

BRAINCASE OF AN EARLY CRETACEOUS TITANOSAURIFORM SAUROPOD FROM TEXAS

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ABSTRACT—The first braincase belonging to an Early Cretaceous sauropod from North America is described. The diagnostic characters of this well preserved partial braincase are: prominent supraoccipital crest, with a distinct median ridge extending almost to the foramen magnum; short, ventrally directed basitubera, divided by a deep groove extending to the basiptyergoid; single foramen for cranial nerve XII; accessory foramen for cranial nerve XI. A lack of juvenile characters suggests this specimen, although quite small, belongs to an adult individual. Comparison of this specimen with other sauropod crania indicates strong similarities with brachiosaurids and titanosaurids.

INTRODUCTION

The braincases of sauropods have not received the same attention as the postcrania, in part because they are either hidden by outer skull bones or are heavily damaged. Even less information is available for sauropod endocasts because of the difficulty of cleaning out the brain cavity. The braincases of various sauropods that have been described are listed in Table 1. Most of these descriptions are of Late Jurassic sauropods. In contrast, Cretaceous sauropod braincases are not as well known, and none have yet been described from North America. Langston (1974) mentioned, but did not describe, a braincase from the Lower Cretaceous Glen Rose Formation of Texas (TMM 40435). Winkler et al. (1995) have determined the age of the Glen Rose in Blanco County to be Upper Aptian or Lower Albian. Because no further description of this specimen has been published, a more complete evaluation is warranted, especially in light of recent accounts of other North American Cretaceous sauropods (Britt et al., 1997, 1998; Gomani et al., 1999; Tidwell et al., 1999).

The braincase TMM 40435 is compared with casts of *Camarasaurus* GNMH 101 (McIntosh et al., 1996) and CM 11338 (Gilmore, 1925), and *Brachiosaurus* sp. USNM 5730 (Carpenter and Tidwell, 1998), as well as published descriptions of specimens listed in Table 1.

Abbreviations—**CM**, Carnegie Museum of Natural History; Pittsburgh; **DNM**, Dinosaur National Monument, Utah; **GMNH**, Gunma Museum of Natural History, Tokyo; **TMM**, Texas Memorial Museum, Austin; **USNM**, United States National Museum (National Museum of Natural History), Washington, D.C.; **YPM**, Yale Peabody Museum, New Haven.

DESCRIPTION

TMM 40435 is a well preserved partial braincase consisting of the supraoccipital, exoccipital–opisthotic complex (incomplete paraoccipital processes), basioccipital, basisphenoid (minus the basiptyergoid processes), and the prootic. All elements are firmly fused, with only a faint suture visible between the supraoccipital and right exoccipital. The braincase is small, measuring 62 mm from the posterior edge of the occipital condyle to the hypophyseal fenestra, and 91 mm from the basitubera to the supraoccipital apex.

The supraoccipital is intact, having fractured from the parietal near their suture (Fig. 1A, B). This sutural region has suffered some weathering, and no distinct sutural articulations are visible. A prominent mediodorsal crest rises above the surrounding bone and is set well apart from the rest of the supra-

occipital region by moderate fossae on each side of the crest. A similar crest is variably developed in *Camarasaurus*, but it is consistently found in *Brachiosaurus*. A distinct ridge extends from the apex of the crest almost to the foramen magnum.

Both paraoccipital processes are truncated a short distance from the foramen magnum. On the prootic, the lateral wing of the crista prootica is also missing; however, the main body of this bone remains fused to the opisthotic. The small occipital condyle is almost spherical and has a moderate groove on the dorsal surface for the spinal cord. The condyle is directed posteriorly on a relatively long neck, 25 mm in length and 42 mm wide measured dorsally. The basioccipital forms short, ventrally directed basitubera that do not meet medially, but remain separate throughout their length. Viewed posteriorly, each tuber is rectangular in shape. A deep, oval fossa extends along the bottom of the basioccipital from the ventral edge of the occipital condyle, between the basitubera, and ends just posterior to the basisphenoid (Fig. 1C). Although the posterior edge of the basisphenoid is fused to the front of the basioccipital, the basiptyergoid processes are missing, leaving the dorsum sellae and pituitary fossa exposed. Anteriorly the lateroventral portion of the prootic is still fused to the opisthotic, forming the anterior border of the otic capsule.

