BIGGEST OF THE BIG: A CRITICAL RE-EVALUATION OF THE MEGA-SAUROPOD *AMPHICOELIAS FRAGILLIMUS* COPE, 1878

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Abstract—Questions about the largest dinosaur have largely ignored or downplayed a discovery made in 1878 of a 1.5 m tall neural arch. The specimen is lost, but the original description by E.D. Cope of *Amphicoelias fragillimus* provides enough information to reconstruct the vertebra as a posterior dorsal of a diplodocid. The estimated 2.7 m height of the dorsal suggests a skeleton 58 m long, about 9.25 m at the highest point of the back, and with a body mass of 122,400 kg. These dimensions indicate that *A. fragillimus* was several orders of magnitude larger than any other sauropod. *A. fragillimus* existed at the peak of a trend toward gigantism in sauropods that progressed since their origin in the Late Triassic. One possible cause for large body size in sauropods, based on studies of extant mammalian megaherbivores, may be due to increased gut size for more efficient digestion of low quality browse by hindgut fermentation.

INTRODUCTION

Discoveries during the past decade or so of very large sauropods (>30 m) have led to the question about which was the largest dinosaur. Van Valen (1969) attempted to answer that question before many of the recent discoveries of large sauropods, such as of *Argentinosaurus*, thus was limited in the data available for his analysis. Contenders today include the diplodocids *Seismosaurus hallorum* from the Upper Jurassic of New Mexico (Gillette, 1991; as *Diplodocus hallorum* by Lucas et al., 2004 and Lucas et al. this volume) and *Supersaurus vivianae* from the Upper Jurassic of Colorado and Wyoming (Jensen, 1985; Lovelace et al., 2005), and the titanosaurids *Argentinosaurus huinculensis* from the Lower Cretaceous of Argentina (Bonaparte and Coria, 1993) and "*Antarctosaurus*" *giganteus* from the Upper Cretaceous of Argentina (Huene, 1929; Powell, 2003). All of these sauropods have estimated lengths of 30-35 m and estimated weights of between 30-90 tons (Mazzetta et al., 2004; Paul,1994) one possible contender, *Paralatitan stromeri* (Smith et al., 2001) is apparently shorter than 30 m. Intriguingly, these sauropods are only known from fragmentary remains. Based on the bone sample study in Amboseli Park by Behrensmeyer and Dechant Boaz (1980), most of the skeleton for such giant sauropods should be present. Although some of the loss is undoubtedly due to erosion of the fossils, most of the specimens consist of disarticulated and scattered skeletons. Considering the great mass of the bones, this dispersal is remarkable in light of the bone dispersal studies by Voorhies (1969) and Behrensmeyer (1975).

One other giant sauropod from the Upper Jurassic of North America, *Amphicoelias fragillimus* Cope, 1878b, is either ignored (e.g., Gillette, 1991) or only briefly mentioned (e.g., Mazzetta et al., 2004). Only Paul (1997), following preliminary work by Carpenter (1996), has discussed this taxon, but even this is brief. Because this taxon may indeed be the largest dinosaur known, a fuller assessment is presented below.

The holotype of *A. fragillimus* consists of a neural arch and spine (Fig. 1) believed to have been from the last or second to last dorsal (D10 or D9). It was collect by Oramel Lucas near the main *Camarasaurus supremus* localities in Garden Park, north of Cañon City, Colorado, as indicated by E.D. Cope's field notes (Fig. 2). Lucas began collecting for Cope in late 1877, and shipped the specimen to Cope during the spring or early summer of 1878 (McIntosh, 1998), who then published it in August 1878. Cope visited Lucas in July, 1879 and recorded in a small notebook the various quarries from which Lucas had been excavating (McIntosh, 1998; Monaco, 1998). Among the entries is "III *Amphicoelias fragillissimus* [sic] from between the two lots" (lots refers to quarries or sites). Specifically, the site is southwest of the "hill" of Cope's notes (now referred to as Cope's Nipple), and south of the *Camarasaurus supremus* I Quarry. The matrix in the vicinity of the quarry is a reddish
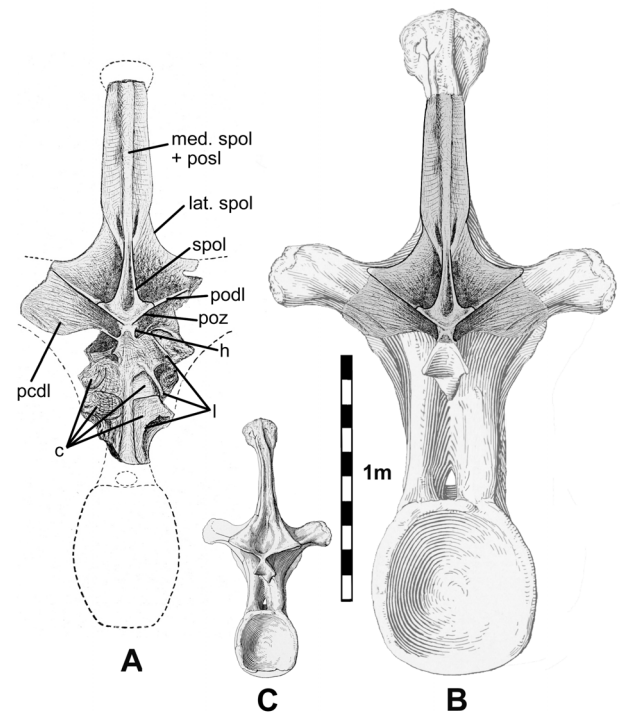

