant Chinese hadrosaurine Shantungosaurus giganteus is also anatomically similar to Edmontosaurus ; M. K. Brett @-@ Surman found the two to differ only in details related to the greater size of Shantungosaurus , based on what had been described of the latter genus .

While the status of Edmontosaurus as a saurolophine or (= " hadrosaurine ") has not been challenged , its exact placement within the clade is uncertain . Early phylogenies , such as that presented in R. S. Lull and Nelda Wright 's influential 1942 monograph , had Edmontosaurus and various species of Anatosaurus (most of which would be later considered as additional species or specimens of Edmontosaurus) as one lineage among several lineages of " flat @-@ headed " hadrosaurs . One of the first analyses using cladistic methods found it to be linked with Anatosaurus (= Anatotitan) and Shantungosaurus in an informal " edmontosaur " clade , which was paired with the spike @-@ crested " saurolophs " and more distantly related to the " brachylophosaurs " and arch @-@ snouted " gryposaurs " . A 2007 study by Terry Gates and Scott Sampson found broadly similar results , in that Edmontosaurus remained close to Saurolophus and Prosaurolophus and distant from Gryposaurus , Brachylophosaurus , and Maiasaura . However , the most recent review of Hadrosauridae , by Jack Horner and colleagues (2004) , came to a noticeably different result : Edmontosaurus was nested between Gryposaurus and the " brachylophosaurs " , and distant from Saurolophus . The discrepancies are complicated by the relative lack of work on hadrosaurine evolutionary relationships .

= = Discovery and history = =

= = = Claosaurus annectens = = =

Edmontosaurus has had a long and complicated history in paleontology , having spent decades with various species classified in other genera . Its taxonomic history intertwines at various points with the genera Agathaumas , Anatosaurus , Anatotitan , Claosaurus , Hadrosaurus , Thespesius , and Trachodon , and references predating the 1980s typically use Anatosaurus , Claosaurus , Thespesius , or Trachodon for edmontosaur fossils (excluding those assigned to E. regalis) , depending on author and date . Although Edmontosaurus was only named in 1917 , its oldest well @-@ supported species (E. annectens) was named in 1892 as a species of Claosaurus .

The first well @-@ supported species of Edmontosaurus was named in 1892 as Claosaurus annectens by Othniel Charles Marsh . This species is based on USNM 2414 , a partial skull @-@ roof and skeleton , with a second skull and skeleton , YPM 2182 , designated the paratype . Both were collected in 1891 by John Bell Hatcher from the late Maastrichtian @-@ age Upper Cretaceous Lance Formation of Niobrara County (then part of Converse County) , Wyoming . This species has some historical footnotes attached : it is among the first dinosaurs to receive a skeletal restoration , and is the first hadrosaurid so restored ; and YPM 2182 and UNSM 2414 are , respectively , the first and second essentially complete mounted dinosaur skeletons in the United States . YPM 2182 was put on display in 1901 , and USNM 2414 in 1904 .

Because of the incomplete understanding of hadrosaurids at the time, following Marsh 's death in 1897 Claosaurus annectens was variously classified as a species of Claosaurus, Thespesius or Trachodon. Opinions varied greatly; textbooks and encyclopedias drew a distinction between the " Iguanodon @-@ like " Claosaurus annectens and the " duck @-@ billed " Hadrosaurus (based on remains now known as adult Edmontosaurus annectens), while Hatcher explicitly identified C. annectens as synonymous with the hadrosaurid represented by those same duck @-@ billed skulls . Hatcher 's revision, published in 1902, was sweeping: he considered almost all hadrosaurid genera then known as synonyms of Trachodon. This included Cionodon, Diclonius, Hadrosaurus, Ornithotarsus, Pteropelyx, and Thespesius, as well as Claorhynchus and Polyonax, fragmentary genera now thought to be horned dinosaurs. Hatcher 's work led to a brief consensus, until after 1910 new material from Canada and Montana showed a greater diversity of hadrosaurids than previously suspected. Charles W. Gilmore in 1915 reassessed hadrosaurids and recommended that Thespesius be reintroduced for hadrosaurids from the Lance Formation and rock units of equivalent age, and that Trachodon, based on inadequate material, should be restricted to a hadrosaurid from the older Judith River Formation and its equivalents. In regards to Claosaurus annectens, he recommended that it be considered the same as Thespesius occidentalis. His reinstatement of Thespesius for Lance @-@ age hadrosaurids would have other consequences for the taxonomy of Edmontosaurus in the following decades.

