Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*

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Sauroposeidon proteles is a large brachiosaurid sauropod recently described from the Antlers Formation (Aptian–Albian) of southeastern Oklahoma. *Sauroposeidon* represents the culmination of brachiosaurid trends toward lengthening and lightening the neck, and its cervical vertebrae are characterized by extensive pneumatic structures. The elaboration of vertebral air sacs during sauropod evolution produced a variety of internal structure types. We propose a new classification system for this array of vertebral characters, using computed tomography (CT) of pneumatic internal structures. Comparisons with birds suggest that the vertebrae of sauropods were pneumatized by a complex system of air sacs in the thorax and abdomen. The presence of a thoraco-abdominal air sac system in sauropods would dramatically affect current estimates of mass, food intake, and respiratory requirements. *Sauroposeidon* was one of the last sauropods in the Early Cretaceous of North America; sauropods disappeared from the continent by the early Cenomanian. The demise of sauropods in the Early Cretaceous of North America predates significant radiations of angiosperms, so the decline and extinction of this dinosaur group cannot be linked to changes in flora.

Key words: Dinosauria, Sauropoda, *Sauroposeidon*, pneumatic structures, Cretaceous, Oklahoma.

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Introduction

Sauropod dinosaurs include the largest terrestrial vertebrates, and they were one of the most wide-ranging and successful groups of dinosaurs. Sauropods achieved a worldwide distribution soon after their appearance in the Early Jurassic (Hunt *et al.* 1994). By the Late Jurassic, sauropods were both abundant and diverse, with diplodocids and brachiosaurids in particular dominating North American and African dinosaur faunas (McIntosh 1990). Sauropods are also well-represented in the Late Cretaceous, when titanosaurids were widely distributed in both hemispheres (Salgado *et al.* 1997).

Despite the abundance of sauropods during the Jurassic and Cretaceous, the systematics of the group is poorly understood. Although there is some consensus regarding general trends in higher-level sauropod phylogeny (Salgado *et al.* 1997; Wilson & Sereno 1998; Upchurch 1998), the systematic positions of many genera are unresolved (see Upchurch 1998, 1999). This is particularly true of sauropods from the Early Cretaceous of North America (Salgado *et al.* 1997; Gomani *et al.* 1999).

Whereas sauropods were widely distributed in the Early Cretaceous of North America, this distribution is sparse, and within each assemblage sauropod remains are relatively rare. Most occurrences consist of isolated or disarticulated elements, many representing juvenile individuals. Until recently, much of the sauropod material from the North American Early Cretaceous was customarily referred to *Pleurocoelus* (Langston 1974; Gallup 1989), a poorly represented taxon founded on juvenile remains. This practice has not improved our understanding of sauropod diversity during this time period.

In this context, any articulated and morphologically informative specimens are noteworthy. *Sauroposeidon proteles*, an unusually large and long-necked sauropod from the Antlers Formation of Oklahoma, was briefly described by Wedel *et al.* (2000). Our purpose here is to more fully describe and illustrate the type material of *Sauroposeidon*, to compare it with relevant taxa and place it in a systematic framework, and to discuss its paleobiology.

Materials and methods

Vertebral terminology. — Janensch (1929, 1950a) provided a comprehensive nomenclature for vertebral laminae and cavities. By using morphologically informative terms, Janensch avoided ambiguity; for example, using 'posterior centrodiapophyseal lamina' instead of the potentially confusing term 'horizontal lamina', which was commonly used in earlier works (Lull 1919; Osborn & Mook 1921). Wilson (1999) revised Janensch's nomenclature and provided a system of four-letter abbreviations to standardize discussion of these features. Herein we follow the terminology set forth by Janensch (1929, 1950a), as modified by Wilson (1999), with one caveat. Janensch (1929, 1950a) distinguished the structure joining the parapophysis to the centrum in the cervical series as the 'hinter Centroparapophysialleiste' or posterior centroparapophyseal lamina. Wilson (1999) did not consider this structure a true lamina, because it is only a minor extension of ventrolateral margin of the centrum in most taxa and does not maintain a connection to the parapophysis in the dorsal series. In *Sauroposeidon* this structure is pronounced, extending posteriorly to the cotyle. Rather than propose a novel term for this structure, we follow Janensch (1929, 1950a) in calling it a centroparapophyseal lamina. We follow Zweers *et al.* (1987) for terminology relating to specific muscle attachment sites. A stylized cervical vertebra illustrating the terminology used herein is shown in Fig. 1.

In the Eusauropoda, the centra of presacral vertebrae are laterally excavated by pleurocentral cavities or pleurocoels (Wilson & Sereno 1998). In the most basal eusauropods such as *Shunosaurus*, the pleurocoels form only slight depressions, but in all more derived taxa the pleurocentral cavities are well developed and are subdivided by at least one bony septum. Seeley (1870) was the first to recognize these features in sauropod vertebrae as osteological correlates of a pneumatic air-sac system. Seeley referred some large vertebrae from the Wealden to a pterodactyl on the basis of their pneumatic charac-

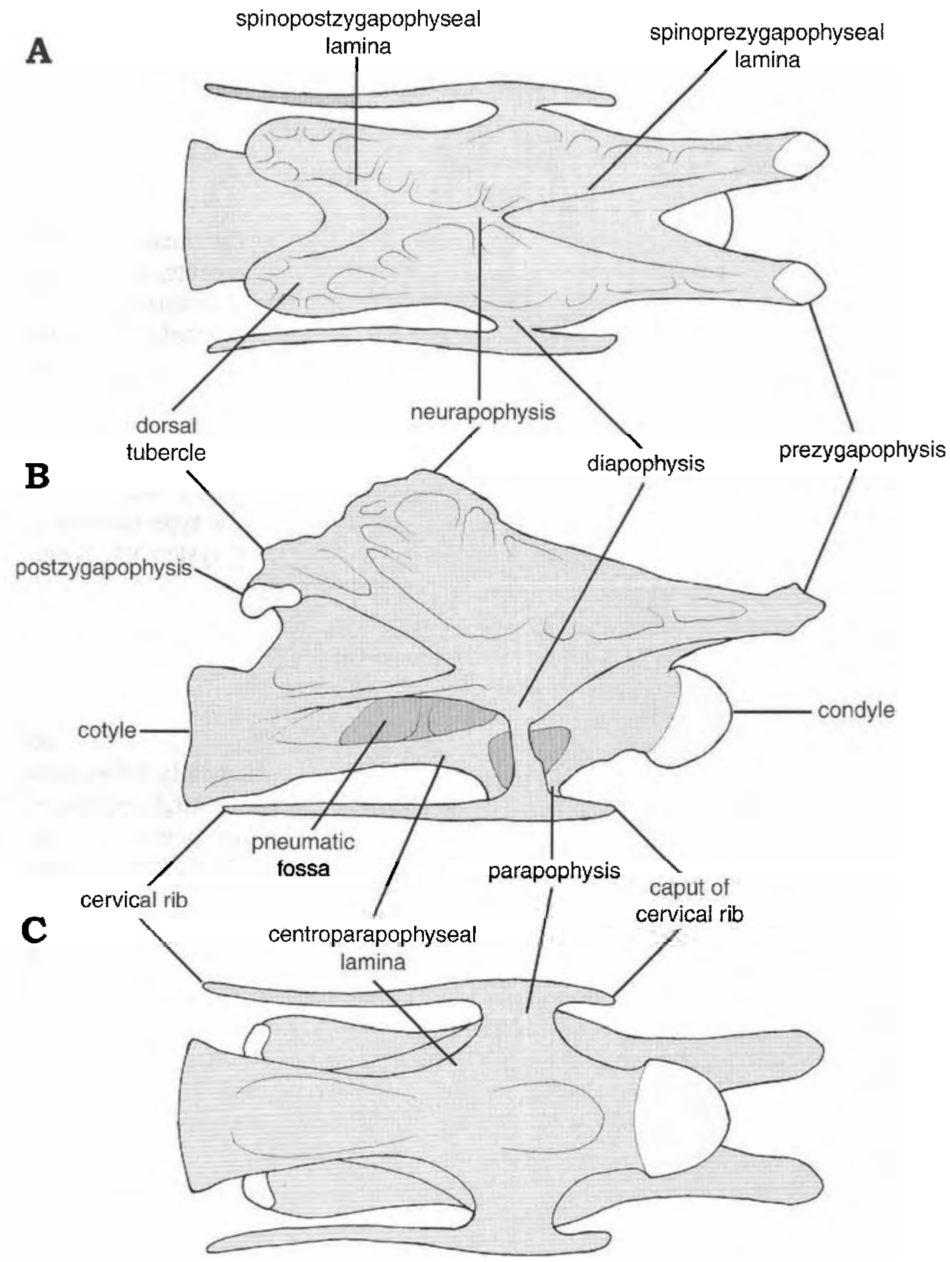


Fig. 1. Vertebral nomenclature. A stylized cervical vertebra of a sauropod in dorsal (**A**), lateral (**B**), and ventral (**C**) views, illustrating the terminology used herein. Anterior is to the right.

ters, although they were later shown to be those of a sauropod (Owen 1875). Cope (1877), Marsh (1877), Janensch (1947), Romer (1966), and Britt (1993, 1997) have all interpreted the lateral excavations and internal cavities of sauropod vertebrae as being pneumatic in nature. Britt (1993, 1997) provided the most comprehensive survey of

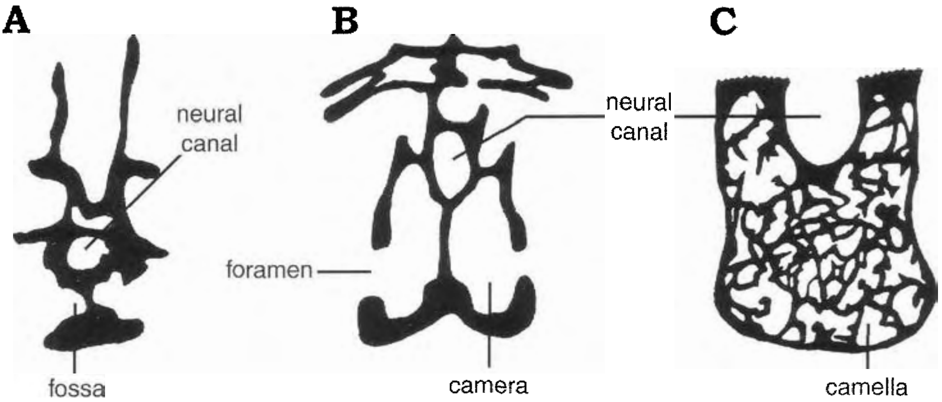


Fig. 2. Axial sections of sauropod vertebrae showing pneumatic features. **A.** *Haplocanthosaurus priscus* (CM 897-7). **B.** *Camarasaurus* sp. (OMNH 01313). **C.** *Saltasaurus loricatus* (PVL 4017-137, redrawn from Powell 1986).

postcranial pneumaticity in the Archosauria to date, and proposed precise terminology for discussing pneumatic vertebral features. Pneumatic cavities can be separated into three broad categories, as shown in Fig. 2. Fossae are bowl-like depressions that are not enclosed by ostial margins. Camerae are large pneumatic cavities separated by thick bony septa (internally) and laminae (externally). Camellae are small pneumatic cavities separated by thin bony trabeculae. Britt (1993, 1997) classified pneumatic vertebrae as simple or complex based on the presence of camerae or camellae, respectively. Britt (1993) also noted that the two types of pneumatic cavity are not mutually exclusive and can occur in the same vertebra. Computed tomography (CT) indicates that sauropod vertebrae can be classified into at least seven groups based on the nature and extent of internal pneumatic cavities (see discussion below). Wilson & Sereno (1998) proposed the clade Somphospondyli for sauropods whose vertebrae are composed of spongy bone. Vertebrae of this nature could be described by the adjective construction somphospondylous. Although this term appears to be equivalent to fully camellate internal structure, in which all internal spaces are camellate and no camerae are present, use of the term Somphospondyli may be useful to distinguish between vertebrae of this type and vertebrae in which camellae are present but less extensive.

When discussing vertebral proportions Upchurch (1998) used the term elongation index (EI), defined as the length of the centrum divided by the width of the cotyle. Although they did not suggest a term for the proportion, Wilson & Sereno (1998) used centrum length divided by the height of the cotyle as a character in their analysis. We prefer the latter defintion of this proportion, as the height of the cotyle is directly related to the range of motion of the intervertebral joint in the dorsoventral plane. For the purposes of the following discussion, we therefore redefine the EI of Upchurch (1998) as the anteroposterior length of the centrum divided by the midline height of the cotyle.

Data collection. — Whenever possible, we measured specimens using a metric tape measure, and these specimens are listed under 'personal observations' in table legends. The dimensions of all other specimens were obtained from the available literature. In a few cases when no published measurements were available for a given specimen, the dimensions were taken from scaled figures.

All radiographic techniques discussed herein were performed at the University Hospital on the University of Oklahoma Health Sciences Center campus in Oklahoma City. The CT protocol we followed was identical to that described by Wedel *et al.* (2000). Magnetic resonance imaging (MRI) scans of *Struthio* were performed on a 1.5 Tesla General Electric Signa magnet to produce spin-echo T1 weighted images.

Institutional abbreviations. — AMNH, American Museum of Natural History, New York City, New York, USA; BMNH, The Natural History Museum, London, UK; BYU, Brigham Young University, Earth Sciences Museum, Provo, Utah, USA; CCG, Chengdu College of Geology, China; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; DGM, Museo de la Divisão Geologia y Mineralogia, Rio de Janeiro, Brazil; FWMSH, Fort Worth Museum of Science and History, Fort Worth, Texas, USA; HM, Humbolt Museum, Berlin, Germany; ISIR, Indian Statistical Institute, Calcutta, India; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; PMU, Paleontological Museum, Uppsala, Sweden; PVL, Paleontología de Vertebrados de la Fundación Miguel Lillo, Argentina; SMU, Southern Methodist University, Schuler Museum of Paleontology, Dallas, Texas, USA; TMM, Texas Memorial Museum, Austin, Texas, USA; UMNH, Utah Museum of Natural History, Salt Lake City, Utah, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

The Early Cretaceous North American sauropod record

During the Late Jurassic, sauropods were the most numerous dinosaurs in North America (see Turner & Peterson 1999). At least 20 valid species in at least 4 families are present in the Morrison Formation (McIntosh 1990). In contrast to the diversity and abundance of sauropods during the Late Jurassic, the fossil record of sauropods from the Early Cretaceous of North America is relatively poor. Although sauropod remains have been recovered from Early Cretaceous deposits across the continent (Fig. 3), specimens are rare, and most of the material is fragmentary or disarticulated. Compounding these problems, a surprising amount of the recovered fossils belong to juvenile individuals, for which corresponding adult material is rare or nonexistent. Before 1990 only two sauropod genera were recognized from the North American Early Cretaceous (*Astrodon* and *Pleurocoelus*), and those two are probably synonymous (Gilmore 1921). However, since 1990 there have been many important finds and diagnostic material is finally coming to light, although much of the new material is not yet prepared or described (Kirkland *et al.* 1998).

Eastern North America. — The Arundel Clay (Aptian) of Maryland yielded the type material of the first sauropod to be described from North America. *Astrodon johnstoni* (see Leidy 1865) was described on the basis of a single tooth from the vicinity of Bladensburg, Prince George's County, Maryland. Marsh (1888) described *Pleurocoelus nanus* on the basis of disarticulated vertebrae from near Muirkirk in the same county. The vertebrae belong to a very young juvenile and are remarkable only for the size of their pneumatic fossae, although this may be an age-related character (see below). A supraoccipital, a dentary, several teeth, and various isolated postcranial bones from the same locality were also referred to *P. nanus*. Marsh (1888) also erected the species *P. altus* on the basis of larger but equally fragmentary postcranial remains from

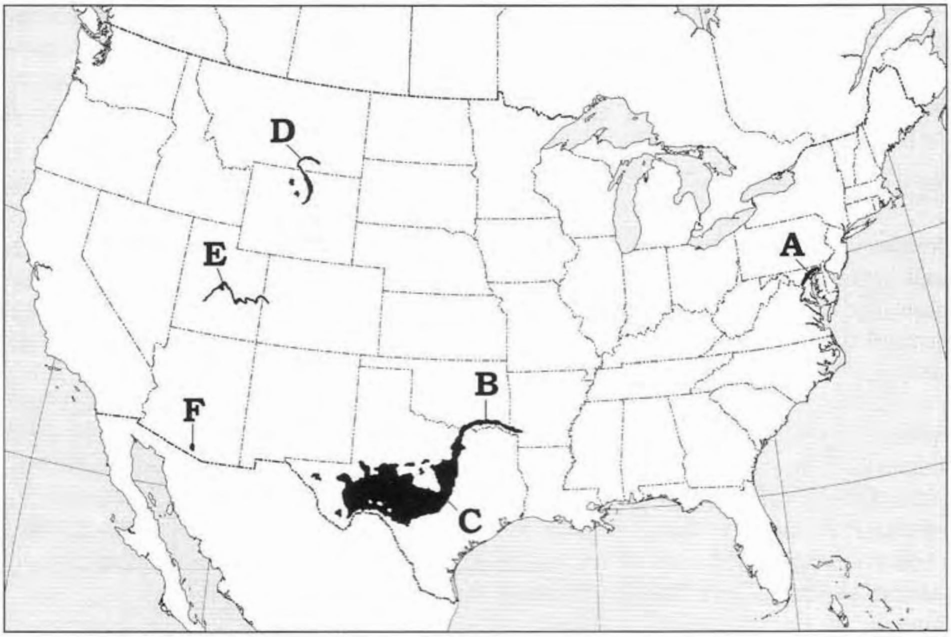


Fig. 3. Sauropod distribution in the Early Cretaceous of North America. Units which have yielded sauropod remains are shown in black. **A**. Arundel Clay, Maryland (Gallup 1988). **B**. Antlers Formation, Texas, Oklahoma, and Arkansas (Langston 1974; Hart & Davis 1981). **C**. Trinity Group, Texas (Langston 1974). **D**. Cloverly Formation, Montana and Wyoming (Ostrom 1970). **E**. Cedar Mountain Formation, Utah and Colorado (Kirkland *et al.* 1999). **F**. Turney Ranch Formation, Arizona (McCord & Tegowski 1996).

the same locality. It is widely accepted that *P. altus* and *P. nanus* represent two growth stages of the same species (e.g., Langston 1974). It is also likely that *Pleurocoelus* is a junior synonym of *Astrodon* (Lull 1911a).

