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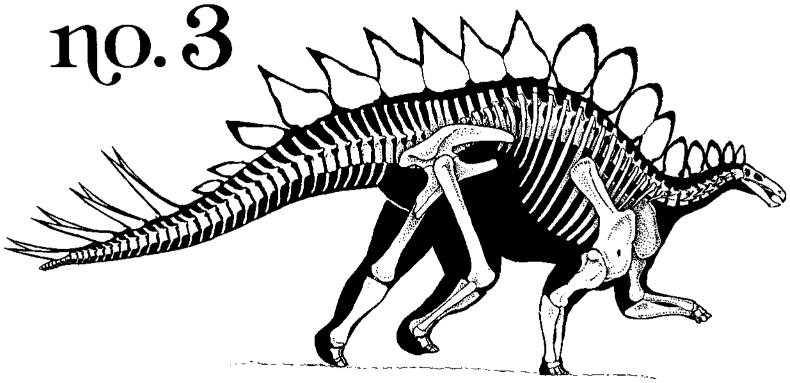

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THE BRACHIOSAUR GIANTS OF THE MORRISON AND TENDAGURU WITH A DESCRIPTION OF A NEW SUBGENUS, GIRAFFATITAN, AND A COMPARISON OF THE WORLD'S LARGEST DINOSAURS

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ABSTRACT

A new skeletal restoration of ***Brachiosaurus brancai*** shows that this gracile, giraffe-like taxon is a distinct subgenus from ***Brachiosaurus altithorax***. ***Ultrasaurus macintoshi*** is a junior synonym of ***B. altithorax*** and is similar in size to the largest ***B. brancai*** specimen. A survey of exceptionally large sauropod remains indicates that the largest weighed about 50 tons in lean condition, but this size was probably not the ultimate limit of the group. ***"Ultrasaurus"*** was not larger than the largest African brachiosaurs and published estimates of a body weight up to 190 tons are unwarranted exaggerations.

INTRODUCTION

Brachiosaurs are not only the largest of the Morrison dinosaurs, they are the largest terrestrial vertebrates of all time for which good remains are known. The first Morrison brachiosaur, ***Brachiosaurus altithorax***, was discovered by Riggs (1901, 1903, 1904) in 1900. The east African Tendaguru quarries that contained ***Brachiosaurus brancai*** were discovered in 1907 (Fraas, 1908; Janensch, 1914). Over the years there has been a tendency to consider the North American and African examples as much the same animal. In the 1970's the uncovering of new Morrison specimens led to claims of brachiosaurs of unprecedented size (Jensen, 1978, 1985a,b). While executing a new skeletal restoration of ***B. brancai,*** the author discovered errors in previous restoration of this species. Correction of the errors revealed that ***B. altithorax*** and ***B. brancai*** differ significantly in dorsal column morphology. The latter taxon is shorter bodied, more gracile, and more giraffe-like than previously realized. ***B. altithorax*** is much heavier bodied and may have been advanced in a different way in the shoulder. Enough differences exist in the two taxa to place them in separate subgenera. ***Ultrasaurus macintoshi*** is probably a junior synonym of ***B. altithorax*** and is little if any larger than ***B. brancai.*** These and the largest remains of other sauropods indicate animals of around 50 tons in lean condition. The temporal and biogeographic implications these taxa have for their respective formations is considered.

Museum abbreviations — AMNH American Museum of Natural History, New York; BMNH British Museum of Natural History, London; BYU Brigham Young University, Provo; CM Carnegie Museum of Natural History, Chicago; HMN Humboldt Museum fur Naturkunde, East Berlin; MLP Museo La Plata, La Plata; MNDN Museum National D'histoire Naturelle, Paris; PEM Port Elizabeth Museum, Port Elizabeth; YMP Yale Peabody Museum, New Haven.

BRACHIOSAURUS BRANCAI

Brachiosaurus brancai Janensch 1914 is by far the best known of the brachiosaurs, so a consideration of the group starts with this species. Although no one complete individual exists, multiple specimens make knowledge of its osteology almost complete. A full understanding of this species has been hindered by the absence of an accurate, detailed skeletal restoration. The Berlin mount, HMN SII, is a composite made of different sized individuals, plus some bones modeled in plaster. Janensch's restoration of SII is schematic and includes postural and proportional errors. The methodologies for restoring sauropods and other dinosaurs are discussed in Paul (1987) and Paul and Chase (in press).

The basis for the new skeletal restoration in Fig. 1 is the holotype and best specimen, and the one on display in Berlin, HMN SII. This individual includes a partial skull (S116, in Janensch, 1935-36), all but the first three neck vertebrae, dorsal vertebrae 1-4, 8?, 10-12 and parts of others, most of the dorsal ribs, a sternal, scapular material, a coracoid, a complete forelimb and hand, the pubes, a partial femur, a fibula, and hindfoot bones. Another important specimen is BMNH M 23, which includes a complete though poorly figured dorsal column (Migeod, 1931, most of this specimen has since been destroyed; McIntosh pers. comm.). The HMN specimens figured by Janensch (1950a, 1961) provide virtually all the rest of the missing elements, including a hip, sacrum, and tail (HMN Aa). Only a few hindfoot bones are absent. In addition to the excellent figures of the various elements provided by Janensch, the author used photographs taken of the HMN mount and material — extreme care was taken in executing the profile of each element in the skeletal restoration. Duplication of parts in the HMN sample of elements allow different sized individuals to be scaled to the size of HMN SII (Table 1); consequently the confidence in the morphology and proportions of the restoration of HMN SII is high.

The skull is the complete HMN t1, modified slightly and scaled up to S116/SII. The ball and socket head-neck articulation was highly mobile, but since the occipital condyle points down and backwards, the head was usually carried at a sharp angle to the neck. The neck articulates in a gentle S curve, a basic dinosaurian adaptation. Ball and socket central facets and very large zygapophyses that remained articulated under a wide range of motion show that the neck was very flexible. The dorsals are wedge shaped and form a gentle arch, another general dinosaur character. Janensch did not have a complete dorsal column and did not explain why he gave ***B. brancai*** 11 dorsals, but BMNH M 23 indicates that there were 12 dorsals (Migeod, 1931, and McIntosh, pers. comm.; dorsal 1 is considered to be the first relatively short-centrum vertebra that supports a long dorsal rib). Although the dorsal centra also have ball and socket central articulations, the following features show that the posterior dorsal region was stiff: partly ossified interspinal ligaments; expanded neural spine heads that supported enlarged interspinal ligaments; auxiliary zygapophyses that interlock transversely; and a tendency for the posterior dorsals to coossify. The ball and socket centra of the posterior dorsals added strength to the rigid column. In a similar manner, birds have stiff backs in association with saddle-shaped central articulations. The anterior dorsals may have been moderately mobile in the vertical plane (Bakker, pers. comm.). The tail-base vertebrae are also wedge shaped and form a gentle upwards arch (Gilmore, 1932, 1937; Janensch, 1950a); moderate sized zygapophyses show a fair degree of flexibility. A multitude of sauropod trackways show that they rarely if ever dragged their tails on the ground (Bird, 1985; Dutuit and Oazzou, 1980; Langston, 1974; Lockley et al., 1986).

Articulated sauropod skeletons show that the anterior ribs are swept backwards relative to the main axis of the body. Proceeding backwards the ribs become more perpendicular relative to the main axis, so the ribs bunch together towards their ends. The anterior ribs are straight shafted and vertical in front view of the body, forming a narrow, slab-sided chest for articulation with the shoulder girdle. The posterior ribs are curved and arch far out to the side, creating a cavernous abdominal cavity.

