A New Sauropod Dinosaur From the Early Cretaceous of Oklahoma

by

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ABSTRACT

An apparently new brachiosaurid sauropod, represented by an articulated series of four mid-cervical vertebrae, has been recovered from the Antlers Formation (Aptian-Albian), 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, the new taxon 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. In addition, the new taxon shares with *Brachiosaurus* a transition point midway through the cervical series, at which the neural spine morphology changes from very low (anteriorly) to very high (posteriorly). The Cretaceous taxon is unique, however, in the posterior placement of the diapophyses, lateral excavation of the neural spines, and the extraordinary degree of vertebral elongation (e.g., C8=1.25 m; 25% longer than *Brachiosaurus*). Additional sauropod material from the Early Cretaceous Cloverly and Trinity formations may be referable to the new Oklahoma taxon, which appears to be the last of the giant North American sauropods and represents the culmination of brachiosaurid trends toward lengthening and lightening of the neck.
INTRODUCTION

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 (Figure 1), most of the material is fragmentary or disarticulated. Compounding these problems, a surprising amount of the recovered material belongs to juvenile individuals, for which corresponding adult material is rare or nonexistent.

The Arundel Formation (Hauterivian-Barremian) of Maryland yielded the type material of *Astrodon* (see Leidy, 1865) and *Pleurocoelus* (see Marsh, 1888). *Astrodon* is based on isolated teeth, while *Pleurocoelus* is based on disarticulated, largely juvenile skeletal elements. It is often assumed that the two genera represent the same animal (Lull, 1911; Langston, 1974), but this assumption cannot be proven on the basis of available evidence, and the two have not been formally synonymized.

The Antlers Formation (late Aptian-middle Albian) of Oklahoma and Texas has produced little sauropod material to date: an indeterminate coracoid (Larkin, 1910), isolated teeth comparable to *Astrodon* (Citelli et al., 1997), and the series of cervical vertebrae which is the subject of this study.

The Trinity Group (Aptian-Albian) of Texas includes the Twin Mountains, Glen Rose, and Paluxy formations. The relationship of these formations to the more northerly Antlers Formation is shown in Figure 2. Although no complete sauropod skeletons have been recovered from Trinity deposits, a large number of isolated bones and teeth suggest that sauropods were abundant in this region during the Early Cretaceous. All of the Texas material has been referred to *Astrodon/Pleurocoelus* (Langston, 1974; Gallup, 1989). Excavation of a new sauropod bonebed promises much valuable information (Winkler et al., 1997), but most of the material remains to be prepared and studied.
The Cloverly Formation (Aptian-Albian) of Montana and Wyoming has produced various postcranial elements that may be referable to the sauropod family Titanosauridae, isolated teeth similar to *Astrodon*, and an anomalous juvenile cervical centrum, YPM 5294, which will be discussed in detail below (Ostrom, 1970).

The Cedar Mountain Formation (Albian) of Utah has yielded the greatest variety of sauropod remains among North American Early Cretaceous deposits. Juvenile elements referred to *Pleurocoelus* were found near adult sauropod remains at the Long Walk Quarry (DeCourten, 1991), and the Dalton Wells locality is notable for having two distinct taxa, a camarasaaurid and a titanosaurid (Britt and Stadtman, 1996, 1997; Britt et al., 1997). The uppermost part of the unit, dated at approximately 98.5 Ma, has produced teeth similar to *Astrodon* from an apparently dwarfed sauropod (R. Cifelli, pers. comm.). This taxon represents the last sauropod in North America prior to reintroduction (via presumed immigration from South America) during the Maastrichtian (Lucas and Hunt, 1989).

The Turney Ranch Formation (Albian-Cenomanian) of Arizona has produced remains of a medium-sized sauropod which was provisionally assigned to the Brachiosauridae (McCord and Tegowski, 1996) following initial classification as a hadrosaur (Thayer and Ratkevich, 1995). The vertebral column is as yet unknown, making any classification tentative. The age of the Turney Ranch Formation is not well established, with upper and lower bounds of 110 and 76 Ma (McCord and Tegowski, 1996).