Central North America. — The Antlers Formation (late Aptian–middle Albian) of Oklahoma and Texas has produced little sauropod material to date. An indeterminate coracoid was the first Early Cretaceous sauropod specimen to be described from west of the Mississippi (Larkin 1910). More recently, OMNH field crews working in Atoka County, Oklahoma, have discovered isolated teeth comparable to those of *Astrodon* (Cifelli, Gardner, *et al.* 1997) and the series of cervical vertebrae designated as the holotype of *Sauroposeidon proteles* (see Wedel *et al.* 2000).

The Trinity Group (Aptian–Albian) of Texas includes the Twin Mountains, Glen Rose, and Paluxy formations, and is laterally equivalent to the thinner, more northerly Antlers Formation. Although no complete sauropod skeletons have been recovered from Trinity deposits, a large number of isolated bones and teeth, together with numerous sauropod trackways, suggest that sauropods were moderately abundant in this region during the Early Cretaceous. Langston (1974) reviewed the Trinity sauropod material and referred isolated teeth to *Astrodon* and skeletal remains to *Pleurocoelus*. Langston based the latter referral on similarities in morphology of caudal vertebrae. The extensive sauropod trackways have received much attention; Farlow *et al.* (1989) provided a thorough review and description. Despite the prevalence of sauropod remains in the Trinity

Group, the lack of articulated skeletons makes comparisons between isolated finds uncertain at best. Gallup (1989) tied morphological characteristics of an isolated hindfoot to sauropod ichnite morphology, but a thorough understanding of the Trinity sauropods awaits the discovery and description of more complete remains. Excavation of a new sauropod bonebed at the Jones Ranch locality promises much valuable information (Winkler *et al.* 1997); preliminary comparisons suggest the presence of a basal titanosauriform more derived than *Brachiosaurus* (Gomani *et al.* 1999).

Western North America. — The Cloverly Formation (Aptian–Albian) of Montana and Wyoming has produced various postcranial elements that may be referrable to the sauropod family Titanosauridae, isolated teeth similar to *Astrodon*, and an anomalous juvenile cervical vertebra (Ostrom 1970). The juvenile cervical vertebra, YPM 5294, exhibits some similarites to *Sauroposeidon* and will be discussed in detail below.

The Cedar Mountain Formation (Barremian–?early Cenomanian) of Utah has yielded the greatest variety of sauropod remains among North American Early Cretaceous deposits. DeCourten (1991) described adult and juvenile remains from the Long Walk Quarry (of presumed Aptian–Albian age) and referred them to *Pleurocoelus* on the basis of juvenile vertebral morphology. The Dalton Wells locality (?Barremian–Aptian) is notable for having at least two distinct taxa, a camarasaurid and a titanosaurid, and for the prevalence of cranial material, which is generally rare for sauropod finds (Britt & Stadtman 1996, 1997; Britt *et al.* 1997, 1998). The uppermost part of the unit (Mussentuchit Member), dated at approximately 98.4 Ma, has produced teeth similar to *Astrodon* from an apparently dwarfed sauropod (Cifelli, Kirkland, *et al.* 1997), which may be the last sauropod in the mid-Cretaceous of North America. Most recently, Tidwell *et al.* (1999) described *Cedarosaurus weiskopfae* based on a partial skeleton from the Yellow Cat member (?Barremian–Aptian) of the Cedar Mountain Formation. Tidwell *et al.* (1999) referred *Cedarosaurus* to the Brachiosauridae.

The Turney Ranch Formation (of uncertain age, but believed to be Albian– Cenomanian) of Arizona has produced remains of a medium-sized sauropod that was provisionally assigned to the Brachiosauridae (McCord & Tegowski 1996) following initial classification as a hadrosaur (Thayer & Ratkevitch 1995). The animal has now been described as *Sonorasaurus thompsoni* and referred to the Brachiosauridae (Ratkevitch 1998). The age of the Turney Ranch Formation is not well established, with upper and lower bounds of 110 and 76 Ma (McCord & Tegowski 1996). Ratkevitch (1998) proposed a tentative age of 97.6 Ma for the unit.

Sauropod trace and body fossils are absent from the Western Interior of North America from the early Cenomanian through the late Campanian (Lucas & Hunt 1989; Sullivan and Lucas 2000). Lucas & Hunt (1989) considered this hiatus to be genuine and not an artifact of incomplete sampling. According to this view, North American sauropods died out by the early Cenomanian and were temporarily unreplaced by other large herbivores (Cifelli, Kirkland, *et al.* 1997). Dinosaur faunas of the later Cretaceous are dominated by low-browsing ornithischians (Coe *et al.* 1987). This dramatic change in herbivore faunas has in turn been linked to reciprocal changes in terrestrial flora, resulting from the rise and radiation of flowering plants (Bakker 1986). However, in North America angiosperms did not become significant elements of the terrestrial flora until the Cenomanian (Lupia *et al.* 1999). Despite our relatively poor knowledge of Early Cretaceous faunas, it is clear that the sauropod decline in North America predates the Albian, and that *Sauroposeidon* was one of the last of its kind on the conti-

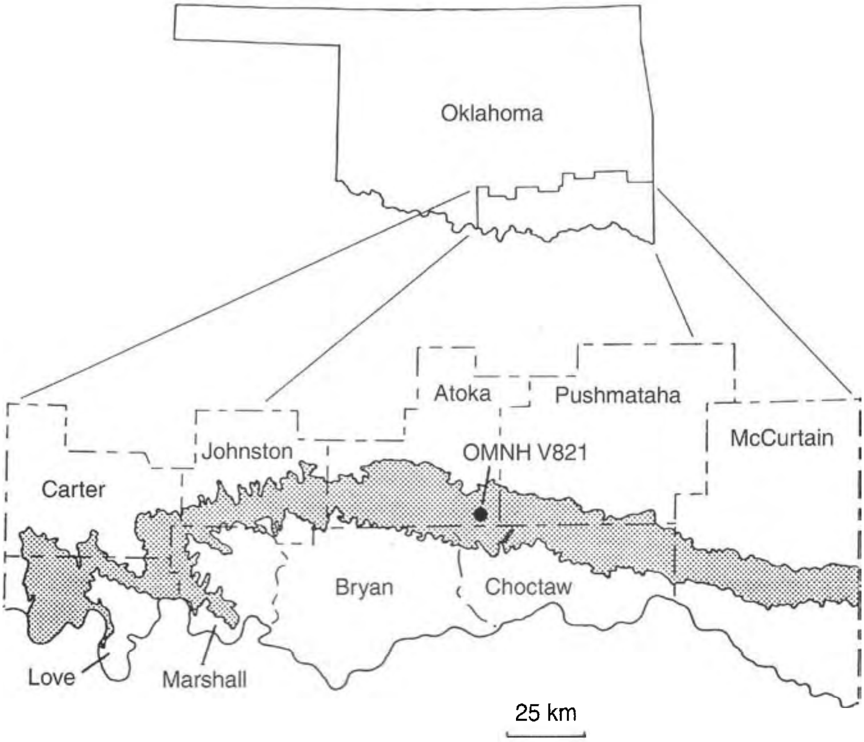


Fig. 4. Surface distribution of the Antlers Formation in Oklahoma and the location of OMNH Locality V821. Modified from Hart & Davis (1981).

nent. Hence, the spread and dominance of flowering plants, which took place later, is an unsatisfactory causal explanation for the extinction of sauropods in the Early Cretaceous of North America.

Geology and taphonomy

OMNH locality V821, about 20 km west of Antlers, Atoka County, lies in the Antlers Formation. The Antlers Formation, which extends across southeastern Oklahoma (Fig. 4) and adjacent parts of Texas and Arkansas, is a lateral equivalent to the Trinity Group of central Texas. Age constraints on the Trinity Group are relatively good, owing to contained marine invertebrates (see Winkler *et al.* 1990; Jacobs *et al.* 1991; Jacobs & Winkler 1998). Northeast of the pinchout of the Glen Rose Limestone, however, the sequence is almost exclusively terrestrial, and the Antlers Formation is conventionally regarded as of Aptian–Albian age (see summary by Brinkman *et al.* 1998). The Antlers Formation consists predominantly of well-sorted, fine, poorly consolidated sandstones, together with interbedded siltstones and claystones, deposited in a fluviodeltaic environment (Hobday *et al.* 1981). The unit is estimated to be about 150 m thick in the vicinity of OMNH locality V821 (Rennison 1996). The site is laterally equivalent to OMNH V706, and thus probably lies in the upper middle part of the Antlers Formation (Brinkman *et al.* 1998).

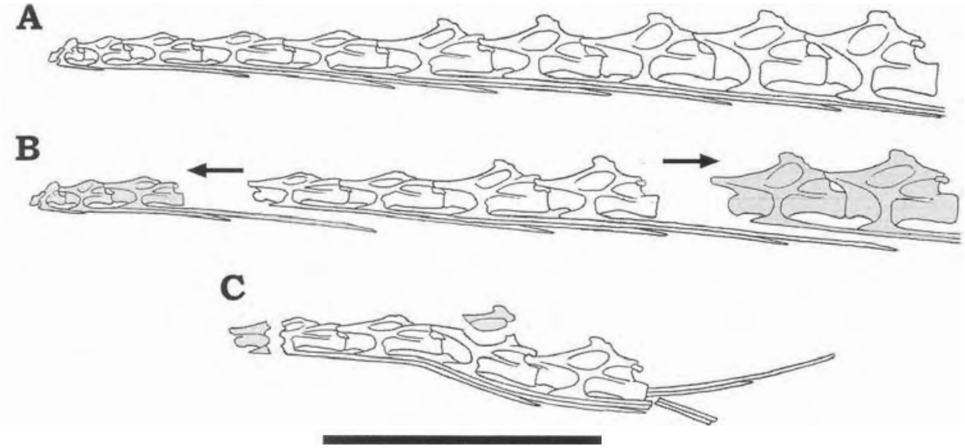


Fig. 5. Taphonomy of the type specimen of *Sauroposeidon proteles* (OMNH 53062). **A**. Anterior and middle cervical vertebrae in articulation. **B**. Disarticulation of C5–C8 by forces acting parallel to the long axis of the vertebrae. **C**. OMNH 53062 as it was found, with posterior cervical ribs partially displaced and material missing from C5 and C7. Missing material is shaded. Scale bar is 3 m.

Regionally, most vertebrate fossils of the Antlers Formation occur in the claystones (e.g., Cifelli, Gardner, *et al.* 1997; Brinkman *et al.* 1998). OMNH V821 is atypical in that the lithography of the fossil horizon is mainly sandstone, with small lenses and stringers of finer clastics (siltstone, claystone). In addition to the holotype specimen of *Sauroposeidon proteles*, OMNH locality V821 has also yielded a number of associated teeth of the theropod *Deinonychus antirrhopus*, associated postcranial and cranial remains of a small crocodylian, and a partly associated skeleton of the ornithopod *Tenontosaurus*. There was no close association of any of these specimens, which were recovered as much as 20 m from the sauropod remains. The partial scattering of the *Tenontosaurus* specimen (OMNH 34191) suggests some fluvial transport, but the preservation of delicate, light, flat skull bones indicates that the energy was moderate.

The type specimen of *Sauroposeidon proteles*, OMNH 53062, consists of four articulated mid-cervical vertebrae with cervical ribs preserved in place. The specimen was found lying on its right side (Fig. 5), angled toward the northwest. The cervical ribs attached to each vertebra extend posteriorly beneath the two succeeding vertebrae, forming a vertically stacked bundle three ribs thick. The cervical ribs of vertebrae anterior to the four recovered centra were not in place, while the cervical ribs of the two posterior vertebrae extend 2.1 meters beyond the end of the last centrum. The preservation of the cervical ribs in their natural positions, undistorted by postmortem contraction, suggests that the specimen was buried with the musculature in place. The loss of cervical ribs from centra anterior to the specimen, and the retention of the cervical ribs pertaining to the specimen, demonstrate that the neck was not likely broken transversely, but was pulled apart parallel to its long axis by unknown forces (Fig. 5).

Extensive excavation at the site has failed to uncover any more sauropod elements. The size of the animal and the delicate state of preservation of the recovered elements would seem to preclude significant fluvial transport of either the vertebrae or the rest of the animal. Work at the locality is ongoing, and it is possible that future discoveries will elucidate the taphonomy of this enigmatic specimen.

Systematic paleontology

Order Saurischia Seeley, 1888
Suborder Sauropodomorpha Huene, 1932
Infrorder Sauropoda Marsh, 1878
Family Brachiosauridae Riggs, 1904
Sauroposeidon proteles Wedel, Cifelli, & Sanders, 2000

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

Locality and horizon: OMNH locality V821, Antlers Formation (Lower Cretaceous: Aptian–Albian), Atoka County, Oklahoma, USA.

Revised diagnosis. — Cervical centra extremely elongate; EI of mid-cervicals greater than 5. 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. The internal structure is entirely composed of pneumatic camellae separated by bony septa ranging in thickness from less than 1 mm to approximately 3 mm. Total length of each cervical rib equals or exceeds three centrum-lengths.

Morphological description

The cervical vertebrae of *Sauroposeidon* are extremely elongate, exceeding the vertebrae of all other sauropods in length, both absolutely and relative to diameter (Fig. 6; Table 1). Because the vertebrae are still in articulation, the condyles are obscured and centrum length must be estimated from CT films. The longest vertebra, C8, has an exposed length of 1200 mm and a total centrum length of approximately 1250 mm. The prezygapophyses project anteriorly to the condyles, so the maximum length of each vertebra (from cotyle to prezygapophyses) is greater than the functional length of centrum (from cotyle to condyle). Measured from the cotyle to the right prezygapophyis, C8 is 1400 mm in length.

Pneumatic features. — The vertebrae of *Sauroposeidon* are extensively pneumatized (Fig. 7). The lateral faces of the centra and neural spines are occupied by large pneumatic fossae that penetrate to a narrow median septum. These fossae are larger, deeper, and more elaborate than those of basal sauropods. If *Sauroposeidon* was descended from a *Brachiosaurus*-like ancestor, then these fossae were probably derived by reducing the exterior walls of the lateral camerae to externalize the lateral air sacs. The absence of enveloping margins on the bounding laminae gives each pneumatic fossa a bowl-like profile. This morphology is especially pronounced in the neural spines, where each pneumatic fossa grows progressively deeper towards its center. In the two anterior vertebrae, C5 and C6, these fossae actually penetrate the median septum of the neural spine to produce a perforation. The edge of each perforation consists of a finished bone surface. This morphology, coupled with the similar placement of the perforation in both vertebrae, suggests that it is an actual morphological character and not an artifact of preparation.

Pneumatic fossae also occupy the lateral faces of the centra, extending from near the condyles to the very rim of the cotyles. Although the borders of these fossae are not sharply-lipped like the pneumatic foramina of other sauropod taxa, the boundaries are

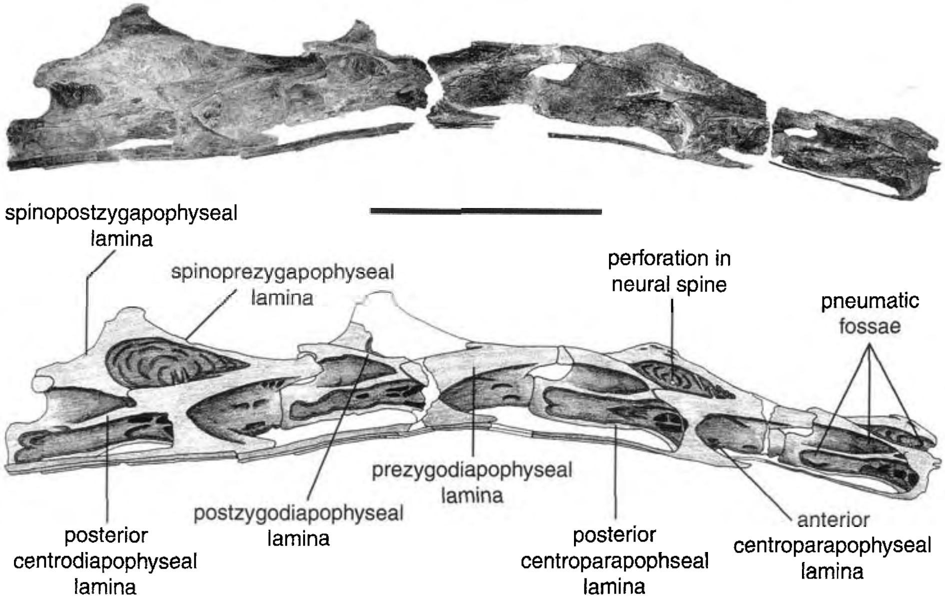


Fig. 6. *Sauroposeidon proteles* (OMNH 53062), articulated cervicals 5–8 in right lateral view. The interpretive drawing emphasizes the laminae and pneumatic fossae (redrawn from Wedel *et al.* 2000: fig. 1). Some cervical ribs segments were removed during excavation and preparation and are not shown in the photograph; these are restored in the drawing. Scale bar is 1 m.

Table 1. Measurements (in mm) of *Sauroposeidon proteles* (OMNH 53062).

