THE EVOLUTION OF VERTEBRAL PNEUMATICITY IN SAUROPOD DINOSAURS

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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 basal sauropods pneumatic features are limited to fossae. 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*, derived diplodocids, and most titanosauriforms is correlated with increasing size and neck length.

The presacral vertebrae of basal 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 were probably present in at least some sauropods.

INTRODUCTION

The pneumaticity of sauropod vertebrae 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 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, 1903; 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 basal 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 deter-

mination 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 expand the number of taxa discussed, to describe the pneumatic morphologies in more detail, and to discuss the evolution of vertebral pneumaticity in sauropods in a more comprehensive fashion.

MATERIALS AND METHODS

Vertebral Terminology

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. 1; abbreviations used in the figures are provided in Table 1). 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) redefined fossae, camerae, and camellae based on geometry, size, septal thickness, degree of enclosure, and pattern of branching (Table 2).

Sauropod vertebrae can be classified into several morphological types based on the presence and distribution of their pneumatic fossae, camerae, and camellae (Fig. 2, Table 3). In addition to the established terms camerate and camellate (Britt, 1993, 1997), Wedel et al. (2000b) proposed the new terms acamerate, procamerate, and semicamellate. They also recognized particularly derived subcategories within camerate and camellate morphologies, which were termed polycamerate and somphospondylous, respectively. These terms are primarily intended as descriptors for individual vertebrae. Where I apply these labels to an entire taxon, for example, stating that *Brachiosau-*

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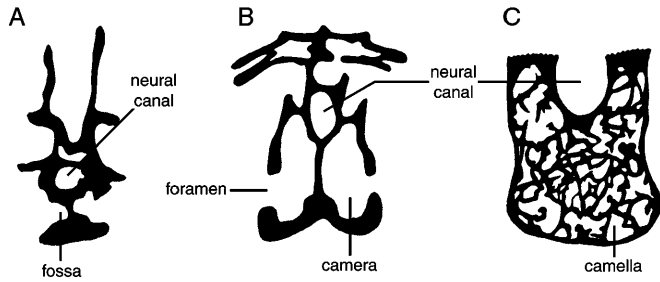
FIGURE 1. Axial sections of sauropod vertebrae showing pneumatic features. **A**, *Haplocanthosaurus priscus* (CM 897-7). **B**, *Camarasaurus* sp. (OMNH 01313). **C**, *Saltasaurus loricatus* (PVL 4017-137, redrawn from Powell, 1986). After Wedel et al. (2000b:fig. 2).

TABLE 1. Abbreviations used herein.

ab	abdominal air sac
al	accessory lamina
at	anterior thoracic air sac
c	cervical air sac
cml	camella
cmr	camera
i	interclavicular air sac
ncl	neural canal
ncs	neurocentral suture
pfm	pneumatic foramen
pfs	pneumatic fossa
pt	posterior thoracic air sac

rus is semicamellate, I use the most complex internal structure type found in that taxon. Because there is so much serial variation in vertebral pneumaticity, a single individual may have vertebrae of several different morphological types. In sauropod taxa I examined, internal pneumatic features are most complex in posterior cervical vertebrae, and dorsals and caudals tend to have simpler internal structures within a given individual or species. This serial variation in character states should be borne in mind when coding data for cladistic analyses.

Sample Size and Radiographic Techniques

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 following description and discussion hinge on those taxa for which vertebrae were available for CT scanning. 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. Such alterations are noted in the figure captions.

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. The CT protocols used were identical to those described by Wedel et al. (2000a, b).

Institutional Abbreviations

CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **MN**, Museu Nacional/Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **OMNH**, Oklahoma Museum of Natural History, Norman, Oklahoma; **PVL**, Paleontología de Vertebrados de la Fundación Miguel Lillo, Argentina; **QG**, National Museum of Zimbabwe, Bulawayo, Zimbabwe; **TMM**, Texas Memorial Museum, Austin, Texas; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **WL**, Wann Langston, Jr., Texas Memorial Museum, Austin, Texas.

POSTCRANIAL SKELETAL PNEUMATICITY

Pneumatization of the postcranial skeleton in various ornithodiran groups, including sauropods, is just one aspect of the more general phenomenon of skeletal pneumatization. Skeletal pneumatization, which includes paranasal, paratympanic, and pulmonary pneumatic spaces, is unique to archosaurs and synapsids (Witmer, 1997). 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 cranial 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 nutshell (Wetherbee, 1951).

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).

In addition to phylogenetic diversity in skeletal pneumatization, 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

