= duck + Greek sauros =

lizard) , had as its type species Marsh 's old Claosaurus annectens . Also assigned to this genus were Thespesius edmontoni , T. saskatchewanensis , a large lower jaw that Marsh had named Trachodon longiceps in 1890 , and a new species , Anatosaurus copei , for two skeletons on display at the American Museum of Natural History that had long been known as Diclonius mirabilis (or variations thereof) . Thus , the various species became Anatosaurus annectens , A. copei , A. edmontoni , A. longiceps , and A. saskatchewanensis . Anatosaurus would come to be called the " classic duck @-@ billed dinosaur . "

This state of affairs persisted for several decades , until Michael K. Brett @-@ Surman reexamined the pertinent material for his graduate studies in the 1970s and 1980s . He concluded that the type species of Anatosaurus , A. annectens , was actually a species of Edmontosaurus and that A. copei was different enough to warrant its own genus . Although theses and dissertations are not regarded as official publications by the International Commission on Zoological Nomenclature , which regulates the naming of organisms , his conclusions were known to other paleontologists , and were adopted by several popular works of the time . Brett @-@ Surman and Ralph Chapman designated a new genus for A. copei (Anatotitan) in 1990 . Of the remaining species , A. saskatchewanensis and A. edmontoni were assigned to Edmontosaurus as well , and A. longiceps went to Anatotitan , as either a second species or as a synonym of A. copei . Because the type species of Anatosaurus (A. annectens) was sunk into Edmontosaurus , the name Anatosaurus is abandoned as a junior synonym of Edmontosaurus .

The conception of Edmontosaurus that emerged included three valid species : the type E. regalis , E. annectens (including Anatosaurus edmontoni , emended to edmontonensis) , and E. saskatchewanensis . The debate about the proper taxonomy of the A. copei specimens continues to the present : returning to Hatcher 's argument of 1902 , Jack Horner , David B. Weishampel , and Catherine Forster regarded Anatotitan copei as representing specimens of Edmontosaurus annectens with crushed skulls . In 2007 another " mummy " was announced ; nicknamed " Dakota " , it was discovered in 1999 by Tyler Lyson , and came from the Hell Creek Formation of North Dakota .

In a 2011 study by Nicolás Campione and David Evans , the authors conducted the first ever morphometric analysis to compare the various specimens assigned to Edmontosaurus . They concluded that only two species are valid : E. regalis , from the late Campanian , and E. annectens , from the late Maastrichtian . Their study provided further evidence that Anatotitan copei is a synonym of E. annectens ; specifically , that the long , low skull of A. copei is the result of ontogenetic change and represents mature E. annectens individuals .

= = Species and distribution = =

Edmontosaurus is currently regarded as having two valid species : type species E. regalis , and E. annectens . E. regalis is known only from the Horseshoe Canyon Formation of Alberta , dating from the late Campanian stage of the late Cretaceous period . At least a dozen individuals are known , including seven skulls with associated postcrania , and five to seven other skulls . The species formerly known as Thespesius edmontoni or Anatosaurus edmontoni represents immature individuals .

E. annectens is known from the Frenchman Formation of Saskatchewan , the Hell Creek Formation of Montana , and the Lance Formation of South Dakota and Wyoming . It is limited to late Maastrichtian rocks , and is represented by at least twenty skulls , some with postcranial remains . One author , Kraig Derstler , has described E. annectens as " perhaps the most perfectly @-@ known dinosaur to date [1994] . " Anatosaurus copei and E. saskatchewanensis are now thought to be growth stages of E. annectens : A. copei as adults , and E. saskatchewanensis as juveniles . Trachodon longiceps may be a synonym of E. annectens as well . Anatosaurus edmontoni was mistakenly listed as a synonym of E. annectens in both reviews of the Dinosauria , but this does not appear to be the case .

E. annectens differed from E. regalis by having a longer , lower , less robust skull . Although Brett

@-@ Surman regarded E. regalis and E. annectens as potentially representing males and females of the same species , all E. regalis specimens come from older formations than E. annectens specimens .