	C5	C6	C7	C8
Centrum length[a]	–	1220	1230	1250
Total length[b]	–	1350	1370	1400
Cervical rib length	3400+	3420	3300[c]	3100[c]
Cotyle height	180	200	220	270
Total height[d]	430	510	–	695

[a] Condyles are somewhat obscured; length determined from CT scans.
[b] Measured from right prezygapophysis to cotyle.
[c] Estimated; preparation of the jacket containing these ribs is not yet complete.
[d] Measured from neurapophysis to ventral margin of the capitulum.

easily recongnizable on the basis of bone texture. When it comes in contact with pneumatic epithelium, the surface of a bone becomes remodeled to produce a distinctive woven texture (Britt 1993). By plotting the boundaries of this pneumatic bone, it is possible to determine the extent of the air sacs that occupied the lateral fossae (Fig. 7). The central pneumatic fossae are deepest just posterior to the diapophyses, at which point they are subdivided into a complex network of accessory laminae and small, sharply-lipped foramina. Other elaborations of the pneumatic fossae occur along major laminae and around the condyles; these accessory fossae and foramina are very similar to the 'Aussenkaverne' described by Janensch for *Brachiosaurus* (Fig. 8; com-

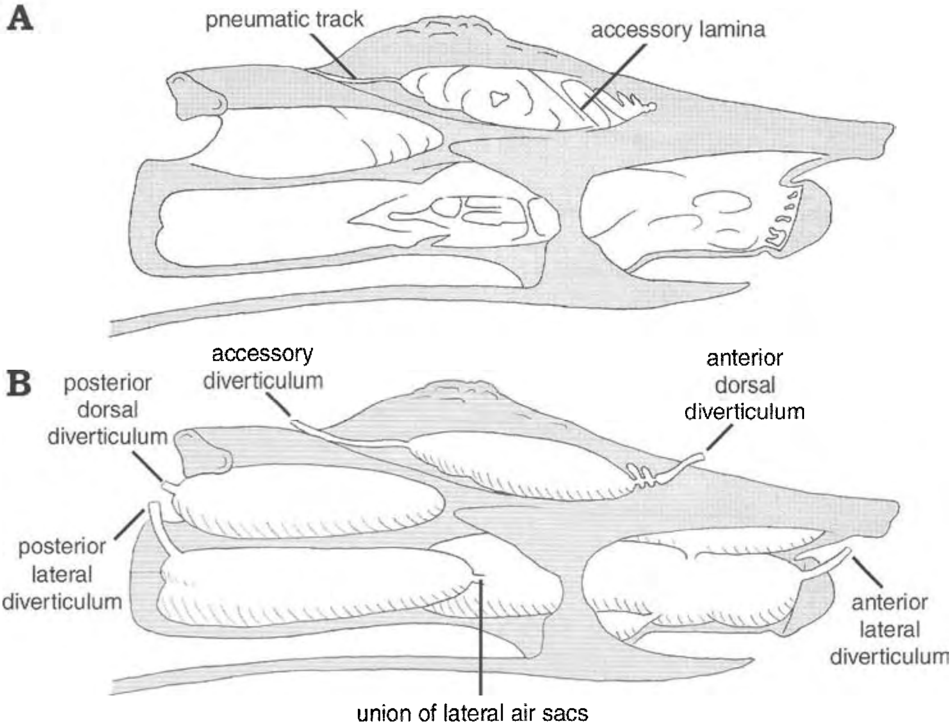


Fig. 7. Pneumatic bone and probable extent of air sacs in *Sauroposeidon*. **A**. C6 of *Sauroposeidon* in right lateral view. Pneumatic bone is unshaded. In addition to the pneumatic fossae, a small pneumatic track runs along the neural spine posterior to the pneumatic fossa. **B**. Hypothetical appearance of the air sac system, reconstructed after that of the ostrich (*Struthio camelus*). The four primary air sacs are pneumatized by diverticula which emerge from the neural canal at the transverse foramina. The continuous distribution of pneumatic bone on the lateral surface of the centrum indicates that the lateral air sacs united to form a continuous airway extending the length of the vertebra, as in modern birds (see Müller 1907).

pare Janensch 1950a: fig. 5). In addition to these external pneumatic characters, the vertebrae of *Sauroposeidon* are also extensively pneumatized internally. These internal pneumatic features are described in the next section.

The size and depth of the pneumatic fossae are so great that the centra appear to be caved in, perhaps as a result of crushing. However, the condyles and cotyles are roughly circular in cross section, and the delicate laminae exhibit considerable lateral relief (Fig. 9). While the vertebrae of *Sauroposeidon* are certainly narrow, they do not exceed the degree of lateral restriction exhibited by other long-necked taxa such as *Brachiosaurus* and *Euhelopus*. Although one of the centroparapophyseal laminae is apparently broken (Fig. 9), this structure is very delicate and could be expected to fail after the death of the individual. When the neck came to rest on its side, the weight of the cervical ribs would have loaded this lamina mediolaterally, placing maximum stress on its minimum dimension. Given the round profiles of the condyles and cotyles, the degree of lateral relief exhibited by the vertebral laminae, and the presence of narrow vertebrae in other long-necked taxa, we find no evidence of significant crushing in the type material of *Sauroposeidon proteles*.

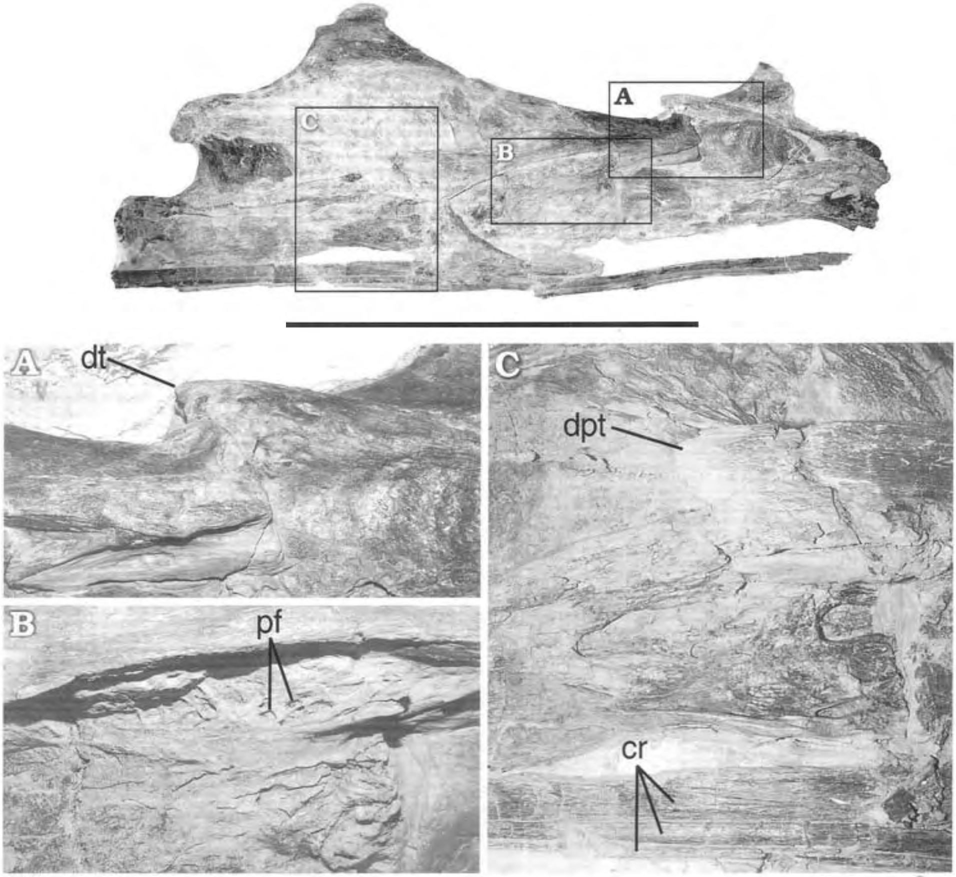
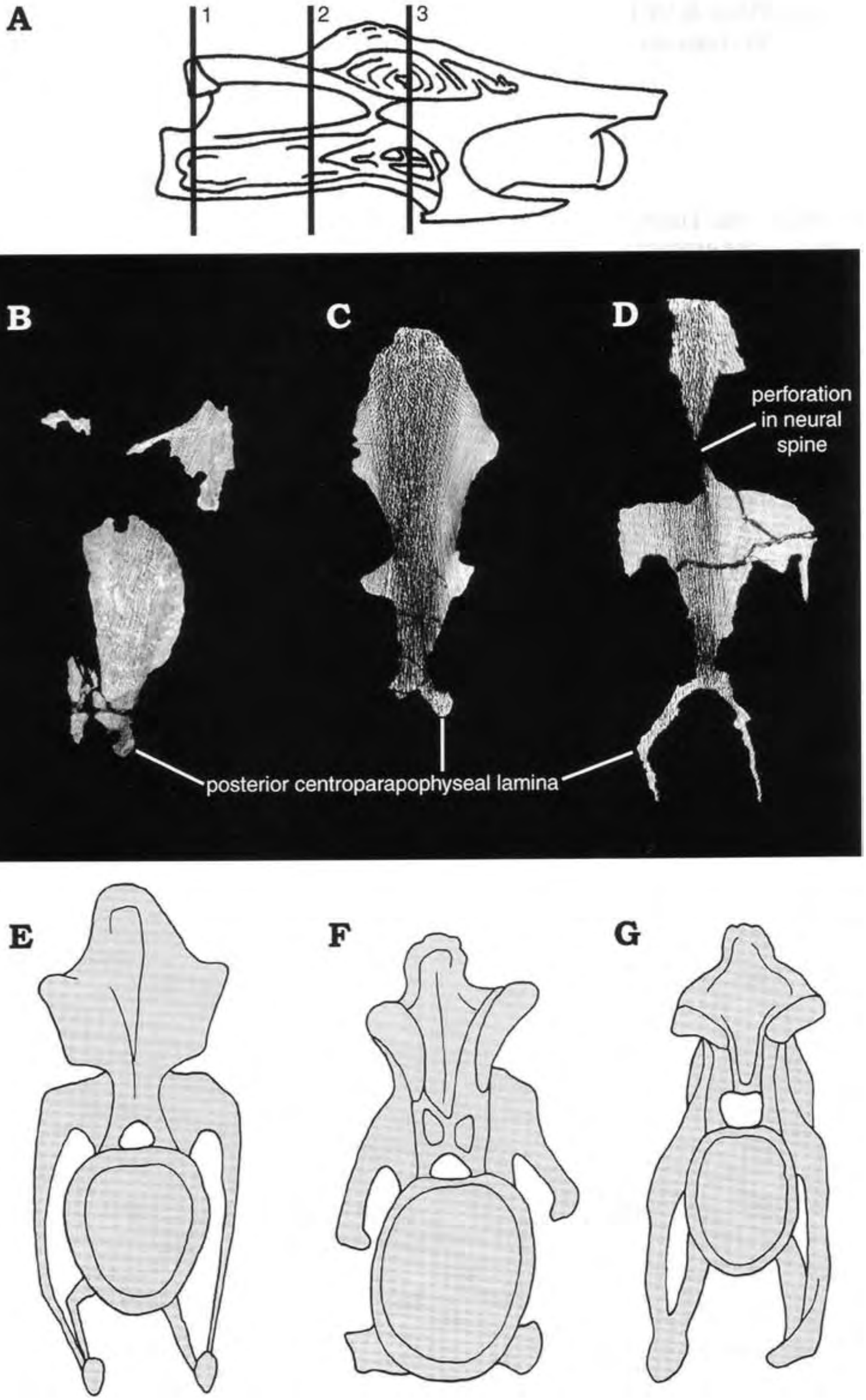


Fig. 8. Detailed anatomy of *Sauroposeidon* vertebrae. **A**. Prominent dorsal tubercles above the postzygapophyses served as insertions of the longus colli dorsalis and cervicalis ascendens muscles. **B**. Pneumatic bone is characterized by its woven texture and the presence of small pneumatic foramina. **C**. The cervical ribs are the ossified tendons of the longus colli ventralis muscles and would have been held together by retinacular bands in life. Diapophyseal tubercles mark the insertions of intertransversalis muscles. Scale baris 1 m. Abbreviations: cr, cervical ribs; dpt, diapophyseal tubercle; dt, dorsal tubercle; pf, pneumatic fossae.

Laminae. — Although the pneumatic features are highly specialized, the laminae that bound them are relatively conservative (Fig. 6). The major laminae arising from and connecting the zygapophyses, neurapophyses, and diapophyses are sharply delineated and are essentially identical to those described for *Brachiosaurus* by Janensch (1950a). There is no inflation of the neural spine or reduction of the neural arch laminae as described by Wilson & Sereno (1998) for titanosaurs. The one major lamina that differs significantly from its condition in *Brachiosaurus* is the centroparapophyseal lamina. In most sauropods this lamina, if present, consists of little more than a ventrolateral extension of the centrum to accomodate the parapophysis. In *Sauroposeidon*, the centroparapophyseal laminae are broad, thin plates, extending ventrolaterally from the base of the median septa at an angle of about 45 degrees. Anteriorly, these laminae blend into the centra well behind the condyles, but posteriorly they extend to the base of the


A
1
2
3
B
C
D
perforation in neural spine
posterior centroparapophyseal lamina
E
F
G

cotyles (Figs. 6, 9). In cross-section, they resemble an inverted 'V' hanging from the base of the centrum (Fig. 9).

As mentioned above, small accessory laminae are present in the centers of the central pneumatic fossae. In addition, accessory laminae are occasionally present in the pneumatic fossae of the neural spines. In C6, a series of small, anteroposteriorly inclined laminae cross the pneumatic fossae anterior to the perforation in the neural spine (Fig. 7). A pair of similar laminae is present in C8, extending dorsally from the diapophyses. These irregular laminae probably formed in reaction to biomechanical stress in the extensively excavated neural spines.

Neural spines. — The neural spines occupy the anterior nine-tenths of each centrum and are not bifurcate. The morphology of the neural spines varies greatly between the two anterior vertebrae and the two posterior vertebrae (Fig. 10). In C5 and C6, the neural spines are long and low, the spinozygapophyseal laminae are very gently inclined relative to the long axis of the centrum, and the neurapophyses are low and rounded. In C8, the neural spine is very high, roughly triangular in lateral view, with steeply inclined spinozygapophyseal laminae and a large, boss-like neurapophysis. Most of the neural spine of C7 is lost. The broken edge that remains approximates the border of the pneumatic fossa that occupied that lateral face of the spine, suggesting that, apart from the spinozygapophyseal laminae, the neural spines were very weak. The remaining portion of the spine slopes up sharply from the postzygapophyses, approximating the contours of the posterior neural spine in C8. This portion of the neural spine of C7 is very different from the same region in C5 and C6, and indicates 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 diamter in posterior vertebrae. Even if the neural spine of C7 was intermediate in morphology, which is unlikely given the portion that remains, there would still be a profound change in neural spine morphology between C6 and C8.

A similar transition point was evidently present in *Brachiosaurus* as well (Fig. 10). In the HM SI specimen of *Brachiosaurus*, the neural spine of C6 is low and rounded, and the neural spine of C7 is high and triangular (Janensch 1950a: figs. 26 and 29). Unfortunately, HM SII lacks neural spines on C6 and C7, but the spines of C5 and C8 are very low and very high, respectively, indicating a transition of some sort between

Fig. 9. Cervical vertebrae in cross-section and end view. **A–E**. *Sauroposeidon proteles* (OMNH 53062), cervical vertebra 6 (modified from Wedel *et al.* 2000: fig. 4). Dark radial streaks on CT images are x-ray beam hardening artifacts caused by the size and density of the specimen. **A**. Outline drawing showing location of CT sections. The cervical ribs were removed to decrease the specimen's diameter for CT scanning. **B**. Section through posterior centrum near cotyle (**A**, position 1). Although the left side of the centrum and left postzygapophysis were damaged by weathering, sufficient material remains to demonstrate that the cotyle was round and not significantly crushed. The centroparapophyseal laminae terminate near this point. **C**. Section through posterior centrum (**A**, position 2) showing reduced centrum and well-developed laminae. **D**. Section through diapophysis (**A**, position 3) showing extreme ventrolateral expansion of centroparapophyseal laminae, with probable breakage of the lamina on the left. Also apparent is the perforation of the neural spine by large pneumatic fossae. **E**. Probable posterior view of C6, reconstructed from CT cross sections. **F**. *Brachiosaurus brancai* (HM SI), cervical vertebra 4 in posterior view (after Janensch 1950a: fig. 22). **G**. *Euhelopus zdanskyi* (PMU.R233), cervical vertebra 10, in posterior view (after Wiman 1929: pl. 3). While the vertebrae of *Sauroposeidon* are laterally restricted, they are no more narrow than the vertebrae of other long-necked taxa.

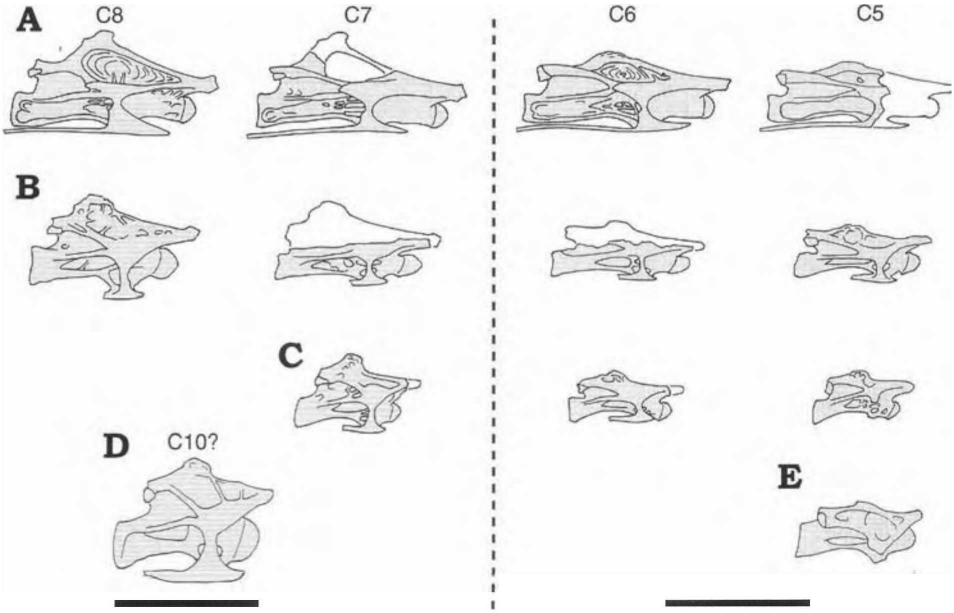


Fig. 10. Mid-cervical transition point in brachiosaurids. All specimens are shown in right lateral view and at the same scale. **A–C**. Cervical vertebrae 5 through 8. **A**. *Sauroposeidon proteles* (OMNH 53062). **B**. *Brachiosaurus brancai* (HM SII, redrawn from Janensch 1950a: figs. 37, 39, 41, and 43). C6 and C7 are dorsoventrally compressed and lack neural spines. **C**. *Brachiosaurus brancai* (HM SI, redrawn from Janensch 1950a: figs. 23, 26, and 29). **D**. *Brachiosaurus* sp. (BYU 12867, this study), probable C10. **E**. *Brachiosaurus* sp. (BYU 12866, this study), probable C5. Scale bars are 1 m.

them. In addition, two cervicals referred to *Brachiosaurus* sp. were recovered from Dry Mesa Quarry (Curtice & Wilhite 1996). Based on comparison to the HM specimens, we interpret these vertebrae as a C5 and a C10. The anterior cervical has a low neural spine, while the posterior cervical has a high neural spine that is very similar to those of posterior vertebrae in the HM specimens and in OMNH 53062. To summarize, available cervicals of *Brachiosaurus* and *Sauroposeidon* fall into two distinct categories, with no overlap and no transitional forms. While only two specimens, HM SI and OMNH 53062, record the actual transition point, we consider the mid-cervical transition point in *Sauroposeidon* and *Brachiosaurus* to be a genuine character.