TABLE 2.   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 Osteal			
Margins with Foramina?	no	yes	yes
Pattern?	—	regular branches	irregular branches
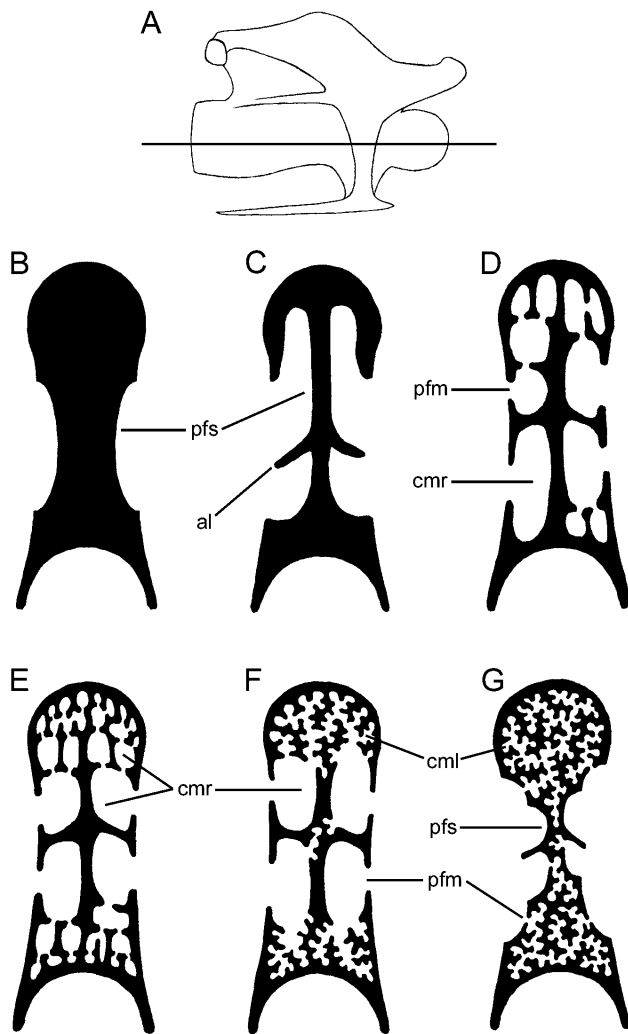
FIGURE 2.   Generalized examples of the internal structure types found in sauropod vertebrae. **A**, a sauropod cervical vertebra in right lateral view, showing the location of cross sections. **B**, in acamerate vertebrae, pneumatic fossae are present but do not significantly invade the centrum. **C**, in procamerate vertebrae, large pneumatic fossae penetrate to the median septum, but are not enclosed by osteal margins. **D**, camerate vertebrae have lateral pneumatic foramina that open into large camerae that occupy most of the centrum. The large camerae may bifurcate to produce successive generations of smaller camerae. **E**, in polycamerate vertebrae, successive bifurcations of the pneumatic diverticula produce three or more generations of camerae, with an increased number of branches at each generation. **F**, in semicamellate vertebrae, camellae are present but do not fill the internal structure, which is mostly occupied by large lateral camerae. **G**, the centra and neural spines of camellate vertebrae are entirely filled with numerous, small, irregularly arrayed camellae. Large external fossae may also be present. Somphospondylous vertebrae are distinguished from other camellate vertebrae by their reduced neural spine lamination (see Fig. 11).

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). The primary vertebral diverticulum is the diverticulum intertransversalis, which follows the brachial plexus and vertebral artery to advance through the transverse foramina (Fig. 4; 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). Diverticula may 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. 5).

In addition to their ventilatory function, the air sacs and their diverticula function in buoyancy, phonation and display, mass reduction, and thermoregulation (Witmer, 1997). These nonventilatory functions of the air sacs are obviously exaptations of a primarily pulmonary system. Skeletal pneumatization 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, 1940; 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 lack postcranial skeletal pneumaticity (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

TABLE 3.   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 osteal 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.

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*, respectively, were pneumatic. 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. Surveying 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. Although Longman did not describe these internal structures as pneumatic, 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 studies of the Tendaguru sauropods. 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
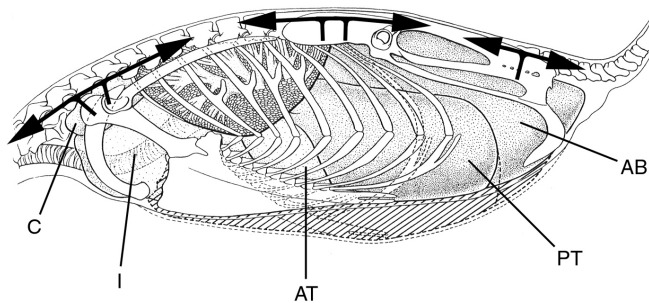

FIGURE 3.   Air sacs and axial pneumatization in an extant avian. The body of bird in left lateral view, showing the cervical, interclavicular, anterior thoracic, posterior thoracic, and abdominal air sacs. The hatched area shows the volume change during exhalation. The cervical and anterior thoracic 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).
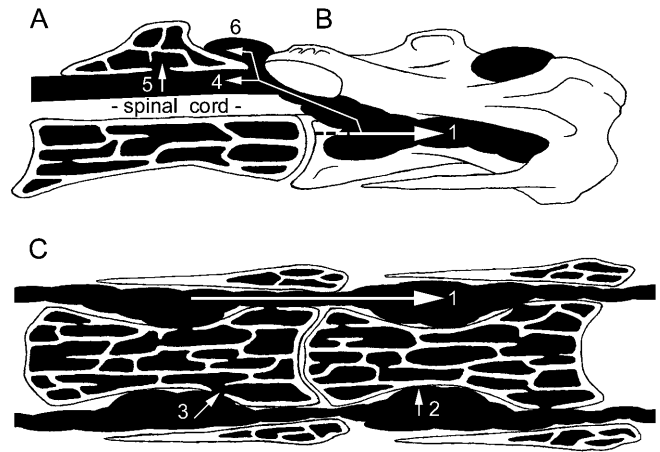

FIGURE 4.   Pneumatization of the cervical series in the ostrich. The vertebrae are shown in midsagittal section (**A**), right lateral view (**B**), and horizontal section (**C**). Anterior is to the right. White arrows show the development of pneumatic diverticula and camellae, which are shown in black. 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 become 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.
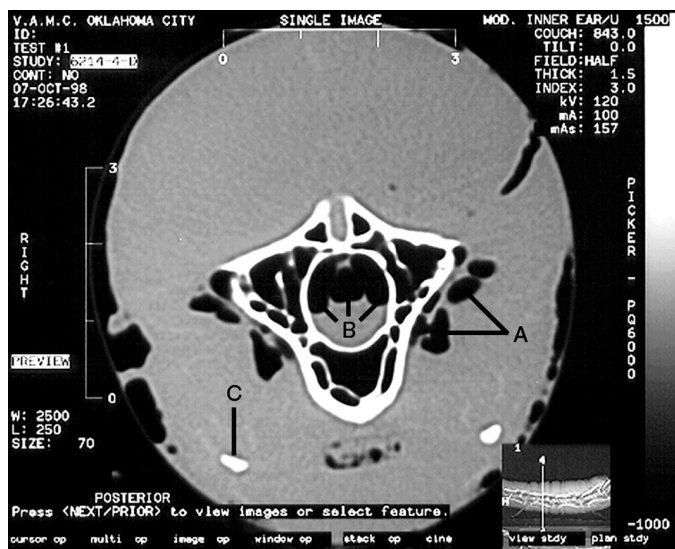
FIGURE 5. CT sections through the neck of an ostrich. The neck section was sealed with surgical gloves and cannulated with an air tube to re-inflate the pneumatic diverticula. In these images, air is black, bone is white, and soft tissues are grey. **A**, note the essentially camellate nature of the 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.

