

= Apatosaurus =

Apatosaurus (/ ˈpæʊtəˈsaʊrəs / ; meaning " deceptive lizard ") is a genus of extinct sauropod dinosaurs that lived in North America during the Late Jurassic period . Othniel Charles Marsh described and named the first @-@ known species , *A. ajax* in 1877 , and a second species , *A. louisae* , was discovered and named by William H. Holland in 1916 . They lived about 152 to 151 million years ago (mya) , during the early Tithonian age , and are now known from fossils in the Morrison Formation of modern @-@ day Colorado , Oklahoma , and Utah , in the United States . *Apatosaurus* had an average length of 21 ? 22 @.@ 8 m (69 ? 75 ft) , and an average mass of 16 @.@ 4 ? 22 @.@ 4 t (16 @.@ 1 ? 22 @.@ 0 long tons ; 18 @.@ 1 ? 24 @.@ 7 short tons) . A few specimens indicate a maximum length of 11 ? 30 % greater than average and a mass of 32 @.@ 7 ? 72 @.@ 6 t (32 @.@ 2 ? 71 @.@ 5 long tons ; 36 @.@ 0 ? 80 @.@ 0 short tons) .

The cervical vertebrae of *Apatosaurus* are less elongated and more heavily constructed than those of *Diplodocus* , a diplodocid like *Apatosaurus* , and the bones of the leg are much stockier despite being longer , implying that *Apatosaurus* was a more robust animal . The tail was held above the ground during normal locomotion . *Apatosaurus* had a single claw on each forelimb and three on each hindlimb . The skull of *Apatosaurus* , long thought to be similar to *Camarasaurus* , is much more similar to that of *Diplodocus* . *Apatosaurus* was a generalized browser that likely held its head elevated . To lighten its vertebrae , *Apatosaurus* had air sacs that made the bones internally full of holes . Like that of other diplodocids , its tail may have been used as a whip to create loud noises .

The skull of *Apatosaurus* was confused with that of *Camarasaurus* and *Brachiosaurus* until 1909 , when the holotype of *A. louisae* was found , and a complete skull just a few meters away from the front of the neck . Henry Fairfield Osborn disagreed with this association , and went on to mount a skeleton of *Apatosaurus* with a *Camarasaurus* skull cast . Until 1970 , *Apatosaurus* skeletons were mounted with speculative skull casts , when McIntosh showed that more robust skulls assigned to *Diplodocus* were more likely from *Apatosaurus* .

Apatosaurus is a genus in the family Diplodocidae . It is one of the more basal genera , with only *Amphicoelias* , and possibly a new , unnamed genus more primitive . While the subfamily Apatosaurinae was named in 1929 , the group was not used validly until an extensive 2015 study . Only *Brontosaurus* is also in the subfamily , with the other genera being considered as synonyms or reclassified as diplodocines . *Brontosaurus* has long been considered a junior synonym of *Apatosaurus* ; its only species was reclassified as *A. excelsus* in 1903 . However , the 2015 study concluded that *Brontosaurus* was a valid genus of sauropod distinct from *Apatosaurus* . Nevertheless , not all paleontologists agree with this division . As it existed in North America during the late Jurassic , *Apatosaurus* would have lived aside dinosaurs such as *Allosaurus* , *Camarasaurus* , *Diplodocus* , and *Stegosaurus* .

= = Description = =

Apatosaurus was a large , long @-@ necked , quadrupedal animal with a long , whip @-@ like tail . Its forelimbs were slightly shorter than its hindlimbs . Most size estimates are based on specimen CM 3018 , the type specimen of *A. louisae* . In 1936 , this was measured to be 21 @.@ 8 m (72 ft) , by measuring the vertebral column . Current estimates are similar , which find the individual was 21 ? 22 @.@ 8 m (69 ? 75 ft) long and had a mass of 16 @.@ 4 ? 22 @.@ 4 t (16 @.@ 1 ? 22 @.@ 0 long tons ; 18 @.@ 1 ? 24 @.@ 7 short tons) . A 2015 study that estimated the mass of volumetric models of *Dreadnoughtus* , *Apatosaurus* , and *Giraffatitan* estimates CM 3018 at 21 @.@ 8 ? 38 @.@ 2 t (21 @.@ 5 ? 37 @.@ 6 long tons ; 24 @.@ 0 ? 42 @.@ 1 short tons) , similar in mass to *Dreadnoughtus* . Past estimates have put the creature 's mass as high as 35 @.@ 0 t (34 @.@ 4 long tons ; 38 @.@ 6 short tons) . Some specimens of *A. ajax* (like OMNH 1670) represent individuals 11 ? 30 % longer , suggesting masses twice that of CM 3018 or 32 @.@ 7 ? 72 @.@ 6 t (32 @.@ 2 ? 71 @.@ 5 long tons ; 36 @.@ 0 ? 80 @.@ 0 short tons) , potentially rivalling the largest titanosaurs .

