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First occurrence of *Brachiosaurus* (Dinosauria: Sauropoda) from the Upper Jurassic Morrison Formation of Oklahoma

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The giant sauropod *Brachiosaurus* is one of the rarest sauropods from the Upper Jurassic of North America. The genus has previously been reported from Colorado, Utah, and Wyoming. OMNH 01138 is a sauropod metacarpal of unusual proportions from the Upper Jurassic Morrison Formation of Oklahoma. The bone is longer and more slender than the metacarpals of diplodocids and *Camarasaurus*, and is most similar in size and proportions to the elongate metacarpals of *Brachiosaurus*. This is the first report of *Brachiosaurus* from Oklahoma.

INTRODUCTION

Brachiosaurus Riggs 1903 is one of the most familiar and distinctive dinosaurs, and a century after its initial description it remains the largest sauropod known from reasonably complete remains. *Brachiosaurus altithorax* Riggs 1903 was first described on the basis of a partial skeleton from the Upper Jurassic Morrison Formation of Colorado, USA. The genus was subsequently recognized in the Upper Saurian beds of Tendaguru, Tanzania, where *Brachiosaurus brancai* Janensch 1914 is represented by numerous partial skeletons. *Brachiosaurus* is the most common sauropod in the Tendaguru assemblage (Russell et al. 1980), in contrast to North America, where it is one of the rarest Jurassic sauropods (Turner and Peterson 1999).

The prolific Kenton Pit 1 (OMNH V92), in the Morrison Formation of the Oklahoma panhandle, yielded the remains of numerous sauropods, including specimens referable to *Apatosaurus* Marsh 1877b, *Camarasaurus* Cope 1877, and *Diplodocus* Marsh 1878 (Stovall 1938, Hunt and Lucas 1987, Czaplewski et al. 1994). While going through the *Camarasaurus* material in the OMNH collection, we noted a metacarpal of unusual proportions. This specimen, OMNH 01138, was previously catalogued as a left MC II of *Camarasaurus* sp. (Fig. 1). However, as we discuss below, this specimen is proportionally distinct from *Camarasaurus* and probably represents *Brachiosaurus*, which was hitherto unrecognized from Oklahoma.

Given the scarcity of *Brachiosaurus* in North America, any new material is significant. Herein we review the occurrence of *Brachiosaurus* in North America, describe the new specimen, and briefly discuss the Jurassic dinosaur fauna of Oklahoma.

Institutional Abbreviations: **AMNH**, American Museum of Natural History, New York; **ASDM**, Arizona Sonora Desert Museum, Tucson, Ariona; **BYU**, Bringham Young University, Provo, Utah; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **DMNS**, Denver Museum of Nature and Science, Denver, Colorado; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **HM**, Humbolt Museum, Berlin, Germany; **KUVP**, University of Kansas Museum of Vertebrate Paleontology, Lawrence, Kansas; **MNN TIG**, Musée National du Niger; **NMNH**, National Museum of Natural History, Washington, D.C.; **OMNH**, Oklahoma Museum of Natural History, Norman, Oklahoma; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

THE FOSSIL RECORD OF *BRACHIOSAURUS* IN NORTH AMERICA

Following the initial discovery and description of *Brachiosaurus altithorax* by Riggs (1901, 1903), remains referable to *Brachiosaurus* have been reported from several other localities in the Morrison Formation (Fig. 2, Table 1). These additional localities include Dry Mesa Quarry and Potter Creek Quarry, both of which have yielded numerous associated elements (Jensen 1985, 1987; Curtice and Wilhite 1996; Curtice et al. 1996), and Felch Quarry 1, which produced the only cranial material of *Brachiosaurus* from North America (Carpenter and Tidwell 1998). Jensen (1987) referred a large rib from the Jensen/Jensen Quarry to *Brachiosaurus*, but this referral was made solely on the basis of size and is therefore suspect. The rib may belong to the very large individual of *Camarasaurus* that is also present in the Jensen/Jensen Quarry (D.R. Wilhite, personal communication). Foster (2003) reported the presence of *Brachiosaurus* in the Fruita Paleontological Area General quarry in Mesa County, Colorado, and in the Freezeout Hills General quarry in Carbon County, Wyoming.

