A RE-EVALUATION OF *BRACHIOSAURUS ALTITHORAX* RIGGS 1903 (DINOSAURIA, SAUROPODA) AND ITS GENERIC SEPARATION FROM *GIRAFFATITAN BRANCAI* (JANENSCH 1914)

MICHAEL P. TAYLOR*

Palaeobiology Research Group, School of Earth and Environmental Sciences, University of Portsmouth,
Burnaby Road, Portsmouth PO1 3QL, United Kingdom, dino@miketaylor.org.uk

ABSTRACT—Although the macronarian sauropod *Brachiosaurus* is one of the most iconic dinosaurs, its popular image is based almost entirely on the referred African species *Brachiosaurus brancai* rather than the North American type species *Brachiosaurus altithorax*. Reconsideration of Janensch's referral of the African species to the American genus shows that it was based on only four synapomorphies and would not be considered a convincing argument today. Detailed study of the bones of both species show that they are distinguished by at least 26 characters of the dorsal and caudal vertebrae, coracoids, humeri, ilia, and femora, with the dorsal vertebrae being particularly different between the two species. These animals must therefore be considered generically separate, and the genus name *Giraffatitan* Paul 1988 must be used for "*Brachiosaurus*" *brancai*, in the combination *Giraffatitan brancai*. A phylogenetic analysis treating the two species as separate OTUs nevertheless recovers them as sister taxa in all most parsimonious trees, reaffirming a monophyletic Brachiosauridae, although only one additional step is required for *Giraffatitan* to clade among somphospondylians to the exclusion of *Brachiosaurus*. The American *Brachiosaurus* is shown to be somewhat different from *Giraffatitan* in overall bodily proportions: it had a longer and deeper trunk and probably a longer and taller tail, carried a greater proportion of its mass on the forelimbs, and may have had somewhat sprawled forelimbs. Even though it was overall a larger animal than the *Giraffatitan* lectotype, the *Brachiosaurus* holotype was probably immature, as its coracoids were not fused to its scapulae.

INTRODUCTION

The sauropod dinosaur *Brachiosaurus* Riggs, 1903 is one of the most iconic of all prehistoric animals, immediately recognizable by its great size, tall shoulders, long neck and helmet-like skull. However, much of the distinctive morphology attributed to *Brachiosaurus* is known only from the referred species, *B. brancai* Janensch, 1914, and not from the type species *B. altithorax* Riggs, 1903. That *B. brancai* belongs to *Brachiosaurus* was asserted but not convincingly demonstrated by Janensch (1914), and contradicted but not disproved by Paul (1988). This study reviews the history of the two species, assesses the similarities and differences between them, assesses their relationships within a broader phylogenetic context, and discusses the implications for the phylogenetic nomenclature of sauropods.

Anatomical Nomenclature—The term Gracility Index (GI) is introduced to quantify the gracility of the humeri and other long bones discussed in this study, and is defined as the ratio between the proximodistal length of the bone and its minimum transverse width.

Many different sets of directions have been used to describe sauropod coracoids, with the edge furthest from the scapular articulation having been variously described as median (e.g., Seeley, 1882), inferior (Riggs, 1904), anteromedial (Powell, 1992), distal (Curry Rogers, 2001) and anterior (Upchurch et al., 2004), and the designation of the other directions varying similarly. I follow Upchurch et al. (2004) in describing the coracoid as though the scapulocoracoid were oriented horizontally: the scapular articular surface is designated posterior, so that the glenoid surface of the coracoid is considered to face posteroventrally.

Nomenclature for vertebral laminae follows that of Wilson (1999).

Anatomical Abbreviations—ACDL, anterior centrodiapophyseal lamina; **PCPL**, posterior centroparapophyseal lamina; **PODL**, postzygadiapophyseal lamina; **PPDL**, paradiapophyseal lamina; **PRPL**, prezygaparapophyseal lamina; **SPPL**, spinoparapophyseal lamina.

Institutional Abbreviations—BMNH, Natural History Museum, London, United Kingdom; **BYU**, Brigham Young University, Provo, Utah; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **HMN**, Humboldt Museum für Naturkunde, Berlin, Germany; **OMNH**, Oklahoma Museum of Natural History, Norman, Oklahoma; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington D.C.

HISTORICAL BACKGROUND

Initial Finds

The type species of the genus *Brachiosaurus* is *Brachiosaurus altithorax*, founded on a partial skeleton collected from the Grand River valley of western Colorado by the Field Columbian Museum paleontological expedition of 1900 under the leadership of Elmer S. Riggs (now accessioned as specimen FMNH P 25107). It comprises the last seven dorsal vertebrae, sacrum, the first two caudal vertebrae (one in very poor condition), left coracoid, right humerus, ilium and femur, fragmentary left ilium, and dorsal ribs. The type specimen does not contain any material from the skull, neck, anterior dorsal region, median or posterior parts of the tail, distal parts of the limbs or feet; nor has such material been confidently referred to the species (although see below).

Brachiosaurus altithorax was first reported, unnamed, by Riggs (1901), and subsequently named and briefly described on the basis of some but not all elements, the dorsal vertebrae not yet having been prepared (Riggs, 1903). After preparation was

*Current address: Department of Earth Sciences, University College London, Gower Street, London WC1E 6BT, United Kingdom

complete, the material was more fully described and figured in a monograph on the new family Brachiosauridae (Riggs, 1904). Riggs (1903:299, 1904:230) assigned the coracoid to the right side, but it is from the left: the orientation of the scapular margin indicates that the coracoid as figured by Riggs (1903:fig. 3, 1904: pl. LXXV, fig. 4) and as displayed in the FMNH collection is either a right coracoid in medial view or a left coracoid in lateral view; and the posteromedial-anterolateral orientation of the coracoid foramen and lateral flaring of the bone to support the glenoid articular surface (observed in photos provided by Phil Mannion) show that it is the latter.

Brachiosaurus is also known from a second species, *Brachiosaurus brancai*, excavated from Tendaguru in Tanzania by the German expeditions of 1909-1912 (Maier, 2003). Janensch (1914) initially also named a second Tendaguru species, *Brachiosaurus fraasi* Janensch, 1914, but subsequently synonymized this species with *B. brancai* (Janensch, 1929:5, 1935-1936:153, 1950a:31). Unlike the type species, *B. brancai* is known from many specimens of varying degrees of completeness, in total including almost all skeletal elements. The original type specimen, "Skelett S" (Janensch, 1914:86) was subsequently found (e.g., Janensch, 1929:8) to consist of two individuals, which were designated SI (the smaller) and SII (the larger and more complete). Janensch never explicitly designated these two specimens as a syntype series or nominated either specimen as a lectotype; I therefore propose HMN SII as the lectotype specimen of *Brachiosaurus brancai*. The skull, with its distinctive nasal arch, and the very long neck, are known only from *B. brancai*, and it is primarily from this species that nearly all previous skeletal reconstructions and life restorations have been executed, beginning with that of Matthew (1915: fig. 24). The sole exception is the partial reconstruction that Paul (1998: fig. 1B) included in a montage of skeletal reconstructions.

Janensch provided comprehensive descriptions of the Tendaguru elements in a series of monographs on the manus (Janensch, 1922), skull (Janensch, 1935-1936), axial skeleton (Janensch, 1950a) and appendicular skeleton (Janensch, 1961), as well as a discussion of pneumatic structures in the vertebrae (Janensch, 1947) and an account of the reconstruction of the mounted skeleton (Janensch, 1950b). In consequence, *B. brancai* is the most comprehensively described of all sauropods, although the papers are not widely read as they were written in High German.

Additional Material

Migeod's Tendaguru Brachiosaur—After the German Tendaguru expeditions were ended by the First World War, Tanzania became a British territory, and a series of expeditions were sent to Tendaguru by the British Museum (Natural History) (now the Natural History Museum) from 1919 to 1931 (Maier, 2003). Although the British were in Tendaguru for much longer than the Germans had been, their expeditions were under-funded and lacked the excellent scientific leadership of the earlier efforts. As a consequence, most of the material recovered by the British was unimpressive, consisting only of disarticulated elements. The sole exception was a nearly complete brachiosaurid sauropod skeleton, BMNH R5937, collected by F. W. H. Migeod in the 1930 field season. Migeod (1931) briefly reported on this specimen, which was said to include a complete and mostly articulated set of vertebrae from the fifth cervical through to the ninth caudal, together with cervical and dorsal ribs. Other material considered to be part of this specimen included three teeth, a scapulocoracoid, two humeri, an ilium, a partial pubis, a broken ischium, an incomplete femur, parts of a second femur and a calcaneum. Unfortunately, the association of some of this material was uncertain, much of it appears to have been lost, and more remains unprepared, although further preparation work is now under way. The preservation of the prepared material varies considerably: a pair of posterior dorsal vertebrae are in excellent condition, while most cervical vertebrae are lacking nearly all processes and laminae. An initial assessment of the material indicates that it probably represents a second distinct Tendaguru brachiosaur (Taylor, 2005).

Apart from the specimens recovered by the German expeditions, Migeod's specimen is the only Tendaguru brachiosaur material to have been been reported. However, several later finds of sauropod material in the U.S.A. have been referred, with varying degrees of certainty, to *Brachiosaurus*.

Potter Creek Humerus—As recounted by Jensen (1985, 1987), Eddie and Vivian Jones collected a large left humerus from the Uncompahgre Upwarp of Colorado and donated it to the Smithsonian Institution where it is accessioned as USNM 21903. It was designated *Brachiosaurus* (Anonymous, 1959) although no reason for this assignment was published; it was subsequently described very briefly and inadequately by Jensen (1987:606-607). Although its great length of 213 cm (pers. obs.) is compatible with a brachiosaurid identity, it is in some other respects different from the humeri of both *B. altithorax* and *B. brancai*, although some of these differences may be due to errors in the significant restoration that this element has undergone. The bone may well represent *Brachiosaurus altithorax*, but cannot be confidently referred to this species, in part because its true proportions are concealed by restoration (Wedel and Taylor, in prep.). It can therefore be discounted in terms of contributing to an understanding of the relationship between *B. altithorax* and *B. brancai*.

Other Potter Creek Material—Further brachiosaurid material was recovered from the Potter Creek quarry in 1971 and 1975 (Jensen, 1987:592-593), including a mid-dorsal vertebra, incomplete left ilium, left radius and right metacarpal. This material is accessioned as BYU 4744 (BYU 9754 of Jensen's usage). The material that overlaps with that of the *B. altithorax* type specimen appears very similar to it, and can be confidently assigned to that species. Preservation is supposedly very good (Jensen, 1987:599), but because the material was restored before figuring, its quality is difficult to assess. Further study is needed.

Dry Mesa Material—Jensen (1985) described further brachiosaurid material from the Dry Mesa quarry, erecting the new genus and species *Ultrasaurus macintoshi* Jensen, 1985 to receive it. It subsequently became apparent that Kim (1983), seemingly unaware of Jensen's informal prior use of the name "*Ultrasaurus*," had used this name for an indeterminate Korean sauropod which therefore has priority. Olshevsky (1991) therefore proposed the replacement genus name *Ultrasauros*, and it is this spelling that will be used herein. The type specimen of *U. macintoshi* is the dorsal vertebra BYU 9044 (BYU 5000 of Jensen's usage); referred specimens included a mid-cervical vertebra BYU 9024 (BYU 5003 of Jensen's usage), an anterior caudal vertebra BYU 9045 (BYU 5002 of Jensen's usage) and a scapulocoracoid BYU 9462 (BYU 5001 of Jensen's usage). Jensen (1987:603) subsequently asserted that the scapulocoracoid was the *U. macintoshi* holotype, but the original designation must stand. Jensen (1987:602) also recovered a large rib, which he considered to belong to *Brachiosaurus* (Jensen, 1987: caption to fig. 1). Unfortunately, little of Jensen's *Ultrasauros* material is actually brachiosaurid. Jensen (1987:600-602) recognized that the cervical vertebra, having a bifid neural spine, could not be brachiosaurid and instead tentatively referred it to Diplodocidae. Curtice (1995) subsequently referred the caudal vertebra to *Supersaurus* Jensen, 1985, leaving only the type dorsal and the scapulocoracoid. Curtice et al. (1996:88) asserted incorrectly that Jensen (1987) had referred the cervical specifically to *Supersaurus* rather than more generally to Diplodocidae, and this identification has been followed subsequently (e.g., Curtice and Stadtman, 2001; Wedel, 2006). Most importantly, Curtice et al. (1996) demonstrated that type type specimen of *U. macintoshi*, the dorsal vertebra, was not an anterior dorsal from a

brachiosaurid as Jensen had believed, but a posterior dorsal from a diplodocid. Curtice et al. (1996) referred this specimen, too, to *Supersaurus*, making *Ultrasauros* a junior subjective synonym of that name. The result of this is that only the scapulocoracoid BYU 9462 is recognized as brachiosaurid. Curtice et al. (1996:95) referred this element to *Brachiosaurus* sp., citing the narrow scapular neck, distal blade expansion and irregular shape of the coracoid as brachiosaurid characters (Curtice et al., 1996:93), and Paul, (1988:6-7) referred it specifically to *B. altithorax*. Its coracoid, however, does not closely resemble that of the *B. altithorax* holotype, lacking the the latter's distinctively strong lateral deflection of the glenoid. Neither is the scapula very similar to that of *B. brancai*, having a less pronounced acromion process – compare Curtice et al. (1996:fig. 1a) with Janensch (1961:pl. XV figs. 1 and 3a). As shown by Curtice et al. (1996:table 1), the coracoid of the "*Ultrasauros*" scapulocoracoid is smaller in both length and breadth than that of the *Brachiosaurus altithorax* holotype FMNH P 25107 (Riggs 1904:241); so the Dry Mesa brachiosaur, often cited as unusually large, was most likely rather smaller than the holotype. In conclusion, none of the Dry Mesa material described by Jensen can be confidently referred to *Brachiosaurus altithorax*.

Curtice and Stadtman (2001) briefly described BYU 13023, a pair of articulated dorsal vertebrae from Dry Mesa. They referred them to *Brachiosaurus ?altithorax*, and figured one of the pair in anterior, right lateral and dorsal views (Curtice and Stadtman, 2001:fig. 1B, 2C, 5B). The figured vertebra resembles those of the *B. altithorax* type specimen in general construction and lamina topology, but is proportionally very short anteroposteriorly: total height is about 4.2 times centrum length (including condyle), compared with values of no more than 2.2 in the *B. altithorax* holotype. This discrepancy might be accounted for by anteroposterior crushing, but since the diapophysis appears unaffected and there is no shearing, this seems unlikely. Therefore, a species-level referral cannot be confidently supported.

Jensen/Jensen Material—Jensen (1987:594-595) very briefly reported "several brachiosaur elements including a rib 2.75 m (9 ft) long …, a distal cervical vertebra, the proximal half of a scapula, and a coracoid" from a locality near Jensen, Utah, but did not describe any of this material and figured only a cast of the rib. The cervical vertebra, if correctly identified, would be particularly significant due to the paucity of North American brachiosaur cervical material.

Felch Quarry Skull—In 1883, a large sauropod skull (81 cm in length) was found in Felch Quarry 1, Garden Park, Colorado. It was shipped to O. C. Marsh in Yale that year and an illustration of the skull was used in the restoration of *Brontosaurus* Marsh, 1879 (=*Apatosaurus* Marsh, 1877) (Marsh, 1891: pl. 16). The skull was subsequently transferred to the National Museum of Natural History, where it was accessioned as USNM 5730. McIntosh and Berman (1975:195-198) recognized that the skull did not pertain to *Apatosaurus*, but described it as being "of the general *Camarasaurus* [Cope, 1877] type" (p. 196). McIntosh subsequently identified the skull tentatively as *Brachiosaurus* (Carpenter and Tidwell, 1998:70) and it was later described by Carpenter and Tidwell (1998), who considered it intermediate between the skulls of *Camarasaurus* and *Brachiosaurus brancai*, and referred it to *Brachiosaurus* sp. The skull may be that of *B. altithorax*, but this is currently impossible to test due to the lack of comparable parts (Carpenter and Tidwell, 1998:82).