Edmontosaurin specimens from the Prince Creek Formation of Alaska formerly assigned to Edmontosaurus sp. have been given their own genus and species name , Ugrunaaluk kuukpikensis . Edmontosaurus was also reported from the Javelina Formation of Big Bend National Park , western Texas , but the remains in question were later referred to Kritosaurus cf. navajovius by Wagner (2001) , and one specimen has been described as the new species Gryposaurus alsatei .

= = Paleoecology = =

Edmontosaurus was a wide @-@ ranging genus in both time and space . The rock units from which it is known can be divided into two groups by age : the older Horseshoe Canyon and St. Mary River formations , and the younger Frenchman , Hell Creek , and Lance formations . The time span covered by the Horseshoe Canyon Formation and equivalents is also known as Edmontonian , and the time span covered by the younger units is also known as Lancian . The Edmontonian and Lancian time intervals had distinct dinosaur faunas .

The Edmontonian land vertebrate age is defined by the first appearance of Edmontosaurus regalis in the fossil record . Although sometimes reported as of exclusively early Maastrichtian age , the Horseshoe Canyon Formation was of somewhat longer duration . Deposition began approximately 73 million years ago , in the late Campanian , and ended between 68 @.@ 0 and 67 @.@ 6 million years ago . Edmontosaurus regalis is known from the lowest of five units within the Horseshoe Canyon Formation , but is absent from at least the second to the top . As many as three quarters of the dinosaur specimens from badlands near Drumheller , Alberta may pertain to Edmontosaurus .

The Lancian time interval was the last interval before the Cretaceous ? Paleogene extinction event that eliminated non @-@ avian dinosaurs . Edmontosaurus was one of the more common dinosaurs of the interval . Robert Bakker reports that it made up one @-@ seventh of the large dinosaur sample , with most of the rest (five @-@ sixths) made up of the horned dinosaur Triceratops . The coastal plain Triceratops ? Edmontosaurus association , dominated by Triceratops , extended from Colorado to Saskatchewan .

The Lance Formation , as typified by exposures approximately 100 kilometres (62 mi) north of Fort Laramie in eastern Wyoming , has been interpreted as a bayou setting similar to the Louisiana coastal plain . It was closer to a large delta than the Hell Creek Formation depositional setting to the north and received much more sediment . Tropical araucarian conifers and palm trees dotted the hardwood forests , differentiating the flora from the northern coastal plain . The climate was humid and subtropical , with conifers , palmettos , and ferns in the swamps , and conifers , ash , live oak , and shrubs in the forests . Freshwater fish , salamanders , turtles , diverse lizards , snakes , shorebirds , and small mammals lived alongside the dinosaurs . Small dinosaurs are not known in as great of abundance here as in the Hell Creek rocks , but Thescelosaurus once again seems to have been relatively common . Triceratops is known from many skulls , which tend to be somewhat smaller than those of more northern individuals . The Lance Formation is the setting of two edmontosaur " mummies " .

= = Paleobiology = =

= = = Growth = = =

In a 2011 study , Campione and Evans recorded data from all known " edmontosaur " skulls from the Campanian and Maastrichtian and used it to plot a morphometric graph , comparing variable features of the skull with skull size . Their results showed that within both recognized Edmontosaurus species , many features previously used to classify additional species or genera were directly correlated with skull size . Campione and Evans interpreted these results as strongly

suggesting that the shape of Edmontosaurus skulls changed dramatically as they grew . This has led to several apparent mistakes in classification in the past . The Campanian species Thespesius edmontoni , previously considered a synonym of E. annectens due to its small size and skull shape , is more likely a subadult specimen of the contemporary E. regalis . Similarly , the three previously recognized Maastrichtian edmontosaur species likely represent growth stages of a single species , with E. saskatchewanensis representing juveniles , E. annectens subadults , and Anatotitan copei fully mature adults . The skulls became longer and flatter as the animals grew .