The major cranial nerve foramina are preserved (Fig. 1D). Whereas two separate openings for the dual branches of cranial nerve XII are commonly found on the exoccipital in sauropod skulls (White, 1958; Berman and McIntosh, 1978; Madsen et al., 1995), in TMM 40435 these two nerves exit the endocranium from a single opening, the hypoglossal foramen, lateral to the foramen magnum. A small foramen located on the anterior side of the exoccipital just below the paraoccipital process probably housed cranial nerve XI. In *Camarasaurus* and *Brachiosaurus* this nerve is usually combined with cranial nerves IX, X, and the jugular vein in the metotic fissure (jugular foramen of White, 1958; Madsen et al., 1995). On this specimen, however, it evidently pierces the exoccipital on the anterior side of a distinct ridge that extends ventrally from the lower margin of the paraoccipital process and along the lateral side of the basioccipital to merge with the basitubera. The vertically elongate metotic fissure is the most prominent lateral opening in this braincase, housing cranial nerves IX, X and the jugular vein. Anterior to this large opening is the fenestra ovalis, a relatively small, circular fossa that, in turn, lies behind a slightly larger foramen for cranial nerve VII. Thus, there are four foramina placed between the crista prootica and the foramen magnum, rather than the three usually found in sauropods.

TABLE 1. Sauropod braincases described.

Taxon	References
<i>Amargasaurus</i>	Salgado and Bonaparte, 1991
<i>Antarctosaurus</i>	Huene, 1929; Chatterjee and Rudra, 1996
<i>Apatosaurus</i>	McIntosh and Berman, 1975; Berman and McIntosh, 1978
<i>Barosaurus</i>	Janensch, 1935–36
<i>Brachiosaurus</i>	Janensch, 1935–36; Carpenter and Tidwell, 1998
<i>Camarasaurus</i>	White, 1958; Madsen et al., 1995
<i>Dicraeosaurus</i>	Janensch, 1935–36
<i>Diplodocus</i>	McIntosh and Berman, 1975; Berman and McIntosh, 1978
<i>Nemegtosaurus</i>	Nowinski, 1971; Upchurch, 1999
<i>Quaesitosaurus</i>	Kurzanov and Bannikov, 1983; Upchurch, 1999
<i>Saltosaurus</i>	Powell, 1992
<i>Shunosaurus</i>	Zhang, 1988
<i>Titanosaurus</i>	Berman and Jain, 1982; Chatterjee and Rudra, 1996
unnamed titanosauriform	this paper