Near this skull was a 99 cm cervical vertebra, probably of *Brachiosaurus*, but this was destroyed during attempts to collect it (McIntosh and Berman, 1975:196).

OMNH Metacarpal—Bonnan and Wedel (2004) described an isolated metacarpal, OMNH 01138, from Kenton Pit 1, Cimarron County, Oklahoma. This element, previously believed to belong to *Camarasaurus*, was referred to *Brachiosaurus* sp. on the basis of its elongation and slenderness.

BYU Cervicals—Cervical vertebrae in the BYU collection have been identified as *Brachiosaurus*, and found indistinguishable from those those of *B. brancai* (Wedel et al., in prep.). Two of these vertebrae, BYU 12866 and 12867, were figured by Wedel et al. (2000:fig. 10D, E, 12A-D) and Wedel (2005:fig. 7.2A). These may be the cervicals of *B. altithorax*, or may represent an as-yet unrecognized form more closely related to *B. brancai*.

Besides the material discussed here, Foster (2003:23) briefly reported a *Brachiosaurus* caudal vertebra from the Freezeout Hills of Wyoming, and Turner and Peterson (1999) mentioned, without discussion, *Brachiosaurus* material from Lower Split Rock Site 1, Mesa County, Colorado (p. 109), Callison's Quarries and Holt's Quarry, both Mesa County, Colorado (p. 110) and Bone Cabin Quarry E, Albany County, Wyoming (p. 144). Further North American specimens of *Brachiosaurus* remain for the moment unavailable, being unprepared, unpublished, or privately held. Discounting these unavailable specimens, very little of the available North American brachiosaur material can be confidently identified as *B. altithorax*, due to the absence of articulated or even associated elements. The Potter Creek radius and metacarpal may perhaps be considered to belong to this species, but their association with elements that overlap with the type material is not made clear in the publications that describe them (Jensen, 1985, 1987). In conclusion, comparisons of *B. altithorax* with the African brachiosaur material can only be safely made on the basis of the type specimen FMNH P 25107 described by Riggs (1904).

Janensch's Referral of *B. brancai* to *Brachiosaurus*

Although Janensch corresponded extensively with palaeontologists around the world, including America, there is no record that he ever visited America (G. Maier, pers. comm., 2007), so he would never have seen the *Brachiosaurus altithorax* type material. Therefore his referral of the Tendaguru brachiosaur material to this genus was based exclusively on the published literature – and perhaps private correspondence, although I have not been able to locate any.

The basis of Janensch's initial referral of his two new species to *Brachiosaurus* was not explicit: "Both species are so close to the genus *Brachiosaurus*, so far as the present state of preparation allows a judgement, that there was no recognizable reason to hold them separate from *Brachiosaurus*" (Janensch, 1914:83). [Here and elsewhere, quotes from Janensch are in English-language translations provided by Gerhard Maier.] This was elaborated as follows: "The referral here of both species to the American genus *Brachiosaurus* Riggs will be based on the description of *B. Fraasii* [sic] below" (p. 94). "All the relationships of the humerus of *Brachiosaurus altithorax* … are very similar to our species" (p. 97), although "the width at the proximal end of [the humerus of] our species is indeed relatively still somewhat larger than in the American sauropods. Above all, the contour of the proximal end is different in so far as it ascends sharply medially from the lateral side" (p. 97). "A left ilium was found with Skeleton J from the Upper Saurian Marl, which resembles to quite an extraordinary degree that of *Brachiosaurus altithorax* … A caudal vertebra of the same skeleton exhibits exactly the same form as that of the second caudal vertebra of the American species … This similarity of the ilium and the caudal vertebra further render it quite likely that the species under consideration cannot be generically separated from *Brachiosaurus*" (p. 97-98). Finally, "A comparison of the East African forms with that of *Brachiosaurus altithorax* Riggs allows very major similarities to be recognized, as cited above, particularly in the description of the individual skeletal elements. This is valid above all for the dorsal vertebrae of the American sauropods and those of *Br. Brancai* [sic, here and elsewhere]. … The similarity in relation to the humerus is particularly great between *Br. altithorax* and

Br. Fraasi [sic, here and elsewhere]; the ilium in these two species has a nearly entirely identical form. Furthermore, the caudal vertebrae of all three species are very similar. Finally, the agreement in the enormous dimensions, which exists especially between *Br. altithorax* and *Br. Brancai*, can also be cited. For all these reasons, it did not appear to me to be justified to hold the two described East African species under consideration generically separate from the cited North American genus" (p. 98).

Because this assessment did not describe specific derived characters shared between the Tendaguru forms and *Brachiosaurus altithorax*, it would not be considered a valid justification for the referral if published today. Lull (1919:42) commented that "Unless the German author, Janensch, actually made a comparison of the dorsals of the Tendaguru genus with those of the American *Brachiosaurus* and found sufficient agreement, I see no reason for including the African form in this genus merely on the ground of the elongated fore limbs, as we have no reason to know that *Brachiosaurus* had huge cervical vertebrae," although he noted that "Further evidence from Berlin, if such were available, might serve . . . to clarify the relationships."

Janensch (1929:20) made a more specific comparison: "The contrasting condition of . . . particularly low neurapophyses of the anterior caudal vertebrae is found in the genus *Brachiosaurus*, and indeed is in complete agreement with the American species *Br. altithorax* Riggs (1904 Pl. 75 Fig. 1, 2) and the East African *Br. Brancai* JAN (including *Br. Fraasi* JAN), as the illustration (Fig. 15) shows. The harmony stressed above also exists, in *Brachiosaurus*, in the low height of the neurapophyses of the anterior caudal vertebrae of this genus, and in those of the sacrum."

The subsequent monograph on the axial skeleton of *B. brancai* (Janensch, 1950a) provided a more rigorous justification for the referral: "The dorsal vertebrae of the African *Brachiosaurus brancai* correspond extensively to those of *Brachiosaurus altithorax* . . . The vertebrae in the two species exhibit extensive pleurocentral excavations and undivided, dorsally widened neurapophyses, which are relatively low in the posterior dorsal vertebrae, but which become taller from the sacrum up to just before the mid-trunk; in addition there are horizontally or almost horizontally oriented diapophyses that are of considerable size prior to the mid-trunk. The considerable increase in the height of the neurapophysis from the sacrum to just before mid-trunk is a characteristic that is found in no other sauropod genus in the same manner; it is also particularly characteristic for *Brachiosaurus*" (p. 72), although "differences between both species can be confirmed, that concern the overall morphology. Thus the centra of the dorsal vertebrae of *B. altithorax* are noticeably longer. In *B. brancai* the neurapophysis and the entire vertebra of what is probably the eighth-last presacral vertebra is taller and the diapophyses longer than in the seventh-last presacral vertebra of *B. altithorax*" (p. 72). Features of the sacrum also contributed to the referral: "The extensive, triangular first sacral rib is completely similar in both species. The long extension by which the sacral rib of the second sacral vertebra attaches to the first and second centrum is also to be found in the American forms and indeed apparently somewhat more so. The characteristically great length of the transverse processes, that confers the sacrum its significant width in comparison to other genera, is again conformable" (p. 76). The caudal vertebrae were also mentioned: "In its construction the second caudal vertebra of *B. altothorax* [sic] that Riggs (1904) illustrated resembles the corresponding vertebra of *Br. brancai* extraordinarily," although in *B. altithorax*, "a lateral depression is not indicated . . . the neurapophysis is particularly thickened block-like dorsally, and . . . the wedge at the ventral end of the postzygapophyses has a stronger zygosphenal character" (p. 76). Finally, Janensch drew attention to pneumaticity in the ribs of both species: "Cavernous construction can be confirmed in the head of the most robust

dorsal ribs . . . I interpret these depressions as manifestations that developed through the formative pressure of air sacs. In *Brachiosaurus altithorax* (Riggs, 1904) a large foramen even sits in the upper section of the shaft, which leads to an internal cavity and is to be interpreted as pneumatic" (p. 87), although "The circumstance that the anterior ribs of *Brachiosaurus altithorax* are even wider than those of *B. brancai* is to be considered. That may be related to the fact that the dorsal vertebrae of the American species are noticeably larger than those of the African" (p. 90).

Janensch's final publication on *Brachiosaurus brancai* was a monograph on the limbs and limb girdles (Janensch, 1961). Here, Janensch provided further arguments for the assignment of his species to *Brachiosaurus* as follows: "The humerus of the type species of the genus *Brachiosaurus altithorax* Riggs (1904) from the Morrison Formation, is in broad terms so similar in outline to *Br. brancai* that a detailed comparison is unnecessary; with a length of 204 cm the proximal width amounts to 65 cm, that is 32% of the length. The distal end is not preserved in its width; the smallest shank width of 28 cm (= 14% of the overall length) is insignificantly larger than in the East African species" (p. 187). "The ilium of *Brachiosaurus altithorax* Riggs corresponds well with the ilium of the African *Brachiosaurus* in the characteristic features of the strong development of the anterior wing of the blade and the compressed shape of the pubic peduncle, so that thereby the assumption of generic association is strongly supported. The differences are not significant. In the American species the posterior wing of the blade, which does not extend over the ischiadic peduncle, is less tapered; the forward wing still somewhat more highly developed" (p. 200). "The outline of the 2.03 cm [sic] long femur of the type species of the genus is very similar [to that of *B. brancai*]. The more exact shape of the distal articular end and its condyles is not presented, therefore cannot be compared" (p. 207). (Janensch was mistaken regarding the preservation of the *B. altithorax* femur: while the distal end of its humerus is eroded, that of the femur is intact.) "*Br. brancai* is very similar to the North American *Br. altithorax* in the form of the humerus and the ilium, it is also similar in the humerus and astragalus to the Portuguese *Br. botalaiensis* [sic]" (p. 231). This final reference is to "*Brachiosaurus*" *atalaiensis* Lapparent and Zbyszewski, 1957, a probable brachiosaurid which was considered by Upchurch et al. (2004:308) to be distinct from *Brachiosaurus* as its ischium has a less steeply inclined distal shaft, and which has been subsequently referred to its own genus, *Lusotitan* Antunes and Mateus, 2003. Similarities between this species and either *B. altithorax* or *B. brancai* cannot be taken to indicate similarities between the latter two species.

Disregarding statements of general similarity, then, Janensch advanced a total of 13 putative shared characters in support of the referral of the Tendaguru species to *Brachiosaurus*, none of which pertain to the coracoid, humerus or femur (Table 1). Of these, one is invalid (does not apply to *B. brancai*), six diagnose more inclusive clades than Brachiosauridae, two are difficult to evaluate, and four appear to be valid synapomorphies: anterior dorsal vertebrae with long diapophyses; neural spines low in posterior dorsals and taller anteriorly; ilium with strongly developed anterior wing; and ilium with compressed pubic peduncle. While four synapomorphies constitute good evidence of a relationship between the two species, they are not in themselves compelling evidence for congenericity.

Paul's Separation of *Giraffatitan* from *Brachiosaurus*

Although Lull (1919:42) had suggested seventy years earlier that *B. brancai* may not belong to *Brachiosaurus*, this idea was ignored in both scientific and popular literature until Paul (1988) executed a new skeletal reconstruction of *B. brancai* and thereby recognized proportional differences between the two species. Although believing that "the caudals, scapula, coracoid, humerus,

TABLE 1. Characters used by Janensch (1929, 1950a, 1961) in support of the referral of the species *Brachiosaurus brancai* to the genus *Brachiosaurus*, with their corresponding character numbers in the analysis of Harris (2006) and their distribution as presently understood.

Character	Reference	Corresponding character in Harris (2006)	Distribution
Dorsal vertebrae with extensive lateral foramina	Janensch (1950a: 72)	123 (state 2)	Neosauropoda + *Haplocanthosaurus* + *Jobaria*
Dorsal vertebrae with undivided neural spines	Janensch (1950a: 72)	120 (state 0)	Saurischia
Dorsal vertebrae with neural spines that broaden dorsally	Janensch (1950a: 72)	148 (state 2)	Macronaria (but reverts to state 1 in Somphospondyli)
Dorsal vertebrae with horizontal diapophyses	Janensch (1950a: 72)	—	(Not present in *B. brancai*, so irrelevant.)
Anterior dorsal vertebrae with long diapophyses	Janensch (1950a: 72)	—	Brachiosauridae (i.e., *B. altithorax* and *B. brancai*)
Neural spines low in posterior dorsals, taller anteriorly	Janensch (1950a: 72)	—	Brachiosauridae
Sacrum with extensive triangular first sacral rib	Janensch (1950a: 72)	—	(Cannot be assessed)
Second sacral rib with extensive attachment to first and second sacral centra	Janensch (1950a: 72)	—	(Cannot be assessed)
Sacrum with long transverse processes	Janensch (1950a: 72)	258	Neosauropoda + *Haplocanthosaurus* + *Jobaria*
Sacrum and proximal caudal vertebrae with low neural spines	Janensch (1929: 20)	164 (state 0)	Saurischia
Dorsal ribs with pneumatic foramina	Janensch (1950a: 87)	197	Titanosauriformes
Ilium with strongly developed anterior wing	Janensch (1961: 200)	—	Brachiosauridae
Ilium with compressed pubic peduncle	Janensch (1961: 200)	—	Brachiosauridae

ilium, and femur of *B. altithorax* and *B. brancai* are very similar" (p. 7), Paul argued that "it is in the dorsal column and trunk that the significant differences occur … the dorsal column of *B. altithorax* is about 25-30% longer relative to the humerus or femur than that of *B. brancai* … the longest dorsal rib [in *B. altithorax*] is some 10% longer relative to the humerus than in *B. brancai* … All the dorsal centra of *B. altithorax* have pleuro-coels that are about 50% larger than those of *B. brancai* … The neural arches are taller and longer in *B. altithorax* [sic; probably a typo for *B. brancai* since the opposite is in fact the case], but are much narrower. The transverse processes form a shallow V in *B. brancai*; in *B. altithorax* they appear to be flatter … Excepting the centrum, dorsal 4 [of *B. brancai*] differs greatly from the posterior dorsals in being much taller and wider. In the upper portions, the anterior dorsals of *B. altithorax* differ relatively little from the more posterior vertebrae … In HMN SII … the anterior dorsals are about the same length as the posterior dorsals. In FMNH P 25107 the mid dorsal centra are abut 50% longer than those of the posterior dorsals." Although the axial variation in centrum lengths is indeed greater in *B. altithorax* than in *B. brancai*, the difference is nowhere near as great as Paul suggests (Table 3).

As recognized by Wilson and Sereno (1998:21), Paul's comparisons were in part based on the wrongly referred specimen BYU 9044 (BYU 5000 of his usage). Paul followed Jensen (1985) in considering this element to be brachiosaurid, but went further in referring it to *B. altithorax* (Paul, 1988:6) and using it "to bolster our knowledge of the shoulder of *B. altithorax*"; but as described above, Curtice et al. (1996) demonstrated convincingly that this element is diplodocid, and referred it to *Supersaurus*, so it can tell us nothing about *Brachiosaurus*. Paul (1988:6-7) also referred the "*Ultrasauros*" scapulocoracoid BYU 9462 to *B. altithorax*, and used its supposed similarity to *B. brancai* scapular material as evidence of the close relationship between the two *Brachiosaurus* species; but this referral is not justified because the fused coracoid that is part of this "*Ultrasauros*" scapulocoracoid is different from that of the *B. altithorax* holotype, lacking that specimen's characteristically strong lateral deflection of the glenoid facet, and having the glenoid facet more nearly continuous with the scapular suture rather than at about 60° to it as in FMNH P 25107.

