The fragile legacy of *Amphicoelias fragillimus* (Dinosauria: Sauropoda; Morrison Formation – latest Jurassic)

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Key words: Amphicoelias fragillimus, E.D. Cope, sauropod, gigantism.

Abstract. In the summer of 1878, American paleontologist Edward Drinker Cope published the discovery of a sauropod dinosaur that he named *Amphicoelias fragillimus*. What distinguishes *A. fragillimus* in the annals of paleontology is the immense magnitude of the skeletal material. The single incomplete dorsal vertebra as reported by Cope was a meter and a half in height, which when fully reconstructed, would make *A. fragillimus* the largest vertebrate ever. After this initial description Cope never mentioned *A. fragillimus* in any of his scientific works for the remainder of his life. More than four decades after its description, a scientific survey at the American Museum of Natural History dedicated to the sauropods collected by Cope failed to locate the remains or whereabouts of *A. fragillimus*. For nearly a century the remains have yet to resurface. The enormous size of the specimen has generally been accepted despite being well beyond the size of even the largest sauropods known from verifiable fossil material (*e.g. Argentinosaurus*). By deciphering the ontogenetic change of Diplodocoidea vertebrae, the science of gigantism, and Cope's own mannerisms, we conclude that the reported size of *A. fragillimus* is most likely an extreme over-estimation.

INTRODUCTION

Described by Edward Drinker Cope in 1878, the holotype (and only) specimen of *A. fragillimus* consisted only of a distal end of a femur and a partial posterior dorsal neural arch and spine. What makes *A. fragillimus* truly unique in all of dinosaurian paleontology is the reported immense size of the material. As reported by Cope, the fragmentary posterior dorsal vertebra of *A. fragillimus* was 1.5 meters tall, which when reconstructed resulted in the complete dorsal vertebra being at least 1.83 meters tall. Later studies based general proportions of *A. fragillimus* on those of *Diplodocus*, resulting in body length estimates of 58–60 meters (Paul, 1994; Carpenter, 2006). Since Cope's report of *A. fragillimus*, all other diplodocoids, sauropodomorphs, and all other dino-

saurs pale in comparative size; thus *A. fragillimus* could be the largest dinosaur, and largest vertebrate in Earth's history (the Blue Whale being approximately 29 meters long [Reilly *et al.*, 2008], Fig. 1).

Surviving correspondence and journal entries between Cope and the collector O. Lucas address the presence and quarry location of *A. fragillimus* (McIntosh, 1998; Monaco, 1998; Carpenter, 2006) prior to Cope's 1878 formal description. However, at some point between Cope's 1878 description and Osborn and Mook's monograph on the sauropods of Cope in 1921, the *A. fragillimus* holotype material disappeared. This material was assigned an American Museum of Natural History collections number when the AMNH acquired the Cope collection in 1895 (AMNH 5777; McIntosh, 1998), so the specimen apparently survived at least until

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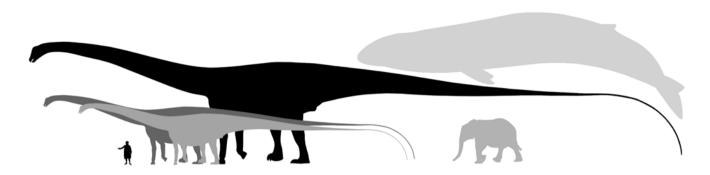


Fig. 1. Scaled life reconstruction of Amphicoelias fragillimus

Light grey is *Diplodocus carnegii* (CM 84), dark grey is *Supersaurus vivianae* (WDC DMJ-021), black is *A. fragillimus*. Sauropod silhouettes used are *Diplodocus carnegii* available from S. Hartman and PhyloPic. The Blue Whale and African Elephant illustrate dwarfed comparative size (silhouettes from PhyloPic). All to scale. Human scale bar is 1.88 m tall

then. In the original description Cope noted the extreme fragile and delicate nature of the material (hence the species name *fragillimus*), and since fossil preservatives were not used at the time, it has been surmised that at some point prior to Osborn and Mook's survey that the deteriorating material was discarded, potentially even by Cope himself (Carpenter, 2006). Regardless of the whereabouts of the holotype material, several works have accepted Cope's measurements without question (Osborn, Mook, 1921; McIntosh, 1998; Carpenter, 2006).

Unfortunately in many respects the study of A. fragillimus represents a forever un-testable scientific endeavor. Due to the disappearance of the holotype material, proportions cannot be re-measured, morphology and anatomy cannot be examined, and phylogeny and taxonomy are practically nonexistent; in essence any further science is hindered. All we are left with is the scant information in Cope's 1878 description. Yet, based on what information survives, presumed body length and body mass have been calculated (Paul, 1994; Mazzetta et al., 2004; Carpenter, 2006). This resulting body size has remained largely unquestioned, and dinosaur paleontology has been largely indoctrinated with the concept that A. fragillimus was possibly the largest dinosaur; although it is rarely mentioned in these discussions due to the missing status of the type material. While any scientific assessment of A. fragillimus is conjectural, it is nonetheless important to question the biology of such a reported organism. If reconstructed elemental size and body length and mass can all be hypothesized, the same should hold true for other biological aspects. Through morphological comparisons this analysis shall examine more plausible elemental reconstructions while also considering biological and historical aspects in order to determine if a sauropod of the reported size of A. fragillimus could have existed.