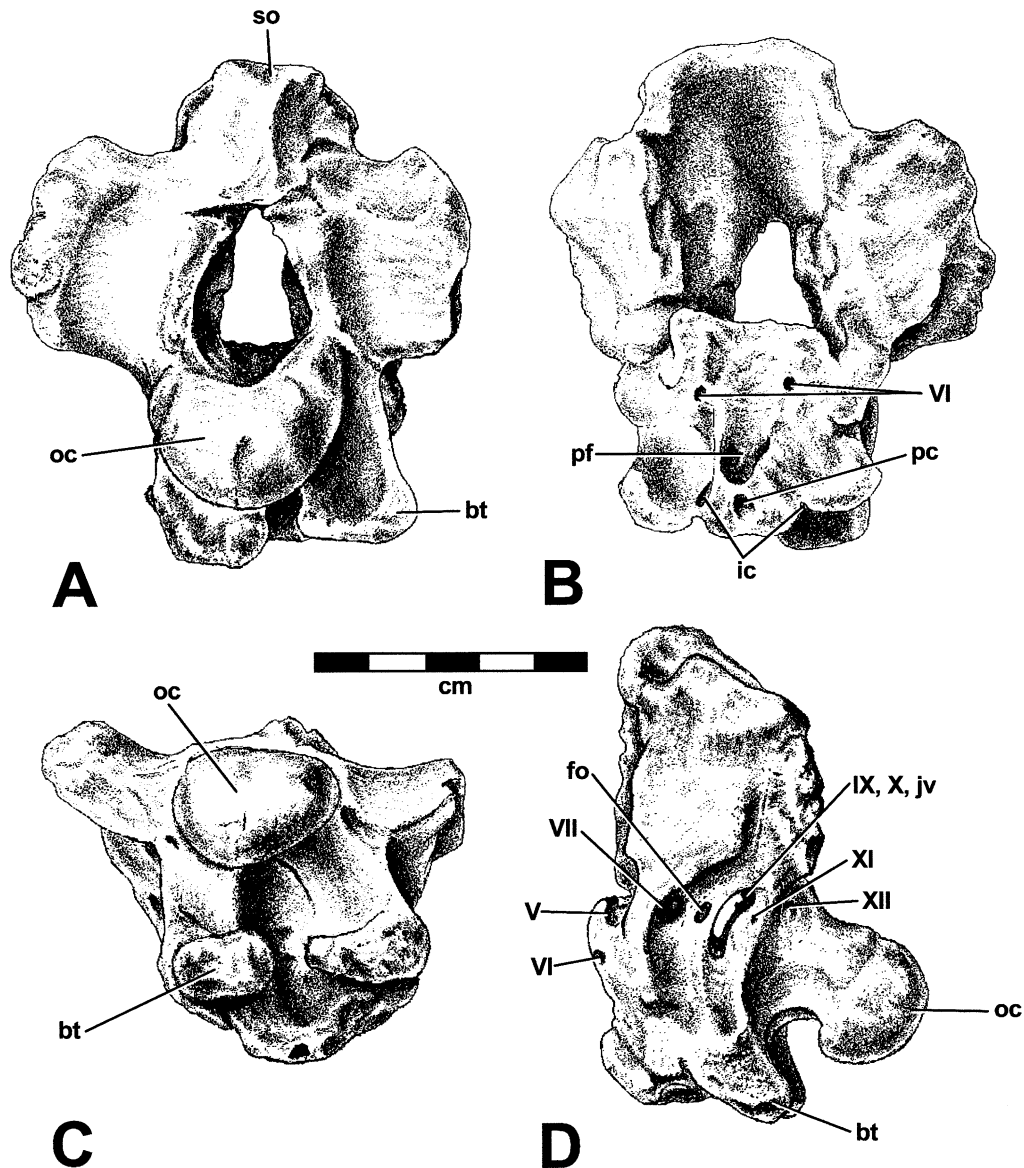


FIGURE 1. Sauropod braincase TMM 40435 in: A, posterior; B, anterior; C, ventral; D, lateral views. **Abbreviations:** *bt*, basitubera; *fo*, fenestra ovalis; *ic*, internal carotid exit; *jv*, jugular vein exit; *oc*, occipital condyle; *pf*, pituitary fossa; *so*, supraoccipital; *V*, trigeminal nerve exit; *VI*, abducens nerve exit; *VII*, facial nerve exit; *IX*, glossopharyngeal nerve exit; *X*, vagus nerve exit; *XI*, accessory nerve exit; *XII*, hypoglossal nerve exit. Scale = 5 cm.

In anterior view (Fig. 1B), the broken surface of the prootic shows the posterior edge of a large fossa for the trigeminal nerve (V), which is positioned on the lateroventral corner of the endocranial cavity. Near the anterior edge of the endocranial floor are two parallel grooves for cranial nerve VI. Anteroventrally, these grooves lead to circular openings located a short distance below the level of the braincase floor, on either side of the pituitary fossa. At the base of the pituitary fossa lies a subtriangular, block-like wedge of bone, which is part of the basiptyergoid. Dorsoventrally directed foramina on each side of the basiptyergoid house the internal carotid artery, and medially, a single short passage extends ventrally from the base of the pituitary fossa. This is possibly the hypophyseal fenestra, which houses the pituitary vein. Because the orbitosphenoid and laterosphenoid are missing from the specimen, the locations of cranial nerves II through IV cannot be determined.

Endocast

An endocast was taken of the endocranial cavity (Fig. 2A) representing the mid- and hindbrain regions. The endocast widens considerably anteriorly indicating that the midbrain was the widest part of the brain, as in other sauropods. The narrowest part is between the otic capsules. The posterior half of the pituitary region shows the crest of the internal carotid at the posteroventral apex, and the exit for the abducens nerve (VI) about mid-height. The exit for the trigeminal nerve (V) is located just above the posterior edge of the pituitary fossa (Fig. 2A), which is slightly more anterior than it occurs in *Brachiosaurus* (Fig. 2B), *Camarasaurus* (Fig. 2C) or *Diplodocus* (Hopson, 1979:fig. 16). Posterior to the trigeminal is the small root of the facial nerve (VII); this nerve is relatively larger in *Brachiosaurus*, and very close to the trigeminal root (compare Fig. 2A, B).