Outside of the quarries listed above, Turner and Peterson (1999) cited several unpublished reports of *Brachiosaurus* material from the Morrison Formation. By kind permission of Clark and Cliff Miles, one of us (MJW) was allowed access to possible *Brachiosaurus* specimens from Bone Cabin Quarry E in the holdings of Western Paleontological Laboratories. These specimens actually pertain to *Barosaurus* Marsh 1890. The other localities listed by Turner and Peterson (1999) with unpublished reports of *Brachiosaurus* material are all in Mesa County, Colorado (see Turner and Peterson 1999: Appendix 3), where the presence of *Brachiosaurus* is already well established.

Fig. 1. Metapodial OMNH 01138 in **A**, anterior, **B**, posterior, **C**, proximal, and **D**, distal views. We interpret the element as a left metacarpal II of *Brachiosaurus.* Scale bar equals 10 cm.

Finally, *Brachiosaurus* is apparently present in the University of Kansas quarry in Weston Co., Wyoming, although the find has only been reported in popular articles to date (e.g., Sherman 2003; see Foster 2003 for further information on the quarry). *Brachiosaurus* material reportedly present in the quarry includes a nearly complete skeleton and a pes of a second individual (Sherman, 2003).

DESCRIPTION AND IDENTIFICATION OF METAPODIAL OMNH 01138

Description of metapodial OMNH 01138

The reader is referred to Figure 1 for the following description. Metapodial OMNH 01138 is an elongate element that is slightly expanded proximally and distally, and, despite a length of 455 mm, it is a surprisingly gracile element. The metapodial has a wedge- or trapezoidal shape proximally—the medial face is the longest, the lateral face is the shortest, and its anterior and posterior faces pinch laterally to form the trapezoid. The posterior face narrows to a blunted point. The proximal articular surface of metapodial OMNH 01138 is roughened and relatively flattened with a slight concavity anterolaterally. Proximally, the shaft curves slightly laterally; otherwise it is straight, expanding slightly as it nears the proximal and distal ends of the element. In cross-section, metapodial OMNH 01138 is roughly triangular, with the base of the triangle anterior and the apex posterior. Posteriorly, a dull but discernable ridge runs from the proximal end of the element and terminates approximately mid-shaft. The distal end of metapodial OMNH 01138 has two poorly developed condyles separated by a shallow concavity. Both condyles expand slightly onto the anterior and posterior faces of the metapodial, but are mostly restricted to the distal surface and are directly almost completely ventrally.

Diagnosis of Metapodial OMNH 01138

Neosauropod metacarpals each have a distinctive morphology which, when articulated, allows the manus to assume a semi-tubular configuration (McIntosh 1990, Upchurch 1995, 1998, Wilson and Sereno 1998, Bonnan 2003). Directional terms are used here as if the metacarpals were articulated and the manus were pronated such that metacarpal III was oriented anteriorly. Proximally, the metacarpals have a triangular or wedge-shaped morphology. Metacarpal I is typically D-shaped and its flattened lateral edge articulates with metacarpal II (Fig. 3). Metacarpals II-IV are triangular proximally. Metacarpal II has a wedge-like shape that narrows to a blunted or squared-off point posteriorly. In diplodocids, metacarpal II typically resembles a distorted trapezoid