In May and August, 1994, crews from the Oklahoma Museum of Natural History recovered a series of four articulated sauropod cervical vertebrae from a OMNH locality V821, in the Antlers Formation of Atoka County, Oklahoma (Figure 3). Over the past three years, the OMNH staff and volunteers have been preparing the specimen, OMNH 53062. While preparation of the series is not yet complete, it is sufficiently advanced to permit description of the specimen and comparison to known sauropod taxa.
VERTEBRAL TERMINOLOGY

The vertebral terminology used herein follows Janensch (1929). This usage is at the suggestion of J.S. McIntosh, and stems from the morphological similarity of OMNH 53062 to *Brachiosaurus*, a genus that was extensively studied by Janensch.

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 all advocated the interpretation of these cavities as containing or leading to pneumatic air 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 discussing neural spine morphology, the term "simple" will be used to describe neural spines that are not divided. Brachiosaurids, cetiosaurids, and titanosaurids have simple neural spines, while camarasaurs, diplodocids, and euheleopods have bifid neural spines (McIntosh, 1990; Upchurch, 1995).

A stylized cervical vertebra illustrating the terminology used in this discussion is shown in Figure 4.

MATERIALS AND METHODS

Whenever possible, the author measured specimens himself, and these specimens are listed under "personal observations" in Table 1. All measurements were made with a metric tape measure. All other specimens were researched in the available literature. In a few cases, no published measurements were available for a given specimen, in which case the dimensions were taken from scaled figures.

Institutional abbreviations used in this text are as follows.

AMNH American Museum of Natural History, New York City, New York.
BYU Brigham Young University, Earth Sciences Museum, Provo, Utah.
CMNH Cleveland Museum of Natural History, Cleveland, Ohio.
Institutional abbreviations (continued).

DAM  Department of Antiquities, Malawi.
DGM  Museo de la Divisao Geologia y Mineralogia, Rio de Janeiro, Brazil.
FWMSH  Fort Worth Museum of Science and History, Fort Worth, Texas.
HM  Humbolt Museum, Berlin, Germany.
ISIR  Indian Statistical Institute, Calcutta, India.
OMNH  Oklahoma Museum of Natural History, Norman, Oklahoma.
USNM  National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

Order SAURISCHIA Seeley, 1888

Suborder SAUROPODAMORPHA Huene, 1932

Infraorder SAUROPODA Marsh, 1878

Family BRACHIOSAURIDAE Riggs, 1904

Gen. et sp. nov. [name to be added in formal publication]

Holotype--OMNH 53062, an articulated series of cervical vertebrae, interpreted as C5 through C8, with intact cervical ribs.

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

Age--Early Cretaceous (late Aptian-early Albian).

Diagnosis--Cervical centra extremely elongate; centrum length more than five times greater than 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, and deeply excavated neural spines which are perforate in anterior cervicals.
Differs from all other sauropods except *Supersaurus vivianae* in possessing pneumatic
fossae that extend into the posterior centra. Neural spines occupy anterior nine-tenths of
dorsal centra and are not bifurcate. Cervical ribs are slender and elongated; with long,
robust anterior processes that extending 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 (Figure 5). At first glance, the vertebrae appear to have been crushed,
especially in the regions of the neural spines and posterior centra. This appearance of
crushing is best explained by the extreme degree of excavation of both the neural spines
and centra. The ends of the centra are circular in cross section and the lateral relief
exhibited by the diapophyses and zygapophyses does not suggest crushing. At some
points the left and right cervical ribs lie very close together, and this may be the result of
distortion or breakage of the thin parapophyses, as all other bony structures appear to be
in place and not significantly distorted. The vertebrae are thought to be 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 1250 mm and an overall length of 1400 mm (see Table 1 for vertebral
dimensions). The cervical ribs are remarkably long as well. The cervical rib of each
vertebra extends posteriorly beneath the two succeeding vertebrae. The longest
measureable cervical rib originates on C6 and finally tapers out at a point even with the
posterior centrum of C8, a total length of 3420 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 (Tables 1 and 2). 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 terminus of each cervical rib is very close to the anterior 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 laterally excavated by deep, bowl-shaped depressions that are perforate in at least the first two vertebrae in the series. 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 diapophysis, at which point it is subdivided into a complex network of accessory laminae and small, sharp-lipped foramina. It is quite probable that the entire cervical series was extensively pneumatized. 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 high, 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 mechanically 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 very high neural spine. There appears to be an abrupt transition in neural spine height between C6 and C7, with the anterior vertebrae having very low neural spines and posterior vertebrae having very high neural spines.