Institutional Abbreviations: AMNH – American Museum of Natural History, New York, NY, U.S.A; CM – Carnegie Museum of Natural History, Pittsburgh, PA, U.S.A.; MOR – Museum of the Rockies, Bozeman, MT, U.S.A.; SMA – Sauriermuseum Aathal, Aathal, Switzerland; WDC – Wyoming Dinosaur Center, Thermopolis, WY, U.S.A.

DISCUSSION

While the attention of A. fragillimus works are generally dedicated to length and weight of the animal (Paul, 1994; Mazzetta et al., 2004), this analysis shall attempt to determine a more accurate reconstruction of the A. fragillimus material. Cope's original reconstructive comparisons were based on Camarasaurus and the second Amphicoelias species A. altus (AMNH 5764). However, based on vertebral morphological similarities, modern analyses prefer to use a diplodocid proxy, such as Diplodocus (Paul, 1994). Phylogentically, both Rauhut et al. (2005) and Whitlock (2011) recover the second Amphicoelias species, A. altus, as a basal diplodocoid. Thus a diplodocid proxy is morphologically and phylogentically supported. However, as Carpenter (2006) pointed out, if A. fragillimus was indeed a diplodocid, then either Apatosaurus, Diplodocus, or Barosaurus are suitable proxies. Indeed, it must be stated first and foremost that differing proxies would produce drastically different outcomes (i.e. the proportional differences between Dicraeosaurus, Diplodocus, and Brachiosaurus). In addition, all analyses presume that supergiant sauropods had proportions respective to their smaller relatives; for the purposes of this analysis, proportions and morphology shall be compared to Diplodocus, Supersaurus, and A. altus. The largest Diplodocus species, D. hallorum, has been temporarily excluded from this analysis since a large portion of the dorsal series remains articulated in a matrix block (Lucas *et al.*, 2006), and therefore comparable vertebral features and orientations cannot be examined.

A. FRAGILLIMUS ELEMENTAL RECONSTRUCTIONS

VERTEBRAL RECONSTRUCTION

In his 1878 description, Cope presumed that the neural arch of A. fragillimus represented the tenth dorsal, and he reconstructed the centrum similar to that of A. altus. Cope's A. fragillimus is reconstructed as having a very narrow and rectangular centrum (nearly twice as tall as wide) with a very small and rounded neural spine apex shortly above the preserved portion (Fig. 2). This reconstruction results in a posterior dorsal vertebra 1.83 meters tall. In 2006, based on presumed morphological similarities, K. Carpenter reconstructed the A. fragillimus vertebra as an extensively modified A. altus posterior dorsal vertebra. Carpenter's reconstruction resulted in a centrum that was slightly more circular (yet still taller than wide),

with a very tall and narrow neural arch, slightly vertically oriented transverse processes, and a larger, more bulbous neural spine apex. This reconstruction, at least being based on a comparative specimen, results in the A. fragillimus posterior dorsal vertebra as being 2.7 meters tall (Fig. 2). Looking at a posterior dorsal from *Diplodocus* carnegii (D 10 from CM 84; Hatcher, 1901), the centrum is very circular, with the height and width being near equal. From the neural canal to the hyposphene, the neural arch is rather tall, but becomes quite narrow proximally to the neural canal. Proportionally, in the case of D. carnegii (D 10 from CM 84) the centrum is approximately 1/4 of the entire vertebral height. In a larger diplodocid, such as Supersaurus vivianae (WDC DMJ-021), the centrum is significantly larger than that of D. carnegii. In S. vivianae the centrum is much wider than it is tall. The neural arch from the neural canal to the hyposphene is much shorter than in D. carnegii, yet still retains the narrow portion proximal to the neural canal. Also, proportionally the centrum is a much larger component of the total vertebral height; in this case approximately 1/3 of the entire height. If these size and proportional differences between D. carnegii and S. vivianae are indicative



Fig. 2. Diplodocid vertebral comparisons and Amphicoelias fragillimus reconstructions

I. Amphicoelias altus (from Osborn, Mook, 1921). II. Diplodocus carnegii (CM 84, from Hatcher, 1901). III. Supersaurus vivianae (WDC DMJ-021). IV. Dorsal neural arch of A. fragillimus with newly reconstructed neural arch height of 1050 mm (from Cope, 1878a). V. Dorsal neural arch of A. fragillimus based on measurements described by Cope (from Cope, 1878b). VI. Reconstructed dorsal vertebra of A. fragillimus modeled after A. altus (from Carpenter, 2006). VII. Reconstruction of A. fragillimus using vertebral trends observed throughout Diplodocidae ontogeny (note the general proportions were modeled assuming A. fragillimus maintained similar proportions to that of S. vivianae). All vertebrae to scale. Scale bar = 1 M

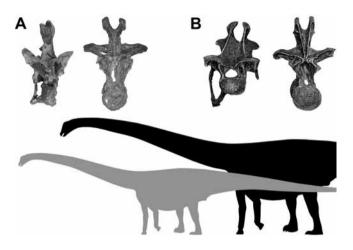


Fig. 3. Representative Diplodocidae (*Diplodocus*) anterior cervical and posterior dorsal vertebral ontogeny

A and the grey silhouette represent the "sub-adult" *Diplodocus* condition. B and the black silhouette the "adult" condition. Silhouettes to relative scale, vertebrae not to scale. Modified from Woodruff and Fowler (2012). Silhouettes from S. Hartman and PhyloPic

of vertebral changes within large diplodocids, then it might be possible to predict the morphologies of even larger diplodocids. Since we do not have any material from a diplodocid between the size of *S. vivianae* and *A. fragillimus*, it is impossible to determine whether or not the centrum continued to widen and dominate more of the total vertebral height. However, assuming that the *A. fragillimus* posterior dorsal was indeed roughly similar in relative proportions to that of *S. vivianae*, this new reconstruction results in a posterior dorsal larger than Carpenter's (2006).

