

= Amphicoelias =

Amphicoelias (/ ˈæmf??si?li?s / , meaning " biconcave " , from the Greek ????? , amphi : " on both sides " , and ?????? , koilos : " hollow , concave ") is a genus of herbivorous sauropod dinosaur that is probably synonymous with the genus Diplodocus . It includes what has sometimes been estimated to be the largest dinosaur specimen ever discovered , originally named " A. fragillimus " . Based on surviving descriptions of a single fossil bone , scientists had over the years estimated A. fragillimus to have been the longest known animal at 58 metres (190 ft) in length , with potentially a mass of up to 122 @. @ 4 tonnes (135 short tons) . However , because the only fossil remains were lost at some point after being studied and described in the 1870s , evidence survived only in drawings and field notes . More recent analysis of the surviving evidence , and the biological plausibility of such a large land animal , has suggested that the enormous size of this animal were over @-@ estimates due partly to typographical errors in the original 1878 description .

= = Description = =

The type species of Amphicoelias , A. altus , was named by paleontologist Edward Drinker Cope in December 1877 (though not published until 1878) for an incomplete skeleton consisting of two vertebrae , a pubis (hip bone) , and a femur (upper leg bone) . Cope also named a second species , A. fragillimus , in the same paper . However , all subsequent researchers have considered A. fragillimus to be a synonym of A. altus . Even by 1881 however , it was recognized that A. altus could not be distinguished from other genera , as the features described by Cope were misinterpreted and are widespread . In 1921 , Osborn and Mook assigned additional bones to A. altus ? a scapula (shoulder blade) , a coracoid (shoulder bone) , an ulna (lower arm bone) , and a tooth . Henry Fairfield Osborn and Charles Craig Mook noted the overall close similarity between Amphicoelias and Diplodocus , as well as a few key differences , such as proportionally longer forelimbs in Amphicoelias than in Diplodocus . The dentition of Amphicoelias is homodont . Its teeth are shaped like long slender cylindrical rods , are spaced apart and project forward towards the front of the mouth . The femur of Amphicoelias is unusually long , slender , and round in cross section ; while this roundness was once thought to be another distinguishing characteristic of Amphicoelias , it has since been found in some specimens of Diplodocus as well . A. altus was also similar in size to Diplodocus , estimated to be about 25 m (82 ft) long . While most scientists have used these details to distinguish Amphicoelias and Diplodocus as separate genera , at least one has suggested that Amphicoelias is probably the senior synonym of Diplodocus .

= = History = =

Amphicoelias fragillimus was collected by Oramel Lucas , a fossil collector employed by E. D. Cope , shortly after he was hired by Cope in 1877 . Lucas discovered a partial vertebra (the neural arch and spine) of the new sauropod species in Garden Park , north of Cañon City , Colorado , close to the quarry that yielded Camarasaurus . The vertebra was in poor condition , but astonishingly large , measuring 1 @. @ 5 metres (4 @. @ 9 ft) up to 2 @. @ 7 metres (8 @. @ 9 ft) in height . Lucas shipped the specimen to Cope in the spring or early summer of 1878 , and Cope published it as the holotype specimen (catalogue number AMNH 5777) of a new species , A. fragillimus , that August . The name derives from the Latin fragillimus (" very fragile ") , referring to the delicateness of the bone produced by very thin laminae (vertebral walls) . As revealed in Cope 's notebooks , which he recorded based on Lucas ' report on excavation site locations in 1879 , the specimen came from a hill south of the Camarasaurus quarry now known as " Cope 's Nipple . " While Cope originally wrote that the site belonged to the Dakota Formation (mid @-@ Cretaceous in age) , the presence of dinosaurs such as Camarasaurus in the same rocks indicates that they probably belong to the Morrison Formation , which places the age of the site at 150 million years ago in the late Jurassic period , specifically the Tithonian age .

