



# GEOLOGY OF THE INTERMOUNTAIN WEST

*an open-access journal of the Utah Geological Association*

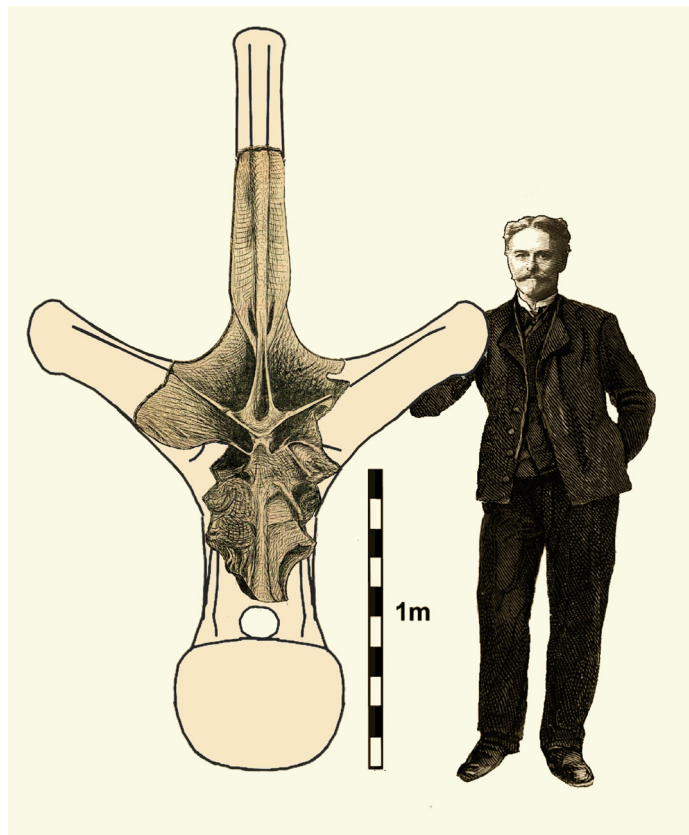
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## MARAAPUNISAURUS FRAGILLIMUS, N.G. (FORMERLY AMPHICOELIAS FRAGILLIMUS), A BASAL REBBACHISAURID FROM THE MORRISON FORMATION (UPPER JURASSIC) OF COLORADO

Kenneth Carpenter



Theme Issue

An Ecosystem We Thought We Knew—

The Emerging Complexities of the Morrison Formation

SOCIETY OF VERTEBRATE PALEONTOLOGY

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*The controversial vertebra of **Maraapunisaurus fragillimus** (formerly **Amphicoelias fragillimus**) and Edward D. Cope who described the specimen in 1878.*



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## *Maraapunisaurus fragillimus*, N.G. (Formerly *Amphicoelias fragillimus*), A Basal Rebbachisaurid From the Morrison Formation (Upper Jurassic) of Colorado

**Kenneth Carpenter**

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### ABSTRACT

In 1878, Oramel Lucas shipped to E.D. Cope of the Academy of Natural Sciences of Philadelphia, a huge 1.5-m-tall neural spine from the dorsal vertebra of a sauropod (from the Upper Jurassic Morrison Formation) that Cope named and illustrated as *Amphicoelias fragillimus*. The holotype was lost and all that is known of the specimen is from Cope's original publication. Reanalysis of Cope's publication in light of other sauropods discovered since 1878 indicates that *Amphicoelias fragillimus* is a basal rebbachisaurid characterized by pneumatic neural spine and arch, and the unambiguous rebbachisaurid character of a festooned spinodiapophyseal lamina. Because the specimen can no longer be referred to the basal diplodocoid *Amphicoelias*, the genus name is replaced with *Maraapunisaurus* n.g. As a rebbachisaurid, revised dimensions indicate a dorsal vertebra 2.4 m tall and a head-to-tail length for the animal of 30.3 to 32 m, significantly less than previous estimates.

### INTRODUCTION

Between 1877 and 1884, school teacher Oramel Lucas and his brother Ira discovered and excavated numerous dinosaur specimens from the vicinity of a prominent conical hill (a.k.a. "Cope's Nipple," "the Nipple," "Saurian Hill") of Upper Jurassic Morrison Formation in Garden Park north of Cañon City, Colorado (for historical review see Carpenter, in press). Among the specimens shipped by Oramel Lucas to Edward D. Cope, loosely affiliated with the Academy of Natural Sciences of Philadelphia, in 1878 was a huge neural spine. The specimen was described and illustrated as *Amphicoelias fragillimus* by Cope (1878f: 564) who wrote that "the total elevation of this vertebra, when complete, was not less than six feet, and probably more" (figure 1A). This

estimation was never challenged by Cope's contemporaries, nor later by Henry Osborn and Charles Mook of the American Museum of Natural History in their monograph of the Cope sauropod collection (Osborn and Mook, 1921). Only more recently have questions been raised about this specimen in the debate about the maximum possible size of terrestrial vertebrates (Paul, 1998; Mazzetta and others, 2004; Carpenter, 2006a; Perry and others, 2009; Woodruff and Foster, 2014).

Osborn and Mook's access to Cope's sauropods was made possible by the purchase of the Cope zoological and paleontological specimens by the American Museum of Natural History, much to the consternation of the Academy of Natural Sciences of Philadelphia, which had hoped to acquire the collections (Anonymous, 1899).

Citation for this article.

Carpenter, K., 2018, *Maraapunisaurus fragillimus*, n.g. (formerly *Amphicoelias fragillimus*), a basal rebbachisaurid from the Morrison Formation (Upper Jurassic) of Colorado: *Geology of the Intermountain West*, v. 5, p. 227–244.

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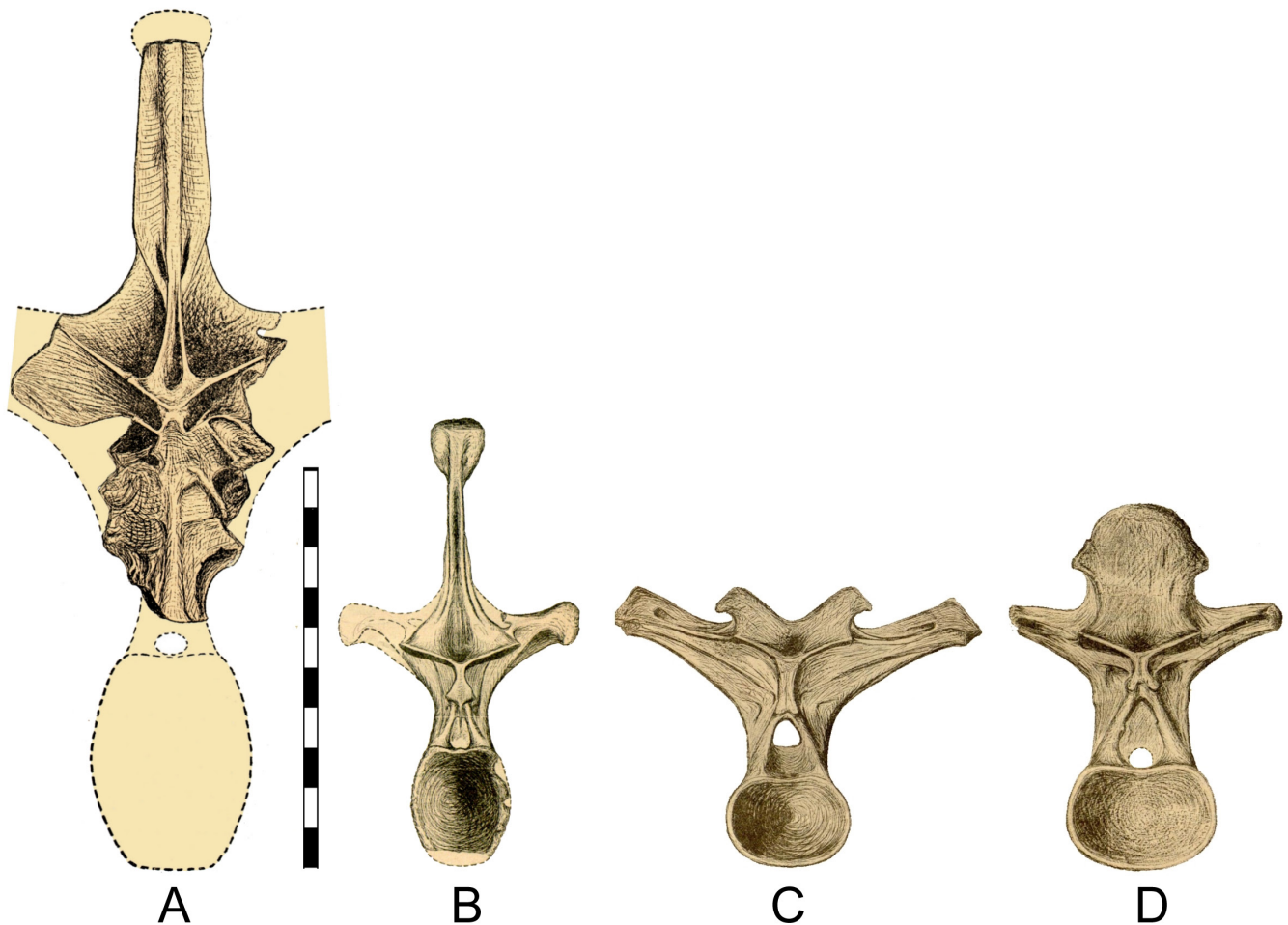


Figure 1. Illustrations of different sauropod dorsals made by Cope to show why he thought that the neural spine of "*Amphicoelias*" *fragillimus* (A) was most similar to that of *Amphicoelias altus* (B) than to *Camarasaurus supremus* (C, mid-dorsal; D, more posterior mid-dorsal). Scale = 1 m. B to D from Cope 1878b; A from Cope 1878f.

