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THE EVOLUTION OF VERTEBRAL PNEUMATICITY IN THE SAUROPODA

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THE EVOLUTION OF VERTEBRAL PNEUMATICITY IN THE SAUROPODA

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DEPARTMENT OF ZOOLOGY

BY

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As a final note, I have previously published some preliminary results of this work in two manuscripts coauthored by Drs. Cifelli and Sanders (Wedel et al., 2000a, b). These manuscripts were submitted with the knowledge and approval of my thesis committee. Although Dr. Cifelli and Sanders made fundamental contributions to those works and to my ideas in general, the functional and evolutionary inferences drawn from analysis of sauropod vertebrae, which form the backbone of this thesis, are mine alone, along with any errors that appear herein. Where the material presented herein reflects the substantial input of Drs. Cifelli and Sanders, I cite it as Wedel et al. (2000b). This manuscript is formatted for the Journal of Vertebrate Paleontology, following the revised guidelines provided in the March, 2001 issue (Volume 21, Number 1).

A NOTE ABOUT THIS VERSION OF THE THESIS

This version of my master's thesis is slightly different from the version that I filed with the University of Oklahoma Graduate College in 2001. At the recommendation of Kevin Padian, I moved the section "Identification of Problematic Elements" from "Survey of Vertebral Pneumaticity in the Sauropoda" to "Materials and Methods". In the filed version, the figure captions were grouped together before the figures. In this version, I have placed each figure adjacent to its caption, so that if the thesis is printed front-and-back each figure and its caption will share a two-page spread. Finally, one or two extra pages (including this one) have been inserted to make the pagination work out for front-and-back printing.

The scientific content of the thesis is not changed at all. In the summer of 2001 I cut the thesis in half and submitted the halves to the Journal of Vertebrate Paleontology and to Paleobiology. The two papers were fortuitously printed within months of each other in 2003. The JVP paper is very little changed from the parts of the thesis from which it was drawn. The Paleobiology paper is substantially different. In particular, I didn't hit on the idea of pneumatic hiatuses until 2002, when the Paleobiology manuscript was going through its second round of peer review, so there is nothing about pneumatic hiatuses in the thesis.

Thank you for your interest.

Matt Wedel
May 26, 2007

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ABSTRACT

The vertebrae of sauropod dinosaurs are characterized by complex architecture involving laminae, fossae, and internal chambers of various shapes and sizes. These structures are interpreted as osteological correlates of an intricate system of air sacs and pneumatic diverticula similar to that of birds. In primitive sauropods, including *Jobaria* and *Haplocanthosaurus*, pneumatic features are limited to fossae. Although these fossae are morphologically simple, lacking the elaborate subdivision of pneumatic chambers observed in more derived taxa, the absence of similar fossae in the axial skeletons of ornithischians suggests that they are pneumatic in origin and not simply adaptations for mass reduction. A well-developed system of vertebral laminae was already present in primitive sauropods and also supports the interpretation of certain vertebral characters as products of pneumatization. Camerae and camellae are internalized pneumatic chambers independently acquired in neosauropods and some Chinese forms. The polycamerate and camellate vertebrae of higher neosauropods are characterized by internal pneumatic chambers of considerable complexity. The independent acquisition of these derived morphologies in *Mamenchisaurus*, advanced diplodocids, and most titanosauriforms is strongly correlated with increasing size and neck length.

The presacral vertebrae of primitive sauropods were probably pneumatized by diverticula of cervical air sacs similar to those of birds. Although pneumatic characters in sauropods are most extensive and complex in presacral vertebrae, the sacrum was also pneumatized in most neosauropods. Pneumatization of the proximal caudal vertebrae was achieved independently in diplodocids and titanosaurids. In birds, the synsacrum is pneumatized via abdominal air sacs which function primarily in lung ventilation. The presence of pneumatized sacral and caudal vertebrae in neosauropods indicates that abdominal air sacs may have been present in at least some sauropods. Postcranial pneumaticity in sauropods may have facilitated the evolution of extremely long necks in some sauropod lineages; thoracoabdominal air sacs would have overcome respiratory dead space, and the pneumatization of the axial skeleton would have reduced mass. The hypothesis that sauropods had thoracoabdominal air sacs is also supported by certain aspects of their paleobiology, especially the observed rapid growth rates.

INTRODUCTION

That sauropod vertebrae were pneumatic was recognized before the scientific community had any clear idea of just what a sauropod was; at least one early specimen was thought to pertain to a giant ally of the pterosaurs (Seeley, 1870). When Cope and Marsh described the first relatively complete sauropod specimens from the American West in the 1870s, they also noted that the vertebrae had well-developed pneumatic features (Cope, 1877; Marsh, 1877). Despite this promising early start, the possibility that sauropod vertebrae might have been pneumatic was largely ignored during the following century. Although the complex system of vertebral laminae was widely used as a systematic tool, later authors tended to acknowledge the weight-saving features of sauropod vertebrae without discussing the possibility of vertebral pneumaticity (e.g., Osborn, 1899; Hatcher, 1903a; Gilmore, 1925). The infrequent acknowledgment that sauropod vertebrae were probably pneumatic (Janensch, 1947; Romer, 1966) did little to alter the prevailing view of sauropods as swamp-bound sluggards; the vertebral air sac system was presumed to be an adaptation for maintaining buoyancy (see discussion in Coombs, 1975). Even after sauropods were recognized as fully terrestrial, giraffe-like herbivores (Bakker, 1971; Coombs, 1975), their complexly excavated vertebrae and elaborate spinal laminae continued to be viewed as anatomical curiosities, weight-saving features of undeniable taxonomic value but little significance otherwise.

In his survey of postcranial pneumaticity in the Archosauria, Britt (1993) described pneumatic features in the vertebrae of five sauropod genera, and noted that derived sauropods tend to have more complex pneumatic morphologies than do primitive taxa. At the time his work was the most detailed analysis ever performed of vertebral pneumaticity in sauropods. However, Britt acknowledged that much work remained to be done; in particular, he suggested that the distribution of specific pneumatic features within Sauropoda be determined and compared with hypotheses of sauropod phylogenetic relationships. That determination and comparison is precisely what I have attempted herein.

Some preliminary results from this study appeared in Wedel et al. (2000a, b). My purpose here is to greatly expand the number of genera discussed, to describe the pneumatic morphology of each genus in more detail, and to discuss the evolution and implications of vertebral pneumaticity in sauropods in a more comprehensive fashion.

MATERIALS AND METHODS

Vertebral Terminology

Janensch (1929, 1950) provided a comprehensive nomenclature for the laminae and cavities of sauropod presacral vertebrae. Wilson (1999) revised Janensch's nomenclature for laminae and provided a system of four-letter abbreviations to standardize discussion of these features. I follow that terminology when discussing the external laminae.

There has been no similar attempt sto standardize the nomenclature of the fossae that are bounded by the major laminae of saurischian vertebrae, and the creation of such a system is beyond the scope of this work. Gilmore (1936) named several of the more important fossae, including two that are of particular interest in the current study. One fossa is bounded by the prezygodiapophyseal, spinoprezygapophyseal, spinopostzygapophyseal, and postzygodiapophyseal laminae. This fossa occurs in the cervical and dorsal vertebrae of almost all sauropods and in the anterior caudals of diplodocids (see Wilson, 1999:fig. 4). In dorsal and sacral vertebrae, this cavity is divided by the spinodiapophyseal lamina into suprapre- and suprapostzygapophyseal cavities of Gilmore (1936). However, the spinodiapophyseal lamina is absent from cervical vertebrae, and the suprapre- and suprapostzygapophyseal cavities form a single broad fossa. This fossa is referred to herein as the supraprezygapophyseal cavity. The other fossa of interest is that bounded antero-dorsally by the postzygodiapophyseal and postcentrodiapophyseal laminae, and referred to as the infrapostzygapophyseal cavity by Gilmore (1936). Although alternate terminology may be applied to these cavities in the future, they can be recognized in cervical, dorsal, and caudal vertebrae if the bounding laminae are present. They are thus serially homologous throughout the vertebral column, meeting one of Wilson's (1999) criteria for appropriate vertebral nomenclature.

A stylized cervical vertebra illustrating some of the more important terms used herein is shown in Figure 1.

Britt (1993, 1997) provided the most comprehensive survey of postcranial pneumaticity in the Archosauria to date, and proposed terminology for discussing vertebral pneumatic spaces. Lateral excavations of saurischian vertebrae had previously been referred to as pleurocoels. The term pleurocoel was never rigorously defined, and was applied indiscriminately to a variety of pneumatic features including fossae, foramina, and camerae. Britt classified external pneumatic features as fossae or foramina, and proposed the terms camerae and camellae to describe internal pneumatic spaces (Fig. 2). Wedel et al. (2000b) proposed empirically-based definitions of fossae, camerae, and camellae based on geometry, size, septal thickness, degree of enclosure, and pattern of branching. These definitions and the rationale behind them are discussed below under ‘Defining Pneumatic Morphologies.’

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 and Sereno (1998) used centrum length divided by the height of the cotyle as a character in their analysis. I prefer the latter definition of this proportion, because 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, I therefore redefine the EI of Upchurch (1998) as the anteroposterior length of the centrum divided by the midline height of the cotyle, following Wedel et al. (2000b).

The arthrology and myology of sauropod vertebrae are also relevant to the following discussion, in that the origins and insertions of various muscles limit the extent of external air sacs. In addition, pneumatic features of sauropod vertebrae have occasionally been explained as muscle attachment points (see Bonaparte et al., 2000), and this point must be addressed in any discussion of vertebral pneumaticity. The extant phylogenetic bracket for sauropods consists of Crocodylia and Aves. Birds and sauropods share an elongated neck and pneumatized presacral vertebrae, which makes birds the most suitable models for interpreting the cervical series of sauropods and making inferences about soft-tissue anatomy. Zweers et al. (1987) provided a comprehensive nomenclature for the cervical musculature of birds, which I follow herein.

The abbreviations used in the figures are provided in Table 1.

Included Taxa and Sample Size

The taxa included in this study fall into three broad categories: those that I was able to image using computed tomography (CT), those that I personally examined but was not able to scan, and those for which observations or interpretations are based solely on available literature. The entry for each genus includes the methods of investigation available to me, with citations of key references. A list of the included taxa in their approximate phylogenetic position is provided in Table 2.

The following description and discussion hinge on those taxa for which vertebrae were available for CT scanning. This includes specimens from the BYU, CM, MAL, OMNH, and TMM collections, which are listed in Table 3. Two factors limited the sample size available for radiographic investigation. First, the logistics of transporting sauropod bones limited the number of institutions from which I could borrow specimens, as well as the size and number of specimens that could be borrowed. Second, the CT scanner used in this study has an aperture of 48 cm, limiting the radiographic study to specimens that did not exceed 48 cm in at least two dimensions. Although the following descriptions include cervical, dorsal, and caudal vertebrae, the radiographic study focused primarily on cervicals. Sauropod cervical vertebrae tend to be long, low, and roughly cylindrical, whereas dorsals tend to be both tall and wide because of their large neural spines and transverse processes. Thus for an individual of any given size, a cervical vertebra was more likely to fit through the CT scanner. Furthermore, Britt (1993) observed that in any given taxon or individual, pneumatic morphology tends to be the most complex in the posterior cervicals. This observation is supported by the results of this study. For some taxa, such as the brachiosaurids, even a single cervical was too large to be accommodated by the scanner in one pass, and such vertebrae had to be imaged in two or more scans. Many vertebrae with broken neural spines and diapophyses were included in the radiographic study because the loss of these peripheral elements made these specimens small enough to fit through the scanner. The proper identification of such incomplete specimens is discussed below.

Although the number of vertebrae that could be scanned for any given taxon was rather small, the CT study still included enough specimens that describing them all would be impractical. In the descriptions below, I have focused on one or more vertebrae from each taxon that illustrate the relevant morphologies.

In most cases, the illustrations derived from the CT scans do not include raw data. Where possible, matrix has been removed from the internal cavities, either digitally during imaging, or manually using Adobe Photoshop® version 5.5.

Identification of Problematic Elements

A significant portion of the specimens described below are from the vertebrate paleontology collection of the OMNH. Between 1935 and 1942, WPA crews working under J. Willis Stovall collected and prepared a vast amount of sauropod material from

Morrison Formation exposures in the Oklahoma panhandle. Most of the workers had only limited training and experience, and preparation techniques were necessarily primitive (Czaplewski et al., 1994). Perhaps as a result of incautious preparation, many of the vertebrae are missing the neural spines and cervical ribs. Accurate referral of these incomplete specimens is problematic, and a few are so incomplete as to preclude identification (see Table 3). However, vertebrae of *Apatosaurus* and *Camarasaurus* can be differentiated based on the orientation of the diapophyseal laminae (Fig. 6). Where possible, more complete and diagnostic material in other collections was also scanned to confirm the identification of the problematic elements.

Several of the OMNH specimens collected during the Stovall era were repaired with metal rods and wires of various sizes, which were plastered into the internal structure. The metalwork is radio-opaque and shows up clearly in the CT scans, but the resulting artifacts are small and generally do not prohibit identification of internal structures.

Radiographic Techniques

The radiographic techniques discussed herein were performed at the University Hospital and Veterans' Hospital, both on the University of Oklahoma Health Sciences Center campus in Oklahoma City. CT scans of sauropod vertebrae were performed using a General Electric 9800 Highlight Advantage® 4th generation CT scanner. Scout images were obtained in lateral or dorsal projection with a technique setting of 120 kVp (kilovolt peak) and 40 mA (milliamperes). Most axial images were produced at 120 kVp and 120 mA, although the size and density of the largest specimens required the maximum technique setting of 140 kVp at 170 mA. Data were reconstructed in bone algorithm using a Star Tech, Inc., One Sun® CPU computed tomography array imaging processor and the GE Advantage® version 1.0 imaging software package. Magnetic resonance imaging (MRI) scans of *Struthio* were performed on a 1.5 Telsa General Electric Signa® magnet to produce spin-echo T1 weighted images.

Institutional Abbreviations

BMNH, The Natural History Museum, London, UK; BYU, Brigham Young University, Earth Sciences Museum, Provo, Utah; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FWMSH, Fort Worth Museum of Science and History, Fort Worth, Texas; HM, Humbolt Museum, Berlin, Germany; MAL, Malawi Department of Antiquities, Lilongwe, Malawi; MN, Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MNN, Musée National du Niger, Niamey, Republic of Niger; MWC, Museum of Western Colorado, Grand Junction, Colorado; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma; PVL, Paleontología de Vertebrados de la Fundación Miguel Lillo, Argentina; TMM, Texas Memorial Museum, Austin, Texas; UMNH, Utah Museum of Natural History, Salt Lake City, Utah; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; WL, Wann Langston, Jr., Texas Memorial Museum, Austin, Texas.

POSTCRANIAL SKELETAL PNEUMATICITY IN EXTANT TAXA

Pneumatization of the postcranial skeleton in various ornithodiran groups, including sauropods, is just one aspect of the more general phenomenon of skeletal pneumatization. The phenomenon of skeletal pneumatization, which includes paranasal, paratympanic, and pulmonary pneumatic spaces, is unique to archosaurs and advanced synapsids (Witmer, 1997). In addition, diverticula of the pulmonary system that do not invade the skeleton are present in representative taxa from most major lineages of tetrapods, and are used in intraspecific or interspecific communication. These diverticula usually arise from the buccal cavity or trachea and are used to inflate specialized structures that are used in display or phonation, and are present in certain species of frogs (Duellman and Trueb, 1986), snakes (Young, 1992), birds (King, 1966; Fowler, 1991), and primates (Janensch, 1947). Such tracheal diverticula do not invade any bones except the hyoid, which is pneumatized in certain species of primates (Janensch, 1947).

Although paranasal and paratympanic pneumatization of the cranium is certainly relevant to skeletal pneumatization in general, the distribution and functions of cranial pneumatization have been thoroughly reviewed elsewhere (see Witmer, 1997 and references therein). Diverticula of paranasal and paratympanic air spaces may extend down the neck in some species of birds, but these diverticula are subcutaneous or intermuscular and do not pneumatize the postcranial skeleton (King, 1966). Extremely rare examples of cervical pneumatization have been reported in humans, but these are pathological cases related to occipito-atlantal fusion (Sadler et al., 1996). Among extant taxa, extensive pneumatization of the postcranial skeleton occurs only in birds. A survey of the distribution and morphology of postcranial pneumaticity in birds is fundamental to any discussion of postcranial pneumaticity in dinosaurs.

The Lung-Air Sac System of Birds

All birds have an extensive air sac system in the thorax and abdomen (Fig. 3). In contrast to the tracheal diverticula mentioned above, the thoracoabdominal air sacs of birds arise directly from the bronchi within the lungs (Duncker, 1971, 1972). There are typically nine thoracoabdominal air sacs, including one interclavicular air sac and paired cervical, anterior thoracic, posterior thoracic, and abdominal air sacs (Duncker, 1974), although this number is reduced in certain taxa by anteroposterior and lateral fusion of adjacent air sacs. The air sacs are present throughout the body cavity and enclose the viscera like a nut-shell (Wetherbee, 1951).

The primary function of the avian pulmonary air sac system is lung ventilation. The air sac system allows ventilation and gas exchange to be decoupled physically; the relatively inflexible lungs are ventilated by changes in air sac volume. The air sacs system is divided into two functional complexes, an anterior complex consisting of the cervical, interclavicular, and anterior thoracic air sacs, and a posterior complex consisting of the posterior thoracic and abdominal air sacs (Duncker, 1971, 1974).

Avian respiration is complex but now quite well understood (see Brackerbury, 1971; Bouverot and Dejours, 1971; Duncker, 1971, 1972, 1974; and Scheid et al. 1972), and merits only a brief description here. Inhalation is accomplished by expanding the air sacs, which draws air through the parabronchi of the lungs and into the air sacs. During exhalation, the air sacs are compressed and air also flows through the parabronchi. Airflow through the parabronchi is unidirectional during both inspiration and expiration. This unidirectional flow allows cross-current gas exchange between the air capillaries of the parabronchi and the capillaries of the circulatory system.

The constant airflow through the lungs and cross-current gas exchange allow birds to have much higher oxygen extraction than mammals (Bernstein, 1976). This greatly increased oxygen extraction allows birds access to physical regimes denied to other vertebrates. For example, geese regularly migrate over the Himalayas at altitudes exceeding 8850 m, whereas human climbers at similar altitudes cannot survive long without artificially supplied oxygen. Outside the lungs, gas exchange in the air sacs is negligible. Most extrapulmonary gas exchange occurs in the posterior thoracic sacs and accounts for less than five percent of the total (Magnussen et al., 1976).

In addition to their ventilatory function, air sacs overcome respiratory dead space in the trachea, which can be quite long in some species (Müller, 1907; Duncker, 1972). The air sacs are also important in thermoregulation. Birds dump exogenous heat through the air sac system through evaporation (Bernstein, 1976). Indeed, in the absence of significant evaporation through the skin, evaporative cooling in the air sac system is the only way for large subtropical birds to maintain a stable body temperature below high ambient temperatures (Schmidt-Nielsen et al., 1969). The complex architecture of lung-air sac system allows the lungs to be excluded from airflow during thermoregulatory panting to avoid respiratory alkalosis (Schmidt-Nielsen et al., 1969; Fowler, 1991).

Skeletal Pneumatization in Birds

The postcranial skeleton is pneumatized by diverticula of cervical, interclavicular, and abdominal air sacs (Müller, 1907; Hogg, 1984b; Bezuidenhout et al., 1999). Diverticula of the cervical air sacs pneumatize the cervical and anterior thoracic vertebrae. The posterior thoracic vertebrae, synsacrum, and hindlimb are pneumatized by diverticula of the abdominal air sacs. The interclavicular air sac pneumatizes the sternum, sternal ribs, coracoid, clavicle, scapula, and forelimb. The anterior and posterior thoracic air sacs lack diverticula (Müller, 1907; Bezuidenhout et al., 1999) and are excluded from the vertebral column by horizontal and oblique septa within the body cavity (Duncker, 1974), and consequently do not pneumatize any bones. The above list contains those bones known to be pneumatized in at least some bird species, but the extent of diverticula and hence pneumatization is quite variable in different lineages. For example, in diving birds such as the loon, there is no pneumatization of the postcranial skeleton whatsoever (Gier, 1952).

Although the paired thoracoabdominal air sacs are simple bags with no internal divisions, pneumatic diverticula consist of narrow pneumatic tubes. A single diverticulum may consist of several small pneumatic tubes separated by thin membranes of epithelial tissue, similar to camellae but lacking the surrounding bone structure (Fig. 4). A similar morphology is seen in the unpaired interclavicular air sac where it attaches to the sternum (Duncker, 1971). The diverticula pass intermuscularly following blood vessels and nerves, and enter bones at existing nutrient and nervous foramina (Bremer, 1940a, b; Rigdon, 1957; Duncker, 1971). The resulting pneumatic foramina occur at areas of low stress, and may shift position ontogenetically as the loading of a particular bone changes (Bremer, 1940b; Witmer, 1997). In addition, the pneumatic foramina may retain their original functions as inlets for blood vessels and nerves, so a given foramen may host circulatory, nervous, and pneumatic components.

The pneumatic diverticula cannot actually “invade” bones, they can only occupy space that has already been evacuated. Air pressure is unimportant in bone pneumatization, as demonstrated by the fact that diverticula may form embryonically prior to aeration of cavities (Witmer, 1997). Rather, an osteoclastic resorptive front resorbs the inner layer of periosteum, which is replaced by mesenchymal tissue (van Limborgh, 1970). This mesenchymal tissue is in turn displaced by the growing air sac (Bremer, 1940b). The osteoclastic resorption of bone ahead of the advancing air sac creates changes in bone histology similar to the effects of osteitis fibrosa cystica in mammals, and is evidently mediated hormonally (Bremer, 1940b).

Once the air sac has penetrated the cortical bone, erythropoietic bone marrow is replaced by pneumatic air spaces (Schepelmann, 1990). This replacement of bone marrow by air sacs means that marrow is restricted to bones that have not been pneumatized or which are only partially pneumatized (King and Kelly, 1956; Schepelmann, 1990).

As an air sac advances, it bypasses and envelops obstructions, which may be resorbed later or preserved as a system of trabeculae (Bremer, 1940b). The morphology of a pneumatized bone is partly a result of the competing mandates of pneumatic epithelium and developing bone. The pneumatic epithelium advances opportunistically and tends to pneumatize bones in an all-or-nothing fashion (Hogg, 1984b). At the same time, bone grows partly in reaction to biomechanical stress. This ‘competition’ between bone and air sacs tends to produce structures that appear mechanically optimal (Witmer, 1997). Furthermore, the interaction between bone and air sac is dynamic, and morphology may change in response to mechanical stress or injury, even late in life (Sadler et al., 1996; Witmer, 1997).

As mentioned above, the extent of pneumatic diverticula and thus pneumatization varies widely in different lineages of birds. In addition to these broad phylogenetic variations, within a single genus there is often significant variation at the individual, population, and species level (King, 1966; Hogg, 1984a, b). In *Gallus*, there is also some evidence for sex-related variation: the skeletons of males tend to be more completely pneumatized than those of females (King and Kelly, 1956; Hogg, 1984a). Furthermore, pneumatization of the postcranial skeleton occurs independently on either side via diverticula of the paired cervical and abdominal air sacs, which may account for high degrees of asymmetry observed within an individual (Hogg, 1984a).

Diverticula of the cervical air sacs pneumatize the cervical and anterior thoracic vertebrae, although the initial point of pneumatization may vary. In *Gallus*, the cervical vertebrae are pneumatized mid-series. Diverticula pneumatize C5-C9 before spreading to the rest of the cervical series and the anterior thoracic vertebrae (Hogg, 1984a). In the closely related *Meleagris*, the anterior thoracics are apparently pneumatized first, and diverticula spread to the cervical series later in ontogeny (Cover, 1953; Rigdon, 1957). The primary diverticulum is the diverticulum intertransversalis, which follows the brachial plexus and vertebral artery to advance through the transverse foramina (Fig. 5; see Müller, 1907 and Duncker, 1971). From these major diverticula on either side of the vertebral column, smaller diverticula contact the neural spine and enter the neural canal to form the canalis supramedullaris (Müller, 1907). Air sacs unite when they come into contact, forming a continuous supramedullary canal that extends along most or all of the spinal column (Cover, 1953). Before this invasion, the neural canal was completely filled by the spinal cord (Shapiro, 1992). The supramedullary canal may form parallel airways that vary in number. For example, there are two in *Columba* (Müller, 1907) and three in *Struthio* (Fig. 4).

The posterior thoracic vertebrae, synsacrum, pelvis and hindlimb are pneumatized by diverticula of the paired abdominal air sacs (Müller, 1907; Hogg, 1984a, b; Bezuidenhout et al., 1999). In *Struthio*, the posterior thoracics and synsacrum are pneumatized independently by extensions of the diverticulum perirenalia (Bezuidenhout et al., 1999). In *Gallus*, variable pneumatization along the synsacrum also indicates more than one diverticular invasion (see Hogg, 1984a:fig. 4).

The thoracic vertebrae are pneumatized by diverticula of two different air sacs. Anterior thoracic vertebrae are pneumatized directly from the cervical air sac (*Meleagris*) or by transverse and supramedullary diverticula advancing posteriorly from the cervical series (*Gallus*, *Struthio*). Posterior thoracic vertebrae are pneumatized by the diverticulum perirenalia or by vertebral diverticula advancing anteriorly from the synsacrum. If the cervical and abdominal diverticula meet, they may anastomose to form a continuous airway extending the entire length of the vertebral column (Cover, 1953).

Because of this dual pneumatization of the thoracic series from two different directions, the middle thoracics are occasionally incompletely pneumatized or not pneumatized at all (King and Kelly, 1956; Hogg, 1984a).

The internal structure of pneumatic bones varies depending on location and gross morphology. The diaphyses of the long bones tend to be filled by a single large chamber that is crossed by a variable number of thin, strut-like trabeculae (McGowan, 1991). The vertebrae, sternum, pelvis, and ends of the long bones are completely filled with a highly interconnected network of small camellae (see Figs. 4 and 5). Except the middle thoracics of some species, the vertebrae tend to pneumatize in an all-or-nothing fashion: camellae fill the entire internal volume of the centrum, condyles, cotyles, neural spine, zygapophyses, diapophyses, parapophyses, and cervical ribs. A striking example of the completeness of vertebral pneumatization is illustrated by Tompsett (1957:pl. 3).

In addition to their primary ventilatory function, the air sacs and their diverticula function in buoyancy, phonation and display, mass reduction, and thermoregulation (Witmer, 1997). These non-ventilatory functions of the air sacs are obviously exaptations of a primarily pulmonary system. Skeletal pneumatization, which results in significant mass reduction, is one of these exaptive aspects of the air sac system. However, given the apparent precision of hormonal control in the pneumatization of bone, its evolutionary origins remain mysterious (Bremer, 1940b; Witmer, 1997).