**COMPARISONS**

**Brachiosauridae**--Although traditional classifications (Romer, 1965; McIntosh, 1990) placed a number of poorly understood taxa in this family, the only well-represented brachiosaurid genus is *Brachiosaurus* itself, and Salgado et al. (1997) challenged the inclusion of any genera other than *Brachiosaurus* in the Brachiosauridae. The cervical series of *Brachiosaurus brancai* is extensively illustrated and described by Janensch (1950). In addition, at least two cervical vertebrae referable to *Brachiosaurus* sp. have been recovered from Dry Mesa Quarry in Colorado (Curtice and Wilhite, 1996).

*Brachiosaurus* cervical vertebrae are quite long, both proportionally and absolutely (Table 2, Figure 6A). The neural spines are simple and are set forward on the centra. The cervical ribs are quite long, extending beyond the posterior centra, but their absolute length is not known for certain (Janensch, 1950). The neural spines of anterior cervical vertebrae (anterior to and including C6) are low and rounded, while those of posterior cervical vertebrae (posterior to and including C7) are high and triangular. This abrupt change in neural spine morphology marks a transition point in the neck, and provided the basis for assigning cervical numbers to the OMNH 53062 vertebrae.

**Camarasauridae**--A family of advanced sauropods that may contain only one genus, *Camarasaurus*. Other genera that have traditionally been referred to the Camarasauridae include *Euhelopus*, which may be a euhelopodid (but see Wilson and Sereno, in press), and *Opisthocoelicaudia*, an anomalous Late Cretaceous form now
almost universally regarded as a titanosaurid (Salgado et al., 1997; Upchurch, 1995, 1997; Wilson and Sereno, in press). *Camarasaurus* itself closely resembles *Haplocanthosaurus* in overall cervical morphology (Figure 7L), with the following differences: better-developed pneumatic fossae, cervical ribs extending well beyond the posterior centrum (character state unknown in *Haplocanthosaurus*), and bifid neural spines (Osborn and Mook, 1921). The bifurcation of the neural spine takes the form of a narrow, V-shaped cleft, as opposed to the broad, U-shaped trough seen in diplodocids (McIntosh, 1990).

**Cetiosauridae**--The Cetiosauridae is a group of generalized primitive sauropods. The cetiosaurids are geographically widespread, largely of Jurassic age, and poorly represented. Cervical vertebrae have been figured for three genera, *Cetiosaurus*, *Haplocanthosaurus*, and *Patagosaurus* (McIntosh, 1990; Hatcher, 1903; Bonaparte, 1979). McIntosh (1990) characterized cetiosaurid cervicals as being moderately elongate, with simple neural spines and shallow pneumatic fossae (Figures 7D-7E). It is not known whether the cervical ribs extended posterior to the vertebrae of origin (McIntosh and Williams, 1988). On the basis of phylogenetic analyses, it is now thought that the cetiosaurids represent a grade of advancement rather than a monophyletic clade (Upchurch 1995, 1997; Wilson and Sereno, in press).

**Diplodocidae**--The Diplodocidae is a large, well-defined group of advanced sauropods. While the group appears to have achieved its greatest diversity and abundance in the Late Jurassic of North America (Gillette, 1996), diplodocids are also known from the Late Jurassic of Africa (Janensch, 1929) and the Early Cretaceous of Europe (Charig, 1980) and South America (Salgado and Bonaparte, 1991). Cervical vertebrae are known for six taxa: *Amargasaurus*, *Apatosaurus*, *Barosaurus*, *Dicraeosaur*us, *Diplodocus*, and *Supersaurus* (Figures 7F-7K). Most diplodocid cervicals are moderately elongate, with well-developed, complexly subdivided pneumatic fossae, strongly bifurcated neural spines that occupy the entire dorsal surface of each centrum, and short cervical ribs that do not extend beyond the posterior centra (McIntosh, 1990). The dicraeosaurines,
Dicraeosaurus and Amargasaurus, are peculiar in having relatively short cervical centra and extremely tall neural spines (McIntosh et al., 1997).

The single available Supersaurus cervical is the longest known vertebra for any chordate, with a centrum length of 1400 mm (Jensen, 1987). The Supersaurus cervical is atypical for diplodocids in possessing shallow, anteroposteriorly expanded pneumatic fossae that contrast strongly with the deep, sharp-lipped fossae seen in other diplodocids (B. Curtice, pers. comm.). This feature will be discussed in more detail below.