B. brancai has enormous sternals. With their postero-lateral corners attaching to the first long, robust dorsal rib (number two) via a short sternal rib, the sternals help determine the breadth of the chest. A cartilaginous anterior sternum is restored in front of the paired sternals as per Norman (1980). The anterior sternum has grooved edges along which the coracoid glided back and forth (Bakker, 1975; Paul, 1987). Observe that the scapulocoracoid does not perform anatomical violations as it rotates, contrary to Bennett and Dalzell (1973). Also note that the backswept ribs set the sternum and coracoids a bit behind a perpendicular to the cervico-dorsal transition, not forward of it. The deep chest and short coracoid are compatible with an upright scapula seen in most tetrapods, instead of a bird-like horizontal one as often shown. This is the normal tetrapod condition — only protobirds and birds with their extremely long coracoids and scapulae have horizontal scapulae.

The detailed limb joint articulations of ***B. brancai*** are discussed elsewhere (Paul, 1987). Forelimb posture is erect and the forefoot gauge is narrow as shown by morphology and trackways (Bakker, 1971a,b,c, 1974, 1975; Bird, 1985; Dutuit and Ouazzou, 1980; Langston, 1974; Paul, 1987). A downwardly facing shoulder glenoid and distally restricted humeral condyles show that the forelimb was also columnar. Janensch (1961) correctly restored the long, unguligrade, circular arcade

TABLE 1

	B. (Giraffatitan) brancai HMN XV2	SII	Y	Ki24	Sa9	Aa	*B. (Brachiosaurus) altithorax* FMNH P25107	BYU	*"Brachiosaurus" ataliensis*	*Rebbachisaurus garasbae* MNDN	titanosaur?*** MLP	*Antarctosaurus giganteus* MLP A2300	*titanosaur?* PEM	titanosaur? L T1	*"Supersaurus" viviane* BYU 5501	BYU 5500	*Amphicoelius altus* AMNH 5764	*Diplodocus carnegii* CM 84	*Apatosaurus "immanis"* YPM 1840	*A.* sp. CM 33994	*A. louisae* CM 3018	*Breviparopus* print	Paluxy print
Lengths mm																							
Skull t		880																					
13 Cervicals c		8996p																					
Longest Cervical	*1300e*	*1155*																					
12 Dorsals c <		3781p					4760p																
Dorsals 6-12 c <		1711p					2475																
5 Sacrals		1150					950																
55 Caudals c <		7404e				6530																	
Longest Rib	2900e	2580					2745	3048															
								5001															
Scapula	2175e	1929e	1540	~ 890	1930			2190		1170													
Scapula-coracoid	2660e	2360e		~ 1090				2690							2700	2440		1600					
Sternal		1100		**D**																			
Humerus	2400e	2130	1700	1600			2040	2420e	1950e														
Radius		*1240*							*1130*														
Metacarpal II		635																					
					J																		
Ilium		1360e			1050	1190	1124																
Pubis		1150			890																		
Ischium		1195e	**XV1**		925																		
Femur	*2350e*	*2090e*	*2140*	*1550*	*1610*		*2030*	*2370e*	*1900e*		*2400+*	*2310*		*1750*	*2600e*	*2350e*	*1770*	*1542*	*~ 1950*		*1785*		
Tibia-astragulus		1150e		900	950				1120														
Fibula	1340	1190		940	960																		
Metatarsal II		276			150																		
Toe Claw I		240e			130																		
Height mm																							
								5000															
Tallest Dorsal	1320e	1170**					910	1360		1500													
Dorsal 12		790					760																
Circumference mm																							
Femur		730							~ 1000			800	~ 920	~ 920					767		845		
Breadth mm																							
Femoral Head			560				602				600+	700	600	550				500	660	615	575		
Hindfoot Pad	~ 850e	~ 750p													~ 870e			~ 500f		~ 650		900	870
Meters																							
Total Length*	25e	22.2p						25e							~ 42e	~ 38e	~ 29e	24.8p*	~ 25e		22.8p*		
Total Height	16e	14.0						16e															
Rearing Height	19e	17.0						19e															
Shoulder Height	6.8e	6.0						6.8e															
Hip Height	5.4e	4.8p						5.4e															
Metric Tonnage	~ 45p	31.5					35p	~ 45-55e			50+e	~ 40-50e			~ 50e	~ 36e	~ 16e	10.7	~ 23e		17.5	~ 50e	~ 50e
Ratios																							
Dorsal 1-12/Humerus		1.78					2.33																
Dorsal 6-12/Humerus		0.80					1.21																
Dorsal 6-12/PVH		2.70					2.68																
Humerus/PVH		2.17					3.26																
Humerus/Femur		1.02					1.00																
k for Humerus		3.26					4.07																

e = estimated, p = partial element or elements allow more precise estimate, t = tip of premaxilla to end of opisthotic wing, * = along centra, PVH = twelfth dorsal total height in mm.

p* - for ***Diplodocus carnegii*** using composite tail of CM 84, 307 and USNM 10865 with total of 82 caudals, greater than 25.8 m estimates for length are excessive (Gilmore, 1932); for ***Apatosaurus louisae*** using combined tails of CM 3018 and 3078 with total of 82 caudals, confidence in length very high, f - from hindfoot of CM 94 scaled up to CM 84.

c - includes space for cartilagenous intervertebral discs.

k - for the formula $m = k(h)^3$ where k is the constant for the humerus, h is humerus length in decameters, and m is mass in kg.

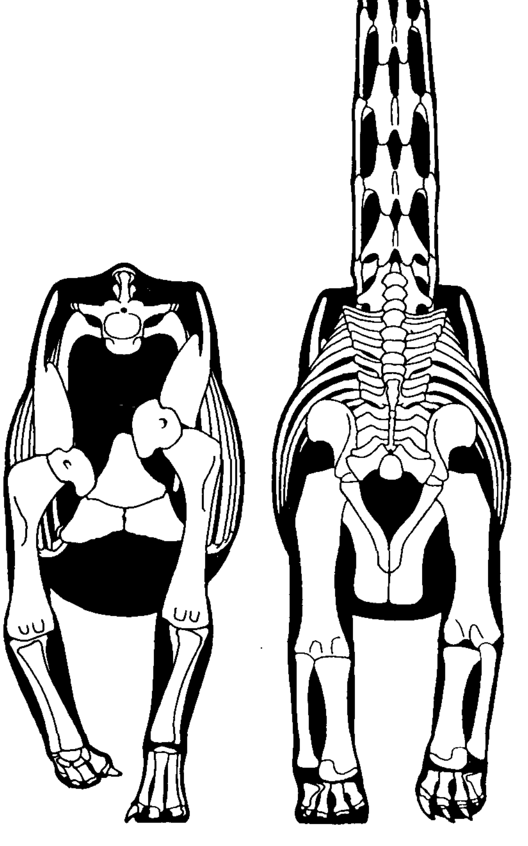
** - incorrectly listed as 1070 mm on p. 44 in Janensch (1950a).

*** - McIntosh, Gasparini pers. comms.

of the hand. Contrary to previous reports, the sauropod hand is not at all elephant-like — in fact it is unique and has only a thumb claw and no hooves. As restored the femur/tibia or fibula ratio of SII is a little higher than in other specimens (Table 1), but as the femur is always just a little shorter than the humerus in brachiosaurs, this ratio must be correct. The hindlimb is also columnar, and the foot is unguligrade and very elephant-like (excepting the three or four big laterally splayed banana claws; the outer one or two toes are neither clawed nor hooved). The astragular distal articulation faces more downwards and less forwards in well preserved sauropod ankles, relative to those of digitigrade prosauropods; therefore the sauropod foot is posturally unguligrade instead of plantigrade as suggested by Cooper (1984). The extremely short metatarsus and toes backed by a big pad show that the ankle was nearly immobile. The animal is shown in an elephant-like amble (Muybridge, 1887), its fastest gait.