RECOGNIZING SKELETAL PNEUMATICITY IN FOSSIL TAXA

Soft tissues are only rarely preserved with fossil remains, and the delicate structure of pneumatic epithelium makes it highly unlikely that a preserved pulmonary system will ever be found for any fossil taxon. Therefore, recognition of skeletal pneumaticity involves a certain level of inference. The degree of inference involved can be determined using the Extant Phylogenetic Bracket (EPB) method described by Witmer (1997). The EPB of all ornithodirans, including sauropods, consists of Crocodylia and Aves.

Crocodylians, both extinct and extant, lack postcranial skeletal pneumaticity of any kind (Britt, 1993). Therefore postcranial skeletal pneumaticity cannot be assumed to be primitive for Archosauria, and its recognition in any fossil archosaur involves a level II inference sensu Witmer (1997). In the absence of convincing phylogenetic support, recognition of postcranial pneumaticity in fossil archosaurs must be based on compelling morphological evidence. “Causal association of hard and soft tissues is the key to the approach in that it allows the soft-tissue attributes to be tested for congruence across both extinct and extant taxa by using the osteological correlates as proxies for the soft tissues” (Witmer, 1997:7).

In his survey of postcranial skeletal pneumaticity in Archosauria, Britt (1993) listed five osteological correlates of pneumaticity: large foramina, fossae with crenulate texture, bones with thin outer walls, smooth or crenulate tracks, and internal chambers with foramina. These features are all present in the pneumatized bones of extant birds, and constitute the compelling morphological evidence by which potentially pneumatic features of fossil taxa may be evaluated.

SURVEY OF VERTEBRAL PNEUMATICITY IN THE SAUROPODA

Historical Context for Discussion

Early Work–Seeley (1870) was the first to recognize certain features of 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 characters. At the time, sauropods were very poorly known and pneumatic vertebrae were only known for pterodactyls and birds, so the referral was entirely appropriate given existing knowledge. Owen (1875) later demonstrated that the vertebrae belonged to a sauropod. Cope (1877) and Marsh (1877) recognized that the vertebrae of the sauropods *Camarasaurus* and *Apatosaurus* were pneumatic, respectively. Cope, in particular, considered the interpretation of the *Camarasaurus* vertebrae as pneumatic to be so obvious that he did not bother to defend it (Britt, 1993).

Longman, 1933–In his description of *Austrosaurus*, Longman noted the presence of both pneumatic fossae and camellae in the dorsal vertebrae. By comparison to the relatively few sauropods known at the time, he also established that sauropod vertebrae fell into two general categories, an open-chambered ‘phanerocamerate’ type and a cancellous ‘cryptocamarillan’ type (Longman, 1933:141). These terms are equivalent to the modern terms camerate and camellate, respectively, and Longman’s description and diagnosis is surprisingly cogent and accurate given how little he had to work with. Longman did not specifically discuss these internal structures as pneumatic in origin, and in fact he questioned whether the internal camellae were connected to each other or to the outside at all. However, he stressed the current and future utility of vertebral internal structure as a phylogenetic tool, saying, “the intramural complex of the vertebral centra exhibits diagnostic characters to which greater attention should be given” (Longman, 1933:141). Although Longman’s work was generally overlooked in later studies of vertebral pneumaticity (e.g. Janensch, 1947; Britt, 1993), his work in diagnosing vertebral internal structures and using them in phylogenetic comparisons was pioneering and deserves to be acknowledged.

Janensch, 1947–Although initially skeptical of the interpretation of sauropod vertebrae as pneumatic, Janensch became convinced of this in the course of his own study. Janensch cited three lines of evidence supporting the pneumatic interpretation: the presence of pleurocentral cavities, including fossae, camerae, and camellae, in the centra; the complex of fossae and laminae that comprise the neural arches; and the presence of fossae, foramina, and internal chambers in the ribs of certain taxa.

Although he mentioned at least ten genera of sauropods in his discussion, Janensch did not attempt to use pneumatic vertebral characters to assess sauropod phylogeny. Rather, his aims were to convince the scientific community that the pneumatic interpretation of the vertebrae of sauropods and other saurischians was well-founded, and to discuss the physiological implications of skeletal pneumaticity. Janensch felt that the function of vertebral pneumaticity in sauropods was to maintain buoyancy, in accordance with their presumed aquatic habits.

Janensch’s work is important because of his wide-ranging survey of skeletal pneumaticity, reliance on comparative anatomy for recognition of pneumatic features, and inquiry into the physiological functions of postcranial pneumaticity.

Britt 1993, 1997–In his survey of postcranial pneumaticity in Archosauria, Britt provided the most comprehensive analysis and discussion of the subject to date. Using dissections of extant ratites as a starting point, Britt identified five osteological correlates of pneumaticity that form the foundation for any attempt to identify pneumatic bones in fossil taxa (see above). Equally pioneering was Britt's use of CT scans to image and identify internal chambers in pneumatic bones. Perhaps the most fundamental of Britt's contributions was the creation of a specific and empirically-derived nomenclature for pneumatic characters. Prior to Britt's work, external features such as fossae and foramina were lumped together with internal features such as camerae and camellae under the all-purpose heading of 'pleurocoels.' 'Pleurocoels' are present in the vertebrae of all sauropods and theropods, so stating that a particular taxon has pleurocoels is a plesiomorphic description rather than an apomorphic diagnosis.

Britt described the pneumatic features of five sauropod genera: *Barapasaurus*, *Haplocanthosaurus*, *Camarasaurus*, *Euhelopus*, and *Diplodocus*. He noted that the pneumatic features of basal forms such as *Barapasaurus* and *Haplocanthosaurus* lacked the complexity observed in more derived taxa, but did not attempt to map pneumatic characters of sauropods onto a systematic framework, in part because sauropod phylogenetics were so poorly understood at the time. The intervening years have seen great advances in both sauropod systematics and CT technology, facilitating the present study. However, Britt's work remains the foundation and guidebook for current and future investigations of postcranial pneumaticity in fossil taxa.

Wilson, 1999–Using the work of Janensch (1929, 1950) as a starting point, Wilson proposed a comprehensive, landmark-based terminology for sauropod vertebral laminae, thus ending more than a century of nomenclatorial confusion. In addition, Wilson discussed two functional interpretations of vertebral laminae, as structural adaptations for resisting biomechanical stress and as osseous septa of pneumatic diverticula. Because the appearance of vertebral laminae in Saurischia and its outgroups predates the evolution of large size and long necks in some saurischian lineages, Wilson favored an interpretation of laminae as primarily pneumatic in origin, with a secondary structural function. The evolutionary implications of this interpretation are discussed below.

Description

The following description and discussion includes both those taxa which I was able to examine personally and those which were unavailable and had to be studied on the basis of available literature. No attempt has been made to describe the pneumatic features of all known sauropods, or to track down every published description of pneumatic morphology in sauropods. Rather, I have focused on the taxa that occupy key phylogenetic positions and are thus the most useful for determining the probable distribution and evolution of pneumatic characters in sauropod phylogeny. In addition, the laminar structure of sauropod vertebrae has been extensively described elsewhere (Wilson, 1999; Bonaparte, 1999), so the following description and discussion focus on vertebral internal structures (camerae and camellae) and their external correlates (fossae and foramina).

In the following description, the taxa studied are listed by genus in approximate phylogenetic order (see Table 2). This order is based primarily on Wilson and Sereno (1998), with supplemental information drawn from Salgado et al. (1997), Upchurch (1998), Sereno et al. (1999), and Wedel et al. (2000b). Where there is disagreement over the phylogenetic position of a particular genus (e.g. *Haplocanthosaurus*, *Euhelopus*), I follow Wilson and Sereno (1998). I do this to maintain consistency throughout the manuscript; the implications of both the phylogenies of Upchurch (1998) and Wilson and Sereno (1998) are outlined in the Discussion (see below).

Sauropoda

Taxon: *Vulcanodon*.

Key references: Cooper (1984).

Age: Early Jurassic, ?Hettangian.

Phylogenetic position: All of the most recent phylogenetic analyses posit *Vulcanodon* as the most primitive sauropod (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998).

Description: The posterior half of a cervical vertebra, QG-1406, is the sole presacral vertebra yet recovered for *Vulcanodon*. The vertebra is strongly waisted at its mid-point by deep fossae that penetrate to a median septum (Fig. 7). Similar but shallower fossae are also present in the proximal caudals. Cooper (1984) proposed that these fossae might represent precursors of the fossae and camerae of more advanced sauropods. The possibility that these fossae were pneumatic is discussed below.

Taxon: *Isanosaurus.*

Key references: Buffetaut et al. (2000).

Age: Late Triassic, late Norian or Rhaetian.

Phylogenetic position: The phylogenetic position of *Isanosaurus* has not been empirically tested. Buffetaut et al. (2000) described some features of *Isanosaurus* as comparable to those of basal sauropods such as *Vulcanodon*, *Gongxianosaurus*, *Barapasaurus*, and *Shunosaurus*, although others characters are more primitive than those of *Barapasaurus*. They referred *Isanosaurus* to Sauropoda incertae sedis. For the purposes of this discussion, *Isanosaurus* is regarded as a basal sauropod not more derived than *Barapasaurus*.

Description: The single available individual of *Isanosaurus* is a juvenile with unfused neural arches. Cervical and dorsal vertebrae have concave fossae on their lateral faces, which are neither as deep nor as complex as those of more advanced sauropods. In addition, simple laminae are present on a dorsal neural spine. These features are not present in the vertebrae of prosauropods, and support the referral of *Isanosaurus* to the Sauropoda. However, the juvenile status of the type material leaves open the possibility that adult individuals may have had more complex pneumatic morphologies, because large, simple fossae are a hallmark of most juvenile sauropods (see discussion below).

Eusauropoda

Taxon: *Barapasaurus.*

Key references: Jain et al. (1979), Britt (1993).

Age: Early Jurassic.

Phylogenetic position: Recent phylogenetic analyses recognize *Barapasaurus* as a basal eusauropod (Salgado et al., 1997; Wilson and Sereno, 1998), or as the sister group to Eusauropoda (Upchurch, 1998).

Description: The presacral vertebrae of *Barapasaurus* bear fossae on the lateral faces of the centra (Fig. 7). Some of these fossae are deeper than others, but at no point do the fossae on opposite sides approach each other closely enough to produce what might be termed a median septum. In addition, several of the dorsal vertebrae have hollow neural spines, the chambers of which communicate directly with the neural canal. Externally, laminae are present in the presacral vertebrae but the laminar system is less complex than that of more derived sauropods (Jain et al., 1979; Wilson, 1999).

Taxon: *Mamenchisaurus*.

Key references: Young and Zhao (1972), Russell and Zheng (1993).

Age: Late Jurassic.

Phylogenetic position: Phylogenetic analyses posit *Mamenchisaurus* as the sister taxon or close relative of *Omeisaurus*, which is a eusauropod more derived than *Barapasaurus* but less derived than basal neosauropods (Russell and Zheng, 1993; Upchurch, 1998; Wilson and Sereno, 1998).

Description: Young and Zhao (1972) described the vertebrae of *Mamenchisaurus hochuanensis* as follows. Two small, elliptical fossae are present on the lateral faces of the centra in the cervical series. The tops of the cervical neural spines are partially fenestrated. Internally, the cervical vertebrae are composed of elaborate, honeycombed laminae (trabeculae of Britt, 1993). The laminae of dorsal vertebrae are not well developed and the dorsal centra bear small fossae. Fossae are absent from the sacrum. Anterior caudal vertebrae are laterally concave, but lack distinct pleurocoels.

Russell and Zheng (1993:2089) provided the following description of the fourth cervical vertebra of *Mamenchisaurus sinocanadorum*.

> Cortical bone varies between 2 and 3 mm in thickness. The right lateral wall of the centrum is pierced by an anteriorly directed channel approximately 12 mm in diameter; the left wall is unbroken in the same region. There are no pleurocoel-like lateral cavities. Fractures indicate that the interior of the centrum is at least partly composed of small (13-15 mm in diameter), closely packed, longitudinal pneumatic tubes. These structures are very similar to, but about half as large as the honeycomb of elongate sinuses (diploe) in the back of elephant skulls.

Taxon: *Jobaria*.

Specimens studied: MNN TIG4, TIG5, and TIG6.

Technique: External examination.

Key references: Sereno et al. (1999), Sanders et al. (2000).

Age: Early Cretaceous, Hauterivian-Barremian.

Phylogenetic position: Sereno et al. (1999) posited *Jobaria* as the sister group to Neosauropoda.

Description: Pneumatic fossae are present in the centra of every postatlantal cervical vertebra (the atlas was not recovered). These fossae are usually extensive, occupying most of the lateral face of the centrum, and are subdivided into anterior and posterior cavities. The middle portion of the centrum is reduced to a narrow median septum. The condyles of some vertebrae are excavated by anterior extensions of the lateral fossae. Cervical vertebrae also have fossae in the supraprezygapophyseal cavities that are sharply lipped at their dorsal margins and occasionally subdivided by accessory laminae. In the dorsal series, pneumatic fossae are only present in the centra of anterior vertebrae. Sharply-lipped laminae are present in the neural spines of dorsal and sacral vertebrae.

Neosauropoda

Diplodocidae

Taxon: *Apatosaurus.*

Specimens studied: CM 87, 555 Df 3, 3390, and 11339; OMNH 01094, 01174, 01210, 01219, 01245, 01340, 01380, 01420, and 04173.

Technique: External examination, CT.

Key references: Marsh (1877), Gilmore (1936).

Age: Late Jurassic, Kimmeridgian-Tithonian.

Phylogenetic position: *Apatosaurus* is a crown-group diplodocid closely related to *Diplodocus* (Upchurch, 1998; Wilson and Sereno, 1998).

Description: The vertebrae of *Apatosaurus* are camerate, but they are more complex than the camerate vertebrae of less derived taxa. The lateral camerae branch within the centrum and give rise to successive generations of smaller camerae, usually with a bifurcating pattern of division. The small tertiary and quaternary camerae produced by these bifurcations fill the condyles, encircle the cotyles, and are variably present in the center of the centrum (Fig. 8). *Apatosaurus* is unique among the taxa described herein in that the arrangement of the camerae in the condyles and cotyles is roughly radially symmetrical.

The vertebrae of very immature specimens are characterized by large lateral fossae similar to those of *Pleurocoelus* (see discussion below). During ontogeny, these fossae develop into camerae. In some specimens, preservation is fine enough to record tiny (≤1 mm) coels in the bone near the developing camera (Fig. 9). Comparisons with birds suggest that these coels represent osteoclastic resorption in proximity to the advancing pneumatic epithelium.

Taxon: *Diplodocus.*

Specimens studied: BYU 12613, CM 33984, and OMNH 10333.

Technique: External examination, CT.

Key references: Osborn (1899), Hatcher (1901), Britt (1993).

Age: Late Jurassic, Kimmeridgian-Tithonian.

Phylogenetic position: *Diplodocus* is a crown-group diplodocid closely related to *Apatosaurus* (Upchurch, 1998; Wilson and Sereno, 1998)

Description: Like those of *Apatosaurus*, the vertebrae of *Diplodocus* are characterized by a camerate internal structure that exceeds the complexity seen in less derived taxa. Pneumatic features of *Diplodocus* are extensive; laminae and pneumatic foramina extend well into the caudal series (Fig. 10). Internally, the vertebrae of *Diplodocus* are, if anything, even more complex than those of *Apatosaurus* (Fig. 11). Division of the lateral camerae produces several generations of smaller chambers, but these tertiary and quaternary camerae are irregularly arrayed and lack the roughly radial symmetry of *Apatosaurus*. A few comparatively large camerae are present near the cotyle, but these do not form a radially-arranged ring as in *Apatosaurus*. There is also considerable elaboration of the external fossae and foramina by numerous accessory laminae. The median septum is rarely regular or symmetrical, regardless of ontogenetic stage (Fig. 12). Vertebrae of juveniles are less complex than those of adults, but still lack the regular bilateral or radial development of pneumatic chambers seen in *Apatosaurus*. It may be worth noting that the general lack of symmetry in the vertebrae of *Diplodocus* is more similar to the irregular development of camellae in Titanosauriformes than is the predictable development seen in *Apatosaurus*. These differing morphologies appear to represent different morphogenetic strategies in the two closely related diplodocids, but the functional significance associated with the difference is unknown at this time.

Macronaria

Taxon: *Haplocanthosaurus*.

Specimens studied: CM 879-7 and 572.

Technique: External examination, CT.

Key references: Hatcher (1903a), Britt (1993).

Age: Late Jurassic, Kimmeridgian-Tithonian.

Phylogenetic position: *Haplocanthosaurus* is either the sister taxon to Neosauropoda (Upchurch, 1998), or a basal neosauropod united with the camarasaur-brachiosaur-titanosaur group in the clade Macronaria (Wilson and Sereno, 1998).

Description: Pneumatic features in *Haplocanthosaurus* are limited to fossae. In cervical vertebrae, the lateral fossae penetrate to the median septum, but are not enclosed by ostial margins (Fig. 13). Extensions of each lateral fossa penetrate the condyles, but these extensions are not separated from the fossae by any sort of bottleneck that would constitute a foramen, as are the secondary and later camerae of the diplodocids described above. The dorsal vertebrae also bear large, simple fossae (Fig. 14). These fossae occur in the same location on the centrum as the foramina of truly camerate vertebrae, but do not open into any larger chambers; they are essentially deep depressions.

Taxon: *Camarasaurus.*

Specimens studied: CM 33929 and 36039; OMNH 01109, 01252, and 01313.

Technique: External examination, CT.

Key references: Cope (1877), Britt (1993).

Age: Late Jurassic, Kimmeridgian-Tithonian.

Phylogenetic position: *Camarasaurus* is a basal neosauropod more closely allied to the brachiosaurids and titanosaurids than to the diplodocids (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998).

Description: *Camarasaurus* is the prototypical camerate sauropod; large camerae are one of the hallmark characters of the genus. The large lateral camerae do give rise to secondary and even tertiary camerae in the condyles and variably along the median septum, but these later generations of camerae are neither as small or as numerous as those of the diplodocids (Fig. 15). Because the internal structure is relatively simple, the vertebrae of juveniles resemble smaller versions of the adult form with fewer generations of camerae.

Taxon: *Tendaguria.*

Key references: Bonaparte et al. (2000).

Age: Late Jurassic, Kimmeridgian-Tithonian.

Phylogenetic position: Bonaparte et al. (2000) compared *Tendaguria* to wide selection of sauropod taxa, but did not suggest an alliance with any one group. They noted that the dorsal vertebrae are superficially similar to those of certain titanosaurids, and that the cervical vertebra is more similar to *Camarasaurus* than to any other sauropod. For the purposes of this discussion, *Tendaguria* will be considered a neosauropod related to *Camarasaurus*, but readers should be aware that this referral is based more out of convenience than any other factor.

Description: The dorsal vertebrae of *Tendaguria* have large pneumatic fossae or foramina in the lateral faces of the centra. These features were described as ‘pleurocoelous cavities' by Bonaparte et al. (2000), hence the uncertainty over whether they are fossae or foramina. The neural arch laminae delimit several deep fossae; particularly noteworthy are those along the undersides of the transverse processes (Fig. 16).

A cervical vertebra referred to *Tendaguria* has complex fossae on the lateral faces of the centrum and in the supraprezygapophyseal and infrapostzygapophyseal cavities. Bonaparte et al. (2000) mentioned that these fossae are deep and penetrate to a median septum, but did not mention whether or not any camerae or camellae were present in the internal structure. The vertebra is unusual in that the fossae in the infrapostzygapophyseal cavity are so extensive. Fossae occur variably in this cavity in other sauropods (Fig. 17), but those of *Tendaguria* are larger, deeper, more numerous, and more complex than those of other sauropods.

Bonaparte et al. (2000) speculated that the fossae on the lateral faces of the centrum may have been apneumatic and served for muscle attachment. This hypothesis is discussed below.

Titanosauriformes

Brachiosauridae

Taxon: *Brachiosaurus.*

Specimens studied: BYU 12866 and 12867.

Technique: External examination, CT.

Key references: Janensch (1947, 1950).

Age: Late Jurassic, Kimmeridgian-Tithonian.

Phylogenetic position: *Brachiosaurus* is the most basal titanosauriform (Salgado *et al.*, 1997; Wilson and Sereno, 1998).

Description: Externally, both cervical and dorsal vertebrae of *Brachiosaurus* bear large foramina on the lateral faces of the centra (Figs. 18, 19). These foramina open into camerae that occupy most of the centrum and that penetrate to a narrow median septum. Although the camerae are large they do not occupy the entirety of the internal structure; the condyles, cotyles, and zygapophyses are filled with camellae (Fig. 20). In addition, camellae are also occasionally present along the median septum and in the neural spine. These camellae are larger and simpler than those of *Sauroposeidon* or more derived titanosaurians, but they can be distinguished from small camerae on the basis of their thin walls, irregular occurrence, and lack of branching pattern.

Taxon: *Sauroposeidon.*

Specimens studied: OMNH 53062.

Technique: External examination, CT.

Key references: Wedel et al. (2000a, b).

Age: Early Cretaceous, Aptian-Albian.

Phylogenetic position: *Sauroposeidon* is linked to *Brachiosaurus* by at least three synapomorphies, including mid-cervical vertebrae with an EI greater than 4, cervical ribs that equal or exceed three centrum-lengths, and a transition in neural spine height and form between C6 and C7 (Wedel et al., 2000b).

Description: The lateral faces of the centra and neural spines are occupied by large pneumatic fossae that penetrate to a narrow median septum (Fig. 21). These fossae are larger, deeper, and more elaborate than those of basal sauropods. 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 easily recongnizable on the basis of the crenulate, remodeled texture typical of pneumatized bone (Britt, 1993). 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* (see Janensch, 1950:fig. 5).

As revealed by CT, the vertebrae of *Sauroposeidon* are fully camellate. Because the specimen is so large and dense, a large portion of each cross-sectional slice is obscured by x-ray beam hardening artifacts, which show up as dark, radially-arranged streaks (Fig. 21). In regions not obscured by this artifact, the internal structure of the vertebrae is 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 thicker than 3 mm is in the cervical ribs, which are solid.

<u>Taxon:</u> Unnamed taxon, Croatia.

<u>Key references:</u> Dalla Vecchia (1998, 1999).

<u>Age:</u> Early Cretaceous, Hauterivian-Barremian.

<u>Phylogenetic position:</u> The assemblage described by Dalla Vecchia (1998, 1999) is almost certainly polyspecific: it contains elements referable to the Diplodocoidea and Titanosauriformes. This discussion will focus on only two elements, WN-V1 and MPCM-V2, which may or may not pertain to the same taxon. WN-V1 is very similar to the cervical vertebrae of *Brachiosaurus* and shares with *Sauroposeidon* an EI greater than 5. I therefore follow Dalla Vecchia (1998) in tentatively referring WN-V1 to the Brachiosauridae. MPCM-V2 is similar to the cervical vertebrae of *Chondrosteosaurus gigas* (see Owen, 1876), which has been referred to the Camarasauridae (McIntosh, 1990). However, *Chondrosteosaurus* is probably a titanosauriform (Dalla Vecchia, 1998), and the camellate internal structure of both *Chondrosteosaurus* and MPCM-V2

would seem to preclude a close relationship with *Camarasaurus*. Dalla Vecchia (1998) considered it unlikely that MPCM-V2 pertained to a brachiosaurid, because the centrum is relatively short and flat. The posterior dorsals of *Brachiosaurus* are also rather short (see Janensch, 1950), and the dorsoventral flatness of MPCM-V2 may be an artifact of its generally poor preservation. In general, I find MPCM-V2 more similar to the vertebrae of brachiosaurids than to those of any other group, and so for the purposes of the present discussion I lump WN-V1 and MPCM-V2 under the same heading and consider them to pertain to a brachiosaurid.

Description: WN-V1 is an anterior or middle cervical vertebra from a long-necked sauropod (Fig. 22). The fully fused neural spine indicates that the individual was mature, and its dimensions (centrum length of 350 mm) suggest a rather small animal, especially compared to *Brachiosaurus* and *Sauroposeidon*. The lateral surfaces of the centrum bear numerous small fossae and foramina that are smaller than those of *Brachiosaurus*. The cortical bone is missing from much of the right side of the vertebra, exposing an internal structure that consists of numerous small, antero-posteriorly oriented tubes. These camellae are smaller, more numerous, and more extensive than the camellae in the anterior centrum of *Brachiosaurus*. An internal pneumatic chamber is also evident inside a broken diapophysis.

MPCM-V2 consists of a centrum from a posterior cervical vertebra (Fig. 22). The neural arch and spine are missing, and the cortical bone is missing from the condyle and anterior centrum. The lateral faces of the centrum each bear three large, deeply invaginated fossae. These fossae do not penetrate to a narrow median septum as in the cervical and dorsal vertebrae of *Brachiosaurus*. Rather, the interior of the centrum is entirely composed of a honeycomb-like complex of camellae. As in WN-V1, many of these camellae are antero-posteriorly elongated.

Titanosauriformes incertae sedis

Taxon: *Pleurocoelus.*

Specimens studied: USNM 4946, 4968, 5640, 5641, 5675, 5678, 5705, and 6101.

Technique: External examination.

Key references: Marsh (1888), Lull (1911a, b), Salgado and Calvo (1997).

Age: Early Cretaceous, Aptian.

Phylogenetic position: Salgado and Calvo (1997) considered *Pleurocoelus* a titanosauriform close to the origin of Titanosauria. However, they uncritically assumed that all of the material referred to *Pleurocoelus* from the Arundel Clay, Cedar Mountain Formation, and Trinity Group pertains to a single, monophyletic genus. The referral of any material outside of the Arundel to *Pleurocoelus* is questionable (Tidwell et al., 1999; Wedel et al., 2000b). For the purposes of this discussion I accept the referral by Salgado and Calvo (1997) of the Arundel *Pleurocoelus* material to the Titanosauriformes, based on the morphology of referred appendicular elements.

Description: The type and referred vertebrae of *Pleurocoelus* from the Arundel Clay all pertain to juvenile individuals too young to have undergone neurocentral fusion, and the neural spine is unknown except in very distal caudals. The cervical, dorsal, and sacral vertebrae bear large lateral fossae that penetrate to a narrow median septum (Fig. 23). However, in the absence of adult material it is impossible to determine whether the lack of internalized pneumatic chambers is of phylogenetic or merely ontogenetic significance (see discussion below).

Taxon: Unnamed taxon, Jones Ranch, Twin Mountains Formation.

Specimens studied: FWMSH 'A' (see below).

Technique: External examination.

Key references: Winkler et al. (1997), Gomani et al. (1999).

Age: Early Cretaceous, Aptian-Albian.

Phylogenetic position: Preliminary analysis of the Jones Ranch sauropod indicates that it lies within Titanosauriformes, but outside Somphospondyli (Gomani et al., 1999). According to Gomani et al. (1999), it is unclear whether the Jones Ranch sauropod is more closely related to Brachiosauridae or Somphospondyli. Certain features of the taxon suggest a closer alliance to Somphospondyli than to Brachiosauridae (see below).

Description: The Jones Ranch sauropod has well developed laminae in the dorsal vertebrae, and apparently lacks camellae. The development of certain laminae suggests a closer alliance with basal titanosaurians than with brachiosaurids. Gomani et al. (1999) also describe the neural arch laminae of cervical vertebrae as being well-developed, unlike those of Somphospondyli.