The relationship between the hyposphene to neural canal height versus the width and height of the centrum in S. vivianae (WDC DMJ-021) results in the A. fragillimus centrum being rather circular, approximately 95 cm across by 80 cm tall. The neural arch was reconstructed as being rather short, as in the case of S. vivianae (WDC DMJ-021), with a thinning, narrow portion proximal to the neural canal. In immature Diplodocidae the lateral sides of the neural arch are tall and straight, and throughout ontogeny the arch shortens in height and narrows lateral to the neural canal (Woodruff, Fowler, 2012). Based on the reported size, we presume that A. fragillimus was a fully mature animal, and thus would follow the same trend. The transverse processes were reconstructed as being slightly more horizontally oriented than in Carpenter's (2006) reconstruction, which is more akin to those observed in D. carnegii (CM 84; the transverse processes of WDC DMJ-021 are not preserved). The neural

spine apex is nearly the same height, but much more bulbous (potentially the continuation of an ontogenetic trend observed by Woodruff and Fowler, 2012; Fig. 3). Using the ratio between the centrum height to the overall vertebral height of *S. vivianae* (WDC DMJ-021), results in a total *A. fragillimus* vertebral height of 2.8 meters (Fig. 2).

FEMORAL RECONSTRUCTION

With regard to the femur of *A. fragillimus*, any attempted reconstruction is purely conjectural. Yet femoral dimensions can provide critical variables for life history information, such as body mass and growth rates. Since the femur can reveal such insightful information about the organism in question, we feel that an attempt to hypothesize the femoral morphology of *A. fragillimus* is a worthwhile endeavor.

In his 1878 description, Cope did mention that a distal end of a femur was located near the dorsal neural arch, and assumedly based on its large size from the same animal. However, Cope never figured or described this element in any detail. For comparative and speculative purposes, Cope noted that in the case of *A. altus* and *Camarasaurus supremus* the femora were roughly twice as tall as the tallest dorsal vertebra (Cope, 1878a). Assuming that the preserved neural arch was indeed from the tallest of the series, this results in a femur over 3.6 meters tall (Cope, 1878a). In using *Diplodocus* proportions, the femur to dorsal 10 ratio is approximately 1.6–1.7. This produces an *A. fragillimus* femur anywhere from 3.10–4.76 meters tall (Paul, 1994; Carpenter, 2006; this analysis).

Assuming that A. fragillimus and A. altus were proportioned similar with respect to femur morphology, then the femur of A. fragillimus should be quite gracile and extremely long and narrow (A. altus displays the "stovepipe" diaphyseal morphology). It would seem rather peculiar for an organism with a potential mass of 122,400 kg (Carpenter, 2006) to be supported by such a proportionally narrow and gracile femur as opposed to a stocky and robust Apatosaurus-like femur. But, as the femur increases in length, so should the relative width. Following the development through Diplodocus femoral ontogeny, some general trends include the femoral head enlarging and inclining progressively horizontal, the greater trochanter protruding much more medially, the diaphysis thickening appositionally, and the tibial and fibular condyles becoming much larger and more robust (Fig. 4). Assuming the same developmental trends hold true (disregarding the questionable diaphyseal morphology mentioned above) in A. fragillimus, the femur of A. altus (AMNH 5764) has been modified in the same manner to reconstruct that of A. fragillimus. The resulting reconstructed femur is 4.76 meters tall (Fig. 5).



Fig. 4. Ontogenetic development of diplodocid (Diplodocus) femora

From left to right: SMA 0009, CM 33976, CM 30762, MOR 790 7-5-95-7, MOR 790 7-23-95-122, MOR 592-35, CM 84. *Diplodocus carnegii* silhouettes reflect the minimum and maximum body lengths of the femoral set (from S. Hartman and PhyloPic). Femora to scale. Scale bar equals 10 cm

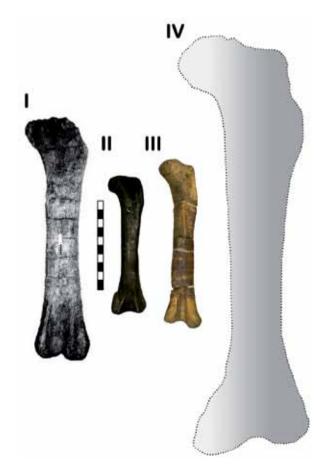


Fig. 5. Hypothetical femur of *Amphicoelias fragillimus* compared to known sauropods