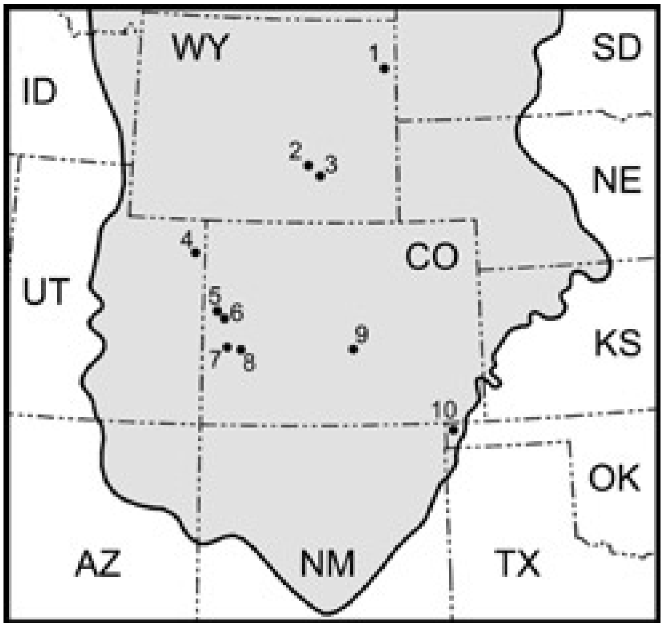

Fig. 2. *Brachiosaurus* localities in North America. The gray area indicates the distribution of the Morrison Formation. **1**, KU Quarry, Weston Co., WY; **2**, Freezeout Hills general, Carbon Co., WY; **3**, Reed's Quarry 13, Albany Co., WY; **4**, Jensen/Jensen Quarry, Uintah Co., UT; **5**, Fruita Paleontological Area general, Mesa Co., CO; **6**, Riggs Quarry 13, Mesa Co., CO; **7**, Dry Mesa Quarry, Mesa Co., CO; **8**, Potter Creek Quarry, Montrose Co., CO; **9**, Felch Quarry 1, Fremont Co., CO; **10**, Kenton Pit 1, Cimarron Co., OK. Modified from Turner and Peterson (1999:fig. 1).

proximally, whereas its shape in macronarians tends to be more triangular (Fig. 3). The proximal surface of metacarpal III typically has a roughly equilateral triangular shape, with no elongate or truncated corners. Metacarpal IV is broad anteriorly but narrows anteroposteriorly into a characteristically narrow flange. Metacarpal V has an oval to sub-oval proximal articular surface that is typically narrow and which slopes anteromedially.

The proximal surface of the lateral third of metacarpal I, the proximal surface of the medial third of metacarpal V, and the proximal, lateral and medial thirds of metacarpals II-IV all bear triangular fossae for articulation with adjacent metapodials (Hatcher 1902, Gilmore 1936, McIntosh 1990). On metacarpals II-IV, a roughened ridge is present posteriorly that extends from the proximal articular surface distally to about mid-shaft in most neosauropods (Fig. 4). In articulation, the ridges of metacarpals II and IV face posterolaterally and posteromedially, respectively, toward the ridge of metacarpal III. The combined ridges of metacarpals II-IV may provide insertion sites for flexor musculature (Bonnan 2001). A reduced but visible posterior ridge is present on the proximal half of metapodial OMNH 01138 (Fig. 5). Distally, the distal articular ginglymus of metacarpal I is offset in most sauropods: its medial condyle lies oblique and superiomedially to the lateral condyle at an angle that varies from 30–45° (Bonnan 2001). As with prosauropods (Galton 1990), this directs the articular ginglymus, and thus phalanx I-1 and the pollex claw, medially. Metacarpals II-V have relatively reduced

TABLE 1. *Brachiosaurus* localities in North America, listed in the same order that they are numbered in Fig. 2. The only element referred to *Brachiosaurus* from the Jensen/Jensen Quarry is a large rib that may belong to *Camarasaurus.* Lists of elements from Reed's Quarry 13 and the FPA General Quarry are not available. Abbreviations: FPA, Fruita Paleontological Area; KU, University of Kansas; MNI, minimum number of individuals.