= = = Brain and nervous system = = =

The brain of Edmontosaurus has been described in several papers and abstracts through the use of endocasts of the cavity where the brain had been . E. annectens and E. regalis , as well as specimens not identified to species , have been studied in this way . The brain was not particularly large for an animal the size of Edmontosaurus . The space holding it was only about a quarter of the length of the skull , and various endocasts have been measured as displacing 374 millilitres (13 US fl oz) to 450 millilitres (15 US fl oz) , which does not take into account that the brain may have occupied as little as 50 % of the space of the endocast , the rest of the space being taken up by the dura mater surrounding the brain . For example , the brain of the specimen with the 374 millilitre endocast is estimated to have had a volume of 268 millilitres (9 US fl oz) . The brain was an elongate structure , and as with other non @-@ mammals , there would have been no neocortex . Like Stegosaurus , the neural canal was expanded in the hips , but not to the same degree : the endosacral space of Stegosaurus had 20 times the volume of its endocranial cast , whereas the endosacral space of Edmontosaurus was only 2 @.@ 59 times larger in volume .

= = = Diet = = =

= = = = Feeding adaptations = = = =

As a hadrosaurid , Edmontosaurus was a large terrestrial herbivore . Its teeth were continually replaced and packed into dental batteries that contained hundreds of teeth , only a relative handful of which were in use at any time . It used its broad beak to cut loose food , perhaps by cropping , or by closing the jaws in a clamshell @-@ like manner over twigs and branches and then stripping off the more nutritious leaves and shoots . Because the tooth rows are deeply indented from the outside of the jaws , and because of other anatomical details , it is inferred that Edmontosaurus and most other ornithischians had cheek @-@ like structures , muscular or non @-@ muscular . The function of the cheeks was to retain food in the mouth . The animal 's feeding range would have been from ground level to around 4 metres (13 ft) above .

Before the 1960s and 1970s , the prevailing interpretation of hadrosaurids like Edmontosaurus was that they were aquatic and fed on aquatic plants . An example of this is William Morris 's 1970 interpretation of an edmontosaur skull with nonbony beak remnants . He proposed that the animal had a diet much like that of some modern ducks , filtering plants and aquatic invertebrates like mollusks and crustaceans from the water and discharging water via V @-@ shaped furrows along the inner face of the upper beak . This interpretation of the beak has been rejected , as the furrows and ridges are more like those of herbivorous turtle beaks than the flexible structures seen in filter @-@ feeding birds .

Between the mid @-@ 1980s and the first decade of the 2000s , the prevailing interpretation of how hadrosaurids processed their food followed the model put forward in 1984 by David B. Weishampel . He proposed that the structure of the skull permitted motion between bones that resulted in backward and forward motion of the lower jaw , and outward bowing of the tooth @-@ bearing bones of the upper jaw when the mouth was closed . The teeth of the upper jaw would grind against the teeth of the lower jaw like rasps , processing plant material trapped between them . Such a motion would parallel the effects of mastication in mammals , although accomplishing the effects in

a completely different way . Work in the early 2000s has challenged the Weishampel model . A study published in 2008 by Casey Holliday and Lawrence Witmer found that ornithopods like Edmontosaurus lacked the types of skull joints seen in those modern animals that are known to have kinetic skulls (skulls that permit motion between their constituent bones) , such as squamates and birds . They proposed that joints that had been interpreted as permitting movement in dinosaur skulls were actually cartilaginous growth zones . An important piece of evidence for Weishampel 's model is the orientation of scratches on the teeth , showing the direction of jaw action . Other movements could produce similar scratches , though , such as movement of the bones of the two halves of the lower jaw . Not all models have been scrutinized under present techniques . Vincent Williams and colleagues (2009) published additional work on hadrosaurid tooth microwear . They found four classes of scratches on Edmontosaurus teeth . The most common class was interpreted as resulting from an oblique motion , not a simple up @-@ down or front @-@ back motion , which is consistent with the Weishampel model . This motion is thought to have been the primary motion for grinding food . Two scratch classes were interpreted as resulting from forward or backward movement of the jaws . The other class was variable and probably resulted from opening the jaws . The combination of movements is more complex than had been previously predicted .