FIGURE 1. **A.** *Amphicoelias fragillimus* (AMNH 5777) as figured by Cope (1878b), modified with identification of features. **B.** Dorsal reconstructed based on modified *A. altus* (extensively modified from Osborn and Mook, 1921, fig. 21. **C.** Dorsal of *A. altus* (AMNH 5764) for comparison (modified from Osborn and Mook, 1921, fig. 21. **C.** cavities bounded by lamina within the neural arch; h, hyposphene; l, lamina within the neural arch (outer bone eroded away exposing interior); lat spol, lateral spinopostzygapophyseal lamina; med spol, medial spinopostzygopophyseal lamina; pcdl, posterior centroparapophyseal lamina; posl, postspinal lamina; poz, postzygapophysis; spol, spinopostzygapophyseal lamina.

mudstone and the specimen was probably very pale tan, tinted with a maroon red, as are all the surviving specimens from this level. Cope also records "IV Immense distal end of femur near 1st broken smaller femur." It seems very likely that this femur belonged to the same specimen as the neural arch and spine because it was found in the next site a few tens of meters away. Unfortunately, the whereabouts of both the neural spine and femur are unknown as first reported by Osborn and Mook (1921), and all attempts to locate the specimens have failed
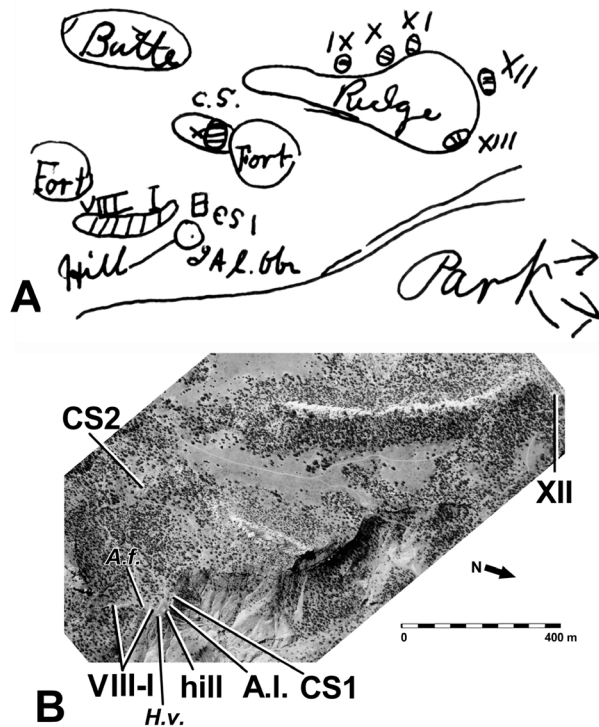
FIGURE 2. **A.** E.D. Cope's 1879 field notebook contains a map showing the location of the Lucas brothers quarries. **B.** This map allowed relocation of many of the quarries. *Amphicoelias fragillimus* was found at quarry III in a string of closely spaced quarries (I-VIII). I-XIII quarries; A.f. *Amphicoelias fragillimus*; A.l., - *Amphicoelias latus* quarry; CS1, 2, *Camarasaurus supremus* 1 and 2 quarries; H.v., probable site for *Hallopus victor* Marsh (see Ague et al., 1995). Most of the quarries along the ridge have not yet been relocated. See McIntosh (1998) for further discussion of the Cope map.

(McIntosh, 1998).