A single cervical vertebra of a sauropod from the Jones Ranch quarry is on display at the Fort Worth Museum of Science and History, and is designated FWMSH 'A' for the purposes of this discussion, following Wedel et al. (2000b). This vertebra closely resembles cervical vertebrae of *Euhelopus* and the unnamed titanosaurid from Peirópolis, Brazil (Fig. 23; see Wiman, 1929, and Powell, 1987, respectively). Unlike the cervical vertebrae from those taxa, it has large foramina on the lateral faces of the centrum. These foramina are more similar to those of camerate taxa than those of camellate taxa, which is consistent with the lack of camellae described by Gomani et al. (1999). However, the cervical neural arch laminae are at least as reduced as those of *Euhelopus* and the Peirópolis titanosaurid, unlike the condition described by Gomani et al. (1999). If all of the sauropod material from the Jones Ranch quarry belongs to one species, that sauropod has an unusual combination of primitive characters (i.e. lack of camellae) and derived ones (reduced lamination on cervical neural arches). Although a more thorough analysis will have to await the publication of a full description of the material, the characters available at present suggest that the Jones Ranch sauropod is more closely allied to Somphospondyli than to Brachiosauridae. The implications of this are discussed below.

Somphospondyli

Taxon: *Euhelopus*.

Key references: Wiman (1929), Britt (1993), Wilson and Sereno (1998).

Age: Late Jurassic or Early Cretaceous (see discussion in Wilson and Sereno, 1998).

Phylogenetic position: The phylogenetic position of *Euhelopus* is currently debated. Upchurch (1995, 1998) considered *Euhelopus* part of a monophyletic and endemic radiation of Chinese sauropods, the Euhelopodidae, and closely related to the basal eusauropods *Shunosaurus*, *Omeisaurus*, and *Mamenchisaurus*. However, Wilson and Sereno (1998) cited 34 characters tying *Euhelopus* more closely to Titanosauria than to *Omeisaurus*, and considered *Euhelopus* the sister group to Titanosauria.

Description: The presacral vertebrae of *Euhelopus* are completely camellate. In addition, the laminae of cervical and anterior dorsal vertebrae are poorly developed compared to those of other sauropods. Both of these characters are synapomorphic for Somphospondyli and unite *Euhelopus* with the Titanosauria.

Titanosauria

Taxon: *Gondwanatitan*.

Key references: Kellner and Azevedo (1999).

Age: Late Cretaceous, Santonian-Maastrichtian.

Phylogenetic position: Kellner and Azevedo (1999) describe *Gondwanatitan* as a member of the Titanosauridae, being more derived than the primitive titanosaurians *Andesaurus* and *Malawisaurus* and less derived than the Saltasaurinae.

Description: Although the material currently available is not complete enough for a rigorous assessment, a partial cervical vertebra has a few, relatively large pneumatic chambers (Fig. 23). The thick cortical bone and presence of a distinct median septum suggest that these chambers are camerae rather than camellae.

Taxon: *Alamosaurus*.

Specimens studied: TMM 41398-1 and WL 362.

Technique: External examination.

Key references: Gilmore (1922, 1946).

Age: Late Cretaceous, Campanian-Maastrichtian (Sullivan and Lucas, 2000).

Phylogenetic position: *Alamosaurus* is a titanosaurid closely allied with the Mongolian *Opisthocoelicaudia* and the South American Saltasaurinae (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998).

Description: TMM 41398-1 consists of the neural spine of a dorsal vertebra. The distal end of the neural spine is broken away, revealing an internal structure that is entirely composed of camellae (Fig. 24). The laminar structure of the neural spine is poorly developed, and the neural spine resembles a partially inflated balloon in overall appearance. A partial cervical vertebra, WL 362, was also examined, but not figured because of its extremely poor preservation. Across most of the centrum the outer cortical bone is entirely missing, and the extremely dense matrix filling the internal camellae is exposed. The matrix casts of the small and irregular camellae, thus exposed, resemble petrified shag carpet.

Taxon: *Saltasaurus*.

Key references: Powell (1986, 1992), Sanz et al. (1999).

Age: Late Cretaceous, Campanian-Maastrichtian.

Phylogenetic position: *Saltasaurus* is generally regarded to be the most derived titanosaurid yet discovered (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998).

Description: The presacral, sacral, and proximal caudal vertebrae of *Saltasaurus* are fully camellate (Fig. 25). Fully camellate caudal vertebrae are autapomorphic for Saltasaurinae (*Saltasaurus* and *Neuquensaurus*). Furthermore, Sanz et al. (1999) mention that the ilium has a cancellous internal structure. This 'cancellous internal structure' is also used to describe the camellate vertebrae, and no distinction is made between the cancellous internal structure of the vertebrae and the ilium. It therefore seems reasonable to assume that Sanz et al. (1999) are actually reporting the presence of camellae in the ilium of *Saltasaurus*. If this is accurate, it is of tremendous importance, because it would represent the only recorded instance of appendicular pneumatization in a sauropod. However, the possibility of ilial camellae was not mentioned by Powell (1992) in his monographic description of the osteology of *Saltasaurus*. In addition, Sanz et al. (1999) did not discuss the 'cancellous internal structure' as pneumatic, and it is therefore difficult to determine at second hand whether they meant the apneumatic medullary bone typical for most vertebrates or the pneumatic camellate bone typical of advanced sauropods and birds.

Taxon: Unnamed taxon, Dalton Wells, Cedar Mountain Formation.

Specimens studied: BYU 7510/9443, 9458, 9460, 11302, and 14063 (but see below).

Technique: External examination.

Key references: Britt and Stadtman (1996, 1997), Britt et al. (1997, 1998).

Age: Early Cretaceous, ?Barremian-Aptian.

Phylogenetic position: Although the Dalton Wells taxon has not been included in a phylogenetic analysis, it is characterized by several titanosaurid synapomorphies (Britt et al., 1998).

Description: The Dalton Wells quarry has yielded elements pertaining to a camarasaurid, a titanosaurid, and possibly a brachiosaurid (B. Britt, personal communication). The titanosaurid is unusual in that it is fully camerate and apparently lacks camellae. When I examined the material, then housed in the MWC collections, vertebrae from both the camarasaurid and the titanosaurid were shelved together and lacked labels other than the specimen number. Therefore, I am certain at least some of the specimens listed above pertain to the camarasaurid. However, the fact that I cannot determine from my notes and photos alone which vertebrae pertain to the titanosaurid only highlights how similar the Dalton Wells titanosaurid is to camarasaurids in general. The *fully* camerate condition of the Dalton Wells taxon is so far unique among described titanosaurids.

DISCUSSION

Defining Pneumatic Morphologies

Pneumatic features, or features that may be interpreted as pneumatic, are present in the presacral vertebrae of all sauropods. In most sauropods, these vertebrae are hollowed 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, so the difference between small camerae and large camellae is vague. In addition, deep pneumatic fossae may be confused with camerae. Therefore, Wedel et al. (2000b) proposed that fossae, camerae, and camellae be differentiated on the basis of discrete criteria (Table 4).

Pneumatic fossae are lateral excavations that are broad in contour and are not enclosed by ostial margins to form a foramen. Camerae are pneumatic chambers enclosed by ostial margins that constitute 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 presence or absence of an identifiable branching pattern.

Wedel et al. (2000b) proposed these definitions to provide a more accurate, empirically based nomenclature for describing pneumatic internal structure. They considered that some cavities described by Britt (1993) as camellae are actually small camerae. For example, Britt described small cavities in the condyles and cotyles of

Diplodocus vertebrae as camellae, but their rounded margins, relatively thick septa, and bifurcating pattern of division suggest that they are small camerae rather than camellae (Wedel et al., 2000b).

Pneumatic characters are highly variable, both within species and serially within individuals (Britt, 1993; Curtice, 1998). In sauropod taxa I examined, internal pneumatic features are most complex in posterior cervical vertebrae. Some character combinations I describe may not exist throughout the presacral series. 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 5). In addition to the established terms camerate and camellate (Britt, 1993, 1997), Wedel et al. (2000b) proposed the new terms acamerate, procamerate, and semicamellate, which are defined below. They also recognized particularly derived subcategories within camerate and camellate morphologies, which were termed 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, they are provided here in order to describe the observed range of morphologies as precisely as possible.

The most primitive condition observed in sauropods is acamerate morphology, in which pneumatic fossae are present but do not significantly invade the centrum. This morphology is found in basal sauropods such as *Isanosaurus* and basal eusauropods such as *Barapasaurus* and *Shunosaurus*. In these taxa, pneumatic fossae are present as simple depressions on the lateral faces of the vertebral centra (Britt, 1993; Wilson and Sereno, 1998), and the centra are not deeply 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. This internal structure is exhibited by *Haplocanthosaurus*, which is either a derived eusauropod (Upchurch, 1998), or a primitive neosauropod (Wilson and Sereno, 1998). 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. 26). 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. 26; cf. Hatcher, 1901:pl. 7). Wedel et al. (2000b) proposed 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. 20). 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. 18) and dorsal vertebrae (Fig. 19). 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 fully camellate; the internal structure of the vertebrae is composed entirely of small pneumatic camellae. 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*. If *Sauroposeidon* evolved from a *Brachiosaurus*-like ancestor, the lateral pneumatic fossae were probably derived by reducing the ostial margins of the camerae to externalize the lateral air sacs.

Wilson and Sereno (1998) proposed the term Somphospondyli (“spongy vertebrae”) to describe the group [*Euhelopus* + Titanosauria]. Wilson and 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. Whereas camellate internal structure as defined by Britt (1993, 1997) has precedence over somphospondyli (used as a condition rather than a taxonomic group), Wedel et al. (2000b) recommended that the latter term be retained and used to designate only those camellate vertebrae that have the 'inflated' neural spines and reduced lamination characteristic of *Euhelopus* and the Titanosauria.

Trends Within Sauropoda

Ontogenetic Considerations–It is axiomatic that animals change as they grow, but ontogenetic variation poses a special problem in any analysis of vertebral pneumaticity. The interaction between the bone and air sac is dynamic and may be actively remodeled even late in life. Therefore, attempting to predict adult morphology from a juvenile specimen, or vice versa, is an exercise in futility unless the ontogenetic changes in a particular feature are well understood for closely related taxa. This problem is of considerable import in studies of sauropod evolution, because several key taxa are known only from juvenile material (e.g., *Isanosaurus, Lapparentosaurus, Phuwiangosaurus*; see Upchurch, 1998). The *Pleurocoelus* problem is a prime example of the hazards of attempting to draw phylogenetically significant information from juvenile material.

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 except in the posterior caudal vertebrae. The sacral and presacral centra are distinctive only in the large size of their pneumatic fossae; in fact, this is the sole diagnostic characteristic of the taxon.

Perhaps because of this lack of diagnostic characters, *Astrodon*/*Pleurocoelus* has been used a taxonomic dustbin for a variety of juvenile material, including vertebrae from young ornithischians (Galton, 1981). Juvenile sauropod vertebrae from the Upper Jurassic Morrison Formation were referred by Marsh (1896) and Hatcher (1903b) to *Pleurocoelus*. McIntosh (1981) considered these vertebrae to belong to *Camarasaurus*, and judged the enlarged pneumatic fossae to be a juvenile character. Carpenter and 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*. The same is true for cervical and dorsal vertebrae from juvenile individuals of *Phuwiangosaurus* described by Martin (1994). *Phuwiangosaurus* is probably a basal titanosauriform more closely allied to Titanosauria than to Brachiosauridae (Upchurch, 1998). These similarities between the vertebrae of juvenile sauropods in at least four nonoverlapping suprageneric taxa (Diplodocidae, Camarasauridae, Brachiosauridae, and Titanosauroidea) suggest that referrals made on the basis of cavernous juvenile vertebrae alone are unfounded (Fig. 27).

Given that vertebrae of juvenile *Apatosaurus* and *Camarasaurus* are characterized by the same large, simple fossae as those of *Pleurocoelus*, there is clearly no barrier to the ontogenetic derivation of camerate and even polycamerate morphologies from procamerate precursors. Indeed, the vertebrae of the youngest *Apatosaurus* individuals in this study are acamerate, and must have lacked any pneumatic features at an even earlier ontogenetic stage. This is obvious, but important, because if camerae can be derived from fossae ontogenetically then they can also be derived from fossae phylogenetically. Jain et al. (1979) maintained that the fossae in the vertebrae of *Barapasaurus* could not have been evolutionary precursors to the camerae of more derived forms because the two morphologies indicated different strategies for lightening the centrum. However, given that fossae may grade into camerae in an individual, either ontogenetically or serially (Britt, 1993), it is clear that fossae and camerae are not fundamentally different, but merely two points in a morphological continuum. Of greater import is the question of whether or not the fossae of primitive sauropods were, in fact, pneumatic; this will be dealt with in the next section.

The regular branching pattern of camerae in camerate and polycamerate forms suggests a clear ontogenetic pathway. First, the pneumatic diverticula would enter the vertebra on either side and replace most of the bony tissue of the centrum, producing the large, simple fossae seen in juveniles of *Apatosaurus* and *Camarasaurus*. As the vertebra grew from either end, an increasing thickness of bone would build up in front of, behind, and between the lateral fossae, which probably remained static for a certain amount of time. At some point the pneumatic epithelium would start expanding again, bifurcating and pushing its way into the new bone that had formed around it. If this cycle repeated several times, the result would be the regularly branching, polycamerate morphology observed in diplodocids (see Fig. 26). The simpler camerate morphology of *Camarasaurus* suggests a smaller number of growth cycles, and hence fewer generations of camerae.

This leapfrogging of bone and air sac could also explain the growth of the ostial margins that enclose the camerae; they are all that is left of the solid bone that once lay above and below the primitive fossae. Alternately, the ostial margins may have grown out from the centrum to enclose the growing air sac. Certainly the interaction of bone and air sac must have been more complex than the simple model suggested here; how else to account for the derivation of a variable number of foramina from a single, juvenile fossa? Unfortunately, the ontogeny of camerate morphologies may be difficult to test empirically, because all extant avians are camellate.

The ontogenetic development of camellate morphologies in sauropods is also mysterious, but for the opposite reason. Whereas extant camellate forms (i.e., birds) abound, juveniles of camellate sauropod taxa are rare. The few juvenile titanosaurids that have been found are in museums outside the U.S., and I have not had the opportunity to examine them. In birds, camellae develop very early in ontogeny and the vertebrae increase in size by several factors after pneumatization. However, it is not clear whether the camellae grow together with the vertebrae or whether the entire system is continuously remodeled throughout ontogeny. The dynamic potential of the bone/air sac interaction certainly makes the latter a viable possibility. Of particular interest will be the eventual elucidation of the ontogeny of semicamellate forms such as *Brachiosaurus*. Do the camellae initially form as branches of the lateral camerae? Does the complex system of camellae develop before pneumatization takes place? The answers to these questions will have to await the discovery of a fairly complete growth series of a semicamellate taxon, but they promise to clear up much of the uncertainty regarding the ontogenetic and phylogenetic derivation of camellate morphologies in general. Finally, separating ontogenetic noise from phylogenetic signal will be one of the key tasks for any future study of postcranial pneumaticity.

Recognizing Skeletal Pneumaticity Revisited: Were Pneumatic Fossae Actually Pneumatic?–The pneumatic features of primitive sauropods are limited to fossae. These fossae range from shallow depressions, as in *Barapasaurus* (Jain et al., 1979), to deep excavations that penetrate to a narrow medium septum, as in *Haplocanthosaurus* (Britt, 1993). Although these fossae are not as obviously pneumatic as the internalized chambers of more advanced sauropods, they were nonetheless pneumatic. If the fossae were simply apneumatic adaptations for mass reduction, we would expect to see similar structures in the largest prosauropods, hadrosaurs, and proboscideans, all of which had apneumatic postcranial skeletons and equaled or exceeded primitive sauropods in size. The absence of such fossae in these non-sauropod taxa is evidence that their appearance in sauropods is related to more than simple mass reduction. In addition, even the most basal sauropods have vertebral laminae (Wilson and Sereno, 1998), which probably evolved initially to partition pneumatic diverticula (Wilson, 1999). Finally, in more advanced taxa fossae may grade into camerae either ontogenetically or serially, indicating that the difference between fossae and camerae is one of degree (Britt, 1993).

Two possibilities exist. One is that the fossae of primitive sauropods constitute a novel adaptation for mass reduction, which failed to evolve in equally large taxa outside Sauropoda, and which are totally unrelated to the more obviously pneumatic features of primitive sauropod vertebrae, such as the neural spine laminae and supramedullary chambers in *Barapasaurus*. Alternatively, the fossae of primitive sauropods are osteological correlates of a system of pneumatic diverticula, which was probably present in basal forms, based on the occurrence of laminae and supramedullary chambers. Based on the available evidence, the latter hypothesis is clearly better supported.

Even the more complex and invasive fossae of neosauropods have not been universally regarded as pneumatic in origin. Bonaparte et al. (2000) speculated that the fossae of *Tendaguria* may have been muscle attachment sites rather than pneumatic features, but do not cite any evidence to support such an interpretation. Indeed, the muscular hypothesis is a poor alternative to the pneumatic hypothesis. No muscles attach to the equivalent position in the vertebrae of birds (Zweers et al., 1987), and the lateral faces of the centrum are largely occupied by the cervical diverticula (see Figs. 4 and 5). On the other hand, several muscle attachment sites in sauropod vertebrae can be homologized with those of birds (Wedel et al., 2000b), and these attachment points are usually marked by reactive bone growth rather than pitting. Pitting is more typically associated with excessive strain or trauma at the interface between bone and tendon or bone and ligament (see Iscan and Kennedy, 1989, and references therein). Even when pitting does occur, it does not penetrate to the center of a bone except in cases of severe infection. In short, no known or inferred muscle originated or inserted at the location of the fossae, and if one had, it would have left different osteological traces. Using the criteria of Britt (1993) and Witmer (1997), the fossae are best explained as osteological correlates of pneumaticity.

Evolution of Pneumatic Morphologies Within Sauropoda–From the outset, one of the goals of this project was to determine how many times various pneumatic characters evolved in sauropod evolution, and to compare the distribution of pneumatic morphologies with currently accepted hypotheses of sauropod relationships.

The two most comprehensive treatments of sauropod systematics in recent years are the cladistic analyses presented by Upchurch (1998) and Wilson and Sereno (1998). The two studies agree on most points, positing *Vulcanodon*, *Barapasaurus*, *Omeisaurus*, the diplodocids, *Camarasaurus*, and Brachiosauridae as successively closer outgroups to Titanosauria. However, the positions of certain taxa such as *Haplocanthosaurus* and *Euhelopus* vary between the two studies. Because the positions of these taxa influence the inferred evolution of pneumatic characters within Sauropoda, I will compare the results of my survey of vertebral pneumaticity with both phylogenies.

Upchurch (1998) placed *Haplocanthosaurus* outside Neosauropoda, and grouped *Euhelopus* with an endemic radiation of Chinese sauropods including *Shunosaurus*, *Omeisaurus*, and *Mamenchisaurus*. This distribution of taxa requires two independent acquisitions of camerae, once in the Chinese sauropods and once in Neosauropoda (Fig. 28). In fact, camerae are synapomorphic for Neosauropoda if this phylogeny is accurate. Camellae also evolved independently a minimum of two times, once in the Chinese sauropods and at least once in Titanosauriformes.

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 and Azevedo, 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 has large pneumatic chambers with thick septations (Fig. 23). Thus *Gondwanatitan* may be a camerate titanosaur. In addition, a sauropod from the Dalton Wells Quarry, Utah, is characterized by several titanosaurid apomorphies (Britt and 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, pers. comm.), demonstrating that at least some titanosaurids had camerate vertebrae.

On the other hand, all known brachiosaurids have camellae, as do the crown-group titanosaurids such as *Alamosaurus* and *Saltasaurus*. Camellae may be synapomorphic for Titanosauriformes, and the camerate taxa listed above may represent numerous reversals. Alternatively, camellae may have evolved independently in Brachiosauridae and within Titanosauridae, and the more basal titanosauriforms may have been primitively camerate. Until one of these hypotheses is supported by a more detailed analysis, it is best to regard the basal titanosauriforms as equivocal with respect to the evolution of camellae.

The results of Wilson and Sereno (1998) differ from those of Upchurch mainly in the alternative placement of *Haplocanthosaurus* and *Euhelopus* (Fig. 29). Wilson and

Sereno (1998) consider *Haplocanthosaurus* to be a basal Macronarian, a neosauropod more closely allied to Titanosauriformes than to Diplodocoidea. The procamerate morphology of *Haplocanthosaurus* suggests that camerae are not synapomorphic for Neosauropoda, and evolved independently in the Chinese forms, Diplodocoidea, and Macronaria. Wilson and Sereno (1998) also group *Euhelopus* with Titanosauria. That the camellate *Euhelopus* is bracketed by camerate taxa such as the Jones Ranch and Dalton Wells forms supports the earlier assertion that the evolution of camellae within Titanosauriformes was complex, and that the condition in basal titanosauriforms is best regarded as equivocal for the present.

Regardless of which phylogeny is preferred, it is clear that camerae and camellae each evolved more than once in sauropods. The Chinese sauropods, derived diplodocoids, brachiosaurids, and some titanosaurians were all relatively long-necked (see Powell, 1986, 1987; Wilson and Sereno, 1998). The presence of complex polycamerate and camellate internal structures in these taxa is thus strongly correlated with neck elongation. Although it has not yet been tested, it is likely that ‘honeycombed’ polycamerate and camellate structures are biomechanically more efficient than ‘I-beam’ camerate structures, and that acquisition of the more complex morphologies facilitated the evolution of the spectacularly long necks observed in certain lineages.

Distribution of Vertebral Pneumaticity and its Implications–The pattern of vertebral pneumatization in sauropod evolution is similar to that seen during avian ontogeny, and allows us to speculate about the nature and extent of the thoracoabdominal air sac system. In primitive sauropods such as *Jobaria*, pneumatic fossae occur only in the cervical and anterior thoracic vertebrae (Sereno et al., 1999). In most neosauropods, the posterior thoracic and sacral vertebrae are also pneumatized. Derived diplodocoids and titanosaurians independently acquired pneumatized caudal vertebrae (Britt, 1993; Sanz et al., 1999). This caudad progression of vertebral pneumaticity in sauropod phylogeny is mirrored in avian ontogeny. In extant birds, the cervical and anterior thoracic vertebrae are pneumatized first, via diverticula from the cervical air sacs (Hogg, 1984b; Bezuidenhout et al., 1999). Diverticula of the abdominal air sacs pneumatize the posterior thoracic vertebrae and synsacrum later in ontogeny. It therefore appears likely that cervical air sacs were present in all sauropods, and abdominal air sacs were probably also present in most neosauropods. A similar caudad progression of pneumatized vertebrae, and hence air sacs, also occurred in the evolution of theropods (Britt, 1993).

Evolution of Postcranial Pneumaticity Within Ornithodira

Sauropods are not the only fossil archosaurs with pneumatic postcranial skeletons. Postcranial pneumaticity is also present in pterosaurs and theropods (Fig. 30), but lacking in ornithischians and, probably, prosauropods (see discussions in Britt, 1993, 1997). This distribution of postcranial pneumaticity is puzzling. The same morphologies and trends observed in sauropods are also present in theropods and pterosaurs (Britt, 1993), and it seems unlikely that the same complex system would have evolved more than once, let alone three times. On the other hand, it appears equally unlikely that an adaptation as potentially useful as skeletal pneumatization would be lost in successful, diverse lineages. Inferences drawn from vertebral characters and from studies of birds may shed some light on the situation.

In his analysis of vertebral laminae in Saurischia, Wilson (1999) discussed two functional interpretations of vertebral laminae, as structural adaptations for resisting biomechanical stress and as bony partitions of vertebral air sacs. He also noted that the two functions are not mutually exclusive; in fact, alignment of bony components to resist biomechanical stress appears to be a fundamental property of the bone/air sac interaction (Witmer, 1997). Because the appearance of vertebral laminae in Saurischia and its outgroups predates the evolution of large size and long necks in some saurischian lineages, Wilson favored an interpretation of laminae as primarily pneumatic in origin, with a secondary structural function. One consequence of this interpretation is that the origin of vertebral pneumaticity must have occurred at about the same time as the origin of Saurischia. But where did the vertebral diverticula come from?

Although the thoracoabdominal air sacs of extinct taxa cannot be observed directly, their presence can be inferred from osteological correlates and by comparative studies with birds (Fig. 31). The postcrania of birds are pneumatized by diverticula of the thoracoabdominal air sacs, not by the airsacs themselves. The thoracoabdominal air sacs must be present before the skeleton can be pneumatized. Furthermore, a complete and functional system of thoracoabdominal air sacs can be present without pneumatizing the skeleton, as in the loon (Gier, 1952).

These observations of extant taxa have important implications for fossil forms. First, it is clear that the evolution of thoracoabdominal air sacs must predate the first appearance in the fossil record of a taxon with pneumatic postcranial bones. Second, because thoracoabdominal air sacs had to originate before the evolution of skeletal pneumaticity, they must have initially evolved for some purpose other than pneumatizing the skeleton. This other purpose was probably not mass reduction. Thoracoabdominal air sacs alone merely displace soft tissues outward; mass reduction is achieved by the diverticula invading the skeleton and actively replacing tissue, which could only have happened later. Nor is it likely that the ancestral thoracoabdominal air sac system evolved primarily for thermoregulatory purposes. The thermoregulatory advantages conveyed on birds by their air sac systems are directly tied to the ventilatory function of the air sacs. Without adequate ventilation, the primitive air sacs would have been of dubious thermoregulatory value. It therefore appears most likely that air sacs initially evolved to fulfill the same purpose they serve in modern birds: to ventilate the lungs. Between the simple septate lungs of extant "reptiles" and the fully evolved air sac system of modern birds, there must have existed an entire spectrum of intermediates. Although the air sac systems of basal ornithodirans would not have been as complex or efficient as those of modern birds, there is no logical reason why they could not have become so in the course of the dinosaurian radiation. And obviously, in time, they did.

All of this still leaves open the question of why pneumatization of the postcranial skeleton apparently never occurred in Ornithischia. The 'invasion' of bone by pneumatic epithelium is essentially opportunistic (Witmer, 1997). Although pneumatic diverticula may radically remodel both the exterior and interior of an affected bone, this remodeling cannot occur if the diverticula never come into contact with the bone. The anterior and posterior thoracic air sacs of birds do not pneumatize any bones because they are excluded from the bony skeleton by the horizontal and oblique septa (Duncker, 1974; also see Müller, 1907, and Bezuidenhout et al., 1999). Furthermore, for all of the potential advantages it conveys, skeletal pneumaticity is still an exaptation of a pre-existing system; in an adaptive sense, lineages that lack skeletal pneumaticity don't know what they're missing. It is possible that at some intermediate stage along the line from septate lung to lung/air sac system, the viscera of primitive ornithischians became arranged in such a way that the primeval air sacs were excluded from the skeleton, and so postcranial pneumaticity never developed. It is pointless to dwell on the advantages that ornithischians 'lost' by never developing postcranial pneumaticity, because that development would have hinged on the incidental contact of bone and air sac and could not have been anticipated or sought by natural selection.