Because of financial reasons, Cope began negotiating with the American Museum in April 1894 to purchase parts of his collections with his friend Henry Osborn acting as a middleman (Osborn, 1931). Although this would be considered a conflict of interest today, Cope counted on his friend's honesty to help him leverage the best possible prices and to recoup the estimated \$50,000 (~ \$1.5 million in 2018) of personal money spent. The Cañon City dinosaurs were part of the final sale negotiated with the Cope estate in 1897 a few months after his death at age 54. In the end, the American Museum spent \$60,550 (~ \$1.8 million in 2018) for just the four vertebrate fossil collections alone (Osborn, 1931).

The process of examining, packing and shipping the

collections was not rushed, but took several years, with the last of the collections not arriving at the American Museum until 1903, six years after Cope's death (Jesup, 1896, 1898, 1899, 1900, 1901, 1903). Osborn, who was head of vertebrate paleontology, put William D. Matthew, curator at the museum, in charge of the vertebrate fossil collection transfers (Matthew, 1915, p. 38; Osborn and Mook, 1921; Osborn, 1931; Colbert, 1992, p. 51–53). Matthew was aided by Albert Thompson and Jim Young, also of the American Museum (Osborn, 1931). Some of Cope's collections were at his house on Pine Street in Philadelphia, but a larger portion was in storage a few miles away in the lower level of the Memorial Hall building in Fairmont Park (Matthew, 1915). Once



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the collections arrived at the American Museum, the cataloguing of the specimens was handled by Walter Granger, Albert Thompson, and William Matthew (see Jessup, 1901, p. 23; Osborn and Mook, 1921, p. 251, 258, and 260).

While Cope was still alive, Osborn did write Cope about various specimens that could not be accounted for by Matthew:

“I write to ask whether you can fix your memory upon the type of *Symborodon torvus* and of *S. ophryas*. We cannot locate definitely the type of either specimen, although one is the type of the genus and the other is described as a nearly complete skull. I hope you will look this up, and if you can, refresh your memory and let me know. Dr. Matthew also reports that the types of marsupials from the White River are apparently missing. Have you seen anything of them?” Osborn to Cope, May 19, 1896, in Osborn (1931, p. 449–450).

Despite these letters, some of these specimens were never found, e.g., *Mesohippus cuneatus*, AMNH 6293, “These types could not be identified when Cope’s Colorado collection was catalogued by W.D. Matthew.” (Osborn, 1918, p. 47).

The situation was worse when the dinosaur collection was finally dealt with six years after Cope’s death. By then it was no longer possible for Osborn to inquire of Cope where the missing specimens might be, or which sets of bones belonged together because Cope never numbered them (see discussion on the comingled specimens in Osborn and Mook, 1921, p. 259–261). Osborn even wrote to Oramel Lucas:

“I find that the records which came to use with the collection from Professor Cope are very inadequate and do not enable us to determine where the various fossils were found. I write to ask whether you have any records of the number and kind of bones taken out of the different quarries which would enable us to clear up this very import question.” (Osborn to Lucas, April 30, 1904, GPPS docs).

Among the Cañon City dinosaurs, the type of *Amphicoelias fragillimus* was missing, as were the type

mandible of *Laelaps trihedrodon*, and parts of the types of *Camarasaurus leptodirus* and *Amphicoelias latus* (Osborn and Mook, 1921; Chure, 2001). McIntosh (1998) also reports that some bones mentioned in the shipping lists of Lucas were missing, an oversight that Osborn knew nothing about because the documents were assumed to be lost (Osborn and Mook, 1921; McIntosh, 1998). Nevertheless, all of the missing specimens (mammalian, as well as dinosaurian) were assigned catalog numbers in the event that they were eventually found.

## ABBREVIATION

AMNH FR – American Museum of Natural History, Fossil Reptile collection, New York City, New York. GPPS docs – archives of the Garden Park Paleontological Society housed at the Royal Gorge Regional Museum and History Center, Cañon City, Colorado.

## COPE’S GIANT NEURAL SPINE

In his description of *Amphicoelias fargillimus*, Cope wrote that he thought the neural spine compared favorably to that of *A. altus* (figure 1B), a taxon he named the previous year (Cope, 1877d):

“It [the neural spine] exhibits the general characteristics of the genus *Amphicoelias*, in the hyposphen [sic], antero-posteriorly placed neural spine, and elevated diapophysis for the rib articulation. The diapophyses are compressed and supported by a superior and inferior, and anterior and posterior, thin buttress, separated by deep cavities.” (Cope, 1878f, p. 563).

At the time of this writing, sauropods had just been discovered in the United States the year before and were very imperfectly known. From Cope’s limited point of view, the two neural spines did indeed resemble one another more than to those of *Camarasaurus supremus*, the only other sauropod known to him that included dorsal vertebrae (compare figures 1A and 1B with 1C and 1D). Only now with many hundreds more sauropod specimens do we know that many of the cited characters are more widely spread.

In differentiating between the two species of *Am-*

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*phicoelias*, Cope wrote (1878f, p. 563):

“As compared with the *Amphicoelias altus*, this reptile differs in the greater elevation and attenuation of the neural spine, as well as its different form; also in the generally more laminar character of its buttresses and walls. The double rib of the anterior border of the spine of *A. altus* is here [*A. fragillimus*] represented by two laminae which extend on each side, so as to give a horizontal section of the spine a T shape. The posterior zygapophyses have less lateral expanse than in *A. altus*, but they continue as horizontal laminae with a deep cavity above and below: their superior surfaces contract into two ridges, which are separated by a deep groove. These ridges, unlike the anterior ones, approximate to each other closely on the border of the spine. The summit of the spine is wanting.”

Despite these differences, Osborn and Mook (1921, p. 279), synonymized the two taxa, arguing that “Cope’s description indicates an animal with the general characters and proportions of *Amphicoelias altus*. It is doubtful, however, if the characters described by Cope warrant the placing of the type in another species different from *A. altus*. The form is therefore provisionally referred to *A. altus*.” This position was accepted by McIntosh (1998). In contrast, as will be shown below, I consider the characters listed by Cope as valid distinctions and will add to them based on his illustration.

The reliability of Cope’s illustrations was never questioned by Osborn and Mook (1921) who were able to match Cope’s illustrated bones to specific bones (see captions for their figures 7 to 14 and 17 to 20). Cope showed an artistic capability as a child (Osborn, 1931) and making his own drawings gave him an eye for detail that is missing in many of O.C. Marsh’s publications. Although Cope’s illustration of the bones from Cañon City lacked the refinement of staff artist Rudolf Weber who did the line drawings for the Osborn and Mook monograph (figure 2), there is no reason not to accept the reliability of the *Amphicoelias fragillimus* illustration.

