SEVEN

Postcranial Skeletal Pneumaticity in Sauropods and Its Implications for Mass Estimates

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ONE OF THE SIGNAL FEATURES of sauropods, and one of the cornerstones of our fascination with them, is their apparent efficiency of design. The presacral neural spines of all sauropods have a complex of bony ridges or plates known as vertebral laminae (fig. 7.1; abbreviations used in the figures are listed below). In addition, the vertebral centra of most sauropods bear deep fossae or have large foramina that open into internal chambers. The laminae and cavities of sauropod vertebrae are often considered to be adaptations for mass reduction (Osborn 1899; Hatcher 1901; Gilmore 1925) and have been important in studies of sauropod evolution (McIntosh 1990; Wilson 1999). The possibility that these structures were pneumatic—that they contained or partitioned air-filled diverticula of the lungs or air sacs—has been recognized for over a century (Seeley 1870; Janensch 1947). However, pneumaticity in sauropods has received little attention until recently (Britt 1997; Wilson 1999; Wedel 2003a, 2003b).

My goal here is to review previous work on pneumaticity in sauropods, discuss some outstanding problems, and outline possible directions for future studies. To that end, the chapter is organized around three questions. What criteria do we use to infer pneumaticity in sauropod fossils? What characteristics of pneumatic bones have been (or could be) described? and How can we apply data on skeletal pneumaticity to paleobiological problems, such as estimating the masses of sauropods? Before attempting to answer these questions, it will be useful to review skeletal pneumaticity in living vertebrates.

Institutional abbreviations: BYU, Earth Sciences Museum, Brigham Young University, Provo, Utah; CM, Carnegie Museum, Pittsburgh, Pennsylvania; DGM, Museo de la Divisão de Geologia y Mineralogia, Rio de Janeiro, Brazil; DMNS, Denver Museum of Nature and Science, Denver, Colorado; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