An attempt was made to relocate the quarry in 1994 including using ground penetrating radar. However, because the density of fossilized bone is the same as the encasing matrix, the technique, which relies on density differences, did not work. In addition, the mudstone containing lots I-IV is nearly stripped down to the underlying sandstone. The local topography suggests that most of the strata had already been stripped off by the time Lucas made his first dinosaur bone discovery in 1877. Thus, it is probable that most of the *Amphicoelias* skeleton was destroyed long before the neural spine was found.

Cope (1878b) states that the *Amphicoelias* "was found in the Dakota formation of Colorado...", which today would imply that the specimen is Aptian-Albian in age (Waagé, 1955). However, Cope also notes that the specimen was found "in the same bed that has thus far produced the known species of *Camarasaurus, Amphicoelias, Hypsirophus,* etc." *Camarasaurus* is a classic Morrison sauropod, and is in fact the most common sauropod found (Dodson et al., 1980). The Morrison has been dated as latest Oxfordian to early Tithonian (Kowallis et al., 1998). Because the Lucas quarries which these specimens came from occur near the top of the Morrison Formation, a Tithonian age for *Amphicoelias fragillimus* seems reasonable (Turner and Peterson, 1999).

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, New York; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; DMNH, Denver Museum of Natural History (now Denver Museum of Nature & Science), Denver, Colorado; USNM, United States National Museum (now National Museum of Natural History), Washington, D.C.

DESCRIPTION

It is unfortunate that the specimen of *Amphicoelias fragillimus* is missing, and that comparisons with other sauropods must rely on Cope's description. Although missing, it has been assigned the catalog number AMNH 5777. The generic referral by Cope was based on his (1878b, p. 563) observation that "[i]t 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 [i.e., spinodiapophyseal lamina] and inferior [i.e., centrodiapophyseal lamina], and anterior [i.e., prezygodiapophyseal lamina] and posterior [i.e., postzygodiapophyseal lamina], thin buttresses [i.e., lamina], separated by deep cavities."

The genus *Amphicoelias* (as *A. altus*) was named by Cope in December, 1877 (published in 1878a) for a mid-dorsal vertebra (D6?), a posterior dorsal vertebra (D10?), a pubis, and a femur (all AMNH 5764) from Quarry XII located at the north end of a long ridge (Fig. 2) about 1.5 km northwest of the main quarries. Osborn and Mook (1921) also referred a scapula, a coracoid, an ulna, and a tooth to the holotype. Quarry XII is stratigraphically the highest in the Morrison Formation in the Garden Park area, being about 15 m higher than the *Camarasaurus supremus* sites (Carpenter, 1998). As noted by Osborn and Mook (1921), the specimen closely resembles *Diplodocus,* especially in the posterior dorsal (best preserved): tall, slender neural spine, tall neural arch, well developed spinodiapophyseal laminae, and prominent posterior centroparapophyseal laminae. However, it also differs from *Diplodocus* having in a centrum that is as long as tall rather than taller than long, having an anteroposteriorly elongated, laterally compressed neural spine, parapophysis separate from the diapophysis, diamond-shaped hyposphene, pleurofossa (defined by Carpenter and Tidwell, 2005, p. 94) restricted to the centrum (not extending onto the neural arch), and less constricted ("pinched") centrum. The ulna is significantly longer relative to the femur length (0.6) than in *Diplodocus* (0.46); thus, the forelimbs were proportionally longer as well. The circular cross-section of the femur, once used to separate *Amphicoelias* from *Diplodocus,* is known to occur in *Diplodocus* as well (V. Tidwell, personal commun.).

The species name, *fragillimus,* apparently reflects the fragility or delicateness of the specimen produced by the thinness of the numerous laminae as noted by Cope (1878b, p. 563): "[in] the extreme tenuity [i.e., thinness] of all its parts, this vertebra exceeds those of this type [i.e., *Amphicoelias altus*] already described...". These laminae not only include the external ones connecting various structures, but also internal struts within the neural arch (Fig. 1A). These internal struts or laminae are exposed because the missing outer cortical bone was lost, probably to erosion. The delicateness of the specimen made collecting difficult, "much care was requisite to secure its preservation" (Cope, 1878b, p. 563), and may provide a clue to its disappearance (as discussed below).

Osborn and Mook (1921) provisionally synonymized *A. fragillimus* with *A. altus,* a position accepted by McIntosh (1998). However, there is reason to suspect that it is a distinct species as noted by Cope (1878b) and even possibly a distinct genus. *A. fragillimus* differs from *A. altus* in having a single postspinal lamina (compare Fig. 1B and 1C), prominent lateral spinopostzygapophyseal lamina, proportionally smaller postzygapophyses with prominent postzygodiapophyseal laminae, and an apparently taller neural arch. Some features are not visible in Cope's figure (Fig. 1A), and must be inferred from Cope's statements: the spinodiaopophyseal laminae are laterally directed so that in horizontal cross section, and the neural spine is T-shaped, rather than H-shaped. Unfortunately, without the holotype, the taxonomic validity of the specimen cannot be resolved.