During this time frame (1902 ? 1915) , two additional important specimens of C. annectens were recovered . The first , the " Trachodon mummy " (AMNH 5060) , was discovered in 1908 by Charles Hazelius Sternberg and his sons in Lance Formation rocks near Lusk , Wyoming . Sternberg was working for the British Museum of Natural History , but Henry Fairfield Osborn of the American Museum of Natural History was able to purchase the specimen for \$ 2 @,@ 000 . The Sternbergs recovered a second similar specimen from the same area in 1910 , not as well preserved but also found with skin impressions . They sold this specimen (SM 4036) to the Senckenberg Museum in Germany .

As a side note , Trachodon selwyni , described by Lawrence Lambe in 1902 for a lower jaw from what is now known as the Dinosaur Park Formation of Alberta , was erroneously described by Glut (1997) as having been assigned to Edmontosaurus regalis by Lull and Wright . It was not , instead being designated " of very doubtful validity . " More recent reviews of hadrosaurids have concurred .

= = = Canadian discoveries = = =

Edmontosaurus itself was coined in 1917 by Lawrence Lambe for two partial skeletons found in the Horseshoe Canyon Formation (formerly the lower Edmonton Formation) along the Red Deer River of southern Alberta, Canada. These rocks are older than the rocks in which Claosaurus annectens

was found . The Edmonton Formation lends Edmontosaurus its name . The type species , E. regalis (" regal " , or , more loosely , " king @-@ sized ") , is based on NMC 2288 , consisting of a skull , articulated vertebrae up to the sixth tail vertebra , ribs , partial hips , an upper arm bone , and most of a hind limb . It was discovered in 1912 by Levi Sternberg . The second specimen , paratype NMC 2289 , consists of a skull and skeleton lacking the beak , most of the tail , and part of the feet . It was discovered in 1916 by George F. Sternberg . Lambe found that his new dinosaur compared best to Diclonius mirabilis (specimens now assigned to Edmontosaurus annectens) , and drew attention to the size and robustness of Edmontosaurus . Initially , Lambe only described the skulls of the two skeletons , but returned to the genus in 1920 to describe the skeleton of NMC 2289 . The postcrania of the type specimen remains undescribed , still in its plaster jackets .

Two more species that would come to be included with Edmontosaurus were named from Canadian remains in the 1920s , but both would initially be assigned to Thespesius . Gilmore named the first , Thespesius edmontoni , in 1924 . T. edmontoni also came from the Horseshoe Canyon Formation . It was based on NMC 8399 , another nearly complete skeleton lacking most of the tail . NMC 8399 was discovered on the Red Deer River in 1912 by a Sternberg party . Its forelimbs , ossified tendons , and skin impressions were briefly described in 1913 and 1914 by Lambe , who at first thought it was an example of a species he had named Trachodon marginatus , but then changed his mind . The specimen became the first dinosaur skeleton to be mounted for exhibition in a Canadian museum . Gilmore found that his new species compared closely to what he called Thespesius annectens , but left the two apart because of details of the arms and hands . He also noted that his species had more vertebrae than Marsh 's in the back and neck , but proposed that Marsh was mistaken in assuming that the annectens specimens were complete in those regions .

In 1926, Charles Mortram Sternberg named Thespesius saskatchewanensis for NMC 8509, a skull and partial skeleton from the Wood Mountain plateau of southern Saskatchewan. He had collected this specimen in 1921, from rocks that were assigned to the Lance Formation, now the Frenchman Formation. NMC 8509 included an almost complete skull, numerous vertebrae, partial shoulder and hip girdles, and partial hind limbs, representing the first substantial dinosaur specimen recovered from Saskatchewan. Sternberg opted to assign it to Thespesius because that was the only hadrosaurid genus known from the Lance Formation at the time. At the time, T. saskatchewanensis was unusual because of its small size, estimated at 7 to 7 @.@ 3 metres (23 to 24 ft) in length.

= = = Anatosaurus to the present = = =