Cervical ribs. — The cervical ribs of *Sauroposeidon* are remarkably long. The cervical ribs of each vertebra extend posteriorly beneath the two succeeding vertebrae. The longest measureable rib originates on C6 and tapers out at a point even with the cotyle of C8, a total length of 3420 mm. This is about 18% longer than the longest rib reported from *Brachiosaurus*, which originated on C7 and spanned 2900 mm (Janensch 1950a). However, the longest cervical rib yet described for a sauropod belonged to *Mamenchisaurus sinocanadorum*, and extends 4100 mm (Russell & Zheng 1993). In *Sauroposeidon*, the cervical ribs of successive vertebrae lie directly 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 individual ribs are ovoid or lunate in cross section, and fit together so that the bundle forms a vertical ellipse in cross section. In life, the ribs were probably held together by retinacular bands, as are the unossified longus colli ventralis tendons of birds. The soft tissue precursors of cervical ribs and their biomechanical significance are discussed below.

Muscle attachment points are also present, and are especially prominent on the posterior vertebrae. Both the dorsal tubercles, located just above the postzygapophyses, and the diapophyseal tubercles, at the posterior margin of the diapophysis, would have provided attachment points for the epaxial neck musculature (Fig. 8). These features are also present in birds (Zweers *et al.* 1987) and serve a similar function.

Vertebral internal structure

Pneumatic features are present in the presacral vertebrae of all eusauropods. In most sauropods, these vertebrae are hollowed out by internal pneumatic chambers of various sizes. Britt (1993, 1997) proposed the terms camerae and camellae to describe large and small chambers, respectively. These terms were defined based on relative size, but in some cases the sizes of the chambers may overlap, leaving the difference between small camerae and large camellae vague. In addition, deep pneumatic fossae may be confused with camerae. Therefore we propose that fossae, camerae, and camellae be differentiated on the basis of the following criteria (Table 2).

Table 2. Definitions of pneumatic excavations and cavities.

Category	fossa	camera	camella
Geometry	bowl-like depression	round cavity	angular cavity
Size (mm)	variable	5–150	2–20
Septal thickness (mm)	–	2–10	1–3
Enclosed by ostial margins with foramina?	no	yes	yes
Pattern?	–	regular branches	irregular branches

Pneumatic fossae are lateral excavations which are broad in contour and are not enclosed by ostial margins to form a foramen. Camerae are pneumatic chambers enclosed by ostial margins constituting a foramen. Although there is some overlap between partially enclosed fossae and large pneumatic foramina, pneumatic foramina are generally less than half the diameter of the camerae they enclose. Camerae are rounded and smoothly contoured cavities ranging in size from 5 mm to more than 150 mm. They are separated by septa ranging in thickness from 2 to 10 mm. They have recognizable branching patterns with interconnecting pneumatic foramina and usually communicate with the lateral foramina. Camellae are pneumatic cavities that range in size from 2 to 20 mm in diameter. The walls are generally angular, with no identifiable branching pattern, and range in thickness from 3 mm to less than 1 mm. The numerous small cavities and angular walls produce a honeycombed pattern in camellate vertebrae. Small camerae and large camellae can be differentiated on the basis of shape, septal thickness, and the presence or absence of an identifiable branching pattern.

We propose these definitions to provide a more accurate, empirically-based nomenclature for describing pneumatic internal structure. We consider some of the cavities de-

Table 3. Classification of sauropod vertebrae based on pneumatic characters.

Category	Definition
Acamerate	Pneumatic characters limited to fossae; fossae do not significantly invade the centrum.
Procamerate	Deep fossae penetrate to median septum, but are not enclosed by ostial margins.
Camerate	Large, enclosed camerae with regular branching pattern; cameral generations usually limited to 3.
Polycamerate	Large, enclosed camerae with regular branching pattern; cameral generations usually 3 or more, with increased number of branches at each generation.
Semicamellate	Camellae present but limited in extent; large camerae may also be present.
Camellate	Internal structure entirely composed of camellae; neural arch laminae not reduced. Large external fossae may also be present.
Somphospondylous	Internal structure entircly composed of camellae; neural arch laminae reduced; neural spine with inflated appearance.

scribed by Britt (1993) as camellae to actually be small camerae. For example, Britt described the small cavities in the condyles and cotyles of *Diplodocus* vertebrae as camellae. Because of their rounded margins, relatively thick septations, and bifurcating pattern of division, we consider these cavities to be small camerae rather than camellae.

It should be noted that pneumatic characters are highly variable, both within species and serially within individuals (Britt 1993; Curtice 1998). In sauropod taxa we have examined, internal pneumatic features are most complex in the posterior cervical vertebrae. For this reason we focus on cervical vertebrae in the following discussion. Some of the character combinations we describe may not exist in other regions of the vertebral column. In general, dorsals and caudals tend to be more camerate than cervicals within a given individual or species. This serial variation in character states should be borne in mind when coding data for cladistic analyses.

Sauropod vertebrae can be classified into five general types based on the presence and distribution of their pneumatic fossae, camerae, and camellae (Table 3). In addition to the established terms camerate and camellate (Britt 1993, 1997), we propose the new terms acamerate, procamerate, and semicamellate, which are defined below. We also recognize particularly derived subcategories within camerate and camellate morphologies, which we term polycamerate and somphospondylous, respectively. The evolutionary derivation of these categories is not yet fully worked out, and although some of these categories may eventually prove too detailed or cumbersome for common usage, we provide them here in order to describe the observed range of morphologies as exactly as possible.

The most primitive condition observed in sauropods is the acamerate morphology, in which pneumatic fossae are present but do not significantly invade the centrum. This morphology is exhibited by basal eusauropods such as *Barapasaurus* and *Shunosaurus*. In these taxa, pneumatic fossae are present as simple depressions on the lateral

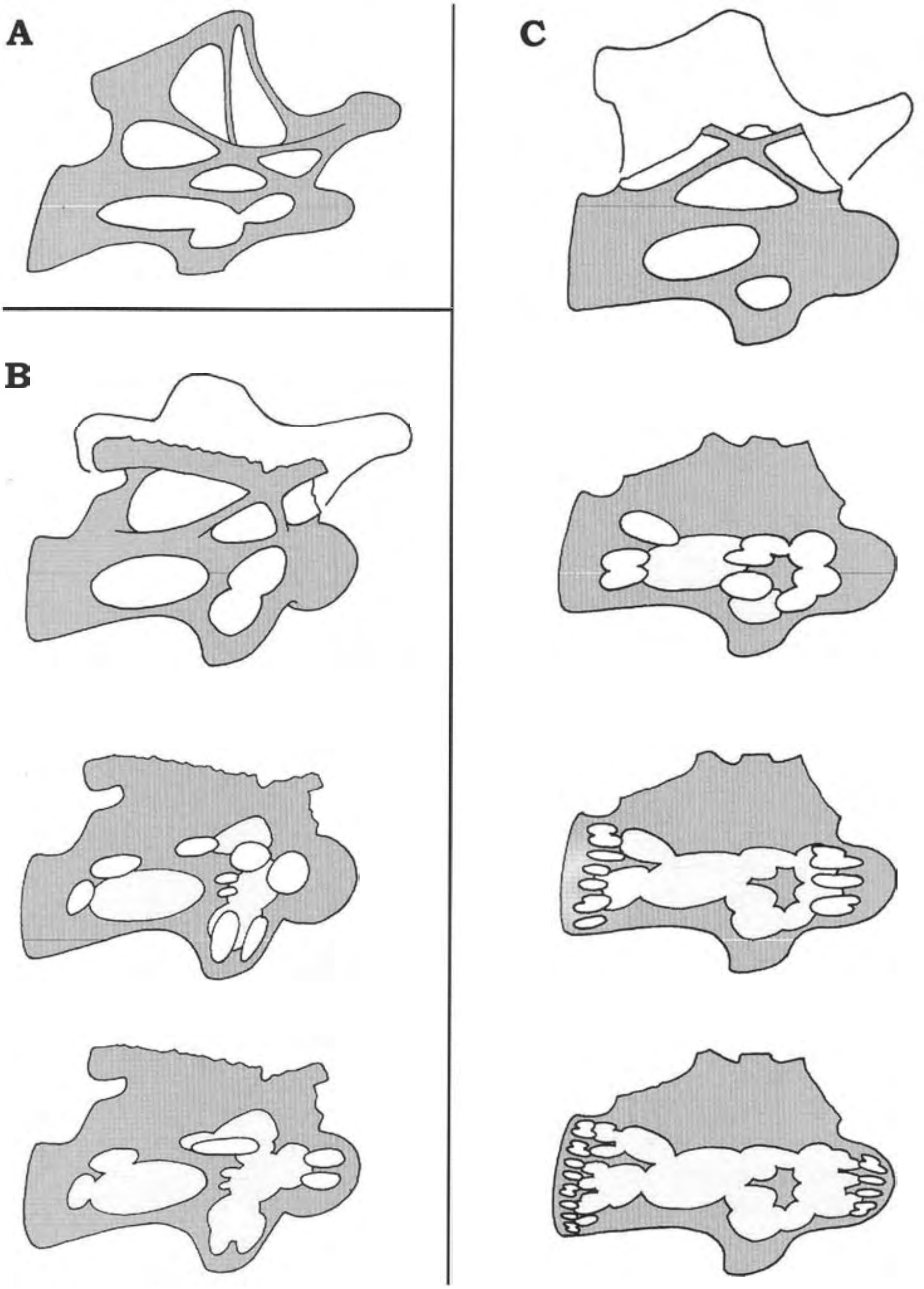


Fig. 11. Generations of cameral divisions in camerate sauropods. Pneumatic features arising at each generation are shown in white, those of previous generations are shown in light grey. **A**. *Haplocanthosaurus priscus* (CM 879-7), illustrating the procamerate condition, in which all pneumatic fossae are exposed to the surface. **B**. *Camarasaurus* sp. (OMNH 01313), illustrating the camerate condition, with three generations of camerae. **C**. *Apatosaurus* sp. (OMNH 01380), illustrating the polycamerate condition, with four generations of camerae and an increased number of camerae at each generation.

faces of the vertebral centra (Britt 1993; Wilson & Sereno 1998), and the centra are not significantly excavated by pneumatic chambers.

In procamerate vertebrae, pneumatic cavities penetrate to the median septum, producing two large lateral fossae that occupy most of the centrum (Fig. 11). This internal structure is exhibited by the primitive neosauropod *Haplocanthosaurus*. In this genus, large pneumatic chambers are present in the condyles, but not in the cotyles, and are separated by thick bony septa. These condylar chambers are formed by anterior extensions of the lateral fossae.

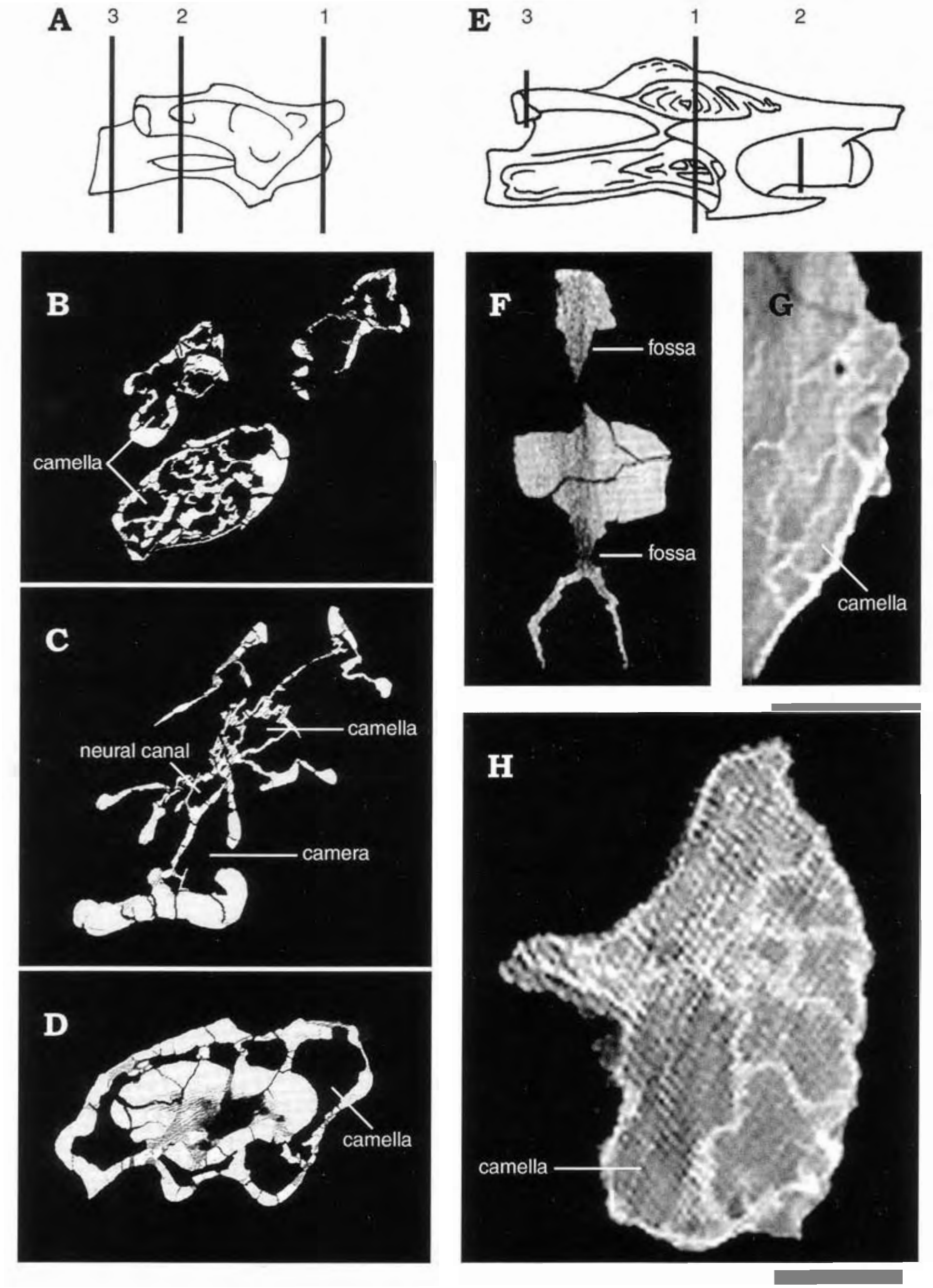
The typical camerate condition is embodied in *Camarasaurus*. Lateral pneumatic foramina open into large camerae that occupy most of the centrum. In addition, the large lateral camerae bifurcate to produce successive generations of smaller camerae that penetrate into the condyle (Fig. 11). These secondary and tertiary camerae may also be present inside the cotyle and parapophyses and along the neural canal.

Apatosaurus and *Diplodocus* exhibit a more complex form of camerate morphology. Large camerae are present in the median portion of the centrum, although they may be subdivided by numerous accessory laminae (see Hatcher 1901: fig. 7). The successive bifurcations of the lateral camerae often proceed to the fourth generation, so that the condyles and cotyles are pneumatized by a large number of small camerae that are often arranged radially (Fig. 11; compare Hatcher 1901: pl. 7). We propose the term polycamerate to describe this morphology, in which the bifurcation of the pneumatic diverticula exceeds the number of generations seen in more primitive taxa such as *Camarasaurus*, to produce numerous small camerae that more extensively pneumatize the centrum.

In *Brachiosaurus*, the condyles, cotyles, and zygapophyses are filled with pneumatic camellae (Fig. 12; compare Janensch 1950a: figs. 68–71). In addition, camellae are also occasionally present along the median septum and in the neural spine. However, the majority of the centrum is taken up by large lateral camerae, in both cervical vertebrae (Fig. 12) and dorsal vertebrae (Janensch 1950a: fig. 67). Thus the vertebrae of *Brachiosaurus* exhibit a semicamellate morphology, wherein camellae are present but do not entirely fill the internal structure.

