Journal of Vertebrate Paleontology 20(1):109–114, March 2000

SAUROPOSEIDON PROTELES, A NEW SAUROPOD FROM THE EARLY CRETACEOUS OF OKLAHOMA

MATHEW J. WEDEL[1], RICHARD L. CIFELLI[1], and R. KENT SANDERS[2]
[1]Sam Noble Oklahoma Museum of Natural History, 2401 Chautauqua, Norman, Oklahoma 73072;
[2]Department of Radiological Sciences University Hospital, Oklahoma City, Oklahoma 73190

ABSTRACT—*Sauroposeidon proteles*, a new brachiosaurid sauropod, is represented by an articulated series of four mid-cervical vertebrae recovered from the Antlers Formation (Aptian–Albian) of southeastern Oklahoma. Most Early Cretaceous North American sauropod material has been referred to *Pleurocoelus*, a genus which is largely represented by juvenile material and is not well understood. Regardless of the status and affinities of *Pleurocoelus*, the new taxon is morphologically and proportionally distinct. Among well-known sauropod taxa, *Sauroposeidon* is most similar to *Brachiosaurus*; particularly noteworthy are the neural spines, which are set forward on the centra and are not bifurcate, and the extremely elongate cervical ribs. *Sauroposeidon* and *Brachiosaurus* also share a derived pattern of pneumatic vertebral ultrastructure and a mid-cervical transition point, at which neural spine morphology changes from very low (anteriorly) to very high (posteriorly). Autapomorphies of *Sauroposeidon* include posterior placement of the diapophyses, hypertrophied pneumatic fossae in the lateral faces of the neural spines and centra, and an extraordinary degree of vertebral elongation (e.g., C8 = 1.25 m; 25% longer than *Brachiosaurus*). Additional sauropod material from the Early Cretaceous Cloverly Formation may be referrable to the new Oklahoma sauropod, which appears to be the last of the giant North American sauropods and represents the culmination of brachiosaurid trends towards lengthening and lightening of the neck.

INTRODUCTION

Sauropod dinosaurs are of general interest because they include the largest of all terrestrial vertebrates and because their great size and tremendously elongate necks pose biomechanical and physiological challenges to paleobiological interpretation. In North America, sauropods are best known from the Late Jurassic, where they were present in considerable abundance and diversity (McIntosh, 1990). They later waned in importance and disappeared from the continent in the mid-Cretaceous (Cifelli et al., 1997b), perhaps as a result of reciprocal effects between terrestrial flora and herbivores (Bakker, 1986).

The fossil record of sauropods from the Early Cretaceous of North America is relatively poor, and the paleogeography and relationships of these animals are not well understood. While sauropod remains have been recovered from Early Cretaceous deposits across the continent, most of the material is fragmentary or disarticulated. Compounding these problems, a significant amount of the recovered material belongs to juvenile animals, for which corresponding adult material is rare or nonexistent. Until recently, almost all Early Cretaceous sauropod material was referred to *Pleurocoelus*, a poorly understood taxon of debatable taxonomic affinities (Langston, 1974; Salgado and Calvo, 1997).

In this context, any new discoveries are significant. In May and August, 1994, crews from the Oklahoma Museum of Natural History recovered a partial cervical series of a large, apparently new sauropod from OMNH locality V821, in the Antlers Formation of southeast Oklahoma. In this paper we describe the specimen and discuss the relationships and paleobiology of the new taxon.

MATERIALS AND METHODS

The centra of presacral vertebrae in sauropods are penetrated by pleurocentral cavities or pleurocoels. Seeley (1870), Wiman (1929), Romer (1933), Janensch (1947), and Britt (1993) have interpreted these cavities as containing or leading to pneumatic spaces. Britt (1993) preferred the term pneumatic fossa over pleurocoel to denote lateral excavations of saurischian vertebral centra, and this preference is followed throughout this work. In addition, Britt (1993, 1997) provided terminology for discussing the internal subdivisions of pneumatized vertebrae. Vertebrae of camerate construction have large pneumatic chambers separated by thick bony septa, whereas vertebrae of camellate construction are characterized by numerous small chambers separated by thin bony septa. Wilson and Sereno (1998) use the term somphospondyli to characterize vertebrae that are composed of ‘‘spongy bone’’; this term appears to be equivalent to camellate internal structure, so we follow the terminology of Britt (1993, 1997) when discussing vertebral pneumatic structure.