The skull is small in comparison with the size of the animal . The jaws are lined with spatulate (

chisel @-@ like) teeth suited to a herbivorous diet . The snout of Apatosaurus and similar diplodocoids are squared , with only Nigersaurus having a squarer skull . The braincase of Apatosaurus is well preserved in specimen BYU 17096 , which also preserved much of the skeleton . A phylogenetic analysis found that the braincase had a similar morphology to those of other diplodocoids . Some skulls of Apatosaurus have been found still in articulation with their teeth . Those teeth that have the enamel surface exposed do not show any scratches on the surface ; instead they display a sugary texture and little wear .

Like those of other sauropods , the neck vertebrae are deeply bifurcated ; they carried neural spines with a large trough in the middle , resulting in a wide , deep neck . The vertebral formula for the holotype of *A. louisae* is 15 cervicals , 10 dorsals , 5 sacals , and 82 caudals . The caudal vertebra number may vary , even within species . The cervical vertebrae of Apatosaurus and Brontosaurus are stouter and more robust than those of other diplodocids , were found to be most similar to Camarasaurus by Charles Whitney Gilmore . In addition , they support cervical ribs that extend farther towards the ground than in diplodocines , and have the vertebrae and ribs narrower towards the top of the neck , making the neck nearly triangular in cross @-@ section . In Apatosaurus *louisae* , the atlas @-@ axis complex of the first cervicals is nearly fused . The dorsal ribs are not fused or tightly attached to their vertebrae , instead being loosely articulated . Apatosaurus has ten dorsal ribs on either side of the body . The large neck was filled with an extensive system of weight @-@ saving air sacs . Apatosaurus , like its close relative Supersaurus , has neural tall spines , which make up more than half the height of the individual bones of its vertebrae . The shape of the tail is unusual for a diplodocid ; it is comparatively slender because of the rapidly decreasing height of the vertebral spines with increasing distance from the hips . Apatosaurus also had very long ribs compared to most other diplodocids , giving it an unusually deep chest . As in other diplodocids , the tail transformed into a whip @-@ like structure towards its end .

The limb bones are also very robust . Within Apatosaurinae , the scapula of Apatosaurus *louisae* is intermediate in morphology between those of *A. ajax* and Brontosaurus *excelsus* . The arm bones are stout , so the humerus of Apatosaurus resembles that of Camarasaurus , as well as Brontosaurus . However , the humeri of Brontosaurus and *A. ajax* are more similar to each other than they are to *A. louisae* . In 1936 , Charles Gilmore noted that previous reconstructions of Apatosaurus forelimbs erroneously proposed that the radius and ulna could cross ; in life they would have remained parallel . Apatosaurus had a single large claw on each forelimb , a feature shared by all sauropods more derived than Shunosaurus . The first three toes had claws on each hindlimb . The phalangeal formula is 2 @-@ 1 @-@ 1 @-@ 1 @-@ 1 , meaning the innermost finger (phalanx) on the forelimb has two bones and the next has one . The single manual claw bone (ungual) is slightly curved and squarely truncated on the anterior end . The pelvic girdle includes the robust ilia , and the fused (co @-@ ossified) pubes and ischia . The femora of Apatosaurus are very stout ; some of the most robust femora of any member of Sauropoda . The tibia and fibula bones are different from the slender bones of Diplodocus , but are nearly indistinguishable from those of Camarasaurus . The fibula is longer and more slender than the tibia . The foot of Apatosaurus has three claws on the innermost digits ; the digit formula is 3 @-@ 4 @-@ 5 @-@ 3 @-@ 2 . The first metatarsal is the stoutest , a feature shared among diplodocids .