The acme of vertebral pneumatization is the camellate condition, in which the centra and neural spines are entirely filled with numerous, small, irregularly arrayed pneumatic camellae (Fig. 2). As revealed by CT, the vertebrae of *Sauroposeidon* are camellate. Due to the size and density of the specimen, a large portion of each cross-sectional slice is obscured by x-ray beam hardening artifacts, which show up as dark, radially-arranged streaks (Figs. 9, 12). In regions not obscured by this artifact, the internal structure of the vertebrae can be seen to be composed entirely of small pneumatic camellae. The bony septa dividing these camellae are extremely thin; throughout the centrum and neural spine, the bone ranges in thickness from less than 1 mm to approximately 3 mm. The only place in the entire specimen that the bone is

Fig. 12. Pneumatic chambers in the vertebrae of brachiosaurids. **A**–**D**. *Brachiosaurus* sp. (BYU 12866), probable cervical vertebra 5. The specimen is somewhat compressed dorsolaterally, causing the distortion or collapse of some internal cavities. **A**. Outline drawing showing location of CT sections. **B**. Section through condyle and prezygapophyses (**A**, position 1). Many camellae in the condyle are collapsed, but several remain relatively undistorted. **C**. Section through the centrum posterior to the neurapophysis (**A**, position 2). Although camellae are present in the neural spine and at the base of the median septum, the most prominent pneumatic cavities are the large, thick-walled camerae. The major laminae are connected to the median septum by thin strips of bone. **D**. Section through the cotyle (**A**, position 3) showing camellae →



surrounding the cotyle. **E–H**, *Sauroposeidon proteles* (OMNH 53062), cervical vertebra 6 (modified from Wedel *et al.* 2000: fig. 4). **E**. Outline drawing showing location of CT sections. **F**. Section through diapophysis (**E**, position 1) showing hypertrophied pneumatic fossae in centrum and neural spine. **G**. Section through anterior centrum (**E**, position 2) showing camellae, which completely fill the internal structure. **H**. Section through postzygapophysis (**E**, position 3) showing camellae. The upper left quadrant of the image is obscured by x-ray beam hardening artifact, caused by the size and density of the specimen.

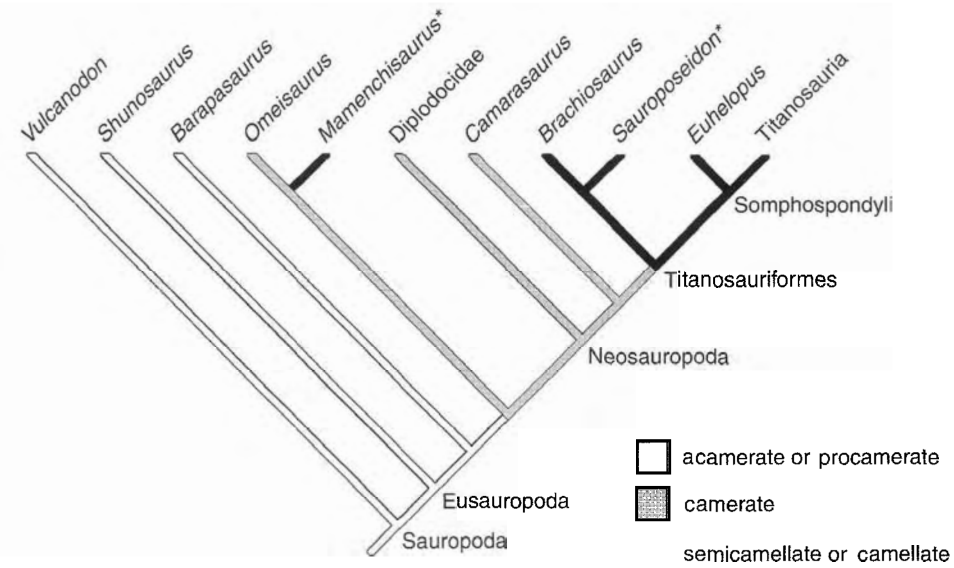


Fig. 13. Evolution of vertebral pneumaticity in the Sauropoda. This phylogenetic tree does not represent the result of a cladistic analysis, but is used to show the probable position of certain taxa, with pneumatic features mapped onto a generally accepted hypothesis of relationships for the group. General tree topology and node terminology is after Wilson & Sereno (1998), with added taxa denoted by an asterisk. Salgado *et al.* (1997) and Upchurch (1998) agree on placement of most major lineages. We follow Russell & Zheng (1994) and Upchurch (1998) in grouping *Mamenchisaurus* with *Omeisaurus*. The grouping of *Brachiosaurus* and *Sauroposeidon* is supported by several synapomorphies. This distribution of taxa requires the independent acquisition of pneumatic camellae in *Mamenchisaurus* and Titanosauriformes. Pneumatic morphologies are defined in Table 3. Acamerate and procamerate forms lack camerae and camellae, and pneumatic structures are limited to fossae. Camerate taxa are characterized by large camerae enclosed by ostial margins. In semicamellate and camellate taxa, the internal structure is composed partly or entirely of camellae.

thicker than 3 mm is in the cervical ribs, which are solid. The lateral pneumatic fossae penetrate to the median septum, but are not enclosed by bone to produce internalized chambers, as are the lateral camerae of *Brachiosaurus*.

Wilson & Sereno (1998) proposed the term Somphospondyli ('spongy vertebrae') to describe the group [*Euhelopus* + Titanosauria]. Wilson & Sereno (1998) noted that, in addition to being completely filled with pneumatic camellae, somphospondylous vertebrae are characterized by reduced neural arch lamination. This often gives the neural spines an 'inflated' appearance. While camellate internal structure as defined by Britt (1993, 1997) has precedence over Somphospondyli, we recommend that the latter term be retained and used to designate only those camellate vertebrae which possess the 'inflated' neural spines and reduced lamination characteristic of *Euhelopus* and the Titanosauria.

Pneumatic camellae evolved independently at least twice in the Sauropoda (Fig. 13): in *Mamenchisaurus* and in the Titanosauriformes. Young & Zhao (1972) reported that the cervical vertebrae of *Mamenchisaurus hochuanensis* were honeycombed with pneumatic cavities. Russell & Zheng (1993) also reported pneumatic camellae in the anterior cervicals of *Mamenchisaurus sinocanadorum*. They described the centrum of C4 as being 'at least partly composed of small (13–15 mm in diameter), closely packed, longitudinal pneumatic tubes.' While the partial composition leaves open the possibility that the vertebra is only semicamellate, the number and density of the camellae suggest the fully camellate condition, as does the lack of lateral camerae in the vertebrae of this taxon (Russell & Zheng 1993). The taxonomic affinities of Chinese sauropods are still debated (see below); however, *Mamenchisaurus* does not appear to have been closely allied with any non-Chinese taxa (Russell & Zheng 1993), and pneumatic camellae were apparently derived independently in this group.

Above the level of *Mamenchisaurus*, pneumatic camellae are present in the vertebrae of most Titanosauriformes (Fig. 13). However, at least some titanosauriforms appear to have lacked camellate internal structure. The Jones Ranch sauropod from the Early Cretaceous of Texas is a titanosauriform that lacks camellae (Gomani *et al.* 1999). *Gondwanatitan faustoi* (Kellner & Avezado 1999) is a recently described titanosaur from the Late Cretaceous of Brazil. Although the material currently available is not complete enough for a rigorous assessment, a partial cervical vertebra exhibits large pneumatic chambers with thick septations (Kellner & Avezado 1999: fig. 5). Thus *Gondwanatitan* may be a semicamellate titanosaur. In addition, a sauropod from the Dalton Wells Quarry, Utah, is characterized by several titanosaurid apomorphies (Britt & Stadtman 1996, 1997; Britt *et al.* 1997, 1998). Vertebrae from this sauropod have large lateral camerae (Britt *et al.* 1997) and lack camellae (B. Britt personal communication), demonstrating that at least some titanosaurs had camerate vertebrae.

Given these character distributions, it appears that semicamellate and camellate internal structures appeared early in the evolution of the Titanosauriformes. Pneumatic camellae are present in most titanosauriforms and their presence may be synapomorphic for the clade. The Jones Ranch sauropod may represent a reversal, or it may indicate that camellae are only synapomorphic for a more exclusive clade within Titanosauriformes. The Dalton Wells titanosaur has camerate vertebrae and probably represents a reversal within Somphospondyli.

Elongation of the cervical centra occurred independently in *Omeisaurus*, advanced diplodocids, and brachiosaurids (Wilson & Sereno 1998), as well as in some titanosaurids (see Powell 1986, 1987). If we take *Mamenchisaurus* to be the sister taxon of *Omeisaurus*, as seems likely (Russell & Zheng 1993; Upchurch 1998), then evolution of polycamerate and camellate internal structures are strongly correlated with centrum elongation. These elaborately subdivided internal structures probably evolved in long-necked lineages as a means of reducing weight. Semicamellate and camellate morphologies are characteristic of the brachiosaurids, which had very long necks, and of the titanosaurids, some of which were relatively long-necked (see Powell 1986, 1987). In addition, the pneumatic characters of *Mamenchisaurus* suggest a second independent derivation of camellae, regardless of the position of *Euhelopus* (see below).

Systematics and affinities

Early Cretaceous North American sauropods

Although the Early Cretaceous North American sauropod record is fairly poor, *Sauroposeidon* differs substantially from almost all other described material, most of which indicates rather small, short-necked taxa. Material pertaining to long-necked forms has been referred to *Astrodon/Pleurocoelus* and to an unnamed sauropod from the Cloverly Formation.

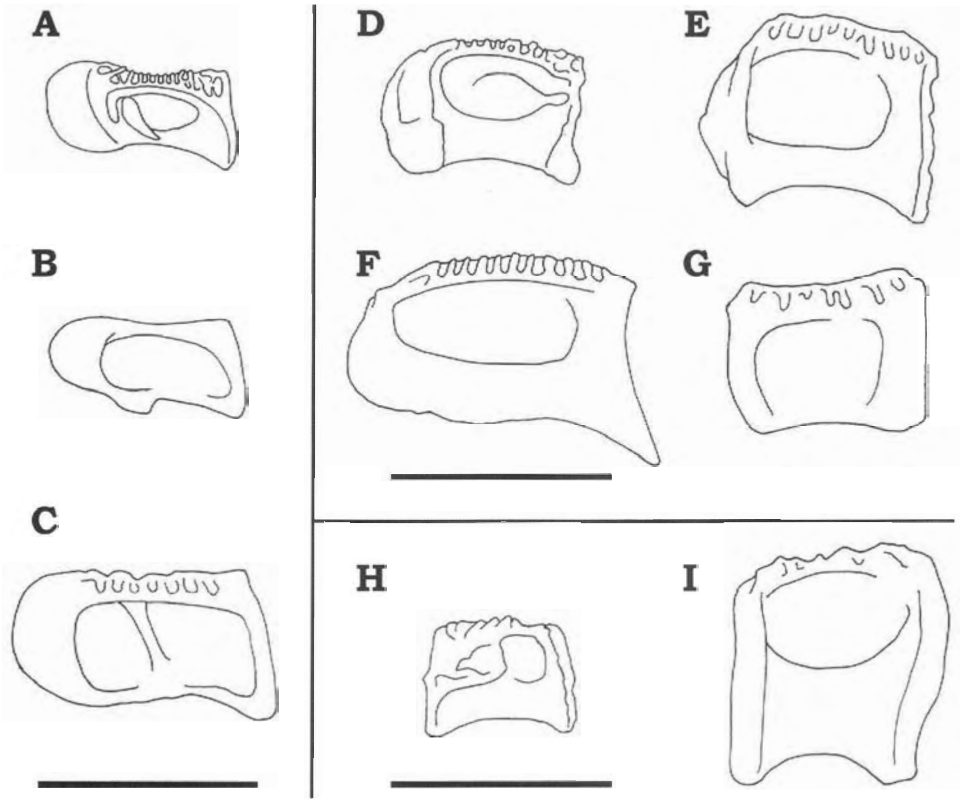


Fig. 14. Vertebrae of *Pleurocoelus* and other juvenile sauropods, in right lateral view. **A–C**. Cervical vertebrae. **A**. *Pleurocoelus nanus* (USNM 5678, redrawn from Lull 1911b: pl. 15). **B**. *Apatosaurus* sp. (OMNH 1251, redrawn from Carpenter & McIntosh 1994: fig. 17.1). **C**. *Camarasaurus* sp. (CM 578, redrawn from Carpenter & McIntosh 1994: fig. 17.1). **D–G**. Dorsal vertebrae. **D**. *Pleurocoelus nanus* (USNM 4968, redrawn from Lull 1911b: pl. 15). **E**. *Eucamerotus foxi* (BMNH R2524, redrawn from Blows 1995: fig. 2). **F**. Dorsal vertebra referred to *Pleurocoelus* sp. (UMNH VP900, redrawn from DeCourten 1991: fig. 6). **G**. *Apatosaurus* sp. (OMNH 1217, redrawn from Carpenter & McIntosh 1994: fig. 17.2). **H–I**. Sacral vertebrae. **H**. *Pleurocoelus nanus* (USNM 4946, redrawn from Lull 1911b: pl. 15). **I**. *Camarasaurus* sp. (CM 578, redrawn from Carpenter & McIntosh 1994: fig. 17.2). In general, vertebrae of juvenile sauropods are characterized by large pneumatic fossae, so this feature is not autapomorphic for *Pleurocoelus* and is not diagnostic at the genus, or even family, level. Scale bars are 10 cm.

Astrodon/Pleurocoelus. — The type species of the genus *Pleurocoelus*, *P. nanus*, is based on juvenile remains. The type vertebrae, which may not belong to a single individual (Lull 1911b), are from an animal or animals too young to have undergone neurocentral fusion, and the neural spine and cervical rib complex are unknown in *Pleurocoelus*, except for very posterior caudals (Figs. 14, 15). The centra are distinctive only in the large size of their pneumatic fossae; in fact, this is the sole defining characteristic of the taxon as originally diagnosed. Referred elements from the type locality are fragmentary and unremarkable, and have done little to improve our understanding of this practically indeterminate genus.

Perhaps because of this lack of diagnostic characters, *Astrodon/Pleurocoelus* has been used as a taxonomic dustbin for a variety of juvenile material, including vertebrae

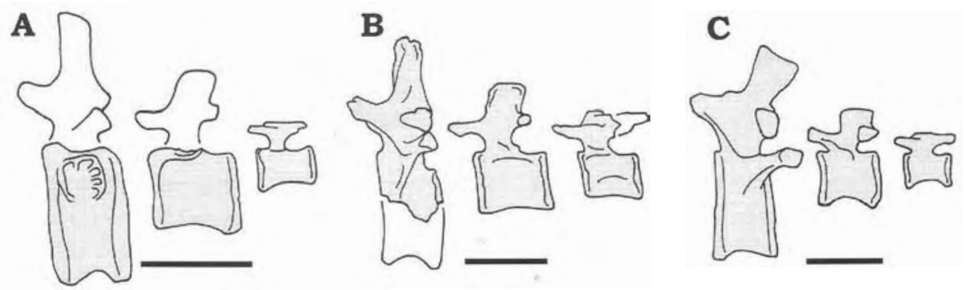


Fig. 15. Caudal vertebrae of *Pleurocoelus* and *Brachiosaurus*. An anterior, middle, and distal caudals are figured for each taxon, in left lateral view. **A**. *Pleurocoelus nanus* (redrawn from Lull 1911b: pl. 16). **B**. Caudal series referred to *Pleurocoelus* sp. (redrawn from Langston 1974: fig. 5). **C**. *Brachiosaurus brancai*, HM Fund D (redrawn from Janensch 1950a: pl. 3). Scale bars: **A**, 5 cm; **B**, 10 cm; **C**, 50 cm.

from young ornithischians (Galton 1981). Juvenile sauropod vertebrae from the Upper Jurassic Morrison Formation were referred by Marsh (1896) and Hatcher (1903) to *Pleurocoelus*. McIntosh (1981) considered these vertebrae to belong to *Camarasaurus*, and judged the enlarged pneumatic fossae to be a juvenile character. Carpenter & McIntosh (1994) described vertebrae from juvenile *Apatosaurus* and *Camarasaurus* in the CM and OMNH collections. These vertebrae do not differ significantly from the type material of *Pleurocoelus* on either proportional or morphological grounds (personal observation). Blows (1995) described dorsal vertebrae of a juvenile brachiosaurid from the Isle of Wight that also appear to be indistinguishable from the type material of *Pleurocoelus*. These similarities between the vertebrae of juvenile sauropods in at least three families (Diplodocidae, Camarasauridae, and Brachiosauridae) suggest that any referrals made on the basis of cavernous juvenile vertebrae alone are suspect (Fig. 14).

Langston (1974) referred the sauropod material from the Trinity Group to *Pleurocoelus* on the basis of caudal vertebral morphology. Sauropod caudal vertebrae from the Trinity, TMM 40435 and SMU 61732, are characterized by an ‘elevated, forwardly-placed neural arch atop a slender, spool-shaped, amphiplatyan centrum’ (Langston 1974: p. 86). Langston also noted the presence of hyposphene-hypantrum articulations in the anterior caudals of the Trinity material. In the Arundel *Pleurocoelus*, neural spine morphology is not known for most of the vertebral column (Lull 1911b, personal observations). A disarticulated neural spine of an anterior caudal vertebra, USNM 5650, shows only a weakly developed hyposphene (see Tidwell *et al.* 1999: fig. 14). In addition, anterior caudal vertebrae from the Arundel *Pleurocoelus* are amphiplatyan, while those of the Trinity material are procoelous, suggesting that the two animals are not congeneric (Tidwell *et al.* 1999). Although caudal vertebrae from both the Arundel and Trinity are very similar to those of *Brachiosaurus* (Fig. 15), the procoelous nature of the Trinity material suggests affinities with the Titanosauria. Salgado & Calvo (1997) discussed the possibility that at least some of the material referred to *Pleurocoelus* pertains to a basal titanosaur.

The presence of caudal hyposphene-hypantrum articulations appears to be autapomorphic for the Trinity *Pleurocoelus* (Tidwell *et al.* 1999). However, there are no synapomorphies linking the Arundel and Trinity material that do not also pertain to *Brachiosaurus*. Despite the very immature condition of the type material, the cervical vertebrae of *Pleurocoelus* contrast sharply with those of *Brachiosaurus* and *Sauropo-*

seidon, and definitely indicate a relatively short-necked sauropod (see below). Because the morphology exhibited by the caudal vertebrae of the Arundel *Pleurocoelus* also occurs in *Brachiosaurus*, it is probably not diagnostic at the genus level. More complete material is needed to elucidate the affinities of both the Arundel *Pleurocoelus* and the referred Trinity material.