The radiographic techniques discussed herein were performed at the University Hospital on the University of Oklahoma Health Sciences Center campus in Oklahoma City. Computed tomography (CT) scans of sauropod vertebrae were performed using a General Electric 9800 Highlight Advantage 4th generation CT scanner. Scout images were obtained in lateral projection with a technique setting of 120 kVp (kilovolt peak) and 40 mA (milliamperes). Most axial images were produced at 120 kVp and 120 mA, although the size and density of the largest specimen, OMNH 53062, required the maximum technique setting of 140 kVp at 170 mA. Data were reconstructed in bone algorithm using a Star Tech, Inc. One Sun CPU computed tomography array imaging processor and the GE Advantage version 1.0 imaging software package.

Institutional abbreviations: DGM, Museo de la Divisao Geologia y Mineralogia, Rio de Janeiro, Brazil; **HM,** Humbolt Museum, Berlin, Germany; **OMNH,** Oklahoma Museum of Natural History, Norman, Oklahoma; **USNM,** National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **YPM,** Yale Peabody Museum, New Haven, Connecticut.

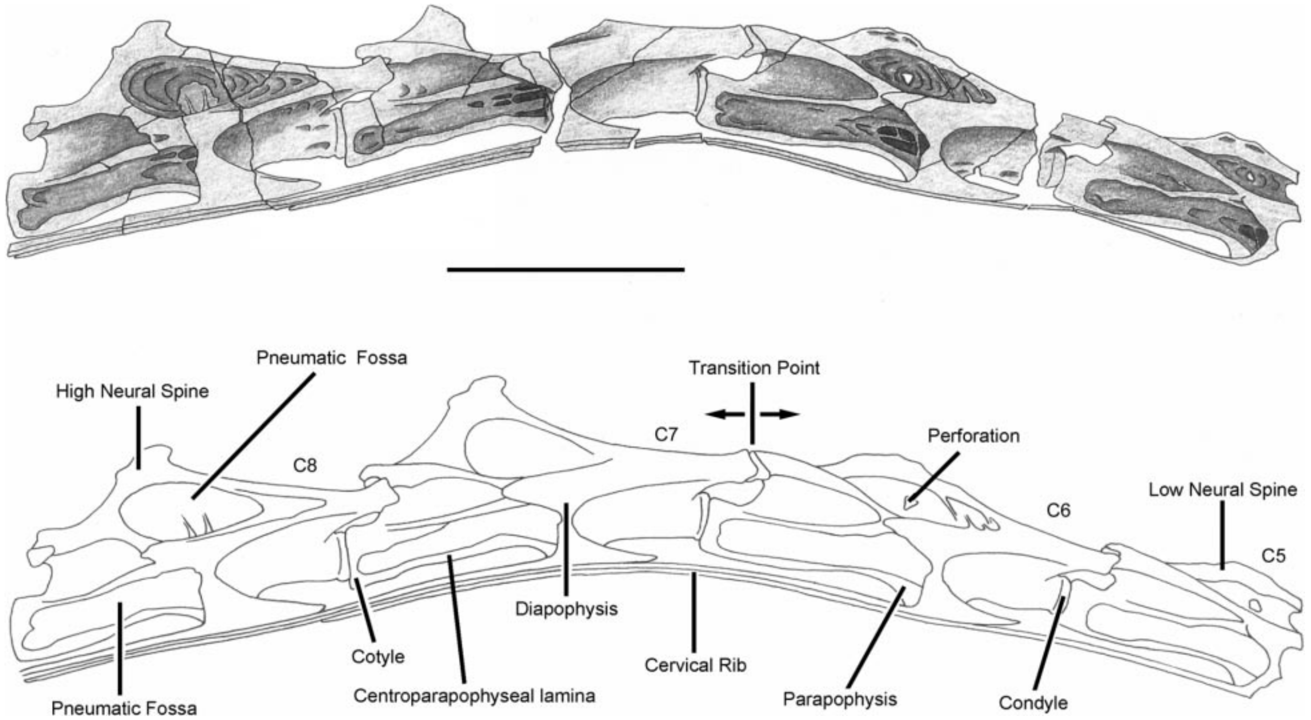

FIGURE 1. *Sauroposeidon proteles,* gen. et. sp. nov. OMNH 53062, articulated cervicals 5–8 in right lateral view. Bottom drawing shows bone restored to missing areas, plus anatomical terminology used in the text. Neural spine of C7 is incomplete but sufficient bone remains to demonstrate that it was high, creating a transition point between C6 and C7. In anterior vertebrae, the height of the neural spine is approximately equal to centrum diameter; in posterior vertebrae, neural spine height is twice centrum diameter. All neural spines are excavated laterally by deep pneumatic fossae, with those of anterior vertebrae being perforate. Scale bar equals 1 m.