= = Discovery and species = =

The name Apatosaurus *ajax* was coined in 1877 by Othniel Charles Marsh , Professor of Paleontology at Yale University , based on a nearly complete skeleton (holotype , YPM 1860) discovered the eastern foothills of the Rocky Mountains in Gunnison County , Colorado . The composite term Apatosaurus comes from the Greek words *apat?* (?????) / *apat?los* (?????????) meaning " deception " / " deceptive " , and *sauros* (?????) meaning " lizard " ; thus , " deceptive lizard " . Marsh gave it this name based on the chevron bones , which are dissimilar to those of other dinosaurs ; instead , the chevron bones of Apatosaurus showed similarities with those of mosasaurs . During excavation and transportation , the bones of the holotype skeleton were mixed

with those of another *Apatosaurus* individual originally described as *Atlantosaurus immanis* ; as a consequence , some elements cannot be ascribed to either specimen with confidence anymore . Marsh distinguished the new genus *Apatosaurus* from *Atlantosaurus* on the basis of the number of sacral vertebrae , with *Apatosaurus* possessing three and *Atlantosaurus* four . Two years later , Marsh announced the discovery of a larger and more complete specimen at Como Bluff , Wyoming . Marsh decided to give this specimen a new name , because conventions and the relative sparse fossil record at that time meant that features then used to distinguish genera and species have now been found to be more widespread among sauropods . He named the new species *Brontosaurus excelsus* . All specimens currently considered *Apatosaurus* were from the Morrison Formation , the location of the excavations of Marsh and his rival Edward Drinker Cope .

Another specimen , in American Museum of Natural History and under the specimen number 460 , which is occasionally assigned to *Apatosaurus* , is very complete ; only the head , feet , and sections of the tail are missing , and it was the first sauropod skeleton mounted . The specimen was found north of Medicine Bow , Wyoming in 1898 by Walter Granger , and took the entire summer to extract . To complete the mount , sauropod feet that were discovered at the same quarry and a tail fashioned to appear as Marsh believed it should ? which had too few vertebrae ? were added . In addition , a sculpted model of what the museum thought the skull of this massive creature might look like was made . This was not a delicate skull like that of *Diplodocus* ? which was later found to be more accurate ? but was based on " the biggest , thickest , strongest skull bones , lower jaws and tooth crowns from three different quarries " . These skulls were likely those of *Camarasaurus* , the only other sauropod for which good skull material was known at the time . The mount construction was overseen by Adam Hermann , who failed to find *Apatosaurus* skulls . Hermann was forced to sculpt a stand @-@ in skull by hand . Osborn said in a publication that the skull was " largely conjectural and based on that of *Morosaurus* " (now *Camarasaurus*) .

In 1903 , Elmer Riggs published a study that described a well @-@ preserved skeleton of a diplodocid from the Grand River Valley near Fruita , Colorado , Field Museum of Natural History specimen P25112 . Riggs thought that the deposits were similar in age to those of the Como Bluff in Wyoming , from which Marsh described *Brontosaurus* . Most of the skeleton was found , and after comparison with both *Brontosaurus* and *Apatosaurus ajax* , Riggs realized that the holotype of *A. ajax* was immature , and thus the features distinguishing the genera were not valid . Since *Apatosaurus* was the earlier name , *Brontosaurus* should be considered a junior synonym of *Apatosaurus* . Because of this , Riggs recombined *Brontosaurus excelsus* as *Apatosaurus excelsus* . Based on comparisons with other species proposed to belong to *Apatosaurus* , Riggs also determined that the Field Columbian Museum specimen was likely most similar to *A. excelsus* .

Despite Riggs ' publication , Henry Fairfield Osborn , who was a strong opponent of Marsh and his taxa , labeled the *Apatosaurus* mount of the American Museum of Natural History *Brontosaurus* . Because of this decision the name *Brontosaurus* was commonly used outside of scientific literature for what Riggs considered *Apatosaurus* , and the museum 's popularity meant that *Brontosaurus* became one of the best known dinosaurs , even though it was invalid throughout nearly all of the 20th and early 21st centuries .

It was not until 1909 that an *Apatosaurus* skull was found during the first expedition , led by Earl Douglass , to what would become the Carnegie Quarry at Dinosaur National Monument . The skull was found a short distance from a skeleton (specimen CM 3018) identified as the new species *Apatosaurus louisae* , named after Louise Carnegie , wife of Andrew Carnegie who funded field research to find complete dinosaur skeletons in the American West . The skull was designated CM 11162 ; it was very similar to the skull of *Diplodocus* . Another smaller skeleton of *A. louisae* was found nearby CM 11162 and CM 3018 . The skull was accepted as belonging to the *Apatosaurus* specimen by Douglass and Carnegie Museum director William H. Holland , although other scientists ? most notably Osborn ? rejected this identification . Holland defended his view in 1914 in an address to the Paleontological Society of America , yet he left the Carnegie Museum mount headless . While some thought Holland was attempting to avoid conflict with Osborn , others suspected Holland was waiting until an articulated skull and neck were found to confirm the association of the skull and skeleton . After Holland 's death in 1934 , museum staff placed a cast of

a *Camarasaurus* skull on the mount .