Quarry	**Location**	**Elements**	**MNI**	**References**
KU Quarry	Weston Co., WY	partial skeleton, pes	2	Sherman 2003, Foster 2003
Freezeout Hills	Carbon Co., WY	caudal vertebra	1	Foster 2003
Reed's Quarry 13	Albany Co., WY	—	—	Foster 2003
Jensen/Jensen Quarry	Uintah Co., UT	rib	1	Jensen 1987
FPA General	Mesa Co., CO	—	—	Foster, 2003
Riggs Quarry 13	Mesa Co., CO	dorsal, sacral, and caudal vertebrae, coracoid, humerus, femur, ribs	1	Riggs 1903
Dry Mesa Quarry	Mesa Co., CO	cervical, dorsal, and caudal vertebrae, scapulocoracoid, fibula, tibia	2	Jensen 1985, 1987, Curtice & Wilhite 1996
Potter Creek	Montrose Co., CO	dorsal vertebra, humerus, radius, metacarpal, ilium, ribs	1	Jensen 1987
Felch Quarry 1	Fremont Co., CO	skull, cervical vertebra	1	McIntosh & Berman 1975, Carpenter & Tidwell 1998
Kenton Pit 1	Cimarron Co., OK	metacarpal, vertebrae?	1	this study

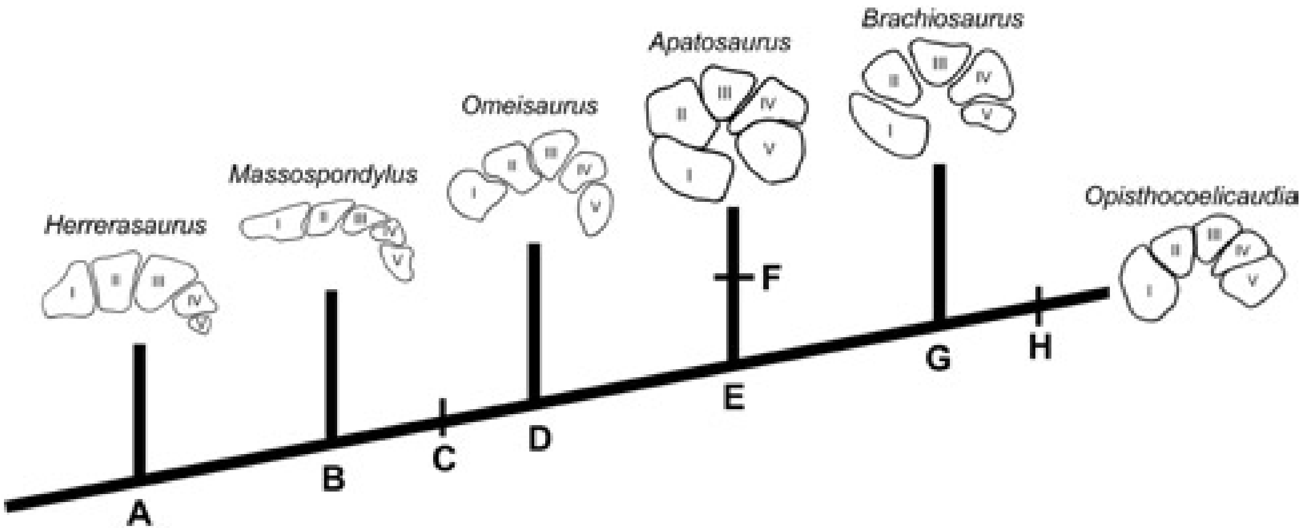

Fig. 3. Phylogenetic diagram of proximal manus shape in *Herrerasaurus*, *Massospondylus*, and selected sauropods; after Bonnan (2003: fig. 1). Nodes/Stems: **A**, Saurischia; **B**, Sauropodamorpha; **C**, Sauropoda; **D**, Eusauropoda; **E**, Neosauropoda; **F**, Diplodocoidea; **G**, Macronaria / "Brachiosauria"; **H**, Titanosauria. Roman numerals indicate metacarpal of same number. Not to scale.