Weishampel developed his model with the aid of a computer simulation . Natalia Rybczynski and colleagues have updated this work with a much more sophisticated three @-@ dimensional animation model , scanning a skull of E. regalis with lasers . They were able to replicate the proposed motion with their model , although they found that additional secondary movements between other bones were required , with maximum separations of 1 @.@ 3 to 1 @.@ 4 centimetres (0 @.@ 51 to 0 @.@ 55 in) between some bones during the chewing cycle . Rybczynski and colleagues were not convinced that the Weishampel model is viable , but noted that they have several improvements to implement to their animation . Planned improvements include incorporating soft tissue and tooth wear marks and scratches , which should better constrain movements . They note that there are several other hypotheses to test as well . Further research published in 2012 by Robin Cuthbertson and colleagues found the motions required for Weishampel 's model to be unlikely , and favored a model in which movements of the lower jaw produced grinding action . The lower jaw 's joint with the upper jaw would permit anterior ? posterior motion along with the usual rotation , and the anterior joint of the two halves of the lower jaw would also permit motion ; in combination , the two halves of the lower jaw could move slightly back and forth as well as rotating slightly along their long axes . These motions would account for the observed tooth wear and a more solidly constructed skull than modeled by Weishampel .

Because scratches dominate the microwear texture of the teeth , Williams et al. suggested Edmontosaurus was a grazer instead of a browser , which would be predicted to have fewer scratches due to eating less abrasive materials . Candidates for ingested abrasives include silica @-@ rich plants like horsetails and soil that was accidentally ingested due to feeding at ground level . The tooth structure indicates combined slicing and grinding capabilities .

Reports of gastroliths , or stomach stones , in the hadrosaurid Claosaurus are actually based on a probable double misidentification . First , the specimen is actually of Edmontosaurus annectens . Barnum Brown , who discovered the specimen in 1900 , referred to it as Claosaurus because E. annectens was thought to be a species of Claosaurus at the time . Additionally , it is more likely that the supposed gastroliths represent gravel washed in during burial .

= = = = Gut contents = = = =

Both of the " mummy " specimens collected by the Sternbergs were reported to have had possible gut contents . Charles H. Sternberg reported the presence of carbonized gut contents in the American Museum of Natural History specimen , but this material has not been described . The plant remains in the Senckenberg Museum specimen have been described , but have proven difficult to interpret . The plants found in the carcass included needles of the conifer Cunninghamites elegans , twigs from conifer and broadleaf trees , and numerous small seeds or fruits . Upon their description in 1922 , they were the subject of a debate in the German @-@ language journal

Paläontologische Zeitschrift . Kräusel , who described the material , interpreted it as the gut contents of the animal , while Abel could not rule out that the plants had been washed into the carcass after death .

At the time , hadrosaurids were thought to have been aquatic animals , and Kräusel made a point of stating that the specimen did not rule out hadrosaurids eating water plants . The discovery of possible gut contents made little impact in English @-@ speaking circles , except for another brief mention of the aquatic @-@ terrestrial dichotomy , until it was brought up by John Ostrom in the course of an article reassessing the old interpretation of hadrosaurids as water @-@ bound . Instead of trying to adapt the discovery to the aquatic model , he used it as a line of evidence that hadrosaurids were terrestrial herbivores . While his interpretation of hadrosaurids as terrestrial animals has been generally accepted , the Senckenberg plant fossils remain equivocal . Kenneth Carpenter has suggested that they may actually represent the gut contents of a starving animal , instead of a typical diet . Other authors have noted that because the plant fossils were removed from their original context in the specimen and were heavily prepared , it is no longer possible to follow up on the original work , leaving open the possibility that the plants were washed @-@ in debris .

= = = Isotopic studies = = =

The diet and physiology of Edmontosaurus have been probed by using stable isotopes of carbon and oxygen as recorded in tooth enamel . When feeding , drinking , and breathing , animals take in carbon and oxygen , which become incorporated into bone . The isotopes of these two elements are determined by various internal and external factors , such as the type of plants being eaten , the physiology of the animal , salinity , and climate . If isotope ratios in fossils are not altered by fossilization and later changes , they can be studied for information about the original factors ; warmblooded animals will have certain isotopic compositions compared to their surroundings , animals that eat certain types of plants or use certain digestive processes will have distinct isotopic compositions , and so on . Enamel is typically used because the structure of the mineral that forms enamel makes it the most resistant material to chemical change in the skeleton .