While most other museums were using cast or sculpted *Camarasaurus* skulls on *Apatosaurus* mounts , the Yale Peabody Museum decided to sculpt a skull based on the lower jaw of a *Camarasaurus* , with the cranium based on Marsh 's 1891 illustration of the skull . The skull also included forward @-@ pointing nasals ? something different to any dinosaur ? and fenestrae differing from the drawing and other skulls .

No *Apatosaurus* skull was mentioned in literature until the 1970s when John Stanton McIntosh and David Berman redescribed the skulls of *Diplodocus* and *Apatosaurus* . They found that though he never published his opinion , Holland was almost certainly correct , that *Apatosaurus* had a *Diplodocus* @-@ like skull . According to them , many skulls long thought to pertain to *Diplodocus* might instead be those of *Apatosaurus* . They reassigned multiple skulls to *Apatosaurus* based on associated and closely associated vertebrae . Even though they supported Holland , it was noted that *Apatosaurus* might have possessed a *Camarasaurus* @-@ like skull , based on a disarticulated *Camarasaurus* @-@ like tooth found at the precise site where an *Apatosaurus* specimen was found years before . On October 20 , 1979 , after the publications by McIntosh and Berman , the first true skull of *Apatosaurus* was mounted on a skeleton in a museum , that of the Carnegie . In 1998 , the Felch Quarry skull that Marsh included in his 1896 skeletal restoration was suggested to belong to *Brachiosaurus* instead . In 2011 , the first specimen of *Apatosaurus* where a skull was found articulated with its cervical vertebrae was described . This specimen , CMC VP 7180 , was found to differ in both skull and neck features from *A. louisae* , but shared many features of the cervical vertebrae with *A. ajax* . Another well @-@ preserved skull is Brigham Young University specimen 17096 , a well preserved skull and skeleton , with a preserved braincase . The specimen was found in Cactus Park Quarry of western Colorado .

Almost all modern paleontologists agreed with Riggs that the two dinosaurs should be classified together in a single genus . According to the rules of the ICZN (which governs the scientific names of animals) , the name *Apatosaurus* , having been published first , has priority as the official name ; *Brontosaurus* was considered a junior synonym and was therefore long discarded from formal use . Despite this , at least one paleontologist ? Robert T. Bakker ? argued in the 1990s that *A. ajax* and *A. excelsus* were in fact sufficiently distinct for the latter to merit a separate genus .

In 2015 Emanuel Tschopp , Octávio Mateus , and Roger Benson released a paper on diplodocoid systematics , and proposed that genera could be diagnosed by 13 differing characters , and species separated based on 6 . The minimum number for generic separation was chosen based on the fact that *A. ajax* and *A. louisae* differ in 12 characters , and *Diplodocus carnegiei* and *D. hallorum* differ in 11 characters . Thus , 13 characters were chosen to validate the separation of genera . The 6 differing features for specific separation were chosen by counting the number of differing features in separate specimens generally agreed to represent one species , with only one differing character in *D. carnegiei* and *A. louisae* , but five differing features in *B. excelsus* . Therefore , Tschopp et al. argued that *Apatosaurus excelsus* , originally classified as *Brontosaurus excelsus* , had enough morphological differences from other species of *Apatosaurus* that it warranted being reclassified as a separate genus again . The conclusion was based on a comparison of 477 morphological characteristics across 81 different dinosaur individuals . Among the many notable differences are the wider ? and presumably stronger ? neck of *Apatosaurus* species compared to *B. excelsus* . Other species previously assigned to *Apatosaurus* , such as *Elosaurus parvus* and *Eobrontosaurus yahnahpin* were also reclassified as *Brontosaurus* . Some features proposed to separate *Brontosaurus* from *Apatosaurus* include : posterior dorsal vertebrae with the centrum longer than wide ; the scapula rear to the acromial edge and the distal blade being excavated ; the acromial edge of the distal scapular blade bears a rounded expansion ; and the ratio of the proximodistal length to transverse breadth of the astragalus is 0 @. @ 55 or greater . Paleontologist Michael D 'Emic made a critique . Palaeontologist Donald Prothero criticized the mass media reaction to this study as superficial and premature , concluding :

Until someone has convincingly addressed the issue , I ? m going to put ? *Brontosaurus* ? in quotes and not follow the latest media fad , nor will I overrule Riggs (1903) and put the name in my books as a valid genus .