Paleobiological Implications: Air Sacs and Metabolism

The possibility that dinosaurs might have had metabolic rates equivalent to modern endotherms, or at least intermediate between those of endotherms and ectothermic reptiles, was widely debated in the late 1970's (see Thomas and Olson, 1980, and references therein). However, even after it became fashionable to envision most non-avian dinosaurs as endotherms or 'intermediates,' sauropods were still viewed as being essentially reptilian in metabolic strategy, or 'warm-blooded' only by virtue of inertial homeothermy (Dodson, 1990; see discussion in Paul, 1998). The tremendous heat buildup in such enormous animals was frequently cited as evidence that sauropods could not possibly have been endothermic (e.g., Spotila et al., 1991).

That sauropods had a highly pneumatic vertebral column and probably a thoracoabdominal air sac system rarely figured in these discussions. The existence of such air sac systems is supported not only by osteological correlates, but also by the timing of acquisition of pneumatic vertebral characters in sauropod evolution. Acknowledging the probable existence of thoracoabdominal air sac systems in sauropods profoundly affects much of what has been proposed regarding their physiology.

If sauropods and theropods had thoracoabdominal air sac systems similar to those of extant birds, we might expect to see some evidence that their metabolic rates were elevated above the basal reptilian condition. Although it is still hotly debated, considerable evidence indicates that theropods had, if not endothermic, then at least ‘intermediate’ metabolic rates (Farlow and Brett-Surman, 1997, and references therein). Sauropods, on the other hand, have traditionally been viewed as ‘gigantotherms,’ whose sheer size made elevated metabolic rates unnecessary or impossible (Dodson, 1990; Spotila et al., 1991). However, discoveries within the past two years suggest that it is time to rethink sauropod metabolism.

Recent studies of bone histology of North American and African sauropods indicate that they reached sexual maturity in 8-12 years and attained full adult size in about two decades (Curry, 1999; Sander, 2000). These sustained rapid growth rates approach those observed in modern birds. The apparent rapid growth of sauropods cannot be explained by inertial homeothermy, which would not have conferred significant metabolic advantages on hatchlings and juveniles. Generally favorable Mesozoic climates are also an insufficient causal explanation, because extant tropical ectotherms have much lower growth rates than those inferred for sauropods.

The traditional view of sauropods as ectotherms rests on three assumptions: that the caloric intake of sauropods was insufficient to support endothermy (Weaver, 1983), that their respiratory systems were likewise inadequate (Hengst and Rigby, 1994), and that the endogenous heat loads associated with endothermy were incompatible with sauropod gigantism (Spotila et al., 1991). None of these assumptions is well supported by available evidence.

Extant elephants and giraffes have to spend the majority of their waking hours gathering food (Weaver, 1983). If sauropods gathered food at the same rate as an elephant or giraffe, as has been alleged, they could not have gathered enough food to sustain endothermy. However, the food-gathering apparatus of most sauropods was much larger, in an absolute sense, than that of an elephant or giraffe (Paul, 1998). More obviously, most sauropods did not perform significant oral processing (Christiansen, 2000; Upchurch and Barrett, 2000), which would greatly increase the rate at which they could gather food compared to large extant mammals.

The assertion that the respiratory systems of sauropods were inadequate to sustain endothermy is based on the assumption that their lungs were essentially identical to those of modern crocodilians (Hengst and Rigby, 1994). No morphological evidence has been cited to support this assumption. Rather, the morphological and phylogenetic development of vertebral pneumaticity in sauropods suggests that their respiratory systems were more similar to those of birds than to those of crocodiles. Diaphragmatically-driven respiratory systems have been postulated for some theropods

(Ruben et al., 1999), but the ‘piston’ has no muscular attachment to the pubis (Hutchinson, 2000). Furthermore, a hepatic-piston diaphragm would exclude the lungs or air sacs from the posterior thoracic vertebrae, and the pneumatization of these vertebrae in many theropods and sauropods is evidence against a hepatic piston in saurischians (Christiansen and Bonde, 2000). Even if sauropods had diaphragmatically driven respiratory systems, such systems are also present in mammals and are clearly no barrier to endothermy.

It has also been argued that the respiratory dead spaces associated with the long necks of sauropods would have prohibited elevated metabolic rates (Gale, 1997, 1998). However, the studies in question explicitly assumed that the respiratory systems of sauropods could be approximated by scaling up monitor lizards to dinosaurian proportions. Using the monitor lizard model, Gale concluded that sauropods either had pharyngeal slits at the base of their necks (1997), or used between 50 and 100 percent of their metabolic energy for lung ventilation (1998), neither of which seems possible, let alone likely. The air sac systems of sauropods may not have been as complex as those of extant birds, but the preponderance of osteological evidence suggests that sauropods were closer to the ‘bird’ end of the morphological spectrum than to the ‘monitor’ end. In birds, the air sacs are sufficient to overcome respiratory dead space. The presence of similar air sacs in sauropods, based on morphological evidence presented herein, provides a far more plausible explanation as to how they were able to breathe through their anomalously long necks.

Spotila et al. (1991) modeled the physiology of *Apatosaurus* and concluded that sauropods could not have had elevated metabolic rates because they couldn't dump heat fast enough to prevent lethally high body temperatures. It was explicitly assumed in that study that *Apatosaurus* had the respiratory system of an 18-ton sea turtle. Once again, osteological evidence suggests that birds are much more suitable as extant analogues for the respiratory physiology of sauropods. As described above, birds dump heat by evaporation in their air sacs, and this form of thermoregulatory cooling is more efficient than that of mammals (Schmidt-Nielsen et al., 1969). This is probably because the air sacs of birds lie between the skeletal muscles and the viscera and can therefore cool the body core directly, whereas mammals must rely on evaporation from more peripheral sites. Future studies of sauropod thermal physiology should at least acknowledge the possibility of efficient, avian-style thermoregulation.

Complicating the picture is the fact that most published estimates of sauropod digestive, respiratory, and thermal physiology (e.g. Daniels and Pratt, 1992; Paladino et al., 1997) have assumed body masses that greatly exceed those obtained from rigorous volumetric estimates (Paul, 1997; Henderson, 1999). The presence of vertebral and thoracoabdominal air sacs in sauropods would have greatly increased the volume of air inside the body and further reduced body mass (Wedel et al., 2000b).

In summation, the traditional arguments for ectothermy in sauropods are largely based on flawed assumptions and inappropriate choices of extant analogs, and are not supported by morphological evidence. More seriously, they fail to explain the observed rapid growth rates in sauropods, which constitute the best available evidence that sauropods were either endothermic or at least intermediate in metabolic strategy.

Elevated metabolic rates in sauropods were probably facilitated by thoracoabdominal air sac systems. Rather than being an aberrant feature solely related to mass reduction, the postcranial pneumaticity of sauropods may be the key to understanding their continued success throughout the Mesozoic.

CONCLUSIONS

The complex external and internal features of sauropod vertebrae are best explained as osteological correlates of skeletal pneumatization. Extant birds are the most appropriate models for understanding the ontogenetic and phylogenetic development of postcranial pneumaticity in sauropods. The evolution of vertebral pneumaticity in sauropods was complex, and most features evolved several times. The evolution of extensively subdivided internal structures in mamenchisaurs, diplodocids, brachiosaurids, and some titanosaurians is correlated with increasing body size and neck length, and suggests that these complex morphologies were mechanically more efficient than the fossae and simple camerae of less derived taxa.

The evolutionary pattern of pneumatization along the axial column in sauropods suggests the presence of both cervical and abdominal air sacs, although the latter were either absent in basal sauropods or failed to pneumatize any bones. Although it may have been less complex and extensive than that of birds, a thoracoabdominal air sac system was definitely present in sauropods. The irregular distribution of postcranial pneumaticity within Ornithodira suggests that the evolution of air sacs within the group was complex. The fact that some groups lacked postcranial pneumaticity is best viewed in light of the exaptive and opportunistic nature of skeletal pneumatization in general.

Ornithodirans, saurischians, and sauropods are all characterized by having longer necks than their immediate outgroups (Gauthier, 1986; Sereno, 1991; Wilson and Sereno, 1998). The continuing trend toward neck elongation in these nested clades may have been related to the progressive evolution of postcranial pneumaticity in the same groups. Air sac systems would have facilitated the evolution of progressively longer necks, first by overcoming tracheal dead space, and later by pneumatizing the axial skeleton, thereby reducing mass. This timing is dictated by the fact that skeletal pneumatization is exaptive; air sacs can be present without pneumatizing the skeleton, but skeletal pneumaticity cannot be present without air sacs.

It therefore seems likely that the air sac systems of ornithodirans evolved primarily for lung ventilation, and this adaptation may have been one of the keys to the success of the group. The potential benefits of a thoracoabdominal air sac system include mass reduction, thermoregulation, and most importantly, efficient lung ventilation. The hypothesis that sauropods had such air sac systems has great explanatory value and reconciles previously inexplicable features of sauropod paleobiology, for example, the observed rapid growth rates. Taken together, the postcranial pneumaticity and rapid growth rates of sauropods point to a synthetic view of these animals as being more active and bird-like than previously recognized.

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FIGURE 1. Vertebral nomenclature. A stylized cervical vertebra of a sauropod in (A) dorsal, (B) lateral, and (C) ventral views, illustrating the terminology used herein. Anterior is to the right. After Wedel et al. (2000b).

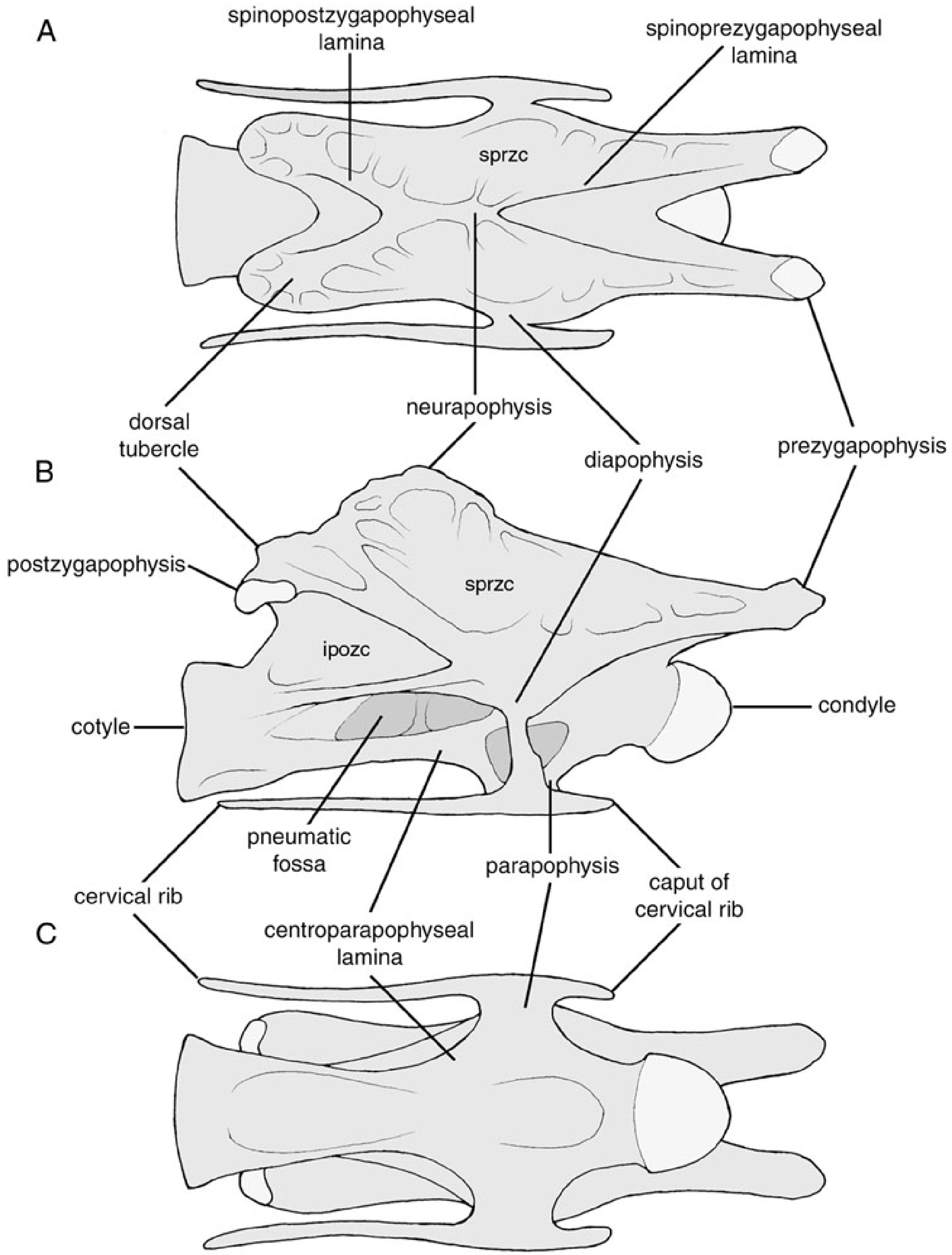

A
spinopostzygapophyseal lamina
spinoprezygapophyseal lamina
sprzc
dorsal tubercle
neurapophysis
diapophysis
prezygapophysis
B
postzygapophysis
sprzc
ipozc
cotyle
condyle
pneumatic fossa
parapophysis
caput of cervical rib
cervical rib
C
centroparapophyseal lamina

FIGURE 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). After Wedel et al. (2000b).

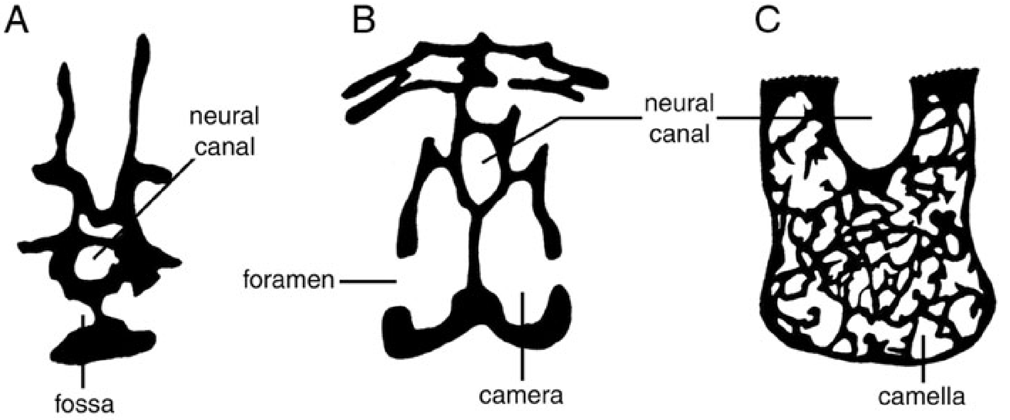

A
B
C
neural canal
neural canal
foramen
fossa
camera
camella

FIGURE 3. Air sacs and axial pneumatization in an extant avian. The body of bird in left lateral view, showing the cervical (C), interclavicular (I), anterior thoracic (AT), posterior thoracic (PT), and abdominal (AB) air sacs. The hatched area shows the volume change during exhalation. The cervical and anterior thoracic vertebrae are pneumatized by diverticula of the cervical air sacs. The posterior thoracic vertebrae and synsacrum are pneumatized via the abdominal air sacs. Diverticula of the abdominal air sacs usually invade the vertebral column at several points. Diverticula often unite when they come into contact, producing a system of continuous vertebral airways extending from the third cervical vertebra to the end of the synsacrum. Modified from Duncker (1971:fig. 8).

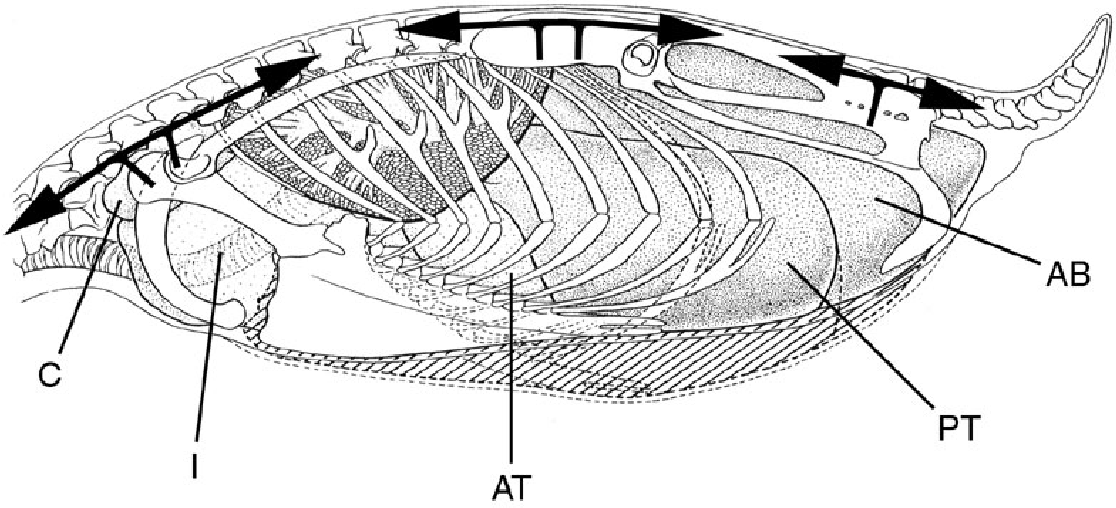

AB
C
PT
I
AT

FIGURE 4. CT sections through the neck of an ostrich. The neck section was sealed with surgical gloves and cannulated with an air tube to re-inflate the pneumatic diverticula. Two axial sections are shown. In these images, air is black, bone is white, and soft tissues are grey. A. Note the essentially camellate nature of the external diverticula, which form aggregates of narrow tubes rather than large, simple sacs. B. The supramedullary airway can be seen to consist of three diverticula separated by thin membranes. C. Also apparent in this view are the cervical ribs, which appear ventrolateral to the centrum on either side. Scale bars are in cm.

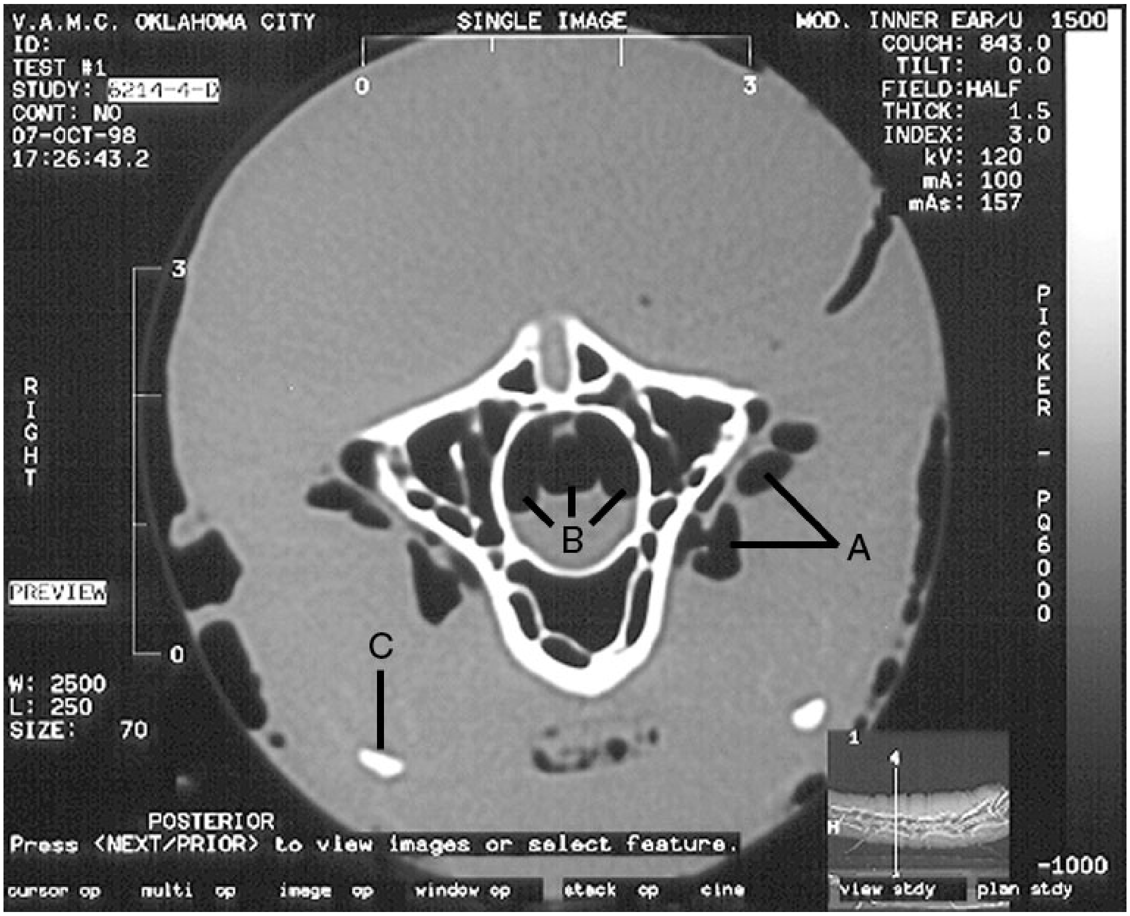

V.A.M.C. OKLAHOMA CITY
ID:
TEST #1
STUDY: 6214-4-D
CONT: NO
07-OCT-98
17:26:43.2
SINGLE IMAGE
0
3
MOD. INNER EAR/U
1500
COUCH: 843.0
TILT: 0.0
FIELD: HALF
THICK: 1.5
INDEX: 3.0
kV: 120
mA: 100
mAs: 157
3
RIGHT
PREVIEW
0
PICKER - PQ6000
A
B
C
W: 2500
L: 250
SIZE: 70
POSTERIOR
Press <NEXT/PRIOR> to view images or select feature.
-1000
cursor op
multi op
image op
window op
stack op
cine
view stdy
plan stdy

FIGURE 5. Pneumatization of the cervical series in the ostrich. The vertebrae are shown in midsagittal section (A), right lateral view (B), and horizontal section (C). Anterior is to the right. White arrows show the development of pneumatic diverticula and camellae, which are shown in black. The pattern of pneumatization is as follows. 1. Cervical diverticula advance through the transverse foramina. 2. Where the diverticula contact the vertebra, the exterior surface of the bone is remodeled. 3. Accessory diverticula enter the bone through existing nutrient foramina, and spread throughout the bone to produce a system of irregular, interconnected camellae. Eventually, even the neural spine and cervical ribs will be filled with pneumatic camellae. 4. Other branches of the main diverticula enter the neural canal at the intervertebral foramina, producing the supramedullary airways. 5. The neural spine may be pneumatized directly from the supramedullary airways. 6. The supramedullary airways evulse at the intervertebral joint to produce the anterior dorsal diverticula.

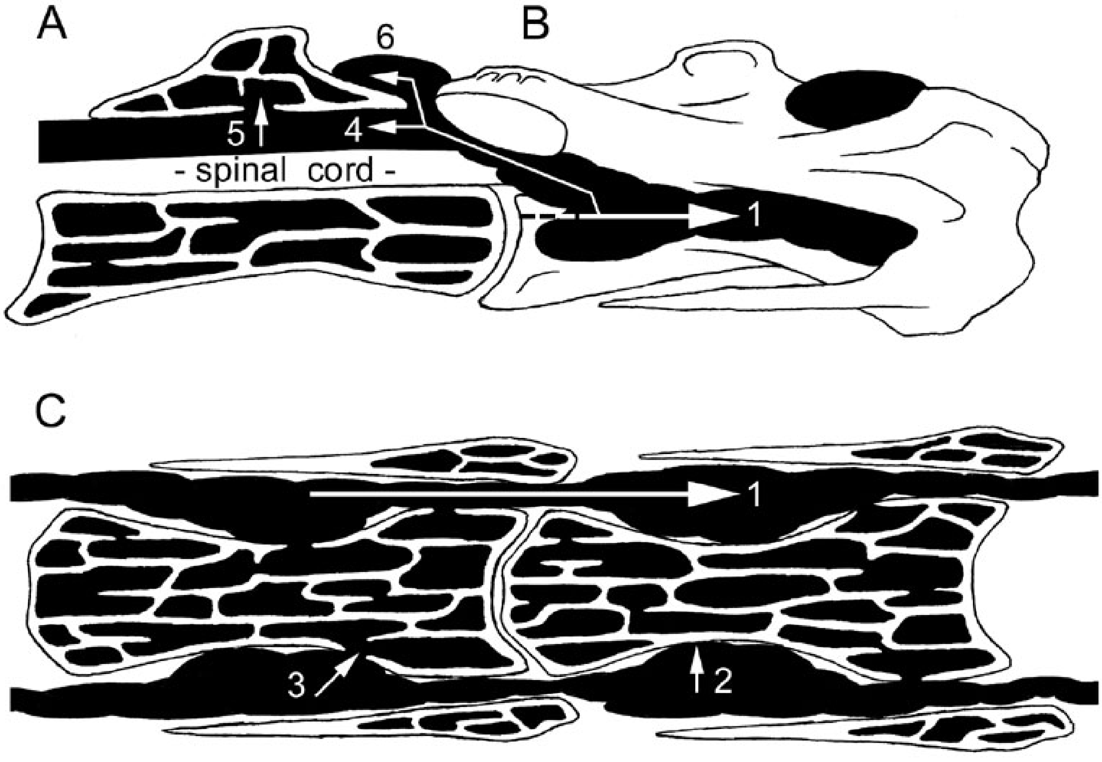

A
6
B
5
4
- spinal cord -
1
C
1
3
2

FIGURE 6. Cervical vertebrae of *Apatosaurus* and *Camarasaurus* differentiated. A. In *Apatosaurus*, the pre- and postzygapophyses are situated more or less directly above the condyle and cotyle, respectively. The intersection of the four diapophyseal laminae is therefore roughly symmetrical. Modified from Gilmore (1936:pl. 24). B. In *Camarasaurus*, the zygapophyses are located well forward of their respective centrum ends, and as a result the intersection of the diapophyseal laminae is anteriorly canted and lacks anter-posterior symmetry. Modified from Osborn and Mook (1921:pl. 67).