Euhelopodidae--The Euhelopodidae is a group of Chinese sauropods including the genera Shunosaurus, Omeisaurus, Datousaurus, Euhelopus, and Mamenchisaurus. Traditional classifications (e.g., McIntosh, 1990) divided these genera among other derived sauropod groups, placing, for example, Euhelopus in the Camarasauridae and Mamenchisaurus in the Diplodocidae. These assignments were based on the presence of advanced characters such as bifid cervical neural spines (?Shunosaurus, Euhelopus, Mamenchisaurus) and forked caudal chevrons (Shunosaurus, Omeisaurus, Datousaurus, Mamenchisaurus). Recent phylogenetic analyses suggest that the Chinese sauropods form a monophyletic assemblage (Upchurch, 1995, 1997), although it should be noted that Wilson and Sereno (in press) exclude Euhelopus, keeping it in its traditional place in the Camarasauridae.

Although Omeisaurus, Euhelopus, and Mamenchisaurus have very long necks, up to 10 meters in Mamenchisaurus hochuanensis (Young and Chao, 1972), the individual vertebrae do not exceed the degree of elongation seen in other long-necked sauropods such as Brachiosaurus and Barosaurus (7A-7C). Rather, elongation of the neck is achieved by increasing the number of cervical vertebrae from the primitive number of 12 to 17 in Omeisaurus and Euhelopus and 19 in Mamenchisaurus. Omeisaurus, Euhelopus, and Mamenchisaurus also have long cervical ribs, which extend under successive centra in an overlapping array similar to that seen in OMNH 53062 (Young, 1939; Wiman, 1929; Young and Chao, 1972).
**Titanosauridae**—A temporally and geographically widespread group, notable for being the only group of sauropods to flourish throughout the Cretaceous. Diagnostic characters for titanosaurids are generally located in the caudal series and appendicular skeleton (McIntosh, 1990), and few titanosaurid cervical series have been recovered. Those which are known exhibit an extraordinary range of morphologies (Figures 7M-7O, 8A-8D). Cervical vertebrae of four taxa have been described and figured: *Saltasaurus loricatus* (Bonaparte and Powell, 1980) and DGM "Serie A" (Powell, 1986, 1987) from South America, *Titanosaurus colberti* from India (Jain et al., 1997), and *Malawisaurus dixeyi* from Africa (Jacobs et al., 1993). *Saltasaurus* differs from all other known sauropods in having the pre- and postzygapophyses that lie posterior to the anterior and posterior ends of the centra, respectively. DGM "Serie A", an unnamed titanosaurid from Brazil, has its pre- and postzygapophyses roughly even with the ends of the centra, but is unusual in having anterior projections of the cervical ribs that extend anteriorly to a point even with the centrum condyle. *Titanosaurus colberti* is unusual in possessing the shortest cervical vertebrae, proportionally, of any sauropod, with the lengths of the posterior centra being only slightly larger than their diameters.

*Malawisaurus dixeyi* presents a problematic case. The single cervical vertebra figured by Jacobs et al. (1993), DAM 89-78, bears some resemblance to the twelfth cervical vertebra of DGM "Serie A" (see Figures 8A and 8C), but is described as lacking any pneumatic fossae in the centrum. The presence of pneumatic fossae in the cervical and dorsal vertebrae is a synapomorphy of the Sauropoda (Upchurch, 1995, 1997; Wilson and Sereno, in press [pneumatic fossae referred to as pleurocoels in these works]), and a complete lack of pneumatic fossae has not been recorded in any known sauropod. The author recently had an opportunity to study the *Malawisaurus* material in the SMU collections. The figured vertebra was not in evidence, and in the complete series of *Malawisaurus* cervical vertebrae, all possessed well-developed pneumatic fossae and none closely resembled DAM 89-78. B. Curtice (pers. comm.) suggests that the *Malawisaurus*
quarry is not a monospecific bonebed and that DAM 89-78 represents a second, non-sauropod dinosaur taxon.

In addition, the author studied the cervical vertebrae referred to the Dalton Wells titanosaur (Britt and Stadtman, 1996, 1997; Britt et al., 1997). The vertebrae have moderately elongate centra and simple neural spines, closely resembling those of *Haplocanthosaurus* except for the better-developed pneumatic fossae in the former (Figure 70).

The affinities of DGM "Serie A" and *Malawisaurus* will be discussed in greater detail below.