The Jones Ranch bonebed described by Winkler *et al.* (1997) has yielded remains of a basal titanosauriform which may or may not pertain to *Pleurocoelus* (Gomani *et al.* 1999). An uncatalogued cervical vertebra from the Jones Ranch quarry is on display in the Fort Worth Museum of Science and History. This 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 *Sauroposeidon* in superficial appearance, possessing an undivided neural spine and a very elongate centrum. However, it lacks the long cervical ribs, posteriorly placed diapophyses, expanded centroparapophyseal laminae, and deeply excavated pneumatic fossae that characterize *Sauroposeidon*. Furthermore, Gomani *et al.* (1999) describe the Jones Ranch sauropod as lacking camellae, which are both present and extensive in *Sauroposeidon*.

Although teeth similar to those of *Astrodon* have been recovered from the Arundel, Cedar Mountain, and Cloverly formations, as well as the Trinity Group, these teeth alone are not very informative. With only two (Upchurch 1998) to at most four (Calvo 1994) tooth morphotypes recognized from all of Sauropoda, sauropod teeth are not diagnostic even to the family level. Furthermore, cladistic analyses demonstrate convergence in tooth morphotypes in the Diplodocoidea and Titanosauria (Salgado & Calvo 1997; Upchurch 1998; Wilson & Sereno 1998), indicating that sauropod taxa that are only distantly related can still have very similar teeth. For these reasons, attempting to draw phylogenetic or paleogeographical significance from isolated teeth is hazardous at best.

Despite the inadequacies of the type material of *Pleurocoelus*, and the uncertainties involved with referred material, the genus can be distinguished from *Brachiosaurus* and *Sauroposeidon*, even considering ontogenetic variation. The cervical vertebrae of *Pleurocoelus* are uniformly short, with a maximum EI of only 2.4 in all of the Arundel material (Table 4). For a juvenile cervical of these proportions to develop into an elongate cervical comparable to those of *Sauroposeidon*, the length of the centrum would have to increase by more than 100% relative to its diameter. Comparisons to taxa whose ontogenetic development can be estimated suggest much more modest increases in length.

Carpenter & McIntosh (1994) described cervical vertebrae from juvenile individuals of *Apatosaurus* and *Camarasaurus*. Measurements and proportions of cervical vertebrae from adults and juveniles of each genus are given in Table 4. The vertebrae from juvenile specimens of *Apatosaurus* have an average EI 2.0. Vertebrae from adult specimens of *Apatosaurus excelsus* and *A. louisae* show an average EI of 2.7, with an upper limit of 3.3. If the juvenile vertebrae are typical for *Apatosaurus*, they suggest that *Apatosaurus* vertebrae lengthened by 35 to 65% relative to centrum diameter in the course of development.

The vertebrae from juvenile specimens of *Camarasaurus* have an average EI of 1.8 and a maximum of 2.3. The relatively long-necked *Camarasaurus lewisi* is represented by a single skeleton, whereas the shorter-necked *C. grandis*, *C. lentus*, and *C. supremus* are each represented by several specimens (McIntosh, Miller, *et al.* 1996), and it is likely that the juvenile individuals of *Camarasaurus* belong to one of the latter species. In AMNH 5761, referred to *C. supremus*, the average EI 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*.

If the ontogenetic changes in EI observed in *Apatosaurus* and *Camarasaurus* are typical for sauropods, then it is very unlikely that *Pleurocoelus* could have achieved the distinctive vertebral proportions of either *Brachiosaurus* or *Sauroposeidon*.

Table 4. Comparative measurements (in mm) of cervical vertebrae from various sauropods. J indicates juvenile individuals.

Taxon	Specimen number	Cervical number	Centrum length	Cotyle height	EI
Apatosaurus excelsus[a]	CM 563	C3	250	80	3.1
		C4	300	125	2.4
		C5	342	11	3.1
		C7	415	166	2.5
		C8	415	184	2.3
		C9	445	201	2.2
		C10	475	199	2.4
Apatosaurus louisae[a]	CM 3018	C2	190	85	2.2
		C3	280	94	3.0
		C4	370	113	3.3
		C6	440	137	3.2
		C8	485	167	2.9
		C9	510	177	2.9
		C10	530	225	2.4
		C11	550	240	2.3
		C12	490	227	2.2
Apatosaurus sp. (J)[b]	OMNH 1245		59	30	2.0
	OMNH 1246		55	27	2.0
	OMNH 1251		45	23	2.0
Barosaurus lentus[c]	YPM 429	C12	930	273	3.4
		C13	890	286	3.1
		C15	720	303	2.4
Brachiosaurus brancai[d]	HM SI	C2	232	100	2.3
		C3	306	116	2.6
		C4	457	138	3.4
		C5	560	147	3.8
		C6	691	157	4.4
		C7	705	200	3.5
	HM SII	C3	420	120	3.5
		C4	663	153	4.3
		C5	810	151	5.4
		C6	900	180[e]	5.0
		C7	930	210[e]	4.4
		C8	973	244	4.0
		C9	980	225	3.8
		C10	1000	223	4.5
Brachiosaurus sp.	BYU 12866	C5?	815	260	3.1
	BYU 12867	C10?	940	300	3.1

Table 4 (continued)

Taxon	Specimen number	Cervical number	Centrum length	Cotyle height	EI
Camarasaurus lewisi[f]	BYU 9047	C2	185	73	2.5
		C3	193	68	2.8
		C4	240	79	3.0
		C5	295	103	2.9
		C6	375	132	2.8
		C7	398	130	3.0
		C8	460	150	3.0
		C9	430	215	2.0
Camarasaurus supremus[g]	AMNH 5761	C2	235	122	1.9
		C3	265	107	2.5
		C4	310	136	2.3
		C5	395	172	2.3
		C7	350	176	3.1
		C8	605	174	3.5
		C9	540	247	2.2
		C12	400	250	1.6
Camarasaurus sp. (J)[b]	OMNH 1239		53	23	2.3
	OMNH 1242		51	36	1.4
	OMNH 1244		53	23	2.3
	OMNH 1249		57	31	1.8
	OMNH 1252		44	26	1.7
	OMNH 1253		35	23	1.5
	OMNH 1254		62	35	1.8
Diplodocus carnegii[h]	CM 84	C2	165	54	3.1
		C3	243	59	4.1
		C4	289	87	3.3
		C5	372	79	4.7
		C6	442	94	4.7
		C7	485	98	4.9
		C8	512	120	4.3
		C9	525	138	3.8
		C10	595	166	3.6
		C11	605	171	3.5
		C12	627	193	3.3
		C13	638	205	3.1
		C14	642	207	3.1
		C15	595	224	2.7
Euhelopus zdanskyi [i]	PMU.R233	C2	94	37	2.5
		C3	130	48	2.7
		C4	222	55[e]	4.0
		C5	234	65	3.6
		C6	238	75	3.2
		C7	260	82	3.2
		C8	262	93	2.8
		C9	274	96	2.9
		C10	282	110	2.6
		C11	283	115	2.5

Table 4 (continued)

Taxon	Specimen number	Cervical number	Centrum length	Cotyle height	EI
Euhelopus zdanskyi[i]	PMU.R233	C12	276	139	2.0
		C13	268	127	2.1
		C14	263	139	1.9
		C15	263	142	1.9
		C16	203	129	1.6
		C17	180	142	1.3
		C18	142	142	1.0
		C19	128	132	1.0
Pleurocoelus nanus (J)	USNM 5640		91	38	2.4
	USNM 5641		101	45	2.2
	USNM 5675		121	64	1.9
	USNM 5678		105	50	2.1
	USNM 5705		95	48	2.0
	USNM 6101		85	45	1.9
Sauroposeidon proteles	OMNH 53062	C6	1220	200	6.1
		C7	1230	220	5.6
		C8	1250	270	4.6
Brachiosauridae? (J)[j]	YPM 5294		470	90[e]	5.2

[a] Gilmore (1936)
[b] Carpenter & McIntosh (1994)
[c] Lull (1919)
[d] Janensch (1950a)
[e] estimated uncrushed diameter
[f] McIntosh, Miller *et al.* (1996)
[g] Osborn & Mook (1921)
[h] Hatcher (1901)
[i] Wiman (1929)
[j] Ostrom (1970)

Cloverly sauropods. — A cervical vertebra of a juvenile sauropod from the Cloverly Formation, YPM 5294, has at least three features in common with *Sauroposeidon* and may represent a young individual from the same taxon or a closely allied taxon (Fig. 16). The vertebra, which had not undergone neurocentral fusion, has a centrum length of 470 mm and an uncrushed centrum diameter of 90 mm (Ostrom 1970). The resulting EI of 5.2 closely approximates the proportions of *Sauroposeidon*. Greatly expanded pneumatic fossae occupy almost the entire lateral surface of the centrum, as in *Sauroposeidon*. Ostrom (1970) described the vertebra as possessing long, thin centroparapophyseal laminae angled ventrolaterally from at least the anterior half of the centrum. Because of their remarkably delicate construction, Ostrom said that he was 'not at all certain that they bore cervical ribs' (p. 82). As described above, *Sauroposeidon* possesses similarly long and thin centroparapophyseal laminae that do indeed bear cervical ribs. None of the type or referred *Pleurocoelus* vertebrae from the Arundel have centroparapophyseal laminae (personal observation).

In addition, a partial postcranial skeleton of a sauropod, YPM 5449, was found in the same quarry as YPM 5294. Though the two specimens were not closely associated,

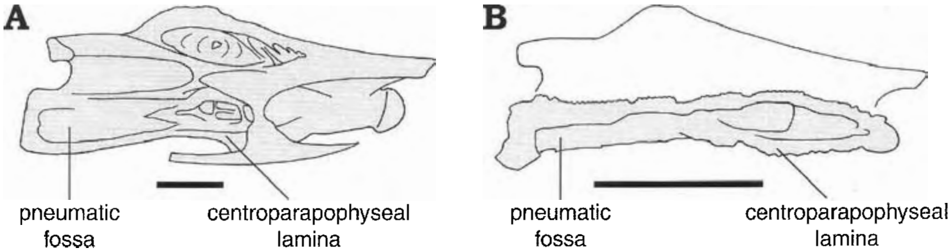


Fig. 16. YPM 5294 and *Sauroposeidon*. The vertebrae are shown in right lateral view, and at the same centrum length to facilitate comparison. **A.** *Sauroposeidon* (OMNH 53062), cervical vertebra 6. **B.** Mid-cervical vertebra of an undescribed sauropod (YPM 5294, redrawn from Ostrom 1970: pl. 15). The vertebra is dorsoventrally compressed, and would have had a larger vertical diameter in life. It shares three synapomorphies with *Sauroposeidon*: centrum EI exceeds 5, hypertrophied pneumatic fossae in centrum, and expanded centroparapophyseal laminae. Scale bars are 20 cm.

they are of similar size and may belong to the same individual (Ostrom 1970). YPM 5449 consists of dorsal vertebrae, a pair of ischia, an ulna, and a possible sternal bone. Ostrom tentatively referred the material to the Titanosauridae, although he noted many similarities to *Brachiosaurus* as well. Interestingly, the dorsal vertebrae possess undivided neural spines and are more extensively excavated than those of most other sauropods (Ostrom 1970). Although these characters might be expected in an advanced brachiosaurid, the appendicular elements of YPM 5449, particularly the ulna, suggest affinities with the Titanosauridae (J.S. McIntosh personal communication).

A stronger case can be made for the referral of YPM 5294, which, despite its juvenile nature, exhibits three of the autapomorphies used to diagnose *Sauroposeidon*: centrum length more than five times diameter; thin, well-defined centroparapophyseal laminae; and hypertrophied central pneumatic fossae that extend posteriorly to the cotyle. Whether or not it is referrable to the new taxon, as we suspect, YPM 5294 demonstrates that the distinctive vertebral proportions exhibited by *Sauroposeidon* can be achieved at a relatively early age, and that the presence of centroparapophyseal laminae predates neurocentral fusion and may be an ontogenetically stable feature. Given the gross porportional differences between *Pleurocoelus* and *Sauroposeidon*, and the example of YPM 5294 as a much better model for a juvenile long-necked sauropod, the Oklahoma taxon can be confidently excluded from the genus *Pleurocoelus*. Because of the lack of diagnostic characters pertaining to the genus *Pleurocoelus*, we recommend that the name be restricted to the Arundel material and to Trinity material that includes associated, *Pleurocoelus*-like caudal vertebrae. At least some of the isolated material from the Cloverly Formation may pertain to *Sauroposeidon* rather than *Pleurocoelus*.

Higher-level sauropod phylogeny

Although affinites within Sauropoda are debated, the most recent cladistic analyses (Salgado *et al.* 1997; Upchurch 1998; Wilson & Sereno 1998) have produced consistent results for the placement of major groups (Fig. 13). Upchurch (1995, 1998) also presented alternative and partly conflicting hypotheses, but the affinities of *Sauroposeidon* would not be affected by alternate placements of major lineages. The great length and derived pneumatic architecture of the vertebrae of *Sauroposeidon* immediately suggest an alliance with one of the four long-necked lineages described above: the Chinese sauropods, Diplodocidae, Brachiosauridae, or Titanosauridae.

Chinese sauropods. — Upchurch (1995, 1998) considered the genera *Shunosaurus*, *Omeisaurus*, *Mamenchisaurus*, and *Euhelopus* to form a monophyletic group of sauropods endemic to China. According to Wilson & Sereno (1998) this group is paraphyletic, including a basal eusauropod (*Shunosaurus*), a derived eusauropod (*Omeisaurus*), and a basal titanosaurian (*Euhelopus*). Regardless of their phylogenetic affinities, the three more derived taxa exhibit similar vertebral characteristics and will be considered as a group for the purposes of this discussion. Although *Omeisaurus*, *Mamenchisaurus*, and *Euhelopus* have very long necks, up to 10 meters in *Mamenchisaurus* (Young& Zhao 1972), the individual vertebrae do not exceed the degree of elongation observed in other long-necked sauropods such as *Brachiosaurus* and *Barosaurus* (Fig. 17). Rather, elongation of the neck is achieved by increasing the number of cervical vertebrae. A cervical count of 12 is primitive for sauropods (Wilson & Sereno 1998); the number of cervicals is increased to 17 in *Omeisaurus* and *Euhelopus* and 19 in *Mamenchisaurus*. These taxa also have long cervical ribs, which extend under successive centra in an overlapping array similar to that seen in *Sauroposeidon* (Wiman 1929; Young & Zhao 1972; Russell & Zheng 1993). The neural spines are generally low and have poorly developed laminae (Russell & Zheng 1993; Wilson & Sereno 1998), characters that contrast strongly with the morphology of *Sauroposeidon*, especially in the posterior cervical vertebrae.

Diplodocidae. — The cervical vertebrae of most diplodocids are moderately elongate, with large, complexly subdivided central camerae, strongly bifurcated neural spines that occupy the entire dorsal surface of each centrum, and short cervical ribs that do not extend beyond the cotyle of the centrum of origin (McIntosh 1990). While some diplodocid taxa, especially *Barosaurus*, had elongate cervical vertebrae (Fig. 17; see Lull 1919), practically all other vertebral characters differ from those of *Sauroposeidon*.

Brachiosauridae. — Although traditional classifications (Romer 1956; Steel 1970; McIntosh 1990) placed a number of poorly understood taxa in this family, the only well-represented brachiosaurid genus is *Brachiosaurus*. The cervical series of *Brachiosaurus* was extensively illustrated and described by Janensch (1950a). In addition, at least two cervical vertebrae referrable to *Brachiosaurus* sp. have been recovered from Dry Mesa Quarry in Colorado (Curtice & Wilhite 1996). The cervical vertebrae of *Brachiosaurus* are quite long, both proportionally and absolutely (Table 4; Fig. 17). The cervical ribs are also very long, up to 2.9 m, and extend under successive centra (Janensch 1950a). The neural spines are undivided and are set forward on the centra, occupying approximately the anterior 5/6 of each centrum. There was apparently a transition point in neural spine height and form between C6 and C7 (Figs. 6, 10; compare Janensch 1950a: figs. 26 and 29).

Sauroposeidon and *Brachiosaurus* share a number of synapomorphies. Elongate cervical centra and long cervical ribs are independently derived in other sauropod lineages, but the relatively short centra and cervical ribs of basal titanosaurians suggest that the elongation of these features in the Brachiosauridae occurred independently. A marked transition in neural spine height and form occurs in the mid-cervical series of both *Brachiosaurus* and *Sauroposeidon* (Fig. 10). The neural spines are set forward on the centra in both taxa, so that the prezygapophyses substantially overhang the condyles. The trends observed in *Brachiosaurus* toward elongation and pneumatization of the cervical series are taken to an extreme in *Sauroposeidon*, which is 30–40 Ma younger. In particular, the pneumatic camellae observed in *Brachiosaurus* have expanded to fill the entire internal volume in the vertebrae of *Sauroposeidon*. However, camellae are present in most titanosauriforms, so camellate internal structure should be considered a symplesiomorphy of *Brachiosaurus* and *Sauroposeidon* (contra Wedel *et al.* 2000).

Brachiosaurus was described by Riggs (1903), who felt that the genus differed enough from other known sauropods to deserve its own family, the Brachiosauridae, which he later erected (Riggs 1904). While numerous other genera have been referred to the Brachiosauridae (McIntosh 1990), most of these taxa are poorly represented and share no unambiguous synapomorphies with *Brachiosaurus*. Salgado *et al.* (1997) argued that the Brachiosauridae consisted of a paraphyletic assemblage of basal titanosauriforms. However, the existence of a monophyletic Brachiosauridae is supported by the discovery of *Sauroposeidon*. Other genera that may be closer to *Brachiosaurus* than to Titanosauria include *Ornithopsis* and *Eucamerotus* (Blows 1995, 1998), *Sonorasaurus* (Ratkevitch 1998), *Cedarosaurus* (Tidwell *et al.* 1999), and the French '*Bothriospondylus*' material (see Wilson & Sereno 1998). While some of the material referred to *Pleurocoelus* conforms closely to *Brachiosaurus* (Langston 1974), Salgado & Calvo (1997) consider *Pleurocoelus* to be a basal titanosaur. As no unequivocal synapomorphies link the material that has been referred to *Pleurocoelus*, it is possible that this material represents multiple taxa, including brachiosaurids and titanosaurids.

