Some Notes on the Diverse Brachiosaurid Sauropods of the Late Jurassic of North America, Europe and Africa

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Abstract: The unusual placement of the parapophyses on elongotated peduncles further distinguishes *Brachiosaurus* from other brachiosaurid genera including *Giraffatitan*. Late Jurassic brachiosaurid taxonomy is probably more complex than has been realized, in part because of evolution over the considerable periods of times recorded in the Morrison and Tendaguru formations. The presence of reduced tails on late Jurassic brachiosaurids is confirmed.

INTRODUCTION

It was long assumed that the brachiosaurid material found in the Late Jurassic Morrison, Tendaguru, and Lourinha Formations from three continents belonged to the genus *Brachiosaurus* (as per Janensch 1950, 1961, Lapparent and Zbyszewski 1957, Jensen 1987) until Paul (1988) noted significant differences between the type species *B. altithorax* (Fig. 1A) from North America and the African *B. brancai* (Fig. 1B) indicated at least a subgeneric separation, and Taylor (2009) formally separated the sauropods, leaving much of the Tendaguru brachiosaurids material titled *Giraffatitan brancai*; the generic separation has been tentatively questioned (Chure et al. 2010). In addition European *B. alatalaiensis* has been retitled *Lusotitan alatalaiensis* (Antunes and Mateus 2003), and a dwarf brachiosaur from the European Mittlere Kimmeridge-Stufe deposits has been designated *Europasaurus holgeri* (Sander et al. 2006).

Institutional Abbreviations: AMNH, American Museum of Natural History, New York; BYU, Brigham Young University, Provo; FMNH, Field Museum of Natural History, Chicago; HMN, Humboldt Museum fur Naturkunde, Berlin; NHMUK, Natural History Museum, London; USNM, United States Natural History Museum, Washington DC.

TAXONOMIC DISCUSSION

Although the feature is in retrospect obvious, it has yet to be observed that the parapophyses of many the *B. altithorax* holotype dorsals are highly unusual in being set on prominent, cranio-laterally projecting, long, and often rather slender peduncles (Fig. 1E; Plate LXXII in Riggs 1904). It is not entirely clear if the goose necked peduncles are actually absent on a few of the preserved dorsals, or lost. Similar parapophysial peduncles have not been documented on other Late Jurassic brachioisaurid dorsals including BYU 4744 (Fig. 1F; Fig. 4A in Jensen 1987), the more cranially positioned BYU 13023 (Fig. 1G, Curtice and Stadtman 2001), any specimen of *G. brancai* (Janensch1950, pers.

observ.), the Tendaguru brachiosaurid NHMUK R5937 (Migeod 1931), or *E. holgeri* (Sander et al. 2006), and there is apparently not a *L. alatalaiensis* dorsal complete enough to assess the parapophyses.

Peduncle parapophyses are present in a few other dinosaurs' dorsals, this researcher is aware of some diplodocids (Hatcher 1901, Curtice and Stadtman 2001), but they are rare in the great group and their presence in one species and absence in another is alone sufficient for generic distinction. It is unlikely that *B. altithorax* was the sole brachiosaurid with the feature, so they were probably were present in some other genera that may have formed a distinct clade that may have been restricted to the northern hemisphere. It follows that *Giraffatitan* is gradistically and probably phylogenetically quite distinct from *Brachiosaurus*, which differ in other regards as detailed by Taylor (2009), at the level of the genus.