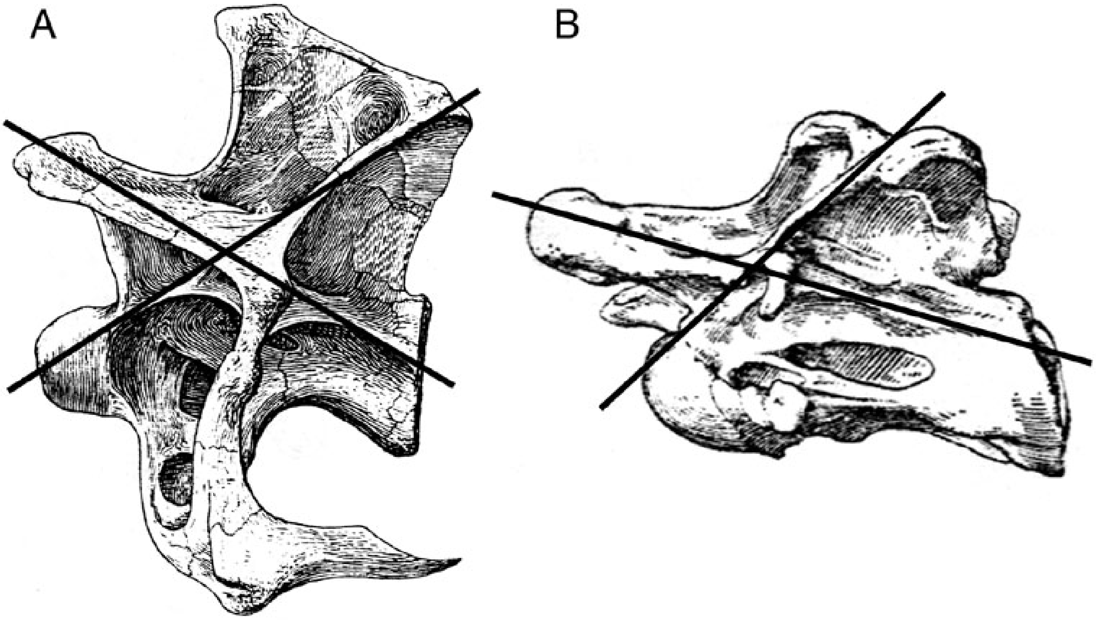

A
B

FIGURE 7. Vertebrae of basal sauropods. A. A section through the single available cervical of *Vulcanodon*. The centrum is strongly waisted by large fossae on either side. Modified from Cooper (1984:fig. 15). B.-F. Dorsal vertebrae of *Barapasaurus*, modified from Jain et al. (1979:pls. 101 and 102). B. A mid-dorsal vertebra in left lateral view. C.-D. Axial sections through mid-dorsal vertebrae, showing the extent of the lateral fossae. E.-F. Sagittal sections through mid-dorsal vertebrae, showing pneumatic chambers extending into the interior of the neural spine from the neural canal. Scale bars: A, 5 cm; B, 10 cm.

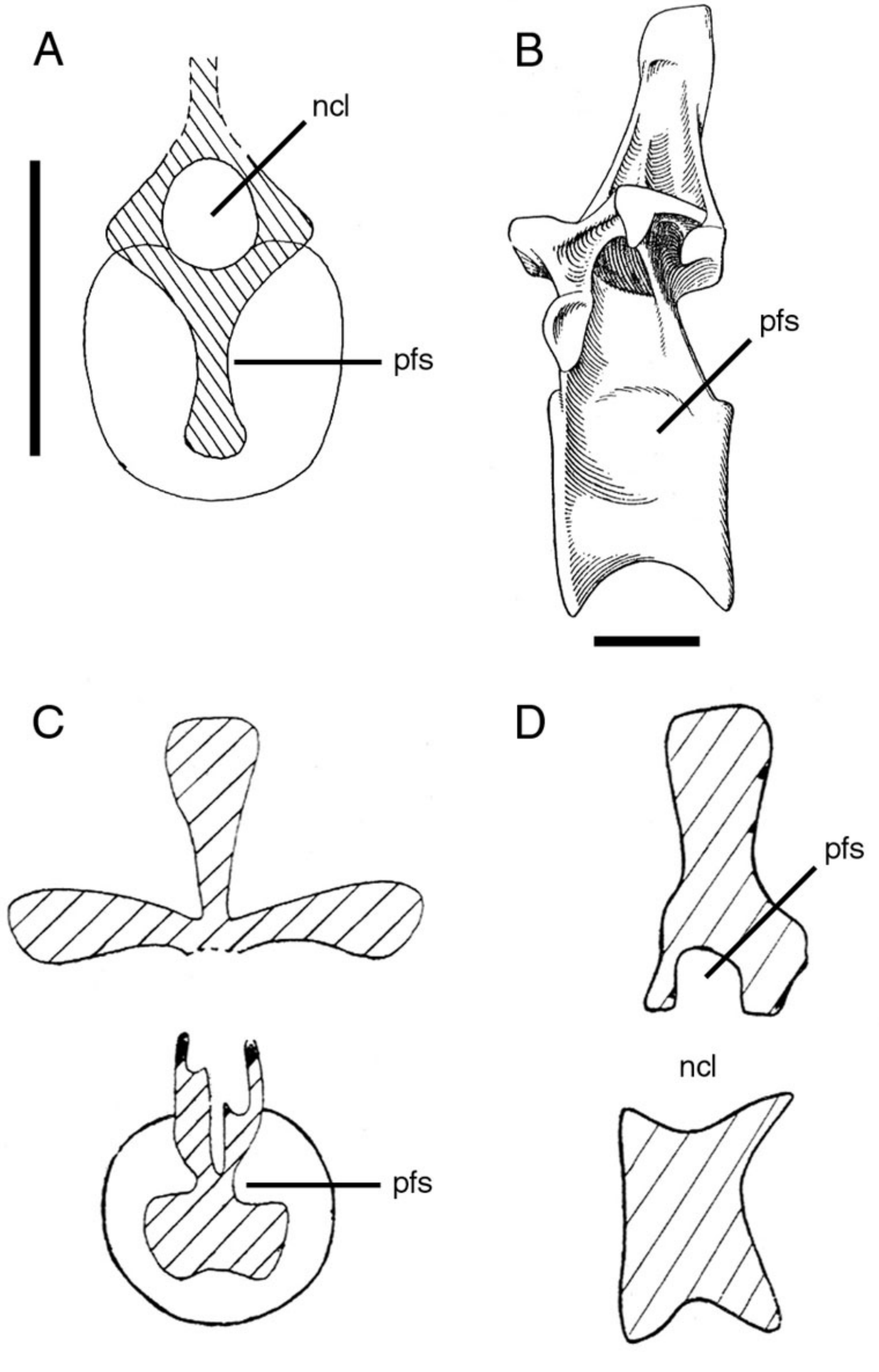

A
ncl
pfs
B
pfs
C
pfs
D
pfs
ncl

FIGURE 8. CT sections through a cervical vertebra of *Apatosaurus*, OMNH 01094. A. Specimen in left lateral view showing the location of CT sections. Two metal pins were used to repair the specimen and can be seen in this image. B. A section through the condyle (A, position 1) showing large, radially arranged camerae. C. A section through the mid-centrum (A, position 2) showing irregular and opportunistic development of camerae within the centrum. D. A section through the cotyle (A, position 3) showing small camerae arranged radially around the cotyle rim. Scale bar is 10 cm.

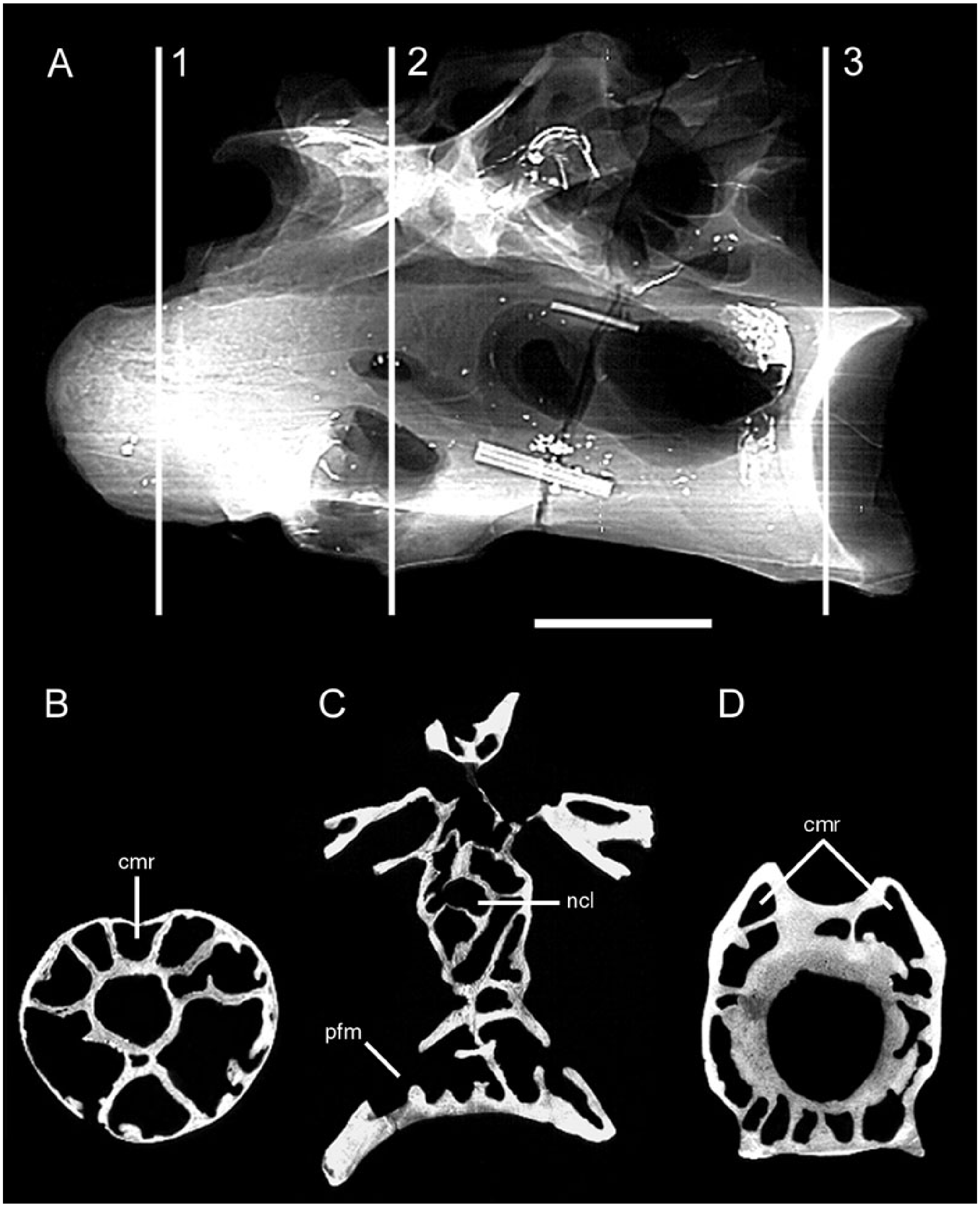

A
1
2
3
B
cmr
C
ncl
pfm
D
cmr

FIGURE 9. Digital model of juvenile vertebrae of *Apatosaurus*. CM 3390 includes two articulated cervical vertebrae from a juvenile animal. These vertebrae were scanned with overlapping slices, and the data were used to construct a digital model of the vertebrae in three dimensions. This digital model could then be sectioned along any axis. A. The digital model in left lateral view. B. The model in ventral view. C. An oblique slice through the centrum of the posterior vertebra (shown as a white line in B) reveals coels developing in the bone ahead of the growing camera. Also apparent in this view is the unfused neurocentral suture. Scale bar is in cm.

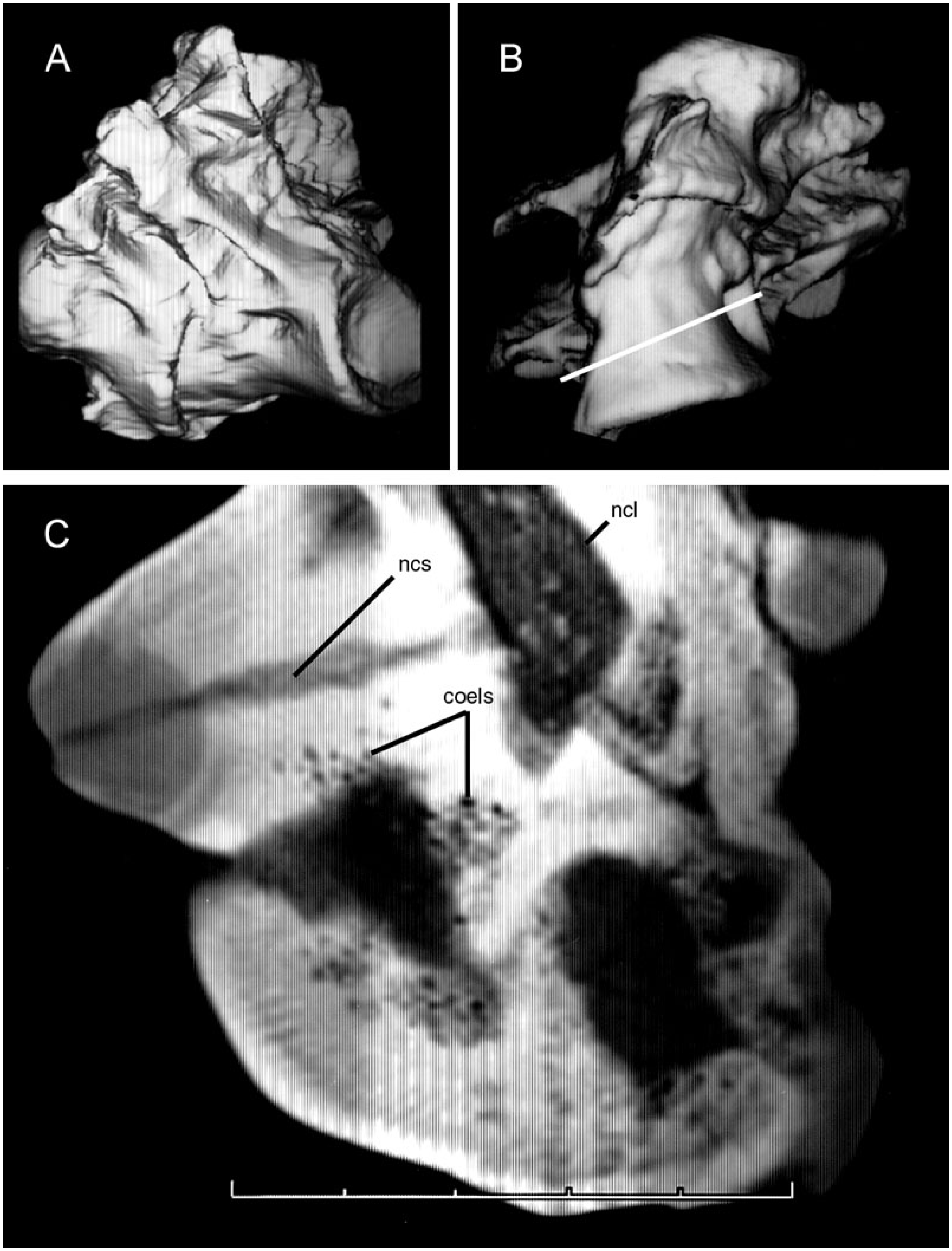

A
B
C
ncl
ncs
coels

FIGURE 10. Dorsal, sacral, and caudal vertebrae of *Diplodocus*. All vertebrae are shown in left lateral view. A. Dorsal vertebrae and sacrum with ilium. Note the complex system of neural spine laminae. B. Caudal vertebrae 1-21. Pneumatic foramina are present on caudals 1-18. Modified from Osborn (1899:figs. 7 and 13). Scale bars are 50 cm.

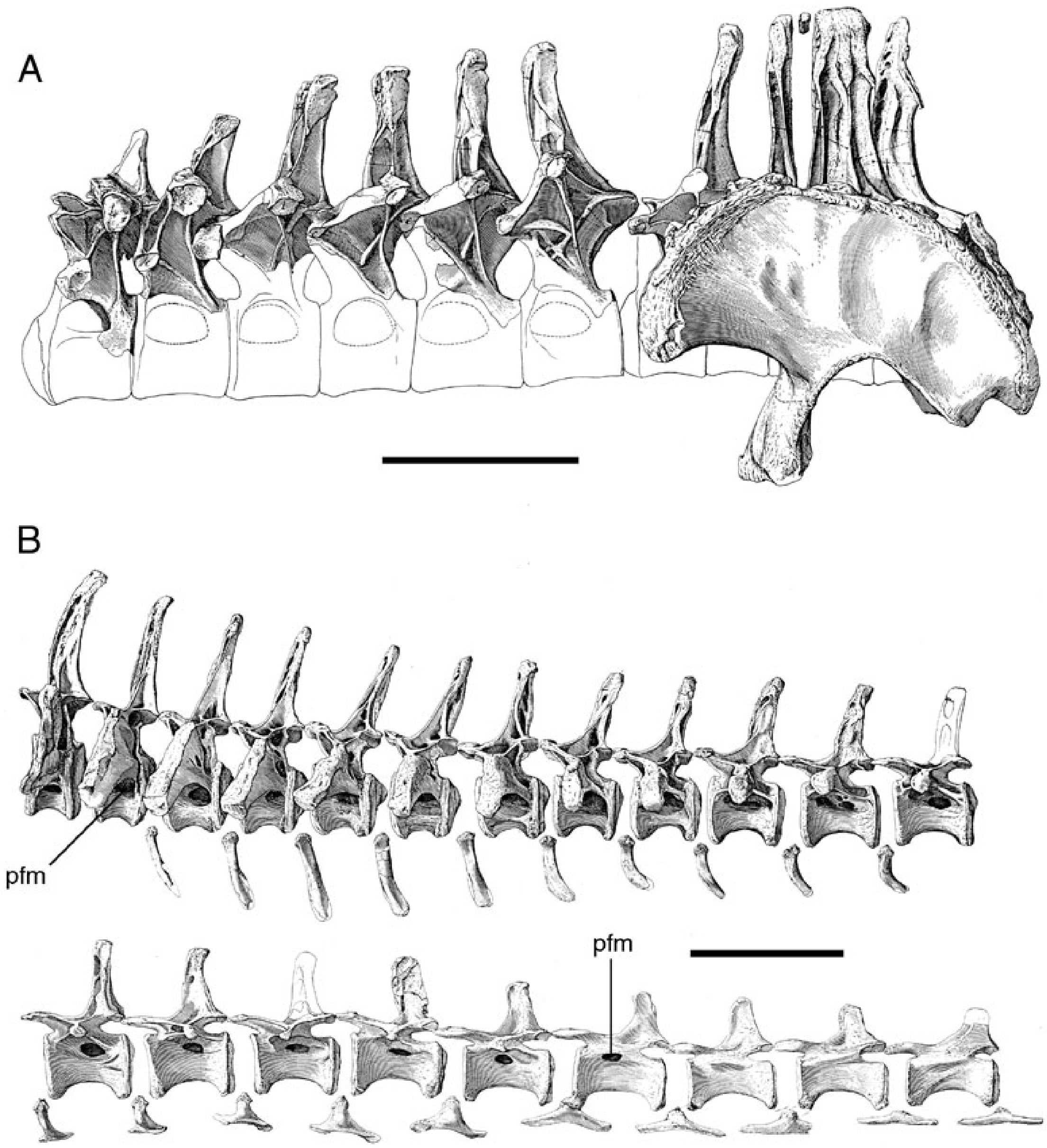

A
B
pfm
pfm

FIGURE 11. CT sections through a cervical vertebra of *Diplodocus*, BYU 12613. A. Specimen in left lateral view showing the location of CT sections. B.-C. Sections through the condyle (A, position 1) and anterior centrum (A, position 2), showing numerous small camerae in the centrum. D. A section through the posterior centrum (A, position 3). Note the irregular, asymmetrical shape of the median septum and the number of large camerae on either side. E. A section through the cotyle (A, position 4). Only a handful of large camerae are present. The regular, radially symmetrical camerae that circle the cotyle in *Apatosaurus* are not present in *Diplodocus*. Scale bar is 10 cm.

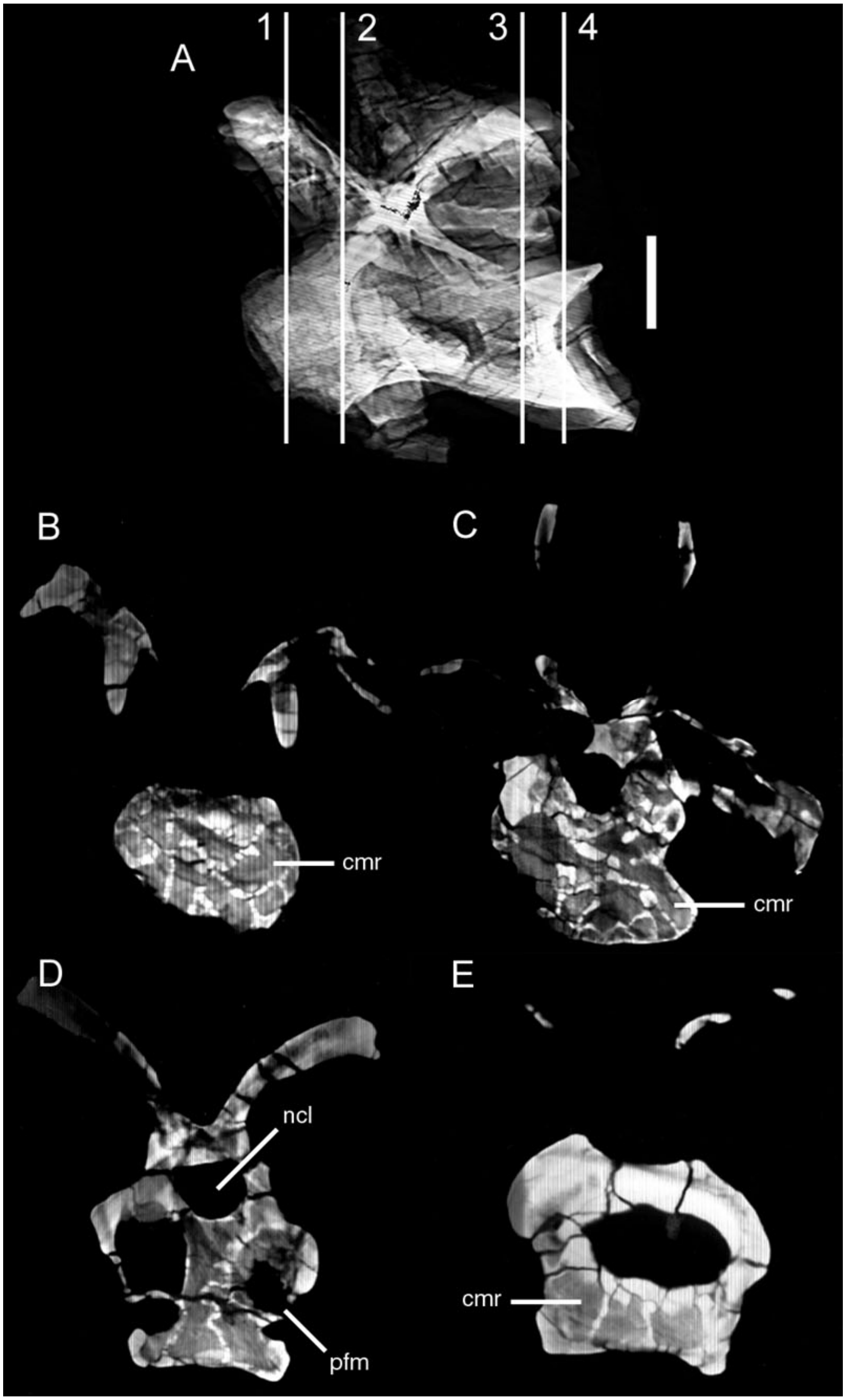

A
1
2
3
4
B
cmr
C
cmr
D
ncl
pfm
E
cmr

FIGURE 12. CT sections through a cervical vertebra from a juvenile individual of *Diplodocus*, CM 33984. The specimen is somewhat distorted diagonally by dorsolateral compression. A. Specimen in left lateral view showing the location of CT sections. B.-C. Sections through the condyle (A, position 1) and anterior centrum (A, position 2), showing the early development of a few relatively large camerae. D. A section through the middle of the centrum (A, position 3) showing large lateral fossae and a camera between the paired median septa. Scale bar is 5 cm.

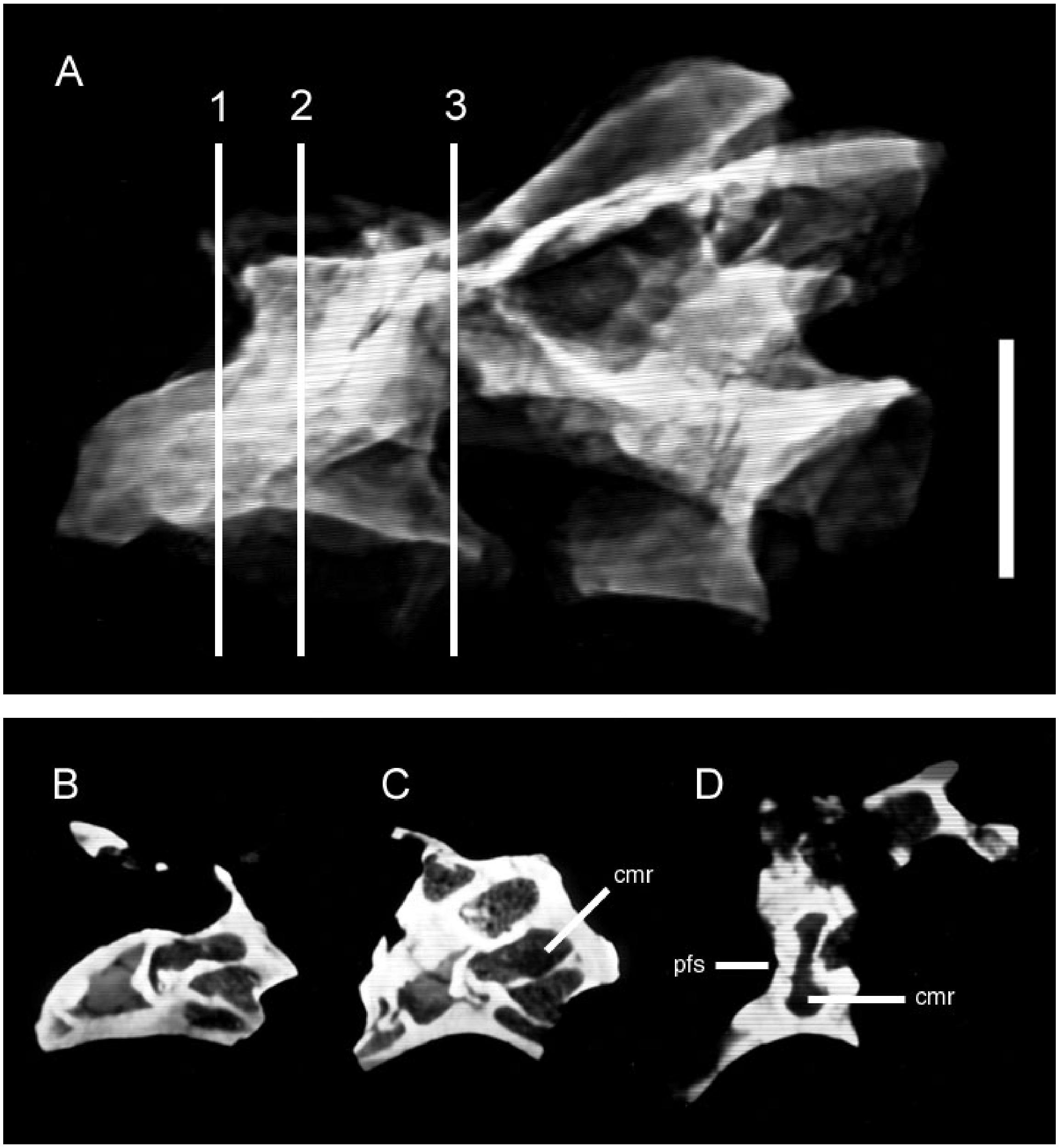

A
1
2
3
B
C
cmr
D
pfs
cmr

FIGURE 13. CT sections through a cervical vertebra of *Haplocanthosaurus*, CM 879-7. A. Line drawing by R.K. Sanders showing the location of CT sections. B. A section through the condyle (A, position 1). The paired chambers are anterior extensions of the lateral fossae. C. A section through the middle of the centrum (A, position 2) showing large lateral fossae, which penetrate to a thin median septum. Scale bar is 10 cm.