A 2004 study by Kathryn Thomas and Sandra Carlson used teeth from the upper jaw of three individuals interpreted as a juvenile , a subadult , and an adult , recovered from a bone bed in the Hell Creek Formation of Corson County , South Dakota . In this study , successive teeth in columns in the edmontosaurs ' dental batteries were sampled from multiple locations along each tooth using a microdrilling system . This sampling method takes advantage of the organization of hadrosaurid dental batteries to find variation in tooth isotopes over a period of time . From their work , it appears that edmontosaur teeth took less than about 0 @.@ 65 years to form , slightly faster in younger edmontosaurs . The teeth of all three individuals appeared to show variation in oxygen isotope ratios that could correspond to warm / dry and cool / wet periods ; Thomas and Carlson considered the possibility that the animals were migrating instead , but favored local seasonal variations because migration would have more likely led to ratio homogenization , as many animals migrate to stay within specific temperature ranges or near particular food sources .

The edmontosaurs also showed enriched carbon isotope values , which for modern mammals would be interpreted as a mixed diet of C3 plants (most plants) and C4 plants (grasses) ; however , C4 plants were extremely rare in the Late Cretaceous if present at all . Thomas and Carlson put forward several factors that may have been operating , and found the most likely to include a diet heavy in gymnosperms , consuming salt @-@ stressed plants from coastal areas adjacent to the Western Interior Seaway , and a physiological difference between dinosaurs and mammals that caused dinosaurs to form tissue with different carbon ratios than would be expected for mammals . A combination of factors is also possible .

= = = Pathologies and health = = =

In 2003 , evidence of tumors , including hemangiomas , desmoplastic fibroma , metastatic cancer ,

and osteoblastoma , was described in Edmontosaurus bones . Rothschild et al. tested dinosaur vertebrae for tumors using computerized tomography and fluoroscope screening . Several other hadrosaurids , including Brachylophosaurus , Gilmoreosaurus , and Bactrosaurus , also tested positive . Although more than 10 @,@ 000 fossils were examined in this manner , the tumors were limited to Edmontosaurus and closely related genera . The tumors may have been caused by environmental factors or genetic propensity .

Osteochondrosis , or surficial pits in bone at places where bones articulate , is also known in Edmontosaurus . This condition , resulting from cartilage failing to be replaced by bone during growth , was found to be present in 2 @.@ 2 % of 224 edmontosaur toe bones . The underlying cause of the condition is unknown . Genetic predisposition , trauma , feeding intensity , alterations in blood supply , excess thyroid hormones , and deficiencies in various growth factors have been suggested . Among dinosaurs , osteochondrosis (like tumors) is most commonly found in hadrosaurids .

= = = Locomotion = = =

Like other hadrosaurids , Edmontosaurus is thought to have been a facultative biped , meaning that it mostly moved on four legs , but could adopt a bipedal stance when needed . It probably went on all fours when standing still or moving slowly , and switched to using the hind legs alone when moving more rapidly . Research conducted by computer modeling in 2007 suggests that Edmontosaurus could run at high speeds , perhaps up to 45 kilometres per hour (28 mph) . Further simulations using a subadult specimen estimated as weighing 715 kilograms (1 @,@ 576 lb) when alive produced a model that could run or hop bipedally , use a trot , pace , or single foot symmetric quadrupedal gait , or move at a gallop . The researchers found to their surprise that the fastest gait was kangaroo @-@ like hopping (maximum simulated speed of 17 @.@ 3 metres per second (62 km / h ; 39 mph)) , which they regarded as unlikely based on the size of the animal and lack of hopping footprints in the fossil record , and instead interpreted the result as indicative of an inaccuracy in their simulation . The fastest non @-@ hopping gaits were galloping (maximum simulated speed of 15 @.@ 7 metres per second (57 km / h ; 35 mph)) and running bipedally (maximum simulated speed of 14 @.@ 0 metres per second (50 km / h ; 31 mph)) . They found weak support for bipedal running as the most likely option for high @-@ speed movement , but did not rule out high @-@ speed quadrupedal movement .