Despite these errors, however, the differences between the dorsal columns of the two *Brachiosaurus* species highlighted by Paul (1988) are mostly correct, and do not depend heavily on the wrongly referred "*Ultrasauros*" dorsal (contra Wilson and Sereno, 1998:21). In particular, the different ways in which the dorsal vertebrae vary along the column in the two species are striking: in *B. altithorax* the more anterior dorsals are more anteroposteriorly elongate but not significantly taller than the more posterior dorsals, whereas in *B. brancai* they are taller but not not significantly more anteroposteriorly elongate. More generally, the seven preserved dorsal vertebrae of the *B. altithorax* holotype form a clear sequence with only small and smooth changes in proportions and morphology between adjacent vertebrae, while the preserved dorsal vertebrae of HMN SII vary much more dramatically, even when corrected for distortion.

Having demonstrated differences between the two *Brachiosaurus* species, however, Paul (1988:8) was circumspect about separating them: "The incompleteness of the remains of *B. altithorax* makes it difficult to prove full generic separation, as does the small sample size of Morrison and Tendaguru dorsal columns. Therefore only a separation at the subgeneric level is proposed." Paul therefore introduced the subgenus *Giraffatitan* Paul, 1988 to contain the species *brancai*, yielding the new combinations *Brachiosaurus* (*Brachiosaurus*) *altithorax* and *Brachiosaurus* (*Giraffatitan*) *brancai*. Subgenera are almost unknown in dinosaur taxonomy, and these combinations have not been used in any subsequent publication. The only subsequent mention of the subgenus *Giraffatitan* was that of McIntosh (1990b:66), who mentioned it only to indicate that he considered subgeneric separation unwarranted. However, Olshevsky (1991:238) raised the subgenus *Giraffatitan* to generic rank, commenting only that "the above genus, initially described as a subgenus of *Brachiosaurus*, is separable therefrom on the basis of the vertebral column figured by Paul (1988)." (Olshevsky's listing gives the publication authority of the name *Giraffatitan* as Paul 1987 [nomen nudum], but he cannot remember what the publication was (G. Olshevsky, pers. comm., 2007); Paul, however, does not recall any published use of the name *Giraffatitan* prior to its 1988 formal erection (G. Paul, pers. comm., 2007)).

Although popular on the Internet, the name *Giraffatitan* has been very little used in the scientific literature: even Paul himself has reverted to using the name *Brachiosaurus* for the Tendaguru brachiosaur (e.g., Paul, 1994:246, 2000:93). Unfortunately, the only subsequent uses of this genus in the literature, in the taxonomic lists of McIntosh (1990a:347) and Upchurch et al. (2004:267), wrongly listed it as containing the species *altithorax* rather than *brancai* – a situation that would be impossible under ICZN rules since *altithorax* is the type species of *Brachiosaurus*.

COMPARISONS

To determine whether the two *Brachiosaurus* species belong in the same genus, an element-by-element comparison is presented here. Even discounting questionable referred *Brachiosaurus altithorax* material such as the "*Ultrasauros*" scapulocoracoid, sufficient elements of the *B. altithorax* holotype are preserved to allow comparison, including both axial and appendicular elements. Except where noted, the following comparisons are based on personal observation of the type material of both species.

Dorsal Vertebrae

As pointed out by Paul (1988:2), Janensch did not give his reasons for assuming that the dorsal column of *Brachiosaurus brancai* consisted of eleven vertebrae, and since Migeod's brachiosaur BMNH R5937 has twelve dorsal vertebrae, this should be considered the most likely number in other brachiosaurids. Although this specimen probably does not belong to *B. brancai* as assumed by Paul (Taylor, 2005), it is important as it includes the only complete dorsal column of any described brachiosaurid. Accordingly, I follow Paul in considering both *Brachiosaurus* species to have had twelve dorsal vertebrae: this means that the seven posterior vertebrae designated by Riggs (1903, 1904) as "presacrals 1-7" (counted forward from the sacrum) are here interpreted as dorsals 6-12, and the posterior dorsal vertebrae of HMN SII designated by Janensch (1950a) as presacrals 20, 22, 23 and 24 (i.e., dorsals 7, 9, 10 and 11) are here reinterpreted as dorsals 8, 10, 11 and 12. Janensch's presacral 17 (dorsal 4) is provisionally retained in this designation, although its true position cannot presently be determined.

As discussed above, the manner in which dorsal vertebrae vary along the column differs between *B. altithorax* and *B. brancai*: in the former, the more anterior dorsal vertebrae are only a little taller than the posterior dorsals but much longer anteroposteriorly, whereas in the latter, the more anterior dorsal vertebrae are much taller than the posterior dorsals but only a little longer anteroposteriorly. The dorsal vertebrae of *B. brancai* also differ from those of the type species in the following characters (Fig. 1):

- Centra are broader transversely than dorsoventrally, rather than subcircular in cross-section.
- As noted by Paul (1988:7), the centra are proportionally less elongate.
- Lateral foramina of centra are proportionally smaller, especially in anterior to middle dorsals.
- Lateral processes are dorsally inclined rather than horizontal.
- Lateral processes are terminated by distinct triangular articular surfaces.
- Neural spines are inclined posterodorsally about 25° in the more anterior vertebrae, rather than vertical.
- Each neural spine is nearly constant in anteroposterior width through much of its height, rather than pronouncedly triangular in lateral view with the base about twice as wide as the narrowest point.
- Each anterior and middle dorsal neural spine is roughly constant in transverse width for much of its height, flaring suddenly rather than gradually at the top.

- The rugosities on the anterior and posterior faces of neural spines are limited to shallow semicircles at the dorsal extremities, rather than the deep inverted triangular rugosities on both faces of the *B. altithorax* dorsals.
- Neural spines bear postspinal laminae.
- Spinodiapophyseal and spinopostzygapophyseal laminae do not contact each other: spinodiapophyseal laminae continue up the neural spine to the lateral flaring near the top rather than merging into the spinopostzygapophyseal laminae half way up the spine.

In addition to these features that apply to the HMN SII dorsals in general, D8 of that specimen (presacral 17 of Janensch's usage) has several other features not observed in any other sauropod, all of them preserved on both sides of the vertebra and therefore probably not pathological. Some of these features may also have existed in the other dorsals of the sequence, but the preservation of the relevant parts of the vertebrae is insufficient to determine this.

- D8 has spinoparapophyseal laminae. This novel lamina, distinct from the "accessory spino-diapophyseal lamina" (ASDL) of Salgado et al. (1997:22-23), is here assigned the standard abbreviation SPPL in accordance with the system of nomenclature for vertebral laminae proposed by Wilson (1999).
- The anterior centroparapophyseal laminae of D8 are unusually broad and flat, and perforated just below the horizontal lamina complex of PRPL, PPDL and PODL. The perforations appear not to be breakage, as the bone is finished around them.
- The horizontal lamina complex is supported ventrally by a dorsally forked lamina which cannot be designated as an ACDL, PCPL or even a generic infradiapophyseal lamina because it does not reach the diapophysis. Instead, the forked dorsal extremities of this lamina meet the horizontal lamina complex either side of the diapophysis, the anterior branch supporting the PPDL and the posterior branch supporting the PODL.

In summary, while the dorsal vertebrae of the two *Brachiosaurus* species are superficially similar, they vary in so many characters that they cannot be considered to support congenericity.
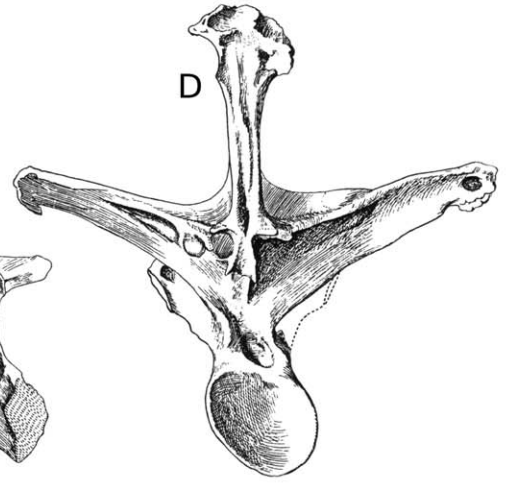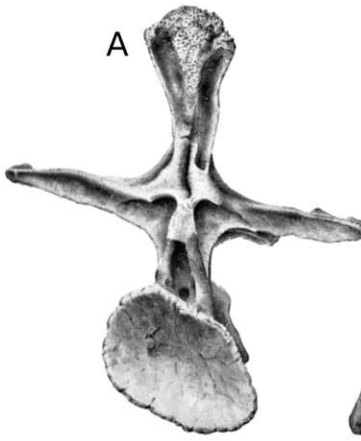
Dorsal Ribs

The dorsal rib heads of *B. altithorax* (figured by Riggs, 1904: pl. LXXV, fig. 5) and *B. brancai* (figured by Janensch, 1950a:fig. 107-108) are similarly proportioned, although the greater curvature of the latter suggests that it may be from a more posterior position. The locations of the pneumatic foramina are notably different, however: in the rib of *B. altithorax*, the rib is invaded on the anterior side by a small foramen in the proximal part of the rib shaft; in that of *B. brancai*, foramina are present on both the anterior and posterior aspects of the tuberculum, very close to the articular surface. The significance of this difference is difficult to assess, however, because the ribs of sauropods vary serially and the serial positions of the figured elements are not known; and also because pneumatic features are generally variable between individuals, between adjacent elements and even between the two sides of a single element – e.g., in *Xenoposeidon* Taylor and Naish, 2007: see Taylor and Naish (2007:1552-1553). Personal observation of the *B. altithorax* type material suggests that at least one rib head of that individual has a large pneumatic opening in its tuberculum similar to that figured by Janensch for *B. brancai*.

Paul (1988:7) stated that the longest dorsal rib of *B. altithorax* is 10% longer than that of *B. brancai*. However, Janensch (1950a:88) gave the length of HMN SII left rib 3 as 2.63 m, so the measurement of 2.75 m for an anterior rib of *Brachiosaurus altithorax* (Riggs, 1904:239) is only 4% longer, a difference that is probably not very significant.
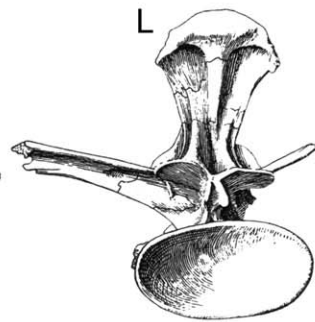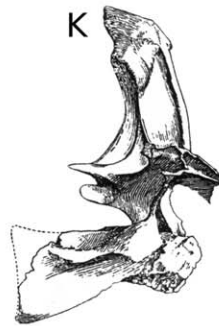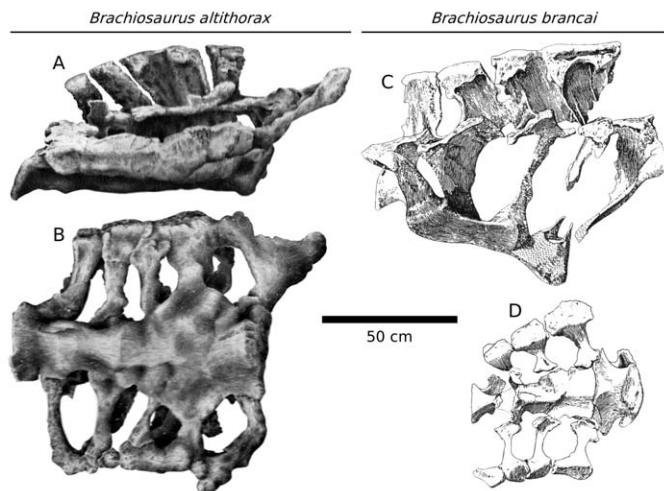
FIGURE 2. Sacra of *Brachiosaurus altithorax* and *Brachiosaurus brancai*, equally scaled. **A**, **B**, *B. altithorax* holotype FMNH P 25107; **C**, *B. brancai* referred specimen HMN Aa; **D**, juvenile *B. brancai* referred specimen HMN T. **A, C**, right lateral; **B, D**, ventral. **A, B** modified from Riggs (1904:pl. LXXIII); **C, D** modified from Janensch (1950a: figs. 74 and 76). Scale bar equals 50 cm.

Sacrum

The sacra of *B. altithorax* and *B. brancai* are difficult to compare because no good material exists of the latter: the sacrum is the only part of the skeleton in which the type species is better represented than the referred species (Fig. 2). While the sacrum of FMNH P 25107 has been subjected to some dorsoventral crushing, it is essentially complete, while the two sacra known for *B. brancai* are unsatisfactory: HMN Aa is distorted and missing the centra of all its sacral vertebrae, and HMN T is juvenile, incomplete and only partly ossified. The sacra of both species are transversely broad, and they share unusually short neural spines, especially when compared to the sacra of diplodocids (Hatcher, 1903b:pl. IV, figs. 1-2), although the spines are not very much shorter proportionally than those of *Camarasaurus* (Osborn and Mook, 1921:fig. 87) or *Haplocanthosaurus* Hatcher, 1903a (Hatcher, 1903b:pl. IV, fig. 3). Apart from these proportional similarities, poor preservation prevents the identification of further similarities between the sacra of the two *Brachiosaurus* species beyond the retention of plesiomorphies such as the sacricostal yoke.