SYSTEMATIC PALEONTOLOGY

Order SAURISCHIA Seeley, 1888
Suborder SAUROPODOMORPHA Huene, 1932
Infraorder SAUROPODA Marsh, 1878
Family BRACHIOSAURIDAE Riggs, 1904

SAUROPOSEIDON PROTELES, gen. et sp. nov.
(Figs. 1, 2B, 4A–E, 5)

Etymology—*Sauroposeidon,* Sauros (lizard, Greek) and Poseidon (the god of earthquakes in Greek mythology); *proteles* (perfected before the end, Greek), in reference to the species' culmination of brachiosaurid adaptations just before the extinction of North American sauropods.

Holotype—OMNH 53062, articulated cervical vertebrae 5–8, with cervical ribs preserved in place.

Locality and Horizon—OMNH locality V821, Antlers Formation, Atoka County, Oklahoma, USA. The locality consists of a claystone outcrop from the middle of the Antlers Formation (Cifelli et al., 1997a).

Age—The occurrence is of Aptian-Albian age (Jacobs et al., 1991).

Diagnosis—Cervical centra extremely elongate; centrum length more than five times posterior centrum height. Differs from all other sauropods in possessing well-defined centroparapophyseal laminae that extend to the posterior ends of the centra, diapophyses located approximately one third of centrum length behind anterior condyles, deeply excavated neural spines which are perforate in anterior cervicals, and hypertrophied central pneumatic fossae that extend posteriorly to the cotyles. Neural spines occupy anterior nine-tenths of centra and are not bifurcate. Cervical ribs are slender and elongated, with long, robust anterior processes that extend nearly to anterior condyles; total length of each cervical rib equals or exceeds 3 centrum-lengths.

DESCRIPTION

OMNH 53062 consists of an articulated series of four mid-cervical vertebrae from a large sauropod, found with their cervical ribs intact and in an excellent state of preservation, despite some lateral compression (Fig. 1). We interpret the vertebrae as being C5–C8, on the basis of a mid-cervical transition point shared with *Brachiosaurus* (see below). The vertebrae are notable for their great length; the longest, C8, has a centrum length of 1,250 mm and an overall length of 1,400 mm. This is approximately twice as long as C8 in *Mamenchisaurus hochuanensis* (Young and Zhao, 1972) and almost a third larger than the same vertebra in the HM SII specimen of *Brachiosaurus brancai* (Janensch, 1950). The cervical ribs are remarkably long as well. The cervical rib of each vertebra extends posteriorly beneath the two succeeding vertebrae. The longest measureable rib originates on C6 and finally tapers out at a point even with the posterior end of the centrum of C8, a total length of 3,420 mm. The cervical ribs of successive vertebrae lie above those of the preceding vertebrae, so that at any point in the series the cervical ribs form a vertically stacked bundle three ribs thick.

The proportions of the individual vertebrae are also noteworthy. The ratio of centrum length to posterior centrum height ranges from 5.1 in C7 to 6.7 in C6. The diapophyses are placed approximately one third of the way back along the centrum. However, the anterior projections of the cervical ribs are also quite elongate, so that the anterior end of each cervical rib lies very close to the condyle of the corresponding centrum.

The vertebrae are of extremely light construction, with the outer layer of bone ranging in thickness from less than 1 mm (literally paper-thin) to approximately 3 mm. The neural spines are excavated laterally by deep, bowl-shaped depressions that are perforate in cervicals 5 and 6. These excavations are bordered by thick struts of bone which connect the zygapophyses with the neural spines and diapophyses. The pneumatic fossae are so extensively developed that no sharply delineated ''pleurocoel'' can be defined. Instead, a broad, shallow excavation extends over almost the entire length of the centrum. This fossa is deepest just posterior to the diapophyses, at which point it is subdivided into a complex network of accessory laminae and small, sharp-lipped foramina. Thin centroparapophyseal laminae extend from the parapophysis to the posterior end of each vertebra, and probably served to stiffen the extensively excavated centrum in a manner structurally analogous to an I-beam.

The neural spines occupy the anterior nine-tenths of each centrum and are not bifurcate. The two anterior vertebrae, C5 and C6, possess long, low neural spines. The most posterior vertebra, C8, has a higher, roughly triangular neural spine that is quite different from those of C5 and C6. In C7 most of the neural spine was lost prior to collection, but the remainder is informative in two ways. First, the broken edge of C7's neural spine approximates the outline of the lateral excavation observed in the other vertebrae, extending ventrally well beyond the break point in the posterior margin of the neural spine, suggesting that apart from the anterior and posterior bony struts the neural spines were structurally very weak. Second, the portion of the posterior neural spine which remains slopes up sharply, suggesting that C7 was similar to C8 in possessing a high, triangular neural spine. This would produce an abrupt transition in neural spine height between C6 and C7, with the height of the neural spines being less than or equal to centrum diameter in anterior vertebrae, and greatly exceeding centrum diameter in posterior vertebrae.