The flexure of the endocast between the floor of the endocranium and pituitary region is rounded as in *Camarasaurus*, rather than deeply notched as in *Brachiosaurus* (compare Fig. 2A, C with B). A large nub located dorsal to the trigeminal is similar to that seen in *Brachiosaurus* as illustrated by Janensch (1935–36) (Fig. 2B). This nub apparently does not occur in *Camarasaurus* (Fig. 2C) or *Diplodocus* (see Hopson, 1979:fig. 16); it may represent the middle cerebral vein.

The large ridge for the vagus (X) nerve and jugular vein occurs low on the medulla oblongata region, adjacent to the inner ear. A small nub for cranial nerve (XI) is found posterior to the vagus nerve (X). Dorsally, a nub adjacent to the ridge may be for the posterior cerebral vein. The hypoglossal nerve (XII) is evident on the endocast, unlike that in *Diplodocus* (Hopson, 1979).

DISCUSSION

By far, the most complete description of the sauropod braincase is the detailed account found in Madsen et al. (1995). They document a significant amount of variation among numerous *Camarasaurus* skulls from North America, which serves as a cautionary statement concerning the role of individual and interspecies variation that could exist within other sauropod genera, as well. With this in mind, the following preliminary comparisons are presented. Unfortunately, the incomplete nature of TMM 40435 necessarily restricts these comparisons to the most posterior elements found in the skull.

The cranium of *Diplodocus* differs considerably from TMM 40435 in morphology. In the two *Diplodocus* skulls illustrated in Berman and McIntosh (1978) the supraoccipital encompasses the top one third of the foramen magnum, while the basitubera are rather elongate. This contrasts with the Glen Rose specimen, in which the supraoccipital contributes only twenty-five percent to the dorsal border of the foramen magnum, and the basitubera are quite short. The occipital condyle in diplodocids is ventrally