OMNH 53062 is characterized by extremely elongate cervical centra, extensively developed pneumatic fossae, very long cervical ribs, simple neural spines set forward on centra, and a mid-cervical transition point in neural spine height. The simple neural spines of OMNH 53062 exclude it from the Camarasauridae, Diplodocidae, or Euhelopodidae, all of which have bifid neural spines. Cetiosaurids possess simple neural spines and centra that are moderately elongated, although no known cetiosaurid approaches OMNH 53062 in degree of centrum elongation. More importantly, the pneumatic fossae of cetiosaurids are shallow and are not subdivided by accessory laminae. These simple pneumatic fossae represent the primitive condition for the Sauropoda, and contrast strongly with the extensively developed, complexly subdivided pneumatic fossae of OMNH 53062.

Among the Titanosauridae, *Saltasaurus loricatus* and *Titanosaurus colberti* are quite different from OMNH 53062 in almost every respect. *Malawisaurus dixeyi* (excluding DAM 89-78) and DGM "Serie A" are much more similar to OMNH 53062. Both *Malawisaurus* and DGM "Serie A" have centrum proportions that approximate those of OMNH 53062, and both have simple neural spines. However, neither taxon possesses the long, slender cervical ribs, expanded pneumatic fossae, elongated centroparapophyseal laminae, or excavated neural spines characteristic of OMNH 53062. In addition, in both *Malawisaurus* and DGM "Serie A" the zygapophyses are roughly even.
with the ends of the centra. In OMNH 53062, the prezygapophyses overhang the anterior ends of the centra and the postzygapophyses are situated forward of the posterior ends of the centra.

The overall resemblance of OMNH 53062 to *Brachiosaurus* is striking. Specific characters shared by the two taxa include: simple neural spines, neural spines set forward on centra, cervical ribs extending well beyond posterior centra, and a mid-cervical transition point. OMNH 53062 and *Brachiosaurus* are the only known sauropods that have both simple neural spines and very long cervical ribs. Cetiosaurids and titanosaurids have simple neural spines, but relatively short cervical ribs. Camarasaurids and euhelopodids have long cervical ribs, but they also have divided neural spines. The transition point in cervical neural spine morphology is unique to OMNH 53062 and *Brachiosaurus*, and may be a synapomorphy of the Brachiosauridae.

Most of the characters which distinguish OMNH 53062 from *Brachiosaurus*, i.e. posteriorly placed diapophyses, expanded pneumatic fossae, elongated centroparapophyseal laminae, and excavated neural spines, can be interpreted as adaptations related to lengthening and lightening the neck, and do not suggest a close relationship between OMNH 53062 and any taxon other than *Brachiosaurus*. The posteriorly placed diapophyses, elongated centroparapophyseal laminae, and excavated neural spines are unique to OMNH 53062. The only other sauropod which possesses expanded pneumatic fossae similar to those of OMNH 53062 is *Supersaurus vivianae*. The cervical vertebra referred to *Supersaurus*, BYU 5003, is typically diplodocid, with a bifid neural spine that occupies the entire upper surface of the centrum. BYU 5003 and OMNH 53062 are the longest known sauropod cervical vertebrae, and the independent evolution of expanded pneumatic fossae in both taxa suggests that this character is a direct consequence of very large size.

OMNH 53062 does not possess any features that preclude placement in the Brachiosauridae, and it cannot be convincingly placed in any sauropod family other than
the Brachiosauridae. It has more points of similarity with *Brachiosaurus* than with any other sauropod, and is best interpreted as an advanced brachiosaurid.

**COMPARISON TO PLEUROCOELUS**

As mentioned in the introduction, the genus *Pleurocoelus* is based on juvenile remains. The type vertebrae are too young to have undergone neurocentral fusion, and the neural spine and cervical rib complex is unknown in *Pleurocoelus* (Figure 6D). 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.

Despite the inadequacies of the type material of *Pleurocoelus*, OMNH 53062 appears to differ substantially from that taxon, even considering ontogenetic differences. *Pleurocoelus* cervicals are uniformly short, with a maximum length-to-diameter ratio of only 2.4 in all of the Arundel material (Table 2). For a juvenile cervical of these proportions to develop into an elongate cervical comparable to OMNH 53062, the length would have to increase by more than 100% relative to the centrum diameter. While it is not inconceivable that such elongation could occur in the process of development, comparisons to taxa whose ontogenetic development can be estimated suggests that it was not common among the Sauropoda.