The gigantic bones attributed to A. fragillimus have often been ignored in summaries of the largest

dinosaurs partly because , according to various subsequent reports , the whereabouts of both the vertebra and the femur are unknown , and all attempts to locate them have failed . Carpenter , in 2006 , presented a possible scenario for the disappearance of the *A. fragillimus* specimens . As Cope noted in his description , the neural arch bone material was very fragile , and techniques to harden and preserve fossil bone had not yet been invented (Cope 's rival , paleontologist O.C. Marsh , was the first to use such chemicals , in the early 1880s) . Carpenter observed that the fossil bones known from the *A. fragillimus* quarry would have been preserved in deeply weathered mudstone , which tends to crumble easily and fragment into small , irregular cubes . Therefore , the bone may have crumbled badly and been discarded by someone at the American Museum of Natural History (possibly even by Cope himself) soon after he illustrated it in rear view for his paper . Carpenter suggested that this may explain why Cope drew the vertebra in only one view , rather than from multiple angles as he did for his other discoveries .

In 1994 , an attempt was made to relocate the original quarry where *A. fragillimus* and other species had been found , using ground @-@ penetrating radar in an attempt to image bones still buried in the ground . This attempt failed because the fossilized mudstone bones were the same density as the surrounding rock , making it impossible to differentiate the two . A study of the local topography also showed that the fossil @-@ bearing rock strata was severely eroded , and probably was so at the time Lucas made his discovery of *A. fragillimus* , indicating that a majority of the skeleton was gone by the time the vertebra and femur were recovered .

Cope 's description of *A. fragillimus* has been met with skepticism , with some researchers noting that there were typographical errors in his measurements . For example , the measurement units are given in (obviously incorrect) centimeters rather than millimeters . Carpenter argued that there is every reason to take Cope at his word , noting that the paleontologist 's reputation was at stake . The discovery took place during the Bone Wars , and Cope 's rival Marsh , who was " ever ready to humiliate " Cope , never called the claims into question . Marsh was known to have employed spies to monitor Cope 's discoveries , and may have even had confirmation of the enormous size of the *Amphicoelias fragillimus* bones . Paleontologists Henry Fairfield Osborn and C.C. Mook in 1921 , as well as John S. McIntosh in 1998 , also accepted Cope 's data without question in published reviews . In 2015 , Woodruff and Foster published an analysis of the evidence and circumstances surrounding the publication and interpretation of *A. fragillimus* .

= = Size = =

Producing an estimate of the complete size of *A. fragillimus* requires scaling the bones of better @-@ known species of diplodocid (a family of extremely long and slender sauropods) in the assumption that their relative proportions were similar . In his original paper , Cope did this by speculating on the size of a hypothetical *A. fragillimus* femur (upper leg bone) . Cope noticed that in other sauropod dinosaurs , specifically *A. altus* and *Camarasaurus supremus* , the femora were always twice as tall as the tallest dorsal vertebra , and estimated the size of an *A. fragillimus* femur to be 12 ft (3 @.@ 6 m) tall .

In 1994 , using the related *Diplodocus* as a reference , Gregory S. Paul estimated a femur length of 3 @.@ 1 to 4 metres (10 to 13 ft) for *A. fragillimus* . The 2006 re @-@ evaluation of *A. fragillimus* by Ken Carpenter also used *Diplodocus* as a scale guide , finding a femur height of 4 @.@ 3 to 4 @.@ 6 metres (14 to 15 ft) . Carpenter went on to estimate the complete size of *A. fragillimus* , though he cautioned that relative proportions in diplodocids could vary from species to species . Assuming the same proportions as the well @-@ known *Diplodocus* , Carpenter presented an estimated total length of 58 m (190 ft) , which he noted fell within the range presented by Paul in 1994 (40 to 60 metres (130 to 200 ft)) . Carpenter pointed out that even the lowest length estimates for *A. fragillimus* were higher than those for other giant sauropods , such as the diplodocid *Supersaurus* (32 @.@ 5 metres (107 ft)) , the brachiosaurid *Sauroposeidon* (34 metres (112 ft)) , and the titanosaur *Argentinosaurus* (30 metres (98 ft)) . Carpenter presented more speculative , specific proportions for *A. fragillimus* (again , based on a scaled @-@ up *Diplodocus*) , including a neck length of 16 @.@ 75 metres (55 @.@ 0 ft) , a body length of 9 @.@ 25 metres (30 @.@ 3 ft

) , and a tail length of 32 metres (105 ft) . He estimated the total forelimb height at 5 @. @ 75 metres (18 @. @ 9 ft) and hind limb height at 7 @. @ 5 metres (25 ft) , and the overall height (at the highest point on the back) at 9 @. @ 25 metres (30 @. @ 3 ft) . By comparison the blue whale , which is on average the longest living creature , reaches 30 metres (98 ft) in length .