I. Ruyangosaurus giganteus (from Lü et al., 2009). II. Diplodocus carnegii (CM 84). III. Amphicoelias altus (AMNH 5764). IV. Amphicoelias fragillimus femur modeled after A. altus with implied features modified after Diplodocus femur ontogeny. Femora to scale. Scale bar = 1 M

THE SCIENTIFIC PLAUSIBILITY OF A. FRAGILLIMUS' MASSIVE SIZE

ECOLOGY

The gargantuan size of *A. fragillimus* and the mystery surrounding the disappearance of the material makes this organism truly unique. That the purported largest terrestrial vertebrate of all time was found and lost before the advent of modern documentation technology is a travesty; and, alas, the memory of *A. fragillimus* may forever remain engrained in the annals of paleontology. While the evidence exists to verify that Cope did indeed extract the remains of some large sauropod from Colorado, the science of gigantism should dispel the potential myth of *A. fragillimus*' purported reconstructed length and body mass. Intrinsic factors such as gravitational forces indicate the maximum weight limit for a terrestrial organism to be 75,000 kg (Günther *et al.*; 2002),

while bone strength and muscles forces have been calculated to max out in terrestrial body sizes over 90,718 kg (Hokkanen, 1986). With regard to large body size, the most critical extrinsic property is resource availability. The larger an organism the more nutritional resource it needs (particularly if it has a higher basal metabolic rate) along with a larger home range for said resources (Burness *et al.*, 2001). If an organism is too large for the geography and biota to support it, that particular organism will be in direct conflict with the ecosystem and shall eventually go extinct. According to MacArthur and Wilson (1967), the larger a particular land area the more individuals per taxon will be present.

If a homogenized Morrison Formation sauropod biota were indeed correct, this means that at least ten genera and potentially twenty-one species with body masses ranging from 7 to 26 tons were all occupying the same landscape (Seebacher, 2001; Foster, 2003; Mazzetta et al., 2004; Taylor, 2009). While there is evidence to suggest generic and ontogenetic niche partitioning (Whitlock et al., 2010; Fowler, Sullivan, 2011), these sauropod genera would undoubtedly have had an impact on the plant biota; so, presumably a sauropod an entire order of magnitude greater in mass would have needed significantly more resources and would have potentially been in direct competition with other coexisting large herbivores, especially as juveniles and subadults. As in the case of the African savanna, the abundance of the largest herbivores is much lower than that of the smaller herbivores (Owen-Smith, Mills, 2008). Assuming the same would hold true for Morrison Fm. time, this could explain the overabundance of the relatively smaller Camarasaurus, compared to the rare giant diplodocids such as Supersaurus and Diplodocus hallorum.

TAPHONOMY AND STRATIGRAPHY

Taphonomically the larger an organism, the more sediment that is needed to entomb the carcass. When one considers the immense size of the giant sauropods such as Puertasaurus reuili (Novas et al., 2005), Turiasaurus riodevensis (Royo-Torres et al., 2006), Paralititan stromeri (Smith et al., 2001), Diplodocus hallorum (Lucas et al., 2006), Futalognkosaurus dukei (Calvo et al., 2007), Sauroposeidon proteles (Wedel et al., 2000), Supersaurus viviana (Jensen, 1985), Alamosaurus sanjuanensis (Gilmore, 1922), Argentinosaurus huinculensis (Bonaparte, Coria, 1993), and Bruhathkavosaurus matlevi (Yadagiri, Avyasami, 1989), all of these sauropods are generally known from relatively sparse remains. So, one could make the argument that if A. fragillimus was considerably larger than any yet-described sauropod, this could support the taphonomic plausibility of a burial bias.

Stratigraphically the A. fragillimus (and A. altus) quarry sits within the Tithonian portion of the upper Brushy Basin Member of the Morrison Formation (Turner, Peterson, 1999). Likewise, the largest Camarasaurus (C. supremus), Apatosaurus (A. louisae), and Diplodocus (D. hallorum) species are all stratigraphically from the slightly lower Kimmeridgian portion of the upper Brushy Basin Member (Turner, Peterson, 1999). Perhaps increasing average body size is a stratigraphic trend in Morrison Formation sauropods; although the stratigraphically highest occurrence of Apatosaurus, in the upper meters of the Brushy Basin Member in Arches National Park, Utah (Foster, 2005), is of a size typical for the average adult lower in the formation. So, it is very likely that O. Lucas did indeed find the remains of a large upper Morrison Formation sauropod; and as Cope said in 1878, the remains were "... the largest saurian I have ever seen." Certainly this could be the case given that a posterior dorsal from A. altus is nearly the same size as that from D. carnegii. Given that most Morrison Formation sauropod quarries are located generally near the division between the lower and upper portions of the Brushy Basin Member (Turner, Peterson, 1999), the rarity of these larger species could also be attributed to collecting biases.

However, even though fragmentary, remains of the largest sauropods are regularly recorded (*i.e. Turiasaurus riodevensis* and *Alamosaurus sanjuanensis*; and the recent discovery of a bone bed of several large sauropods from Argentina with reported femoral lengths of nearly 2.5 meters). Considering the time and resources that have been spent exploring the vastness of the Morrison Formation, not a single substantiating piece of an *A. fragillimus* sized sauropod has been reported. Taphonomically at the very least, some partial fragment should have been quite evident and found in the intervening years. As of this publication no such secondary material is scientifically known.