HOW BIG WAS *AMPHICOELIAS FRAGILLIMUS*?

There is every reason to suspect that *Amphicoelias fragillimus* was indeed one of the largest, if not the largest dinosaur to ever walk the earth (the validity of the immense size is discussed below). As Cope (1878b, p. 563) noted regarding the specimen, it represents "the neural arch of the

vertebra of the largest saurian I have ever seen." Indeed the measurements Cope gives support this hyperbole: total height of specimen 1500 mm; from preserved base to postzygapophyses 585 mm; greatest width of postzygapophyses 190 mm; vertical diameter of the base of the diapophysis 390 mm. Cope estimated the total height of the vertebra as at least 6 feet (1.83 m) and probably more. Indeed, scaling the dorsal of *A. altus* to restore the missing parts of *A. fragillimus* (Fig. 1B) results in a vertebra 2.7 m tall! Paul (1994) estimated the size as 2.4-2.6m. Regardless of the exact measurements, Cope (1878b, p. 564) rightly states that "[t]he dimensions of its vertebra much exceed those of any known land animal."

In order to put *A. fragillimus* into perspective, Cope (1878b) speculates on the size of the femur. He notes that the femora of *A. altus* and *Camarasaurus supremus* were about twice as tall as their tallest dorsals, and he conjectured that the femur of *A. fragillimus* was over 12 feet (3.6 m) tall. In *Diplodocus*, the ratio of femur to D10 ranges from 1.6 (CM 84) to 1.7 (USNM 10865). Assuming a similar range in *A. fragillimus*, the femur was 4.3-4.6 m tall (Paul [1994] estimated a femur length of 3.1-4.0 m). Taking speculation further, what are some of the other dimensions for *A. fragillimus*? Much of this depends on the relative proportions of the body, which can be considerably variable in diplodocids (e.g., relative proportion of the ulna to femur as mentioned above for *A. altus*; proportionally longer distal caudals in *Diplodocus* than in *Barosaurus*, or longer neck in *Barosaurus* than in *Apatosaurus* (McIntosh, 2005). Should *A. fragillimus* be viewed as a scaled up version of *Diplodocus*, *Barosaurus*, or *Apatosaurus*? At present this question cannot be answered. For the sake of illustration, *A. fragillimus* is shown as a scaled up *Diplodocus* in Figure 3A. The estimated length is 58 m (190 ft), whereas Paul (1994) estimated a total length of 40-60 m. In comparison, *Seismosaurus* is 33.5 m and *Supersaurus* is 32.5 m (estimated from Fig. 3C,D). The fragmentary brachiosaurid *Sauroposeidon* is estimated to have been about 34 m long (Fig. 3E). In contrast, the fragmentary titanosaurid sauropods *Argentinosaurus*, *Paralititan* and "*Antarctosaurus*" *giganteus* are viewed as scaled up titanosaurid *Saltosaurus*, rather than a modified *Brachiosaurus* (e.g., Smith et al., 2001: fig. 2D). The mega-sauropod *Argentinosaurus* is 30 m, and the super-sauropods *Paralatitan* only 26 m and "*A*" *giganteus* 23 m (30 m is the arbitrary division between super- and mega-sauropods).

Some other speculative dimensions of *A. fragillimus* assuming *Diplodcus* proportions include a neck length of 16.75 m, body length (base of neck-end of sacrum) of 9.25 m, and a tail length of 32 m. The forelimb is 5.75 m and hind limb 7.5 m.

The mass of mega-sauropods is more difficult to ascertain. Assuming that the mega-diplodocids are scaled up versions of *Diplodocus*, then the volume (hence mass) changes in proportion to the third power of the linear dimension (Schmidt-Nielsen, 1984). Thus, if *Diplodocus carnegii* had a length of 26.25 m and mass of 11,500 kg (Paul, 1994), then *A. fragillimus* had a mass of around 122,400 kg, which is still within the hypothesized maximum mass for a terrestrial animal (Hokkanen, 1986). *Seismosaurus* and *Supersaurus* are each estimated to have had a mass of around 38,800 kg.