Caudal Vertebrae

The *Brachiosaurus altithorax* type specimen includes the first two caudal vertebrae, of which the first consists only of a heavily crushed centrum and is uninformative but the second is well preserved (Fig. 3). In contrast, several nearly complete caudal sequences of *B. brancai* are known, of which that of HMN Aa is best preserved (Janensch, 1950a:60) and includes the second caudal. The corresponding caudals of the two species resemble each other in their gently amphicoelous centra, absence of lateral foramina, short and simple lateral processes, and neural spines
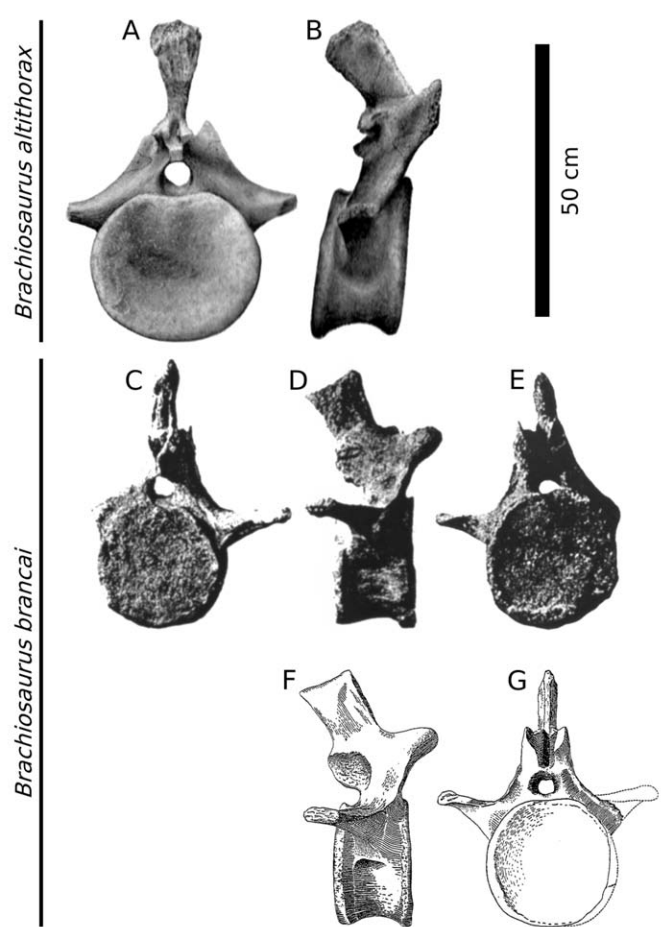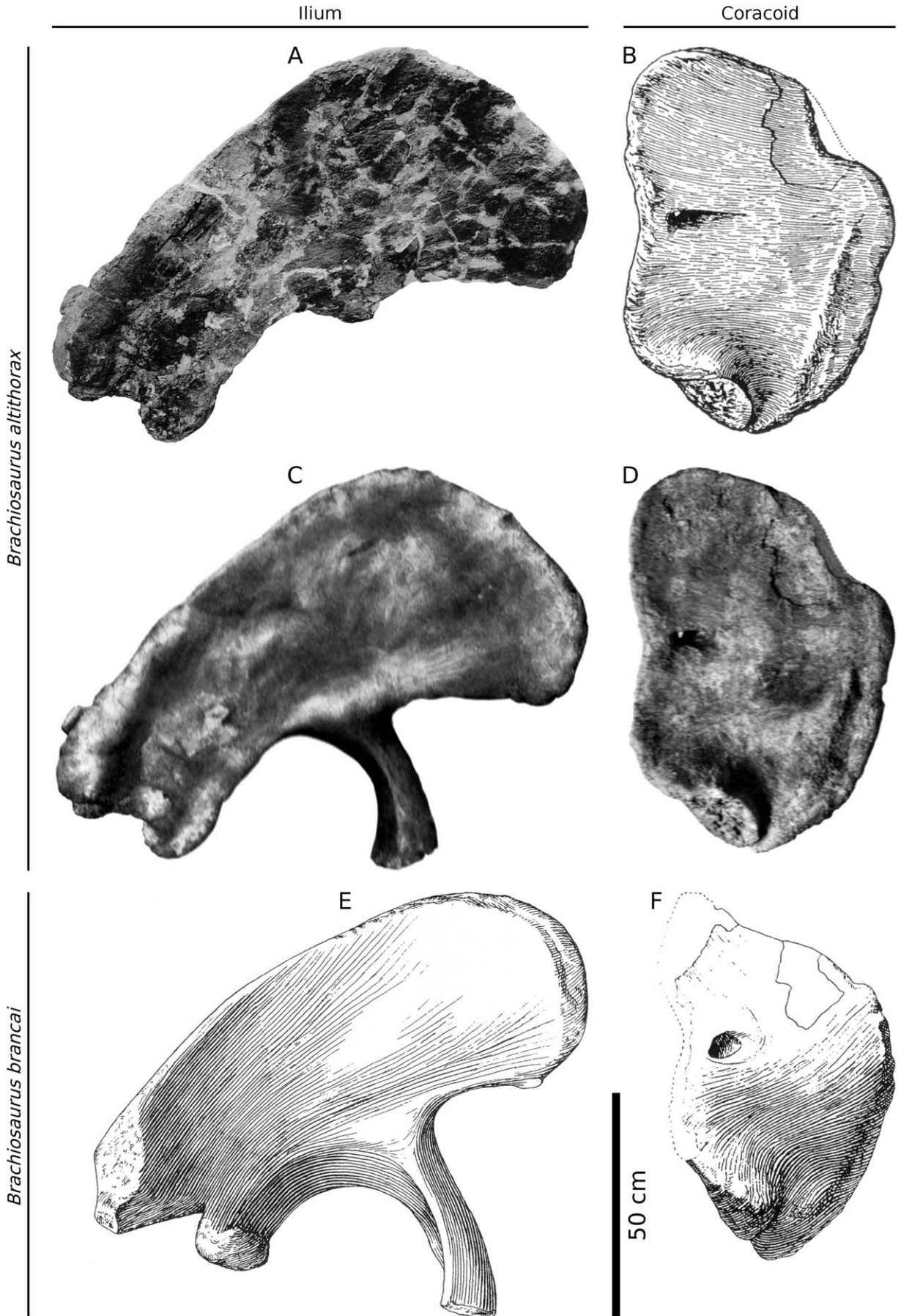

FIGURE 3. Second caudal vertebrae of *Brachiosaurus altithorax* and *Brachiosaurus brancai*, equally scaled. **A**, **B**, *B. altithorax* holotype FMNH P 25107; **C-G**, *B. brancai* referred specimen HMN Aa. **A, C**, posterior; **B, D, F**, right lateral; **E, G**, anterior. **A-B** modified from Riggs (1904:pl. LXXV); **C-E** modified from Janensch (1950a:pl. 2), **F-G** modified from Janensch (1929:fig. 15). Scale bar equals 50 cm.

that are short and simple, rectangular in lateral view and somewhat swept back.

The caudal vertebrae of the two species also differ in several respects, however: the caudal of *B. altithorax*, although very nearly the same length anteroposteriorly as that of *B. brancai*, is about 30% taller, due to a relatively taller neural arch and spine. The articular face is also broader in *B. altithorax*, so that the total articular area is about 55% greater than in *B. brancai*. While the neural spines of all *B. brancai* caudals are laterally compressed, that of *B. altithorax* expands dorsally to about three times its minimum transverse width. The neural spine of the *B. altithorax* caudal is posteriorly inclined more steeply than those of *B. brancai* – about 30° as opposed to about 20°. The caudal ribs of *B. brancai* are swept back by about 30° while those of *B. altithorax* project directly laterally. The *B. altithorax* caudal has a distinct, block-like hyposphene whereas those of *B. brancai*

← FIGURE 1. Dorsal vertebrae of *Brachiosaurus altithorax* and *Brachiosaurus brancai* in posterior and lateral views, equally scaled. **A**, **B**, **E**, **F**, **I**, **J**, **M**, **N**, *B. altithorax* holotype FMNH P 25107, modified from Riggs (1904:pl. LXXII); **C**, **D**, **G**, **H**, **K**, **L**, **O**, **P**, *B. brancai* lectotype HMN SII, modified from Janensch (1950a:figs. 53, 54, 56, 60-62, 64) except **H**, photograph by author. Neural arch and spine of **K** sheared to correct for distortion. **A, D, E, H, I, L, M, P**, posterior; **B, F, G, J, N**, right lateral; **C, K, O**, left lateral reflected. **A, B**, dorsal 6; **C, D**, dorsal 4; **E-H**, dorsal 8; **I-L**, dorsal 10; **M, N, P**, dorsal 12; **O**, dorsals 11 and 12. Corresponding vertebrae from each specimen are shown together except that dorsal 4 is not known from *B. altithorax* so dorsal 6, the most anterior known vertebra, is instead shown next to dorsal 4 of *B. brancai*. Scale bar equals 50 cm.

Ilium   Coracoid

have at most a slender hyposphenal ridge. While the postzyga-pophyseal facets of both species face ventrolaterally, those of *B. altithorax* are closer to a ventral orientation but those of *B. brancai* are more nearly laterally oriented. Finally, while the caudal vertebra of *B. altithorax* has no lateral depressions at all, the anterior caudals of *B. brancai* have pronounced lateral fossae, distinctly visible in the tail HMN Fund no that is incorporated in the mounted skeleton at the Humboldt Museum.

Coracoid

The coracoids of the two *Brachiosaurus* species resemble each other in being somewhat taller dorsoventrally than they are broad anteroposteriorly, in their roughly semicircular shape, and in the possession of an indentation in the anterodorsal margin (Fig. 4). However, the coracoids of *B. brancai* differ from that of *B. altithorax* in having a less straight scapular suture, a more pronounced anteroventral expansion in front of the glenoid, and a more slender, almost pointed, dorsal extremity. Most significantly, the glenoid surface of the coracoid of *B. altithorax* is strongly deflected laterally rather than facing directly postero-ventrally – a feature not found in *B. brancai* or indeed in any other sauropod. The glenoid surface is also mediolaterally broader in *B. altithorax*, extending laterally on a thick buttress which is lacking in the coracoid of *B. brancai*.

Humerus

As noted above, Janensch did not identify any synapomorphies between the humeri of the two *Brachiosaurus* species, observing only that "the similarity in relation to the humerus is particularly great between *Br. altithorax* and *Br. Fraasi* [= *B. brancai*]" (Janensch, 1914:98) (Fig. 5). The superficial similarity is indeed striking, the humeri of both species being more gracile than those of any other sauropods. Discarding a single outlier, the ratio of proximodistal length to minimum transverse width (Gracility Index or GI) in humeri of *B. brancai* varies between 7.86 for the right humerus HMN F2 and 9.19 for the left humerus HMN J12, with the type specimen's right humerus scoring 8.69, slightly more gracile than the middle of the range. (It is notable that the juvenile left humerus HMN XX19 has a GI of 8.63, and so is as gracile as the humeri of adult specimens, corroborating in *B. brancai* the findings of Carpenter and McIntosh (1994:277) for *Apatosaurus*, Ikejiri et al. (2005:176) for *Camarasaurus,* and Tidwell and Wilhite (2005) for *Venenosaurus* Tidwell, Carpenter and Meyer, 2001 that sauropod limb bones, unlike their vertebrae, scale isometrically during ontogeny.) For the *B. altithorax* type specimen, the GI is 8.50, based on the length of 204 cm and the minimum transverse width of 24 cm reported by Riggs (1904:241). However, the *B. altithorax* humerus looks rather less gracile to the naked eye than that of *B. brancai*, and careful measurement from Riggs's plate LXXIV yields a GI of 7.12, indicating that the true value of the minimum transverse width is closer to 28.5 cm. As noted by Riggs (1903:300-301), the surface of the distal end of this humerus has flaked away in the process of weathering. Careful comparison of the humeral proportions with those of other sauropods (Taylor and Wedel, in prep.) indicates that the missing portion of this bone would have extended approximately a further 12 cm, extending the total length to 216 cm and so increasing the GI to 7.53 – still less gracile than any *B. brancai* humerus except the outlier, but more

gracile than any other sauropod species except *Lusotitan atalaiensis* (8.91), and much more gracile than the humerus of any non-brachiosaurid sauropod (e.g., *Diplodocus* Marsh, 1878 sp., 6.76; *Malawisaurus dixeyi* Jacobs, Winkler, Downs and Gomani, 1993, 6.20; *Mamenchisaurus constructus* Young, 1958, 5.54; *Camarasaurus supremus* Cope, 1877, 5.12; *Opisthocoelicaudia skarzynskii* Borsuk-Bialynicka, 1977, 5.00 – see Taylor and Wedel, in prep.) The humeri of the two *Brachiosaurus* species are also alike in their deltopectoral crests: although that of the *B. altithorax* humerus is broken near its tip, enough remains to indicate that, like that of *B. brancai*, it was sharply pronounced, located about one third of the way down the shaft, and oriented directly in a distal direction rather than sloping distomedially across the anterior face of the shaft as in some other sauropods.

However, the profiles of the lateral edges of the humeri are rather different, progressing smoothly upwards in *B. brancai* to the rounded proximolateral corner, whereas in *B. altithorax* there is a low but distinct lateral bulge one fifth of the way down the humerus, proximal to which the lateral margin is directed somewhat proximomedially rather than continuing in its gently proximolateral trajectory (Fig. 5B, H). Inspection of the bone shows that this is a genuine osteological feature, not caused by erosion, breakage or distortion. The maximum width of the *B. altithorax* humerus proximally is about 10% greater than that of *B. brancai*, and the reconstructed distal end (Taylor and Wedel, in prep.) is similarly broader than in *B. brancai*. Taken together with the 16% broader minimum width, these measurements show the *B. altithorax* humerus to be altogether more robust than that of *B. brancai*. The anteroposterior width of the *B. altithorax* humerus is presently impossible to measure accurately because the bone is half enclosed in a plaster jacket, but inspection of a cast of this element incorporated in the FMNH's mounted *Brachiosaurus* skeleton indicates that it is at least as anteroposteriorly broad as in *B. brancai*, perhaps a little more so.

Ilium

As noted by Janensch (1961:200), the ilia of the two *Brachiosaurus* species resemble one another in the great development of the anterior wing and the "compressed" pubic peduncle, which I understand to mean elongate and gracile (Fig. 4). The peduncle appears more recurved in *B. altithorax*, but this may be an error in reconstruction, since the right ilium figured by Riggs (1904:pl. LXXV) did not have its pubic peduncle preserved, and it was restored in the figure after the public peduncle of the otherwise uninformative left ilium (Riggs, 1904:238). A photograph of the preserved ilium shows how poor a condition it is in compared with the illustration produced by Riggs (Fig. 4A, C). Other proportional differences may therefore also be less significant than they appear: for example, the different trajectories of the dorsal borders of the ilia of the two species may be due to the distortion mentioned by Riggs (1904:238). With this caveat, however, there remain several potentially important differences between the ilia. The ischiadic peduncle of the *B. altithorax* ilium, though not pronounced, extends further ventrally than that of *B. brancai*, so that a line projected through the most ventral portions of both peduncles passes some distance ventrally of the posterior extremity of the *B. altithorax* ilium but is coincident with this extremity in *B. brancai*. In *B. brancai*, there is a distinct and acute notch between the ischiadic peduncle and the posterior extremity whereas *B. altithorax* has a much less pronounced indentation.

← FIGURE 4. Limb girdle bones of *Brachiosaurus altithorax* and *Brachiosaurus brancai*, equally scaled. **A**, **C**, right ilium of *B. altithorax* holotype FMNH P 25107; **B**, **D**, left coracoid of same, reflected; **E**, right ilium of *B. brancai* referred specimen Aa 13, scaled to size of restored ilium of *B. brancai* lectotype HMN SII as estimated by Janensch (1950b:99); **F**, right coracoid of *B. brancai* lectotype HMN SII. **A** modified from FMNH neg. #GEO-16152, showing poor preservation and absence of public peduncle; **B** modified from Riggs (1903:fig. 3); **C**, **D** modified from Riggs (1904:pl. LXXV); **E** modified from Janensch (1961:Beilage E, fig. 1a); **F** modified from Janensch (1961:fig. 1a). Scale bar equals 50 cm.

Finally, the dorsal surface of the postacetabular region of the *B. altithorax* ilium bears a distinct tubercle which *B. brancai* lacks, and which also seems not to be present in any other sauropod.

Femur

The femora of *B. altithorax* and *B. brancai* are similar in most respects, sharing a prominent medially directed head, a flat proximal end, a sharply defined proximolateral corner, a fourth trochanter projecting somewhat medially and therefore visible in anterior view, and extreme eccentricity with the mediolateral width being more than twice the anteroposterior diameter for most of the length of the shaft (Fig. 5).

As with the humerus, the femur is somewhat more gracile in *B. brancai* than in *B. altithorax* (GI = 6.21 compared with 5.49). The fourth trochanter of *B. altithorax* is more prominent in anterior view than that of *B. brancai*, and is located more distally, at the half-way point rather than about 40% of the way down the shaft. The distal condyles do not project as far posteriorly in *B. altithorax* as in *B. brancai* (Figs. 5F, N), and while the tibial and fibular condyles are equally wide in the former, the fibular condyle is rather wider than the tibial condyle in the latter. Finally, the femur of *B. brancai* has a prominent lateral bulge one quarter of the way down its lateral margin, which *B. altithorax* lacks. This bulge was proposed as a titanosauriform synapomorphy by Salgado et al. (1997:16) but its distribution appears to be more complex.