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 hypothesized 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, his reliance on comparative anatomy for recognition of pneumatic features, and his 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 to state that a particular taxon has pleurocoels is to describe a plesiomorphy rather than diagnose an apomorphy.

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 phylogeny was 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.

Description

The vertebral pneumaticity of sauropods was briefly discussed by Wedel et al. (2000b). The following description focuses on specimens and taxa that were not discussed in that work. 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 described elsewhere (Wilson, 1999), so the following description and discussion focus on vertebral internal structures (camerae and camellae) and their external correlates (fossae and foramina).

The taxa discussed below are listed in approximate phylogenetic order. 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—Basal sauropods such as *Vulcanodon* and *Isanosaurus* have pneumatic features that are limited to fossae. 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 (see Cooper, 1984:fig. 15). 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 derived sauropods.

Isanosaurus is a basal sauropod recently described from the Late Triassic of Thailand (Buffetaut et al., 2000). 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 derived sauropods. In addition, simple laminae are present on a dorsal neural spine.

Eusauropoda—*Barapasaurus*, from the Early Jurassic of India, is either a basal eusauropod (Salgado et al., 1997; Wilson and Sereno, 1998), or the sister group to Eusauropoda (Upchurch, 1998). The presacral vertebrae of *Barapasaurus* bear

fossae on the lateral faces of the centra (see Jain et al., 1979: pls. 101 and 102). 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 (Jain et al., 1979; Britt, 1993).

Other eusauropods which lie outside the neosauropod radiation include *Mamenchisaurus* and *Jobaria*. *Mamenchisaurus* is closely related to *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). Young and Zhao (1972) described the vertebrae of *Mamenchisaurus hochuanensis* as having small, elliptical fossae on the lateral faces of the cervical and dorsal centra, and internally honeycombed by many small cavities. Russell and Zheng (1993) also described the internal structure of a cervical vertebra of *Mamenchisaurus sinocanadorum* as resembling a honeycomb. The size and geometry of the internal chambers of *Mamenchisaurus* is consistent with camellate internal structure.

The recently described *Jobaria*, from the Early Cretaceous of North Africa, is apparently the sister group to Neosauropoda (Sereno et al., 1999). Pneumatic fossae are present in the centra of every postatlantal cervical vertebra (the atlas was not recovered). 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. In the dorsal series, pneumatic fossae are only present in the centra of anterior vertebrae.

Diplodocidae—*Apatosaurus* and *Diplodocus* from the Late Jurassic of North America are the best known diplodocids. As described by Wedel et al. (2000b), the vertebrae of *Apatosaurus* are polycamerate, with a branching pattern of successively smaller camerae. 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. 6). 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 developed into camerae. In some specimens, preservation is fine enough to record tiny (<1 mm) coels in the bone near the developing camera (Fig. 7A–C). Comparisons with birds suggest that these coels represent osteoclastic resorption in proximity to the advancing pneumatic epithelium.

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 (see Osborn, 1899:figs. 7 and 13). 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* (see Hatcher, 1901:pl. 7). The median septum is rarely regular or symmetrical, regardless of ontogenetic stage (Fig. 7D–G).

Macronaria—*Haplocanthosaurus*, also from the Late Jurassic of North America, 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). Pneumatic features in *Haplocanthosaurus* are limited to fossae. In cervical vertebrae, extensions of the lateral fossae 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. 8). These fossae occur in the same location on the centrum as the foramina of truly ca-
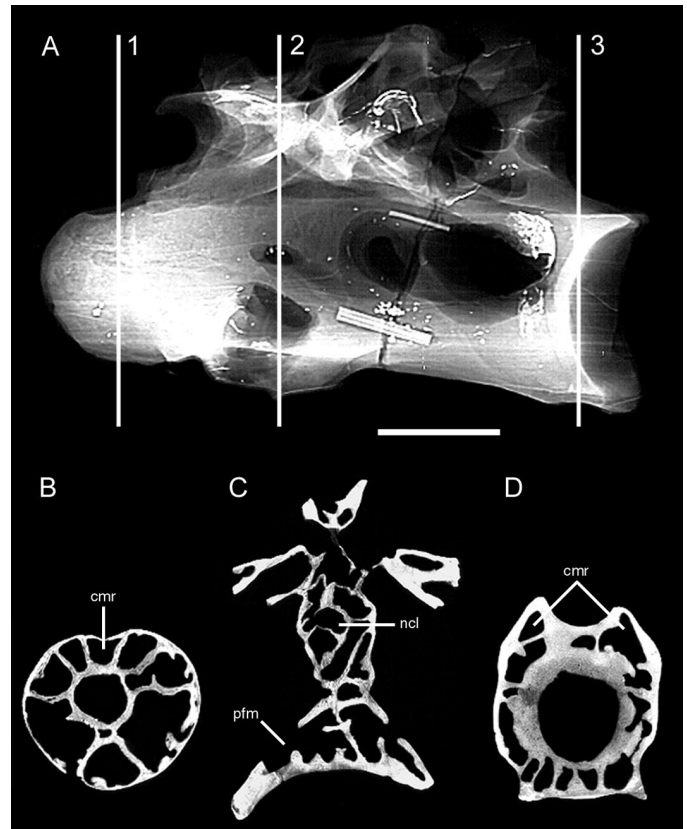

FIGURE 6. CT sections through a cervical vertebra of *Apatosaurus*, OMNH 01094. **A**, specimen in left lateral view showing the location of CT sections. Two metal pins were used to repair the specimen and can be seen in this image. **B**, a section through the condyle (A, position 1) showing large, 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. In **B**, **C**, and **D**, matrix filling the camerae was erased using Adobe Photoshop© version 5.5. Scale bar is 10 cm.

merate vertebrae, but do not open into any larger chambers; they are essentially deep depressions.