One potentially diagnostic character cited by Taylor (2009), differing orientations of the coracoid glenoid, is dubious because this may reflect differing ossification of the joint. It is also open to question that the assumed *B. altithorax* coracoid belongs to the holotype. A very large coracoid relative to the ilium is typical of *Camarasaurus* (Paul 2010); the distal edge of the oversized acromion process can accomodate a coracoid so large that the ratio between the length of the scapula versus across the coracoid is a low 2.8 to 3.1 in USNM 11338 and AMNH 814 (Fig. 1D), and the coracoid is elongated. Such large coracoids have not been documented in other sauropods; in articulated brachiosaurid scapula-coracoids BYU 9462 (Fig. 1C) and HMN MB.R.2746 (= Ki24; Pl. XV, Fig. 3a in Janensch 1961) the ratio is a much higher approximately 4.5. The coracoid attached to the very large scapula BYU 9462 is just 570 mm across (Curtice, Stadtman and Curtice 1996). The exact size of the *G. brancai* HMN MB.R.2181 (= S II) coraocids is not certain because previously published measurements are inconsistent, and the elements are not currently accessible. A cranial view photograph of the original mount of the skeleton of the length of the humerus was used to cross measure the coracoids at approximately 650 mm across, far under the 840 mm value listed by Janensch (1961), greater than the approximately 530 mm that is implied by Fig. 1 in the same paper, and less than the approximately 740 mm implied in Fig. 1F in Taylor (2009). *Giraffatitan brancai* coracoids appear to have been small relative to the ilium (Fig. 1B). Brachiosaurid coracoids appear to be fairly square in shape. The great size of the big coracoid has been obscured by substituting and also scaling down the coracoid of BYU 9462 along with its scapula in skeletal restorations centered on the *Brachiosaurus* holotype to the exclusion of the element found with the rest of the remains (as per Fig. 7 in Taylor 2009). At 870 mm across from the cranial to caudal edge the big coracoid is very large relative to the ilium of the *B. altithorax* holotype (compare at same scale in Pl. LXXV in Riggs, 1904 and Fig. 1A-D in Taylor 2009), is so big that it is awkward to fit into the skeletal restoration (Fig. 1A), is large relative to other large brachiosaurids' coracoids, and is elongated rather than squarish in shape. If the big coracoid belongs to the *B. altithorax* holotype then the scapula-coracoid dimension ratio should have been a camarasaurid like 2.8. That the big coracoid belongs to a larger individual, and perhaps even a camarsaurid at the upper end of that group's size range, is possible. If it is part of the *B. altithorax* holotype then the element's exceptional size and shape may be another diagnostic character of the taxon, which may have had a correspondingly prominent acromion

process. It is doubtful that BYU 9462 is assignable to the same taxon that the big coracoid belongs to, so if the latter is *B. altithorax* then the BYU 9462 is probably not. If the big coracoid is from another taxon then BYU 9462 may or may not belong to *B. altithorax*.

It is interesting that ilia referred to *Giraffatitan* (Fig. 1E in Taylor 2009) and BYU 4744 (Fig. 3A in Jensen 1987) lack the cranially longer and deeper cranial process of the *Brachiosaurus* holotype (Fig. 1A, C in Taylor 2009), so it is possible that the first two taxa are more closely related (possibly at the genus level) than to *Brachiosaurus*. Nor is BYU 4744 within *Brachiosaurus* (contra Taylor [2009], Jensen [1987] realized it was at least a different species). Also not assignable to *Brachiosaurus* is BYU 13023. Although some crushing may be involved, the short centrum of 13023 does not favor its being the same taxon as 4744 either. A juvenile brachiosaurid (Carballido 2012) appears to lack prominent parapophyses, reducing the likelihood that it is *Brachiosaurus* although ontogeny may be a factor.

It is also necessary to consider the stratigraphic level of fossil remains within a given formation if the latter formed over an extended period of time because species often turn over rapidly (Paul 2008, 2010; Ryan and Evans 2005; Mallon and Holmes 2006, Scannella, 2010), and the Morrison Formation was deposited over a period of over 6 million years (Carpenter and Wilson 2008). This is not a serious issue with the *B. altithorax* holotype and BYU 4744, 9462 and 13023 because they are all from the middle Morrison, and the juvenile brachiosaurid (Carballido 2012) may be temporally close enough. But brachiosaurid skull USNM 5730 is from much lower in the formation than the *B. altithorax* holotype (Carpenter and Tidwell 1998), so it is unlikely that they are the same taxon. Likewise, the three "Saurian Beds" of the Tendaguru Formation were laid down over a considerable span of time (Sames 2008), and assigning specimens from more than one of the deposits to the same species should be done only if the remains are sufficiently complete and similar to compel the assignment. Nor should it be presumed that brachiosaurids remains from the same level of a formation represent one species unless the anatomical evidence for unity is sufficient.