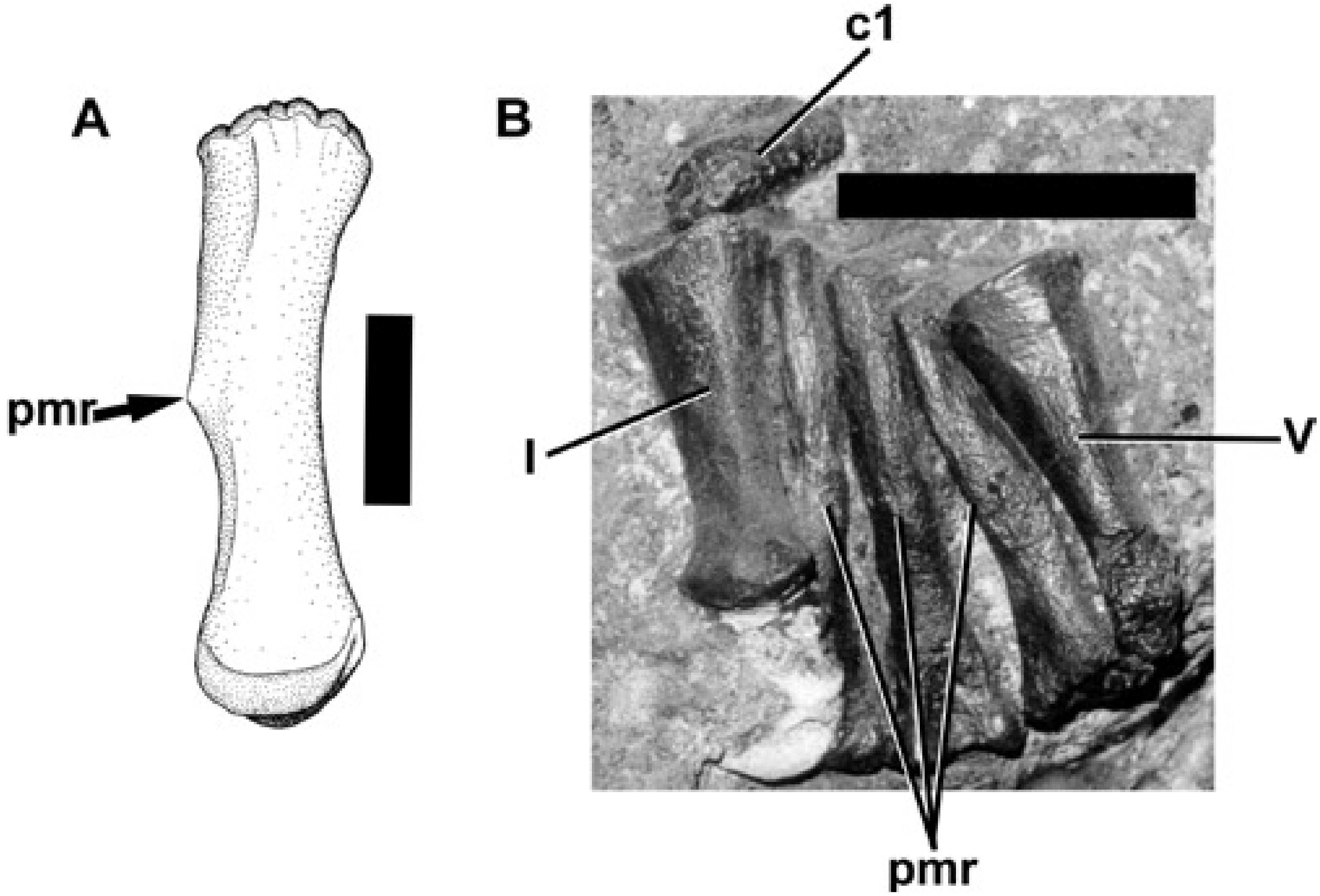

Fig. 4. Posterior metacarpal ridges in *Camarasaurus*. **A.** Medial view of *Camarasaurus grandis* AMNH 965 metacarpal II. **B.** Posterior view of *Camarasaurus lentus* CM 11338 articulated right manus. Scale bars equal 10 cm. Abbreviations: **pmr**, posterior metacarpal ridge; **I**, metacarpal I; **V**, metacarpal V; **c1**, medial carpal.