Camarasaurus is the prototypical camerate sauropod; large camerae are one of the hallmark characters of the genus. The large lateral camerae 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. 9). The internal structure is relatively simple, and the vertebrae of juveniles resemble smaller versions of the adult form with fewer generations of camerae.

Brachiosauridae—*Brachiosaurus*, from the Late Jurassic of North America and East Africa, is the most basal titanosauriform (Salgado et al., 1997; Wilson and Sereno, 1998). Externally, both cervical and dorsal vertebrae of *Brachiosaurus* bear large foramina which open into camerae (see Janensch, 1950: figs. 43 and 53). Although the camerae are large they do not occupy the entirety of the internal structure; the condyles, cotyles, and zygapophyses are filled with camellae (Wedel et al., 2000b:fig. 12; cf. Janensch, 1950:figs. 67–73). 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.
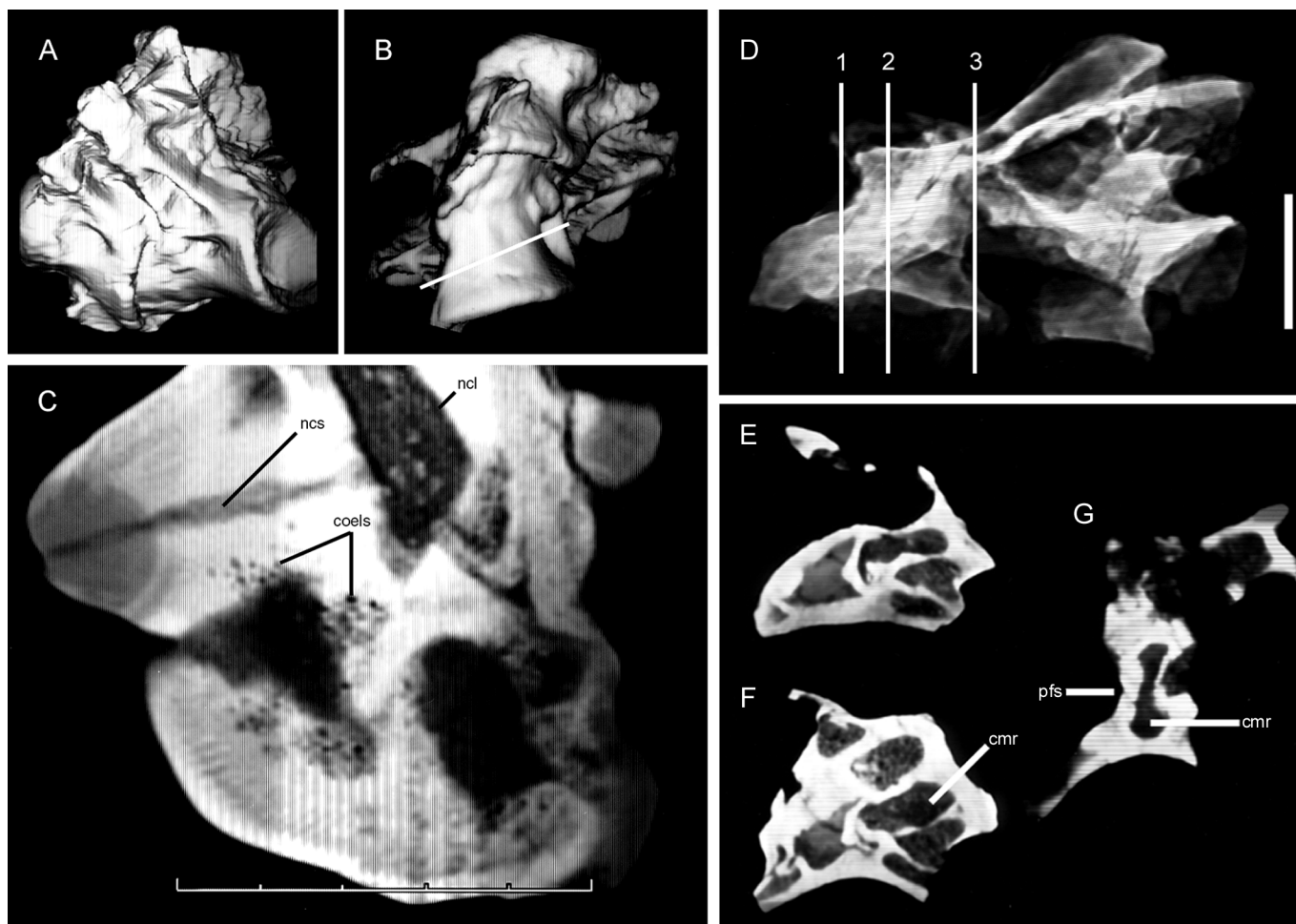
FIGURE 7.   Vertebrae from juvenile diplodocids. **A–C**, Digital model of juvenile vertebrae of *Apatosaurus*. CM 3390 includes two articulated cervical vertebrae from a juvenile animal. These vertebrae were scanned with overlapping slices, and the data were used to construct a digital model which could 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. **D–G**, CT sections through a cervical vertebra from a juvenile individual of *Diplodocus*, CM 33984. The specimen is somewhat distorted diagonally by dorsolateral compression. **D**, specimen in left lateral view showing the location of CT sections. **E–F**, sections through the condyle (D, position 1) and anterior centrum (D, position 2), showing the early development of a few relatively large camerae. **G**, a section through the middle of the centrum (D, position 3) showing large lateral fossae and a camera between the paired median septa. Scale bar is 5 cm.