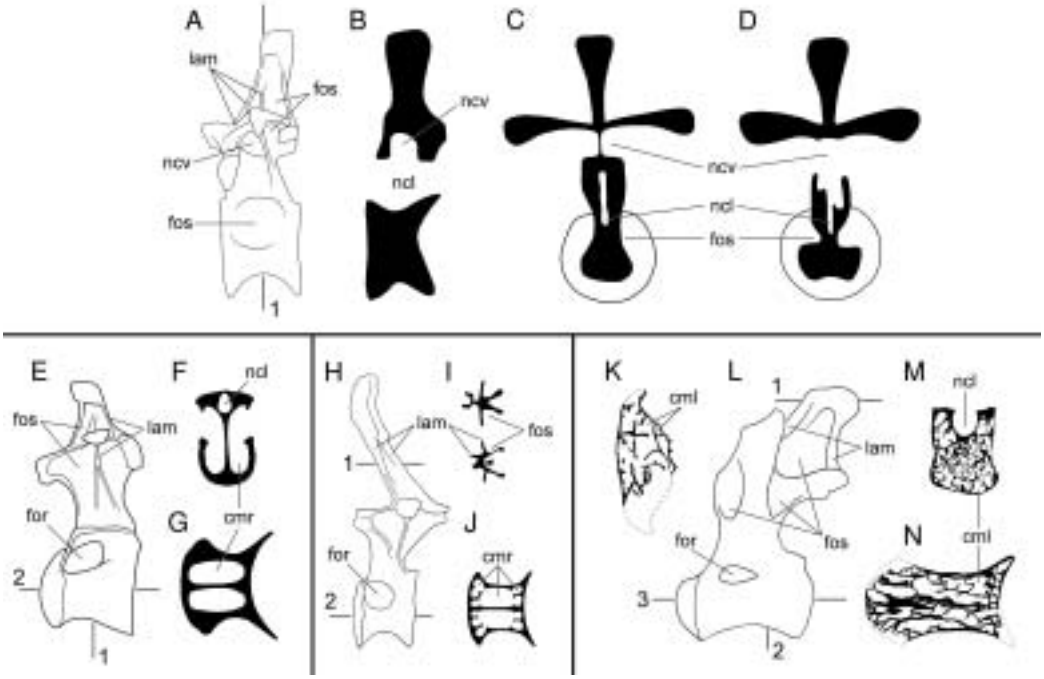

FIGURE 7.1. Pneumatic features in dorsal vertebrae of *Barapasaurus* (A–D), *Camarasaurus* (E–G), *Diplodocus* (H–J), and *Saltasaurus* (K–N). Anterior is to the left; different elements are not to scale. A, A posterior dorsal vertebra of *Barapasaurus*. The opening of the neural cavity is under the transverse process. B, A midsagittal section through a middorsal vertebra of *Barapasaurus* showing the neural cavity above the neural canal. C, A transverse section through the posterior dorsal shown in A (position 1). In this vertebra, the neural cavities on either side are separated by a narrow median septum and do not communicate with the neural canal. The centrum bears large, shallow fossae. D, A transverse section through the middorsal shown in B. The neural cavity opens to either side beneath the transverse processes. No bony structures separate the neural cavity from the neural canal. The fossae on the centrum are smaller and deeper than in the previous example. (A–D redrawn from Jain et al. 1979:pl. 101, 102.) E, An anterior dorsal vertebra of *Camarasaurus*. F, A transverse section through the centrum (E, position 1) showing the large camerae that occupy most of the volume of the centrum. G, a horizontal section (E, position 2). (E–G redrawn from Ostrom and McIntosh 1966:pl. 24.) H, A posterior dorsal vertebra of *Diplodocus*. (Modified from Gilmore 1932:fig. 2.) I, Transverse sections through the neural spines of other *Diplodocus* dorsals (similar to H, position 1). The neural spine has no body or central corpus of bone for most of its length. Instead it is composed of intersecting bony laminae. This form of construction is typical for the presacral neural spines of most sauropods outside the clade Somphospondyli. (Modified from Osborn 1899:fig. 4.) J, A horizontal section through a generalized *Diplodocus* dorsal (similar to H, position 2). This diagram is based on several broken elements and is not intended to represent a specific specimen. The large camerae in the midcentrum connect to several smaller chambers at either end. K, A transverse section through the top of the neural spine of an anterior dorsal vertebra of *Saltasaurus* (L, position 1). Compare the internal pneumatic chambers in the neural spine of *Saltasaurus* with the external fossae in the neural spine of *Diplodocus* shown in J. L, An anterior dorsal vertebra of *Saltasaurus*. M, A transverse section through the centrum (L, position 2). N, A horizontal section (L, position 3). In most members of the clade Somphospondyli the neural spines and centra are filled with small camellae. (K–N modified from Powell 1992:fig. 16.)

Anatomical abbreviations: al, accessory lamina; *cit*, canalis intertransversarius; *cml*, camella; *cmr*, camera; *dsv*, diverticulum supervertebrale; *for*, foramen; *fos*, fossa; *lam*, lamina; *nad*, neural arch diverticulum; *naf*, neural arch fossa; *ncl*, neural canal; *ncs*, neurocentral suture; *ncv*, neural cavity; *nsf*, neural spine fossa; *pcdl*, posterior centrodiapophyseal lamina; *podl*, postzygodiapophyseal lamina; *prdl*, prezygodiapophyseal lamina; *spol*, spinopostzygapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *vk*, ventral keel.

SKELETAL PNEUMATICITY IN EXTANT TAXA

Pneumatization of the postcranial skeleton in various ornithodiran groups, including sauropods, is just one instance of the more

general phenomenon of skeletal pneumatization. Skeletal pneumatization, which includes paranasal, paratympanic, and pulmonary pneumatic spaces, is unique to archosaurs and advanced synapsids (Witmer 1997, 1999). However, diverticula (epithelium-lined outgrowths) of the pharynx or trachea are present in representative taxa from most major lineages of tetrapods, including frogs (Duellman and Trueb 1986), snakes (Young 1991, 1992), birds (King 1966; McClelland 1989a), and primates (Janensch 1947). Pharyngeal and tracheal diverticula are often used to inflate specialized structures used in phonation or visual display. These diverticula do not invade any bones except the hyoid, which is pneumatized by tracheal diverticula in the howler monkey *Alouatta* (Janensch 1947; *Mycetes* of his usage). Diverticula of paranasal and paratympanic air spaces 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 occipitoatlantal fusion (Sadler et al. 1996). Among extant taxa, only birds have extensive postcranial skeletal pneumaticity (PSP).

Extant birds have relatively small, inflexible lungs and an extensive system of air sacs in the thorax and abdomen. The air sacs are flexible and devoid of parenchymal tissue, and their primary function is to ventilate the lungs (King 1966; Duncker 1971; McClelland 1989b). In most birds, the air sacs also give rise to a network of diverticula. Diverticula pass into the viscera, between muscles, and under the skin in various taxa (Richardson 1939; King 1966; Duncker 1971). If a diverticulum comes into contact with a bone, the bone may become pneumatized. Bremer (1940) described the pneumatization of the humerus in the chicken (*Gallus*) as follows. The diverticulum enters the bone because osteoclasts break down the bony tissue ahead of it. The bony tissue immediately adjacent to the diverticulum is replaced by mesenchymal tissue, which degenerates or is resorbed and is in turn replaced by the growing diverticulum. As the diverticulum bores through the cortical bone it produces a pneumatic foramen, which must remain open for pneumatization to proceed normally (Ojala 1957). Once the bone has been penetrated, branches of the diverticulum spread through the marrow cavity by replacing bony trabeculae. The marrow is reduced to small islands of tissue surrounded by the diverticulum. As these islands of marrow degenerate, the branches of the diverticulum anastomose and form a single, epithelium-lined air cavity that occupies most of the internal volume of the bone. The trabecular structure of the bone is greatly reduced, and the inner layers of the cortex are resorbed.