TAXONOMY

In terms of the genus level taxonomy, this analysis agrees with Osborn and Mook (1921) and McIntosh (1998) that the second species, "A. latus", is simply a synonym of A. altus. The distinct stout femur of "A. latus" could possibly be pathologic or individual variation. However, in terms of A. altus, this analysis agrees with Foster (2007) that there are not enough characters to separate A. altus from the genus Diplodocus. In the past, A. altus has been considered either likely a large cf. Diplodocus (Foster, 2001) or at least of uncertain status (Harris, 2006). Even Osborn and Mook (1921) noted the similarities of Amphicoelias to Diplodocus; specifically the similarity in the morphology of the neural spine, neural arch, spinodiapophyseal and centroparapophyseal

laminae. However, Osborn and Mook (1921) do state that *A. altus* differs in that the centrum is as long as it is tall, different than that of *Diplodocus*, which is taller than it is long. Such "autapomorphies", such as the circular femoral cross-section ("stovepipe" diaphysis) in *A. altus* are now recognized to be present in many *Diplodocus* specimens (Carpenter, 2006; Woodruff and Fowler, 2012; R. Wilhite – pers. comm.; C. Woodruff, J. Foster – pers. obs.), while the proportionally longer ulna to femur (Carpenter, 2006), the taller and wider neural arch (Carpenter, 2006), a taller than wider centrum, and other minor vertebral differences are primarily indicative of juvenile characteristics (Woodruff, Fowler, 2012).

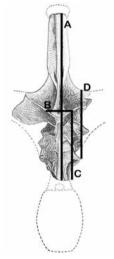
This analysis shall go one step further and suggest that if the differences between the comparable elements of A. altus and A. fragillimus are indeed correct, then this is indicative of an ontogenetic trajectory (comparable to the ontogenetic vertebral changes documented by Woodruff and Fowler, 2012). Thus, the A. altus material represents an immature animal, and A. fragillimus the more mature form. As A. altus was erected in 1887 and A. fragillimus in 1878, fragillimus should be synonomized into altus (likewise suggested by McIntosh, 1998). Stratigraphically and ontogenetically there is coinciding support for a very large uppermost Brushy Basin Member, Tithonian-aged diplodocine. In lieu of the lack of legitimate autapomorphies and distinction to the genus *Diplodocus*, this analysis supports the referral of the collective Amphicoelias material to the genus and species Diplodocus altus. As the genus Amphicoelias (Cope, 1877) takes priority over Diplodocus (Marsh, 1878), this would mean that the genus level identification should be assigned as Amphicoelias, and Diplodocus would now be a junior subjective synonym. However, in consideration of the historical and cultural significance, coupled with the copious material and significant paleontological understanding of material referred to as Diplodocus, this analysis calls for Amphicoelias being deemed the nomen oblitum and Diplodocus as a nomen protectum.

COULD E.D. COPE HAVE BEEN WRONG?

In the face of the historical evidence and Cope's detailed anatomical training, it would seem hard to deny the existence of *A. fragillimus*. We will never know the answers as to why Cope never published more on *A. fragillimus*, why O.C. Marsh did not publicly question the material, and why the AMNH never publicly expressed vivid interest in displaying the world's largest dinosaur. All of these questions are intangible. However, with regard specifically to the described material, it is our belief that the measurements are a typographical error.

TYPOGRAPHICAL ERROR

In the 1878 description of A. fragillimus Cope lists the measurements as follows, "total elevation of the neural arch preserved, 1500 m; elevation of the posterior zygapophyses, 585; transverse expanse of posterior zygapophyses, 190; vertical diameter of base of diapophysis, 390" (Cope, 1878a). This list of measurements is interesting because all subsequent works (such as Carpenter, 2006) refer to the units as mm (other 19th century works denote meters as "M." and millimeters as "mm"). Obviously, Cope did not mean to say that the neural arch was 1,500 meters tall, but immediately in the very first line of given measurements is a typographical error. With regard to the values themselves, some care should be taken as to the literal dimensions. In his 1877 description of A. altus. Cope described the femur as being exactly "six feet four inches" (Cope, 1877), while in his table the value given is "1.542 M" (1542 mm; approximately 5 feet; Cope, 1877). While this error does not result in a total re-evaluation of the relative size of the element, it is off by over 38 cm.



	New arch reconstruction (in mm)	Cope's measurement (in mm)	Percent difference
Α	1050		
В	168.52	190	11%
С	437.5	585	25%
D	333	390	14%
	Cop's arch reconstruction (in mm)	Cope's measurement (in mm)	Percent difference
Α	Cop's arch reconstruction (in mm) 1500	Cope's measurement (in mm)	Percent difference
A B		Cope's measurement (in mm) 190	Percent difference 20%
	1500	. , ,	

Fig. 6. Neural arch measurement reference points

A. Neural arch height.
 B. Transverse expanse of posterior zygapophyses.
 C. Elevation of the posterior zygapophyses.
 D. Vertical diameter of the base of diapophysis.
 Amphicoelias fragillimus drawing from Cope (1878a)