There is also no reason not to accept the measurements given by Cope contrary to Woodruff and Foster

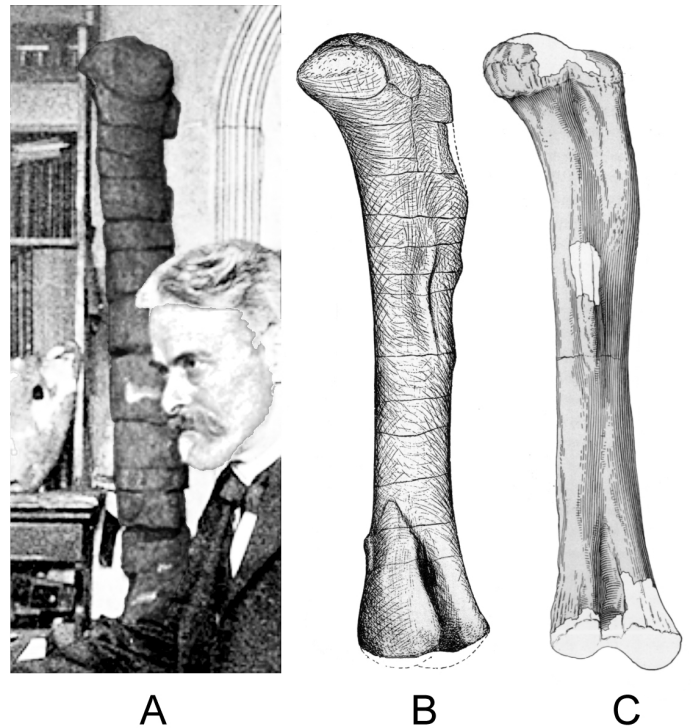


Figure 2. The reliability of the drawings made by Cope is seen in this example with the femur of *Amphicoelias altus*. (A) Femur as displayed in Cope’s office, circa 1895, slightly rotated with head towards the viewer (from Osborn, 1931). (B) Femur illustrated by Cope (1878b). (C) Femur as illustrated by Rudolf Weber (from Osborn and Mook, 1921).

(2014), who suggest “a typographical error” is likely in the vertebra’s height measurement because they perceive another such error in the use of the abbreviation “m” alone for millimeter, rather than the commonly used “mm” today. In point of fact, both meter and millimeter used the same abbreviation at that time (Anonymous, 1878, p. 316), and is understood by context. Cope also used “M” (upper case) for meter (e.g., Cope, 1877b, measurements for *Camarasaurus supremus*) and “m” (lower case) for millimeter (e.g., Cope, 1878f, for *Amphicoelias fragillimus*). Woodruff and Foster (2014, p. 217) also seek to cast doubt as to the reliability of Cope’s measurements by focusing on what they contend to be contradictory measurements given by Cope for the femur of *A. altus* (note: Cope, 1878b, printed January 12, 1878, as given at bottom of p. 233, not Cope, 1877, as stated by Woodruff and Foster, 2014). Cope does write

on page 244, “The length of the femur is six feet four inches” (= 1.930 meters) and on page 245 “Length of femur 1.524 M.” The illustration by Cope (1878b, 1877c; figure 2B) of the femur shows that the distal condyles were missing, therefore Cope’s measurement of 1.524 meters is reasonable as a minimum length, whereas Osborn and Mook (1921) gave a maximum preserved measurement of 1.77 meters. Osborn and Mook (1921) also note and illustrate the distal half of the left femur, which Cope undoubtedly used to estimate the femur length of *A. altus* as being “six feet four inches.” Today, we would qualify this as a “reconstructed” length, but such terminology was not in use at the time. Despite this possible alternative explanation, we really have no way of knowing Cope’s thinking and might find his explanation logical if we could ask him.

## AMNH FR 5777 AS A BASAL REBBACHISAURID

Traditionally, AMNH FR 5777, *Amphicoelias fragillimus*, was considered a diplodocid beginning with Osborn and Mook (1921) and continuing to this day (Woodruff and Foster, 2014). Even I had previously considered the specimen a diplodocid (Carpenter, 2006a), but reanalysis of Cope’s description and figure suggests otherwise, and that it is a basal rebbachisaurid.

I begin with some points of observation by Cope (1878f, p. 563). He stresses the fragility of the bone in several ways, “In the extreme tenuity [i.e., lack of solidity or substance] of all its parts, this vertebra exceeds those of this type already described [i.e., *A. altus*], so that much care was requisite to secure its preservation.” He also noted the “... attenuation of the neural spine.” Compared to the neural spine of *A. altus*, and all diplodocids for that matter, the neural spine is indeed “attenuated,” meaning it had a “simplified” structure in that there are few laminae and fossa. He notes, for example, that “The double rib [i.e., ridges or laminae] of the anterior border of the spine [i.e., paired spinoprezygapophyseal laminae] of *A. altus* is here [*A. fragillimus*] represented by two laminae which extend on each side [i.e., spinoprezygapophyseal + spinodiapophyseal laminae, see figure 3] so as to give a horizontal section of the

spine a T shape...” He says nothing about a prespinal lamina, but neither does he of the postspinal lamina, which is seen in figure 1A. Thus, it is not clear whether he means the “T-cross section” lacked a prespinal process, or whether he means “t-cross section” with a prespinal lamina. Either interpretation is possible (figure 4A). The tetra-radiate cross section (a.k.a. “t-cross section”) was considered by Carvalho and Santucci (2018) as a distinctly rebbachisaurid character, but in fact also occurs in dicraeosaurids (figure 4C). Cope also notes the many laminae of the neural arch (“generally more laminar character of its buttresses and walls”) that in the figure define various pneumatic cavities (figure 3).

Other rebbachisaurid features of the neural spine given by Whitlock (2011) can be gleaned from Cope’s illustration (figure 3). (1) The festooned spinodiapophyseal lamina, which is the sheet of bone between the neural spine and transverse process, is an unambiguously rebbachisaurid character (figures 4D to 4L; Sereno and others, 2007; Whitlock, 2011). (2) Pneumatic chambers dorsolateral to neural canal are implied by the paired foramina on each side of the postspinal lamina. This character occurs in *Comahuesaurus* (Carbadillo and others, 2012), *Demandasaurus* (Torcida Fernández-Baldor and others, 2011), and *Rebbachisaurus* (Wilson and Allain, 2015). Other pneumatic chambers appear to have been widespread throughout the neural arch as revealed by the damaged area below the postzygapophyses. There is a large pneumatic cavity (camera) that probably extended dorsally from the pneumatic cavity of the centrum. This feature is also seen in the damaged D4 of CM 94 (*Diplodocus carnegii*) and in *Barosaurus* (J. Foster, Utah Field House of Natural History State Park Museum, written communication, 2018). Pneumatized neural arches also occur in the rebbachisaurids *Comahuesaurus* (Carbadillo and others, 2012), *Demandasaurus* (Torcida Fernández-Baldor and others, 2011), *Katepensaurus* (Ibiricu and others, 2017) and *Rebbachisaurus* (Wilson and Allain, 2015). (3) The height of the neural arch below the postzygapophyses is very high among rebbachisaurids, but this character is also shared with *Haplocanthosaurus*, *Dicraeosaurus*, and the last dorsals of *Apatosaurus* (figure 4B, 4C, and 4Q).

One character that occurs in rebbachisaurids, as



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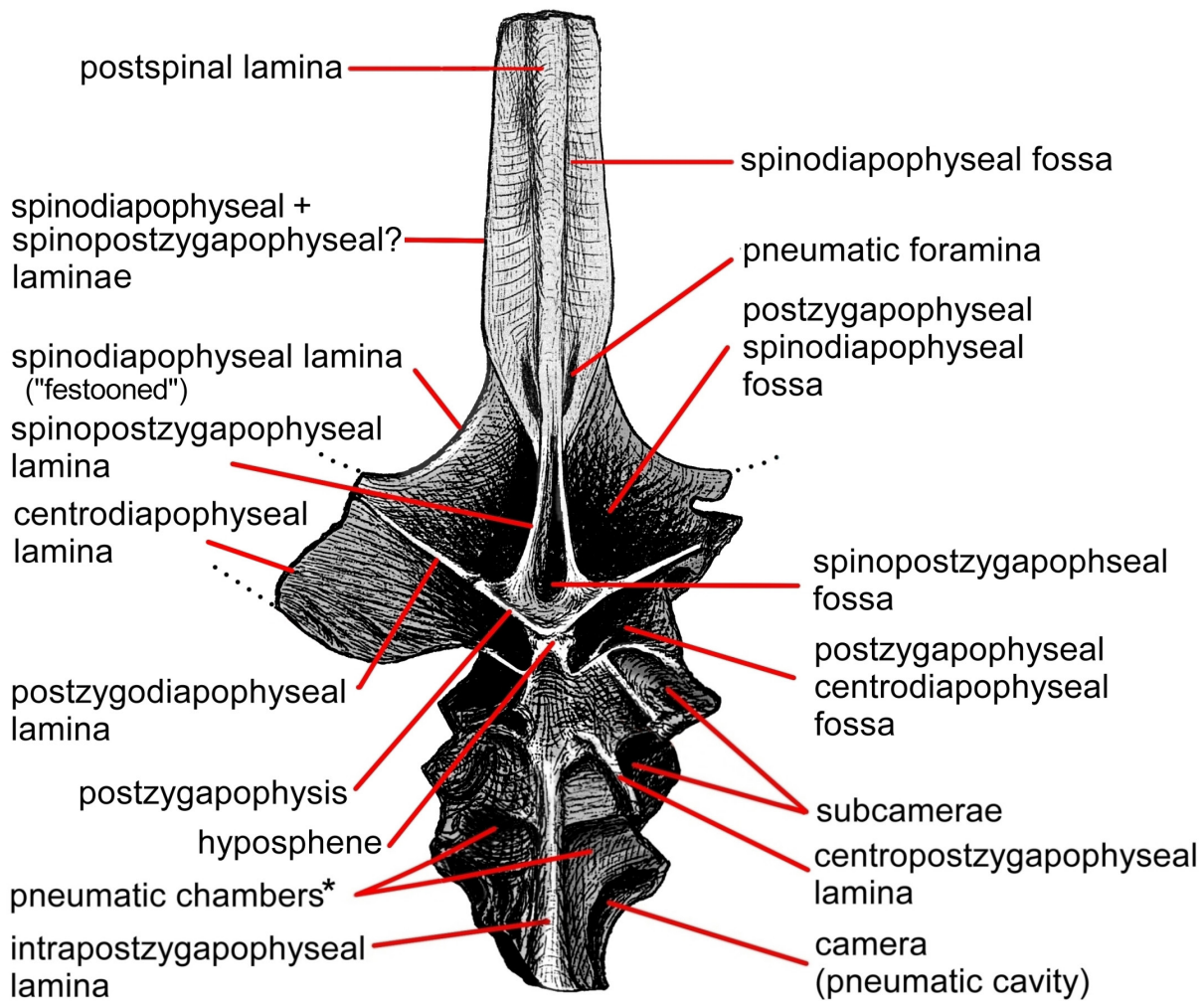