Titanosauridae. — Although cervical vertebrae have only been described for a few titanosaurid taxa, those that are known exhibit considerable diversity. For example, *Titanosaurus colberti* is unusual in possessing the shortest cervical vertebrae, proportionally, of any sauropod, with the lengths of posterior centra only slightly exceeding their diameters (Jain & Bandyopadhyay 1997; Fig. 17). The most elongate cervical vertebrae that have been described from a titanosaurid are those of an unnamed taxon from Brazil, DGM 'Série A' (Powell 1986, 1987). The vertebrae are otherwise dissimilar to those of *Sauroposeidon*, lacking the very elongate cervical ribs, expanded centroparapophyseal laminae, and hypertrophied pneumatic fossae that characterize the Oklahoma taxon (Fig. 17).

Paleobiology

Size estimates. — By comparing *Sauroposeidon* to better known taxa, especially *Brachiosaurus*, we can make inferences regarding its dimensions, paleobiology, and probable appearance. Paul (1988) provided an extensive discussion of the size and probable habits of the giant brachiosaurids. The most complete specimen of *Brachiosaurus* that has been assembled to date is HM SII, the holotype of *Brachiosaurus brancai*, which is mounted in the Humboldt Museum in Berlin. The specimen is a composite of different-sized individuals, and while its proportions are not entirely accurate (Paul 1988; Gunga *et al.* 1995), it is the best available example. HM SII includes a complete, articulated cervical series which is 9 m (29.5 ft.) long. The vertebrae of *Sauroposeidon* are between 25 and 33% longer than the corresponding vertebrae from HM SII (Table 3), which would give *Sauroposeidon* a neck length of 11.25–12 m

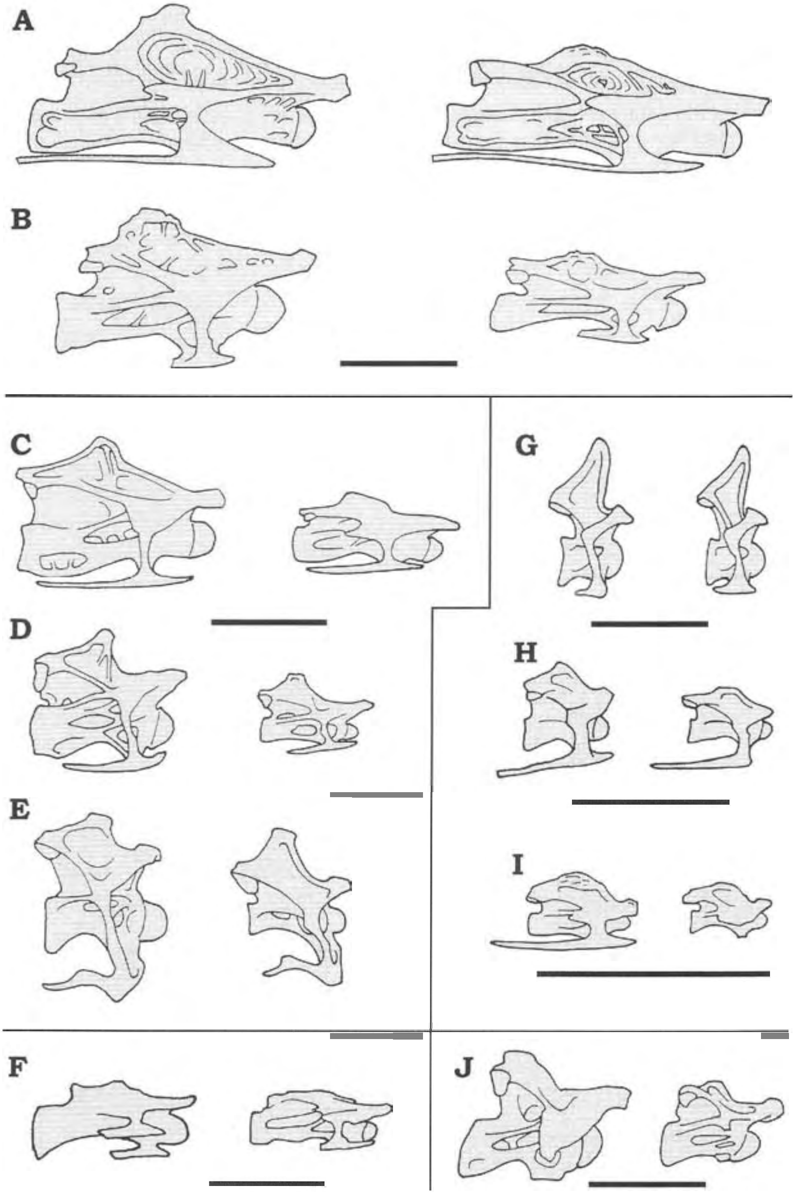


Fig. 17. Cervical vertebrae of various sauropods. An anterior and posterior cervical is illustrated for each taxon, in right lateral view. All except for H and I are shown at the same scale. **A–B**. Brachiosaurids. **A**. *Sauroposeidon proteles* (OMNH 53062). **B**. *Brachiosaurus brancai* (HM SII, redrawn from Janensch 1950a: figs. 37 and 43). **C–E**. Diplodocids. **C**. *Barosaurus lentus* (CM 11984, this study). **D**. *Diplodocus carnegii* (CM 84, redrawn from Hatcher 1901: pl. 4). **E**. *Apatosaurus louisae* (CM 3018, redrawn from Gilmore 1936: pl. 24). **F**. *Omeisaurus tianfuensis* (CCG T5701, redrawn from He *et al.* 1988). **G–I**. Titanosauriforms. **G**. *Titanosaurus colberti* (ISIR 335, redrawn from Jain & Bandyopadhyay 1997: figs. 3 and 5). **H**. *Euhelopus zdanskyi* (PMU R233, redrawn from Wiman 1929: pl. 3). **I**. Unnamed titanosaur (DGM 'Série A', redrawn from Powell 1986: pls. 13 and 14). **J**. *Camarasaurus supremus* (AMNH 5761, redrawn from Osborn & Mook 1921: pls. 67 and 68). Scale bars are 50 cm.

(37–39.5 ft.), assuming that the remainder of the neck of *Sauroposeidon* was proportioned similarly to that of *Brachiosaurus*.

Estimating the size of the body of *Sauroposeidon* requires another level of inference, and thus uncertainty. While the vertebrae of *Sauroposeidon* are much longer than those of the HM SII specimen of *Brachiosaurus*, they are only slightly larger in diameter (Table 4). If we use centrum diameter as an estimate of body size, then *Sauroposeidon* was probably only slightly larger than HM SII, but with a much longer neck. However, as *Mamenchisaurus hochuanensis* demonstrates, a very long neck can be attached to a relatively small body. Though we consider it unlikely, it is possible that *Sauroposeidon* was as small or smaller than the HM SII *Brachiosaurus*.

In the absence of any material from the limbs or body, any mass estimates of *Sauroposeidon* must be considered tentative. Colbert (1962), Paul (1988), and Alexander (1989) used volumetric displacement to estimate the mass of *Brachiosaurus*, obtaining estimates of 78.3, 32, and 46.6 metric tons. Russell *et al.* (1980) and Anderson *et al.* (1985) estimated the mass of *Brachiosaurus* using limb bone allometry, and obtained mass estimates of 15 and 29 metric tons, respectively. The average of these five estimates is 40 metric tons, or 36 tons if we reject the estimates of 78 and 15 tons as outliers. Because mass increases with the cube of the linear dimension, relatively small increases in linear size produce much larger masses. For example, the HM XV2 specimen of *Brachiosaurus* is only 12% larger than the individual represented by HM SII, but would have weighed 40% more, perhaps as much as 50 or 60 metric tons.

If *Sauroposeidon* had a build similar to that of *Brachiosaurus*, it may also have massed between 50 and 60 tons. On the other hand, it is possible, given the gracility of the neck, that *Sauroposeidon's* body was equally slender, in which case the animal could have weighed less than the HM SII specimen of *Brachiosaurus*. An analogous situation exists between *Apatosaurus* and the longer, more gracile *Diplodocus*, which are estimated to have weighed 30 and 10 tons, respectively (Colbert 1962). Furthermore, no published mass estimates of sauropods take into account thoracic and abdominal air sacs, which were probably present and would have reduced mass signficantly (see below).

Neck posture and biomechanics. — While brachiosaurids have traditionally been restored as carrying their necks in a nearly vertical pose (e.g., Janensch 1950b; Paul 1987, 1988), there is little evidence that they actually did so. The neural spines of the posterior cervicals and anterior dorsals of HM SII are missing, and are reconstructed from plaster in the skeletal mount. Therefore the posture of the neck in the skeletal mount should not be taken as evidence for a vertical pose in life. Paul & Leahy (1994) asserted that the posterior cervicals and anterior dorsals of *Camarasaurus* were 'beveled' to produce a sharp dorsiflexion in neutral pose, and Paul (1987, 1988) restored the base of the neck of *Brachiosaurus* similarly. The posterior cervicals of *Brachiosaurus* are not beveled, and were discovered articulated and in a nearly straight line (Janensch 1950a). Parrish & Stevens (1998) used computer modeling to demonstrate that the dorsiflexion of the basal cervical series observed in *Camarasaurus* skeletons is due to postmortem contraction, and suggested that this dorsiflexion exceeds the range of motion possible during life.

Based on computer modeling of the range of motion in the cervical series, Stevens & Parrish (1999) found that the diplodocids *Apatosaurus* and *Diplodocus* were capable of only limited dorsiflexion, but could ventroflex deeply and had a large lateral range of motion as well. They proposed that the long necks of diplodocids allowed the animals to feed from near the ground, over a broad area. The long forelimbs and ex-

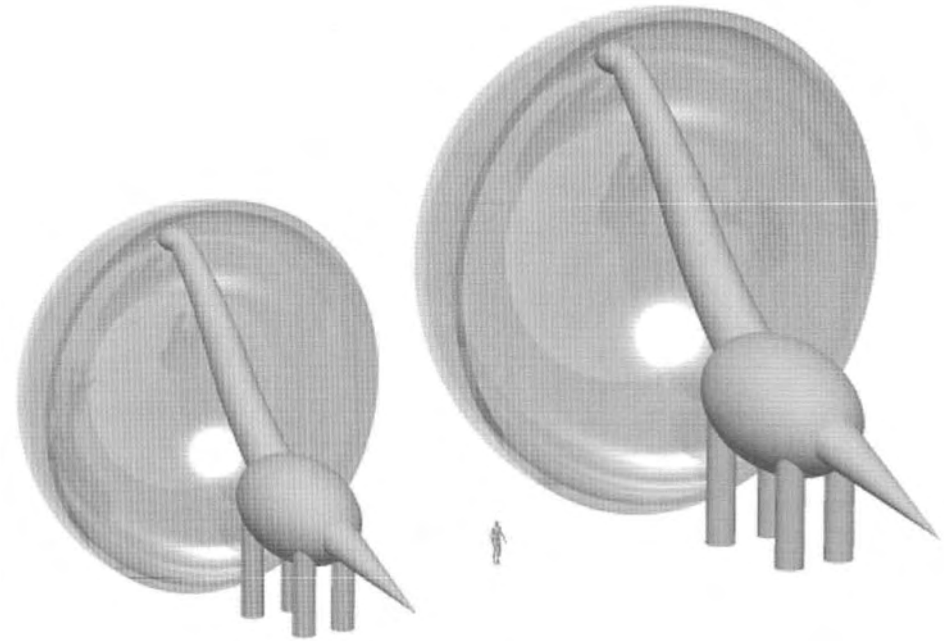


Fig. 18. Feeding envelopes of *Brachiosaurus* (left) and *Sauroposeidon* (right). The shapes of the feeding envelopes were probably complex; we have deliberately simplified them for the purposes of this illustration. Because volume increases with the cube of the linear dimension, the increase in neck length of 25 to 33% in *Sauroposeidon* would have effectively doubled the volume of its feeding envelope over that of *Brachiosaurus* ($1.25^3 = 1.95$, $1.33^3 = 2.35$). The human figure is 1.8 m tall.

tremely long necks of brachiosaurids, on the other hand, are suggestive of high-level browsing, by analogy with giraffes and other ungulate mammals.

While the extremely long neck of the Late Jurassic *Brachiosaurus* may have evolved to permit access to food resources unavailable to shorter taxa, this competition-based scenario does not explain the even greater elongation of the neck in *Sauroposeidon*. The next-largest herbivore present in the Antlers fauna is the ornithopod *Tenontosaurus* (Cifelli, Gardner, *et al.* 1997). It is unlikely that *Tenontosaurus* and *Sauroposeidon*, with maximum heights of approximately 3 and 18 m, respectively, competed in any significant fashion for available vegetation. Even Early Cretaceous sauropods from other formations do not appear to have been large enough or abundant enough to exert competition-based selective pressures. However, the additional 2–3 m of neck in *Sauroposeidon* would have doubled the volume of the feeding envelope over that of *Brachiosaurus* (Fig. 18). Although the feeding envelope could also be extended by simple locomotion, forests are mechanically difficult environments (Wing & Tiffney 1987), and a long, mobile neck may have evolved in part to overcome the mobility limitations imposed by large body size.

The sauropod neck would have been supported by the interspinous ligaments and epaxial musculature. Alexander (1985, 1989) speculated that a large elastin ligament might have provided much of the necessary support in at least some sauropod taxa. Several sauropod groups, including diplodocids and camarasaurids, have bifurcated neural spines in their cervical and anterior dorsal vertebrae (Fig. 19). Some birds, including

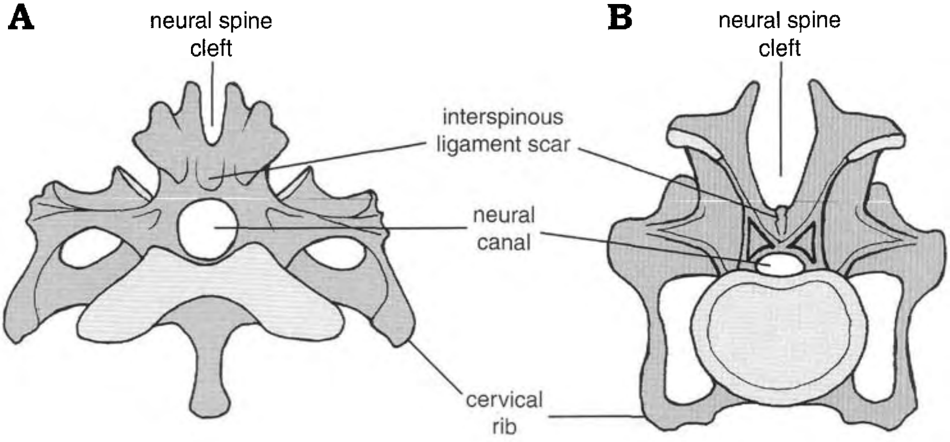


Fig. 19. Cleft neural spines and interspinous ligament scars in ratites and sauropods. **A**. In *Rhea americana* the interspinous ligaments attach well below the cleft in the neural spine, which is occupied by the biventer cervicis muscle. **B**. In *Diplodocus carnegii* (CM 84, redrawn from Hatcher 1901: pl. 5) there is a prominent attachment scar for the interspinous ligament at the base of the neural spine cleft, but there is no osteological evidence that the ligament was either continuous or large enough to fill the cleft.

Rhea americana, also have bifurcated neural spines in their posterior cervical and anterior dorsal vertebrae (Fig. 19). In these birds, the cleft in the bifurcated neural spine is occupied by the biventer cervicis muscle. A large elastin ligament, the ligamentum elasticum interlaminare (Zweers *et al.* 1987), is also present. Unlike the ligamentum nuchae of artiodactyls, this ligament is discontinuous, connecting only the neural spines of successive cervical vertebrae (Fig. 20). The ligament attaches to each spine below the level of the neural spine cleft, leaving a visible scar. In groups with simple, undivided neural spines, such as brachiosaurids, the interspinous ligament was probably discontinuous, as in birds. In those taxa with bifurcated neural spines, the ligament attachment scars are usually at the anterior and posterior ends of the cleft. This could indicate discontinous ligaments, or a continuous ligament that also anchored to each vertebra.

The large elastin ligaments of artiodactyls and birds function as energy-return systems, helping to raise the neck following ventroflexion. These ligaments are taut in all normal positions of the neck, but even at maximum ventroflexion the ligaments alone are insufficient to support the neck; additional support must be provided by epaxial muscle groups (Dimery *et al.* 1985; Bennett & Alexander 1987; Alexander 1989). In birds, the largest dorsal muscles are the longus colli dorsalis and cervicalis ascendens, which insert on the dorsal tubercles (processes) above the postzygapophyses (Zweers *et al.* 1987; Heidweiller 1989). The prominent dorsal tubercles of many sauropod cervical vertebrae, particularly the posterior cervical vertebrae (Figs. 8, 17), suggest equally impressive dorsal musculature. Large epaxial muscles would have been necessary to raise the neck (Alexander 1985; Dodson 1990), and probably contributed significantly to support of the neck in all poses.