This analysis agrees with subsequent work in that the unit "m." was a typographical error, which was intended to be mm. Yet a 1,500 mm neural arch still leads to the titanic vertebral reconstructions. It is historically unsupported and speculative, but if the value 1,500 mm is altered to 1,050 mm, then this results in a vertebral reconstruction significantly more comparable in size to the largest sauropods in the world and still represents the largest ever found in the Morrison Formation. Since Cope did not indicate where his precise measured reference points were, the newly calculated values are not identical, but they are surprisingly close. Based on Cope's drawing (which assumes the drawing to be perfectly scaled and an exact 1:1 with the fossil material), with a 1,050 mm neural arch height, the elevation of the posterior zygapophyses is approximately 520 mm; the transverse expanse of posterior zygapophyses is approximately 160 mm; and the vertical diameter of the base of diapophysis is approximately 320 mm. While these values do differ from the originals (aside from the neural arch height the mean difference is 55 mm), proportionally these new values fit much better with a 1,050 mm neural arch than the originals do with one 1,500 mm. This new arch value still produces a reconstructed total vertebral height nearly 1.83 m, which is close to the value estimated by Cope (Fig. 6).

DISAPPEARANCE OF THE A. FRAGILLIMUS MATERIAL

Given this new possible explanation, this analysis presents two new potential scenarios as to the disappearance of the A. fragillimus material: 1) O. Lucas did collect a large diplodocid partial vertebra, which Cope quickly described. However, the remains were of such poor preservation that Cope discarded the material soon after description (similar to Carpenter's [2006] explanation; and the assigned AMNH collection number probably was assigned after the acquisition of Cope's collection). While this scenario could only be substantiated by a confession, Cope's history is marked with typographical errors (Cope even referred to his own species on occasion as "fragillimus" and "fragillisimus"). Cope himself claimed credit for the theory that unitatheres possessed trunks and that secretaries and printers had left this information out through a series of errors (Wallace, 1999). And even Cope's longtime friend, H.F. Osborn noted that Cope's own furious rush to describe and publish on fossil material had led to numerous scientific errors (Osborn, 1931). 2) Considering the immense volume of scientific work Cope had compiled for himself, coupled with the fact that his publication finances were significantly limited compared with those of O.C. Marsh, it is possible that Cope deliberately chose not to pursue further in depth works on *A. fragillimus*. It is even possible that Cope himself was never aware of this potential typographical error. And, if O.C Marsh's spies had reported on the specimen in Colorado, this could be why Marsh never disputed the description. If Cope did not personally dispose of *A. fragillimus*, then it is just as likely that at some point after the AMNH acquired the Cope collection in 1895, a fragmentary, poorly preserved portion of neural arch may have inadvertently slipped "under the radar" of the collections staff and was subsequently disposed of.

CONCLUSION

Whichever scenario holds true as to the disappearance of A. fragillimus, it is unfortunately most likely that the material was in one way or another destroyed. While this analysis does not wish to claim that Cope had ulterior motives nor is it believed that Cope purposefully inflated measurement values, some strikingly absent historical events do raise questions. While it is a fact that Cope did not have the near limitless financial or supportive backing of O.C. Marsh, it is curious that Cope never mentioned A. fragillimus in any further detail (its discovery and taxonomy were extremely briefly addressed in a publication in 1881 - Cope, 1881). Some speculations suggest that it was the limited resources that hindered any further works, yet merely mentioning or referencing A. fragillimus would not have been a grievous task. In December 1877, Cope described A. altus and "A. latus" in a review of dinosaurs from Colorado, and another on the same subject in February 1878 (Cope, 1877, 1878b). If A. fragillimus was indeed discovered in the summer of 1877, it is curious as to why was it not addressed in either of these sizeable works (the former was released within 6 months before the formal description). The entire formal description of A. fragillimus is only two paragraphs long, so certainly it was not omitted from either due to limited text space. Potentially Cope purposefully chose to do a separate description, but given the sparse size of the description this seems rather odd. In addition, it is perplexing as to why Cope did not even mention A. fragillimus within his theory of lineages increasing in body size through time (a theory now called Cope's Rule - Cope, 1896). While Cope's Rule is a loose general trend (and fraught with exceptions, i.e. Hone et al., 2005; Carrano, 2006; Hone et al., 2008; Sander et al., 2011), considering he discovered the largest terrestrial vertebrate at the time, it is striking that Cope did not speculate on A. fragillimus and its evolutionary lineage contribution.

To confirm the story and size of *Amphicoelias fragillimus* may be nearly every sauropod paleontologist's Holy Grail. When in the heart of Morrison Formation country one cannot help but think that the long lost *A. fragillimus* rests around the next bend. But, as in a mythical treasure hunt, the spoils may forever remain unattainable. While the mysteries surrounding *A. fragillimus* are alluring, when we stop to consider the validity of a gargantuan terrestrial organism through several aspects such as biology, ecology, and ontogeny (opposed to making these variables fit around it) the end result is that it is highly unlikely that a terrestrial quadruped of such a purported body size could have existed. Whatever the secrets of *A. fragillimus* are, Cope took them to his grave.

Acknowledgements. We would like to thank J. Horner, H. Woodward-Ballard, J. Scannella, D. Fowler, L. Freedman-Fowler, S. Lucas, R. Sullivan, K. Nordén, R. Hunt-Foster, and two anonymous reviewers for invaluable insight, comments, help, and review of this paper.