Although poorly represented, the Early Cretaceous *Sauroposeidon* is linked to *Brachiosaurus* by several synapomorphies. The lateral faces of the centra and neural spines are occupied by pneumatic fossae that are larger, deeper, and more elaborate than those of basal sauropods (Wedel et al., 2000b: fig. 6). Internally, the vertebrae of *Sauroposeidon* are entirely filled by small pneumatic camellae (see Wedel et al., 2000b:fig. 12). The bony septa dividing these camellae range in thickness from less than 1 mm to approximately 3 mm.

Titanosauriformes Incertae Sedis—*Pleurocoelus* is a poorly understood genus from the Early Cretaceous of North America. Salgado and Calvo (1997) referred *Pleurocoelus* to the Titanosauriformes, based on the morphology of referred appendicular elements. The type and referred vertebrae of *Pleurocoelus* from the Arundel Clay all pertain to juvenile individuals. Cervical, dorsal, and sacral vertebrae bear large lateral fossae that penetrate to a narrow median septum (Fig. 10A). However, in the absence of adult material it is impossible to determine whether the lack of internalized pneumatic chambers is of phy-

logenetic or merely ontogenetic significance (see discussion below).

An unnamed taxon from the Jones Ranch Quarry in the Twin Mountains Formation (Aptian–Albian) of Texas represents a sauropod of unknown affinities (Winkler et al., 1997). Preliminary analysis of the Jones Ranch sauropod indicates that it lies within Titanosauriformes, but outside Somphospondyli (Gomani et al., 1999). 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 closely resembles cervical vertebrae of *Euhelopus* and the unnamed titanosaurid from Peirópolis, Brazil (Fig. 10B; 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).

Somphospondyli—*Euhelopus* is a long-necked sauropod from Late Jurassic or Early Cretaceous of China (see discussion
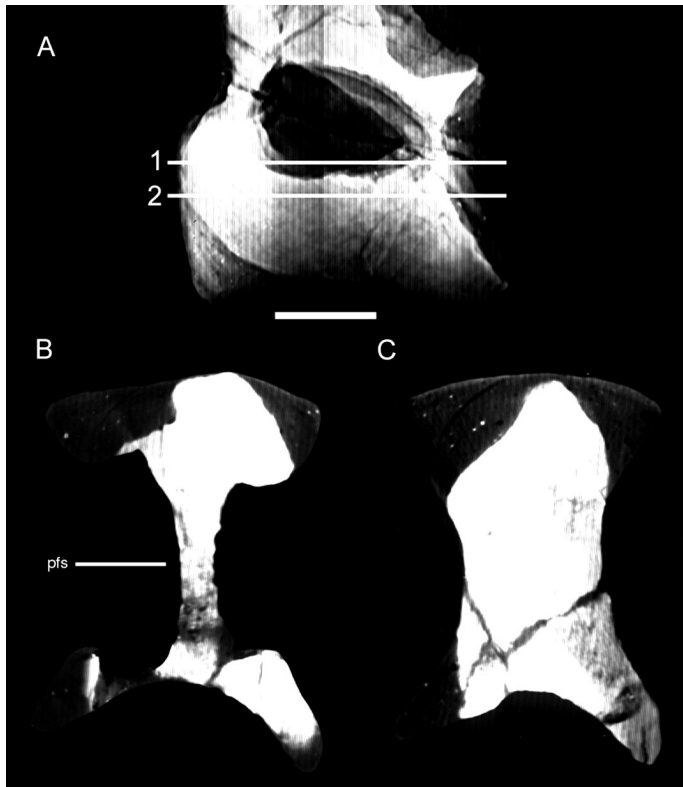
FIGURE 8. CT sections through a dorsal vertebra of *Haplocantho-saurus*, CM 572. The vertebra is complete, but only the centrum is shown here. **A**, the centrum in left lateral view showing the location of CT sections. **B**, horizontal section through the mid-centrum (A, position 1) showing the large 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.
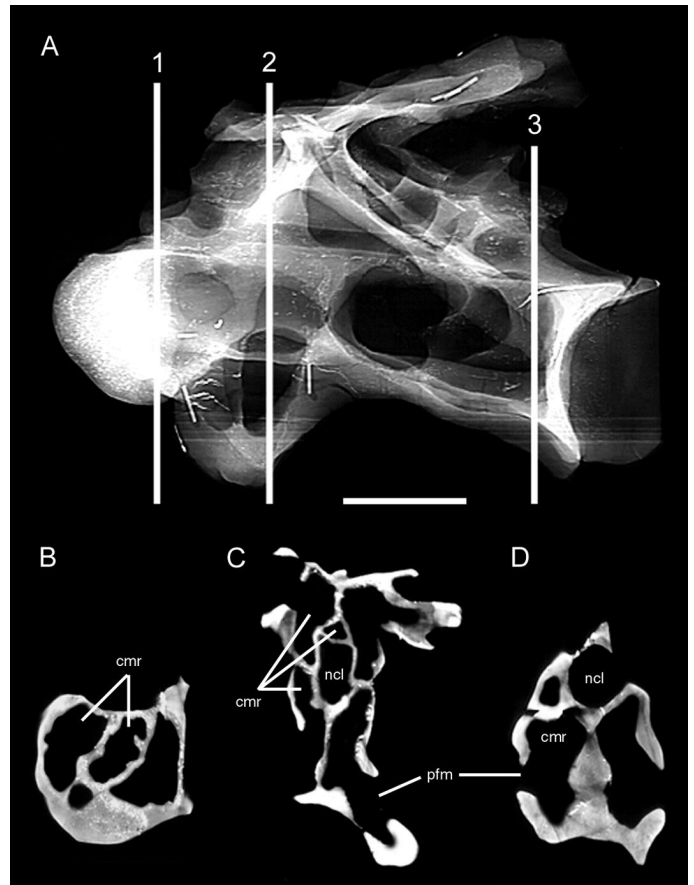