Currently, adult and juvenile cervical vertebrae are available for two genera, *Apatosaurus* and *Camarasaurus*. Measurements and proportions of cervical vertebrae of two species from each genus, as well as juvenile cervicals referred to each genus, are given in Table 2. The juvenile *Apatosaurus* vertebrae, OMNH 1246 and 1251, have length-to-diameter ratios of 2.0. Vertebrae from adult specimens of *A. excelsus* and *A. louisae* show an average length-to-diameter ratio of 2.4, with a maximum of 3.7 among the vertebrae considered in this study, for C4 of CM 3018. This vertebra is the only one from either specimen with a length-to-diameter of greater than 2.9. It is unlikely that both of the known juvenile *Apatosaurus* cervical vertebrae represent anomalously long vertebrae.
like C4 of CM 3018. If OMNH 1246 and 1251 are typical of juvenile *Apatosaurus* cervical vertebrae, they suggest that in the course of development *Apatosaurus* vertebrae may have lengthened by 20% to 50% relative to centrum diameter.

The juvenile *Camarasaurus* vertebrae have an average length-to-diameter ratio of 1.8 and a maximum of 2.3. There is a species of *Camarasaurus*, *C. lewisi*, which exhibits length-to-diameter ratios of up to 5.1 in its cervical vertebrae. If the OMNH juvenile *Camarasaurus* belongs to *C. lewisi*, then *Camarasaurus* cervicals may have lengthened by more than 100% during ontogeny. However, *Camarasaurus lewisi* is represented by a single partial skeleton. It is much more likely that the OMNH juvenile *Camarasaurus* belongs to *C. lentus* or *C. supremus*. These species are represented by numerous specimens (McIntosh et al., 1996), and have cervical vertebrae that are proportionally much shorter than those of *C. lewisi*. In AMNH 5761, referred to *C. supremus*, the average length-to-diameter ratio of the cervical vertebrae is 2.4, with a maximum of 3.5. These ratios represent an increase in length relative to diameter of 30% to 50% over the juvenile *Camarasaurus*.

Interestingly, a juvenile sauropod cervical from the Cloverly Formation, YPM 5294, has at least two features in common with OMNH 53062 and may represent a young animal from the same taxon, or a closely allied taxon (Figure 6C). 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 OMNH 53062. In addition, YPM 5294 possesses long, thin centroparapophyseal laminae similar to those observed in OMNH 53062. 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 extended all the way to the posterior end of the centrum, as do those of OMNH 53062. *Pleurocoelus* lacks centroparapophyseal laminae of any sort. YPM 5294 demonstrates that the distinctive vertebral proportions seen in OMNH
53062 can be achieved at a relatively early age, and that the presence of
centroparapophyseal laminae predates fusion of the neural elements and may be an
ontogenetically stable feature.

Given the gross proportional differences between the *Pleurocoelus* type material
and OMNH 53062, 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*.

An uncatalogued, undescribed cervical vertebra from the Jones Ranch Quarry,
Trinity Group of Texas, has been prepared and placed on display in the Fort Worth
Museum of Science and History. The vertebra, which will be referred to here as FWMSH
"A," possesses several features of interest and merits a short discussion. FWMSH "A" is
similar to OMNH 53062 in possessing an undivided neural spine and a long centrum with
large pneumatic fossae (Figure 8B). These features, coupled with the length of the
vertebra, led the author to the initial conclusion that FWMSH "A" belonged to the same
taxon OMNH 53062. However, a careful morphological comparison, together with an
examination of titanosaurid material from Brazil and Malawi, suggests that this is not the
case. The cervical rib of FWMSH "A" extends to the end of the centrum. While it is not
uncommon for partial or entire cervical ribs to become detached and lost, the degree of
tapering observed in FWMSH "A" suggests that, when intact, the cervical rib would have
been little if any longer. The diapophyses of FWMSH "A" are set well forward on the
centrum, contra the condition observed in OMNH 53062. The pneumatic fossae are large
and well-defined, but lack the extreme expansion seen in OMNH 53062, and there is no
evidence that the centroparapophyseal lamina extended any significant distance posterior
to the parapophyses. Finally, the neural spine lacks the lateral excavations characteristic
of OMNH 53062, and is very different in lateral outline from either the anterior or
posterior neural spines of OMNH 53062.
As with OMNH 53062, the centrum proportions of FWMSH "A" preclude its referral to *Pleurocoelus*. FWMSH "A" does bear a strong resemblance to DGM "Serie A" and to C3 from *Malawisaurus*. In all three taxa the cervical ribs are rather short, between 1 and 1.5 centrum-lengths overall. If this feature is genuine, and not due to breakage or poor preservation, it may be a synapomorphy linking the three taxa. FWMSH "A" is also similar to DGM "Serie A" and *Malawisaurus* in having a high, rounded neural spine. In "Serie A" this distinctive neural spine shape persists throughout the series. In *Malawisaurus* only C3 has this sort of spine. The neural spines of succeeding vertebrae are progressively shorter (anteroposteriorly), taller, and more transversely expanded. If FWMSH "A" is the third cervical from an animal similar to *Malawisaurus* then it represents a prodigious animal indeed, far larger than OMNH 53062 or even *Supersaurus*. It is more likely that FWMSH "A" is a mid-cervical from a moderate- to large-sized titanosaur similar to DGM "Serie A."