Summary

Although McIntosh (1990b:65) felt that "the coracoid, femur, and sacrum of the two species are in complete accord," differences exist in both coracoid and femur, as well as the humerus, ilium, caudals, and most significantly the dorsal vertebrae. Since poor preservation prevents detailed comparison of the sacra, and lack of information about ribs makes it impossible to evaluate the significance of observed differences, these elements are therefore uninformative for comparative purposes. All elements sufficiently well preserved in both species, then, exhibit distinct differences, and generic separation is warranted since the two species are more different from each other than, for example, *Diplodocus* and *Barosaurus* Marsh, 1890. Accordingly, the name *Giraffatitan* will be used in the remainder of this paper.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
SAUROPODA Marsh, 1878
NEOSAUROPODA Bonaparte, 1986
MACRONARIA Wilson and Sereno, 1998
TITANOSAURIFORMES Salgado, Coria and Calvo, 1997
BRACHIOSAURIDAE Riggs, 1904

Revised Diagnosis—Ratio of humerus:femur length ≥ 0.90 (character 206); centroprezygapophyseal lamina on middle and posterior dorsal vertebrae undivided at upper end (character 138); anterior dorsal vertebrae with long diapophyses (Janensch, 1950a:72); neural spines low in posterior dorsals, taller anteriorly (Janensch, 1950a:72); ilium with strongly developed anterior

wing (Janensch, 1961:200); ilium with compressed pubic peduncle (Janensch, 1961:200); ratio of mediolateral:anteroposterior diameter of femur at midshaft ≥ 1.85 (character 284).

BRACHIOSAURUS RIGGS, 1903

BRACHIOSAURUS ALTITHORAX Riggs, 1903
(Figs. 1–5 in part, 7)

Brachiosaurus (*Brachiosaurus*) *altithorax* (Riggs): Paul, 1988:8, figs. 2A, 3F, 4B.

Holotype—FMNH P 25107, partial skeleton comprising last seven dorsal vertebrae, sacrum, first two caudal vertebrae, left coracoid, right humerus, ilium and femur, fragmentary left ilium, and dorsal ribs.

Referred Specimens—USNM 21903, left humerus; BYU 4744, dorsal vertebra, left ilium and radius, right metacarpal III; BYU 9462, right scapulocoracoid, dorsal rib; BYU 13023, two dorsal vertebrae; USNM 5730, nearly complete skull; OMNH 01138, left metacarpal II; BYU 12866 and 12867, mid-cervical vertebrae; undescribed specimens. Not all referrals are certain.

Occurrence and Distribution—Morrison Formation, North America (Colorado, Utah, Oklahoma).

Age—Latest Jurassic (Kimmeridgian-Tithonian), 155.6-145.5 Mya.

Revised Diagnosis—Postspinal lamina absent from dorsal vertebrae (character 130); distal ends of transverse processes of dorsal vertebrae transition smoothly onto dorsal surfaces of transverse processes (character 142); spinodiapophyseal and spinopostzygapophyseal laminae on middle and posterior dorsal vertebrae contact each other (character 146); posterior dorsal centra subcircular in cross-section (character 151); posterior dorsal neural spines progressively expand mediolaterally through most of their length ("petal" or "paddle" shaped) (character 155); mid-dorsals about one third longer than posterior dorsals (see Paul, 1988:7); mid-dorsals only about 20% taller than posterior dorsals (see Paul, 1988:8); dorsal centra long (Janensch, 1950a:72) so that dorsal column is over twice humerus length (Paul, 1988:8); transverse processes of dorsal vertebrae oriented horizontally (Paul, 1988:8); dorsal neural spines oriented close to vertical in lateral view; dorsal neural spines triangular in lateral view, diminishing smoothly in anteroposterior width from wide base upwards; deep inverted triangular ligament rugosities on anterior and posterior faces of neural spines; hyposphenes present on anterior caudal vertebrae (character 178); anterior caudal vertebrae have transversely widened neurapophyses (Janensch, 1950a:76); anterior caudal vertebrae lack lateral fossae (Janensch, 1950a:76); glenoid articular surface of coracoid oriented somewhat laterally; glenoid articular surface of coracoid mediolaterally broad, extending laterally onto thick buttress; humerus relatively robust (GI = 7.5); lateral margin of humerus with low bulge one fifth of the way down; projected line connecting articular surfaces of ischiadic and pubic processes of ilium passes ventral to ventral margin of postacetabular lobe (character 264); subtle posterior notch between ischiadic peduncle and postacetabular lobe of ilium; tubercle present on dorsal margin of postacetabular lobe of ilium; distal tip of fourth trochanter lies at femoral midshaft height (character 282); lateral margin of femoral shaft in anterior or posterior view straight (character 285); femur relatively robust (GI = 5.5); tibial and fibular condyles of femur equal in width.

← FIGURE 5. Right limb bones of *Brachiosaurus altithorax* and *Brachiosaurus brancai*, equally scaled. **A-C**, humerus of *B. altithorax* holotype FMNH P 25107; **D-F**, femur of same; **G-K**, humerus of *B. brancai* lectotype HMN SII; **L-P**, femur of *B. brancai* referred specimen HMN St 291, scaled to size of restored femur of HMN SII as estimated by Janensch (1950b:99). **A, D, G, L**, proximal; **B, E, H, M**, anterior; **C, K, P**, posterior; **J, O**, medial; **F, I, N**, distal. **A, B, D, E** modified from Riggs (1904:pl. LXXIV); **C** modified from Riggs (1904:fig. 1); **F** modified from Riggs (1903:fig. 7); **G-K** modified from Janensch (1961:Beilage A); **L-P** modified from Janensch (1961:Beilage J). Scale bar equals 50 cm.

GIRAFFATITAN Paul, 1988

GIRAFFATITAN BRANCAI (Janensch, 1914)
(Figs. 1–5 in part)

Brachiosaurus brancai Janensch, 1914:86, figs. 1–4 (original description)
Brachiosaurus fraasi Janensch, 1914:94, figs. 5, 6 (original description)
Brachiosaurus (*Giraffatitan*) *brancai* (Janensch): Paul, 1988:9, figs. 1, 2B, 3G, 4B.

Lectotype—HMN SII, partial skeleton comprising skull fragments including dentaries, eleven cervical vertebrae, cervical ribs, seven dorsal vertebrae, nearly complete set of dorsal ribs, distal caudal vertebrae, chevrons, left scapula, both coracoids and sternal plates, right forelimb and manus, left humerus, ulna and radius, both pubes, partial left femur, right tibia and fibula (Janensch, 1950b). Contra Janensch, the right femur of the mounted skeleton is complete while the left femur has a reconstructed shaft, and is presumably the partial femur of SII while the right femur is that of the referred specimen from locality Ni.

Paralectotype—HMN SI, skull and cervical vertebrae 2-7.

Referred Specimens—As listed by Janensch (1929:7-9) for "Brachiosaurus Brancai und Br. Fraasi Janensch."

Occurrence and Distribution—Middle and Upper Saurian Members, Tendaguru Formation, Tanzania, east Africa.

Age—Latest Jurassic (Kimmeridgian-Tithonian), 155.6-145.5 Mya.

Revised Diagnosis—Postspinal laminae present on dorsal vertebrae (character 130); distal ends of transverse processes of dorsal vertebrae possess distinctive, elevated areas with dorsally-facing surface that is connected to the dorsal surface of the remaining process only by a sloping region (character 142); spinodiapophyseal and spinopostzygapophyseal laminae on middle and posterior dorsal vertebrae do not contact each other (character 146); posterior dorsal centra dorsoventrally compressed in cross-section (character 151); posterior dorsal neural spines rectangular for most of their length with little or no lateral expansion except at distal end (character 155); mid-dorsals only about one quarter longer than posterior dorsals (see Paul, 1988:7); mid-dorsals about 40% taller than posterior dorsals (see Paul, 1988:9); dorsal centra short (Janensch, 1950a:72) so that dorsal column is less than twice humerus length (Paul, 1988:9); transverse processes of dorsal vertebrae oriented dorsolaterally (Paul, 1988:9); dorsal neural spines oriented posterodorsally in lateral view; dorsal neural spines are nearly constant in anteroposterior width through much of their height; ligament rugosities on anterior and posterior faces of neural spines limited to shallow semicircles at the dorsal extremity; spinoparapophyseal laminae on some dorsal vertebrae; broad, perforated anterior centroparapophyseal laminae on some dorsal vertebrae; horizontal lamina complex (PRPL, PPDL and PODL) supported from below by forked lamina that does not contact the diapophysis in some dorsal vertebrae; hyposphenal ridge weakly developed or absent from anterior caudal vertebrae (character 178); anterior caudal vertebrae have transversely narrow neural spines (Janensch, 1950a:76); anterior caudal vertebrae with lateral fossae (Janensch, 1950a:76); glenoid articular surface of coracoid oriented directly posteroventrally; glenoid articular surface of coracoid mediolaterally narrow; humerus very gracile (GI = 8.7); lateral margin of humerus straight; projected line connecting articular surfaces of ischiadic and pubic processes of ilium passes through ventral edge of postacetabular lobe (character 264); acute posterior notch between ischiadic peduncle and postacetabular lobe of ilium; tubercle absent from dorsal margin of postacetabular lobe of ilium; distal tip of fourth trochanter lies above midshaft height (character 282); lateral margin of femoral shaft in anterior view with distinct bulge 1/3 down (character 285); femur relatively gracile (GI = 6.2); fibular condyle of femur wider than tibial condyle.

PHYLOGENETIC ANALYSIS

Salgado and Calvo (1997:43) suggested that the two "*Brachiosaurus*" species may not form a clade, as they were unable to identify any unequivocal synapomorphies linking the species. However, they did not test their own hypothesis by codifying the two species as separate OTUs in the phylogenetic analysis of the companion paper, Salgado et al. (1997). Neither have subsequent studies done so: in the phylogenetic analysis of Harris (2006), and those of Wilson (2002) and Upchurch et al. (2004) on which that of Harris is largely based, and in Wilson and Sereno (1998), a single *Brachiosaurus* OTU is used, the scoring for which represents a combination of states observed in the two species (J. Harris, J. Wilson, P. Upchurch; pers. comms., 2007). As no published phylogenetic analysis treats the two species separately, there is no numerical evidence either for or against the paraphyly proposed by Salgado and Calvo (1997).

To address this deficiency, I adapted the matrix of Harris (2006) by splitting the composite *Brachiosaurus* OTU into two separate OTUs representing *Brachiosaurus altithorax* and *Giraffatitan brancai*, yielding a matrix of 31 taxa (29 ingroups and two outgroups) and 331 characters. While rescoring the two brachiosaurid species, it became apparent that the composite *Brachiosaurus* OTU of Harris (2006) was incorrectly scored for several characters, having been assigned states that do not occur in either species (Table 2). These were corrected for both new OTUs.

Following Harris (2006), PAUP* 4.0b10 (Swofford, 2002) was used to perform a heuristic search using random stepwise addition with 50 replicates and with maximum trees = 500000. The analysis yielded 72 equally parsimonious trees with length = 791, consistency index (CI) = 0.5196, retention index (RI) = 0.6846 and rescaled consistency index (RC) = 0.3557. The statistics indicate a slightly less consistent tree than that of Harris (CI = 0.526, RI = 0.687) because additional homoplasy is introduced by splitting the *Brachiosaurus* OTU.

The strict consensus tree (Fig. 6) is identical to that of Harris (2006) in the relationships of the 29 taxa that they share. (It does not appear identical to the strict consensus tree figured by Harris (2006:fig. 5a) due to a drawing error that resulted in the positions of *Haplocanthosaurus* and *Losillasaurus* Casanovas, Santafé and Sanz, 2001 being exchanged in that figure, as is confirmed by both the text and the majority rule tree in fig. 5b.) Within the current study's strict consensus tree, Neosauropoda is fully resolved except for a trichotomy of the three rebbachisaurids, *Nigersaurus* Sereno, Beck, Dutheil, Larsson, Lyon, Moussa, Sadleir, Sidor, Varricchio, Wilson and Wilson, 1999, *Rebbachisaurus* Lavocat, 1954 and *Limaysaurus* Salgado, Garrido, Cocca and Cocca, 2004. The two "*Brachiosaurus*" species form a clade to the exclusion of all other sauropods, and together occupy the same position as did the composite *Brachiosaurus* OTU in Harris (2006), as basal titanosauriforms forming the outgroup to the (*Euhelopus* [Romer, 1956]+ Titanosauria) clade. This result does not rule out the possibility that other brachiosaurid species, if included in the analysis, might break up the *Brachiosaurus-Giraffatitan* clade, but does argue against the possibility that *Giraffatitan* is more closely related to titanosaurs than to *Brachiosaurus* as was suggested by Naish et al. (2004:793). However, only a single further step is required for *Giraffatitan* to fall closer to titanosaurs than to *Brachiosaurus*; strict consensus of all most parsimonious trees under this constraint maintains the topology (*Camarasaurus* (*Brachiosaurus* (*Giraffatitan* (*Euhelopus*, titanosaurs)))). Four further steps are required for *Brachiosaurus* to fall closer to titanosaurs than to *Giraffatitan*, and the strict consensus of trees satisfying this constraint also keeps *Brachiosaurus* outside the (*Euhelopus* + titanosaurs) clade. Further phylogenetic work including more brachiosaurid OTUs is needed.

TABLE 2. Corrected character codings for the compound "*Brachiosaurus*" OTU in the analysis of Harris (2006). Owenian anatomical nomenclature is used in place of the avian nomenclature of Harris.

Character in Harris (2006)	Coding in Harris (2006)	Corrected coding	Comments
128. Dorsal vertebrae with spinodiapophyseal lamina	On posterior dorsals only (1)	On middle and posterior dorsals (2)	This lamina is clearly visible in middle dorsals of both *Brachiosaurus* (Riggs, 1904: plate LXXII) and *Giraffatitan* (Janensch, 1950a: figs. 53 and 54).
133. Morphology of posterior margins of lateral fossae on anterior dorsal vertebrae	Acute (1)	Unknown (?) in *Brachiosaurus*; rounded (0) in *Giraffatitan*.	Figured for *Giraffatitan* by Janensch (1950a: fig. 53)
134. Morphology of ventral surfaces of anterior dorsal centra	With sagittal crest (creating two ventrolaterally facing surfaces) (2)	Unknown (?) in *Brachiosaurus*; variable (?) in *Giraffatitan*.	In *Giraffatitan*, the ventral morphology of the centra changes along the vertebral column as described by Janensch (1950a: 44-46)[1]
138. Morphology of centroprezygapophyseal lamina on middle and posterior dorsal vertebral arches	Bifurcate toward upper end (= infraprezygapophyseal fossa present) (1)	Single (0)	No infraprezygapophyseal fossa is present in any dorsal vertebra of either species.
141. Posterior centroparapophyseal lamina on middle and posterior dorsal vertebral arches	Present (1)	Uncertain (?) in *Brachiosaurus*; variable (?) in *Giraffatitan*.	Preservation is not good enough in *Brachiosaurus* to be sure about this character. There are no PCPLs in D8 of the *Giraffatitan* type specimen HMN SII, but they are present in the last two dorsals.
143. Lamination on anterior face of (non-bifid) neural spine of middle and posterior dorsal vertebrae	Both prespinal and spinoprezygapophyseal laminae present and connected to each other either directly (merging) or via accessory laminae (3)	Prespinal lamina absent, spinoprezygapophyseal laminae present (2)	No prespinal lamina is present in any dorsal vertebra of either species.
154. Ratio of mediolateral width to anteroposterior length of posterior (non-bifid) dorsal neural spines	<=1.0 (longer than wide) (0)	>1.0 (wider than long) (1)	Only the neural spine of the last dorsal of *Brachiosaurus* is narrower transversely than anteroposteriorly.
160. Ratio of height of sacral neural spines to anteroposterior length of centrum	2.0-3.49 (1)	<2.0 (0)	The partial sacrum of *Giraffatitan* figured by Janensch (1950a: fig. 74) shows the height of the sacral spines to be less than 1.5 times the average sacral centrum length.
169. Morphology of articular surfaces in anterior caudal centra	Dorsoventrally compressed (1)	Subcircular (0)	Circular anterior caudal articular surfaces are figured for both *Brachiosaurus* (Riggs, 1904: plate LVVI, fig. 1) and *Giraffatitan* (Janensch, 1950a: plates II and III).
182. Morphology of anterior centrodiapophyseal lamina on anterior caudal transverse processes	Single (0)	Inapplicable (?)	These laminae do not exist in the caudal vertebrae of either species.
218. Morphology of anterodorsal margin of coracoid	Rectangular (meet at abrupt angle) (1)	Rounded (anterior and dorsal margins grade into one another) (0)	See Riggs (1904: plate LXXV, fig. 4).
284. Ratio of mediolateral to anteroposterior diameter of femur at midshaft	1.25-1.50 (1)	1.85 (2)	This ratio is 2.1 in *Brachiosaurus* (pers. obs. of cast) and 2.3 in *Giraffatitan* (Janensch, 1961: Beilage J, figs. 1a, c).
287. Relative mediolateral breadth of distal femoral condyles	Tibial condyle much broader than fibular condyle (1)	Subequal (0)	The condyles are subequal in width in *Brachiosaurus* (Riggs, 1903: fig. 4, 1904: plate LXXIV, fig. 2); in *Giraffatitan*, the fibular condyle is about 1.5 times as wide as the tibial condyle (Janensch, 1961: Beilage J, fig. 1b).