At this time it is not possible to confidently refer any additional brachiosaurid specimens from the Morrison Formation or any other sediments to *B. altithorax* or the genus *Brachiosaurus*, nor are any of the fossils sufficiently complete and diagnostic to warrant new taxa, so until further remains become sufficient to warrant a major systematic and stratigraphic review of Morrison brachiosaurids all remains aside from the *B. altithorax* holotype should be considered Brachiosauridae *incertae sedis*. In this view the *B. altithorax* skeleton restoration in Taylor (2009) may be a multitaxa chimera. At this time a substantial diversity of Late Jurassic brachiosaurids appears to have inhabited North America, Europe and Africa, both at the same time and over time. The available fossils do not provide biogeographic evidence of faunal uniformity between Late Jurassic continents, and may favor the opposite.

In a rare nontechnical critique Taylor (2009) expresses a negative personal opinion of the name *Giraffatitan*. Taylor is erroneous because *Giraffatitan*, carefully formed because the species is this researcher's favorite dinosaur, is a marvelously evocative title for a sauropod that shared the continent and the unusual form of today's

highest browsing ungulate *Giraffa*, and is indubitably superior to any alternative that could have been proffered.

DIMENSIONAL AND MASS ISSUES

The suggestion by Taylor (2009) that the brachiosaur mass estimates by Paul (1988, 1997) are significantly higher than his because the former were not based on my skeletal restorations is not correct. All of my mass estimates are from volumetric models based directly on the skeletal restorations, and methodological testing by repeated models of the same skeleton indicates they replicate the volume of the skeletal drawings to within a few percent. Other mass estimates of brachiosaurids are in closer agreement with those by Paul (Christiansen 1997, Stoinski 2010). BYU 9462 still appears to have been about a third heavier than the *B. altithorax* holotype (Paul 1988) even though the scapula-coraocid length listed in Curtice et al. (1996) is shorter than was previously stated.

Henderson (2006) suggested that the tail of *Giraffatitan* was proportionally larger than restored by Paul (1988, 1997, 2010) on the premise that titanosauriforms had proportionally more substantial tails. The cranial caudal of *Brachiosaurus* FMNH 25107 is only three quarters the height of the caudal dorsals, which are already low in stature (Fig. 1A; Riggs 1904). The quarry map (Figure 1) and description in Migeod (1931) emphasizes the small dimensions of the caudal dorsals, sacrum and tail of NHMUK R5937 relative to the oversized shoulders and neck (Paul, 1988). The cranial-most sacral (apparently lost in WW II) tentatively refered to *Giraffatitan* HMN MB.R.2921 (= Aa) is similar in height to the caudalmost dorsal of HMN MB.R.2181, the sacrum tapers strongly caudally, and first caudals of the cranially complete HMN MB.R.2921 tail are about three quarters the height of the caudal dorsal of HMN MB.R.2181 (Figure 1A), as they are in FMNH 25107. Enlarging the caudal series of *Giraffatitan* requires expanding the hips and tail so they are much larger than they actually were. *Europasaurus* also appears to have a small tail (Paul 2010). Therefore, a number of Late Jurassic brachiosaurids had much smaller hips and shorter, slenderer tails than normal for sauropods, emphasizing their peculiarly mammalian, giraffe-like proportions.