FIGURE 9. CT sections through a cervical vertebra of *Camarasaurus*, OMNH 01313. **A**, specimen in left lateral view showing the location of CT sections. Small wires used in repairing the specimen can be seen in the condyle, cotyle, neural spine, and parapophysis. **B**, a section through the condyle (A, position 1). The camerae 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. In **B**, **C**, and **D**, matrix filling the camerae was erased using Adobe Photoshop© version 5.5. Scale bar is 10 cm.

in Wilson and Sereno, 1998). 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. The presacral vertebrae of *Euhelopus* are completely camellate (Britt, 1993; Wilson and Sereno, 1998). In addition, the laminae of cervical and anterior dorsal vertebrae are poorly developed compared to those of other sauropods.

Titanosauria—Kellner and Azevedo (1999) described *Gondwanatitan*, from the Late Cretaceous of Brazil, as a titanosaurid more derived than the basal titanosaurians *Andesaurus* and *Malawisaurus* and less derived than the Saltasaurinae. 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. 10C). The thick cortical bone and presence of a distinct median septum suggest that these chambers are camerae rather than camellae.

Another Late Cretaceous titanosaurid, the North American *Alamosaurus* is closely allied with the Mongolian *Opisthocoelicaudia* and the South American Saltasaurinae (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998). 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. 11A, B). The laminar structure of the neural spine is poorly developed, and the neural spine resembles a partially inflated balloon. A fragmentary 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 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.

Saltasaurus, from the Late Cretaceous of Argentina, is generally regarded to be the most derived titanosaurid yet discovered (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998). The presacral, sacral, and proximal caudal vertebrae of *Saltasaurus* are fully camellate (Fig. 11C–F). Fully camellate caudal vertebrae are synapomorphic for Saltasaurinae (*Saltasaurus* and *Neuquensaurus*). Furthermore, Sanz et al. (1999) mentioned 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
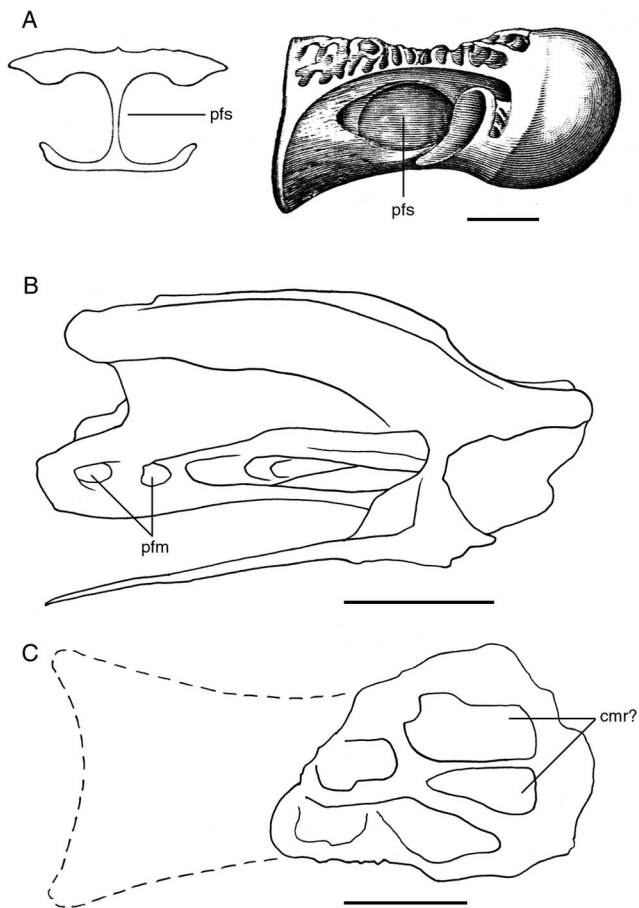
FIGURE 10. Cervical vertebrae of various titanosauriforms. **A**, USNM 5678, holotype cervical vertebra of *Pleurocoelus*. The presence of large lateral fossae is presumed to be a juvenile character. After Lull (1911b:pl. 15). **B**, a cervical vertebra of the Jones Ranch sauropod on display in the Fort 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 *Saltasaurus* (Fig. 11). Redrawn from Kellner and Azevedo (1999:fig. 5). Scale bars are **A**, 2 cm; **B**, 20 cm; **C**, 5 cm.

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 derived sauropods and birds.

The earliest known titanosaurid in North America is an unnamed taxon from the Dalton Wells Quarry in the Cedar Mountain Formation (?Barremian–Aptian) of Utah (Britt and Stadtman, 1996, 1997; Britt et al., 1997, 1998). Although the Dalton Wells taxon has not been included in a phylogenetic analysis, it is characterized by several titanosaurid synapomorphies (Britt et al., 1998). However, it is unusual in that it is camerate and apparently lacks camellae. The fully camerate condition of the Dalton Wells taxon is so far unique among described titanosaurids.