While *A. fragillimus* was relatively thin , its enormous size still made it very massive . Weight is much more difficult to determine than length in sauropods , as the more complex equations needed are prone to greater margins of error based on smaller variations in the overall proportions of the animal . Carpenter used Paul 's 1994 estimate of the mass of *Diplodocus carnegii* (11 @. @ 5 metric tons (11 @. @ 3 long tons ; 12 @. @ 7 short tons)) to speculate that *A. fragillimus* could have weighed up to 122 @. @ 4 metric tons (120 @. @ 5 long tons ; 134 @. @ 9 short tons) . The heaviest blue whale on record weighed about 190 metric tons (190 long tons ; 210 short tons) , and the heaviest dinosaur known from reasonably good remains , *Argentinosaurus* , weighed 80 to 100 metric tons (79 to 98 long tons ; 88 to 110 short tons) , although if the size estimates can be validated , it could still be lighter than *Bruhathkayosaurus* , which has been estimated to have weighed 126 metric tons (124 long tons ; 139 short tons) , but is also known from highly fragmentary remains .

Other unpublished estimates have appeared online . A paleoartist on DeviantArt estimated the length of *A. fragillimus* to be around 73 m (240 ft) , based on a linear scaling of a 26 @. @ 25 meter long , 11 @. @ 5 tonne *Diplodocus* , assuming that *A. fragillimus* was 2 @. @ 79 times larger in linear dimension . In 2010 , Mike Taylor addressed the issue of *A. fragillimus* 's size on the blog SV @- @ POW (Sauropod Vertebrae Picture of the Week) . Based on comparisons to *A. altus* and to *Diplodocus* , he estimated that it may have been around 49 m (161 ft) long and 78 @. @ 5 tonnes . However , he concluded with the disclaimer that it is impossible to determine with any degree of certainty at all how large *A. fragillimus* was in reality because of the lack of accurate information .

= = Classification and species = =

Edward Drinker Cope described his finds in two 1878 issues of the *American Naturalist* , and assigned them to the new genus *Amphicoelias* . He placed it in a unique family , *Amphicoeliidae* , though this is now considered a *nomen oblitum* (forgotten name) . The genus is usually assigned to the family *Diplodocidae* , though some modern analyses have found it at the base of the larger group *Diplodocoidea* or as a *diplodocid incertae sedis* (uncertain placement) . The first named species in the genus , *Amphicoelias altus* (holotype specimen AMHD 5764) , was discovered by Cope in 1877 . But while it is only represented by a partial skeleton , there are enough diagnostic characteristics to provisionally define the genus . *A. altus* is known from better remains , but is smaller than *A. fragillimus* . Cope also named a second species in 1878 : *Amphicoelias latus* .

The third named *Amphicoelias* species , *A. fragillimus* , was known only from a single , incomplete 1 @. @ 5 m tall neural arch (the part of a vertebra with spines and processes) , either last or second to last in the series of back vertebrae , D (dorsal) 10 or D9 . Based only on an illustration published in 1878 , this vertebra would have measured 2 @. @ 7 metres (8 @. @ 9 ft) tall in life . However , it has been argued that the scale bar in the published description contained a typographical error , and the fossil vertebra was in fact only 1 @. @ 38 metres (4 @. @ 5 ft) tall . In addition to this vertebra , Cope 's field notes contain an entry for an " [i] mmense distal end of femur ? , located only a few tens of meters away from the giant vertebra . It is likely that this undescribed leg bone belonged to the same individual animal as the neural spine .

In 2010 , a monograph was made available , but not formally published , by Henry Galiano and Raimund Albersdorfer in which they referred a fourth species to *Amphicoelias* , as " *A. brontodiplodocus* " based on several complete specimens found in the Dana Quarry of Big Horn Basin , Wyoming and held in a private collection . The specific name referred to their hypothesis based on these specimens that nearly all Morrison diplodocid species are either growth stages or represent sexual dimorphism among members of the genus *Amphicoelias* , but this analysis has been met with skepticism and the publication itself has been disclaimed by its lead author , explaining that it is " obviously a drafted manuscript complete with typos , etc . , and not a final

paper . In fact , no printing or distribution has been attempted " .