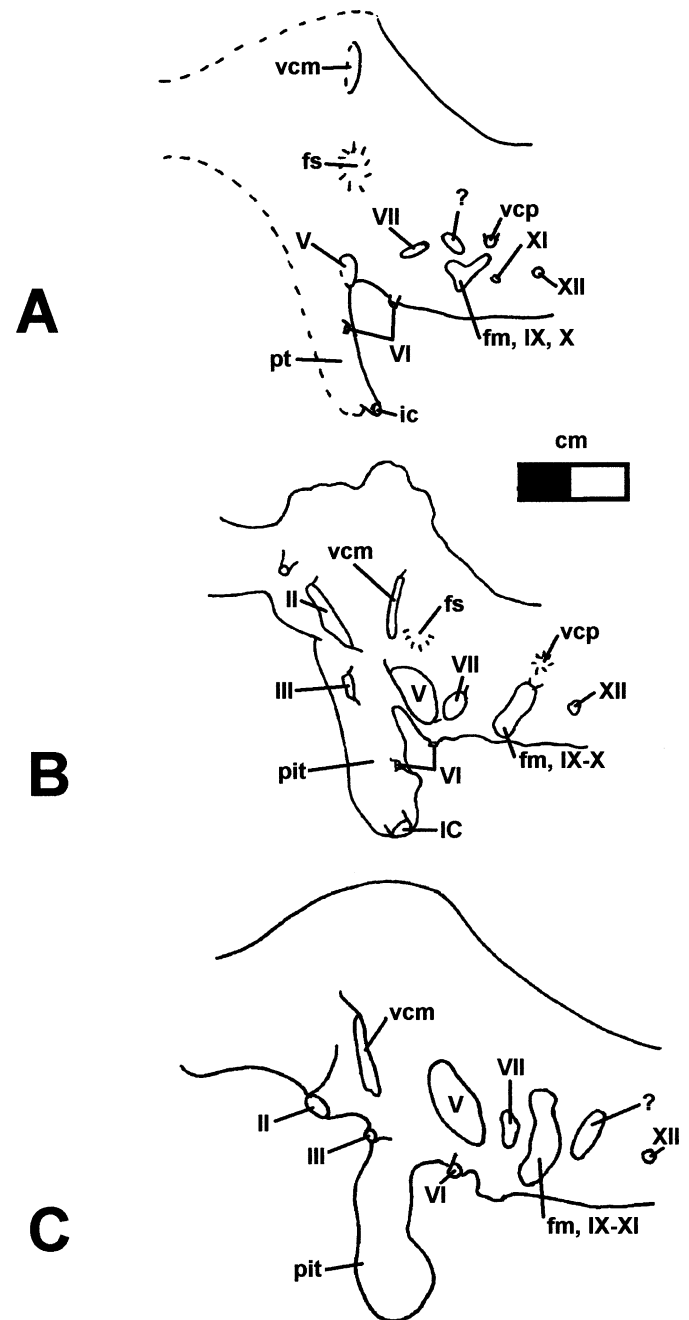


FIGURE 2. **A**, endocast of mid- and hindbrain portions of TMM 40435. **B**, endocast of *Brachiosaurus* (reversed, modified from Janensch, 1935–36). **C**, endocast of *Camarasaurus* (redrawn from Ostrom and McIntosh, 1966). **Abbreviations:** fs, exit for part of mid-cerebral vein?; ic, internal carotid artery; pit, pituitary gland; vcm, mid-cerebral vein; vcp, posterior cerebral vein; II, optic nerve; III, oculomotor nerve; V, trigeminal nerve; VI, abducens nerve; VII, facial nerve; X, vagus nerve; XI, accessory nerve; XII, hypoglossal nerve. Scales in cm.

directed, a derived trait shared with the titanosaur *Saltasaurus* (see Upchurch, 1999:fig. 8) This element on the TMM specimen is posteriorly directed.

Of the numerous *Camarasaurus* skulls described in the literature, the braincase of DNM 28 (White, 1958) demonstrates two features found in common with the Glen Rose specimen: a prominent supraoccipital crest, and a strong dorsoventral ridge

extending from the apex almost to the foramen magnum. However, in other *Camarasaurus* specimens this crest and ridge are poorly developed. The basitubera in *Camarasaurus* are fairly long, posteroventrally recurved, and medially joined along much of their length. No *Camarasaurus* skull shows the short, well separated, ventrally directed basitubera found in TMM 40435.

Of the skull fragments referred to *Pleurocoelus* by Lull (1911) only the supraoccipital is directly comparable. It evidently comes from a much younger individual, because it is not yet fused to the other braincase elements. The medial crest is only slightly raised and bears a prominent medial ridge.

Several sauropod braincases from the Late Cretaceous of India and South America have been referred, at least provisionally, to the titanosauria. These specimens share several features in common with TMM 40435: fully fused sutures throughout a relatively small braincase, a robust supraoccipital crest, and a single opening for cranial nerve XII. The partial braincase from India described by Berman and Jain (1982), also shows a separate opening for the cranial nerve XI, like the Texas specimen. This cranium is referred to *T. indicus* by Chatterjee and Rudra (1996). A second cranium from India also described by Chatterjee and Rudra (1996) is referred to *Antarctosaurus*, contra Hunt et al. (1994). However, both of these crania show the basitubera fused together over most of their length, diverging only slightly at their distal ends. This feature is also shared with *Saltasaurus* (Powell, 1992), and *Nemegtosaurus* (Nowinski, 1971), but differs greatly from the two, short, well-separated stalks forming the basitubera of TMM 40435.

The skull of *Brachiosaurus* has long been known from Africa (Janensch, 1935–36). A recently described skull from North America (Carpenter and Tidwell 1998) provides additional information. In comparing the skull of *Brachiosaurus* to TMM 40435, several similarities become evident. The medial crest of the supraoccipital is prominently displayed and bears a strong sagittal ridge. All known crania of *Brachiosaurus* exhibit relatively short, individually divergent, ventrally directed basitubera, which are very similar to those in the Glen Rose braincase. Although *Brachiosaurus* and TMM 40435 show several similarities, they differ in the relative length of the occipital condyle. This measurement is obtained by dividing the occipital condyle-hypophysial fenestra length by the total height of the cranium. In *Brachiosaurus*, this ratio is 0.51, which is significantly shorter than the ratio of 0.68 in TMM 40435. Overall, the skull of *Brachiosaurus* shares the greatest number of characteristics with the Glen Rose specimen. Nevertheless, TMM 40435 cannot be placed phylogenetically with confidence because key regions of the specimen are missing, and because of the limited number of sauropod skulls available for comparison. Although several authors have recently published phylogenies for the Sauropoda (Salgado and Calvo, 1997; Upchurch, 1998; Wilson and Sereno, 1998), the number of specimens with skulls remains very limited.