DISCUSSION

Ontogenetic Considerations

It is axiomatic that animals change as they grow, but ontogenetic variation poses a special problem in any analysis of vertebral pneumaticity. In extant mammals and archosaurs, the interaction between the bone and air sac is dynamic and may be remodeled actively, even late in life (Witmer, 1997). 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 some key taxa are known only from juvenile material (e.g., *Isanosaurus*, *Lapparentosaurus*; 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 (Marsh, 1888). The type vertebrae, which may not belong to a single individual (Lull, 1911a, b), 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. However, large pneumatic fossae are typical of juvenile sauropods regardless of their phylogenetic affinities. Vertebrae from juvenile specimens *Apatosaurus* and *Camarasaurus* do not differ significantly from the type material of *Pleurocoelus* on either proportional or morphological grounds (see Wedel et al., 2000b:fig. 14), and have been confused with *Pleurocoelus* in the past (McIntosh, 1981). 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.

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.
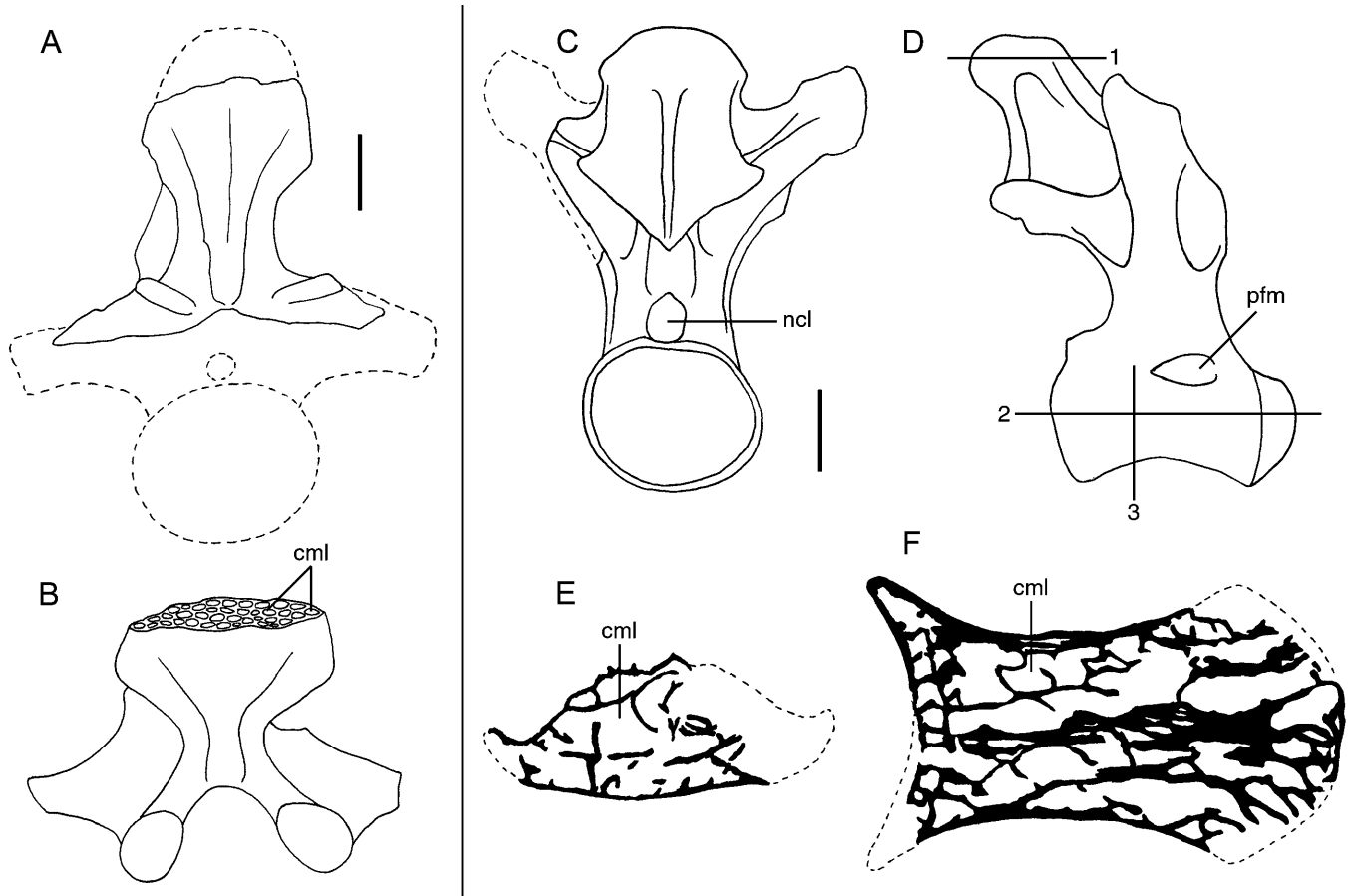
The regular branching pattern of camerae in camerate and

FIGURE 11. Somphospondylous vertebrae of titanosaurids. **A–B**, 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. **C–F**, PVL 4017-137, a dorsal vertebra of *Saltasaurus*. **C**, posterior view. **D**, lateral view, showing the location of cross sections. **E**, horizontal section through neural spine (D, position 1). **F**, horizontal section through centrum (D, position 2). A vertical section through centrum (D, position 3) is shown in Figure 1C. Redrawn from Powell (1986: pls. 28 and 30). Note the reduced neural arch laminae and overall 'inflated' appearance in both vertebrae. Scale bars are **A**, 10 cm; **B**, 5 cm.