Osborn and Mook , in 1921 , provisionally synonymized the three species , sinking *A. latus* into *Camarasaurus supremus* , and suggesting also that *A. fragillimus* is just a very large individual of *A. altus* , a position which most subsequent studies , including McIntosh 1998 , Foster (2007) , and Woodruff and Foster (2015) have agreed with . Carpenter (2006) disagreed about the synonymy of *A. altus* and *A. fragillimus* , however , citing numerous differences in the construction of the vertebra also noted by Cope , and suggested these differences are enough to warrant a separate species or even a separate genus for *A. fragillimus* . However , he went on to caution that the validity of *A. fragillimus* as a separate species is nearly impossible to determine without the original specimen to study . Although *Amphicoelias latus* is clearly not *Amphicoelias* , it is probably synonymous with *Camarasaurus grandis* rather than *C. supremus* because it was found lower in the Morrison Formation and the deeply concave articular faces on the caudal vertebrae are more consistent with *C. grandis* .

In 2007 , John Foster suggested that the differences usually cited to differentiate *Amphicoelias altus* from the more well known *Diplodocus* are not significant and may be due to individual variation . Foster argued that *Amphicoelias* is probably the senior synonym of *Diplodocus* , and that if further research bears this out , the familiar name *Diplodocus* would need to be abandoned in favor of *Amphicoelias* , as was the case with *Brontosaurus* and its senior synonym *Apatosaurus* . In 2015 , Woodruff and Foster reiterated this conclusion , stating that there is only one species of *Amphicoelias* and that it could be referred to *Diplodocus* as *Diplodocus altus* . They considered the name *Amphicoelias* to be a *nomen oblitum* . It has also been hypothesized that *Amphicoelias* should be considered an *apatosaurine* , and therefore should be placed in the subfamily *Apatosaurinae* .

The following cladogram of the *Diplodocidae* after Tschopp , Mateus , and Benson (2015) instead shows *A. altus* outside *Diplodocinae* .

= = Paleobiology = =

In his 2006 re @-@ evaluation , Carpenter examined the paleobiology of giant sauropods , including *Amphicoelias* , and addresses the question of why this group attained such a huge size . He pointed out that gigantic sizes were reached early in sauropod evolution , with very large sized species present as early as the late Triassic Period , and concluded that whatever evolutionary pressure caused large size was present from the early origins of the group . Carpenter cited several studies of giant mammalian herbivores , such as elephants and rhinoceros , which showed that larger size in plant @-@ eating animals leads to greater efficiency in digesting food . Since larger animals have longer digestive systems , food is kept in digestion for significantly longer periods of time , allowing large animals to survive on lower @-@ quality food sources . This is especially true of animals with a large number of ' fermentation chambers ' along the intestine which allow microbes to accumulate and ferment plant material , aiding digestion . Throughout their evolutionary history , sauropod dinosaurs were found primarily in semi @-@ arid , seasonally dry environments , with a corresponding seasonal drop in the quality of food during the dry season . The environment of *Amphicoelias* was essentially a savanna , similar to the arid environments in which modern giant herbivores are found , supporting the idea that poor @-@ quality food in an arid environment promotes the evolution of giant herbivores . Carpenter argued that other benefits of large size , such as relative immunity from predators , lower energy expenditure , and longer life span , are probably secondary advantages .

The Morrison Formation environment in which *Amphicoelias* lived would have resembled a modern savanna , though since grass did not appear until the Late Cretaceous , ferns were probably the dominant plant and main food source for *Amphicoelias* . Though Engelmann et al . (2004) dismissed ferns as a sauropod food source due to their relatively low caloric content , Carpenter argued that the sauropod digestive system , well adapted to handle low @-@ quality food , allows for the consumption of ferns as a large part of the sauropod diet . Carpenter also noted that the occasional presence of large petrified logs indicate the presence of 20 ? 30 m (66 ? 98 ft) tall trees , which would seem to conflict with the savanna comparison . However , the trees are rare , and

since tall trees require more water than the savanna environment could generally provide , they probably existed in narrow tracts or " gallery forests " along rivers and gulleys where water could accumulate . Carpenter speculated that giant herbivores like *Amphicoelias* may have used the shade of the gallery forests to stay cool during the day , and done most of their feeding on the open savanna at night .