Fig. 5. Comparison of *Camarasaurus* metacarpal II and metapodial OMNH 01138. Medial views of *Camarasaurus grandis* AMNH 965 (left) and OMNH 01138 (right). Adjusted to same scale for comparison. Scale bars equal 10 cm.

articular surfaces that are poorly subdivided, and which face almost completely ventrally (Bonnan 2001). Among the neosauropods, the metacarpals of diplodocoids are short and robust, whereas macronarian metacarpals are more elongate and gracile (McIntosh 1990, Wilson and Sereno 1998).

Based on the preceding observations, metapodial OMNH 01138 is identified here as a left second metacarpal because its proximal articular surface is triangular and wedge-like with a narrow, blunted posterior projection, and it lacks well-defined or developed condyles as would be present on metacarpal I. Moreover, metacarpal OMNH 01138 is very elongate and slender, which strongly suggests it is of macronarian affinities. Furthermore, metacarpal OMNH 01138 is longer, proportionally, than any metacarpals that can be reliably identified as *Camarasaurus* (Figs. 5, 6, 7 and Tables 2 and 3). On the other hand, the specimen is very similar in proportions and overall morphology to the elongate metacarpals of brachiosaurids, including *Brachiosaurus brancai* (Tables 2 and 3, Fig. 7), *Brachiosaurus* sp. (Jensen 1987), *Sonorasaurus* Ratkevitch 1998, and *Cedarosaurus* Tidwell et al. 1999. Although brachiosaurids were fairly diverse in the

Fig. 6. Left metacarpal II of *Brachiosaurus brancai* (HM MBR 2249) in **A**, anterior, **B**, oblique posterior, **C**, proximal, and **D**, distal views. Compare to Figures 1, 4, and 5. Scale bars equal 10 cm.

Early Cretaceous of North America (Wedel et al. 2000), *Brachiosaurus* is the only member of the clade recognized from the continent during the Late Jurassic. We therefore identify metapodial OMNH 01138 as a macronarian left metacarpal II, and refer this specimen to *Brachiosaurus* sp.

DISCUSSION

To date, OMNH 01138 is the only element from Kenton Pit 1 that can be reliably identified as *Brachiosaurus*. However, several cervical centra in the OMNH collection are exceedingly long and slender, with length-to-diameter ratios of up to 4.6 (MJW, unpublished data). In contrast, the cervical vertebrae of *Apatosaurus* and *Camarasaurus* do not exceed a length-to-diameter ratio of 3.3 (see Table 4 in Wedel et al. 2000). The centra in question are proportionally similar to those of *Diplodocus*, *Barosaurus*, and *Brachiosaurus*, but lack the ventral ridges typical of *Diplodocus* and *Barosaurus*. At least some of these elements may pertain to *Brachiosaurus*, although more work will be required to adequately assess this possibility.

Brachiosaurus is the eighth dinosaur genus reported from the Morrison Formation of Oklahoma. Previously reported taxa include the sauropods *Apatosaurus*, *Diplodocus*, and *Camarasaurus*, the theropods *Allosaurus* Marsh 1877b and *Saurophaganax* Chure 1995, and the ornithischians *Camptosaurus* Marsh 1885 and *Stegosaurus* Marsh 1877a (Stovall 1938, 1943, Hunt and Lucas 1987, Czaplewski et al. 1994, Chure 1995). The presence of the three previously reported sauropod genera has been confirmed by recent radiographic studies (Wedel and Sanders 1998, Wedel 2001).

Of the eight genera present in Kenton Pit 1, all except *Brachiosaurus* and *Saurophaganax* are common at other Morrison localities (see Turner and Peterson 1999). Also typical