The most important point about the mounted HMN SII is that the presacrals on display are not the originals, they are plaster models. The centra of the dorsal models are significantly larger than those of the originals, and Janensch's (1950b) paper skeletal restoration includes the same error. Why the modeled centra are so long is not clear, for although the dorsals are moderately crushed and too fragile to mount, most of the centra appear to be little altered in length. With centra of proper length, the dorsal column of ***B. brancai*** is some 20% shorter relative to the limbs than indicated by Janensch, even though one more vertebra is included in the new restoration. Other errors in Janensch's restoration include vertical anterior dorsal ribs and a shoulder girdle that is consequently too far forward — as well as too high — on the ribcage; scapula and humerus too short, a sprawling forelimb, and a tail that is too long, too heavy, and droops. Burian's well known restoration of the species emphasizes these errors, and also shows the neck much too short (Spinar and Burian, 1972). In addition the claws are incorrect. Because the new restoration has a scaled up HMN Aa tail that is longer than it is in the mount and a dorsal column that is shorter, the differences cancel each other and the new restoration and the mount share nearly the same length of over 22 m.

A very unusual feature of ***B. brancai*** is the extreme height of dorsal vertebra 4, especially the neural spine, relative to both the cervicals and posterior dorsals. Unfortunately the immediately surrounding neural spines are not preserved, but it appears that this sauropod had "withers", tall neural spines over the shoulders (Figs. 1, 2B). ***Rebbachisaurus garasbae***, a species possibly assignable to the Brachiosauridae, may have even taller withers (Lavocat, 1952). Withers are fairly common among mammals, but are unknown among other dinosaurs except for the chasmosaurian ceratopsids. This feature suggests that nuchal ligaments helped to support the neck. The withers' modest height and the long neck suggest the ligaments were rather low, like a camel's (Knight, 1947; Dimery et al., 1985). The ossified cervical "ligaments" cited by Migeod (1931) and Alexander (1985) are more probably displaced ends of the long cervical ribs (McIntosh, pers. comm.). Also unusual is the *small* size of the posterior dorsals, especially the centra. HMN SII and BMNH M 26 have posterior centra that are only 9 inches long! Although brachiosaur posterior dorsals are very different from the great posterior dorsals and sacrals of diplodocids, it does not follow that brachiosaurs were weak in the back. Obviously these giants did perfectly well with the posterior dorsals they had. Brachiosaur dorsals were not as specialized for rearing up as were diplodocid dorsals (Bakker, 1971c, 1978). On the other hand brachiosaurs were like all other dinosaurs in being hindlimb dominant — the center of gravity was towards the rear so the hindlimb was more robust and supported more weight than the forelimb. This weight distribution made it easier for brachiosaurs to rear in search of choice



food items or to fight than it is for elephants, which, despite their forelimb dominance, also have the capacity to rear (Eltringham, 1982). Note that brachiosaurs are less hindlimb dominant than diplodocids (Anderson et al., 1985).

Corrected with shorter trunk, taller forelimbs, and withers ***B. brancai*** is even more giraffe-like than previously realized. It is the only quadrupedal dinosaur which one would have to reach up to slap the belly as one walked under it! Most

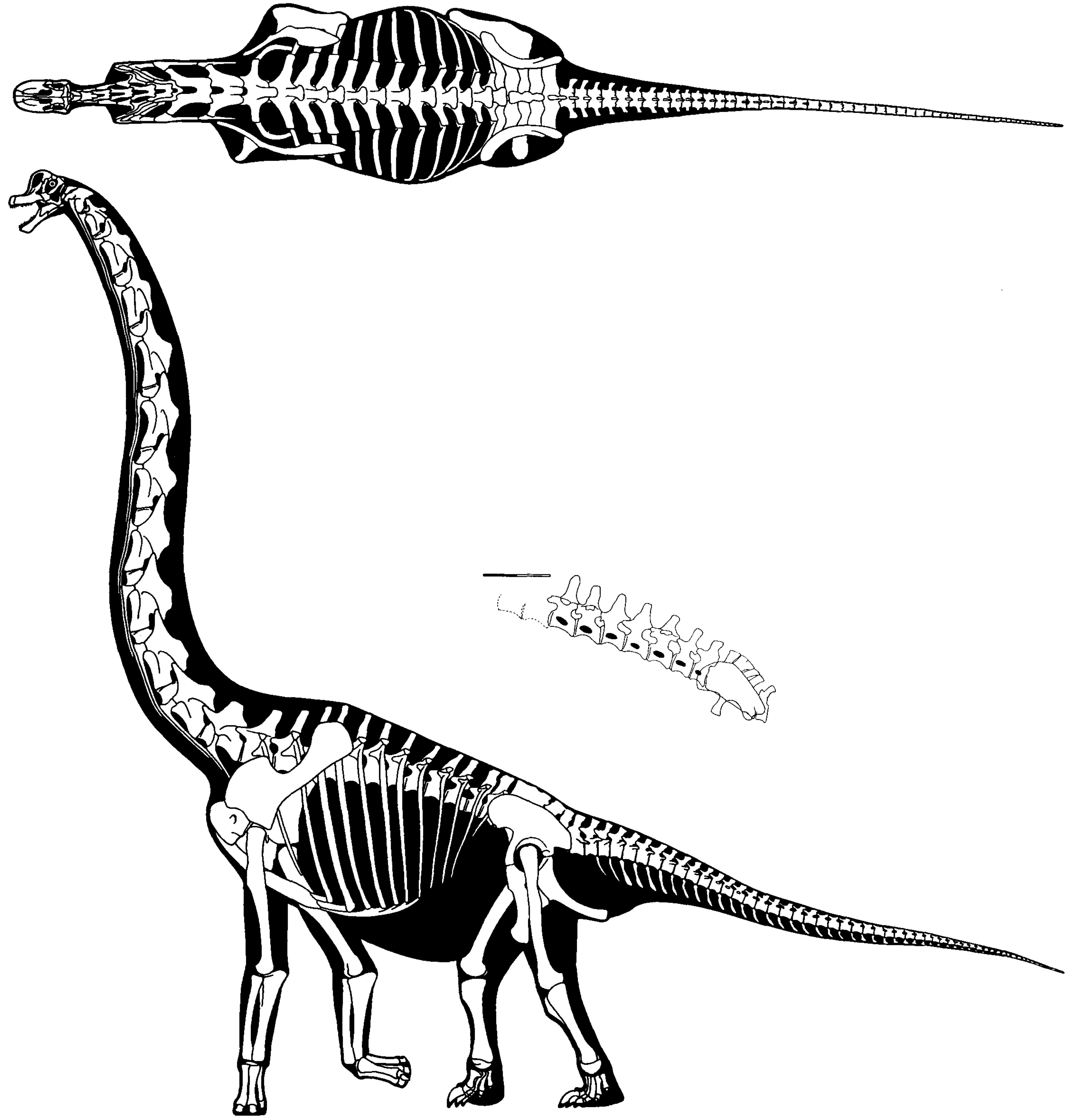


Figure 1—Multiview skeletal restoration of ***Brachiosaurus (Giraffatitan) brancai*** holotype SII/S116 (skull), with some proportions and elements from other HMN specimens. Inset shows dorsal-sacral column and ilium of ***B. (Brachiosaurus) altithorax*** holotype FMNH P25107 to same scale. Measurements in Table 1.

unusual for a tetrapod, much less a dinosaur, it is an exceptionally elegant and majestic design.

A COMPARISON OF B. BRANCAI WITH B. *ALTITHORAX* AND THE DELTA GIANT

The holotype of ***Brachiosaurus altithorax*** Riggs 1903 FMNH, P25107 is the most complete North American brachiosaur specimen. It includes dorsals 6-12, ribs, sacrum, caudals 1 and 2, coracoid, humerus, ilium, and femur (Figs. 2A, 3F). This specimen is crushed to varying degrees, especially in the sacrum (dorso-ventrally) and, to a lesser degree in the dorsals (downwards to the right).