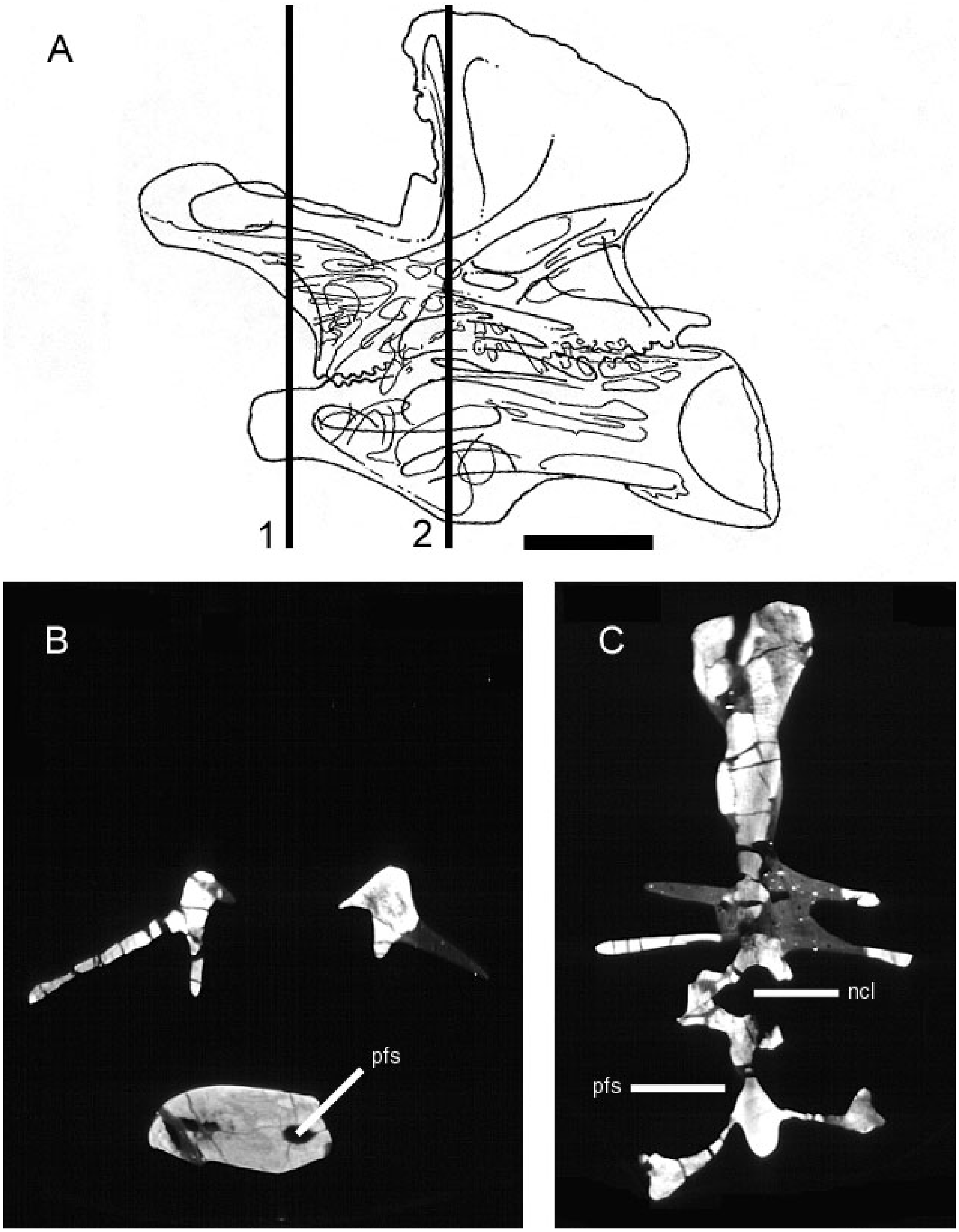

A
1
2
B
pfs
C
ncl
pfs

FIGURE 14. CT sections through a dorsal vertebra of *Haplocanthosaurus*, CM 572. The vertebra is complete, but only the centrum is shown here. A. The centrum in left lateral view showing the location of CT sections. B. Horizontal section through the mid-centrum (A, position 1) showing the large lateral fossae. C. Horizontal section through the mid-centrum just below the rim of the lateral fossae (A, position 2). The centrum is solid at this point, and the lack of internalized chambers indicates that the lateral chambers are in fact fossae, rather than camerae. Scale bar is 5 cm.

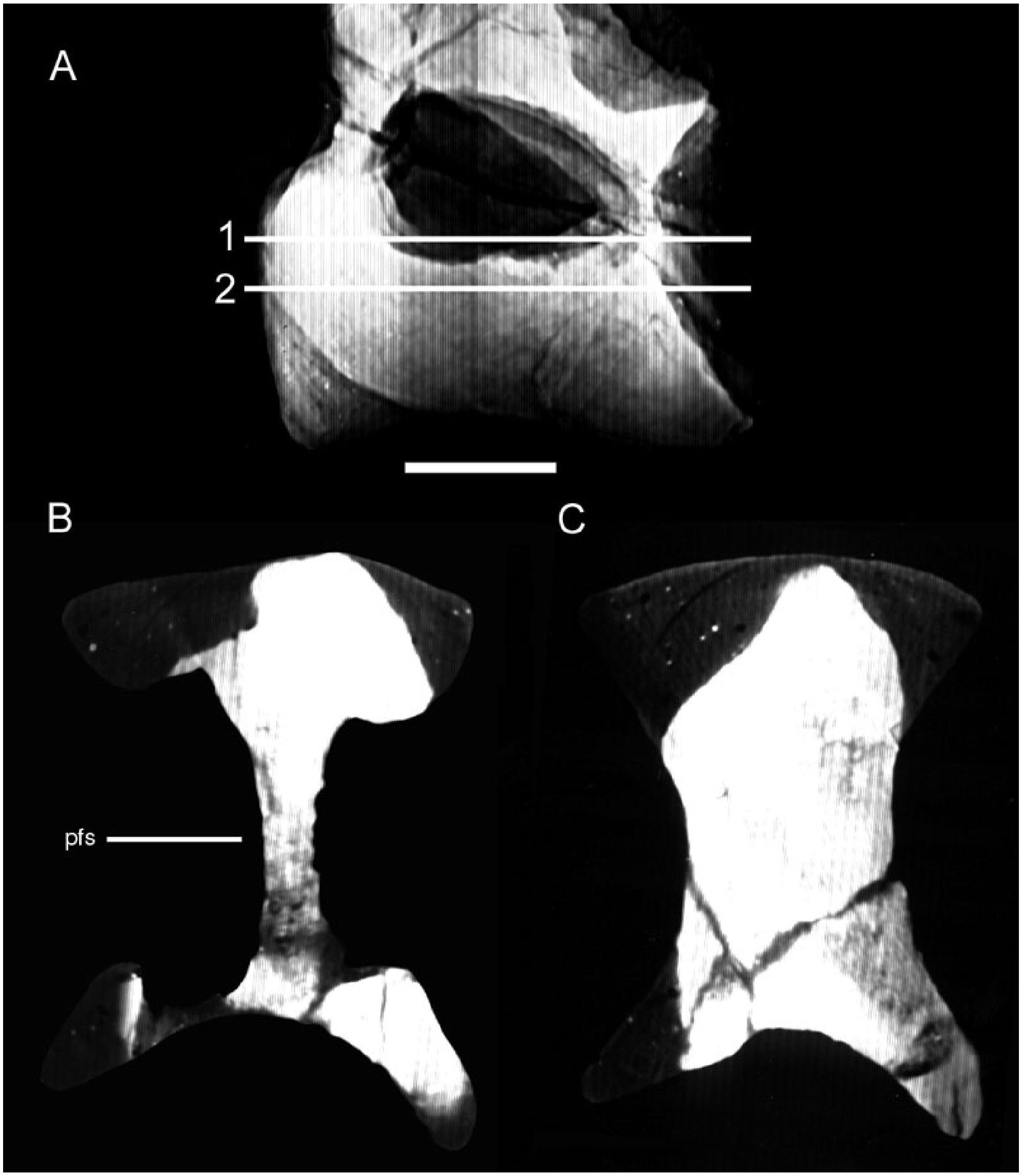

A
1
2
B
C
pfs

FIGURE 15. CT sections through a cervical vertebra of *Camarasaurus*, OMNH 01313. A. Specimen in left lateral view showing the location of CT sections. Small wires used in repairing the specimen can be seen in the condyle, cotyle, neural spine, and parapophysis. B. A section through the condyle (A, position 1). The camerae here are fewer and less complex than those in *Apatosaurus* and *Diplodocus*. C. A section through the mid-centrum (A, position 2) showing the relatively simple internal structure, composed mainly of large camerae. D. A section near the cotyle (A, position 3). The large lateral camerae extend posteriorly to the anterior side of the cotyle, but the smaller camerae seen in *Apatosaurus* and *Diplodocus* are absent. Scale bar is 10 cm.

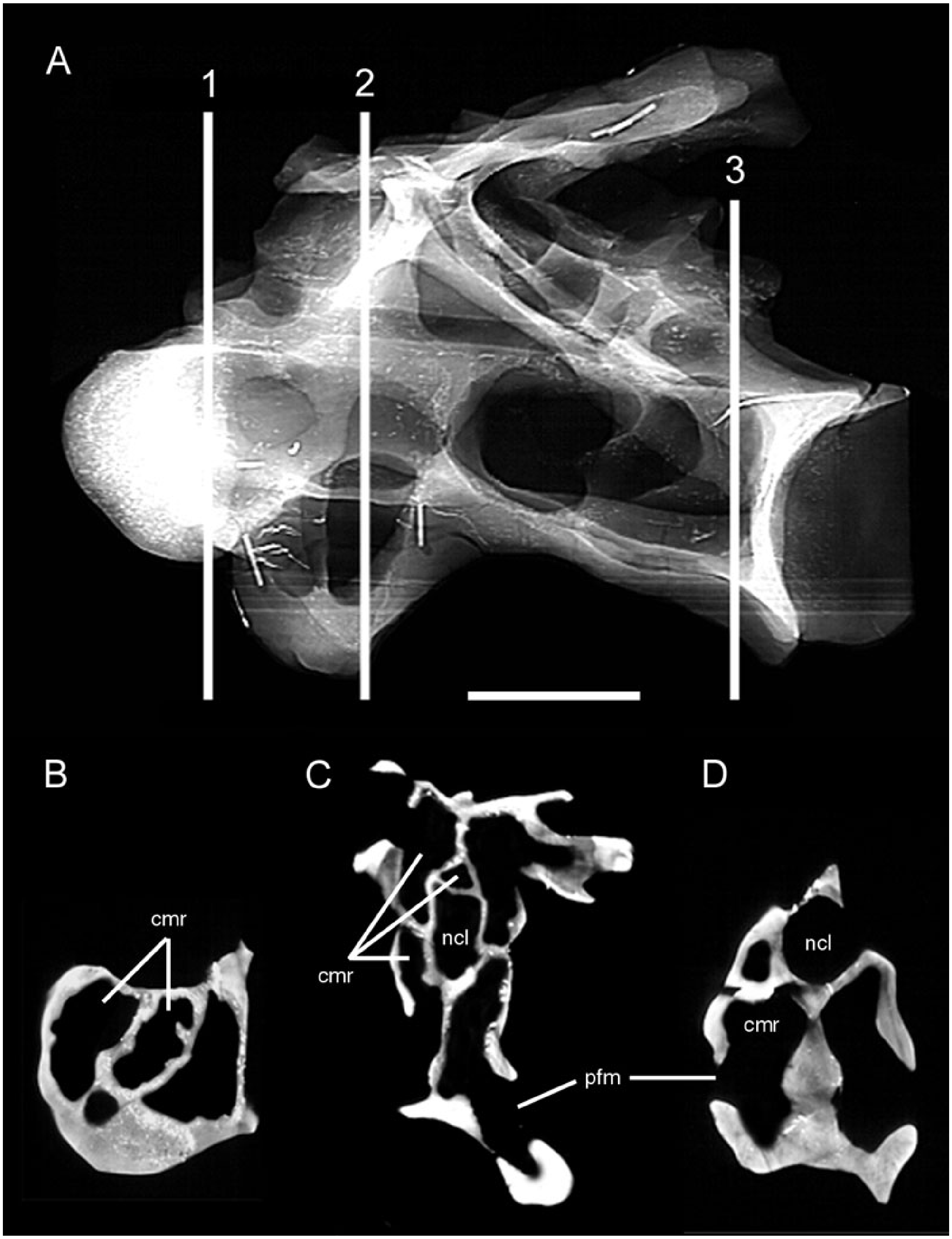

A
1
2
3
B
cmr
C
cmr
ncl
pfm
D
ncl
cmr

FIGURE 16. Vertebrae of *Tendaguria*. A. The single available cervical shown in left lateral view. In addition to the pneumatic foramina on the sides of the centrum, pneumatic fossae or foramina are also present in the supraprezyapophyseal and infrapostzygapophyseal cavities. B. A dorsal shown in right antero-lateral view. Note the fossae along the underside of the transverse processes. Modified from Bonaparte et al. (2000:fig. 17 and pl. 8). Scale bars are 10 cm.

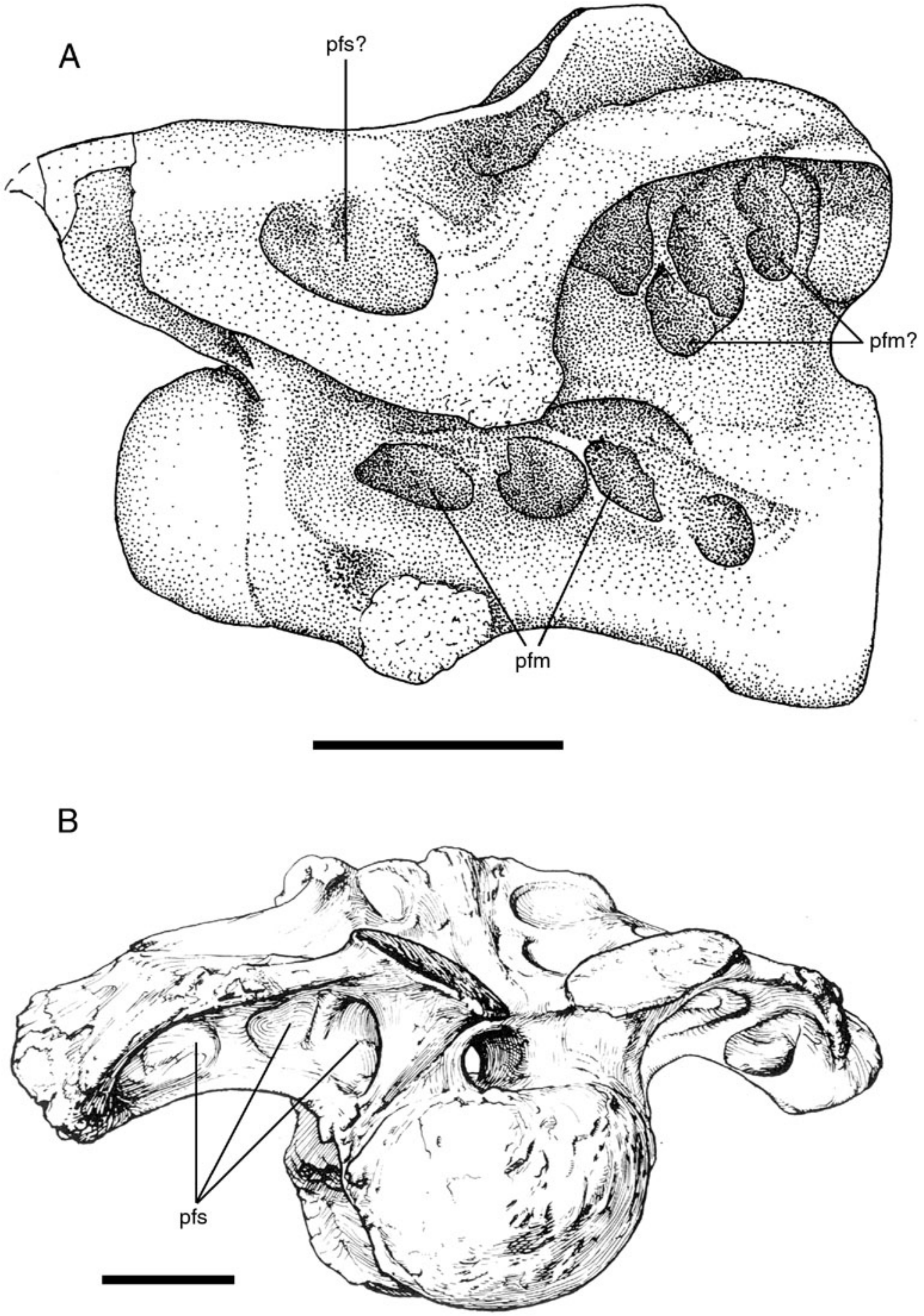

A
pfs?
pfm?
pfm
B
pfs

FIGURE 17. Cervical vertebrae of *Camarasaurus* and *Tendaguria* compared. Both vertebrae are shown in right lateral view. A. *Camarasaurus*. B. *Tendaguria*. Pneumatic fossae and foramina are shown in black. Deep, invasive pneumatic features are present in the supraprezygapophyseal and infrapostzygapophyseal cavities in these taxa, some diplodocids, and brachiosaurids (cf. Hatcher, 1901:pl. 7; Janensch, 1950:fig. 5, and Dalla Vecchia, 1998:fig. 2). Modified from Bonaparte et al. (2000:fig. 18).

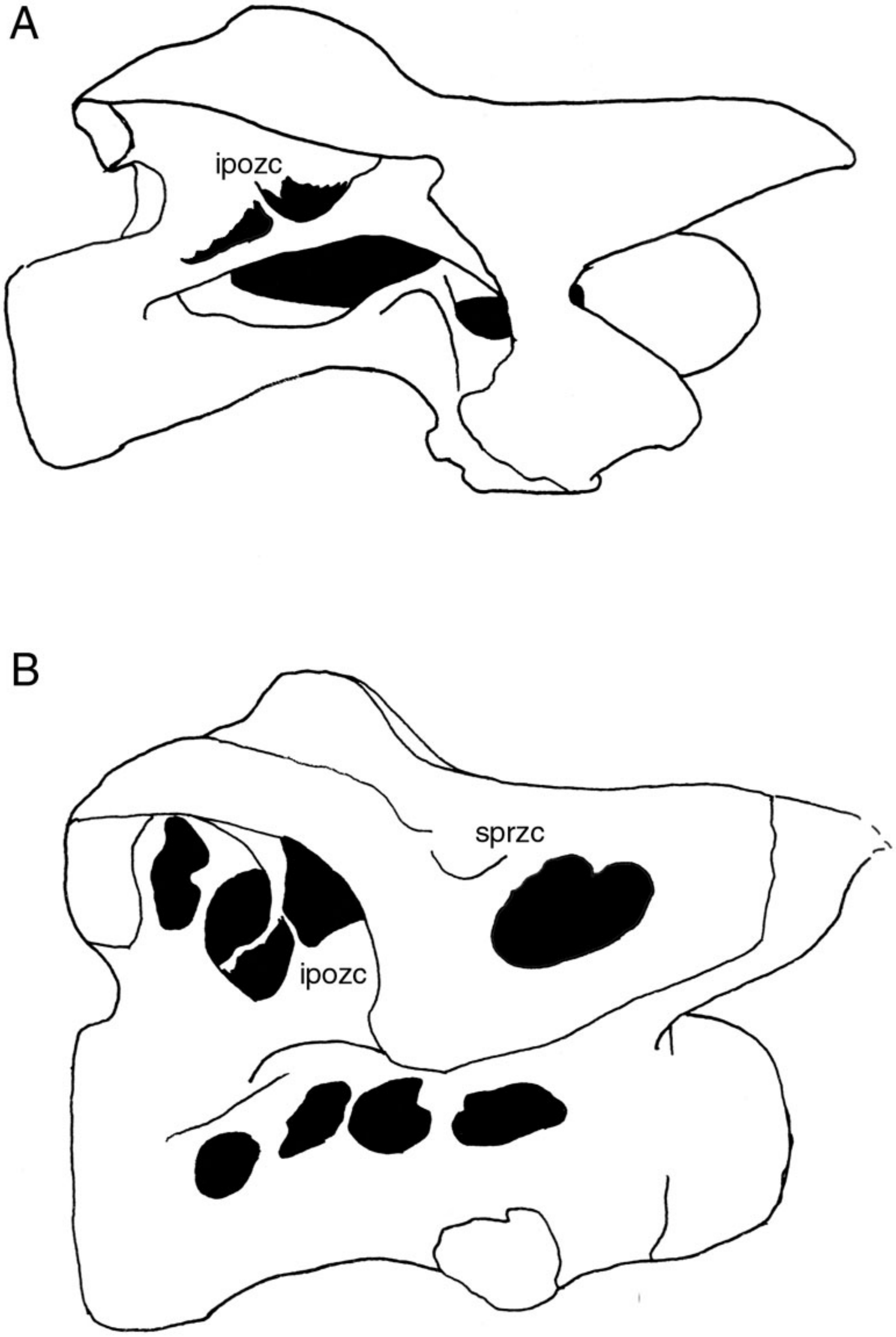

A
ipozc
B
sprzc
ipozc

FIGURE 18. Cervical vertebrae of *Brachiosaurus*. A. Atlas. B. Eighth cervical vertebra. In addition to the large foramina on the centrum, note the small, irregular fossae within the supraprezygapophyseal and infrapostzygapophyseal cavities. C. A sagittal section through the condyle of a cervical vertebra. D. An axial section through another condyle. Note the thin walls and irregular layout of the camellae. Modified from Janensch (1950:figs. 12, 43, 70, and 71). Scale bars: A, 10 cm; B, 20 cm.

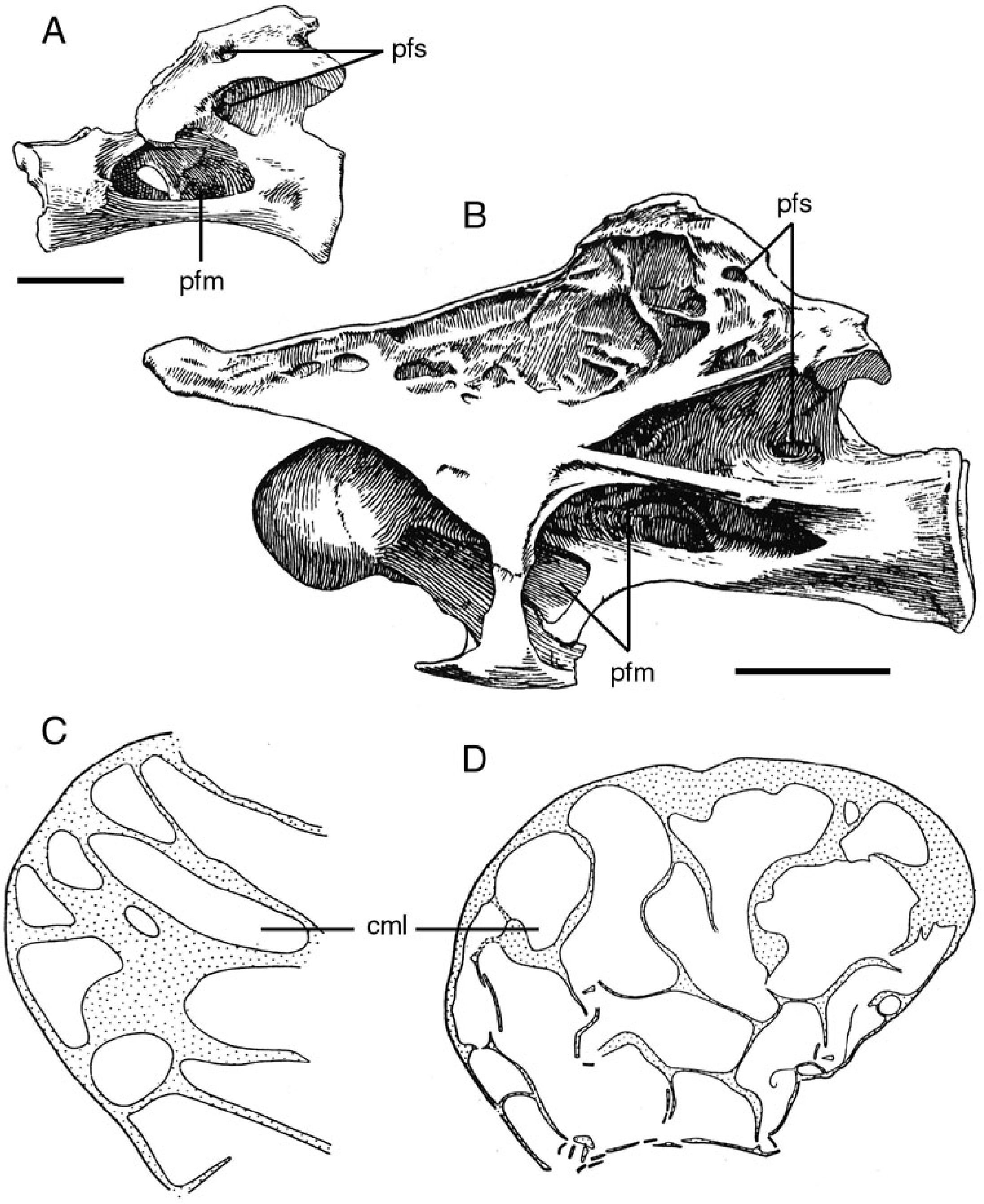

A
pfs
pfm
B
pfs
pfm
C
D
cml

FIGURE 19. Dorsal vertebrae of *Brachiosaurus*. A. Fourth dorsal vertebra in posterior view. B. The same vertebra in lateral view. C. Sagittal section through the anterior portion of a dorsal vertebra. D. Axial section through the middle of a dorsal vertebra. As in the cervical vertebrae, most of the centrum is occupied by large camerae, and camellae are restricted to the ends of the centrum. Modified from Janensch (1950:figs. 53, 54, 67, and 72). Scale bar is 20 cm.