Figure 3. Drawing made by E.D. Cope of the holotype of *Maraapunisaurus fragillimus* (Cope, 1878f) with parts labeled. "Pneumatic chambers\*" indicate the pneumatic cavities dorsolateral of the neural canal, a feature also seen in several rebbachisaurids. Terminology from Wilson (1999, 2011) and Wilson and others (2011).

well as dicraeosaurids and *Haplocanthosaurus*, that is equivocal in AMNH FR 5777 is the rather steep angle of the transverse process. Much of this process is missing and Cope implies that it was nearly horizontal with dashes (figure 1A), but I believe he was influenced by *A. altus* to which he thought the giant spine was most similar. There appears to be a slight upwards curvature of the distal portion of the spinodiapophyseal lamina best seen on the more complete left side which suggests that the transverse process could have been angled upwards, perhaps as much as 30° (figure 5A). This possibility is also supported by the angle of the lower edge

of the centrodiapophyseal laminae and by the angle of the postzygodiapophyseal lamina. As a general rule, the angle of the postzygapophysis also mirrors the angle of the transverse process among diplodocoids, with some noticeable exceptions: dorsal 7 of *Diplodocus carnegii* (Hatcher, 1901, plate 8) and dorsals 11–14 in *Haplocanthosaurus* where the postzygapophyses are nearly horizontal, but the transverse processes are steeply angled (Hatcher, 1903, plate 1). However, in the latter, the postzygodiapophyseal laminae do reflect the upward angle.

The postzygapophyses are proportionally smaller than they are in *A. altus* where they are very large as not-



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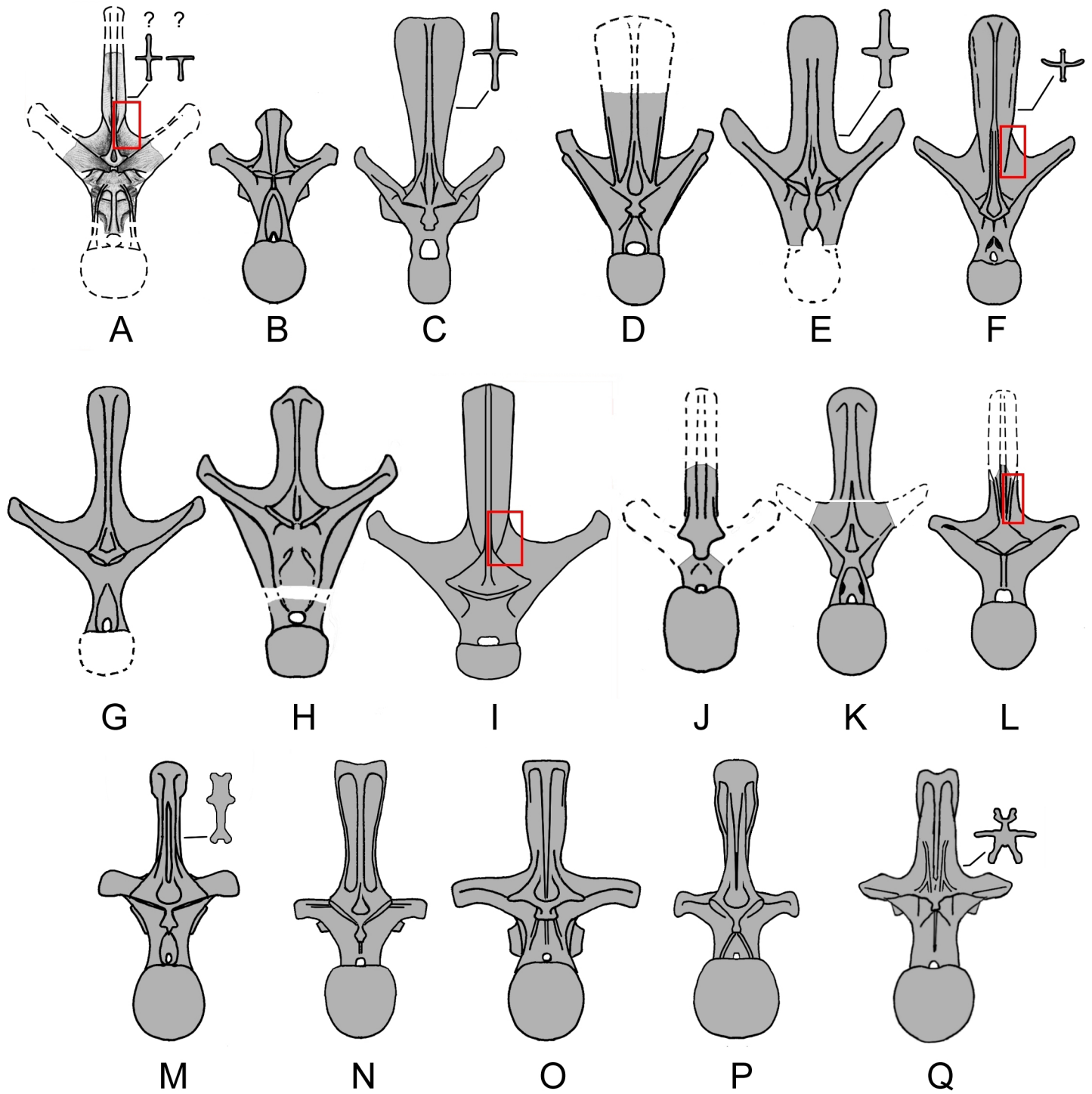


Figure 4. Caption is on the following page.

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Figure 4 (figure is on previous page). Comparison of various sauropod dorsal vertebrae in posterior view: (A) *Maraapunisaurus* as a rebbachisaurid, (B) *Haplocanthosaurus* (modified from Hatcher, 1903), and (C) *Dicraeosaurus* (modified from Janensch, 1929). Rebbachisaurids: (D) *Histriasaurus* (reconstructed from Dalla Vecchi, 1999), (E) unnamed (modified from Apesteguía, 2007), (F) *Rebbachisaurus* (reconstructed from Wilson and Allain, 2015), (G) *Limaysaurus* (modified from Calvo and Salgado, 1995), (H) *Nopcsaspondylus* (reconstructed from Nopcsa, 1902), (I) unnamed (modified from Carvalho and Santucci, 2018), (J) *Comahuesaurus* (reconstructed from Carballido and others, 2012), (K) *Demandasaurus* (reconstructed from Torcida Fernandez-Baldor and others, 2011) with neural spine of first caudal, and (L) *Katepensaurus* (reconstructed from Ibiricu and others, 2013). Basal Diplodocoid: (M) *Amphicoelias* (modified from Osborn and Mook, 1921). Diplodocids: (N) *Apatosaurus* (modified from Gilmore, 1936), (O) *Barosaurus* (reconstructed from photographs), (P) *Supersaurus* (reconstructed from photographs), (Q) *Diplodocus* (reconstructed from photographs; cross section modified from Osborn, 1899). Cross sections of neural spines also shown for A, C, E, F, M, and Q. All scaled to same height, except for B. Small red boxes in A, F, I, and L show divergence of the lateral spinopostzygapophyseal laminae from the postspinal lamina. Images are not to equal scale.