DISCUSSION

The present whereabouts of the holotype of *A. fragillimus* is unknown. The first to note its absence were Osborn and Mook (1921, p. 279): "The type of this species has not been found in the Cope Collection..." Subsequent attempts to locate the specimen by McIntosh (personal
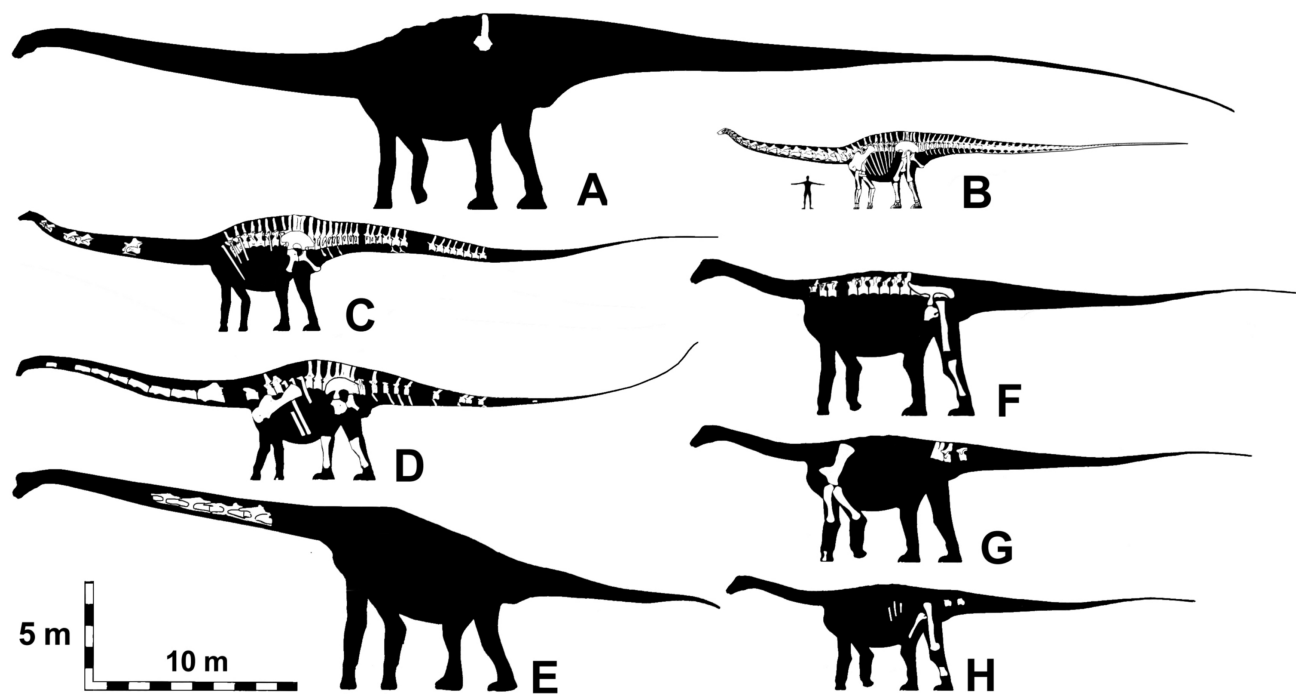

FIGURE 3. Body size comparison of mega- and super-sauropods. See text for lengths. Diplodocids: **A.** *Amphicoelias fragillimus*; **B.** *Diplodocus*; **C.** *Seismosaurus*; **D.** *Supersaurus*. Brachiosaurid: **E.** *Sauroposeidon*. Titanosaurids: **F.** *Argentinosaurus*; **G.** *Paralatitan*; **H.** "*Antarctosaurus*" *giganteus*. Except for *Diplodocus*, the body outlines are conjecture because of the fragmentary nature of the specimens. The titanosaurids are modeled after the titanosaurid *Saltosaurus*, rather than a brachiosaurid. Reconstructions are scaled to known bone measurements.

commun.) have also failed. The fate of the specimen is intriguing and a possible hypothesis is presented. As noted by Cope (1878b), the specimen was very delicate and required great care in its collecting. At the time, preservatives had not yet been employed to harden fossil bone, the first of which was a sodium silicate solution used in O.C. Marsh's preparation lab at Yale University beginning in the early 1880s (M.P. Felch letter to Marsh, October 30, 1883). The extreme fragility of large bone from the vicinity of the *A. fragillimus* quarry is attested to by the crumbling into small pieces of half of a large dorsal of *C. supremus* (DMNH 27228) at the Denver Museum of Nature & Science (the discovery and excavation of this *C. supremus* partial skeleton is given in Carpenter [2002]). The stratum in the vicinity of quarries (lots) I-IV is deeply weathered mixed illitic-smectitic mudstone that breaks into small irregular cubes. Bone in this level is also weathered, and the battered, incomplete appearance of the *A. fragillimus* as figured by Cope (1878b) suggests it lay partially exposed in the weathered zone. Thus, the specimen was extremely fragile and it is possible that it crumbled badly and was discarded by Cope soon after it was figured in posterior view (which may explain why no other views were offered by Cope in contrast to his description of other specimens).