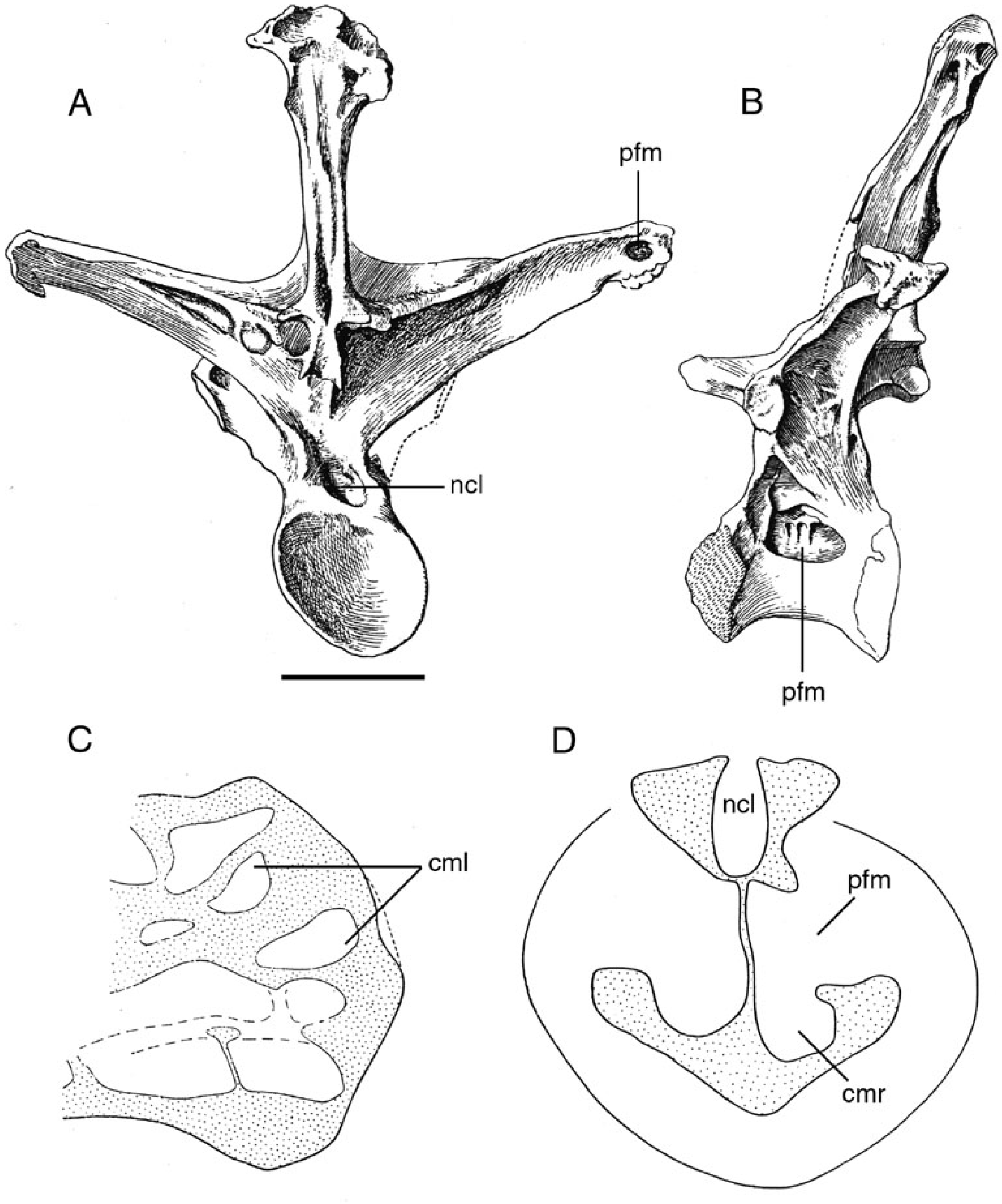

A
B
pfm
ncl
pfm
C
D
cml
ncl
pfm
cmr

FIGURE 20. CT sections through a cervical vertebra of *Brachiosaurus*, BYU 12866. The specimen is somewhat distorted diagonally, causing the distortion or collapse of some internal cavities. A. Specimen in left lateral view showing the 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. Modified from Wedel et al. (2000b:fig. 12). Scale bar is 20 cm.

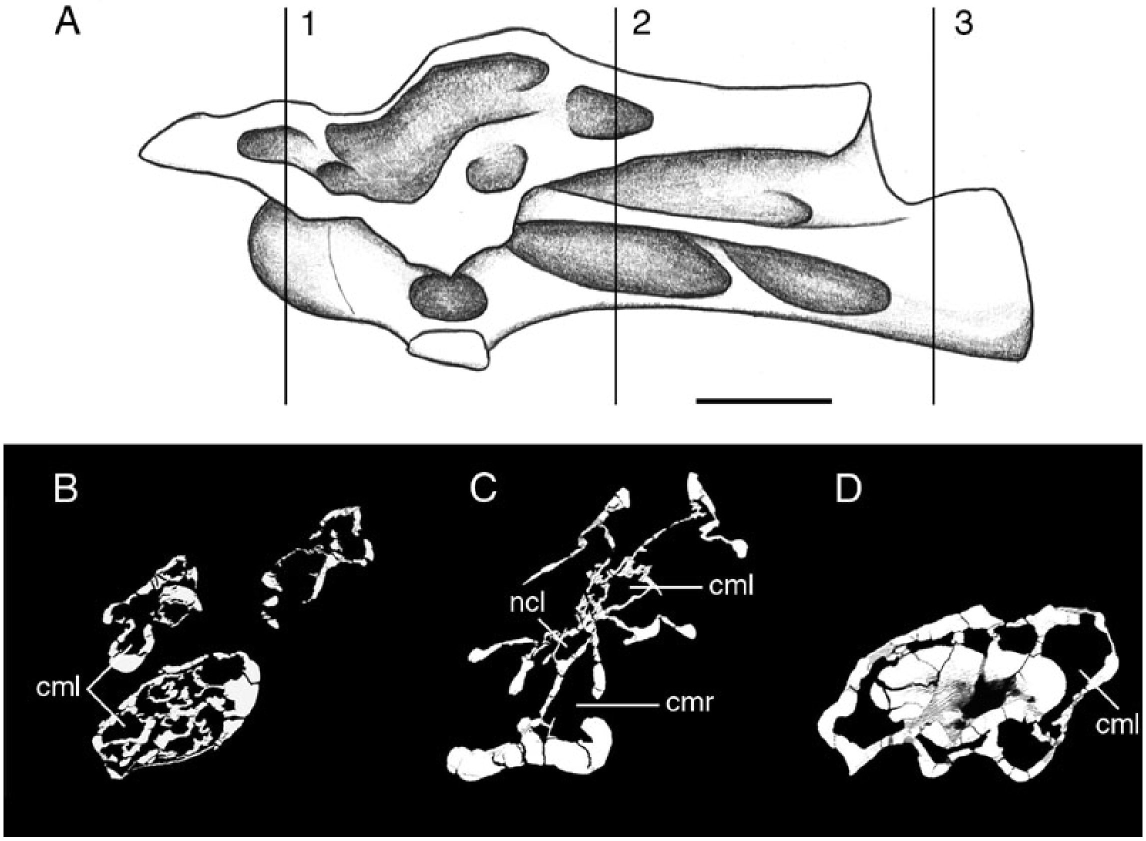

A
1
2
3
B
cml
C
ncl
cml
cmr
D
cml

FIGURE 21. CT sections through a cervical vertebra of *Sauroposeidon*, OMNH 53062. A. Specimen in right lateral view showing the location of CT sections. B. Section through diapophysis (A, position 1) showing hypertrophied pneumatic fossae in the centrum and neural spine. C. Section through anterior centrum (A, position 2) showing camellae, which completely fill the internal structure. D. Section through postzygapophysis (A, 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. Modified from Wedel et al. (2000b:fig. 12). Scale bar is 20 cm.

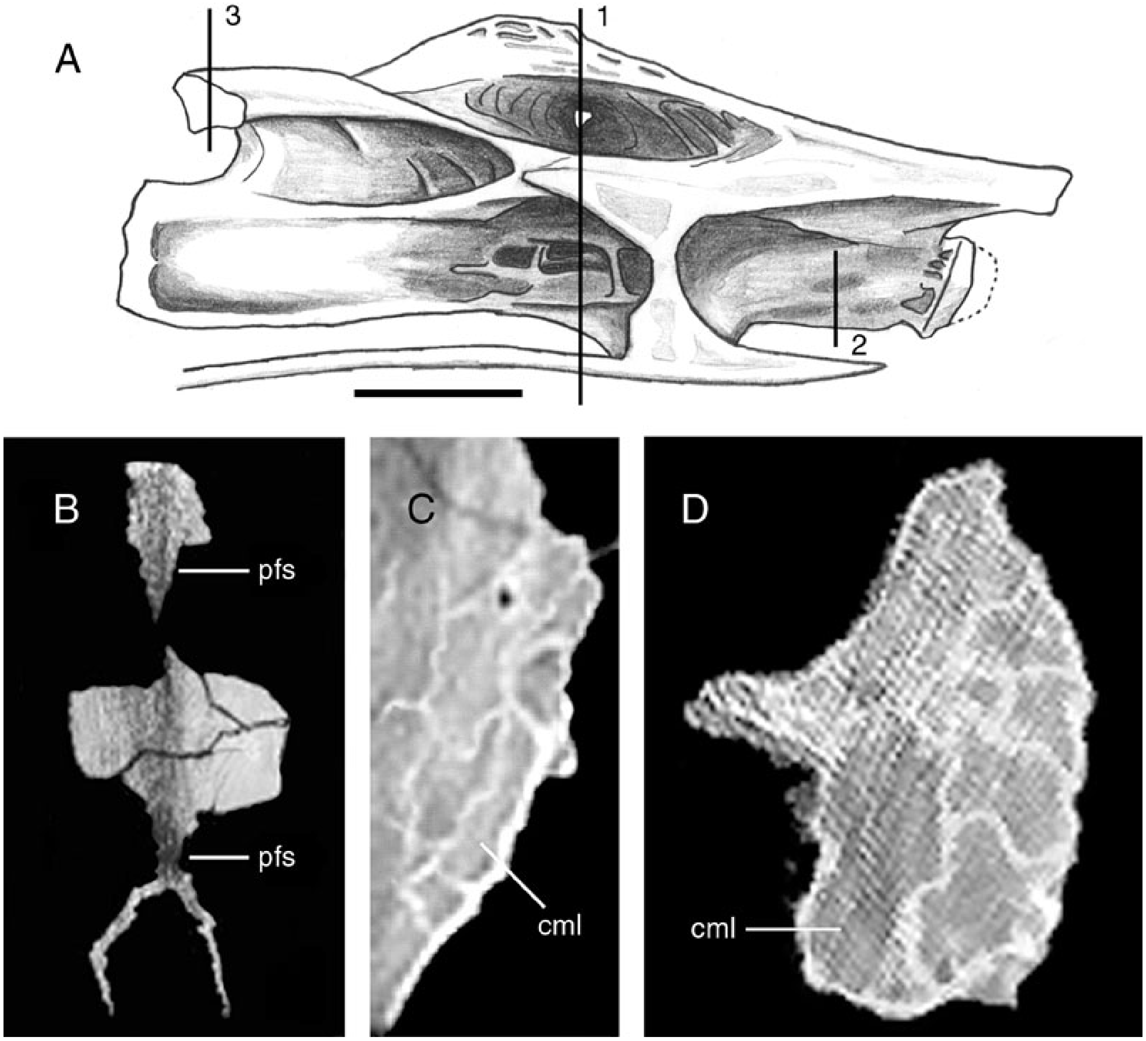

A
3
1
2
B
pfs
pfs
C
cml
D
cml

FIGURE 22. Cervical vertebrae of an unnamed brachiosaurid from Croatia. A. WN-V1, an anterior or middle cervical vertebra, shown in right lateral view. B. MPCM-V2, a posterior cervical vertebra, shown in antero-dorsal view. Note the complex ‘honeycomb’ of camellae in the anterior part of each vertebra. Modified from Dalla Vecchia (1999:figs. 2 and 19). Scale bars are in cm.

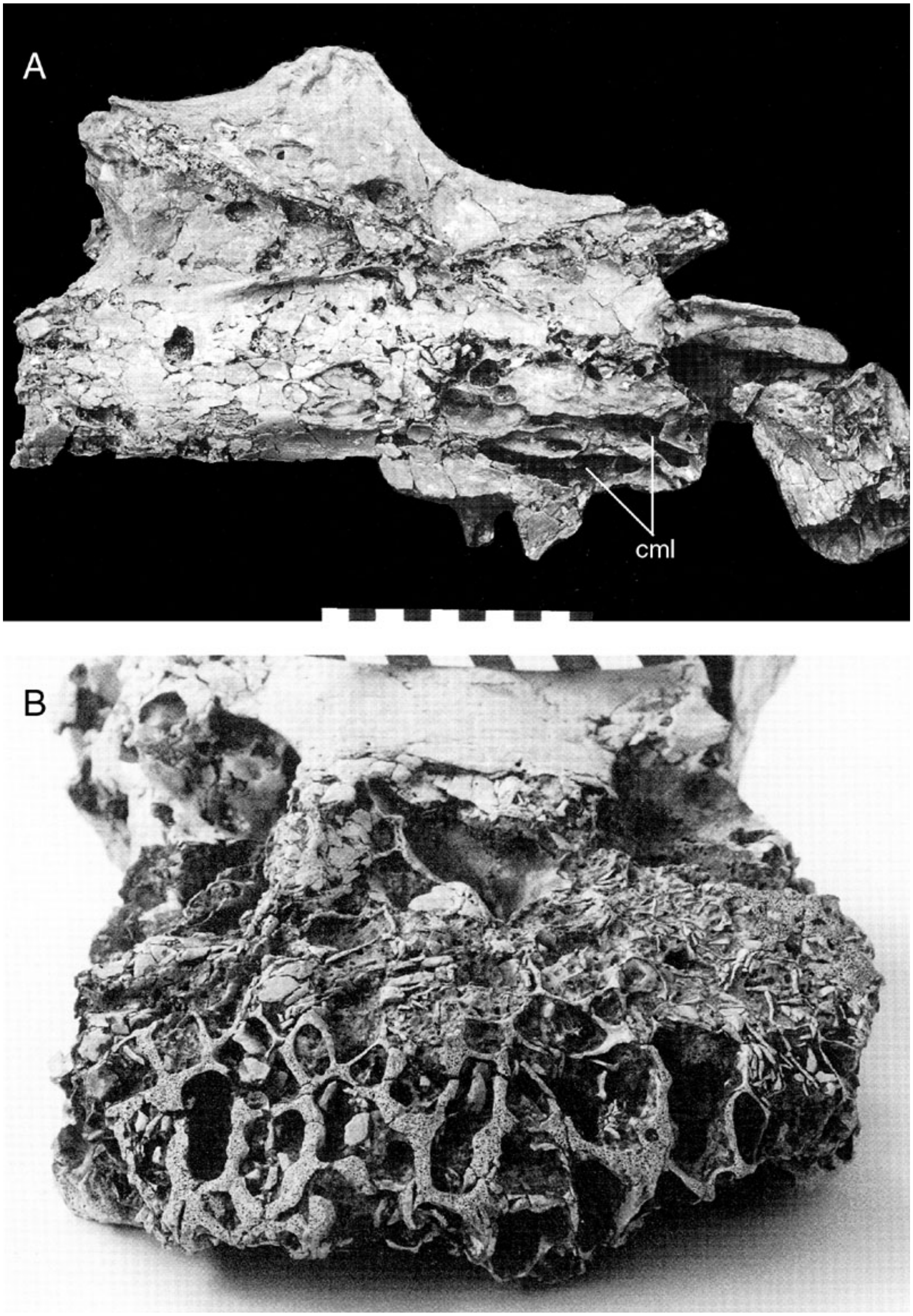

A
cml
B

FIGURE 23. Cervical vertebrae of various titanosauriforms. A. USNM 5678, holotype cervical vertebra of *Pleurocoelus*. The presence of large lateral fossae is presumed to be a juvenile character. After Lull (1911b:pl. 15). B. FWMSH 'A', a cervical vertebra of the Jones Ranch sauropod on display in the Fort Worth Museum of Science and History. C. MN 4111-V, a partial cervical vertebra of *Gondwanatitan*. Note the relatively thick cortical bone and the presence of a median septum separating the few, relatively large cavities. Compare to the camellate vertebrae of *Sauroposeidon* (see Fig. 22) and *Saltasaurus* (see Fig. 26). Redrawn from Kellner and Azevedo (1999:fig. 5). Scale bars: A, 2 cm; B, 20 cm; C, 5 cm.

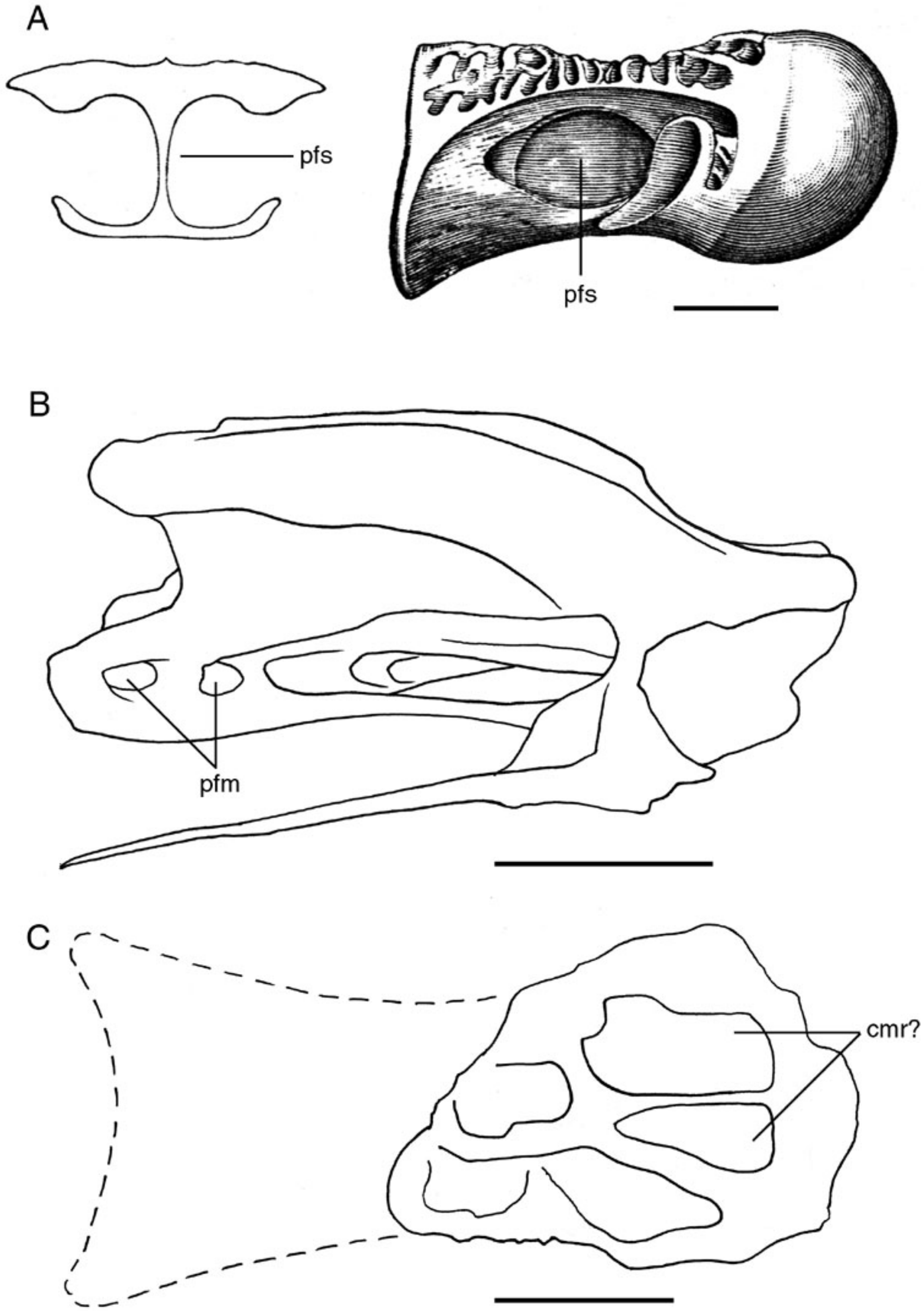

A
pfs
pfs
B
pfm
C
cmr?

FIGURE 24. TMM 41398-1, a dorsal neural spine of *Alamosaurus*. A. Anterior view. B. Dorsal view. The top of the neural spine is broken, revealing the camellate internal structure. Also note the reduced neural arch laminae and overall ‘inflated’ appearance. Scale bar is 10 cm.

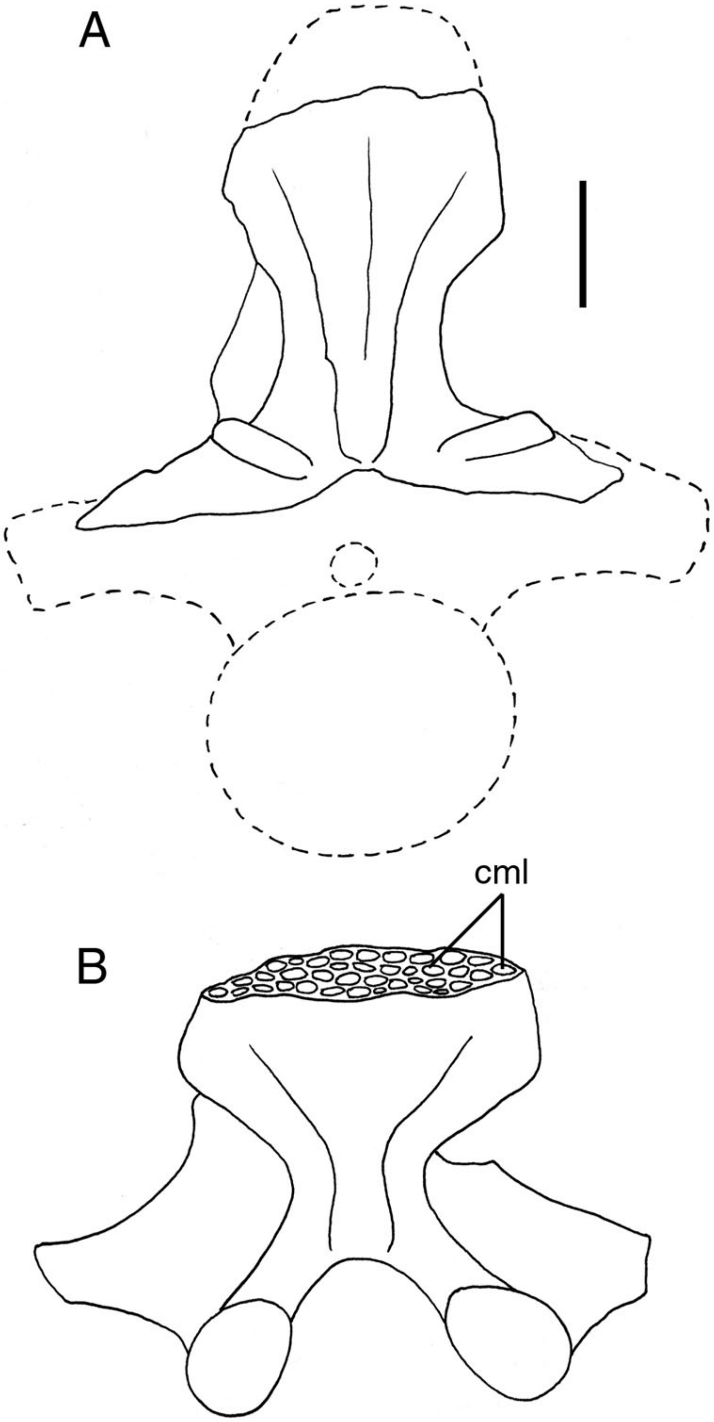

A
B
cml

FIGURE 25. PVL 4017-137, a dorsal vertebra of *Saltasaurus*. A. Posterior view. B. Lateral view, showing the location of cross sections. C. Horizontal section through centrum (B, position 1). D. Vertical section through centrum (B, position 2). E. Horizontal section through neural spine (B, position 3). Redrawn from Powell (1986:pls. 28 and 30). Scale bar is 5 cm.

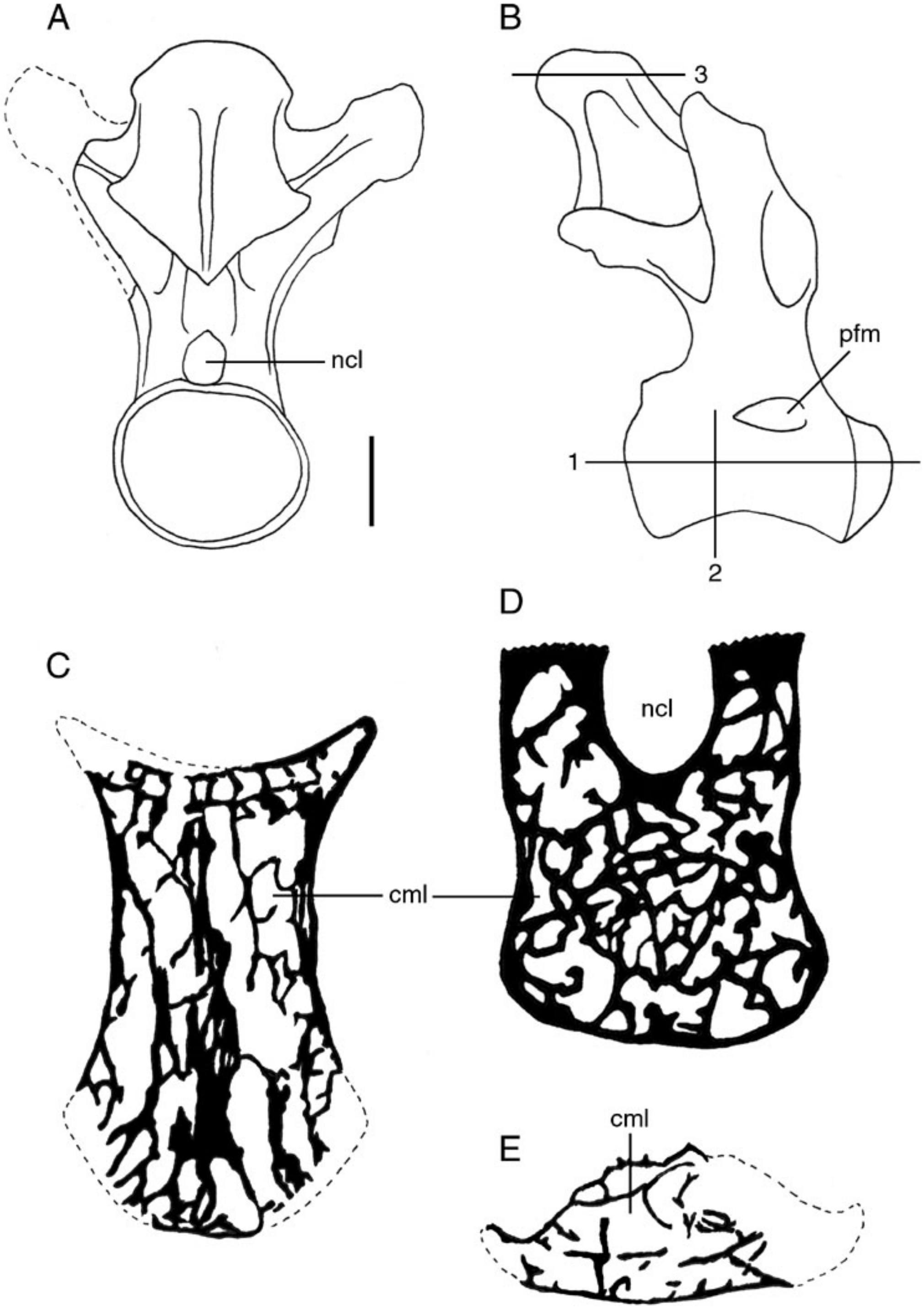

A
ncl
B
3
pfm
1
2
C
cml
D
ncl
E
cml

FIGURE 26. 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. After Wedel et al. (2000b:fig. 11).