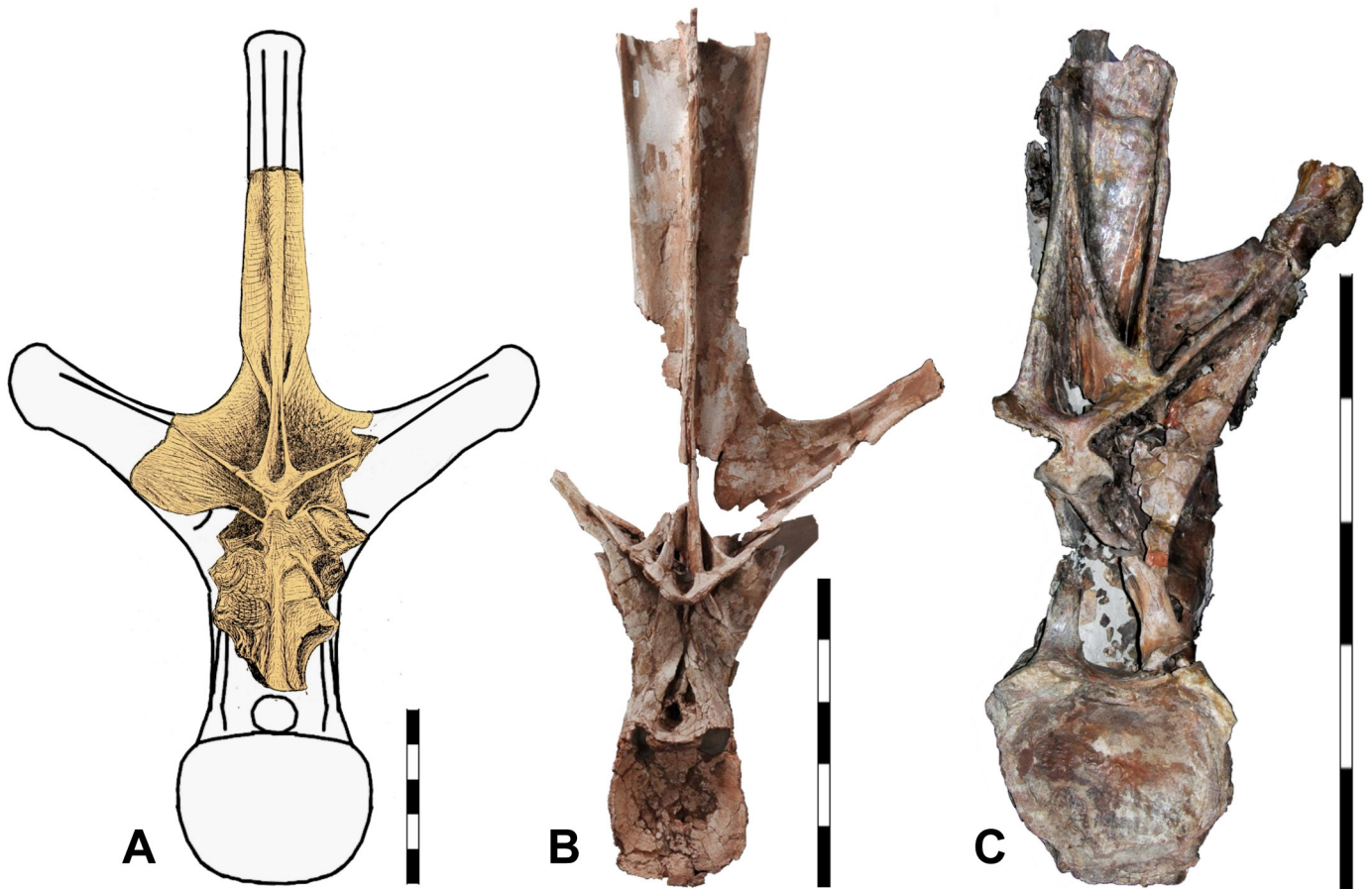


Figure 5. Comparison of the neural spine of *Maraapunisaurus fragillimus* restored as a rebbachisaurid (A), and the dorsal vertebrae of *Rebbachisaurus garasbae* (B), and *Histriasaurus boscarollii* (C). Increments on scale bars = 10 cm.

ed by Osborn and Mook (1921; figure 1C). The articular surfaces in AMNH FR 5777 are angled approximately 30°, noticeably steeper than in *A. altus*. The postzygodiapophyseal lamina connects the postzygapophyses

with the spinodiapophyseal lamina just below its dorsal rim. The spinopostzygapophyseal laminae extend dorsomedially from the postzygapophyses to join and form the postspinal lamina as they typically do in reb-

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bachisaurids, such as *Rebbachisaurus* and *Histriasaurus* (figure 5B and 5C), but also in the dicraeosaurids *Amargasaurus* and *Dicraeosaurus*. The postspinal lamina extends the entire preserved length of the neural spine. The spinopostzygapophyseal laminae form a triangular or lachrymiform spinopostzygapophyseal fossa between them. Laterally adjacent to where the postspinal lamina is formed, two short laminae diverge and extend dorsolaterally to combine with the spinodiapophyseal laminae along the sides of the neural spine. The identity of these laminae is problematic because they do not extend to the postzygapophyses. Nevertheless, a similar divergence involving the lateral spinopostzygapophyseal laminae occurs in several rebbachisaurids (red boxes in figures 4A, 4F, 4I, and 4L). In diplodocids, the lateral spinopostzygapophyseal laminae of the posterior dorsal vertebrae do not contact the postspinal lamina but are separate.

The evidences above show that AMNH FR 5777 cannot be referred to the genus *Amphicoelias* as Cope (1878f) had originally suggested based on the very limited information available to him. Therefore, a new generic name is warranted, but first I need to defend naming the missing type. The fact that the specimen is missing does not invalidate giving it a new generic name (ICZN 1999; Article 72.5.6). “In the case of a nominal species-group taxon based on an illustration or description, or on a bibliographic reference to an illustration or description, the name-bearing type is the specimen or specimens illustrated or described (and not the illustration or description itself).” This is reiterated in Article 73.1.4 (ICZN, 1999). Some researchers have objected to this provision in the Code, but as Krell and Marshall (2017, p. 4) have noted, “It is important to understand that a change in the Code to disallow the use of photographs [or illustrations] as proxies for lost types would not change the underlying taxonomy. The processes of discovery and description of species, which are matters of taxonomic judgment rather than rules, would remain the same.” It must also be remembered that the Code is meant for all branches of zoology, not just vertebrate paleontology. A binding rule that physical type specimens must exist would exclude some branches of zoology from the Code as listed in Krell and Marshall (2017).

Finally, lest it be thought that the Code gives free reign to naming taxa from illustrations of existing specimens, it also states “Preference for specimens studied by author. An author should designate as holotype a specimen actually studied by him or her, not a specimen known to the author only from descriptions or illustrations in the literature.” (ICZN 1999, Recommendation 73B). This nonbinding guideline is given as a recommendation because there are instances where the material is missing or destroyed, as was the case for the rebbachisaurid *Nopcsaspondylus alarconensis* named by Apesteguía (2007) for a vertebra described and figured (but not named) by Nopcsa (1902), for the stegosaur *Alcovasaurus longispinus* by Galton and Carpenter (2016), and for AMNH FR 5777. The recently issued nonbinding Declaration 45 (ICZN 2017) seeks to promote good taxonomic practice regarding an unpreserved specimen as the name-bearing type. As Krell and Marshall (2017) commented, “The Code cannot dictate what quality or quantity of evidence is enough; that is a matter of taxonomic judgment.”

## SYSTEMATIC PALEONTOLOGY

### Sauropoda Marsh, 1878

#### Diplodocidae Marsh, 1884 (Upchurch, 1998)

#### Rebbachisauridae Bonaparte, 1997

*Maraapunisaurus fragillimus* (Cope, 1878f) n.g.

Figures 1A, 3, 4A

*Amphicoelias fragillimus* Cope, 1878f

*Amphicoelias altus* Osborn and Mook, 1921 in part

*Amphicoelias altus* McIntosh, 1998 in part

*Amphicoelias fragillimus* Cope, 1878f (Carpenter, 2006a)

### Etymology

Ma-ra-pu-ni (pronounced mah-rah-poo-nee) — Southern Ute for “huge” used here in reference to the huge size of the animal, and *saurus*, Greek for reptile. The Garden Park area was traditionally Ute tribal territory before they were displaced by settlers in the mid-1800s. The name was recommended by the Southern Ute Cultural Department, Ignacio, Colorado.