The holotype of the Delta or Uncompahgre giant ***Ultrasaurus macintoshi*** Jensen 1985 is the crushed vertebra BYU 5000 (note that the specimen numbers applied to the Uncompahgre material by Jensen are sometimes contradictory, and hence those cited here are tentative). This vertebra has been identified as a posterior dorsal (Fig. 3E). However, its transversely narrow neural spine with a small head shows that it is an anterior dorsal. Clearly brachiosaurian in design, it is very similar to the anterior dorsals of ***B. altithorax***. As far as can be told, BYU 5000 belongs to ***B. altithorax*** and is referred to it. Hence, ***U. macintoshi*** is not considered valid. The slenderness of the neural spine suggests that BYU 5000 is forward of dorsal 6, so it bolsters our knowledge of the shoulder of ***B. altithorax***. Also referable to ***B. altithorax*** is the extremely large (2690 mm long) Uncompahgre

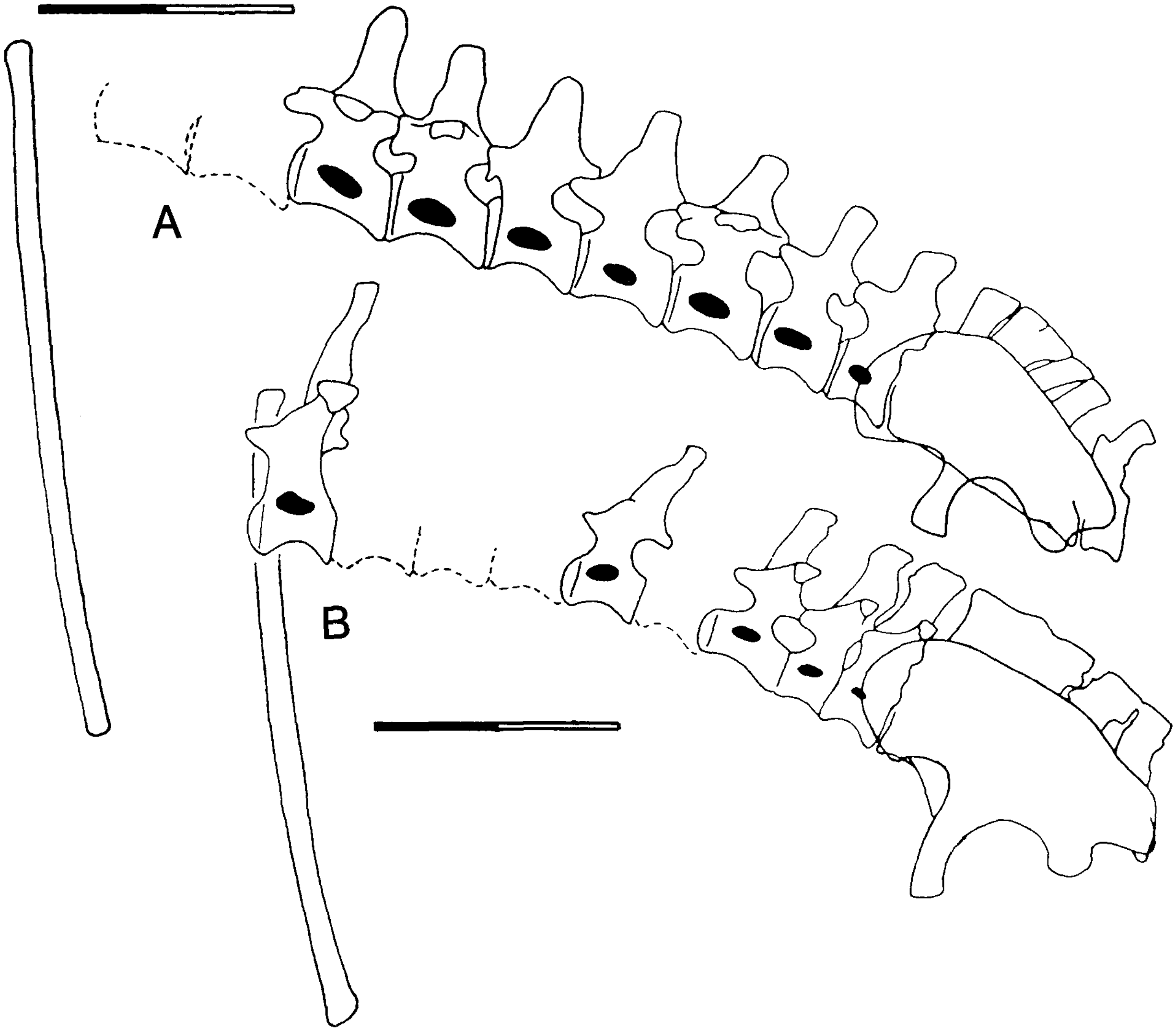


Figure 2—Dorsals 6-12 and sacrals, longest rib and ilia of A) ***Brachiosaurus (Brachiosaurus) altithorax*** holotype FMNH P25107 and B) ***B. (Giraffatitan) brancai*** holotype HMN SII and Aa. Drawn so that their respective humeri are to the same length, scale bars equal 1 m. Neither column is complete, the sacrals and ilia of HMN Aa are scaled up to SII, the position of the longest dorsal rib is not certain in either, and some crushing is removed from both examples.

scapulocoracoid (Jensen 1985a, BYU 5001, Fig 4A, popularly labeled ***"Ultrasaurus"***). It has the short, rounded anterior scapular process, short rounded coracoid, narrow scapular neck, and broad, rounded blade fully compatible with a brachiosaur. Jensen suggests that the scapula blade was not as broad as in ***Brachiosaurus***, but some ***B. brancai*** blades are similar in breadth.

The caudals, scapula, coracoid, humerus, ilium, and femur of ***B. altithorax*** and ***B. brancai*** are very similar, and though the limb bones of the former are a bit more robust these elements could belong to the same species. It is in the dorsal column and trunk that the significant differences occur. To start with, at any given point, the dorsal column of ***B. altithorax*** is about 25-30% longer relative to the humerus or femur than that of ***B. brancai*** (Fig. 2, Table 1). Riggs (1903) commented on the unusually long ribs of the Morrison sauropod, and indeed the longest dorsal rib is some 10% longer relative to the humerus than in ***B. brancai.***

The dorsals of both species are crushed, hampering comparison, especially quantitative. The posterior dorsals appear to be fairly similar. However, all the dorsal centra of ***B. altithorax*** have pleurocoels that are about 50% larger than those of ***B. brancai*** (Fig. 3E-G). The neural arches are taller and longer in ***B. altithorax***, but are much narrower. The transverse processes form a shallow V in ***B. brancai***; in ***B. altithorax*** they appear to be flatter.

The anterior and mid dorsals differ the most. In ***B. brancai,*** dorsal 4 is very gracile, with very long, proximally deep, distally tapering transverse processes and a tall, slender neural spine. The centrum is rather small and short. Excepting the centrum, dorsal 4 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 — their neural spines and transverse processes are only a little longer. Compared to the posterior arches, the anterior arches are longer both vertically and fore and aft.

Very notable is the length of the anterior dorsal centra relative to those of the posterior dorsals in ***B. altithorax***. Incomplete columns, crushing, centra fusion, and incomplete measurements hamper quantitative comparisons. But in HMN SII and BMNH M 26, the anterior dorsals are about the same length as the posterior dorsals. In FMNH P25107 the mid dorsal centra are about 50% longer than those of the posterior dorsals (Fig. 2). Such elongation of mid-anterior dorsals is most unusual for sauropods and dinosaurs — even in ***Diplodocus*** and ***Barosaurus*** only the first two dorsals