== Valid species ==

Multiple species of *Apatosaurus* have been designated from scant material . Marsh named as many species as he could , which resulted in many being based upon fragmentary and indistinguishable remains . In 2005 , Paul Upchurch and colleagues published a study that analyzed the species and specimen relationships of *Apatosaurus* . They found that *A. louisae* was the most basal species , followed by FMNH P25112 , and then a polytomy of *A. ajax* , *A. parvus* , and *A. excelsus* . Their analysis was revised and expanded with many additional diplodocid specimens in 2015 , which resolved the relationships of *Apatosaurus* slightly differently , and also supported separating *Brontosaurus* from *Apatosaurus* .

Apatosaurus ajax was named by Marsh in 1877 after Ajax , a hero from Greek mythology . Marsh designated the incomplete , juvenile skeleton YPM 1860 as its holotype . The species is less studied than *Brontosaurus* and *A. louisae* , especially because of the incomplete nature of the holotype . In 2005 , many specimens in addition to the holotype were found assignable to *A. ajax* , YPM 1840 , NSMT @-@ PV 20375 , YPM 1861 , and AMNH 460 . The specimens date from the late Kimmeridgian to the early Tithonian ages . In 2015 , only the *A. ajax* holotype YPM 1860 assigned to the species , with AMNH 460 found either to be within *Brontosaurus* , or potentially its own taxon . However , YPM 1861 and NSMT @-@ PV 20375 only differed in a few characteristics , and cannot be distinguished specifically or generically from *A. ajax* . YPM 1861 is the holotype of " *Atlantosaurus* " *immanis* , which means it might be a junior synonym of *A. ajax* .

Apatosaurus louisae was named by Holland in 1916 , being first known from a partial skeleton that was found in Utah . The holotype is CM 3018 , with referred specimens including CM 3378 , CM 11162 , and LACM 52844 . The former two consist of a vertebral column ; the latter two consist of a skull and a nearly complete skeleton , respectively . Its specimens all come from the late Kimmeridgian of Dinosaur National Monument . In 2015 , Tschopp et al. found the type specimen of *Apatosaurus laticollis* to nest closely with CM 3018 , meaning the former is likely a junior synonym of *A. louisae* .

The cladogram below is the result of an analysis by Tschopp , Mateus , and Benson (2015) . The authors analyzed most diplodocid type specimens separately to deduce which specimen belonged to which species and genus .

== Reassigned species ==

Apatosaurus grandis was named in 1877 by Marsh in the article that described *A. ajax* . It was briefly described , figured , and diagnosed . Marsh later mentioned it was only provisionally assigned to *Apatosaurus* when he reassigned it to his new genus *Morosaurus* in 1878 . Since *Morvosaurus* has been considered a synonym of *Camarasaurus* , *C. grandis* is the oldest @-@ named species of the latter genus .

Apatosaurus excelsus was the original type species of *Brontosaurus* , first named by Marsh in 1879 . Elmer Riggs reclassified *Brontosaurus* as a synonym of *Apatosaurus* in 1903 , transferring the species *B. excelsus* to *A. excelsus* . In 2015 , Tschopp , Mateus , and Benson argued that the species was distinct enough to be placed in its own genus so they reclassified it back into *Brontosaurus* .

Apatosaurus parvus , first described from a juvenile specimen as *Elosaurus* in 1902 by Peterson and Gilmore , was reassigned to *Apatosaurus* in 1994 , and then to *Brontosaurus* in 2015 . Multiple other , more mature specimens were assigned to it following the 2015 study .

Apatosaurus minimus was originally described as a specimen of *Brontosaurus* sp. in 1904 by Osborn . In 1917 , Henry Mook named it as its own species , *A. minimus* , for a pair of ilia and their sacrum . In 2012 , Mike P. Taylor and Matt J. Wedel published a short abstract describing the material of " *A.* *minimus* , finding it hard @-@ to @-@ place among either *Diplodocoidea* or *Macronaria* . While it was placed with *Saltasaurus* in a phylogenetic analysis , it was thought to represent instead some form with convergent features from many groups . The study of Tschopp et

al. did find that a camarasaurid position for the taxon was supported , but noted that the position of the taxon was found to be highly variable and there was no clearly more likely position .

Apatosaurus alenquerensis was named in 1957 by Albert @-@ Félix de Lapparent and Georges Zbyweski . It was based on post cranial material from Portugal . In 1990 , this material was reassigned to *Camarasaurus* , but in 1998 it was given its own genus , *Lourinhasaurus* . This was further supported by the findings of Tschopp et al. in 2015 , where *Lourinhasaurus* was found to be sister to *Camarasaurus* and other camarasaurids .