polycamerate forms suggests a clear ontogenetic pathway (Fig. 12). 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 ei-
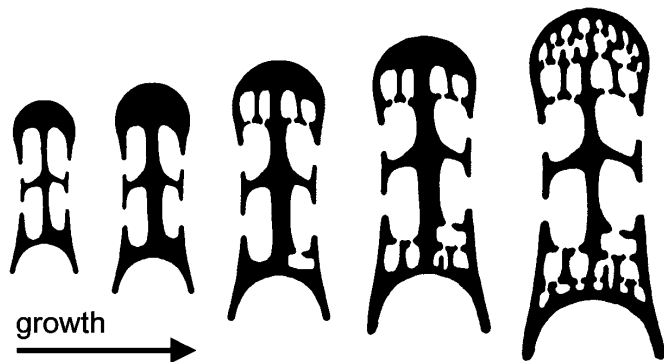
FIGURE 12. Hypothetical ontogeny of camerate vertebrae. The regular branching pattern of camerae in camerate and polycamerate vertebrae suggests that pneumatization of the centrum occurred in pulses. As the vertebra grew, new bone would build up around existing fossae and camerae. The pneumatic epithelium would then bifurcate and push into the new bone, producing a regular branching pattern.

ther 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. The simpler camerate morphology of *Camarasaurus* suggests a smaller number of growth cycles, and hence fewer generations of camerae.

This leap-frogging of bone and air sac could also explain the growth of the osteal 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 osteal 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, and I have not had the opportunity to examine them. In birds, camellae develop very

early in ontogeny and the vertebrae grow considerably following 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 derived 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 derived 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 did 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 centra are largely occupied by the cervical diverticula (see Figs. 4, 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 (Fig. 13).

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. 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, 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). As discussed above, the vertebral morphology of *Gondwanatitan* suggests that it is a camerate titanosaurid. In addition, vertebrae from the Dalton Wells titanosaurid have large lateral camerae and lack camellae (Britt et al., 1997), demonstrating that at least some titanosaurids had camerate vertebrae.

On the other hand, all known brachiosaurids have camellae, as do derived 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*. 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* may be 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
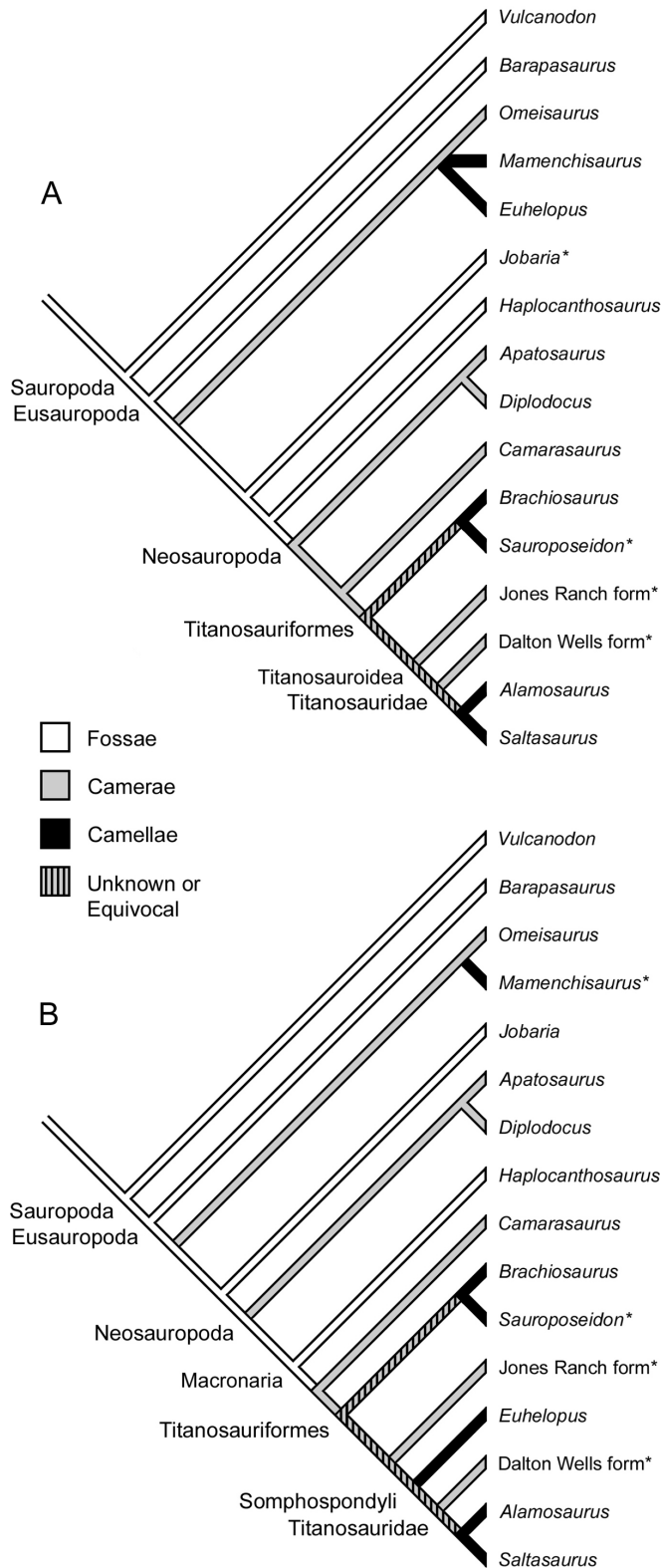
condition in basal titanosauriforms is best regarded as equivocal for the present.

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 is thus correlated with the evolution of large body size and long necks in these taxa. The biomechanical implications of different pneumatic morphologies remain to be investigated.

Distribution of Vertebral Pneumaticity and Air Sacs

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 basal 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).

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. 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.

ACKNOWLEDGMENTS

FIGURE 13. Evolution of vertebral pneumatic structures in sauropods, following the phylogenies of Upchurch (1998) and Wilson and Sereno (1998). In each diagram, added taxa are placed in their probable phylogenetic position and denoted with an asterisk. **A**, sauropod phylogeny after Upchurch (1998). 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 titanosauri-

forms as equivocal with respect to this character. **B**, sauropod phylogeny after Wilson and Sereno (1998). 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.

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