Witmer (1990) pointed out that a pneumatic foramen does not have to be located on the pneumatic bone in question; the intraosseous diverticulum may have spread across a suture from an adjacent pneumatic bone. He called this *extramural pneumatization* and contrasted it with *intramural pneumatization*, in which a diverticulum directly invades a bone and produces a pneumatic foramen. Although Witmer (1990) was concerned with cranial pneumatization, extramural pneumatization also occurs in the postcranial skeleton, for example, between fused vertebrae in the chicken (King 1957; Hogg 1984a).

The term *air sac* has been used by some authors for any reservoir of air in an animal that is lined by epithelium and devoid of parenchymal tissue (e.g., Brattstrom 1959; Cranford et al. 1996). The same term is often used in the ornithological literature to refer specifically to the pulmonary air sacs of birds (e.g., Müller 1907). In this paper, the term air sac is restricted to indicate the pulmonary air sacs of birds. All other epithelium-lined air reservoirs, including those that develop from the lungs and air sacs, are called diverticula. Another important difference is between a pneumatic diverticulum, which is a soft-tissue structure, and the bony recess that it may occupy (Witmer 1999). In many cases, the bony recess is produced by the

diverticulum through the process of pneumatization. This causal relationship allows us to infer the presence of diverticula from certain kinds of bony recesses. The study of skeletal pneumaticity in fossil taxa is founded on such inferences.

WHAT CRITERIA DO WE USE TO INFER PNEUMATICITY IN FOSSILS?

How do we recognize skeletal pneumaticity? More specifically, what are the osteological correlates (*sensu* Witmer 1995, 1997) of pneumatic diverticula, such that the presence of the latter can be inferred from the former? Several authors, including Hunter (1774) and Müller (1907), list differences between pneumatic and apneumatic bones. These authors focused on recognizing pneumaticity in extant birds and thus referred to attributes that tend not to fossilize, such as vascularity, oil content, and color. Britt (1993, 1997) provided the most comprehensive list of pneumatic features identifiable in fossil bones: internal chambers with foramina, fossae with crenulate texture, smooth or crenulate tracks (grooves), bones with thin outer walls, and large foramina.

INTERNAL CHAMBERS WITH FORAMINA

The most obvious osteological correlate of pneumaticity is the presence of foramina that lead to large internal chambers. Large chambers, often called "pleurocoels," are present in the presacral vertebrae of most sauropods. They may also be present in the sacral and caudal vertebrae, as in *Apatosaurus* and *Diplodocus* (see Ostrom and McIntosh 1966:pl. 30 and Osborn 1899:fig. 13, respectively). In extant birds, such chambers are invariably associated with pneumatic diverticula (Britt 1993). The presence of similar chambers in the bones of sauropods, theropods, and pterosaurs has been accepted by most authors as prima facie evidence of pneumaticity (Seeley 1870; Cope 1877; Marsh 1877; Janensch 1947; Romer 1966; Britt 1993, 1997; O'Connor 2002). As far as I am aware, no substantive alternative hypotheses have been advanced; as Janensch (1947:10: translated from the German by G. Maier) said, "There is no basis to consider the pleurocentral cavities in sauropod vertebrae as different from similar structures in the vertebrae of birds." In short, no soft tissues other than pneumatic diverticula are known to produce large foramina that lead to internal chambers, and these chambers constitute unequivocal evidence of pneumaticity.

One of the primary differences among the pneumatic vertebrae of different sauropod taxa is the subdivision of the internal chambers. Some taxa, such as *Camarasaurus*, have only a few large chambers, whereas others, such as *Saltasaurus*, have many small chambers (fig. 7.1). Vertebrae with many small chambers have been characterized as "complex" (Britt 1993; Wedel 2003b), in contrast to "simple" vertebrae with few chambers. The concept of "biological complexity" has several potential meanings (McShea 1996). In this paper, complexity refers only to the level of internal subdivision of pneumatic bones; complex bones have more chambers than simple ones. This is "nonhierarchical object complexity" in the terminology of McShea (1996).