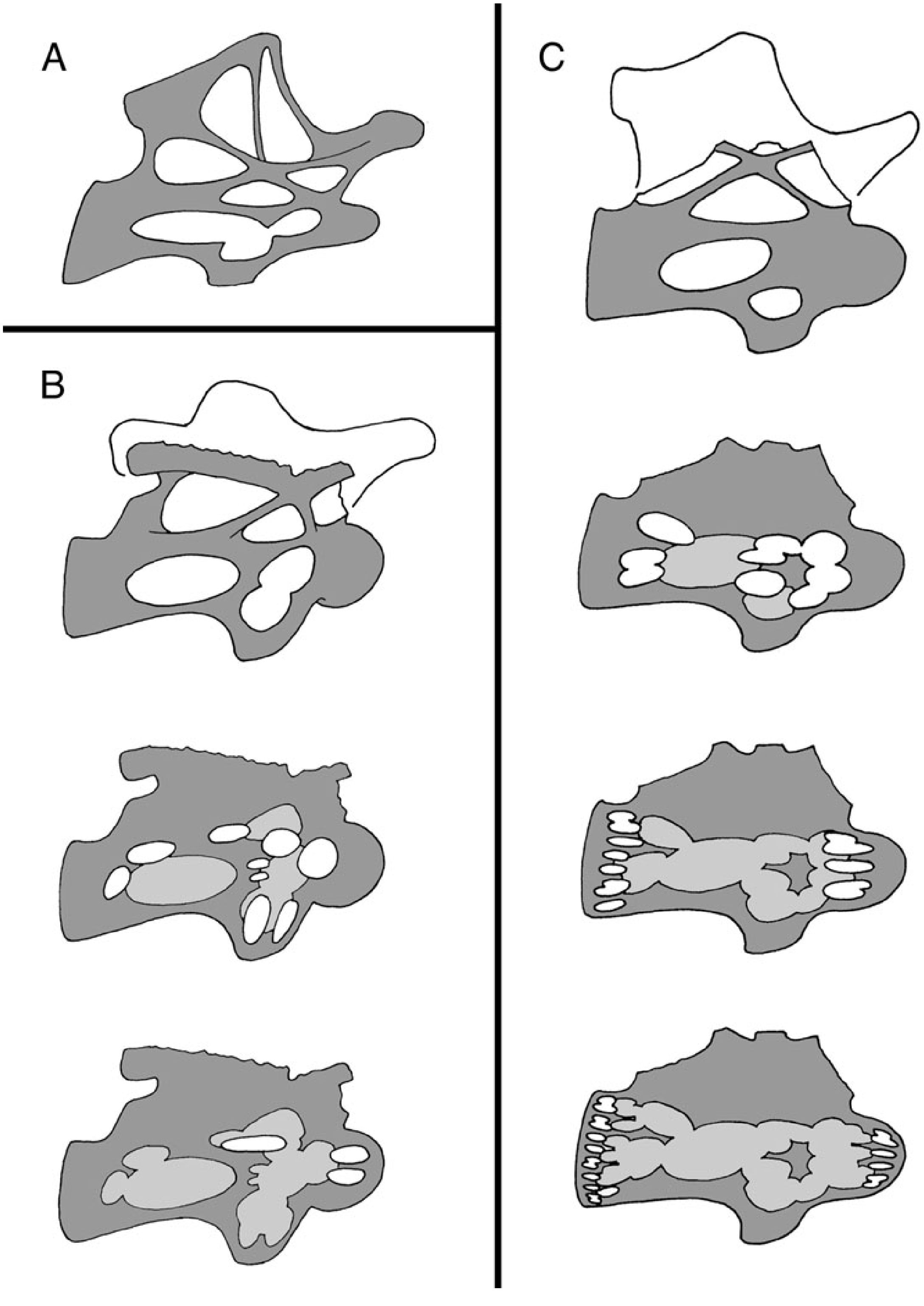

A
B
C

FIGURE 27. 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 and McIntosh, 1994:fig. 17.1). C. *Camarasaurus* sp. (CM 578, redrawn from Carpenter and 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 and 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 and 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 = 10 cm. After Wedel et al. (2000b:fig. 14).

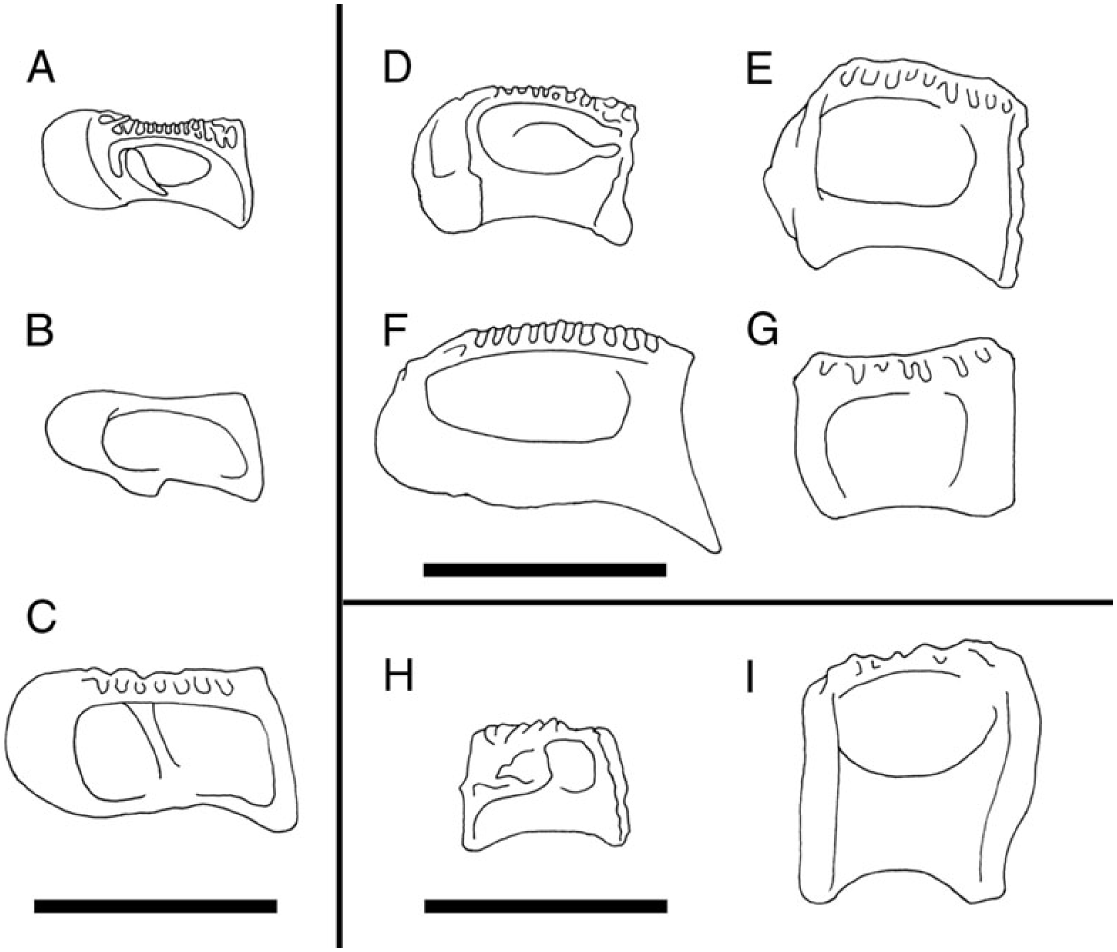

A
B
C
D
E
F
G
H
I

FIGURE 28. Evolution of vertebral pneumatic structures in sauropods, following the phylogeny of Upchurch (1998). Added taxa are placed in their probable phylogenetic position and denoted with an asterisk. This distribution of taxa requires the independent acquisition of camerae in the Chinese sauropods and Neosauropoda. Camellae evolved either two or three times, depending on state in basal titanosauriforms. Given that several titanosauriforms are known to lack camellae, it seems best to regard the state of basal titanosauriforms as equivocal with respect to this character.

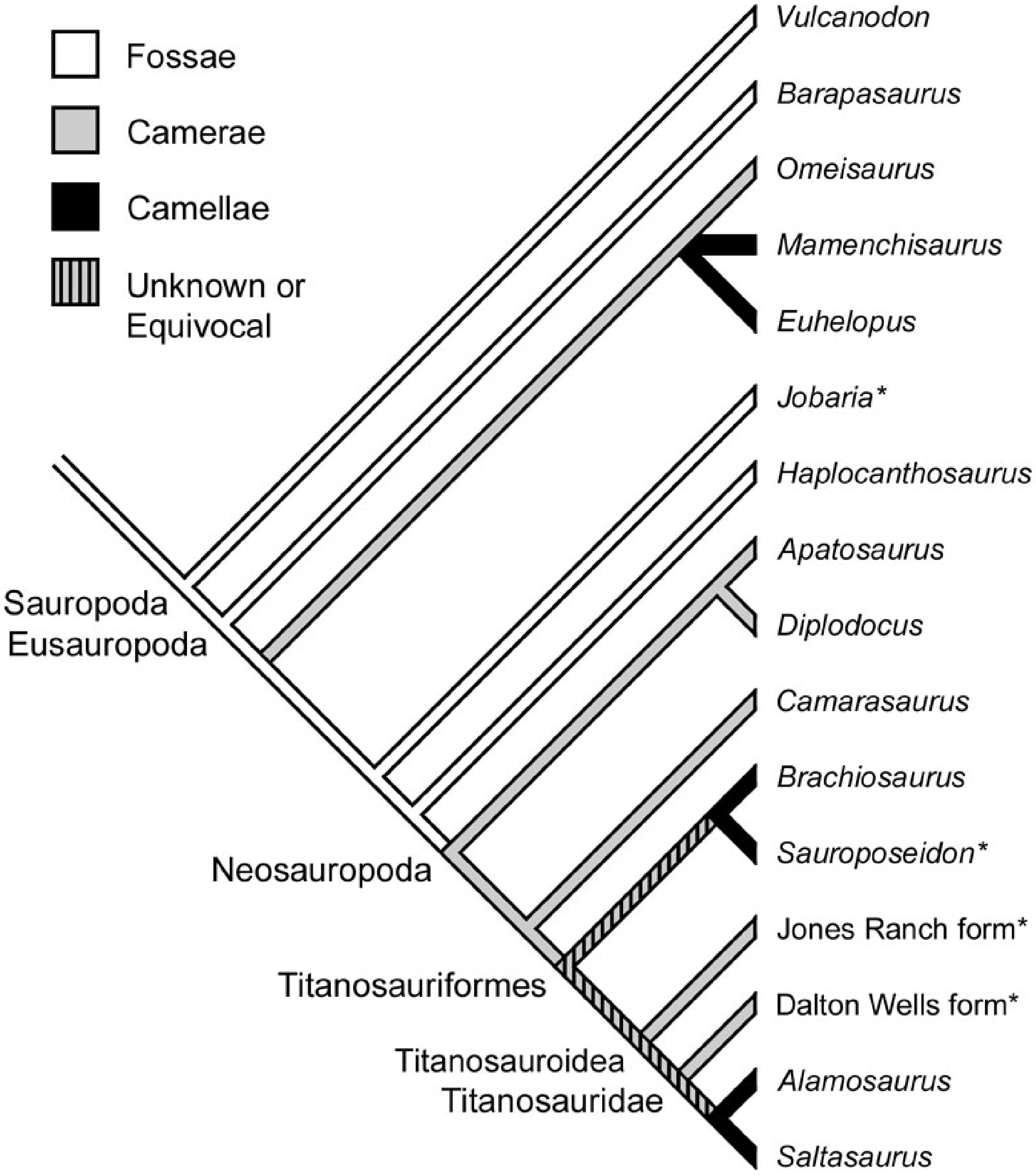
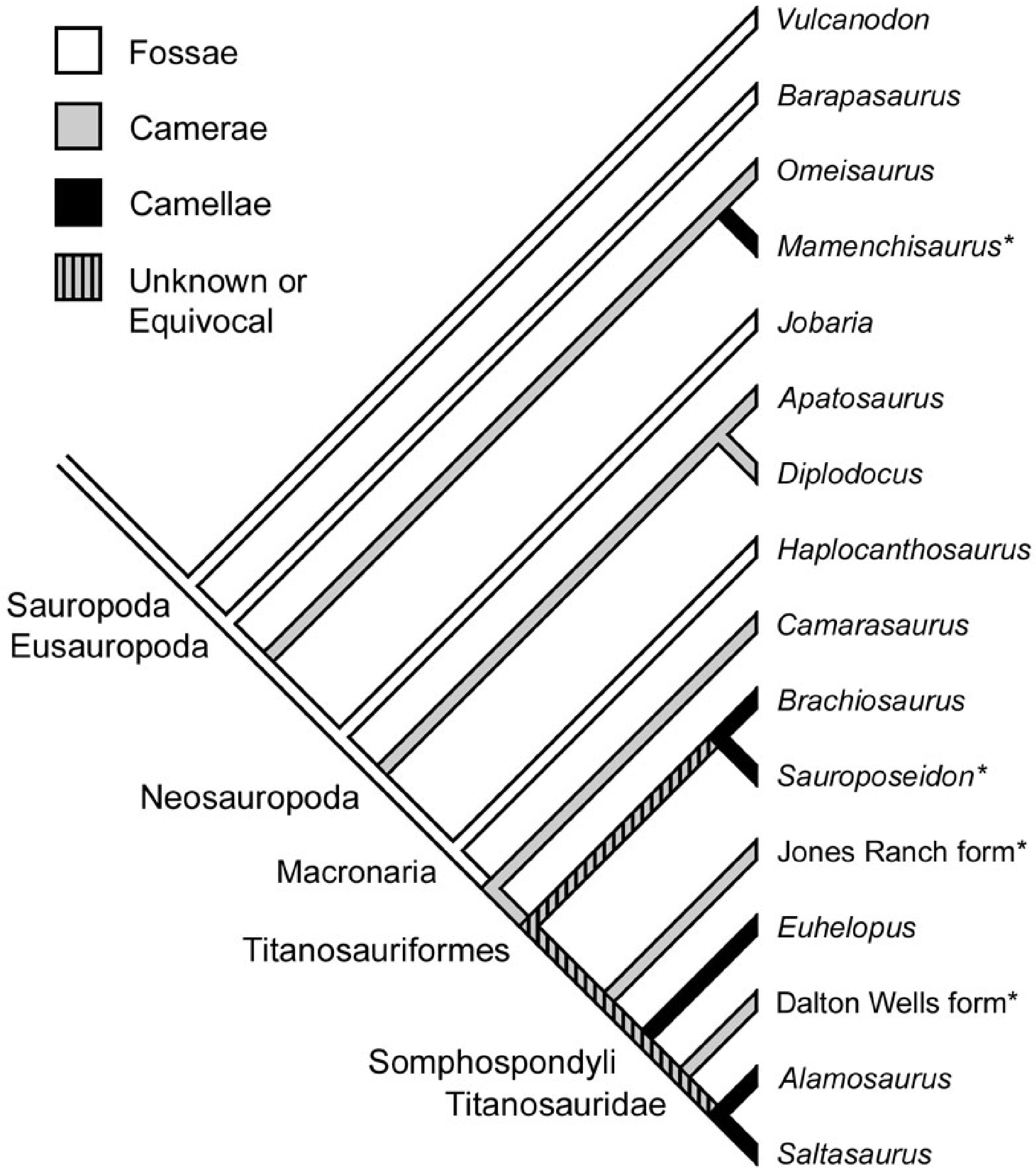

Fossae
Camerae
Camellae
Unknown or Equivocal
Vulcanodon
Barapasaurus
Omeisaurus
Mamenchisaurus
Euhelopus
Jobaria*
Haplocanthosaurus
Apatosaurus
Diplodocus
Camarasaurus
Brachiosaurus
Sauroposeidon*
Jones Ranch form*
Dalton Wells form*
Alamosaurus
Saltasaurus
Sauropoda
Eusauropoda
Neosauropoda
Titanosauriformes
Titanosauroidea
Titanosauridae

FIGURE 29. Evolution of vertebral pneumatic structure in sauropods, following the phylogeny of Wilson and Sereno (1998). Added taxa are placed in their probable phylogenetic position and denoted with an asterisk. The alternative placement of *Haplocanthosaurus*, with respect to Upchurch (1998), requires the independent acquisition of camerae in the Chinese sauropods, Diplodocidae, and Macronaria. Again, the evolution of camellae within Titanosauriformes is complex, and included either several independent origins or numerous reversals.



Fossae
Camerae
Camellae
Unknown or Equivocal
Vulcanodon
Barapasaurus
Omeisaurus
Mamenchisaurus*
Jobaria
Apatosaurus
Diplodocus
Haplocanthosaurus
Camarasaurus
Brachiosaurus
Sauroposeidon*
Jones Ranch form*
Euhelopus
Dalton Wells form*
Alamosaurus
Saltasaurus
Sauropoda
Eusauropoda
Neosauropoda
Macronaria
Titanosauriformes
Somphospondyli
Titanosauridae

FIGURE 30. Postcranial pneumaticity in Ornithodira. General tree topology and node terminology after Sereno (1991, 1999). Clades with pneumatized postcrania are denoted with asterisks. Pneumatization of the postcranial skeleton is either primitive for Ornithodira and secondarily lost in some dinosaurs, or evolved independently two or more times.

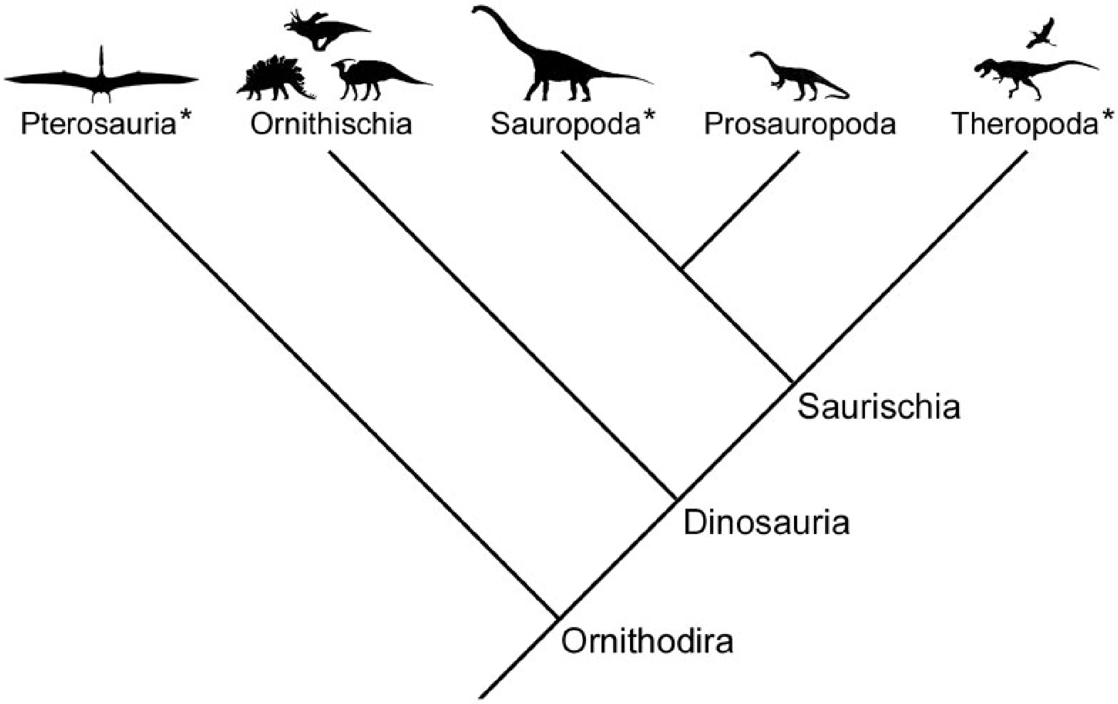

Pterosauria*
Ornithischia
Sauropoda*
Prosauropoda
Theropoda*
Saurischia
Dinosauria
Ornithodira

FIGURE 31. Hypothetical system of thoracoabdominal air sacs in a sauropod, based on that of the ostrich (see Bezuidenhout et al., 1999). The presence of even a limited air sac system would profoundly affect interpretation of sauropod paleobiology.

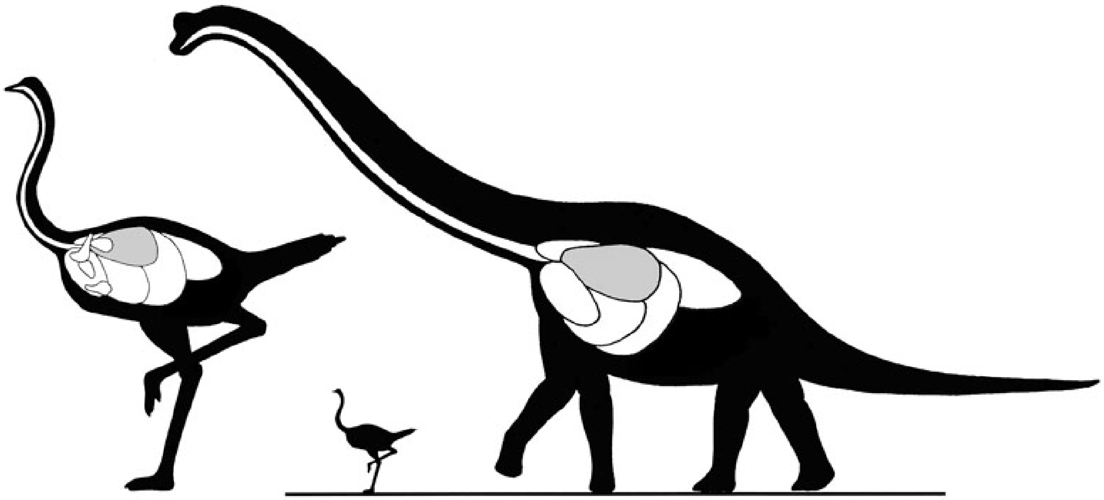


TABLE 1. Abbreviations used herein.

cml	camella
cmr	camera
ipozc	infrapostzygapophyseal cavity
ncl	neural canal
ncs	neurocentral suture
pfm	pneumatic foramen
pfs	pneumatic fossa
sprzc	supraprezygapophyseal cavity

TABLE 2. Taxa included in this analysis and their phylogenetic position. Phylogeny after Wilson and Sereno (1998), with supplemental information drawn from Salgado et al. (1997), Upchurch (1998), Sereno et al. (1999), and Wedel et al. (2000b). Taxa not included in those studies are placed in approximate position (see discussion in text). Taxa included in the CT analysis are indicated with an asterisk.

- Sauropoda
  - *Vulcanodon*
  - Sauropoda incertae sedis
    - *Isanosaurus*
  - Eusauropoda
    - *Barapasaurus*
    - *Mamenchisaurus*
    - *Jobaria*
    - Neosauropoda
      - Diplodocidae
        - *Apatosaurus* *
        - *Diplodocus* *
      - Macronaria
        - *Haplocanthosaurus* *
        - *Camarasaurus* *
        - *Tendaguria*
        - Titanosauriformes
          - Brachiosauridae
            - *Brachiosaurus* *
            - *Sauroposeidon* *
            - Unnamed taxon, Croatia
          - Titanosauriformes incertae sedis
            - *Pleurocoelus*
            - Unnamed taxon, Jones Ranch
          - Somphospondyli
            - *Euhelopus*
            - Titanosauria
              - *Gondwanatitan*
              - *Alamosaurus*
              - *Saltasaurus*
              - Unnamed taxon, Dalton Wells

TABLE 3. Sauropod material examined in the CT study. Axial position (i.e., cervical, dorsal, or caudal) is given for each vertebra. Numbers are assigned if they are known or can be reliably estimated. Maturity categories used in this study are as follows. Juveniles are individuals less than half of adult size, and lack neurocentral fusion. Subadults are individuals at least half of adult size with incomplete neurocentral fusion. Adults individuals are recognized on the basis of complete neurocentral fusion throughout the vertebral column.

Taxon	Specimen Number	Position	Maturity
Apatosaurus	CM 87	Dorsal	Adult
	CM 555 Df 3	Cervical	Subadult
	CM 3390	Dorsal	Juvenile
	CM 11339	Dorsal	Juvenile
	OMNH 01094	Cervical	Adult
	OMNH 01174	Cervical	Juvenile
	OMNH 01210	Dorsal	Juvenile
	OMNH 01219	Dorsal	Juvenile
	OMNH 01245	Cervical	Juvenile
	OMNH 01340	Cervical 14?	Adult
	OMNH 01380	Cervical	Adult
	OMNH 01420	Cervical	Adult
	OMNH 04173	Cervical	Adult
Brachiosaurus	BYU 12866	Cervical 5?	Adult
Camarasaurus	CM 33929	2 cervicals	Juvenile
	CM 36039	Cervical	Juvenile
	OMNH 01109	Cervical	Adult
	OMNH 01252	Cervical	Juvenile
	OMNH 01313	Cervical	Adult
Diplodocus	BYU 12613	Cervical	Adult
	CM 33984	Cervical	Juvenile
	OMNH 01093	Cervical	Adult
	OMNH 10333	Caudal	Adult
Haplocanthosaurus	CM 879 / 7	Cervical	Subadult
	CM 572	Dorsal	Adult

TABLE 3 (continued).

Taxon	Specimen Number	Position	Maturity
*Malawisaurus**	MAL 243	Cervical 3	Adult
	MAL 180	Cervical 4	Adult
	MAL 278-3	Cervical 7	Adult
	MAL 280-1	Cervical 8	Adult
	MAL 280-4	Cervical 11	Adult
	MAL 239	Dorsal 2	Adult
	MAL 200	Caudal 2	Adult
Sauroposeidon	OMNH 53062	Cervicals 5-7	Adult
Sauropoda indet.	OMNH 01418	Partial cervical	Adult
	OMNH 01649	Partial cervical	Adult
	TMM 42158-10	Anterior cervical	Adult

* Vertebrae from *Malawisaurus* were scanned as part of the CT study, but are not described herein. They will be described in a future manuscript, pending further work by E.M. Gomani and me.

TABLE 4. Definitions of pneumatic excavations and cavities. After Wedel et al. (2000b).

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

TABLE 5. Classification of sauropod vertebrae into morphologic categories based on pneumatic characters. After Wedel et al. (2000b).

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 entirely composed of camellae; neural arch laminae reduced; neural spine with inflated appearance.