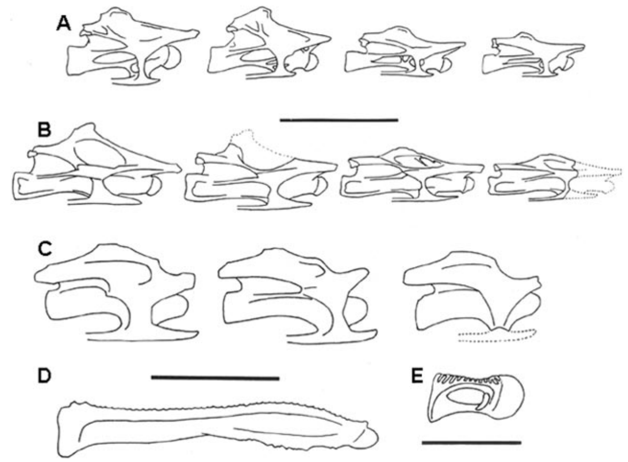

FIGURE 2. Titanosauridae and Brachiosauridae; comparative series illustrating cervical vertebrae in right lateral view. **A**, *Brachiosaurus brancai* C5–C8 (HM SI and SII, Janensch, 1950). **B**, *Sauroposeidon proteles* C5–C8 (OMNH 53062). **C**, unnamed titanosaurid C4, C7, and C8 (DGM serie a, Powell, 1987). **D**, Unnamed taxon (YPM 5294, Ostrom, 1970). **E**, *Pleurocoelus nanus* (USNM 5678, Marsh, 1888). Scale bars equal 1 m, **A**, **B**; 20 cm, **C**, **D**; 10 cm, **E**.

SYSTEMATICS AND AFFINITIES

Status of *Sauroposeidon* With Respect to Other Early Cretaceous North American Sauropods

Our understanding of sauropod evolution and extinction in the Early Cretaceous of North America is hampered primarily by the paucity of diagnostic material. Vertebrae are generally the most diagnostic elements in the sauropod skeleton (McIntosh, 1990), but almost all of the sauropod vertebrae that have described from the Early Cretaceous of North America belong to very immature animals and are phylogenetically uninformative. The prevalence of *Astrodon*-like teeth in Early Cretaceous deposits indicates that sauropods were widely distributed, but with only 2 or 3 tooth morphotypes recognized from all of Sauropoda (Upchurch, 1998; Wilson and Sereno, 1998), isolated teeth convey little information about sauropod diversity and abundance. In addition, much of the sauropod material that has been reported has yet to be prepared and described (Kirkland et al., 1998).

Much of the sauropod material that has been described from the Early Cretaceous of North America has been referred to the genus *Pleurocoelus*. The type of *Pleurocoelus* consists of four disarticulated vertebrae from a very young animal. The type vertebrae are at too early an ontogenetic stage to have undergone neurocentral fusion, and the neural spine and cervical rib complex is unknown in *Pleurocoelus* (Fig. 2E). The centra are distinctive only in the large size of their pleurocoels. Referred elements from the type locality are fragmentary and unremarkable, and have done little to improve our understanding of this practically indeterminate genus.

Interestingly, a juvenile sauropod cervical from the Cloverly Formation, YPM 5294, has at least two features in common with *Sauroposeidon* and may represent a young animal from the same taxon, or a closely allied taxon (Fig. 2D). The vertebra, which has not undergone fusion, has a centrum length of 470 mm and an uncrushed centrum height of 90 mm (Ostrom, 1970). The length-to-diameter ratio of 5.2 closely approximates the proportions of *Sauroposeidon.* In addition, YPM 5294 possesses long, thin centroparapophyseal laminae similar to those observed in *Sauroposeidon.* These laminae extend posteriorly from the parapophyses about halfway to the posterior end of the centrum. Because of the rather poor preservation of YPM 5294, it is not possible to determine whether these laminae extend all the way to the posterior end of the centrum, as do those of *Sauroposeidon*. *Pleurocoelus* lacks centroparapophyseal laminae. YPM 5294 demonstrates that the distinctive vertebral proportions seen in *Sauroposeidon* can be achieved at a relatively early age, and that the development of centroparapophyseal laminae in some long-necked taxa predates fusion of the neural elements and may be an ontogenetically stable feature. Given the gross proportional differences between the *Pleurocoelus* type material and *Sauroposeidon,* and the example of YPM 5294 as a much better model for a juvenile long-necked sauropod, the Oklahoma sauropod can be confidently excluded from the genus *Pleurocoelus.* The customary assignment of any sauropod remains from the Aptian–Albian of North America to the genus *Pleurocoelus* should be reexamined in light of the discovery of *Sauroposeidon.*