REFERENCES

- BONAPARTE J., CORIA R., 1993 Un nuevo y gigantesco sauropodo titanosaurio de la Formacion Rio Limay (Albiano—Cenomaniano) de la Provincia del Neuquen, Argentina. *Ameghiniana*, **30**: 271–282.
- BURNESS G.P., DIAMOND J., FLANNERY T., 2001 Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. Proceedings of the National Academy of Sciences, 98: 14,518–14,523.
- CALVO J.O., PORFIRI J.D., GONZÁLEZ-RIGA B.J., KELLNER A.W., 2007 A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais Academia Brasileira Ciencia*, **79**: 529–541.
- CARPENTER K., 2006 Biggest of the big: a critical re-evaluation of the mega-sauropod *Amphicoelias fragillimus* Cope, 1878. *Bulletin of the New Mexico Museum of Natural History and Science*, **36**: 131–137.
- CARRANO M.T., 2006 Body-size evolution in the Dinosauria. *In*: Amniote paleobiology: perspectives on the evolution of mammals, birds, and reptiles (eds M.T. Carrano *et al.*). University of Chicago Press, Chicago.
- COPE E.D., 1877 On the vertebrata of the Dakota Epoch of Colorado. *Proceedings of the American Philosophical Society*, 17: 233–247.
- COPE E.D., 1878a A new species of *Amphicoelias: American Naturalist*, **12**: 563–565.
- COPE E.D., 1878b On the saurians recently discovered in the Dakota Beds of Colorado. *American Naturalist*, **12**: 72–85.
- COPE E.D., 1881 Geological News. *American Naturalist*, **15**: 254–1053.
- COPE E.D., 1896 The primary factors of organic evolution. Open Court Publishing Company, Chicago.
- FOSTER J.R., 2001 Relative abundances of the Sauropoda (Dinosauria, Saurischia) of the Morrison Formation and implications for Late Jurassic paleoecology of North America. *Mesa Southwest Museum Bulletin*, **8**: 47–60.

- FOSTER J.R., 2003 Paleoecological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain Region, U.S.A. New Mexico Museum of Natural History and Science Bulletin, 23.
- FOSTER J.R., 2005 New sauropod dinosaur specimens found near Moab, Utah, and the sauropod fauna of the Morrison Formation. *Canyon Legacy*, **55**: 22–27.
- FOSTER J.R., 2007 Thunder Feet: The sauropod dinosaurs: *In:* 183–208. Jurassic West: The dinosaurs of the Morrison Formation and their world. Indiana University Press.
- FOWLER D.W., SULLIVAN R.M., 2011 The first giant titanosaurian sauropod from the Upper Cretaceous of North America. *Acta Palaeontologica Polonica*, **56**: 685–690.
- GILMORE C.W., 1922 A new sauropod dinosaur from the Ojo Alamo Formation of New Mexico. Smithsonian Miscellaneous Collections, 72: 1–9.
- GÜNTHER B., MORGADO E., KIRSCH K., GUNGA H.C., 2002
 Gravitational tolerance and size of *Brachiosaurus brancai*.

 Mitteilungen aus dem Museum für Naturkunde in Berlin,
 Geowissenschaftliche Reihe, 5: 265–269.
- HATCHER J.B., 1901 Diplodocus (Marsh): Its osteology, taxonomy, and probable habits, with a restoration of the skeleton. Memoirs of the Carnegie Museum, 1: 1–63.
- HARRIS J.D., 2006 The significance of Suuwassea emilieae (Dinosauria: Sauropoda) for flagellicaudatan intrarelationships and evolution. Journal of Systematic Palaeontology, 4: 185–198.
- HONE D.W.E., KEESEY T.M., PISANI D., PURVIS A., 2005 Macroevolutionary trends in the Dinosauria: Cope's rule. *Journal of Evolutionary Biology*, 18: 587–595.
- HONE W., DYKE J., HADEN M., BENTON J., 2008 Body size evolution in Mesozoic birds. *Journal of Evolutionary Biology*, 21: 618–624.
- HOKKANEN J.E.I., 1986 The size of the biggest land animal. *Journal of Theoretical Biology*, **118**: 491–499.
- JAFFE M., 2000 The gilded dinosaur: the fossil war between E.D. Cope and O.C. Marsh and the rise of American science. Crown Publishing Group, New York.
- JENSEN J.A., 1985 Three new sauropod dinosaurs from the Upper Jurassic of Colorado. *Great Basin Naturalist*, **45**: 697–709.
- LUCAS S.G., SPIELMAN J.A., RINEHART L.A., HECKERT A.B., HERNE M.C., HUNT A.P., FOSTER J.R., SULLIVAN R.M., 2006 Taxonomic status of Seismosaurus hallorum, a Late Jurassic sauropod dinosaur from New Mexico. New Mexico Museum of Natural History and Science Bulletin, 36: 149–161.
- LŰ J., XU L., JIA S., ZHANG X., ZHANG J., YANG L., YOU H., JI Q., 2009 A new gigantic sauropod dinosaur from the Cretaceous of Ruyang, Henan, China". *Geological Bulletin of China*, **28**: 1–10.
- MACARTHUR R.H., WILSON E.O., 1967 The theory of island biogeography. Reprint in 2001. Princeton University Press, Princeton.
- MARSH O.C., 1878 Principal characters of American Jurassic dinosaurs. Part I. *American Journal of Science*, **16**: 411–416.
- MAZZETTA G.V., CHRISTIANSEN P., FARIÑA R.A., 2004 Giants and bizarres: body size of some southern South American Cretaceous dinosaurs. *Historical Biology*, **16**: 71–83.