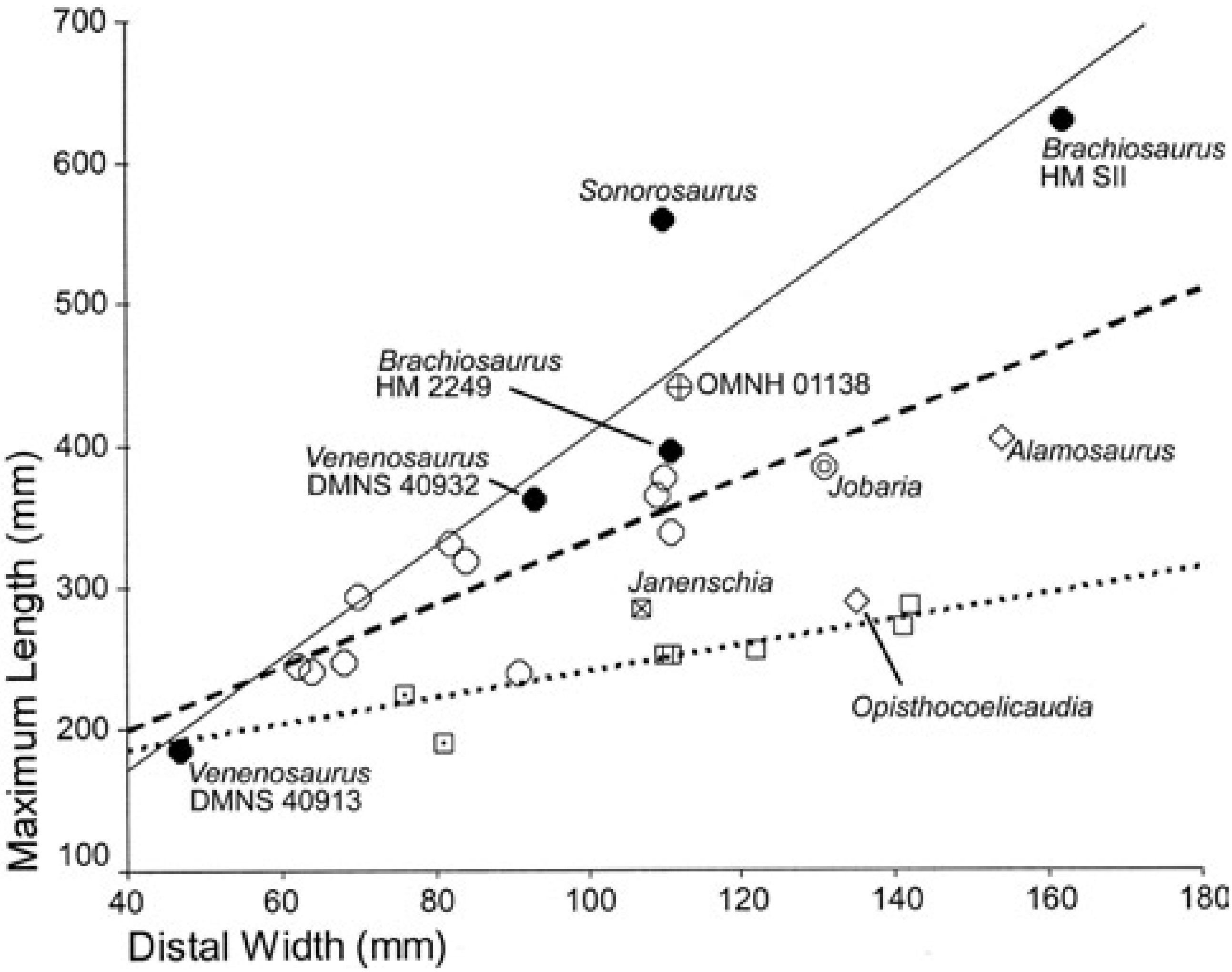

Fig. 7. Bivariate plot of maximum length versus distal width of metacarpal II for several sauropod taxa. The slope for the brachiosaurids (*Brachiosaurus*, *Sonorosaurus*, *Venenosaurus*) is indicated by a solid line, that of *Camarasaurus* by long dashes, and that of *Apatosaurus* by short dashes. Note that specimen OMNH 01138 (open circle with cross-hair) plots above all of the *Camarasaurus* specimens and falls close to the predicted slope for the brachiosaurids. Note also that *Jobaria* (circle with bullseye) falls along the predicted slope for *Camarasaurus*. Brachiosaurids are indicated by dark circles, OMNH 01138 by an open circle with cross-hair, *Camarasaurus* by open circles, *Jobaria* by an open circle with bullseye, saltasaurids (*Alamosaurus*, *Opitsthocoelicaudia*) by open diamonds, *Apatosaurus* by open squares, *Diplodocus* by open squares with dots, and *Janenschia* by a square with an X.