Affinities of *Sauroposeidon* in Higher-Level Sauropod Phylogeny

Although affinities within Sauropoda are debated, the most recent cladistic analyses (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998) have produced consistent results for the placement of major groups (Fig. 3), although Upchurch (1995, 1998) also presents alternative and partly conflicting hypotheses. The great length and complex pneumatic architecture of the vertebrae of *Sauroposeidon* clearly separate it from basal neosauropods such as *Haplocanthosaurus*, *Camarasaurus*, and the Diplodocidae. While derived diplodocids such as *Diplodocus* did achieve complex vertebral internal structure independently (see below), the very high, bifid neural spines and deep, robust centra of such taxa contrast with the morphology exhib-

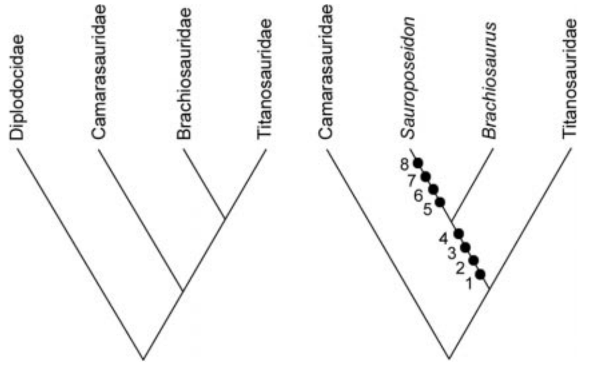

FIGURE 3. Hypothesized relationships among selected Sauropoda and the phylogenetic position of *Sauroposeidon.* Suprageneric phylogeny represents a concensus view of recent analyses (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998). Synapomorphies of *Sauroposeidon* and *Brachiosaurus* (right cladogram), all based on cervical series: **1**, centrum length more than four times diameter; **2**, cervical ribs exceed 2 centra in length; **3**, camellate internal structure (see text); **4**, mid-cervical transition point (see Fig. 1). Autapomorphies of *Sauroposeidon*: **5**, centroparapophyseal laminae greatly expanded; **6**, diapophyses posteriorly placed on centra; **7**, pneumatic fossae extend posteriorly to cotyles; **8**, deep or perforate pneumatic fossae in neural spines.

ited by *Sauroposeidon.* Titanosaurids, most diverse on southern continents but now reported from the Early Cretaceous of North America (Britt and Stadtman, 1997), show considerable diversity in neck morphology. The most elongate vertebrae that have been described from a titanosaurid belong to an unnamed taxon from Brazil, DGM ''Serie A'' (Powell, 1987:fig. 2). The vertebrae are otherwise dissimilar to *Sauroposeidon,* lacking the very elongate cervical ribs, expanded centroparapophyseal laminae, and hypertrophied pneumatic fossae that characterize the new taxon.

Sauroposeidon and *Brachiosaurus,* on the other hand, share a number of synapomorphies. Elongate cervical centra and long cervical ribs are independently derived in other sauropod lineages, but still serve to separate the advanced Brachiosauridae from the Titanosauridae. While some species of *Camarasaurus* had relatively long cervical ribs (Jensen, 1988), camarasaurid vertebral morphology is distinct from that of brachiosaurids. Likewise, the derived camellate pattern of internal pneumatic structure appears to be a synapomorphy of the Brachiosauridae (see below). Finally, the marked transition in neural spine height and morphology between C6–C7 in *Sauroposeidon* is also present in *Brachiosaurus* (Janensch 1950:figs. 26 and 29). This transition point provided the basis for our interpretation of OMNH 53062 as representing C5–C8. The trends observed in *Brachiosaurus* towards elongation and penumatization of the cervical series are taken to an extreme in *Sauroposeidon,* 30–40 Ma younger. The cervical vertebrae of *Sauroposeidon* are the longest among the Sauropoda and, based on comparison to the HM SII specimen of *Brachiosaurus,* we estimate its neck to have been at least 12 m in length—the longest of any known vertebrate.