Apatosaurus yahnahpin was named by James Filla and Patrick Redman in 1994 . Bakker made *A. yahnahpin* the type species of a new genus , *Eobrontosaurus* in 1998 , and Tschopp reclassified it as *Brontosaurus yahnahpin* in 2015 .

= = Classification = =

Apatosaurus is a member of the family Diplodocidae , a clade of gigantic sauropod dinosaurs . The family includes some of the longest creatures ever to walk the earth , including *Diplodocus* , *Supersaurus* , and *Barosaurus* . *Apatosaurus* is sometimes classified in the subfamily *Apatosaurinae* , which may also include *Suuwassea* , *Supersaurus* , and *Brontosaurus* . Othniel Charles Marsh described *Apatosaurus* as allied to *Atlantosaurus* within the now @-@ defunct group *Atlantosauridae* . In 1878 , Marsh raised his family to the rank of suborder , including *Apatosaurus* , *Atlantosaurus* , *Morosaurus* (= *Camarasaurus*) and *Diplodocus* . He classified this group within *Sauropoda* , a group he erected in the same study . In 1903 , Elmer S. Riggs said the name *Sauropoda* would be a junior synonym of earlier names ; he grouped *Apatosaurus* within *Opisthocoelia* . *Sauropoda* is still used as the group name . In 2011 , John Whitlock published a study that placed *Apatosaurus* a more basal diplodocid , sometimes less basal than *Supersaurus* .

Cladogram of the Diplodocidae after Tschopp , Mateus , and Benson (2015) .

= = Palaeobiology = =

It was believed throughout the 19th and early 20th centuries that sauropods like *Apatosaurus* were too massive to support their own weight on dry land . It was theorized that they lived partly submerged in water , perhaps in swamps . Recent findings do not support this ; sauropods are now thought to have been fully terrestrial animals . A study of diplodocid snouts showed that the square snout , large proportion of pits , and fine , subparallel scratches of the teeth of *Apatosaurus* suggests it was a ground @-@ height , nonselective browser . It may have eaten ferns , cycadeoids , seed ferns , horsetails , and algae . Stevens and Parish (2005) speculate that these sauropods fed from riverbanks on submerged water plants .

A 2015 study of the necks of *Apatosaurus* and *Brontosaurus* found many differences between them and other diplodocids , and that these variations may have shown that the necks of *Apatosaurus* and *Brontosaurus* were used for intraspecific combat . Various uses for the single claw on the forelimb of sauropods have been proposed . One suggestion is that they were used for defense , but their shape and size makes this unlikely . It was also possible they were for feeding , but the most probable use for the claw was grasping objects such as tree trunks when rearing .

Trackways of sauropods like *Apatosaurus* show that they may have had a range of around 25 ? 40 km (16 ? 25 mi) per day , and they could potentially reach a top speed of 20 ? 30 km (12 ? 19 mi) per hour . The slow locomotion of sauropods may be due to their minimal muscling , or to recoil after strides . A trackway of a juvenile has led some to believe that they were capable of bipedalism , though this is disputed .

= = = Neck posture = = =

Diplodocids like *Apatosaurus* are often portrayed with their necks held high up in the air , allowing them to browse on tall trees . Some studies state diplodocid necks were less flexible than previously believed because the structure of the neck vertebrae would not have allowed the neck to bend far

upwards , and that sauropods like Apatosaurus were adapted to low browsing or ground feeding .

Other studies by Taylor find that all tetrapods appear to hold their necks at the maximum possible vertical extension when in a normal , alert posture ; they argue the same would hold true for sauropods barring any unknown , unique characteristics that set the soft tissue anatomy of their necks apart from that of other animals . Apatosaurus , like Diplodocus , would have held its neck angled upwards with the head pointing downwards in a resting posture . Kent Stevens and Michael Parrish (1999 and 2005) state Apatosaurus had a great feeding range ; its neck could bend into a U @-@ shape laterally . The neck 's range of movement would have also allowed the head to feed at the level of the feet .

Matthew Cobley et al . (2013) dispute this , finding that large muscles and cartilage would have limited movement of the neck . They state the feeding ranges for sauropods like Diplodocus were smaller than previously believed and the animals may have had to move their whole bodies around to better access areas where they could browse vegetation . As such , they might have spent more time foraging to meet their minimum energy needs . The conclusions of Cobley et al. are disputed by Taylor , who analyzed the amount and positioning of intervertebral cartilage to determine the flexibility of the neck of Apatosaurus and Diplodocus . He found that the neck of Apatosaurus was very flexible .