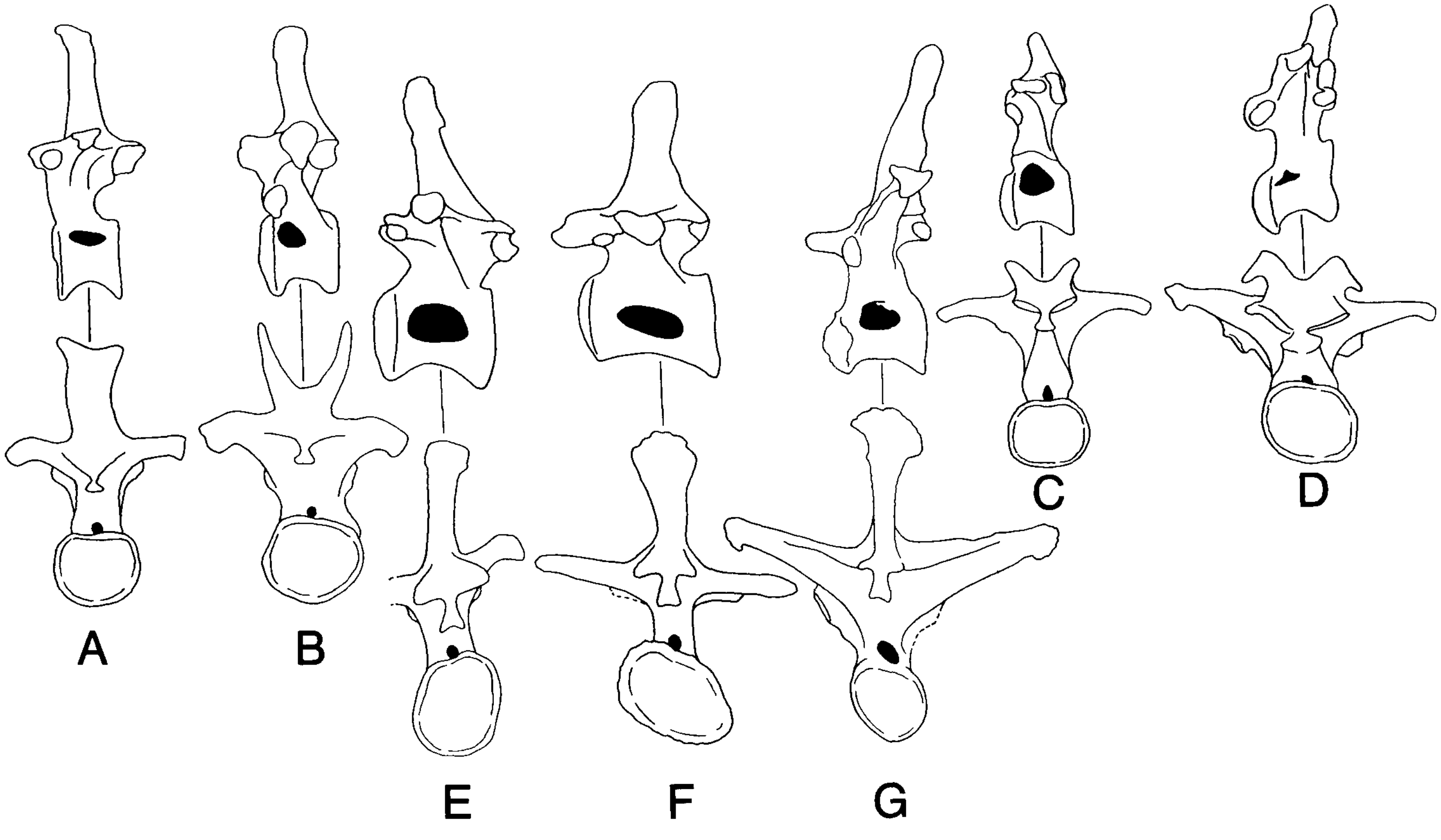


Figure 3—Anterior dorsals in left lateral (top) and posterior (bottom) views, drawn to the same zygapophysis-to-bottom-of-centrum height. Dorsal 5 in A) ***Apatosaurus louisae*** CM 3018; B) ***Diplodocus carnegii*** CM 84; C) ***Camarasaurus grandis*** YPM 1901 or 1902; and D) ***Camarasaurus supremus*** AMNH 5761. Anterior dorsal in E) ***B. (Brachiosaurus) altithorax*** referred BYU 5000; dorsal 6 in F) ***B. (B.) altithorax*** holotype FMNH P25107; and dorsal 4 in G) ***Brachiosaurus (Giraffatitan) brancai*** holotype HMN SII. Data from Gilmore, 1937; Hatcher, 1901; Janensch, 1950a; Jensen, 1985a; Osborn and Mook, 1921; Ostrom and McIntosh, 1966; Riggs, 1903.

are elongated. The combination of lower anterior dorsal vertebrae and the apparent lack of a sharp change between the anterior and posterior dorsals shows that ***B. altithorax*** lacked the tall withers of ***B. brancai***. If this is correct, then ***B. altithorax*** *may* have had a less developed, shorter neck than ***B. brancai***.

It appears that the two brachiosaurs are both derived relative to other sauropods in anterior dorsal design, but in different ways. ***B. brancai*** has tall withers but is normal in anterior dorsal centra length. ***B. altithorax*** is more normal in the shoulder spines, but has unusually long anterior dorsals. The latter is also longer, deeper, and much bulkier in the body relative to the limbs (see below).

Janensch (1914) recognized the differences between the North American and African forms and separated them at the species level. The next question is how do the differences between ***B. altithorax*** and ***B. brancai*** compare to those between other tetrapod genera and species. Simple proportional differences do not necessarily a genus make. A combination of proportional and morphological differences is more significant. In the context of other sauropods, the differences between these two brachiosaurs are more extreme than those found within other genera. In ***Camarasaurus supremus*** and ***C. grandis,*** dorsal 5 differs significantly, especially in the neural arch (Fig. 3C,D). The difference is great enough to question whether these species should be placed in the same genus, but the differences appear to be less than between ***B. altithorax*** and ***B. brancai***. Even ***Diplodocus*** and ***Apatosaurus*** show about the same degree of difference in their anterior dorsals as shown in the two brachiosaurs (Fig. 3A,B). There is much less difference between the anterior dorsals of ***Diplodocus*** and ***Barosaurus*** (Lull, 1919). Indeed the latter may be considered subgenera, rather than full genera.

Among other dinosaurs it is difficult to come up with a genus that shows as much variation in anterior dorsal design. For example ***Tyrannosaurus***, ***Tarbosaurus*** and ***Daspletosaurus*** — which may form a single genus — do not. Indeed, such widely accepted large tetrapod genera as ***Varanus***, ***Anas***, and ***Canis*** show much more uniformity. An example of considerable variation in withers height is found in recent and living species of ***Bison***. However, the withers are an important species-specific display device in bison; the functional importance of differences in neck movement is reduced in these short necked animals. In brachiosaurs the long neck implies that differences in the withers were probably associated with differences in neck size and movement.

A basic definition of any one genus should include an important functional distinction from related species. The Morrison and Tendaguru brachiosaurs not only appear to show a significant functional difference, they appear to be phylogenetically derived in different ways. Since they also vary more from one another than most genera, it is considered probable that they represent different genera. Generic separation would also be useful in preventing the two taxa from being considered more similar than they really are. However, 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 below, with the option of raising the separation to the generic level left open for future developments.

SYSTEMATIC PALEONTOLOGY

Family Brachiosauridae Riggs 1903

Genus *Brachiosaurus* Riggs 1903
Synonym — *Ultrasaurus* Jensen 1985
Type species — *B. altithorax* Riggs 1903

Diagnosis. as per Riggs (1903, 1904) and Janensch (1914, 1929, 1935-36, 1950a,b)

Subgenus *Brachiosaurus (Brachiosaurus)* (Riggs 1903)

Diagnosis. as for species.

Brachiosaurus (Brachiosaurus) altithorax Riggs 1903
Synonym — *Ultrasaurus macintoshi*
Holotype — FMNH F25107
Referred specimens — USNM 21903, BYU 5000, BYU 5001, BYU Potter Creek vertebra.

Diagnosis. Robust overall; mid dorsal centra much longer than posterior dorsal centra, anterior dorsal spines and transverse processes not much taller or wider than those of posterior dorsals; neural arches long, tall and narrow; transverse processes flat; dorsal centra pleurocoels large; dorsal column over twice humerus length and very long relative to vertebrae height; body massive relative to limbs.

Discussion. So far most Morrison brachiosaurs, including the USNM humerus 21903 and the BYU Potter Creek posterior dorsal (Jensen, 1985a), appear to be referable to this species. An Uncompahgre anterior caudal BYU 5002 was incorrectly referred to ***U. macintoshi*** (Jensen, 1985a); its cleft neural spine and handle bar transverse processes are clearly those of a diplodocid, not a brachiosaur.