**CONCLUSIONS**

OMNH 53062 is clearly distinct from previously described sauropod taxa, and possesses several unique characters. These are: deeply excavated neural spines, centroparapophyseal laminae which continue posteriorly to the end of the centra, and diapophyses which are situated more posteriorly than those of other sauropods. At the same time, OMNH 53062 shares several characters with *Brachiosaurus*, including simple neural spines set forward from the posterior ends of the centra, long cervical ribs, and an abrupt transition in neural spine height and morphology in the middle of the cervical series.

OMNH 53062 represents a large sauropod which is quite specialized with regard to neck elongation. Individual vertebrae are between 24% and 34% longer than the corresponding vertebrae from the Humbolt Museum's SII *Brachiosaurus*, indicating a total neck length of at least 11 meters (36 feet). The mechanical problems posed by such a long neck are considerable. The thin bony construction, excavation of the neural spines,
and expansion of the pneumatic fossae and supporting laminae would serve to reduce weight without sacrificing mechanical strength.

The Oklahoma sauropod was evidently related to *Brachiosaurus*, but lived approximately 30 million years later. *Brachiosaurus* itself was advanced in the lengthening and lightening of the neck, and OMNH 53062 represents the culmination of those trends.

ACKNOWLEDGMENTS

I would like to thank Michael Brett-Surman, Brooks Britt, Jim Diffily, Janet Gillette, Ken Stadtman, and Dale Winkler for access to specimens in their care. Many thanks also to Dan Brinkman, Brooks Britt, Dan Chure, Wann Langston, Jr., Chris McGowan, and Tom Rich for providing literature and photographs, and to Elizabeth Gomani and Dewey Ray Wilhite for access to unpublished data. I especially thank Brian Curtice, Jack McIntosh, and Kent Stevens for providing much valuable information and advice. This project was undertaken at the suggestion of Richard Cifelli and has proceeded under his expert supervision, and I owe him a tremendous debt of gratitude. Thanks also to the OMNH field crew, staff, and volunteers for the excavation and preparation of OMNH 53062, and to Richard Cifelli, Nicholas Czaplewski, and Randy Nydam for reviewing this ms. Funding was provided by the University of Oklahoma's Undergraduate Research Opportunities Program and by an NSF grant to Richard Cifelli.
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491 pp.

687 pp.

*Amargasaurus cazau* gen. et sp. nov., de la Formacion La Amarga, Neocomiano 


TABLE CAPTIONS

Table 1. The dimensions of OMNH 53062. All measurements are given in mm.

Table 2. Comparison of centrum length to posterior centrum height in the Sauropoda.
Length (L) is the horizontal length of the centrum, and Height (H) is the vertical height of the posterior end of the centrum. The conventions followed in obtaining these measurements are shown in Figures 4B and 4C. "J" indicates a juvenile specimen or specimens in which neurocentral fusion has not occurred. All dimensions are given in mm.
Data were obtained from the following sources: Carpenter and McIntosh, 1994 (Apatosaurus sp., Camarasaurus sp.); Gilmore, 1936 (Apatosaurus louisae, Apatosaurus excelsus); Hatcher, 1901 (Diplodocus carnegii); Jacobs et al., 1993 (Malawisaurus dixeyi [DAM 89-78]); Jain et al., 1997 (Titanosaurus colberti); Janensch, 1950 (Brachiosaurus brancai); McIntosh et al., 1996 (Camarasaurus lewisi); McIntosh and Williams, 1988 (Haplocanthosaurus delfsi); Osborn and Mook, 1921 (Camarasaurus supremus); Ostrom, 1970 (YPM 5294); Powell, 1986 (DGM "Serie A"); Young, 1939 (Omeisaurus junghsienis); and personal observations (Brachiosaurus sp., FWMSH "A", Malawisaurus dixeyi [excluding DAM 89-78], OMNH 53062, Pleurocoelus nanus, and Supersaurus vivianaec).
FIGURE CAPTIONS