= = = Physiology = = =

Given the large body mass and long neck of sauropods like Apatosaurus , physiologists have encountered problems determining how these animals breathed . Beginning with the assumption that like crocodilians , Apatosaurus did not have a diaphragm , the dead @-@ space volume (the amount of unused air remaining in the mouth , trachea and air tubes after each breath) has been estimated at about 0 @. @ 184 m³ (184 l) for a 30 t (30 long tons ; 33 short tons) specimen . Paladino calculates its tidal volume (the amount of air moved in or out during a single breath) at 0 @. @ 904 m³ (904 l) with an avian respiratory system , 0 @. @ 225 m³ (225 l) if mammalian , and 0 @. @ 019 m³ (19 l) if reptilian .

On this basis , its respiratory system would likely have been parabronchi , with multiple pulmonary air sacs as in avian lungs , and a flow @-@ through lung . An avian respiratory system would need a lung volume of about 0 @. @ 60 m³ (600 l) compared with a mammalian requirement of 2 @. @ 95 m³ (2 @, @ 950 l) , which would exceed the space available . The overall thoracic volume of Apatosaurus has been estimated at 1 @. @ 7 m³ (1 @, @ 700 l) , allowing for a 0 @. @ 50 m³ (500 l) , four @-@ chambered heart and a 0 @. @ 90 m³ (900 l) lung capacity . That would allow about 0 @. @ 30 m³ (300 l) for the necessary tissue . Evidence for the avian system in Apatosaurus and other sauropods is also present in the pneumaticity of the vertebrae . Though this plays a role in reducing the weight of the animal , Wedel (2003) states they are also likely connected to air sacs , as in birds .

James Spotila et al . (1991) concludes that the large body size of sauropods would have made them unable to maintain high metabolic rates because they would not be able to release enough heat . They assumed sauropods had a reptilian respiratory system . Wedel says that an avian system would have allowed it to dump more heat . Some scientists state that the heart would have had trouble sustaining sufficient blood pressure to oxygenate the brain . Others suggest that the near @-@ horizontal posture of the head and neck would have eliminated the problem of supplying blood to the brain because it would not have been elevated .

James Farlow (1987) calculates that an Apatosaurus @-@ sized dinosaur about 35 t (34 long tons ; 39 short tons) would have possessed 5 @. @ 7 t (5 @. @ 6 long tons ; 6 @. @ 3 short tons) of fermentation contents . Assuming Apatosaurus had an avian respiratory system and a reptilian resting @-@ metabolism , Frank Paladino et al . (1997) estimate the animal would need to consume only about 262 litres (58 imp gal ; 69 US gal) of water per day .

= = = Growth = = =

A 1999 microscopic study of Apatosaurus and Brontosaurus bones concluded the animals grew rapidly when young and reached near adult sizes in about 10 years . In 2008 , a study on the growth rates of sauropods was published by Thomas Lehman and Holly Woodward . They said that by using growth lines and length to mass ratios , Apatosaurus would have grown to 25 t (25 long tons ; 28 short tons) in 15 years , with growth peaking at 5 @, @ 000 kg (11 @, @ 000 lb) in a single year . An alternative method , using limb length and body mass , found Apatosaurus grew 520 kg (1 @, @ 150 lb) per year , and reached its full mass before it was about 70 years old . These estimates have been called unreliable because the calculation methods are not sound ; old growth lines would have been obliterated by bone remodelling . One of the first identified growth factors of Apatosaurus was the number of sacral vertebrae , which increased to five by the time of the creatures ' maturity . This was first noted in 1903 and again in 1936 .

Long bone histology enables researchers to estimate the age that a specific individual reached . A study by Eva Griebeler et al . (2013) examined long bone histological data and concluded the Apatosaurus sp . SMA 0014 weighed 20 @, @ 206 kg (22 @. @ 3 short tons) , reached sexual maturity at 21 years , and died aged 28 . The same growth model indicated Apatosaurus sp . BYU 601 ? 17328 weighed 18 @, @ 178 kg (20 @. @ 0 short tons) , reached sexual maturity at 19 years , and died aged 31 .