FUNCTIONAL MORPHOLOGY

Vertebral Pneumatic Architecture

While vertebral internal structure is not yet known for many sauropods, it has the potential for yielding characters of systematic value. Britt (1993, 1997) reviews pneumatic vertebral morphology in dinosaurs and other archosaurs and provides terminology for vertebral internal structure. More primitive sau-

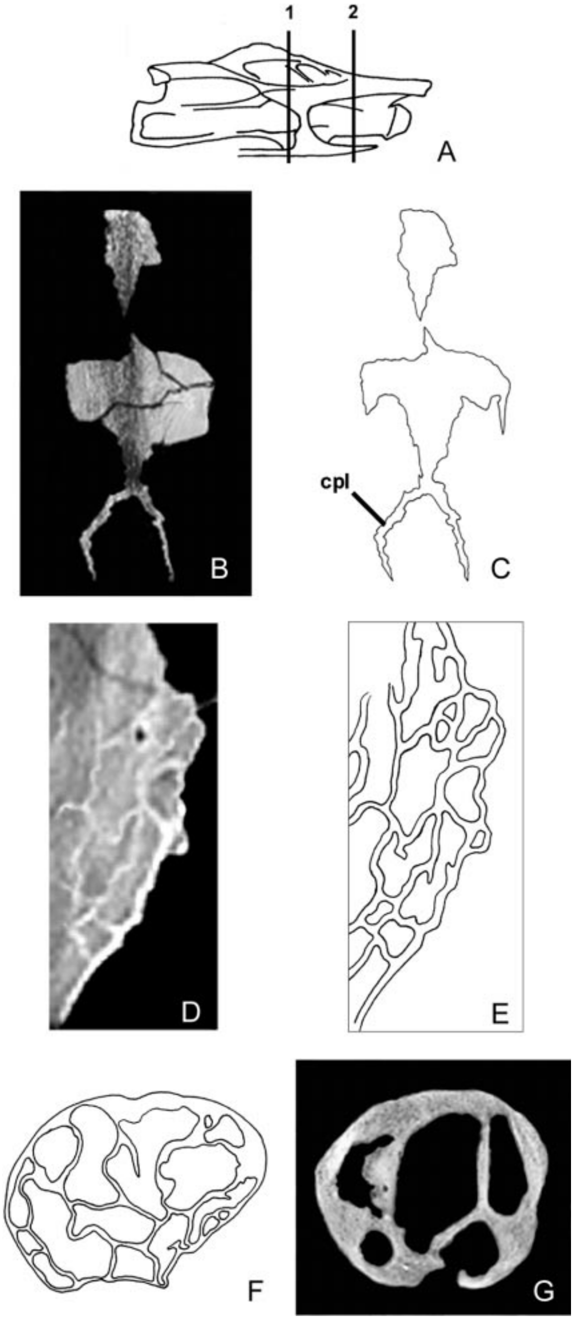

FIGURE 4. Vertebral ultrastructure. **A–E**, *Sauroposeidon proteles* (OMNH 53062), cervical vertebra 6. **A**, outline drawing showing location of CT sections. **B**, **C**, cross-section (**A**, position 1) showing extreme reduction of centrum and ventrolateral expansion of centroparapophyseal laminae (**B**, unretouched CT image; C, outline with some of the rock matrix removed). Central portion of B is affected by an x-ray beam-hardening artifact due to the large diameter of the specimen. **D**, **E**, CT and outline drawing from anterior centrum (**A**, position 2), showing finely subdivided structure of internal bone. This camellate pattern is similar to that of *Brachiosaurus* (**F**, section through condyle, after Janensch, 1950) and differs from the primitive camerate pattern seen in taxa such as *Camarasaurus* (**G**, section through condyle, OMNH 01313). Abbreviation: cpl, centroparapophyseal lamina.