The immense size of the measurements given by Cope and the inferred vertebra size have been met with skepticism (several individuals, verbal to Carpenter), with typographical errors in the measurements being the most commonly assumed explanation. There is, however, every reason to accept Cope at his word. First, Cope never made any subsequent corrections in his publications; furthermore, his reputation was at stake. Marsh, who was ever so ready to humiliate Cope, never called into question the measurements. Marsh is known to have employed spies to keep tabs on what Cope was collecting, and it is quite possible that he had independent confirmation for the immense size of *A. fragillimus*. Osborn and Mook (1921) accept Cope's measurements without question, as does McIntosh (1998). Thus, there is historical precedence for accepting the measurements as correct.

WHY ARE SAUROPODS SO BIG?

The immense size of *A. fragillimus* raises some very interesting questions regarding mega-sauropod biology. The trend towards gigantism in sauropods was established early in their evolution (Fig. 4). The earliest sauropods from the Late Triassic were already as big as some of the later ones. Therefore, whatever mechanism caused sauropods to become big affected them early in their evolution. Some possible clues can be derived from extant megaherbivores (as defined by Owen-Smith, 1988): elephants, hippopotamus, giraffe, and rhinoceros. In analyzing possible causes for sauropod gigantism, it is difficult to separate primary and secondary causes. For example, large body size confers protection against predators, but is this a primary or secondary cause? In other words, did gigantism originate primarily as an anti-predatory feature, or is the anti-predatory role an exaptation of gigantism that evolved for some other reason?

Several studies of mammalian megaherbivores demonstrate a positive relation between large body size and digestive efficiency, especially of low nutrient quality browse (Fritz et al., 2002; Illius and Gordon, 1992; Owen-Smith, 1988). The longer retention time of ingesta in megaherbivores increases digestive efficiency as compared to small animals, thus permitting them to survive on lower quality food. Karasov et al. (1986) noted that passage time of ingesta increased with body size in both reptiles and mammals, and the same was undoubtedly true for dinosaurian herbivores as well. Fermentative digestion relies extensively on microbes, with anaerobes numerically dominating, to hydrolyze and ferment cellulose (Mackie et al., 2004). Although microbes are prevalent throughout the digestive tract, they are especially abundant in fermentation chambers or sacs in the foregut or hindgut (Mackie et al., 2004; McBee, 1971). Hindgut fermentation, involving enlargement of the cecum or colon, is the most primitive and most widespread adaptation (Mackie et al., 2004). The cecum is an expanded sac located between the small and large intestine and occurs in a variety of mammals and birds (McBee, 1971). In contrast, all
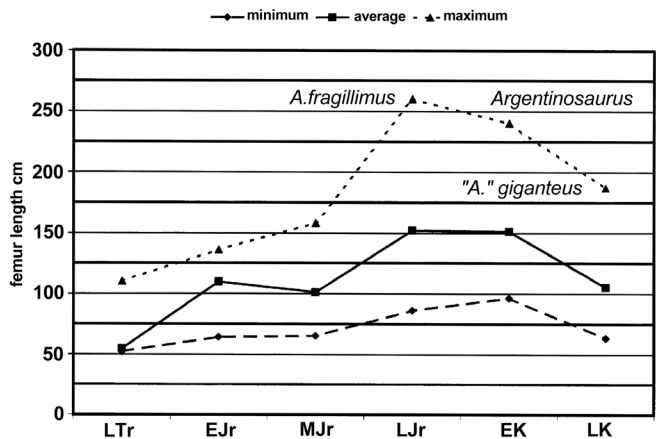

FIGURE 4. Graph showing the gradual increase in femur length, which also correlates with increase in body size. Note peak during the Late Jurassic. The graph also shows the largest specimens (maximum), average-sized specimens, and smallest adult sizes. LTr - Late Triassic (227-206 million years ago - mya); EJr - Early Jurassic (206-180 mya); MJr - Middle Jurassic (180-159 mya); LJr - Late Jurassic (159-144 mya); EK - Early Cretaceous (144-99 mya); LK - Late Cretaceous (99-65 mya). Data from Carpenter in preparation.

extant herbivorous reptiles have elongate intestines and septa or valves within the enlarged colon that slow the passage of ingesta (Iverson, 1982; Cooper and Vitt, 2002). Sauropods most likely also used hindgut fermentation, rather than foregut or rumen, but whether it was cecal, colonic, or a combination is unknown. The elongation and enlargement of the digestive tract, whether expansion of the cecum or colon, requires a larger body to accommodate it in both megaherbivores and herbivorous lizards (Cooper and Vitt, 2002; Illius and Gordon, 1992), and is probably true for sauropods and other large-bodied herbivorous dinosaurs (DiCroce et al., 2005).