## Holotype

AMNH FR 5777 (missing) consisting of a posterior dorsal neural arch, including neural spine (minus the distal apex), the proximal parts of the transverse processes, and both postzygapophyses. Woodruff and Foster (2014, p. 211 and 214) also claim “a distal end of a femur” as part of the type, despite no mention of that by Cope (1878f) nor Osborn and Mook (1921). The only mention of a distal end of a femur occurs in Cope’s field notes for 1879. It is here not considered part of the holotype because it could just as easily belong to a large specimen of *C. supremus* or *A. altus* which also occurred nearby.

## Diagnosis

Combination of characters, including extremely tall neural arch to the base of the postzygapophyses (estimated approximately 1/3 total height of the specimen); unbifurcated, simply structured neural spine with spinopostzygapophyseal laminae joined dorsally to form the postspinal lamina; pneumatic camerae in neural arch and paired pneumatic foramina pierce the neural spine on each side of the postspinal lamina just above where spinopostzygapophyseal laminae join; hyposphene present; the postspinal lamina extends dorsally the entire preserved length of neural spine and with the spinodiapophyseal + spinopostzygapophyseal(?) laminae give the neural spine a simple T-shaped cross section.

## Description and Discussion

The general assumption for AMNH FR 5777 is that it is from a posterior dorsal, possibly D-9 or D-10 (Osborn and Mook, 1921), D-10 (Carpenter, 2006a). Cope, however, simply referred to the specimen as a “posterior dorsal vertebrae” and could not have identified it as a D-10 contrary to Woodruff and Foster (2014, p. 213) because the sauropod dorsal counts were unknown at this time.

The neural arch below the postzygapophyses is damaged, but exceptionally tall. It has a very prominent intrapostzygapophyseal lamina that slightly wid-

ens ventrally towards the missing neural canal (figure 3). Dorsally, it merges into a broad surface below the hyposphene. This region appears to be undamaged and what may be the right centropostzygapophyseal lamina indicates that the laminae ended well below the hyposphene, rather than uniting with that structure. The hyposphene is proportionally small for the size of the neural arch and a simple, rectangular structure (figure 3). The hyposphene is plesiomorphic for sauropods (Apes-teguía, 2005), commonly occurring in Flagellicaudata, and only in basal rebbachisaurids (e.g., *Histriasaurus*, *Comahuesaurus*, and *Demandasaurus*).

The damaged area of the neural arch reveals several pneumatic chambers (camerae and subcamerae), including a large one (figure 3) that probably extended dorsally from the pneumatic cavity of the centrum. This latter feature is also seen in the damaged D-4 of CM-94 (*Diplodocus carnegii*) and *Barosaurus* (J. Foster, Utah Field House of Natural History State Park Museum, written communication, 2018). Pneumatized neural arches also occur in the rebbachisaurids *Demandasaurus* (Torcida Fernández-Baldor and others, 2011), *Comahuesaurus* (Carbadillo and others, 2012), *Rebbachisaurus* (Wilson and Allain, 2015), and *Katepensaurus* (Ibiricu and others, 2017). There also appears to be a pair of pneumatic chambers in the neural arch dorsolateral to where the neural canal is assumed to have been (figure 3 “pneumatic chambers\*”). This character is shared with *Demandasaurus* (Torcida Fernández-Baldor and others, 2011), *Comahuesaurus* (Carbadillo and others, 2012), and *Rebbachisaurus* (Wilson and Allain, 2015).

The postzygapophyses are proportionally smaller than they are in *A. altus* where they are very large as noted by Osborn and Mook (1921; figure 1B). The articular surfaces in AMNH FR 5777 are angled approximately 30 degrees, noticeably steeper than in *A. altus*.

## Size of *Maraapunisaurus*

It is impossible to discuss AMNH FR 5777 without delving into the issue of its size and that of the animal to whom it belonged. In his description of “*Amphicoelias fragillimus*,” Cope (1878f, p. 564) wrote:



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“These figures [the measurements] show that the total elevation of this vertebra, when complete, was not less than six feet, and probably more.”

Woodruff and Foster (2014, p. 219) make it plain they do not believe Cope, writing:

“...that it is highly unlikely that a terrestrial quadruped of such a purported body size could have existed.”

It is unfortunate that they seek to disprove Cope’s claim by casting aspersions about the quality of his work and go so far as to alter Cope’s measurements, claiming that “proportionally these new values fit much better...”

There is, however, corroborative evidence for the existence of the big neural spine as stated by Cope. In late 1877, when word began to circulate of the large bones being uncovered in Garden Park, U.S. Geological Survey geologist Hayden visited Lucas as reported by Pangborn (1878, p. 51). Lucas maintained contact with Hayden and wrote to him on November 18, 1878 (GPPS docs):

“You have doubtless seen Prof Cope’s report on the *Amphicoelias fragillimus*, the vertebra of which is six feet in elevation, requiring a femur twelve feet long, almost fabulous dimensions.”

We know from the GPPS docs archives that Cope sent Lucas copies of his publications. Lucas would certainly have noticed if the measurements of the neural spine were in error. Instead, he corroborates Cope’s estimate of a six-foot vertebra in the letter. We also know from copies of the letters he sent to Cope that he did measure many of the bones before shipment. For example:

“33 caudal vt of all sizes from 2 inches to 14 inches in diameter.” (Lucas letter to Cope, February 10, 1879, GPPS docs).

Even more detailed measurements were given in annotated drawings he sent with letters to Cope, which included various thicknesses as well (e.g., figure 6). Thus, it is doubtful that Lucas was merely parroting Cope when he wrote to Hayden. In addition, such a large and impressive fossil is not easily forgotten, as Lucas was to

recount in an autobiography written for the 50th reunion of the Oberlin class of 1880:

“I found a single bone a vertebra of another animal. This vertebra was six feet in elevation, i.e., the width of the back bone up and down. What a monster this animal must have been.” (Lucas 50th, GPPS docs.)

Given the corroborative evidence, what is the estimated restored size of the vertebra AMNH FR 5777? Cope modeled the missing centrum after *A. altus*, as did I initially (Carpenter, 2006a). Woodruff and Foster (2014) preferred a proportionally larger and rounder centrum modeled on *Supersaurus vivianae* on the basis that the

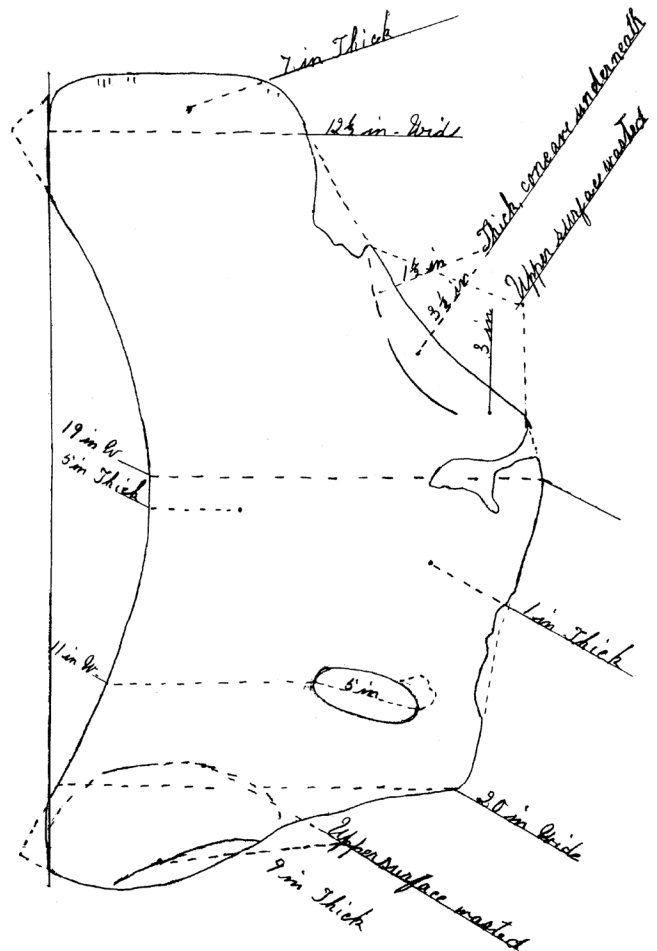


Figure 6. Copy by Oramel Lucas of one of his illustrations that accompanied one of his letters to Cope. The illustrations show the location of various measurements. This and other drawings were apparently made in the field before crating (GPPS docs).