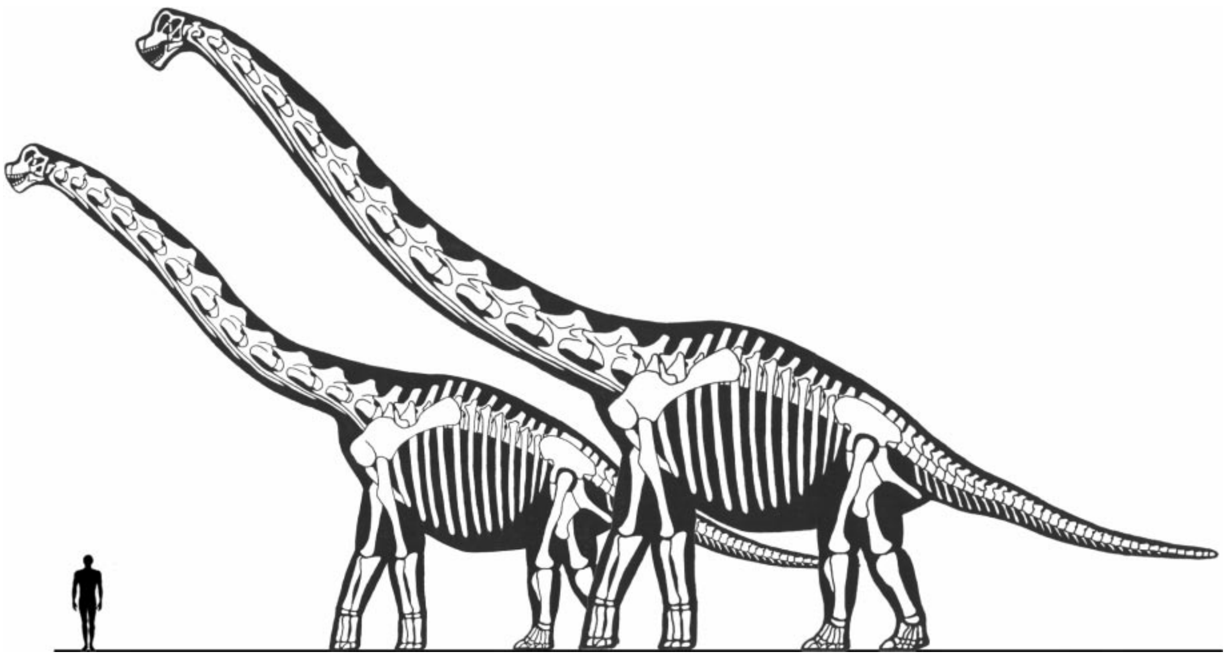

FIGURE 5. Comparison of *Sauroposeidon* and *Brachiosaurus.* The reconstruction of *Sauroposeidon proteles* (right) is hypothetical, based on the skeleton of *Brachiosaurus. Brachiosaurus brancai* (left) is scaled after the HM SII specimen mounted in Berlin. Both taxa are reconstructed with the transition point between C6–C7 producing a gentle s-curve in the posture of the neck. The human figure is 1.8 m tall.

ropods, e.g., *Camarasaurus,* have a camerate internal structure, wherein thick bony struts subdivide a small number of large pneumatic cavities. *Sauroposeidon* is similar to *Brachiosaurus* in the presence of a camellate internal structure, wherein the bone is characterized by numerous irregular, extremely thin septa dividing small pneumatic camellae. Externally, the cross-sectional area of the cervical centra and neural spines is greatly reduced by large pneumatic fossae, so that the centrum is reduced from a cylindrical structure to a series of thin laminae attached to a narrow median septum (Fig. 4).

The presence of pneumatic camellae has previously been regarded as a synapomorphy of (*Euhelopus* + Titanosauria) (Wilson and Sereno, 1998) or of Titanosauria alone (Powell, 1987). However, some basal titanosaurs had a simple, camerate structure (MW, unpubl. data), while the derived pneumatic camellae have been recognized in the cervical series of *Brachiosaurus* (see Britt, 1993; Upchurch, 1998) and in the posterior cervicals of *Diplodocus* (see Britt, 1993). This suggests that camellate internal structure is homoplasic in sauropods and evolved in long-necked lineages as a means of reducing weight.

Biomechanics

Elongation of the neck poses biomechanical problems because of the conflicting demands of strength and lightness. All sauropods are characterized by some specializations to meet these demands; *Sauroposeidon* is notable for lightening the cervical series to an extreme degree while apparently achieving the necessary degree of structural integrity. The intersection of vertical septa of bone, such as the median septum of the centrum, with bony laminae extending laterally to support the diapophyses and ventrolaterally to support the parapophyses (centroparapophyseal laminae) gives the vertebra a longitudinal structure similar to that of an I-beam (Fig. 4C), and allows for great mechanical strength with little cross-sectional area.

The mid-cervical transition point shared by *Sauroposeidon* and *Brachiosaurus* (Fig. 2) is of biomechanical as well as taxonomic significance. The high neural spines of the posterior cervicals would have increased the leverage of the dorsal muscle groups that supported the neck, while the more slender morphology of the anterior cervicals served to increase the flexibility of the head and distal neck. The transition point marks the change from a more upright (extension) posture in the base of the neck to a more horizontal (flexion) posture in the distal third of the neck, and would probably have given the neck a shallow S-curve in neutral pose (Fig. 5). This hypothesis could potentially be tested using a computer model such as that described by Stevens and Parrish (1999).

CONCLUSIONS

Sauroposeidon proteles represents a new genus and species of large sauropod. Autapomorphies characterizing the new taxon include expanded centroparapophyseal laminae, posteriorly positioned diapophyses, and hypertrophied pnuematic fossae in the centra and neural spines. *Sauroposeidon* is proportionally and morphologically distinct from *Pleurocoelus,* and is best interpreted as a very derived brachiosaurid. Synapomorphies linking it to *Brachiosaurus* include elongate centra and cervical ribs, a mid-cervical transition point, and camellate internal structure. Camellate internal structure evolved independently at least three times in sauropod evolution and appears to have been a weight-saving adaptation related to neck elongation.