If the Uncompahgre fauna come from the uppermost Morrison (Jensen, 1985b), then it is possible that the fauna's brachiosaurs represent a distinct population of oversized animals (see below). These could either be a temporal subspecies, which does not require formal recognition, or a separate species. The Morrison brachiosaur material is much too limited to prove any of these options.

The name ***Ultrasaurus*** has appeared informally a number of times since 1978 (Jensen, 1978, 1985a; Lambert, 1983; McWhirter and McWhirter, 1986; Norman, 1985). However, lacking a designated type species and formal technical description, it does not meet the International Code of Zoological Nomenclature criteria for availability. ***Ultrasaurus tabriensis*** Kim (1983) was applied to a medium sized and nondiagnostic Korean sauropod humeral head that was mistaken for a gigantic proximal ulna. Despite these problems, a holotype (DGBU-1973) was effectively designated and described in a public technical text, sufficient to give the generic and specific names a place in formal systematics. Since the type and referred material (a caudal? neural spine) are nondiagnostic, they should be considered Sauropoda incertae sedis, and **Ultrasaurus** should be considered no longer valid. This result is unfortunate because it effectively bars Jensen's (1985a) subsequent formal use of **Ultrasaurus** to designate any Uncompahgre remains.

Subgenus *Brachiosaurus (Giraffatitan)* n. subgen.

Etymology — Loosely "gigantic giraffe", in recognition of the taxon's giraffe-like form.

Diagnosis. as for species.

Discussion. Arkell (1956) suggested that ***Brachiosaurus (Giraffatitan)*** was first named **Gigantosaurus.** Actually ***Gigantosaurus megalonyx*** Seeley 1869 was applied to some ambiguous European sauropod remains. ***Gigantosaurus robustus*** Fraas 1908 was used to accommodate Tendaguru remains that he could not place in other Tendaguru taxa. Much of this material was later placed in ***Tornieria robusta*** Sternfeld 1911.

Brachiosaurus (Giraffatitan) brancai Janensch 1914
Synonym — ***B. fraasi*** Janensch 1914
Holotype — HMN SII and SI
Referred specimens — As per Janensch (1914, 1929, 1935-36, 1950a,b, 1961)

Diagnosis. Gracile overall; 25 presacrals and 12 dorsals; mid dorsal centra about same length as posterior dorsal centra, anterior dorsal spines and transverse processes much taller and wider than those of posterior dorsals and form shoulder withers; neural arches short vertically and fore and aft; transversely broad transverse processes that form a shallow V; dorsal centra pleurocoels moderate in size; dorsal column less than twice humerus length and short relative to vertebra height; body mass relatively modest relative to limbs.

Discussion. All Tendaguru brachiosaur specimens are referred to this species, including ***B. fraasi***, the type (HMN Y) of which Janensch (1961) in later years listed under ***B. brancai***. However, the possibility that some of the Tendaguru remains belong to another taxon remains open.

THE MORRISON AND TENDAGURU FORMATIONS AND THEIR BRACHIOSAURS

That ***B. (B.) altithorax*** and ***B. (G.) brancai*** are probably less similar than thought somewhat reduces the similarities between the Morrison and Tendaguru Formation faunas (Arkell, 1956; Galton, 1977, 1980, 1982). This does not, by any means, discredit the probability of a land connection between North America and Africa. One possibility is that habitat differences between the two formations may be responsible for the differences in the brachiosaurs, even though both formations seem to have been seasonally dry (Dodson et al., 1980; Russell, 1980). That the two brachiosaurs are about equally advanced is compatible with their respective formations being roughly equal in age — within the Upper Kimeridgian-Tithonian (Aitken, 1961; Arkell, 1956; Stokes, 1985). Comparable age is suggested too by the very close similarity of some other elements of the two faunas (Galton, 1977, 1980, 1982). Besides, it remains possible that ***B. (B.) altithorax*** or something like it lies unrecognized in the Tendaguru material, and that ***B. (G.) brancai*** is present in the Morrison.

WHAT WAS THE BIGGEST?

Riggs realized he had discovered an exceptionally great dinosaur, and the actual mass of these animals has aroused curiosity ever since. In order to determine their mass, which is a function of their volume, we must first consider their musculature. A detailed restoration of the contour muscles of ***B. (G.) brancai*** HMN SII is presented elsewhere (Paul, 1987). The muscles are also profiled in solid black around the skeletal restoration given here.

Generally ***B. (G.) brancai*** has been restored as a massively muscled animal wtih a heavy neck and tail and stout limbs (Colbert, 1962; Jackson and Matternes, 1972; Norman, 1985; Ostrom, 1978; Spinar and Burian, 1972; Watson and Zallinger, 1960; BMNH commercial model). Burian's restoration is perhaps the epitome of this style. It is certainly incorrect. The intensely pneumatic and very bird-like neck vertebrae of sauropods were much lighter in life than they look as mineralized fossils, and the skulls they supported were small. This suggests that the cervical musculature was also light and rather bird-like, just sufficient to properly operate the head-neck system. The bulge of each neck vertebra was probably visible in life, as is the case in large ground birds, camels and giraffes.

The rigid, bird-like ribcage was lightly muscled also. However, like all herbivores, sauropods must have had big bellies that they kept filled with fermenting fodder to support the flourishing gut flora necessary to break down plant materials. A ruminant-like system is, however, neither efficient or necessary for high digestive efficiency in animals of this size (Demmont and Soest, 1985). In ungulates and proboscideans the belly is as broad as it is deep (see rear views in Muybridge 1887), and the arching posterior ribs of ***B. (G.) brancai*** show this was the case here. Indeed it had an exceptionally large abdomen for a sauropod; only **Camarasaurus** matches it in this regard. The tail of ***B. (G.) brancai*** is very reduced, and muscles were probably extended only as far as the bones (as mummies show is true of hadrosaurs, Paul, 1987), except for the caudofemoralis, which bulges beyond the transverse processes. All of the author's sauropod restorations show the animals "lean", without fat reserves, as they would be toward the end of the dry season. Large herbivores sometimes carry an additional 15-33% of their lean mass as fat by the end of the heavy feeding season, although elephants are not noted for carrying large fat deposits (Carrington, 1959). Hence the maximum masses of each individual sauropod would likely have been about a sixth higher than listed in Table 1, perhaps as much as a third. Such fat was probably borne towards the base of the belly, and Bakker (pers. comm.) notes that crocodilians and adult monitor lizards have substantial fat deposits on their tail. Sauropods may have had the same in season. On the other hand, being terrestrial animals that carried their tails aloft as weapons, it is possible that the tail was never so burdened. Because the restored tail makes up only 5% of the total mass in brachiosaurs, and just 15% even in big tailed ***Apatosaurus***, even doubling the tail mass will not alter the total mass value much.

The small size and shortness of such muscle leverage attachments as the deltoid crest, olecranon process, ilium, cnemial crest, and hypotarsus relative to other dinosaurs indicates a modest limb musculature in ***B. (G.) brancai***. That the foot was immobile confirms that only light shank muscles were needed to operate it. The lightness of sauropod limb muscles is logical since sauropods were elephantinely slow, and modern elephants also have slender limb muscles (Knight, 1947; Muybridge, 1887). Since brachiosaurs were as hindlimb dominant as other sauropods, the forelimb musculature was more slender than that of the hindlimb. All sauropod trackways show that the hand lacked a large central palm pad; instead it was hollow aft and half moon shaped (Paul, 1987). The hindfoot differs in having a great elephant-like heel pad.