Cervical ribs are present in both birds and sauropods and are anchored to the cervical centra at the diapophyses and parapophyses (Fig. 1). The longus colli ventralis muscles attach to the caudal edge of the parapophyses via tendinous attachments. The cervical rib itself is formed by ossification of tendinous elements that proceeds caudally along the

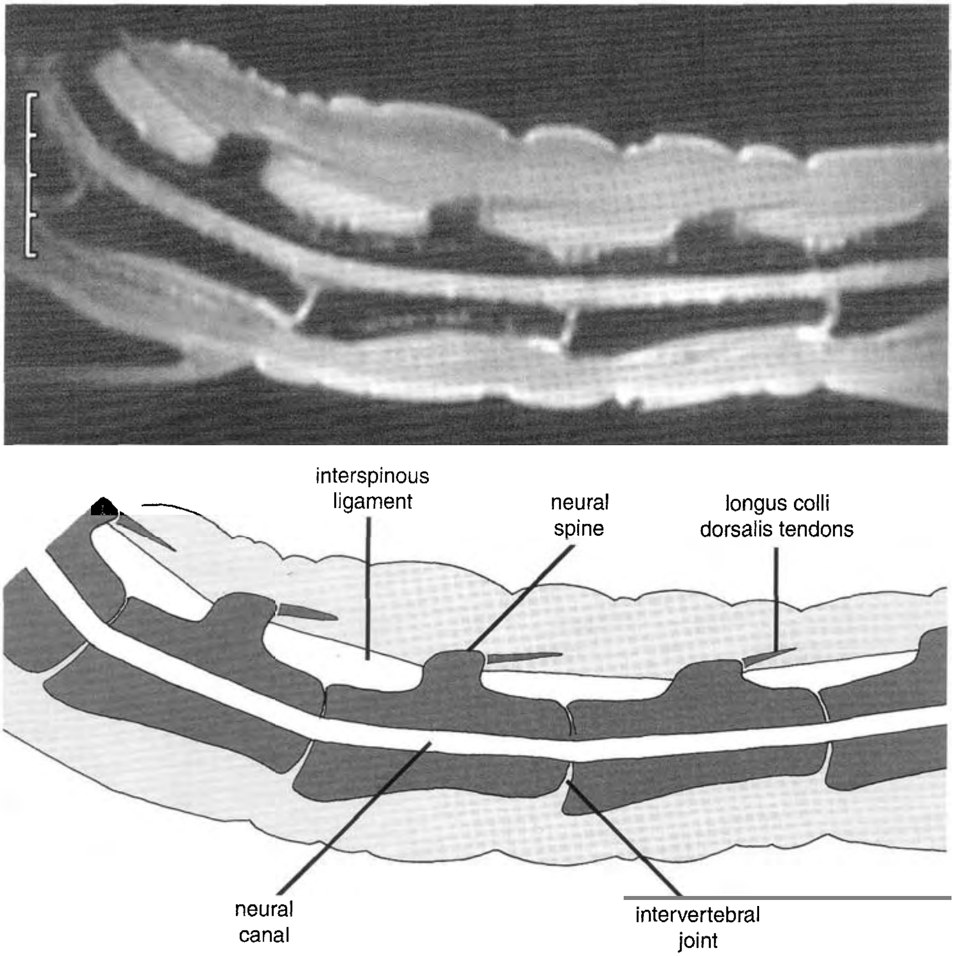


Fig. 20. An MRI of the mid-cervical series of an ostrich (*Struthio camelus*). In sagittal section, the interspinous ligaments are lighter than the surrounding muscle because of their high fat content. The neural canal is occupied by the spinal cord and supramedullary pneumatic airways. Also apparent in this image are the tendons of the longus colli dorsalis muscle originating from the neural spine. Scale bar is 4 cm.

line of attachment (Zweers *et al.* 1987). In birds the cervical ribs tend to be fairly short, although in the ostrich they extend for the entire length of the centrum. In sauropods, the cervical ribs are often much longer, exceeding two or even three centrum-lengths. These long cervical ribs are ovoid or lunate in cross-section and lie in vertically stacked bundles where they overlap (Fig. 8). In life these bundles would have been held together by retinacular bands, as are the unossified longus colli ventralis tendons of birds. These retinacular bands would have allowed the cervical ribs to slide past each other, in the same manner as tendons, during flexion and extension of the neck.

Frey & Martin (1997) proposed that the long cervical ribs of some sauropod taxa served to support the neck by forming an incompressible ventral bracing system. This proposition is anatomically and mechanically untenable. The entire cervical rib complex is present in a less-ossified state in extant avians, where it functions as the inser-

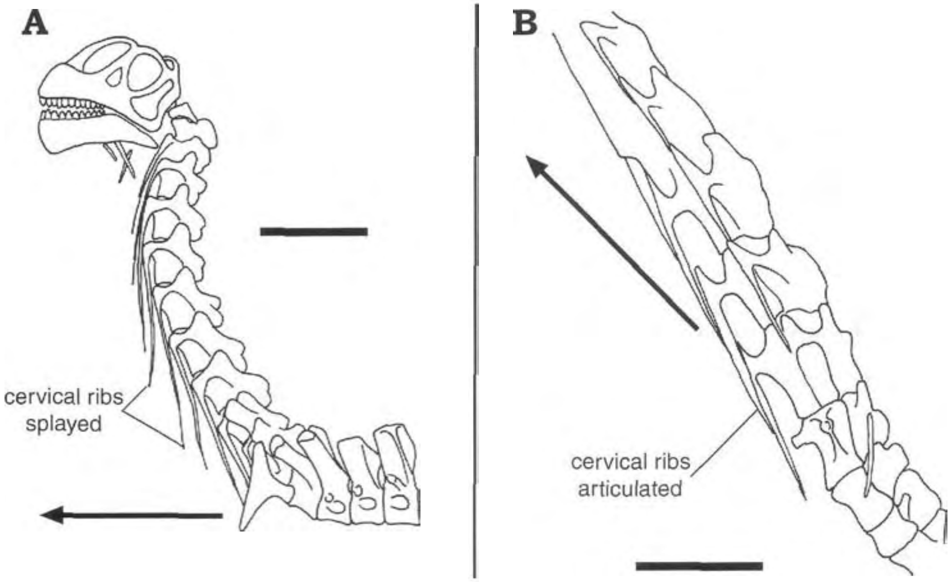


Fig. 21. Cervical ribs as taphonomic indicators. In each case, the arrow represents the orientation of the anterior dorsal vertebrae. **A**. In this specimen of *Camarasaurus lentus* (CM 11338, redrawn from Gilmore 1925: pl. 14) the splayed cervical ribs suggest that the longus colli ventralis muscles were no longer attached, allowing the neck to hyperextend as the interspinous ligaments contracted. **B**. The holotype of *Mamenchisaurus hochuanensis* (CCG V 20401, redrawn from Young & Chao 1972) was preserved with the cervical ribs in articulation, and the cervical series is oriented in more or less the same direction as the anterior dorsal vertebrae. Scale bars: **A**, 25 cm; **B**, 1 m.

tion of the longus colli ventralis muscle. Therefore, there is no need to propose a novel explanation for the character in sauropods. Furthermore, there is no evidence from either comparative anatomy or the structure of articulated ribs that the retinacular bands encircling the cervical ribs would have limited their ability to slide past each other, as would be required in an incompressible, ventrally-braced system. Finally, such a ventrally braced system would have to be completely inflexible in order to support itself. The neck would sag until it reached the maximum ventroflexion allowed by the ventral bracing, so the lowest possible posture would be the only possible posture.

A series of incompressible elements was already present in the sauropod neck: the articulated vertebral centra. The epaxial musculature and articulated vertebrae formed the tensile and compressive elements, respectively, of a horizontally loaded beam. Given that the segments articulated at highly mobile ball-and-socket joints, the stability of the system was probably low. The ossification of the longus colli ventralis tendons to produce elongate cervical ribs in sauropods may have been necessary to maintain tension, not compression, in the ventral portion of the neck. The magnitude of the suspensory forces exerted by the dorsal musculature may have created a tendency for the neck to dorsiflex sharply (i.e., snap) at each of the highly mobile intervertebral joints. The tension provided by the longus colli ventralis muscles and the attendant cervical ribs would have countered this tendency and kept the neck in dynamic equilibrium.

In articulated skeletons, it is not uncommon for the neck to be hyperextended dorsally into a tight curve, producing the familiar 'death pose' (Fig. 21; see McIntosh, Miles, *et al.*

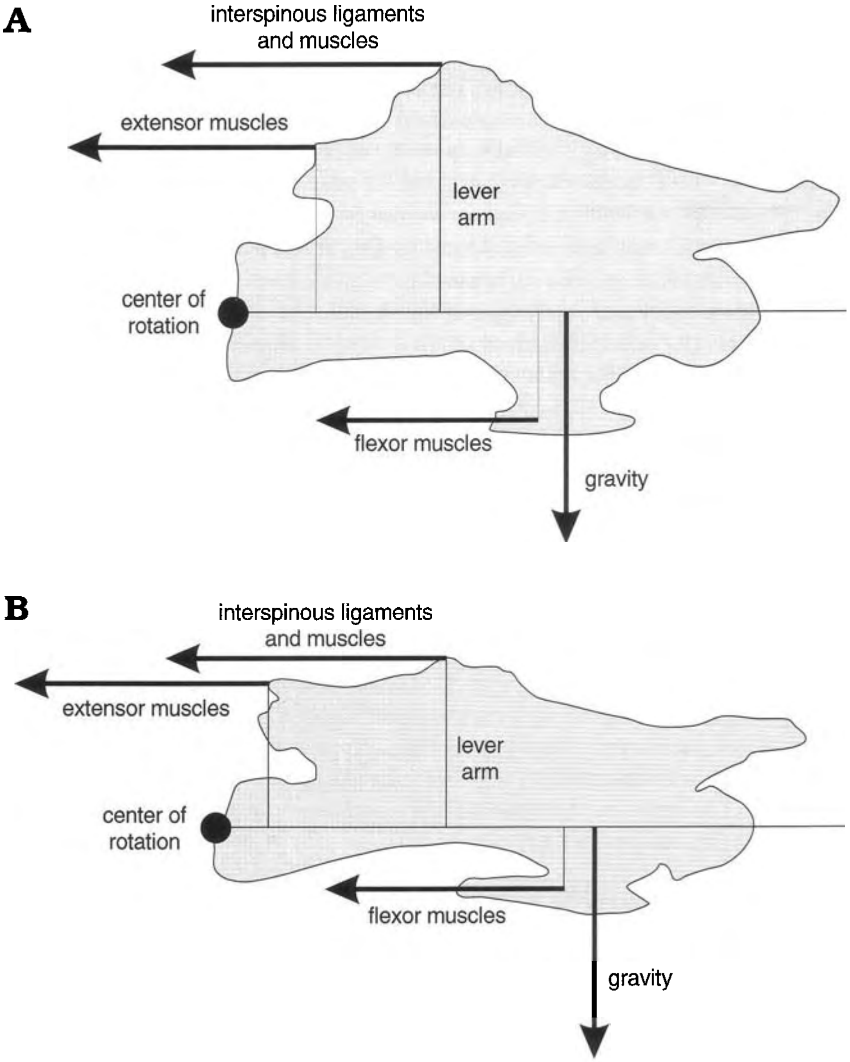


Fig. 22. Forces acting on the cervical vertebrae. In brachiosaurids, the tall neural spines of the posterior cervicals (**A**) would have increased the lever arm, and therefore the mechanical advantage, of the epaxial musculature, while the lower neural spines of the anterior cervicals (**B**) indicate that support was less important in the anterior portion of the neck.

1996). That an articulated neck can assume this pose in death has been used as evidence that the pose must also have been possible in life (Paul & Leahy 1994; Sereno *et al.* 1999). In fact, the dehydration and contraction of the interspinous ligament is powerful enough to pull the cervical vertebrae out of articulation (Parrish & Stevens 1998). The vertebrae may still articulate at the zygapophyses after the condylar joint capsule has separated, producing the appearance of full articulation. In such death pose specimens the cervical ribs are usually splayed, fanning out ventrally from the cervical series (Fig. 21). In birds, the longus colli ventralis tendons lie parallel in life, regardless of the orientation of the neck (personal observation). The cervical ribs of sauropods also lay parallel in specimens in which neck posture is not distorted into a death pose (Fig. 21). The dorsal ligaments and epaxial musculature had to support the weight of the neck and were probably much stronger than the ventral muscle groups. The splayed cervical ribs of the death pose specimens suggest that the postmortem contraction of the dorsal ligaments and musculature disarticulated the longus colli ventralis tendons, which normally lay parallel. If this occurred, the neck would be free to hyperextend dorsally with no opposing force from the hypaxial musculature, a condition that would not have occurred in life.

The mid-cervical transition point shared by *Brachiosaurus* and *Sauroposeidon* (Fig. 10) is of biomechanical as well as taxonomic significance. In the posterior cervicals, high neural spines increased the height of the dorsal tubercles and neurapophyses. The development of high neural spines moved these muscle attachment sites farther from the cotyle, thereby increasing the lever arm relative to the axis of rotation in the dorsoventral plane (Fig. 22). This would have increased the torque exerted by the dorsal musculature, and may indicate an extension posture in the base of the neck. In contrast, the more slender morphology of the anterior cervicals may have served to increase the mobility of the head and distal neck. In particular, the low neural spines would have provided less mechanical advantage for the supporting muscles (Alexander 1985), and indicate that support was less important in the distal neck. The transition point may have marked 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 (Wedel *et al.* 2000: fig. 5). This hypothesis could potentially be tested using a computer model such as that described by Stevens & Parrish (1999). However, construction of a such a model requires knowledge of the size, position, and orientation of the zygapophyses throughout the cervical series. The zygapophyses of most posterior cervical vertebrae are unknown in either *Brachiosaurus* or *Sauroposeidon*, so empirical testing of brachiosaurid neck posture may have to wait until more complete specimens are discovered.

Air sac systems. — One aspect of sauropod paleobiology that has received little attention to date is the nature and extent of the air sac system and its implications for sauropod physiology. Central to this issue is the question of sauropod lung ventilation; presence of air sacs does not necessarily imply an avian-style breathing apparatus. The extensive pneumatization of the cervical series in sauropods points to the existence of cervical air sacs similar to those of birds. However, in birds the lungs are ventilated by abdominal air sacs (Schmidt-Nielsen 1971), so cervical air sacs alone cannot be taken as evidence of bird-like aspiration. It is possible that sauropods also possessed abdominal air sacs. In the chicken, *Gallus domesticus*, the posterior thoracic vertebrae and synsacrum are pneumatized by diverticula of the abdominal air sacs (Hogg 1984). Most sauropods possess pneumatic sacral vertebrae, and in diplodocids the proximal caudals were also pneumatic (Britt 1993, 1997). As the homology of these features with those of birds is well supported (Britt 1993; Reid 1997), it is most parsimonious to assume that they were produced in the same fashion: by pneumatic diverticula extending from abdominal air sacs.

Although the air sac system in sauropods was probably not as complex or extensive as that of birds, the existence of even a limited air sac system in sauropods would dramatically affect current mass estimates. Alexander (1985, 1989) assumed that the lungs of dinosaurs occupied between 8 and 10 percent of the internal volume, based on comparisons with mammals. A thoraco-abdominal air sac system would double or triple the volume of air inside the body cavity, lightening the animal considerably. None of the available mass estimates for sauropods take the possibility of such an air sac system into account, so current estimates may be too heavy by 20 percent or more. Because mass affects food intake (Weaver 1983) and respiratory requirements (Paladino *et al.* 1997), the presence of air sacs in sauropods would change most of what has been proposed regarding sauropod metabolism.

Conclusions

Sauroposeidon proteles represents a large brachiosaurid sauropod. Autapomorphies characterizing the new taxon include expanded centroparapophyseal laminae, posteriorly positioned diapophyses, hypertrophied pneumatic fossae in the centra and neural spines, and a length-to-diameter ratio greater than 5 for mid-cervical vertebrae. YPM 5294, a cervical vertebra of a juvenile sauropod from the Cloverly Formation, exhibits several of these characters and probably represents *Sauroposeidon* or a closely allied taxon. *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, long cervical ribs, and a mid-cervical transition point. Pneumatic camellae evolved independently at least twice in sauropod evolution, and their presence appears to have been weight-saving adaptation related to neck elongation. Weight may have been further reduced by the presence of an air sac system in the thorax and abdomen, although the exact nature and extent of this air sac system cannot be determined at this time. Comparisons to birds suggest that, in sauropods, cervical ribs formed as ossifications of the longus colli ventralis tendons, and may have functioned to maintain tension in the ventral portion of the neck. *Sauroposeidon* had a neck length of 11.25–12 m, stood approximately 17 m tall, and may have weighed as much as 50 or 60 metric tons. This specialized sauropod was one of the last sauropods in the Early Cretaceous of North America. The spread and dominance of angiosperms in the North American mid-Cretaceous postdates the decline of the Early Cretaceous sauropods, and is an insufficient causal explanation for the disappearance of these spectacular animals.

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Osteologia, paleobiologia i pokrewieństwa zauropoda *Sauroposeidon*

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Streszczenie

Sauroposeidon proteles to wielki dinozaur z rodziny brachiozaurów, opisany niedawno z formacji Antlers (apt–alb) z południowo-wschodniej Oklahomy (USA). Stanowi on kulminację widocznej u brachiozaurów tendencji do wydłużania szyi i zmniejszania jej ciężaru – kręgi szyjne odznaczają się intensywną pneumatyzacją. Rozrost worków powietrznych w kręgach szyjnych doprowadził do wytworzenia rozmaitych wariantów ich budowy wewnętrznej. Autorzy proponują nowy podział owych struktur anatomicznych, oparty na obserwacji tomograficznej spneumatyzowanych kręgów. Porównania z ptakami sugerują, że kręgi zauropodów mieściły rozbudowany system worków powietrznych obejmujących też tułów. Obecność piersiowo-brzusznych worków powietrznych oznaczałaby radykalne zmiany dotychczasowych oszacowań masy ciała, zapotrzebowania pokarmowego i wydolności oddechowej zauropodów. Zauroposejdon był jednym z ostatnich zauropodów zamieszkujących Amerykę Północną we wczesnej kredzie (we wczesnym cenomanie brak już zauropodów na tym kontynencie). Zniknięcie zauropodów z Ameryki Północnej poprzedziło większe radiacje adaptacyjne roślin okrytozalążkowych, toteż nie można wiązać upadku i zaniku tej grupy dinozaurów ze zmianami flory.