== = Juveniles == = =

Compared with most sauropods , a relatively large amount of juvenile material is known from Apatosaurus . Multiple specimens in the OMNH are from juveniles of an undetermined species of Apatosaurus ; this material includes partial shoulder and pelvic girdles , some vertebrae , and limb bones . OMNH juvenile material is from at least two different age groups and based on overlapping bones likely comes from more than three individuals . The specimens exhibit features that distinguish Apatosaurus from its relatives , and thus likely belong to the genus . Juvenile sauropods tend to have proportionally shorter necks and tails , and a more pronounced forelimb @-@ hindlimb disparity than in adults .

== = Tail == =

An article published in 1997 reported research of the mechanics of Apatosaurus tails by Nathan Myhrvold and paleontologist Philip J. Currie . Myhrvold carried out a computer simulation of the tail , which in diplodocids like Apatosaurus was a very long , tapering structure resembling a bullwhip . This computer modeling suggested sauropods were capable of producing a whiplike cracking sound of over 200 decibels , comparable to the volume of a cannon being fired .

A pathology has been identified on the tail of Apatosaurus , caused by a growth defect . Two caudal vertebrae are seamlessly fused along the entire articulating surface of the bone , including the arches of the neural spines . This defect might have been caused by the lack or inhibition of the substance that forms intervertebral disks or joints . It has been proposed that the whips could have been used in combat , but the tails of diplodocids were quite light and narrow compared to Shunosaurus and mamenchisaurids , and thus to injure another animal with the tail would severely injure the tail itself .

== = Paleoecology == =

The Morrison Formation is a sequence of shallow marine and alluvial sediments which , according to radiometric dating , dates from between 156 @. @ 3 mya at its base , and 146 @. @ 8 mya at the top , placing it in the late Oxfordian , Kimmeridgian , and early Tithonian stages of the Late Jurassic period . This formation is interpreted as originating in a locally semiarid environment with distinct wet and dry seasons . The Morrison Basin , where dinosaurs lived , stretched from New Mexico to Alberta and Saskatchewan ; it was formed when the precursors to the Front Range of the Rocky Mountains started pushing up to the west . The deposits from their east @-@ facing drainage basins

were carried by streams and rivers and deposited in swampy lowlands , lakes , river channels , and floodplains . This formation is similar in age to the Lourinhã Formation in Portugal and the Tendaguru Formation in Tanzania .

Apatosaurus was the second @-@ commonest sauropod in the Morrison Formation ecosystem , after Camarasaurus . Apatosaurus may have been more solitary than other Morrison Formation dinosaurs . Supersaurus has a greater total length and is the greatest of all sauropods from the Morrison Formation . Apatosaurus fossils have only been found in the upper levels of the formation . Those of Apatosaurus ajax are known exclusively from the upper Brushy Basin Member , about 152 ? 151 mya . A. louisae fossils are rare , known only from one site in the upper Brushy Basin Member ; they date to the late Kimmeridgian stage , about 151 mya . Additional Apatosaurus remains are known from similarly aged or slightly younger rocks , but they have not been identified as any particular species , and thus may instead belong to Brontosaurus .

The Morrison Formation records a time when the local environment was dominated by gigantic sauropod dinosaurs . Dinosaurs known from the Morrison Formation include the theropods Allosaurus , Ceratosaurus , Ornitholestes , Saurophaganax and Torvosaurus ; the sauropods Brontosaurus , Brachiosaurus , Camarasaurus , and Diplodocus ; and the ornithischians Camptosaurus , Dryosaurus , and Stegosaurus . Apatosaurus is commonly found at the same sites as Allosaurus , Camarasaurus , Diplodocus , and Stegosaurus . Allosaurus accounted for 70 ? 75 % of theropod specimens and was at the top trophic level of the Morrison food web . Many of the dinosaurs of the Morrison Formation are of the same genera as those seen in Portuguese rocks of the Lourinhã Formation ? mainly Allosaurus , Ceratosaurus , and Torvosaurus ? or have a close counterpart ? Brachiosaurus and Lusotitan , Camptosaurus and Draconyx , Apatosaurus and Dinheirosaurus . Other vertebrates that are known to have shared this paleo @-@ environment include ray @-@ finned fishes , frogs , salamanders , turtles , sphenodonts , lizards , terrestrial and aquatic crocodylomorphans , and several species of pterosaur . Shells of bivalves and aquatic snails are also common . The flora of the period has been evidenced in fossils of green algae , fungi , mosses , horsetails , cycads , ginkgoes , and several families of conifers . Vegetation varied from river @-@ lining forests of tree ferns and ferns (gallery forests) , to fern savannas with occasional trees such as the Araucaria @-@ like conifer Brachyphyllum .