A model of HMN SII was sculpted in plasticine and its volume measured by water immersion. Since most live animals float, the specific gravity was assumed to be 0.9. The exception was the highly pneumatic neck which was measured separately and assigned a tentative specific gravity of 0.6. In this species the neck was 13% of the total volume. HMN SII proved to weigh about 32 tons. This is far less than Colbert's (1962) estimate of 78 tons for the same specimen. Why there is so much difference is hard to judge because no plans of the model Colbert used were published. Colbert's museum model was presumably based on an overly long-bodied version of HMN SII. The neck is too heavily muscled; even more so is the tail which is restored heavier at the base than it is in the accompanying ***Apatosaurus*** model. The reverse is actually the case. Both pairs of brachiosaur limbs are muscled much too heavily, especially the forelimb which appears more robust than the hindlimb. In summary so much flesh could not be borne by even SII's giant skeleton. Bakker's (1975) estimate of 50 tons for brachiosaurs is also excessive for average sized individuals.

On the other hand, Russell et al.'s (1980) estimate, based on vaguely defined limb bone circumference/mass estimate, is far too low at 15 tons — so little flesh simply cannot be stretched over the animal's great frame. In a more rigorous analysis of limb element circumference relative to mass in living and fossil tetrapods, Anderson et al. (1985) arrived at a much more reasonable 29 ton estimate. However, the apparent agreement between this and my estimate means less than it appears. Bone robustness can give only a "ball park" estimate because in modern animals mass varies up to a factor of two at any given limb circumference (Anderson et al., 1985). Comparable variation was certainly present in sauropods also. For example the limb bone circumference of ***Apatosaurus louisae*** CM 3018 predicts a mass of 35 tons, bigger than SII. However, the latter's skeleton is definitely more voluminous than CM 3018, and a model shows the apatosaur weighed only 18 tons (Table 1). Clearly ***A. louisae*** was much more strong limbed relative to its mass than was ***B. (G.) brancai***.

The largest specimen of ***B. (G.) brancai*** is the fibula HMN XV2 (Janensch, 1950b, 1961); claims of bigger specimens are unsubstantiated. There is variability in fibula/humerus or femur ratios in various specimens, but assuming it is similar to SII in proportions, XV2 is about 13% larger (Table 1). In this case this individual would weigh up to 45 tons.

The mass of ***B. (B.) altithorax*** FMNH P25107 is less readily determined. To get a rough estimate it was assumed that the neck, tail, and limbs weighed the same relative to the femur as in ***B. (G.) brancai***. This is a fairly safe assumption, except that the neck may actually be somewhat smaller. A new model of the trunk incorporating 12 dorsals was sculpted to determine this portion of the total mass. FMNH P25107 appears to have weighed about 35 tons; despite its shorter limbs it may have been heavier than HMN SII.

Jensen (1978, 1985a,b) suggests that the Uncompahgre brachiosaurs represent uniquely large individuals. However, the great scapulocoracoid BYU 5001 is not especially large because cross scaling indicates that ***B. (G.) brancai*** HMN XV2 also had a scapulocoracoid about this length (Table 1), and several other ***B. (G.) brancai*** scapulocoracoids are not much smaller (Fig. 4A,B). Presumably the gross dimensions of XV2 and BYU 5001 were similar too. If so, then estimates that BYU 5001 weighed up to 190 tons (Lambert, 1983; McWhirter and McWhirter, 1986; Norman, 1985) are overstated. Assuming that BYU 5001 belongs to ***B. (B.) altithorax***, this individual was closer to 45-50 tons. Reported 3038 mm long Uncompahgre ribs (Jensen, 1985b) may be brachiosaurid and are in the same range as estimated for 5001 and XV2 (Table 1). If the giant 1360 mm long Uncompahgre cervical BYU 5002 actually is a single spined brachiosaur as Jensen (1985a) indicates (but see below), then it too has a size similar to that estimated for 5001 and XV2. The indefinite position of anterior dorsal BYU 5000 and the lack of comparable dorsals in FMNH P25107 makes it difficult to compare the two individuals' masses. Besides, vertebra height may be more variable relative to mass than long bone length. It is notable that ***B. (G.) brancai*** HMN XV2 probably had anterior dorsals of similar size to BYU 5000 (Table 1). The Potter Creek posterior dorsal is also in the 5000-XV2 size class. In summary, the fragmentary Uncompahgre remains indicate that ***B. (B.) altithorax*** was in much the same size class as — perhaps a little heavier than — the biggest ***B. (G.) brancai*** specimens. That "ultrasaurs" are unique species of truly exceptional size is unconfirmed.

Having found that ***B. (G.) brancai*** and ***B. (B.) altithorax*** were similar in size, the question arises as to whether they were the largest known terrestrial tetrapods. The Uncompahgre holotype of ***Dystylosaurus edwini***, dorsal BYU 5750, may be brachiosaurian. It cannot belong to the same taxon as BYU 5000 because these two anterior dorsals are too different to belong within the dorsal series of one single species. In having a transversely broad neural arch, BYU 5750 is rather like ***B. (G.) brancai***, but otherwise it is very different, especially in its short, broad spine. With a height of about 1100 mm, BYU 5750 is very large but not uniquely so and, without further data on the animal's form, its weight can not be determined more precisely. Among other brachiosaurs, Russell (1980) and Anderson et al. (1985) suggested that ***"Brachiosaurus" ataliensis*** was unusually large. If the specimen cited is the same one in Lapparent and Zbyszewski (1957), then the radius and tibia are shorter than those of HMN SII (Table 1). The 1500 mm dorsals of the bizarre brachiosaur ***Rebbachisaurus garasbae*** are much taller than those of the biggest of the other brachiosaurs. This height is due to its unusually tall spines; the limb material shows the body is not overall very large (Lavocat, 1952).

The largest of the Paluxy River prints, which may have been made by the brachiosaur ***Pleurocoelus*** (Bird, 1985), are in the very large size class (Table 1). Russell (1980) notes that the ***Breviparopus*** trackways (Dutuit and Ouazzou, 1980) also indicate very large sauropods. Indeed they are about the size of the biggest brachiosaurs. That these trackways were made by animals unbuoyed by water, and that sauropods were terrestrial in habits, proves that animals much bigger than elephants and as big as most whales can be land creatures.

Bakker (1971c) suggested that Morrison apatosaurs and camarasaurs were as large as brachiosaurs. The largest ***Apatosaurus*** specimen is an incomplete femur YPM 1840 described by Marsh. He first estimated it to be over 2.4 m long (Marsh, 1878), but the final restoration is more correct at about 1950 mm (Marsh, 1896). Scaling up from CM 3018, the animal should have weighed only some 23 tons (Table 1). Two proximal ***Apatosaurus*** femora, CM 83 and CM 33994 (McIntosh, 1981), are not as large as YPM 1840; CM 83 is not as large as CM 3018. It is more difficult to calculate mass in ***Camarasaurus*** because a high fidelity skeletal model of a complete adult specimen has yet to be completed. Scaling up of complete juveniles suggests that the biggest known adult specimens (in the Cope collection, including a 1800 mm femur, Osborn and Mook, 1921) weighed 22 to 26 tons.

At least one other Morrison sauropod may be as massive and much longer than the brachiosaurs. A 2440 mm long Uncompahgre scapulocoracoid (BYU 5500, popularly labeled ***"Supersaurus"***) was initially identified as a brachiosaur (Fig. 4D). Jensen (1985a) no longer supports this identification. Instead its long, rectangular anterior scapular process with a sharp anterodorsal corner, long rectangular coracoid, fairly broad scapular neck and short, modestly expanded scapular blade indicate it is a gracile, ***Diplodocus***- or ***Barosaurus***-like diplodocid. A 2700 mm long Uncompahgre scapulocoracoid (BYU 5501) is very similar and was correctly referred to the same taxon as BYU 5500 by Jensen (Fig 4C). Jensen placed the two shoulder girdles in the new ***Supersaurus viviane*** Jensen 1985. However, except for a longer upper blade, they are so extremely similar to ***Diplodocus*** (Hatcher, 1901) that congeneric status is very possible (Fig. 4C-E). On the other hand, the giant neck vertebra BYU 5003 is reconstructed with diplodocid-type double neural spines. If this reconstruction is correct, then the vertebra's great length suggests that these diplodocids are long necked ***Barosaurus***. Scapulocoracoid BYU 5501 may belong to an animal with a 2600 mm femur, if the proportions were diplodocid-like. But because such gracile diplodocids are lightly built they probably weighed "only" some 50 tons, as large as the biggest brachiosaurs. Length is another matter, for assuming that BYU 5501 had about the same total length to scapulocoracoid length ratio as ***Diplodocus*** (Table 1) then it was some 42 m long. At 1130 mm the diplodocid anterior caudal BYU 5002 is not much taller than those of ***Diplodocus*** CM 84 and USNM 10865, so it is not an especially large individual. Likewise the 12 articulated diplodocid caudals (BYU 5502) have a length of 300 mm, no longer than those of CM 84. Since these Uncompahgre caudals are so small, it is very unlikely that they belong to the same individuals as do either of the scapulocoracoids.