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centrum becomes larger and rounder in diplodocids with increased size. As a rebbachisaurid, Cope was correct in giving his reconstruction a proportionally small centrum (figure 1A). Using rebbachisaurid vertebrae (figure 5) as a guide does imply a small centrum that was wider than deep. In the new reconstruction (figure 5A), it is difficult to know how much of the neural spine and diapophyses are missing, or the actual height of the centrum. The reconstructed proportions are based on *Rebbachisaurus* because of the best fit of two easily identified landmarks when the neural spine is scaled down and overlain other vertebrae. These include the base of the neural pedicle (must be at least slightly above the top of the neural canal) and the upper curved edge of the spinodiapophyseal lamina. Using other rebbachisaurid vertebrae, including the basal *Histriasaurus*, was less successful because they have proportionally shorter neural arches. The reconstruction gives a vertebrae 2.4 m tall and less than the previous 2.7 m by me (Carpenter, 2006a) and 2.8 m by Woodruff and Foster (2014).

To better understand the possible size of *Maraapunisaurus*, knowing the femur length would be ideal. To give perspective of the huge size of the animal for his readers, Cope (1878f, p. 564) estimated the femur length as 3.66 m based on his observation that the femur was twice the height of the dorsal vertebra in *A. altus* and *Camarasaurus supremus*. The ratio may be significantly different in rebbachisaurids, although few specimens have useable elements. One example is *Limaysaurus*, where the incomplete dorsal is restored as 120 cm tall, whereas the complete femur is 144 cm (Calvo and Sal-

gado, 1995, as *Rebbachisaurus tessonei*). In this case, the vertebra is 83% the femur length, rather than 50%. If this pattern is representative of most rebbachisaurids, then the femur of *Maraapunisaurus* was approximately 2.9 m tall, which is smaller than estimated by Cope and significantly less than my previous estimate of 4.3 to 4.6 m (Carpenter, 2006a) assuming skeletal proportions similar to *Diplodocus*. Paul (1994) estimated the femur as 3.1 to 4 m, and Woodruff and Foster (2014) estimated 4.76 m. In comparison, the currently largest known sauropod femur is 2.31 m belonging to cf. *Antarctosaurus giganteus* (Huene, 1929).

Revised as a rebbachisaurid modeled after *Limaysaurus*, one of the few specimens complete enough to for a skeletal reconstruction, *Maraapunisaurus* is only 30.3 m long, and 7.95 m at the hips (figure 7). This is significantly less than my previous estimate length of 58 m (Carpenter, 2006a) and Paul's (1994) estimate of 40 to 60 m. Woodruff and Foster (2014) did not give an estimated length based on their revised size of the vertebra. However, Parrish (2006) found that neck length in sauropods scales to torso length to the power of 1.35. That would mean that the neck of *Maraapunisaurus* was 7.6 m long rather than the 6 m long, which it would have if *Limaysaurus* were simply scaled larger. The result is that *Maraapunisaurus* might have been 32 m long, which puts it within the range estimates for *Supersaurus* and *Diplodocus hallorum* (Lovelace and others, 2008).

Finally, the speculative reconstructed hindfoot length of *Maraapunisaurus*, 1.36 m, is in the size range for some of the type A sauropod tracks from Broome,

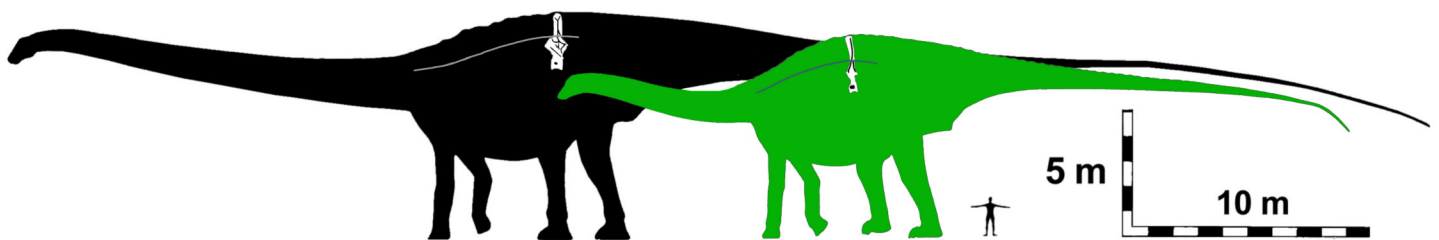


Figure 7. Body comparisons of *Maraapunisaurus* as a 30.3-m-long rebbachisaurid (green) compared with previous version as a 58-m-long diplodocid (black). Lines within the silhouettes approximate the distal end of the diapophyses (i.e., top of the ribcage). Rebbachisaurid version based on *Limaysaurus* by Paul (2016), with outline of dorsal based on *Rebbachisaurus*; diplodocid version modified from Carpenter (2006).

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Australia (Salisbury and others, 2016). I would note, however, that the largest pes track (Salisbury and others, 2016, figure 29) is most likely closely set manus and pes prints (compare their figures 27C and 28C; note manus track behind pes). Regardless, some of the other tracks in the 1.35 to 1.40 m range contradict Woodruff and Foster (2014, p. 219) that such huge sauropods were impossible. Salisbury and others (2016) rightly note that the Broome tracks have major ramifications on the upper size-limits of terrestrial vertebrates.

### Loss of the Neural Spine

As noted above, the holotype of *Maraapunisaurus fragillimus* is one of several specimens that were missing when the American Museum of Natural History took possession of the Cope collection. I have previously hypothesized that the specimen crumbled and was disposed of by Cope years before the collection was sold (Carpenter, 2006a, p. 134). I still believe that to be the strongest hypothesis, although I now consider that the destruction may have occurred by mishandling or rough handling of the crate with the specimen during its move 8 km to the Memorial Hall basement storage where Cope kept most of the Lucas specimens (Osborn, 1931). We do know that hay was often used to pack the fossils in crates as Cope wrote regarding the shipping of *Elasmosaurus*:

“It is very desirable that the specimens should be packed in such a way as to avoid friction or breakage in case of sudden jars. To accomplish this each single piece or mass, should be so surrounded in the hay or other packing as to allow of some elasticity of contact with the next. It is also important that any box should not be too large to bear the rough handling of so much weight: otherwise it may be broken, even much lost.” (Cope to Theophilus Turner, February 13, 1868, given in Almy, 1987, p. 188).

That the use of hay to pack fossils was widespread at this time is seen by the instructions Marsh gave his collectors:

“Pack fossils in boxes of moderate size, and made of inch boards. Plenty of hay or straw should be put

on the bottom, and closely around sacks of fossils, so that they cannot move when the box is turned over.” (Schuchert and LeVene, 1940, p. 173; see also Davidson and Everhart, 2017).

The major problem with hay is its compaction under heavy weight, a serious problem as Cope noted in a letter regarding the shipment of the *Elasmosaurus*:

“Each mass should have had a thicker wrapping of hay (still more when paper is used) & the box should be so packed as to prevent the rubbing and moving of the pieces. The largest box had 1/3 to 1/4 vacant space when it arrived & it as well as others, suffered some injury on that account.” (Cope to Turner, February 13, 1868, given in Almy, 1987, p. 189).

The large and heavy neural spine of *Maraapunisaurus* would have been difficult to crate and ship safely from Colorado to Philadelphia where it was described and illustrated by Cope, as well as from Cope’s home to his Memorial Hall storage. Given that preservatives were not yet in use, it is amazing that the specimen arrived in Philadelphia in the first place. Lucas does mention that he solved the problem of keeping the fractured bones he was excavating together:

“They [the fossil bones] were taken out with great care, each piece for the most part, especially in all the more fragile bones, being secured in its proper position relative to those about it, by pasting paper on the surface of the bones.” (Lucas to Marsh, March 11, 1879).

This precursor to the use of plaster of Paris jackets was independently arrived at by different people (see Schuchert and LeVene, 1940). Ultimately, however, we will never know what happened to this and other Cope specimens that went missing.

## PALEOBIOGEOGRAPHICAL IMPLICATIONS

*Maraapunisaurus fragillimus* as a rebbachisaurid has profound paleobiogeographical and temporal implications. Previously, rebbachisaurids were only known from the Cretaceous and have not been report-



ed from North America. However, the phylogenetic study by Wilson and Allain (2015) estimated a 20-million-year ghost lineage for rebbachisaurids extending back to the Late Jurassic, and thus to the age of *Maraapunisaurus*. This 20-million-year ghost lineage has been shortened recently to 10 million years by *Xenoposeidon* (Taylor, 2018). The previous absence of rebbachisaurids from North America does not exclude *Maraapunisaurus* from being the first reported. *Suuwassea*, for example, has only recently been identified as a dicraeosaurid from the Morrison Formation, making it the first (Whitlock, 2011).

Although *Maraapunisaurus* is a basal rebbachisaurid because of the presence of a hyposphene (shared with *Histriasaurus*, *Comahuesaurus*, and *Demandasaurus*), it also has pneumatic chambers dorsolateral to neural canal as in *Comahuesaurus*, *Demandasaurus*, and *Rebbachisaurus*, but which is apparently lacking in *Histriasaurus*. The neural arch is also very tall and is proportional to that of *Rebbachisaurus*. Thus, in some ways *Maraapunisaurus* is more derived than other basal rebbachisaurids, especially *Histriasaurus* in a few of its features (figure 5).