Figure 1. Sauropod distribution in the Early Cretaceous of North America.
A. Arundel Formation, Maryland.
B. Antlers Formation, Oklahoma and Texas.
C. Trinity Group, Texas.
D. Cloverly Formation, Montana and Wyoming.
E. Cedar Mountain Formation, Utah.
F. Turney Ranch Formation, Arizona.

Figure 2. Stratigraphic relationships of the Trinity Group and Antlers Formation.
Modified from Langston (1974).

Figure 3. OMNH locality V821 in Atoka County, Oklahoma. Modified from Cifelli et al. (1997).

Figure 4. The vertebral terminology and measuring conventions used in this text.
A. A stylized sauropod cervical vertebra illustrating vertebral terminology, shown in right lateral view.
B. Determination of centrum dimensions. $A =$ height of anterior centrum condyle,
   $P =$ height of posterior end of centrum.
C. Determination of posterior centrum height. $W =$ maximum width of posterior end of centrum.

Figure 5. OMNH 53062 in right lateral view.
A. The four vertebrae in articulation.
B. Detail of C6 showing laminae and cavities.
Figure 6. Comparing OMNH 53062 to other sauropods. All vertebrae are shown in right lateral view, and the cervical ribs have been truncated for clarity.

A. *Brachiosaurus*, from Humbolt Museum SI and SII.

B. OMNH 53062. The condyles have been restored.

C. YPM 5294, a juvenile sauropod from the Cloverly.

D. *Pleurocoelus namus* (holotype) cervical vertebra, a juvenile from the Arundel.

Figure 7. Cervical vertebrae of euhelopodids, diplodocids, a camarasaurid, and titanosaurids. Vertebrae are shown in left lateral view, and are not to scale.

A. *Euhelopus zdanskyi*, after Wiman, 1929.

B. *Omeisaurus junghsiensis*, after Young, 1939.

C. *Mamenchisaurus hochuanensis*, after Young and Chao, 1972.

D. *Cetiosaurus oxoniensis*, after McIntosh, 1990.

E. *Haplocanthosaurus priscus*, after McIntosh, 1990.

F. *Apatosaurus excelsus*, after Gilmore, 1936.

G. *Diplodocus carnegii*, after Hatcher, 1901.

H. *Barosaurus lentus*, after Lull, 1919.


K. *Dicraeosaurus hansemanni*, after Janensch, 1929.

L. *Camarasaurus lentus*, after Holland, 1924.

M. *Saltasaurus loricatus*, after Powell, 1986.


O. Dalton Wells titanosaur, from personal observations.
Figure 8. Various titanosaurid cervical vertebrae. All vertebrae are shown in right lateral view. Scale bar = 200 mm.

B. FWMSH "A", from personal observations.
D. *Malawisaurus dixeyi*, from personal observations.
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<td>1100*</td>
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<td>Total height, neurapophysis to ventral margin of centrum</td>
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<td>-</td>
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* In the process of collection, C7 was broken into two pieces at a point even with the diapophyses. There is a small amount of material missing at the break point, and even reconstructing the vertebra from photographs is difficult. Any horizontal measurements that cross this break may be off by up to 50 mm.

** The anterior processes of the cervical ribs are missing on C5, and these measurements are estimates based on the proportions of the other vertebrae.

*** At the current stage of preparation, the vertebrae are still articulated, and determining the maximum height of the posterior centra is very difficult. The numbers given here are minimum values that may be 10 to 20 mm less than the actual values. C8 is the last vertebrae in the series, which allows for more accurate measurement of the posterior centrum.
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* For *Apatosaurus louisae*, *Apatosaurus excelsus*, and *Diplodocus carnegii*, the measurements given in the Height (H) column are the maximum diameters of the posterior centra. The posterior ends of diplodocid cervical centra are very nearly circular, and these diameters may be taken as close approximations of Height (H).

** The specimen numbers of the *Malawisaurus dixeyi* vertebrae in the SMU collections are unavailable at this time. These vertebrae are the same ones discussed in the text and illustrated in Figure 7D.