1: "With the transition [from the neck] to the trunk in the 13th presacral vertebra, and increasingly in the two subsequent first dorsal vertebrae, the flatness of the ventral surface behind the parapophyses gives way to vaulting; in the 15th presacral vertebra the middle section is completely cylindrical ventrally … The centrum of the 15th to 17th presacral vertebrae exhibits a somewhat depressed ventral field bordered by two rounded margins; in the remaining dorsal vertebrae in contrast, as in the three SII 121-123 (essentially preserved only as centra), they exhibit a median ventral ridge" (translated from Janensch, 1950a:44-46).

In the analysis of Taylor and Naish (2007), which used the composite *Brachiosaurus* OTU of Harris (2006), *Xenoposeidon* emerged as the sister taxon to "*Brachiosaurus*" in 72 of 1089 trees (6.6%). When it is added to the new analysis, it is never sister taxon to *Brachiosaurus altithorax*, but is sister to *Giraffatitan* in 72 of 1014 trees (7.1%). Splitting the brachiosaurs, then, reduces the number of most parsimonious trees by 75 (6.9%); in the initial analysis *Xenoposeidon* was attracted to the *Giraffatitan* component of the composite OTU rather than the *Brachiosaurus altithorax* component.

DISCUSSION

Association of the *Giraffatitan* Lectotype Material

As noted by Paul (1988:7), the anterior dorsal vertebra considered by Janensch to be D4 of the *Giraffatitan* lectotype HMN
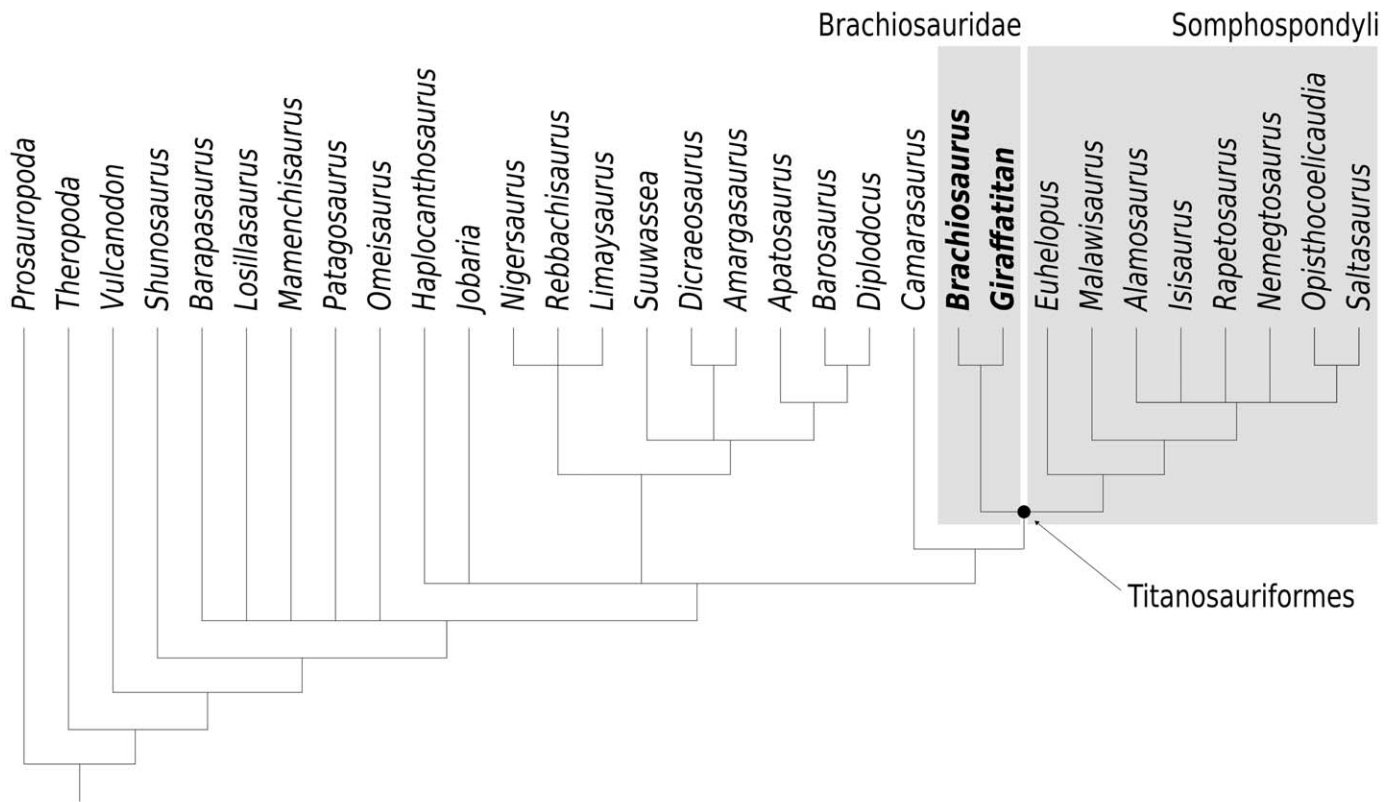
FIGURE 6. Phylogenetic relationships of *Brachiosaurus* and *Giraffatitan*, produced using PAUP* 4.0b10 on the matrix of Harris (2006) modified by splitting the composite "*Brachiosaurus*" OTU into two separate OTUs for the two species, having 31 taxa and 331 characters. Strict consensus of 72 most parsimonious trees (length = 791; CI = 0.5196; RI = 0.6846, RC = 0.3557). Three clades forming a node-stem triplet are highlighted: the node-based Titanosauriformes, and the branch-based sister clades Brachiosauridae and Somphospondyli.

SII differs markedly from the more posterior dorsal vertebrae of the same specimen, being much taller, having a more slender neural spine, and bearing notably broad diapophyses. However, another possibility should be considered: that the aberrant anterior dorsal vertebra does not in fact belong to HMN SII. As noted by Janensch (1950a:33), the excavation at Site S yielded presacral material from two individuals, designated SI and SII. The material assigned to SI consists of a partial skull and an articulated sequence of cervicals 2-7, with all remaining Site S material assigned to SII. However, the dorsal vertebrae posterior to the third were disarticulated, isolated from one another and jumbled together with other skeletal elements. Although Janensch (1929:8) had previously considered it possible that some of the Site S dorsal vertebrae belonged to specimen SI, he subsequently asserted that "These individually embedded vertebrae are far too large to have belonged to the smaller *Brachiosaurus* SI … In size they completely match the articulated vertebral series and can thus be associated with Skeleton SII without hesitation" (Janensch, 1950a:33). However, while the overall size of D4 is commensurate with that of D8, his statement is misleading because its centrum is significantly smaller and its processes much longer. The association of D4 with SII, then, cannot be considered certain. Janensch's preserved field sketches, reproduced by Heinrich (1999:figs. 16, 18) do not indicate the relative positions of the vertebrae, and his field notes subsequent to his first week at Tendaguru are lost (G. Maier, pers. comm., 2007), so further information will probably not be forthcoming.

A dorsal neural spine that is part of Migeod's specimen BMNH R5937 closely resembles that of the vertebra D4

assigned to HMN SII (Taylor, in prep.) Since this specimen, though brachiosaurid, does not belong to *Giraffatitan* (Taylor 2005), it must be possible that the anterior dorsal vertebra assigned to SII actually belongs to SI, and that SI belongs to the same taxon as BMNH R5937. If this is correct, then the cervical vertebrae of this taxon very closely resemble those of *Giraffatitan*. Since the North American cervical vertebrae BYU 12866 and 12867, which may belong to *Brachiosaurus altithorax*, are also indistinguishable from those of *Giraffatitan*, it is possible that cervical morphology is highly conserved in brachiosaurids while more variation is found in the dorsal column. If so, this would be the converse of the situation among diplodocids, among which *Diplodocus*, *Apatosaurus* and *Barosaurus* have rather similar dorsal vertebrae but very different cervicals.

Differences in Body Proportions

Having made a careful element-by-element comparison between the two brachiosaurid species, it is now possible to consider how the osteological differences between the species might have been reflected in differences in gross bodily proportions.

First, as stated by Paul (1988:7), the trunk is proportionally longer in *Brachiosaurus* than in *Giraffatitan* due to the greater length of its dorsal centra. Paul states that the difference is "25%-30%" on the basis of his figure 2. Independent calculation of the lengths of the sequences of dorsals 6-12 in both species corroborates this, finding that the posterior dorsal centra of *Brachiosaurus* are about 23% longer than those of *Giraffatitan* (Table 3). This is a significant proportional difference, apparent to the naked eye.

TABLE 3. Functional lengths of dorsal centra of *Brachiosaurus* and *Giraffatitan*, omitting condyles.

Dorsal	*Brachiosaurus altithorax* Length (cm)	*Giraffatitan brancai* Length (cm)
D4	—	28.5
D5	—	28.7
D6	37	29
D7	38	29.2
D8	34	29.4
D9	32	27.3
D10	35	25.1
D11	28	23
D12	22	20
Total D6–D12	226	183

Measurements for *Brachiosaurus* taken from Riggs (1904:pl. LXXII) and scaled according to total vertebra heights as given by Riggs (1904:234). Measurements for *Giraffatitan* taken from Janensch (1950a:44) for D4 and D8, scaled from Janensch (1950a:fig. 62) for D11 and D12, and linearly interpolated for D5-D7, D9 and D10.

Paul (1988:8) argued that *Brachiosaurus* lacked the "withers" (tall neural spines over the shoulders) of *Giraffatitan*. This cannot be substantiated, however, because the anterior dorsal vertebrae of *Brachiosaurus* are not known, the putative fourth dorsal vertebra of *Giraffatitan* being from a location two places forward of the most anterior known *Brachiosaurus* dorsal. Bearing in mind that the association of the supposed fourth dorsal of *Giraffatitan* may not be secure, it is apparent that nothing can be confidently said about differences between the genera in the anterior dorsal region.

More significant are the differences between the single known caudal vertebra of *Brachiosaurus* and those of *Giraffatitan*. Many caudals of the latter are known, and are remarkably consistent in morphology, while the single known caudal of the former is unambiguously associated with the remainder of the specimen and differs from those of *Giraffatitan* in two mechanically significant ways: first, although it is from a similarly sized animal as the *G. brancai* type specimen, and is comparable in anteroposterior length, it is taller in both the centrum and the neural arch (Fig. 3B, D); and second, the transverse broadening of the neural spine towards its extremity allows a much greater area for ligament attachment – about 2.25 times as great. The former character certainly indicates that the tail was taller in the American taxon, and the latter suggests that it was longer, perhaps by about 20%-25%.

Since *Brachiosaurus* had both a longer trunk and tail than *Giraffatitan*, it is tempting to wonder whether its neck was also longer, contra the suggestion of Paul (1988:8) that it was shorter. However, the example of *Diplodocus* and *Barosaurus* demonstrates that even closely related sauropods may vary unpredictably in proportions: the longer tail of *Diplodocus*, taken alone, might be thought to imply that it also had a longer neck than its cousin, but the opposite is the case. Therefore, conclusions about the neck of *Brachiosaurus* cannot be drawn from elongation in other parts of the body; and indeed the North American brachiosaur cervicals BYU 12866 and 12867, if correctly referred to *Brachiosaurus*, indicate that its neck proportions were identical to those of *Giraffatitan*.

One of the most distinctive osteological features of *Brachiosaurus* is the strong lateral deflection of the glenoid surface of its coracoid, which in other sauropods including *Giraffatitan* faces directly posteroventrally. This may indicate that the humeri were also directed somewhat laterally, again in contrast to the parasagittally oriented forelimbs of other sauropods. Janensch restored the skeleton of *Giraffatitan* with somewhat sprawling upper arms, reasoning that "In the forelimb the humerus [...] displays characters that are similar to the conditions of the

humerus of lacertilians, crocodylians and *Sphenodon*, even if pronounced to a lesser degree, which, however, show that, in the type of motion of the upper arm, a component of lateral splaying was included" (Janensch, 1950b:99). Ironically, while it is now established that sauropods in general held their limbs vertically, it seems possible that *Giraffatitan*'s sister taxon *Brachiosaurus* may have been the sole exception to this rule. If correct, this would be surprising: the bending stress on a sprawled humerus would greatly exceed the compressive stress on one held vertically (Alexander, 1985:18), and the proportionally slender humeri of *Brachiosaurus* would seem particularly unsuited to such a posture.

Finally, while slender, the humeri of *Brachiosaurus* are less so than those of *Giraffatitan*, having a GI of 7.12 compared with 8.69. The femora of the two species, however are proportionally very similar. Since the humerus of *Brachiosaurus*, then, is more robust in comparison with its femur than in *Giraffatitan*, it is possible that the American species carried a greater proportion of its weight on its forelimbs than the African species.

In conclusion, the osteological evidence suggests that *Brachiosaurus* differed from the popular *Giraffatitan*-based conception of the genus in that its trunk was 23% longer, its tail 20%-25% longer and thicker, its forelimbs were possibly somewhat sprawled, and a greater concentration of its mass was probably above the forelimbs. Taking these differences into account, I prepared a skeletal reconstruction of *Brachiosaurus altithorax* (Fig. 7), including the holotype and all referred skeletal elements, with the remaining elements modified from Paul's (1988) reconstruction of *Giraffatitan*. Comparison with Paul's *Giraffatitan* clearly illustrates the differences.

Martin et al. (1998:120) argued that "*Brachiosaurus*" (i.e. *Giraffatitan*) "had front and hind limbs of roughly equal length," that "the now 'traditional' disparity of the fore- and hind-limb proportions (about 1.2:1) has been based on the 1937 mounted skeleton in the Humboldt-Museum, Berlin, which is a composite reconstruction," and that "other taxa referred to *Brachiosaurus* (including *B. altithorax* Riggs, 1903 and *B. atalaiensis* Lapparent and Zbyszewski, 1957) appear, as far as the evidence permits us to say, to have had front and hind limbs of roughly equal length." While it is true that the Humboldt mount is a composite, Janensch (1950b:99) explained that it includes a forelimb, complete except for one carpal, and a tibia, fibula and partial femur, all from the same individual (HMN SII), and that the femur's reconstructed length was "calculated from other finds." Therefore the limb proportions of this skeleton are reliable. It is true that the humeri and femora are nearly identical in length in both *Brachiosaurus* and *Giraffatitan*, but this does not mean that the torso was held horizontal for three reasons: first, the vertically oriented metacarpal arcade of sauropods causes the wrist to be held higher than the ankle, especially in the case of brachiosaurids, which have particularly elongate metacarpals; second, as shown by Janensch (1950b:pl. 8), the lower forelimb (ulna and radius) is longer than the lower hind-limb (tibia and fibula), causing the shoulder to be higher than the hip; third, the shoulder joint is mounted much lower on the rib-cage than the hip joint is on the sacrum, so that shoulder vertebrae must have been higher than hip vertebrae. In conclusion, the forelimbs of brachiosaurids were indeed longer than their hindlimbs, and their backs were strongly inclined anterodorsally, as reconstructed by Janensch (1950b), Paul (1988), Wedel (2000) and others.