- McINTOSH J.S., 1998 New information about the Cope collection of sauropods from Garden Park, Colorado. *Modern Geology*, 23: 481–506.
- MONACO P.E., 1998 A short history of dinosaur collecting in the Garden Park Fossil Area, Cañon City, Colorado. *Modern Geology*, 23: 465–480.
- NOVAS F.E., SALGADO L., CALVO J., AGNOLIN F., 2005 Giant titanosaur (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia. Revisto del Museo Argentino de Ciencias Naturales, 7: 37–41.
- OSBORN H.F., 1931 Cope: Master Naturalist: Life and Letters of Edward Drinker Cope, With a Bibliography of His Writings. Manchester, New Hampshire: Ayer Company Publishing.
- OSBORN H.F., MOOK C.C., 1921 Camarasaurus, Amphicoelias and other sauropods of Cope. Memoirs of the American Museum of Natural History, 3: 249–387.
- OWEN-SMITH N., MILLS M.G.L., 2008 Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology*, 77: 173–183.
- PAUL G.S., 1994 Big sauropods really, really big sauropods. *In*: The dinosaur report. The Dinosaur Society: 12–13.
- RAUHUT O., REMES K., FECHNER R., CLADERA G., PUERTA P., 2005 Discovery of a short-necked sauropod dinosaur from the Late Jurassic period of Patagonia. *Nature*, **435**: 670–672.
- REILLEY S.B., BANNISTER J.L., BEST P.B., BROWN M.,
 BROWNELL R.L. Jr., BUTTERWORTH D.S., LAPHAM P.J.,
 COOKE J., DONOVAN G.P., RBÁN J., ZERBINI A.N., 2008
 Balaenoptera musculus. IUCN Red List of Threatened Species. Version 2013.1. International Union for Conservation of Nature.
- ROYO-TORRES R., COBOS A., ALCALÁ L., 2006 A giant European dinosaur and a new sauropod clade. *Science*, **314**: 1925–1927.
- SANDER P.M., CHRISTIAN A., CLAUSS M., FECHNER R., GEE C., GRIEBELER E.M., GUNGA H.C., HUMMEL J., MALLISON H., PERRY S., PREUSCHOFT H., RAUHUT O., REMES K., TÜTKEN T., WINGS O., WITZEL U., 2011 Biology of the sauropod dinosaurs: The evolution of gigantism. *Biology Letters*, **86**: 117–155.

- SEEBACHER F., 2001 A new method to calculate allometric length-mass relationships of dinosaurs. *Journal of Vertebrate Paleontology*, **21**: 51–60.
- SMITH J.B., LAMANNA M.C., LACOVARA K.J., DODSON P.,
 SMITH J.R., POOLE J.C., GIEGENGACK R., ATTIA Y., 2001
 A giant sauropod dinosaur from an Upper Cretaceous mangrove deposit in Egypt. *Science*, 292: 1704–1706.
- SUKUMAR R., 2003 The living elephants: evolutionary ecology, behaviour, and conservation. Oxford University Press.
- TAYLOR M.P., 2009 A re-evaluation of *Brachiosaurus altitho*rax Riggs 1903 (Dinosauria, Sauropoda) and its generic separation from *Giraffatitan brancai* (Janensh 1914). *Journal of Ver*tebrate Paleontology, **29**: 787–806.
- TURNER C.E., PETERSON F., 1999 Biostratigraphy of dinosaurs in the upper Jurassic Morrison Formation of the western interior, USA. Vertebrate paleontology in Utah. 1999: 77–114.
- WALLACE D.R., 1999 The Bonehunters' Revenge. Dinosaurs, Greed, and the Greatest Scientific Feud of the Gilded Age. Houghton Mifflin, New York.
- WEDEL M.J., CIFELLI R.L., SANDERS R.K., 2000 Sauroposeidon proteles, a new sauropod from the Early Cretaceous of Oklahoma. Journal of Vertebrate Paleontology, 20: 109–114.
- WHITLOCK J.A., 2011 A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). Zoological Journal of the Linnean Society, 161: 872–915.
- WHITLOCK J.A., WILSON J.A., LAMANNA M.C., 2010 Description of a nearly complete juvenile skull of (Sauropoda: Diplodocoidea) from the Late Jurassic of North America. *Journal of Vertebrate Paleontology*, 30: 442–457.
- WOODRUFF D.C., FOWLER D., 2012 Ontogenetic influence on neural spine bifurcation in Diplodocoidea (Dinosauria: Sauropoda): A critical phylogenetic character. *Journal of Morphology*, 273: 754–764.
- YADAGIRI P., AYYASAMI K., 1989 A carnosaurian dinosaur from the Kallamedu Formation (Maestrichtian horizon), Tamilnadu. *In*: Symposium on three decades of development in palaeontology and stratigraphy in India (eds M.V.A. Sastry *et al.*): 523–528. Volume 1. Precambrian to Mesozoic. *Geological Society of India Special Publication*, 11.