The ability to live on low nutrition (i.e., low caloric) plants is common to all megaherbivores as noted above and suggests it may be the main reason why large body size occurs in different, unrelated animals (e.g., elephant, rhinoceros, hippopotamus). This ability may also explain why sauropods got so big. The first sauropods appear in the Late Triassic (227-208 mya) and were already big animals (Fig. 4). They apparently lived in seasonally dry, semiarid environments (Parrish et al., 1986) where plants, based on modern studies (e.g., Prior et al., 2003, 2004), probably had low nutritional value during the dry season. This ability to survive on low nutrition for part of the year explains why sauropods were so successful and why they mostly occur in dry environments. Sauropod remains are unknown in perpetually wet environments, such as represented by the Hell Creek Formation (Russell and Manabe, 2002), but are known from xeric and semi-arid coastal environments, such as represented by the Bahariya Formation of Egypt (Smith et al., 2001 with Russell and Paesler, 2004).

The numerical dominance of sauropods in the Morrison Formation (Dodson et al., 1980) is seemingly at odds with statements that the Morrison was deposited in a semiarid environment with seasonal rainfall (summarized by Turner and Peterson [2004]). This apparent anomaly lead Tidwell (1990) to argue for a wet environment to support abundant vegetation that the sauropods would require. Indeed, large, > 1 m diameter logs (probably conifer) are known in the Morrison Formation at Escalante Petrified Forest State Park in southern Utah, as well as a partial 24 m log near Dinosaur National Monument (F. Peterson, personal commun.). These logs demonstrate the presence of very tall (20-30+ m) trees during deposition of the Morrison Formation, but do not necessarily prove the existence of widespread forests of tall trees. Such tall trees can be accommodated in a gallery (i.e., riverine, Fig. 5A) forest as advocated by Parrish et al. (2004), but require considerably more water than postulated by climatic models (e.g., Moore, et al., 1992; Rees et al., 2000; Sellwood et al., 2000; Valdes and Sellwood, 1992). Demko et al. (2004) suggested the water, mostly as ground water, originated as rainfall on the Cordillera to the west (although how such water managed to flow uphill away from the alleged Lake (Playa?)
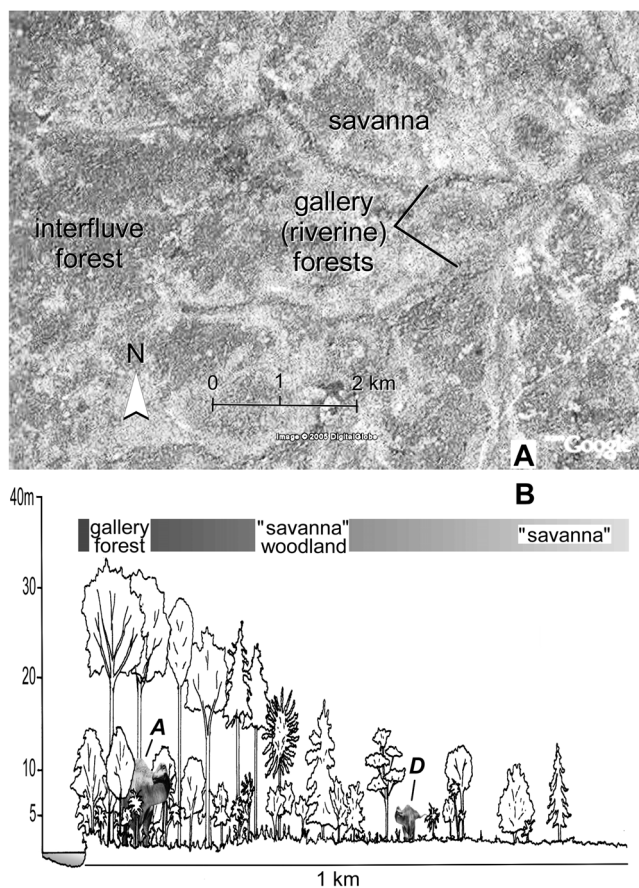
nifer *Brachyphyllum*) among the ferns would produce a savanna-like landscape (Parrish et al. 2004; Fig. 5B).