ACKNOWLEDGMENTS

The authors would like to thank B. G. Eaton for use of CT facilities; Michael Brett-Surman, Brooks Britt, Jim Diffily, Janet Gillette, Wann Langston, Jr., Ken Stadtman, and Dale Winkler for access to specimens in their care; Dan Brinkman, Brooks Britt, Dan Chure, Brian Curtice, Wann Langston, Jr., Jack McIntosh, John Ostrom, Tom Rich, and Kent Stevens for providing literature and photographs; and Elizabeth Gomani and Ray Wilhite for access to unpublished data. We thank Wann Langston, Jr., David D. Gillette, and John S. McIntosh for helpful review comments. Funding was provided by the University of

Oklahoma's Undergraduate Research Opportunities Program and by NSF and NGS grants to RLC.

LITERATURE CITED

Bakker, R. T. 1986. The Dinosaur Heresies. Kensington Publishing Co., New York, 481 pp.

Britt, B. B. 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. Ph.D. dissertation, University of Calgary, Calgary, pp.??.

——— 1997. Postcranial pneumaticity; pp. 590–593 *in* P. J. Currie and K. Padian (eds.), Encyclopedia of Dinosaurs. Academic Press, New York.

———, and K. L. Stadtman. 1997. Dalton Wells Quarry; pp. 165–166 *in* P. J. Currie and K. Padian (eds.), Encyclopedia of Dinosaurs. Academic Press, New York.

Cifelli, R. L., J. D. Gardner, R. L. Nydam, and D. L. Brinkman. 1997a. Additions to the vertebrae fauna of the Antlers Formation (Lower Cretaceous), southeastern Oklahoma. Oklahoma Geology Notes, Oklahoma Geological Survey 57:124–131.

———, J. I. Kirkland, A. Weil, A. L. Deino, and B. J. Kowallis. 1997b. High-precision $^{40}Ar/^{39}Ar$ geochronology and the advent of North America's Late Cretaceous terrestrial fauna. Proceedings of the National Academy of Sciences USA 94:11163–11167.

Jacobs, L. L., D. A. Winkler, and P. A. Murray. 1991. On the age and correlation of the Trinity mammals, Early Cretaceous of Texas, USA. Newsletters on Stratigraphy 24:35–43.

Janensch, W. 1947. Pneumatizitat bei Wirbeln von Sauropoden und anderen Saurischien. Palaeontographica, supplement 7:1–25.

——— 1950. Die Wirbelsaule von *Brachiosaurus brancai.* Palaeontographica 3:27–93.

Kirkland, J. I., B. Britt., D. L. Burge, K.C. Carpenter, R. L. Cifelli, F. DeCourten, S Hasiotis, and T. Lawton. 1998. Lower to middle Cretaceous dinosaur faunas of the central Colorado Plateau: a key to understanding 35 million years of tectonics, sedimentology, evolution, and biogeography. Brigham Young University Geology Studies 42:69–103.

Langston, W., Jr. 1974. Nonmammalian Comanchean tetrapods. Geoscience and Man 8:77–102.

Marsh, O. C. 1888. Notice of a new genus of Sauropoda and other new dinosaurs from the Potomac Formation. American Journal of Science 35:89–94.

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

Ostrom, J. H. 1970. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Montana and Wyoming. Peabody Museum of Natural History Bulletin 35: 1–234.

Powell, J. E. 1987. Morphologia del esqueleto axial de los dinosaurios titanosauridos (Saurischia, Sauropoda) del Estado de Minas gerais, Brasil. Anais do Congreso Brasiliero del Paleontologia 10:155–171.

Romer, A. S. 1933. Vertebrate Paleontology. University of Chicago Press, Chicago, 491 pp.

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

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

Seeley, H. G. 1870. On *Ornithopsis,* a gigantic animal of the pterodactyle kind from the Wealden. Annals of the Magazine of Natural History, series 4 5:279–283.

Stevens, K. A., and J. M. Parrish. 1999. Neck posture and feeding habits of two Jurassic sauropod dinosaurs. Science 284:798–800.

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

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

Wilson, J. A., and P. C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Journal of Vertebrate Paleontology 18, memoir 5:1–68.

Wiman, C. 1929. Die Kriede-Dinosaurier aus Shantung. Palaeontologica Sinica 6:1–67.

Young, C. C., and Zhao X.-J. 1972. *Mamenchisaurus hochuanesis* sp. nov. Institute of Vertebrate Paleontology and Paleoanthropology Monographs, A, 8:1–30.

Received 29 May 1999; accepted 29 October 1999.