The most striking feature of TMM 40435 is the very small size, closely resembling that of the juvenile *Camarasaurus* (CM 11338) from Dinosaur National Monument. It is somewhat smaller than the juvenile *Camarasaurus* specimens YPM 1905 and YPM 1901. In these skulls, the individual elements are articulated, but not completely fused together. The small size of TMM 40435 initially suggested that it also comes from a juvenile, but there is a nearly total absence of sutures between elements. This high degree of fusion for such a small braincase suggests that it belongs to remarkably small adult sauropod as suggested by Langston (1974), approximately 6 m in overall length. While this is much smaller than the Late Jurassic brachiosaurs, it compares well with the two Early Cretaceous titanosauriforms from Utah *Cedarosaurus* and *Venenosaurus* (Tidwell et al., 1999, 2001). Complete neurocentral fusion in

the vertebrae of these new taxa indicates their adult status, suggesting that a number of small sauropods inhabited Western North America during the Early Cretaceous.

ACKNOWLEDGMENTS

We thank Dr. Tim Rowe, Texas Memorial Museum, for the loan of the specimen, and Cliff Miles, Western Paleontological Labs, for a cast of the *Camarasaurus* skull, GMNH 101. Our thanks to Judy Peterson for the braincase illustrations, and to Bryan Small for his helpful insights into basal archosaur cranial morphology.

LITERATURE CITED

- Berman, D. S., and S. L. Jain. 1982. The braincase of a small sauropod dinosaur (Reptilia: Saurischia) from the Upper Cretaceous Lameta Group, Central India, with review of Lameta Group localities. *Annals of Carnegie Museum* 51:405–422.
- , and J. S. McIntosh. 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Bulletin of Carnegie Museum of Natural History* 8:1–35.
- Britt, B. B., K. L. Stadman, R. D. Scheetz, and J. S. McIntosh. 1997. *Camarasaurid* and *titanosaurid* Sauropods from the Early Cretaceous Dalton Wells Quarry (Cedar Mountain Formation), Utah. *Journal of Vertebrate Paleontology* 17(3, suppl.):34A.
- , R. D. Scheetz, J. S. McIntosh, and K. L. Stadman. 1998. Osteological characters of an Early Cretaceous titanosaurid sauropod dinosaur from the Cedar Mountain Formation of Utah. *Journal of Vertebrate Paleontology* 18(3, suppl.):29A.
- Carpenter, K., and V. Tidwell. 1998. A preliminary description of a *Brachiosaurus* skull from Felch Quarry 1, Garden Park, Colorado. *Modern Geology* 23:69–84.
- Chatterjee, S., and D. K. Rudra. 1996. KT events in India: impact, rifting, volcanism and dinosaur extinction. *Memoirs of the Queensland Museum* 39:489–532.
- Gilmore, C. W. 1925. A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from the Dinosaur National Monument, Utah. *Carnegie Museum Memoirs* 10:347–384.
- Gomani, E., L. Jacobs, and D. Winkler. 1999. Comparison of the African titanosaurian *Malavosaurus*, with a North American Early Cretaceous sauropod; pp. 223–233 in Y. Tomida, T. H. Rich, P. Vickers-Rich (eds.), *Proceedings of the Second Gondwanan Dinosaur Symposium*. National Science Museum Monographs, No. 15. Tokyo.
- Hopson, J. A. 1979. Paleoneurology; 39–146 in C. Gans, R. Northcutt, and P. Ulinski (eds.), *Biology of the Reptilia*, Vol. 9. Academic Press.
- Huene, F. von. 1929. Los Saurisquios y Ornitisquios Del Cretaceo Argentino. *Anales Museo La Plata Series 2*, 3:1–196.
- Hunt, A. P., M. G. Lockley, S. G. Lucas, and C. A. Meyer. 1994. The global sauropod fossil record. *Gaia: Revista de Geociencias, Museo Nacional de Historia Natural* 10:261–279.
- Janensch, W. 1935–36. Die schädel der sauropoden *Brachiosaurus*, *Barosaurus*, und *Dicraeosaurus* aus den Tendaguruschichten Deutsch-Ostafrikas. *Paleontographica* 2:147–298.
- Kurzanov, S. M., and A. F. Bannikov. 1983. A new sauropod from the Upper Cretaceous of Mongolia. *Paleontologicheskyy Zhurnal* 1983: 91–97.
- Langston, W., Jr. 1974. Nonmammalian Comanchean tetrapods. *Geoscience and Man* 8:77–102.
- Lull, R. S. 1911. The reptilian fauna of the Arundel Formation; pp. 181–211 in *Lower Cretaceous Volume*. Maryland Geological Survey.
- Madsen, J., J. S. McIntosh, and D. S. Berman. 1995. Skull and atlas-axis complex of the Upper Jurassic sauropod *Camarasaurus* Cope (Reptilia:Saurischia). *Bulletin of the Carnegie Museum of Natural History* 31:1–115.
- 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.
- , C. Miles, K. Cloward, and J. Parker. 1996. A new nearly complete skeleton of *Camarasaurus*. *Bulletin of Gunma Museum of Natural History* 1:1–87.