TABLE 2. Measurements of OMNH 01138 and the right metacarpals of *Brachiosaurus brancai* HM SII (see Janensch 1922), in milimeters. Measurements marked with an asterisk are listed by Janensch (1922) as approximate. Abbreviation: MC, metacarpal.

	OMNH 01138	HM SII				
		MC 1	MC 2	MC 3	MC 4	MC 5
Total length	455	586	634	597*	572	490
Length of proximal end	120	214	170	120	151	127
Width of proximal end	118	104	121	163	246	76
Length of distal end	95	97	136	110*	102*	102*
Width of distal end	111	112	172*	166	150*	142*
Least width of shaft	67	101	89	84	73	56
Least circumference of shaft	227	269	265	251	246	224

TABLE 3. Comparison of metapodial dimensions in OMNH 01138 and other macronarians. The four dimensions reported here were selected because they best summarize metacarpal robustness and were measured or reported for the greatest number of specimens. *Janenschia* is included here because it may be a macronarian. Asterisk indicates measurements were obtained from the literature: *Brachiosaurus brancai* (Janensch 1922), *Sonorosaurus thompsoni* (Ratkevitch 1998), *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka 1977). Abbreviations: ML, maximum length; DW, distal width (mediolateral); LW, least width (mediolateral); LB, least breadth (anteroposterior).

Taxon	Specimen #	ML	DW	LW	LB
Brachiosaurus sp.	OMNH 01138	455	111	67	78
Camarasaurus grandis	AMNH 664	244	62	52	43
Camarasaurus grandis	AMNH 712	365	109	63	68
Camarasaurus grandis	FMNH P25120	293	70	42	30
Camarasaurus supremus	KUVP 129713	377	110	75	72
Camarasaurus supremus	KUVP 129716	339	111	63	60
Camarasaurus sp.	AMNH 332	247	68	45	50
Camarasaurus sp.	AMNH 823	241	64	46	41
Camarasaurus sp.	AMNH 965	331	82	54	64
Camarasaurus sp.	BYU 661/9047	318	84	66	50
Camarasaurus sp.	FMNH P6641	239	91	54	40
Jobaria tiguidensis	MNN TIG 3	385	131	61	67
Brachiosaurus brancai	HM SII*	634	172	89	—
Brachiosaurus brancai	HM 2249	396	111	69	60
Janenschia robusta	HM 2095.7	285	131	66	82
Sonorosaurus thompsoni	ASDM 500*	560	110	70	—
Venenosaurus dicrocei	DMNS 40932	358	87	51	49
Venenosaurus dicrocei, juv.	DMNS 40913	185	47	26	26
Alamosaurus sanjuanensis	NMNH 15560	405	154	96	—
Opisthocoelicaudia skarzynskii	ZPAL MgD-I/48*	290	135	60	65

is the preponderance of sauropod elements. The quarry is unusual in that it yielded the remains of several juvenile sauropods, including baby specimens of *Apatosaurus* and *Camarasaurus* (Carpenter and McIntosh 1994). Baby sauropods are rare in the Morrison Formation, although Dry Mesa Quarry also contains juveniles of more than one sauropod genus (Curtice and Wilhite 1996). The numerous juvenile specimens from Kenton Pit 1 indicate that the absence of small-bodied dinosaur taxa from the quarry is probably not a result of taphonomic bias.

CONCLUSIONS

OMNH 01138, an unusual metacarpal from Kenton Pit 1, is more similar to *Brachiosaurus* than to *Camarasaurus*, and is referred to *B.* sp. This is the first report of *Brachiosaurus* from Oklahoma, although some anomalously long cervical centra in the OMNH collection may also pertain to *Brachiosaurus.*

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