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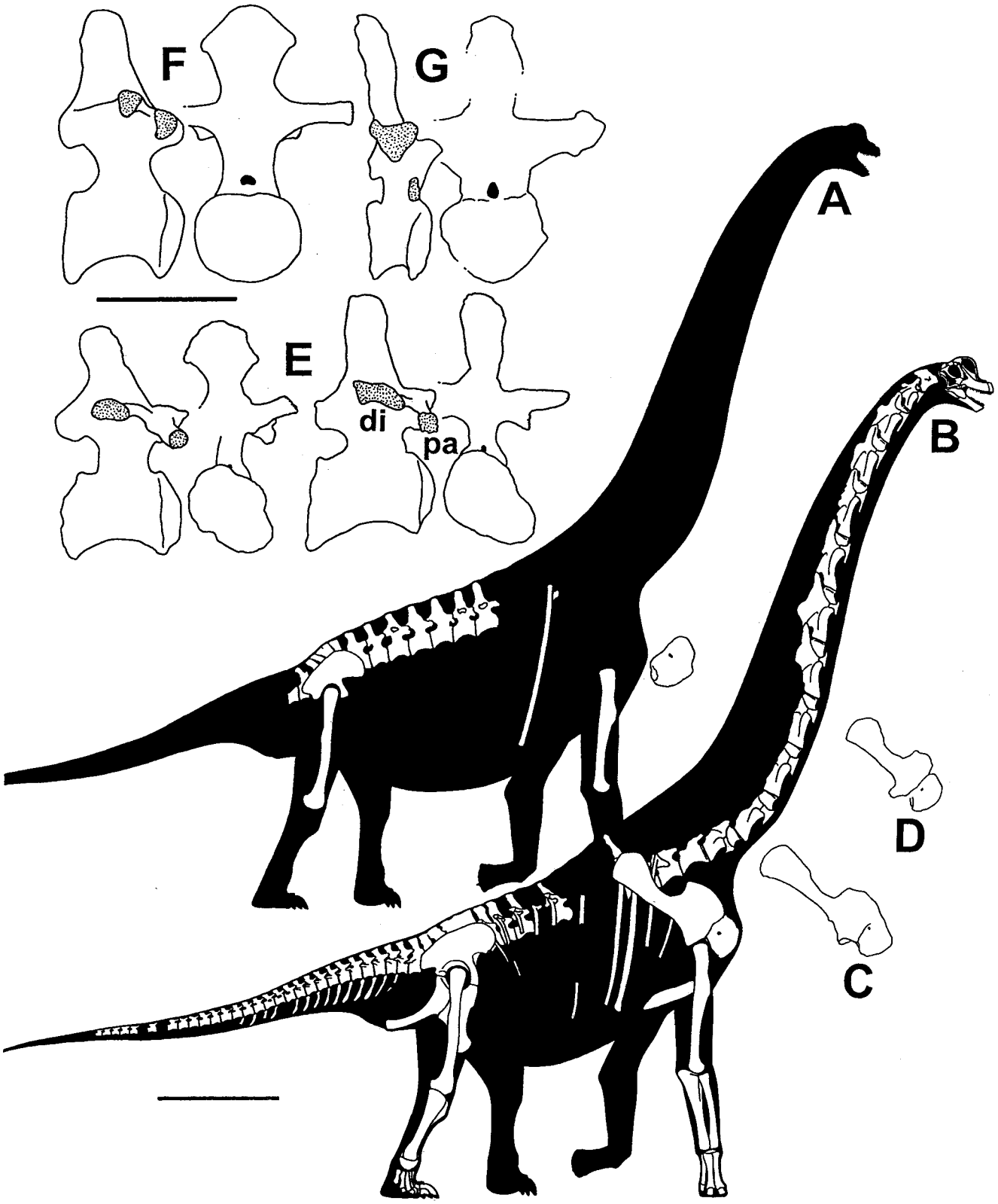

FIGURE 1. Same scale, known bone skeletal restorations of **A**, *Brachiosaurus altithorax* holotype FMNH P 25107 with exceptionally large coracoid shown separately; **B**, *Giraffatitan brancai* published elements

composite consisting mainly of HMN MB.R.2181/2921/2746. Scapula-coracoids of **C**, brachiosaurid BYU 9462; **D**, *Camarasaurus supremus* AMNH 814. Same scale comparison of Morrison brachiosaurid dorsals in lateral and caudal view of **E**, *Brachiosaurus altithorax* holotype, positions 7 (right) and 10; **F**, brachiosaurid BYU 4744; **G**, brachiosaurid BYU 13023; parapophyses (**pa**) and diapophyses (**di**) stippled. Scale bars equal 2 m for A–D, 0.5 m for E–G.