Masses of *Brachiosaurus* and *Giraffatitan*

To determine the effects that these proportional differences would have had on the mass of *Brachiosaurus* as compared with its better known cousin, I estimated the volumes of the type specimens of both species using Graphic Double Integration
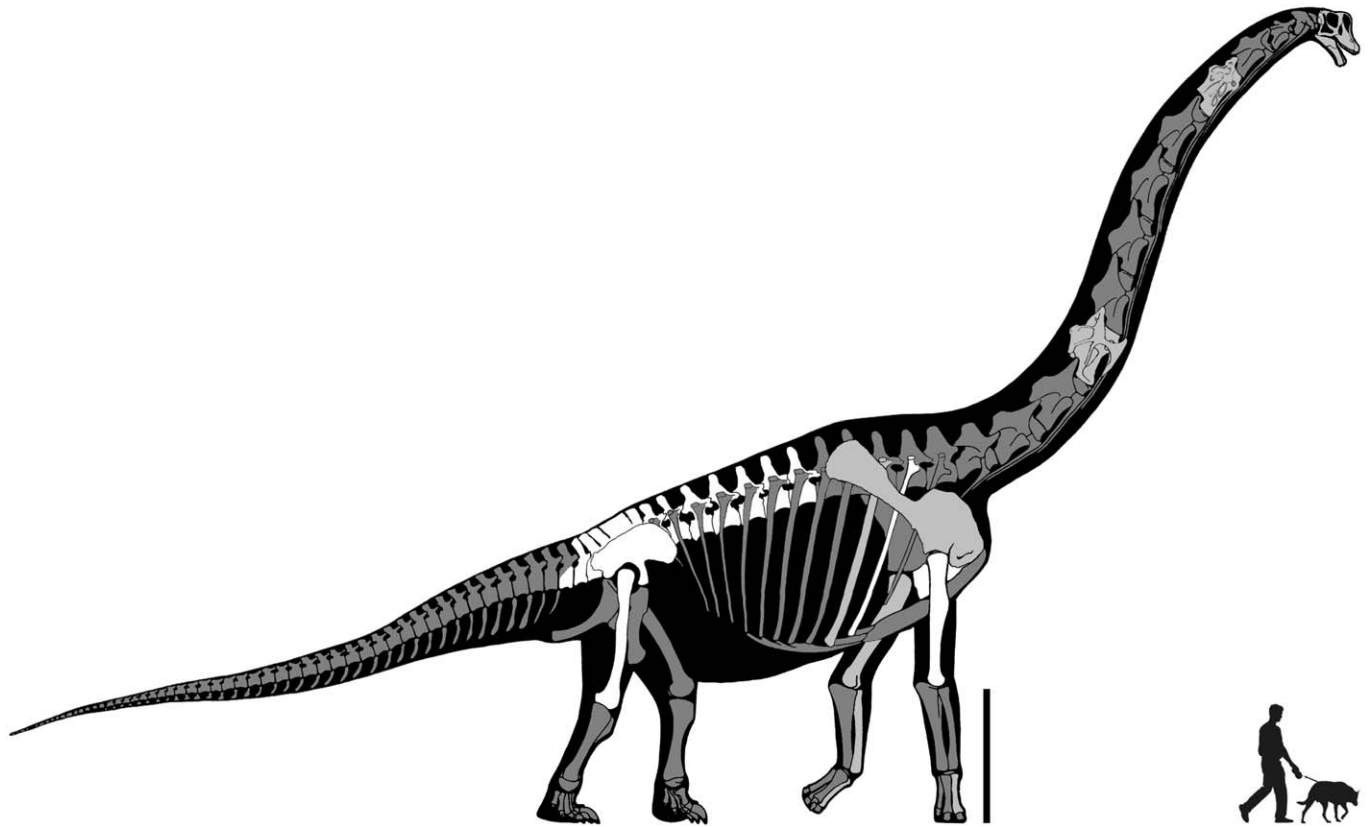
FIGURE 7. Skeletal reconstruction of *Brachiosaurus altithorax*. White bones represent the elements of the holotype FMNH P 25107. Light grey bones represent material referred to *B. altithorax*: the Felch Quarry skull USNM 5730, the cervical vertebrae BYU 12866 (C?5) and BYU 12867 (C?10), the "*Ultrasauros*" scapulocoracoid BYU 9462, the Potter Creek left humerus USNM 21903, left radius and right metacarpal III BYU 4744, and the left metacarpal II OMNH 01138. Dark grey bones modified from Paul's (1988) reconstruction of *Giraffatitan brancai*. Scale bar equals 2 m.

(Jerison, 1973; Hurlburt, 1999; Murray and Vickers-Rich, 2004). For the lateral silhouette of *Brachiosaurus*, I used the reconstruction of Fig. 7; for the corresponding dorsal, anterior and posterior silhouettes, I modified Paul's (1998:fig. 1) reconstruction of *Giraffatitan* as follows: head, neck, forelimbs and hindlimbs I left unmodified. I stretched the dorsal view of the torso by 12.8% to match the length of the lateral view, and conservatively increased the transverse width by half this proportion, 6.4%. Similarly, I stretched the dorsal view of the tail by 20% to match the lateral view, and increased transverse width by 10%. The selected increases in transverse width are unavoidably arbitrary, because the ribs of *Brachiosaurus* are not sufficiently well known to inform a rigorous dorsal-view reconstruction. As pointed out by Murray and Vickers-Rich (2004:211), such guess-

work is unavoidable in mass estimation: the best we can do is to be explicit about what the assumptions are, to facilitate repeatability and the subsequent construction of better models.

The results are summarized, by body-part, in Table 4. Most significantly, the volume, and hence mass, of *Brachiosaurus* is calculated to be 23% greater than that of *Giraffatitan*, whereas Paul (1988:3) found *Brachiosaurus* to be only 11% heavier than *Giraffatitan* (35000 kg vs. 31500 kg). This is partly explained by the larger tail of *Brachiosaurus* in this reconstruction, where Paul assigned it a similarly sized tail to that of *Giraffatitan*, but Paul must also have modelled the torso of *Brachiosaurus* as much narrower that I have. The absolute masses calculated here are significantly lower than those of Paul (1988:3) – 28688 kg for *Brachiosaurus* is 82% of Paul's 35000 kg, and 23337 kg for

TABLE 4. Volumes and masses of *Brachiosaurus* and *Giraffatitan*, estimated by Graphic Double Integration and broken down by body part.

Body part	*Brachiosaurus*		*Giraffatitan*		
	Volume (l)	%Total	Volume (l)	%Total	Volume ratio
Head	140	0.39	140	0.48	
Neck	4117	11.48	4117	14.11	
Forelimbs (pair)	1344	3.75	1344	4.61	
Hindlimbs (pair)	1462	4.08	1462	5.01	
Torso	26469	73.81	20588	70.58	1.29
Tail	2328	6.49	1520	5.21	1.53
Total volume	35860		29171		1.23
Total mass (kg)	28688		23337		

Volume ratio indicates *Brachiosaurus* volumes as a proportion of corresponding *Giraffatitan* volumes. Masses assume a density of 0.8 kg/l (Wedel 2005:220).

Giraffatitan is only 74% of Paul's 31500 kg. One reason for this is that I have assumed a density of 0.8 kg/l based on the average density of *Diplodocus* calculated by Wedel (2005:220) whereas Paul (1988:10) used 0.6 for the neck and 0.9 for the remainder of the animal, yielding an average density of 0.861. However, even using Paul's higher value for density, my mass estimates would be only 88% and 80% of Paul's. This may be because the models used by Paul (1988:10) for his mass estimates were sculpted separately from his execution of the skeletal reconstructions that I used as the basis of my calculations, and may have been bulkier. The mass of 23337 kg for *Giraffatitan*, while surprisingly light for so large an animal, compares well with the 25789 kg of Henderson (2004:S181).

Size of the Largest Brachiosaurid Sauropods

The largest brachiosaurid sauropods known from reasonably complete remains are still the type specimens of *Brachiosaurus altithorax* and *Giraffatitan brancai*, which are of very similar sizes: their humeri differ in length by only 3 cm (1.4%) and their femora by 8 cm (4%). As noted by Janensch (1950b:102) and Paul (1988:10), the fibula HMN XV2 is about 13% longer than that of the type specimen, indicating that *Giraffatitan* grew significantly larger than the type specimen. Curtice et al. (1996:93) noted that the "*Ultrasauros*" scapulocoracoid BYU 9462 belonged to an animal no larger than the largest Tendaguru specimens. It has not been noted, however, that while the scapula and coracoid that constitute BYU 9462 are fully fused, with the suture obliterated, the coracoid of the *B. altithorax* type specimen is unfused, indicating that it belonged to a subadult individual. It is possible that this individual would have grown significantly larger had it survived.

Phylogenetic Nomenclature

The genus *Brachiosaurus* is important in three widely used phylogenetic definitions: those of the clades Brachiosauridae, Somphospondyli, and Titanosauriformes. In all formulations of these three clades together, they form a node-stem triplet with the first two as sisters to each other within the last; therefore the same two specifiers should be used in their definitions.

Although the name Brachiosauridae has been in use as a "family" since Riggs (1904), its earliest phylogenetic definition is that of Wilson and Sereno (1998:20) as "titanosauriforms more closely related to *Brachiosaurus* than to *Saltasaurus*." This same definition was also proposed by Sereno (1998:63); no other definition has been published.

Wilson and Sereno (1998:53) erected the taxon Somphospondyli as the sister group to Brachiosauridae, defining it as "Titanosauriformes more closely related to *Saltasaurus* than to *Brachiosaurus*"; this definition was affirmed by Sereno (1998:63) and no alternative has been published. This clade was proposed in the context of a scheme in which Titanosauria was defined as "Titanosauriforms more closely related to *Saltasaurus* than to either *Brachiosaurus* or *Euhelopus*" (Wilson and Sereno, 1998:22). Upchurch et al. (2004:308), however, noting that this definition is confusing in its use of three reference taxa and that the distinction between the Somphospondyli and Titanosauria of Wilson and Sereno (1998) depended on the controversial position of *Euhelopus* as a basal somphospondylian, instead dispensed with the name Somphospondyli altogether and defined Titanosauria as "Titanosauriformes more closely related to *Saltasaurus* than to *Brachiosaurus*." At the time of that writing, *Euhelopus* was indeed controversial, having been recovered as a mamenchisaurid (euhelopodid of his usage) by Upchurch (1995, 1998), as a basal somphospondylian by Wilson and Sereno (1998) and Wilson (2002), and as a near outgroup of Neosauropoda by Upchurch et al. (2004). However, a subsequent joint

study between these two schools of sauropod phylogeny (Upchurch and Wilson, 2007) has more firmly established *Euhelopus* as more closely related to titanosaurs sensu stricto than to brachiosaurids, so the name Somphospondyli retains some utility. For this reason, and because the precise definition of Titanosauria remains controversial, I recommend the retention of the name Somphospondyli as part of the Titanosauriformes-Brachiosauridae node-stem triplet, and leave the matter of the definition of Titanosauria to others.

Titanosauriformes was initially defined by Salgado et al. (1997:12) as "the clade including the most recent common ancestor of *Brachiosaurus brancai*, *Chubutisaurus insignis*, and Titanosauria and all its descendants." In accordance with recommendation 2 of Taylor (2007:2), this definition should be interpreted according to the apparent intentions of the author, and it seems obvious that Salgado et al. intended to indicate the least inclusive clade containing the specified taxa rather than any of the more inclusive clades that also do. Subsequent redefinitions have all been similar to this one. Wilson and Sereno (1998:51) redefined this taxon as "*Brachiosaurus*, *Saltasaurus*, their common ancestor, and all of its descendants," which improves on the original definition by omitting the unstable and poorly represented specifier *Chubutisaurus insignis*, but which uses genera rather than species.

All of these definitions are in need of revision to comply with the requirements of the draft PhyloCode (Cantino and de Queiroz, 2006) which requires that species rather than genera must be used as specifiers, and that a species used as the internal specifier in a phylogenetic definition of a clade whose name is based on a genus must be the type of that genus (article 11.7). So, for example, Sereno's (2005) refinement of Titanosauriformes as "The least inclusive clade containing *Brachiosaurus brancai* Janensch 1914 and *Saltasaurus loricatus* Bonaparte and Powell 1980" (published only on the Internet) falls into the same trap as the original definition in anchoring on the non-type species *B. brancai*, with the result that, under some topologies, the type species *Brachiosaurus altithorax* is excluded from Titanosauriformes.

To avoid this eventuality, then, I offer the following triplet of definitions:

Titanosauriformes = the most recent common ancestor of *Brachiosaurus altithorax* Riggs 1903 and *Saltasaurus loricatus* Bonaparte and Powell 1980 and all its descendants.

Brachiosauridae = all taxa more closely related to *Brachiosaurus altithorax* Riggs 1903 than to *Saltasaurus loricatus* Bonaparte and Powell 1980.

Somphospondyli = all taxa more closely related to *Saltasaurus loricatus* Bonaparte and Powell 1980 than to *Brachiosaurus altithorax* Riggs 1903.

CONCLUSIONS

The popular image of *Brachiosaurus* is based on *Giraffatitan*, a generically distinct animal that is separated from *Brachiosaurus* by at least 26 osteological characters. The two genera remain closely related within Brachiosauridae, but would have appeared distinctly different in life.

ACKNOWLEDGMENTS

Indispensable translations of Janensch (1914, 1950a, b) were provided by G. Maier, who also provided invaluable assistance in other points relating to Janensch's German. In all cases where I have quoted translated portions of Janensch's papers, I used Maier's translations. Those translations are now freely available at the Polyglot Paleontologist Web site, http://ravenel.si.edu/paleo/paleoglot/, from which translations of other papers were also obtained.

M. Wedel and J. Harris provided excellent and very detailed reviews, and H.-D. Sues handled the manuscript with admirable tact and efficiency. E. Schweizerbart'sche Verlagsbuchhandlung (http://www.schweizerbart.de/) kindly gave permission for Janensch's Palaeontographica figures to be reproduced for the comparative figures.

Finally, I beg forgiveness from all brachiosaur lovers, that so beautiful an animal as "*Brachiosaurus*" *brancai* now has to be known by so inelegant a name as *Giraffatitan*.

LITERATURE CITED

Alexander, R. M. 1985. Mechanics of posture and gait of some large dinosaurs. Zoological Journal of the Linnean Society 83:1–25.

Anonymous. 1959. *Brachiosaurus* exhibit at the Smithsonian Institution. Nature 183:649–650.

Antunes, M. T., and O. Mateus. 2003. Dinosaurs of Portugal. Comptes Rendus Palevol 2:77–95.

Bonaparte, J. F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique moyen de Cerro Cóndor (Chubut, Argentina). Annales de Paléontologie 72:325–386.

Bonnan, M. F., and M. J. Wedel. 2004. First occurrence of *Brachiosaurus* (Dinosauria: Sauropoda) from the Upper Jurassic Morrison Formation of Oklahoma. PaleoBios 24:13–21.