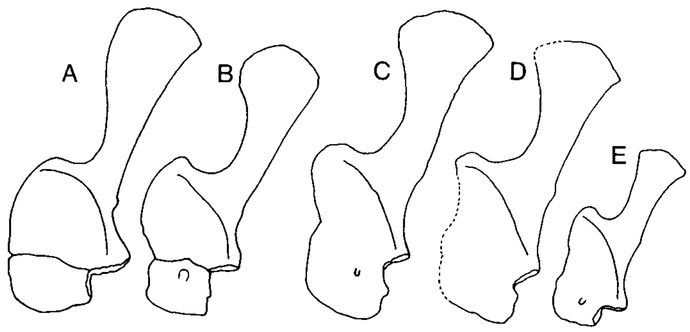


Figure 4—Scapulocoracoids drawn to the same scale of A) ***B. (Brachiosaurus) altithorax*** referred BYU 5001; B) ***B. (Giraffatitan) brancai*** HMN Sa 9 with coracoid scaled in from HMN Ki 74; C) ***Supersaurus vivanae*** referred BYU 5501; D) ***S. vivanae*** holotype BYU 5500; E) ***Diplodocus carnegii*** CM 84. Measurements in Table 1.

"Seismosaurus" has been based on some fragmentary remains from the Morrison Formation (Gillette, 1987). The tall neural spined caudals are clearly those of a gracile diplodocid. They are of unusually large size, but since truly large ***Supersaurus*** caudals are not available for comparison, it is difficult to tell just how much so. If the total length was 37 m long as suggested by Gillette, then it may have been smaller than ***Supersaurus***. Note that the tall neural spines of the ***Supersaurus*** and "Seismosaurus" caudals mean that they probably had the massive hips typical of diplodocids — a rearing-up adaptation (Bakker, 1971c, 1978) that indicates that they also had the short forelimbs found in all complete diplodocid skeletons.

Amphicoelias altus is another large gracile diplodocid (Osborn and Mook, 1921; the straight instead of forward-sloping posterior dorsal neural spine indicates it is a different taxon from other ***Diplodocus*** and ***Barosaurus*** species). The longest 1770 mm femur indicates a 16 ton animal, substantially heavier than regular sized ***Diplodocus*** and ***Barosaurus*** specimens (Table 1). It is possible that ***Amphicoelias***, ***Supersaurus***, and "Seismosaurus" all represent one giant species. All the specimens may be from the uppermost Morrison, and, because not enough parts are shared in common to determine their real taxonomic status, the new names may be premature.

Outside the Morrison a number of sauropods from southerly latitudes, which may represent titanosaurs, exhibit a tendency towards gigantism. A broken and incomplete MLP femur measures nearly 2200 mm, but was much longer when complete (Table 1). Assuming a typical sauropod mass/femur length ratio it may have weighed over 50 tons. Lacking further data it is not possible to estimate the animal's total length. Another super-sized sauropod is the femur of the titanosaur ***Antarctosaurus giganteus*** (Huene, 1929; Van Valen, 1969; Table 1). It is in the same class as the biggest brachiosaur femora, but since the rest of the animal is poorly known, the best that can be said is that it was probably similar in mass too. The South African (McLachlan and McMillan, 1976) and Laotian (Hoffet, 1942) femora Anderson et al. (1985) cited are not from uniquely large individuals (Table 1).

In the final analysis, ***B. (G.) brancai*** and ***B. (B.) altithorax*** were about as big as any other known sauropods. Just as importantly, ***B. (G.) brancai*** holds the record for the biggest species for which all of the skeleton is known. It was also the tallest, but not the longest. The largest known sauropods appear to cluster around 50 tons in lean condition, perhaps a third more in prime fat-bearing condition. This should not be taken as an ultimate limit. The sample of all known sauropods is a tiny fraction of the sampled populations available for many single species of living animals. Even larger sauropods certainly await discovery, and it is improbable that the largest were preserved in the fossil record. It is interesting that, in living tetrapods, extremely rare "world record" individuals are often twice as massive as average individuals (McWhirter and McWhirter, 1986). In this view sauropods of 100 tons are not unrealistic, especially if bearing large amounts of seasonal fat.

In comparison, ***Balaenoptera musculus*** typically weighs 80-100 tons, and may reach 200 in feeding season (Ellis, 1980; McWhirter and McWhirter, 1986). Unfortunately there has never been a rigorous study of the mass of baluchitheres and the largest fossil proboscideans, which may rival each other as the biggest of terrestrial mammals. The baluchitheres and bigger mammoths appear to be rather gracile, and may not have been as massive as sometimes suggested. At perhaps 20 tons or less, they certainly do not match the bigger sauropods in size. As for the greatest living land animal, ***Loxodonta africana*** bulls average 5 tons, often reach 7.5, and rarely reach about 10+ (Laws et al., 1975; McWhirter and McWhirter, 1986).

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NOTES ADDED IN PROOF

The neck of ***B. (G.) brancai*** HMN 211 is about 0.3 m shorter than the 9.3 m neck of the primitive, 9 ton diplodocid ***Mamenchisaurus hochuanensis*** PMNH 3 (Young and Chow, 1972). It is likely that ***Supersaurus*** also had a longer neck than the largest ***Brachiosaurus.***

Martin (1987) restores the neck of the sauropod ***Cetiosaurus*** as barely able to reach the ground, rise above the height of the shoulders, or swing to either side. That such a neck of 14 bird-like vertebrae would be far less flexible than the giraffe's neck of 7 vertebrae is untenable. A high number of vertebrae directly implies great flexibility, since a stiff long neck is better achieved by lengthening a few vertebrae, as in the giraffe. Errors in Martin's restoration include a maximum raised neck posture that is really its normal, neutral S curve, zygapophyses that are virtually immobile, and an average of only 1.4° of motion from the centerline between each cervical. Instead, the sauropod cervical combination of ball and socket centra articulations with large zygapophyses was designed to maintain articulation over a much greater range of motion than Martin shows, especially when the bony joint areas were expanded by cartilagenous surfaces. Exactly how much more I am not sure, what one can learn from dry bone manipulations or paper studies is useful, but not necessarily true to life. Sauropod and giraffe cervicals are remarkably similar; study of the latter might prove helpful to the problem. Note that a modest 12° or so of rotation between successive segments in 6 posterior cervicals would allow the sauropod head to reach high up. This mobility is plausible since many mammals can do the same with only 7 cervicals. The extreme neck inflexibility Martin restores in sauropods is also functionally illogical, since shorter necked ungulates can reach as far up and to the side relative to their size. Long necks are an extreme adaptation, and among land herbivores their only useful purpose is to increase the vertical reach of high browsers. Low browsers and grazers invariably have modest necks because they can always reach what they want by just taking a few steps towards it.

Contrary to Martin (1987), the ilial pubic penducles of all sauropods were massive, buttressed from the front and inside by stout sacral ribs, and well able to bear the mass of a rearing individual. Note that sauropods only stood, or occasionally slowly walked, bipedally. They did not incur the stresses of fast bipedal motion.

PMNH – Beijing Museum of Natural History, Beijing.

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