The coeval presence of *Maraapunisaurus* and diplodocids in the Morrison Formation raises interesting issues about the paleobiogeographical origins of rebbachisaurids. The Late Jurassic age for *Maraapunisaurus* does support the hypothesis for a Middle Jurassic split of the diplodocoids into the diplodocids and rebbachisaurids (Serenó and others, 2007; Wilson and Allain, 2015). Given that there is greater similarities between Late Jurassic and pre-Aptian faunas of North America and Europe (Galton, 1980; Kirkland and others, 1997, 2016; Carpenter and others, 2002; Carpenter, 2006b; Mateus, 2006) than there is between North and South America for the same time interval, it seems more probable that the migration of rebbachisaurids was from North America to Europe during the latest Late Jurassic and earliest Early Cretaceous, with a later arrival in South America via Europe and Africa (figure 8). This direction of migration is the reverse to that previously hypothesized (Torcida Fernandez-Baldor and others, 2011; Fanti and others, 2013). Nevertheless, temporal distribution does seem to support this possibility (figure

8C) and that the presence of post-Berriasian–pre-Aptian rebbachisaurids in Africa are predicted.

## DISCUSSION AND CONCLUSION

It has been over 140 years since Oramel Lucas discovered the giant neural spine that was named *Amphicoelias fragillimus* by Edward Cope in 1878. This specimen was lost prior to 1902, the year the Cope reptile collection was transferred to the American Museum of Natural History. The specimen has long been referred to *Amphicoelias altus*, which is now considered a basal diplodocoid (Whitlock, 2011). Reanalysis of Cope's description and figure demonstrate at least two unambiguous rebbachisaurid characters: the festooned spinodiapophyseal lamina and pneumatic neural spine. Because the specimen cannot be referred to the genus *Amphicoelias*, a new name is proposed, *Maraapunisaurus fragillimus* (Cope, 1878f). As a rebbachisaurid, *Maraapunisaurus* from the Late Jurassic of North America is both the oldest rebbachisaurid and the first from North America and it may be the center of the group's origin.

## ACKNOWLEDGMENTS

Special thanks to Pat Monaco and the late Donna Engard for sharing various documents pertaining to Oramel Lucas. These are now housed at the Royal Gorge Regional Museum and History Center, Cañon City, Colorado. Andrew Smith and Melissa Smeins (Bureau of Land Management, Royal Gorge Field Office, Cañon City, Colorado), and Dan Grenard (unaffiliated, Cañon City, Colorado) made additional documents from the Garden Park Paleontology Society available. Thanks to Fabio M. Dalla Vecchia (Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain) for sharing his unpublished illustration of *Histriasaurus boscarollii*. Thanks to Ursula Göhlich and Andreas Kroh (Natural History Museum Vienna and Jürgen Kriwet, University of Vienna), for searching their collections for the holotype of *Nopcsaspondylus alarconensis*; the specimen remains lost. The name *Maraapunisaurus* was suggested by Hanley Frost, Sr., Edward Box III, and Garrett Briggs of the Southern Ute Cultural Department, Ignacio, Colorado. I am pleased to acknowledge that Zachary Taylor Ward Armstrong (Independent



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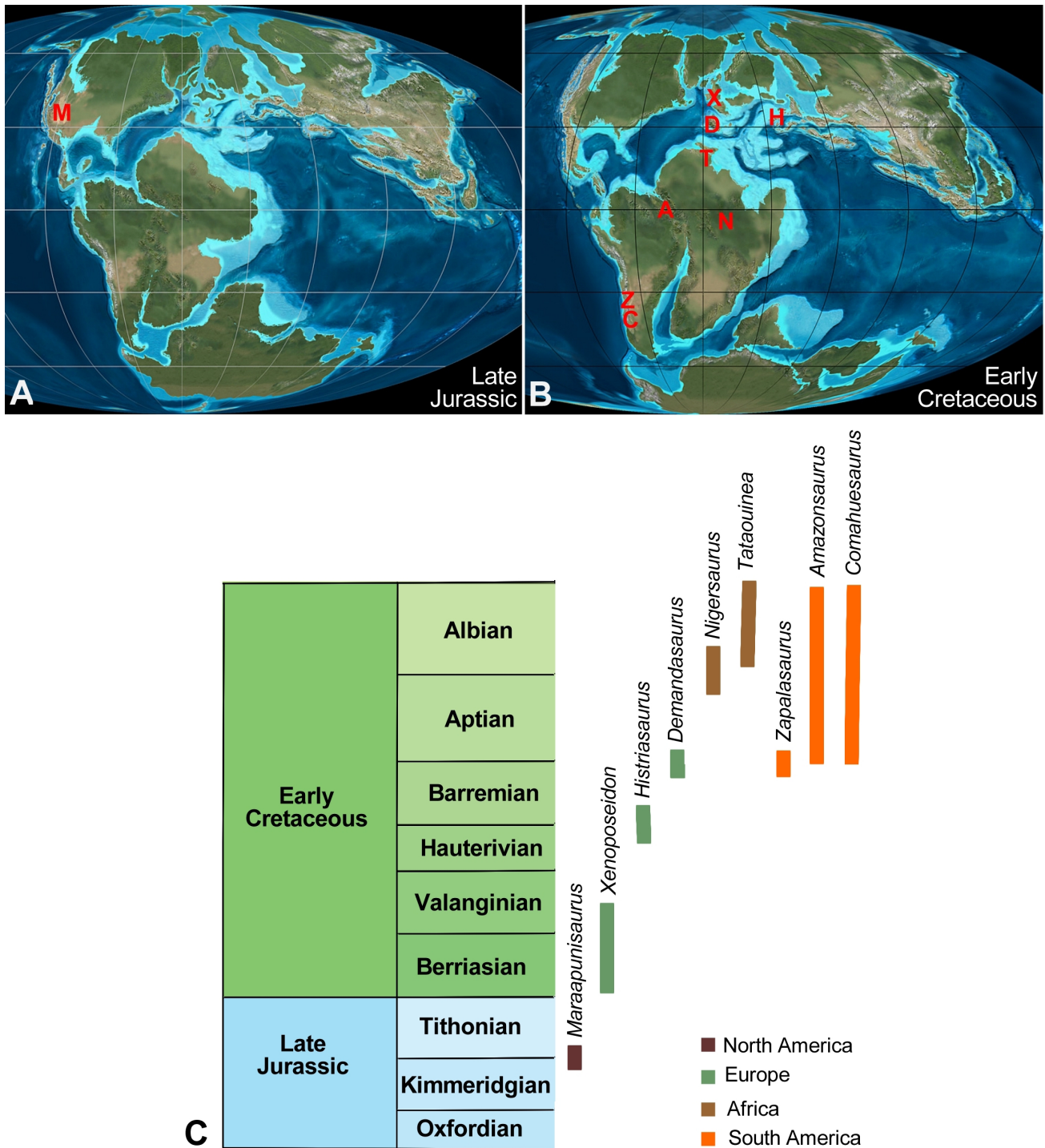


Figure 8. Paleogeographic maps showing the distribution of rebbachisaurids during the Late Jurassic (A) and Early Cretaceous (B). Abbreviations: M–*Maraapunisaurus* (Kimmeridgian-Tithonian), A–*Amazonasaurus* (Aptian-Albian), C–*Comahuesaurus* (Aptian-Albian), D–*Demandasaurus* (Upper Barremian-Lower Aptian), H–*Histriasaurus* (Upper Hauterivian-Lower Barremian), N–*Nigersaurus* (Aptian-Albian), T–*Tataouinea* (Albian), X–*Xenoposeidon* (Berriasian-Valanginian), and Z–*Zapalasaurus* (Barremian-lower Aptian). (C) Temporal and paleogeographic distribution of Late Jurassic and Early Cretaceous rebbachisaurids. Paleogeographic maps from the commercial version of Ron Blakey’s “Paleogeography of Western North America” that is licensed to the Prehistoric Museum.

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dinosaur blogger) who independently considered the possibility that AMNH FR 5777 was a rebbachisaurid four years before me in his blog: <https://palaeozoologist.deviantart.com/journal/Was-Amphicoelias-a-rebbachisaur-440611550>. I came to a similar conclusion based on Carvalho and Santucci (2018) and Apesteguía and others (2010). Finally, review comments by Greg Paul (independent dinosaur artist), John Whitlock (Mount Aloysius College), Mike Taylor (University of Bristol), and John Foster (Museum of Moab) are gratefully acknowledged.

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