Borsuk-Bialynicka, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n., sp. n., from the Upper Cretaceous of Mongolia. Palaeontologica Polonica 37:5–64.

Cantino, P. D., and K. de Queiroz. 2006. PhyloCode: A Phylogenetic Code of Biological Nomenclature (Version 4b, September 12, 2007). http://www.ohiou.edu/phylocode/PhyloCode4b.pdf.

Carpenter, K., and J. S. McIntosh. 1994. Upper Jurassic sauropod babies from the Morrison Formation; pp. 265–278 in K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), Dinosaur Eggs and Babies. Cambridge University Press, Cambridge.

Carpenter, K., and V. Tidwell. 1998. Preliminary description of a *Brachiosaurus* skull from Felch Quarry 1, Garden Park, Colorado. Modern Geology 23:69–84.

Casanovas, M. L., J. V. Santafé, and J. L. Sanz. 2001. *Losillasaurus giganteus*, un neuvo saurópodo del tránsito Jurásico-Cretácico de la cuenca de "Los Serranos" (Valencia, España). Paleontologia i Evolució 32-33:99–122.

Cope, E. D. 1877. On a gigantic saurian from the Dakota epoch of Colorado. Paleontology Bulletin 25:5–10.

Curry Rogers, K. 2001. The evolutionary history of the Titanosauria. (Ph.D. dissertation). State University of New York, Stony Brook, 573 pp.

Curtice, B. D. 1995. A description of the anterior caudal vertebrae of *Supersaurus vivianae*. Journal of Vertebrate Paleontology 15:3–25A.

Curtice, B. D., and K. L. Stadtman. 2001. The demise of *Dystylosaurus edwini* and a revision of *Supersaurus vivianae*. Western Association of Vertebrate Paleontologists and Mesa Southwest Paleontological Symposium, Mesa Southwest Museum Bulletin 8:33–40.

Curtice, B. D., K. L. Stadtman, and L. J. Curtice. 1996. A reassessment of *Ultrasauros macintoshi* (Jensen, 1985). Museum of Northern Arizona Bulletin 60:87–95.

Foster, J. R. 2003. Paleoecological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain Region, U.S.A. (NMMNHS bulletin 23). New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, 95 pp.

Harris, J. D. 2006. The significance of *Suuwassea emiliae* (Dinosauria: Sauropoda) for flagellicaudatan intrarelationships and evolution. Journal of Systematic Palaeontology 4:185–198.

Hatcher, J. B. 1903a. A new name for the dinosaur *Haplocanthus* Hatcher. Proceedings of the Biological Society of Washington 16:100.

Hatcher, J. B. 1903b. Osteology of *Haplocanthosaurus* with description of a new species, and remarks on the probable habits of the Sauropoda and the age and origin of the Atlantosaurus beds. Memoirs of the Carnegie Museum 2:1–72.

Heinrich, W.-D. 1999. The taphonomy of dinosaurs from the Upper Jurassic of Tendaguru (Tanzania) based on field sketches of the German Tendaguru Expedition (1909–1913). Mitteilungen aus dem Museum für Naturkunde, Berlin, Geowissenschaften, Reihe 2:25–61.

Henderson, D. M. 2004. Tipsy punters: sauropod dinosaur pneumaticity, buoyancy and aquatic habits. Proceedings of the Royal Society of London B, 271(Suppl. 4):S180–S183.

Hurlburt, G. R. 1999. Comparison of body mass estimation techniques, using Recent reptiles and the pelycosaur *Edaphosaurus boanerges*. Journal of Vertebrate Paleontology 19:338–350.

Ikejiri, T., V. Tidwell, and D. L. Trexler. 2005. new adult specimens of *Camarasaurus lentus* highlight ontogenetic variation within the species; pp. 154–179 in V. Tidwell, and K. Carpenter (eds.), Thunder Lizards: the Sauropodomorph Dinosaurs. Indiana University Press, Bloomington, Indiana.

Jacobs, L. L., D. A. Winkler, W. R. Downs, and E. M. Gomani. 1993. New material of an Early Cretaceous titanosaurid sauropod dinosaur from Malawi. Palaeontology 36:523–534.

Janensch, W. 1914. Übersicht über der Wirbeltierfauna der Tendaguru-Schichten nebst einer kurzen Charakterisierung der neu aufgefuhrten Arten von Sauropoden. Archiv fur Biontologie 3:81–110.

Janensch, W. 1922. Das Handskelett von *Gigantosaurus robustus* u. *Brachiosaurus Brancai* aus den Tendaguru-Schichten Deutsch-Ostafrikas. Centralblatt für Mineralogie, Geologie und Paläontologie 15:464–480.

Janensch, W. 1929. Material und Formengehalt der Sauropoden in der Ausbeute der Tendaguru-Expedition. Palaeontographica (Suppl. 7) 2:1–34.

Janensch, W. 1935–1936. Die Schadel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus* aus den Tendaguru-Schichten Deutsch-Ostafrikas. Palaeontographica (Suppl. 7) 2:147–298.

Janensch, W. 1947. Pneumatizitat bei Wirbeln von Sauropoden und anderen Saurischien. Palaeontographica (Suppl. 7) 3:1–25.

Janensch, W. 1950a. Die Wirbelsaule von *Brachiosaurus brancai*. Palaeontographica (Suppl. 7) 3:27–93.

Janensch, W. 1950b. Die Skelettrekonstruktion von *Brachiosaurus brancai*. Palaeontographica (Suppl. 7) 3:97–103.

Janensch, W. 1961. Die Gliedmaszen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. Palaeontographica (Suppl. 7) 3:177–235.

Jensen, J. A. 1985. Three new sauropod dinosaurs from the Upper Jurassic of Colorado. Great Basin Naturalist 45:697–709.

Jensen, J. A. 1987. New brachiosaur material from the Late Jurassic of Utah and Colorado. Great Basin Naturalist 47:592–608.

Jerison, H. J. 1973. Evolution of the brain and intelligence. Academic Press, New York, 482 pp.

Kim, H. M. 1983. Cretaceous dinosaurs from Korea. Journal of the Geology Society of Korea 19:115–126.

Lapparent, A. F. d., and G. Zbyszewski. 1957. Mémoire no. 2 (nouvelle série): les dinosauriens du Portugal. Services Géologiques du Portugal, Lisbon, Portugal, 63 pp.

Lavocat, R. 1954. Sur les Dinosauriens du continental intercalaire des Kem-Kem de la Daoura. Comptes Rendus 19th Intenational Geological Congress 1952, 1:65–68.

Lull, R. S. 1919. The sauropod dinosaur *Barosaurus* Marsh. Memoirs of the Connecticut Academy of Arts and Sciences 6:1–42.

Maier, G. 2003. African Dinosaurs Unearthed: The Tendaguru Expeditions. Indiana University Press, Bloomington and Indianapolis, 380 pp.

Marsh, O. C. 1877. Notice of new dinosaurian reptiles from the Jurassic formation. American Journal of Science and Arts 14:514–516.

Marsh, O. C. 1878. Principal characters of American Jurassic dinosaurs. Part I. American Journal of Science, Series 3, 16:411–416.

Marsh, O. C. 1879. Notice of new Jurassic reptiles. American Journal of Science, Series 3, 18:501–505.

Marsh, O. C. 1890. Description of new dinosaurian reptiles. American Journal of Science, Series 3, 39:81–86 and plate I.

Marsh, O. C. 1891. Restoration of *Triceratops*. American Journal of Science, Series 3, 41:339–342.

Martin, J., V. Martin-Rolland, and E. Frey. 1998. Not cranes or masts, but beams: the biomechanics of sauropod necks. Oryctos 1:113–120.

Matthew, W. D. 1915. Dinosaurs, with special reference to the American Museum collections. American Museum of Natural History, New York, 164 pp.

McIntosh, J. S. 1990a. Sauropoda; pp. 345–401 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. University of California Press, Berkeley and Los Angeles.

McIntosh, J. S. 1990b. Species determination in sauropod dinosaurs with tentative suggestions for the their classification; pp. 53–69 in K. Carpenter, and P. J. Currie (eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge.

McIntosh, J. S., and D. S. Berman. 1975. Description of the palate and lower jaw of the sauropod dinosaur *Diplodocus* (Reptilia: Saurischia) with remarks on the nature of the skull of *Apatosaurus*. Journal of Paleontology 49:187–199.

Migeod, F. W. H. 1931. British Museum East Africa Expedition: Account of the work done in 1930. Natural History Magazine 3:87–103.

Murray, P. F., and Vickers-Rich, P. 2004. Magnificent mihirungs. Indiana University Press, Bloomington, Indiana, 410 pp.

Naish, D., D. M. Martill, D. Cooper, and K. A. Stevens. 2004. Europe's largest dinosaur? A giant brachiosaurid cervical vertebra from the Wessex Formation (Early Cretaceous) of southern England. Cretaceous Research 25:787–795.

Olshevsky, G. 1991. A revision of the parainfraclass Archosauria Cope, 1869, excluding the advanced Crocodylia. Mesozoic Meanderings 2:1–196.

Osborn, H. F., and C. C. Mook. 1921. *Camarasaurus*, *Amphicoelias* and other sauropods of Cope. Memoirs of the American Museum of Natural History, n.s. 3:247–387.

Owen, R. 1842. Report on British fossil reptiles, Part II. Reports of the British Association for the Advancement of Sciences 11:60–204.

Paul, G. S. 1988. The brachiosaur giants of the Morrison and Tendaguru with a description of a new subgenus, *Giraffatitan*, and a comparison of the world's largest dinosaurs. Hunteria 2:1–14.

Paul, G. S. 1994. Dinosaur reproduction in the fast lane: implications for size, success and extinction; pp. 244–255 in K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), Dinosaur Eggs and Babies. Cambridge University Press, Cambridge.

Paul, G. S. 1998. Terramegathermy and Cope's rule in the land of titans. Modern Geology 23:179–217.

Paul, G. S. 2000. Restoring the life appearances of dinosaurs; pp. 78–106 in G. S. Paul (ed.), The Scientific American book of dinosaurs. St. Martin's Press, New York.

Powell, J. E. 1992. Osteología de *Saltasaurus loricatus* (Sauropoda-Titanosauridae) del Cretácico Superior del Noroeste Argentino; pp. 165–230 in J. L. Sanz, and A. D. Buscalioni (eds.), Los Dinosaurios y su Entorno Biotico. Actas del Segundo Curso de Paleontologia en Cuenca. Instituto Juan de Valdés, Ayuntamiento de Cuenca.

Riggs, E. S. 1901. The largest known dinosaur. Science 13:549–550.

Riggs, E. S. 1903. *Brachiosaurus altithorax*, the largest known dinosaur. American Journal of Science 15:299–306.

Riggs, E. S. 1904. Structure and relationships of opisthocoelian dinosaurs. Part II, the Brachiosauridae. Field Columbian Museum, Geological Series 2, 6:229–247.

Romer, A. S. 1956. Osteology of the Reptiles. University of Chicago Press, Chicago, 772 pp.

Salgado, L., and J. O. Calvo. 1997. Evolution of titanosaurid sauropods. II: the cranial evidence. Ameghiniana 34:33–48.

Salgado, L., R. A. Coria, and J. O. Calvo. 1997. Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. Ameghiniana 34:3–32.

Salgado, L., A. Garrido, S. E. Cocca, and J. R. Cocca. 2004. Lower Cretaceous rebbachisaurid sauropods from Cerro Aguada Del Leon (Lohan Cura Formation), Neuquen Province, Northwestern Patagonia, Argentina. Journal of Vertebrate Paleontology 24:903–912.

Seeley, H. G. 1882. On a remarkable dinosaurian coracoid from the Wealden of Brook in the Isle of Wight, preserved in the Woodwardian Museum of Cambridge, probably referable to *Ornithopsis*. Quarterly Journal of the Geological Society, London 38:367–371.

Seeley, H. G. 1888. On the classification of the fossil animals commonly named Dinosauria. Proceedings of the Royal Society of London 43:165–171.

Sereno, P. C. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 210:41–83.

Sereno, P. C., A. L. Beck, D. B. Dutheil, H. C. E. Larsson, G. H. Lyon, B. Moussa, R. W. Sadleir, C. A. Sidor, D. J. Varricchio, G. P. Wilson, and J. A. Wilson. 1999. Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. Science 282:1342–1347.

Swofford, D. L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (* and Other Methods). Sinauer Associates, Sunderland, Massachusetts.

Taylor, M. P. 2005. Sweet seventy-five and never been kissed: the Natural History Museum's Tendaguru brachiosaur; pp. 25–25 in P. M. Barrett (ed.), Abstracts volume for 53rd Symposium of Vertebrae Palaeontology and Comparative Anatomy. The Natural History Museum, London.

Taylor, M. P. 2007. Phylogenetic definitions in the pre-PhyloCode era; implications for naming clades under the PhyloCode. PaleoBios 27:1–6.

Taylor, M. P., and D. Naish. 2007. An unusual new neosauropod dinosaur from the Lower Cretaceous Hastings Beds Group of East Sussex, England. Palaeontology 50:1547–1564.

Tidwell, V., and D. R. Wilhite. 2005. Ontogenetic variation and isometric growth in the forelimb of the Early Cretaceous sauropod *Venenosaurus*; pp. 187–198 in V. Tidwell, and K. Carpenter (eds.), Thunder Lizards: the Sauropodomorph Dinosaurs. Indiana University Press, Bloomington, Indiana.

Tidwell, V., K. Carpenter, and S. Meyer. 2001. New Titanosauriform (Sauropoda) from the Poison Strip Member of the Cedar Mountain Formation (Lower Cretaceous), Utah; pp. 139–165 in D. H. Tanke, and K. Carpenter (eds.), Mesozoic Vertebrate Life: New Research inspired by the Paleontology of Philip J. Currie. Indiana University Press, Bloomington and Indianapolis, Indiana.

Turner, C. E., and F. Peterson. 1999. Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the Western Interior, U.S.A; pp. 77–114 in D. D. Gillette (ed.), Vertebrate Paleontology in Utah (Utah Geological Survey Miscellaneous Publication 99-1). Utah Geological Survey, Salt Lake City, Utah.

Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. Philosophical Transactions of the Royal Society of London, Series B 349:365–390.

Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. Zoological Journal of the Linnean Society 124:43–103.

Upchurch, P., and J. A. Wilson. 2007. *Euhelopus zdanksyi* and its bearing on the evolution of East Asian sauropod dinosaurs; pp. 30–30 in J. Liston (ed.), Abstracts volume for 55th Symposium of Vertebrae Palaeontology and Comparative Anatomy. University of Glasgow, Glasgow.

Upchurch, P., P. M. Barrett, and P. Dodson. 2004. Sauropoda; pp. 259–322 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria. 2nd edition. University of California Press, Berkeley and Los Angeles.

Wedel, M. J. 2000. Reconstructing *Brachiosaurus*. Prehistoric Times 42:47.

Wedel, M. J. 2005. Postcranial skeletal pneumaticity in sauropods and its implications for mass estimates; pp. 201–228 in J. A. Wilson, and K. Curry-Rogers (eds.), The Sauropods: Evolution and Paleobiology. University of California Press, Berkeley.

Wedel, M. J. 2006. Pneumaticity, neck length, and body size in sauropods. Journal of Vertebrate Paleontology 26:3–137A.

Wedel, M. J., R. L. Cifelli, and R. K. Sanders. 2000. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. Acta Palaeontologica Polonica 45:343–388.

Wilson, J. A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. Journal of Vertebrate Paleontology 19:639–653.

Wilson, J. A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society 136:217–276.

Wilson, J. A., and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Society of Vertebrate Paleontology Memoir 5:1–68.

Young, C.-C. 1958. New sauropods from China. Vertebrata Palasiatica 2:1–28.