The diversity and abundance of ferns from the Morrison (Litwin et al., 1998), coupled with the apparently low feeding range of diplodocid sauropods (Stevens and Parrish, 1999), suggests that ferns may have played an important role in the diet of diplodocids. Although Fiorillo (1998) and Engelmann et al. (2004) dismissed ferns as a component of the sauropod diet following the low rating given by Weaver (1983), in point of fact the kcal/g data given by Weaver (1983, table 3) for ferns (3.369-4653 kcal/g, $\nabla = 4.205$ kcal/g) is not that much different for most of the other plants listed by her (3.347-5.393 kcal/g,$\nabla = 4.411$kcal/g). In addition, the most of the ferns listed have higher kcal/g values (4.0-4.16 kcal/g) than that given by Bassey et al. (2001) for the fern *Diplazium sammatii*,which is regularly consumed by humans. But even if Morrison ferns had a low caloric content, the large body size of sauropods, with their large gut, would allow them to easily survive on low nutrient browse as is true for extant megaherbivores (Owen-Smith 1988). Whereas diplodocid sauropods increased their gut volume by increasing the entire body size, titanosaurids did so primarily by flaring the ilium laterally thereby making more room for the enlarged hindgut.

The only possible restriction to a diet of ferns are their phytochemical defenses, although most target arthropods (Page, 2002). However, there is reason to believe that not all ferns are equally toxic, as evidenced by selective browsing of tree ferns (*Dicksonia*) by deer in New Zealand (Nugent and Callies, 1988), although it is also true that the distribution of chemical toxins in modern ferns is poorly known (Page, 2002).

If the origin and evolution of large body size among sauropods is related to diet as it is in extant megaherbivores, then all other advantages conferred by large body size are secondary. These would include lower energy expenditure, protection against predators, and life longevity, among others. One major disadvantage frequently cited, that of thermal stress (e.g., Engelmann et al., 2004), need not be a problem because sauropods, including a 10 m tall *Amphicoelias fragillimus*, could seek shade during the day in gallery forests (Fig. 5B) and feed primarily at night.

CONCLUSION

The origin and evolution of large body size in sauropods may be closely linked to a diet of generally poor quality food resources growing on low nutrient, calcareous soils. This giantism culminated in the largest known sauropod, *Amphicoelias fragillimus* during the Late Jurassic. Several lineages of sauropods have independently achieved megasauropod (>30m length) status. Two different strategies of gut enlargement were utilized: diplodocids increased the overall size of the body, and titanosaurids increased the hindgut by flaring the ilium laterally.

ACKNOWLEDGMENTS

FIGURE 5. **A.** Satellite image of northwestern Ghana in the vicinity of 7°48.5'N, 2°26.5'W showing the dendritic pattern of riverine forests and interfluve savanna and forests. The soil and vegetation here was described by Markham and Babbedge (1979). **B.** Hypothetical, gradational cross-section of the Morrison landscape modeled on **A** from gallery forest to savanna. Note that the extremely tall trees in the gallery forest could easily provide shade to *Amphicoelias fragillimus* (*A*) thereby preventing it from overheating during the day. The gallery forest was probably a two story canopy: upper canopy of various coniferophytes, a lower canopy of tree ferns and smaller coniferophytes, and ground cover dominated by ferns. The "savanna" woodland was probably a single story canopy dominated by ginkgos and coniferophytes, with a ground cover dominated by ferns and cycadophytes. The woodland was probably the gradual transition zone to the "savanna." It was probably considerably wider in the more northern, wetter regions of the Western Interior (e.g., northern Wyoming), than in the southern, drier portions (southern Utah) during the Late Jurassic. In the northern regions it probably dominated the interfluve regions, being equivalent to the interfluve forests of Ghana. The "savanna" was probably dominated by sclerophyllous ferns and cycadophytes, with a scattering of coniferophytes, predominately *Brachyphyllum*.

T'oodichi in the back-bulge basin as groundwater is not described). The region between the gallery forests may have been savanna-like (Parrish et al. 2004). Although a savanna is variously defined (e.g., contrast Bourlière and Hadley [1970] and Scholes and Archer [1997]), grass and scattered trees are today the dominant components. However, grasses did not appear until the Late Cretaceous, when they are known from sauropod coprolites (Prasad et al., 2005). During the Late Jurassic, ferns may have dominated the niche now occupied by grasses (Litwin et al., 1998). A scattering of sclerophyllous trees (e.g., the co-

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