- Nowinski, A. 1971. *Nemegtosaurus mongoliensis* n. gen., n. sp. (Sauropoda) from the Uppermost Cretaceous of Mongolia. *Palaeontologica Polonica* 25:57–81.
- Ostrom, J., and J. S. McIntosh. 1966. *Marsh's Dinosaurs*. Yale University Press, New Haven, 388 pp.
- Powell, J. E. 1992. Osteologia de *Saltasaurus loricatus* (Sauropoda–Titanosauridae) del Cretacico Superior del Noroeste Argentino; pp. 165–230 in J. L. Sanz and A. D. Buscalioni (coords), *Los Dinosaurios y su entorno Biotico*. Actas 2 Carso de Paleontologia en Cuenca, Instituto “Juan de Valdes.” Ayuntamiento de Cuenca.
- Salgado, L., and J. F. Bonaparte. 1991. Un nuevo sauropodo dicraosauridae, *Amargasaurus cazauai*, gen. et sp. nov., de la Formacion La Amarga, Neocomiano de la Provincia del Neuquen, Argentina. *Ameghiniana* 28:333–346.
- , and J. Calvo. 1997. Evolution of titanosaurid sauropods. II: the cranial evidence. *Ameghiniana* 34:33–48.
- Tidwell, V., K. Carpenter, and B. Brooks. 1999. New sauropod from the Lower Cretaceous of Utah. *Oryctos* 2:21–37.
- , K. Carpenter, and Susanne Meyer. 2001. A new Titanosauriform (Sauropoda) from the Poison Strip Member of the Cedar Mountain Formation, Lower Cretaceous, Utah; pp. 137–165 in D. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life*. Indiana University Press.
- Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* 124:43–103.
- 1999. The phylogenetic relationships of the *Nemegtosauridae* (Saurischia, Sauropoda). *Journal of Vertebrate Paleontology* 19: 106–125.
- White, T. E. 1958. The braincase of *Camarasaurus lentus* (Marsh). *Journal of Paleontology* 32:477–494.
- Wilson, J., and P. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology* Memoir 5:1–68.
- Winkler, D., L. Jacobs, Y. Lee, and P. Murry. 1995. Sea level fluctuation and terrestrial faunal change in North-Central Texas; pp. 175–177 in Ailing Sun and Yuanqing Wang (eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, short papers. China Ocean Press, Beijing.
- Zheng, Z. 1991. Morphology of the braincase of *Shunosaurus*. *Vertebrata Palasiatica* 4:108–118.
- 1996. Cranial anatomy of *Shunosaurus* and *Camarasaurus* (Dinosauria: Sauropoda) and the phylogeny of the Sauropoda. Ph.D. dissertation, Texas Tech University, Lubbock, 194 pp.

Received 1 November 2000; accepted 16 January 2002.