While long thought to have been aquatic or semiaquatic , hadrosaurids were not as well @-@ suited for swimming as other dinosaurs (particularly theropods , who were once thought to have been unable to pursue hadrosaurids into water) . Hadrosaurids had slim hands with short fingers , making their forelimbs ineffective for propulsion , and the tail was also not useful for propulsion because of the ossified tendons that increased its rigidity , and the poorly developed attachment points for muscles that would have moved the tail from side to side .

= = = Interactions with theropods = = =

The time span and geographic range of Edmontosaurus overlapped with Tyrannosaurus , and an adult specimen of E. annectens on display in the Denver Museum of Nature and Science shows evidence of a theropod bite in the tail . Counting back from the hip , the thirteenth to seventeenth vertebrae have damaged spines consistent with an attack from the right rear of the animal . One spine has a portion sheared away , and the others are kinked ; three have apparent tooth puncture marks . The top of the tail was at least 2 @.@ 9 metres (9 @.@ 5 ft) high , and the only theropod species known from the same rock formation that was tall enough to make such an attack is T. rex . The bones are partially healed , but the edmontosaur died before the traces of damage were completely obliterated . The damage also shows signs of bone infection . Kenneth Carpenter , who studied the specimen , noted that there also seems to be a healed fracture in the left hip which predated the attack because it was more fully healed . He suggested that the edmontosaur was a target because it may have been limping from this earlier injury . Because it survived the attack ,

Carpenter suggested that it may have outmaneuvered or outrun its attacker , or that the damage to its tail was incurred by the hadrosaurid using it as a weapon against the tyrannosaur .

Another specimen of E. annectens , pertaining to a 7 @.@ 6 metres (25 ft) long individual from South Dakota , shows evidence of tooth marks from small theropods on its lower jaws . Some of the marks are partially healed . Michael Triebold , informally reporting on the specimen , suggested a scenario where small theropods attacked the throat of the edmontosaur ; the animal survived the initial attack but succumbed to its injuries shortly thereafter . Some edmontosaur bone beds were sites of scavenging . Albertosaurus and Saurornitholestes tooth marks are common at one Alberta bone bed , and Daspletosaurus fed on Edmontosaurus and fellow hadrosaurid Saurolophus at another Alberta site .

= = = Social behavior = = =

Extensive bone beds are known for Edmontosaurus , and such groupings of hadrosaurids are used to suggest that they were gregarious , living in groups . Three quarries containing Edmontosaurus remains are identified in a 2007 database of fossil bone beds , from Alberta (Horseshoe Canyon Formation) , South Dakota (Hell Creek Formation) , and Wyoming (Lance Formation) . One edmontosaur bone bed , from claystone and mudstone of the Lance Formation in eastern Wyoming , covers more than a square kilometre , although Edmontosaurus bones are most concentrated in a 40 hectares (0 @.@ 15 sq mi) subsection of this site . It is estimated that disassociated remains pertaining to 10 @,@ 000 to 25 @,@ 000 edmontosaurs are present here .

Unlike many other hadrosaurids , Edmontosaurus lacked a bony crest . It may have had soft @-@ tissue display structures in the skull , though : the bones around the nasal openings had deep indentations surrounding the openings , and this pair of recesses are postulated to have held inflatable air sacs , perhaps allowing for both visual and auditory signaling . Edmontosaurus may have been dimorphic , with more robust and more lightly built forms , but it has not been established if this is related to sexual dimorphism .

Edmontosaurus has been considered a possibly migratory hadrosaurid by some authors . A 2008 review of dinosaur migration studies by Phil R. Bell and Eric Snively proposed that E. regalis was capable of an annual 2 @,@ 600 kilometres (1 @,@ 600 mi) round @-@ trip journey , provided it had the requisite metabolism and fat deposition rates . Such a trip would have required speeds of about 2 to 10 kilometres per hour (1 to 6 mph) , and could have brought it from Alaska to Alberta . In contrast to Bell and Snively , Anusuya Chinsamy and colleagues concluded from a study of bone microstructure that polar Edmontosaurus overwintered .