EXTRAMURAL PNEUMATIZATION

The only obvious opportunities for extramural pneumatization in the postcranial skeletons of sauropods are between fused sacral and caudal vertebrae and between the sacrum and the ilium. Sacral vertebrae of baby sauropods have deep fossae (Wedel et al. 2000:fig. 14), and at least in *Apatosaurus*, a complex of internal chambers is present before the sacral vertebrae fuse (Ostrom and McIntosh 1966:pl. 30). The co-ossified blocks of caudal vertebrae in *Diplodocus* often include centra with large pneumatic foramina (Gilmore 1932:fig. 3). It is possible that co-ossified centra without foramina could be pneumatized by intraosseous diverticula of adjacent pneumatic vertebrae, although this has not been demonstrated.

Sanz et al. (1999) reported that "cancellous tissue" is present in the presacral vertebrae, ribs, and ilium of *Epachthosaurus* and *Saltasaurus*. The

presacral vertebrae of *Saltasaurus* are pneumatic and have a camellate internal structure (fig. 7.1K–N), and pneumatic ribs are known in several titanosaurs (Wilson and Sereno 1998). Further, spongiosa (*sensu* Francillon-Vieillot et al. 1990) are present in apneumatic vertebrae of many—possibly all—sauropods (see "Application to a Paleobiological Problem: Mass Estimates," below), so cancellous bone is not limited to titanosaurs. For these reasons, it seems that the "cancellous tissue" of Sanz et al. (1990) is synonymous with camellate pneumatic bone. If so, then the ilia of some titanosaurs may have been pneumatic. Two possible routes for pneumatization of the ilium are by diverticula of abdominal air sacs and by extramural pneumatization from the sacrum. However, the possibility of ilial pneumatization must remain speculative until better evidence for it is presented.

NEURAL CAVITIES

In many sauropods, the neural spines of the dorsal vertebrae contain large chambers. These chambers communicate with the outside by way of large foramina beneath the diapophyses. Upchurch and Martin (2003) called such chambers neural cavities and discussed their occurrence in *Cetiosaurus*, *Barapasaurus*, and *Patagosaurus*. According to Upchurch and Martin (2003:218), "In *Barapasaurus* and *Patagosaurus*, the neural cavity is linked to the external surface of the arch by a lateral foramen which lies immediately below the base of the transverse process, just in front of the posterior centrodiapophyseal lamina [pcdl]" (see fig. 7.1A). In some dorsal vertebrae of *Barapasaurus*, the neural canal is open dorsally and communicates with the neural cavity (Jain et al. 1979). Upchurch and Martin (2003) mentioned that similar cavities are present in some neosauropods, and Bonaparte (1986:fig. 19.7) illustrated neural cavities in *Camarasaurus* and *Diplodocus*. Jain et al. (1979) and Upchurch and Martin (2003) also described a second morphology (in *Barapasaurus* and *Cetiosaurus*, respectively), in which the neural cavity is divided into two halves by a median septum and does not communicate with the neural canal (fig. 7.1C). Neural cavities are interpreted as pneumatic for the same reason that the more familiar cavities in vertebral centra are: they are large internal chambers connected to the outside through prominent foramina (Britt 1993).

PNEUMATIC RIBS

The dorsal ribs of some sauropods have large foramina that lead to internal chambers. The best-known examples of costal pneumaticity in sauropods are the pneumatic ribs of *Brachiosaurus* (Riggs 1904; Janensch 1950). Pneumatic dorsal ribs are also present in *Euhelopus* and some titanosaurs (Wilson and Sereno 1998). Gilmore (1936) described a foramen that leads to an internal cavity in a dorsal rib of *Apatosaurus*, and pneumatic dorsal ribs have also been reported in the diplodocid *Supersaurus* (Lovelace et al. 2003). Pneumatic dorsal ribs have not been found in *Haplocanthosaurus*, *Camarasaurus*, or any basal diplodocoids, so the character evidently evolved independently in diplodocids and titanosauriforms. Pneumatic ribs are part of a growing list of pneumatic characters that evolved in parallel in diplodocids and titanosauriforms, along with complex vertebral chambers and pneumatic caudal vertebrae (see below).

FOSSAE AND LAMINAE

PNEUMATIC FOSSAE

Fossae are ubiquitous in sauropod vertebrae and are often the sole evidence of pneumaticity. For example, basal sauropods such as *Barapasaurus* have shallow fossae on the presacral centra and neural spines but lack the large internal chambers typical of later sauropods (fig. 7.1). Are these fossae pneumatic? The naive assumption that all fossae are pneumatic will surely lead to the overestimation of pneumaticity. On the other hand, to deny that any fossae are pneumatic unless they contain foramina that lead to large internal chambers is equally false. We need criteria to distinguish pneumatic fossae from nonpneumatic fossae.

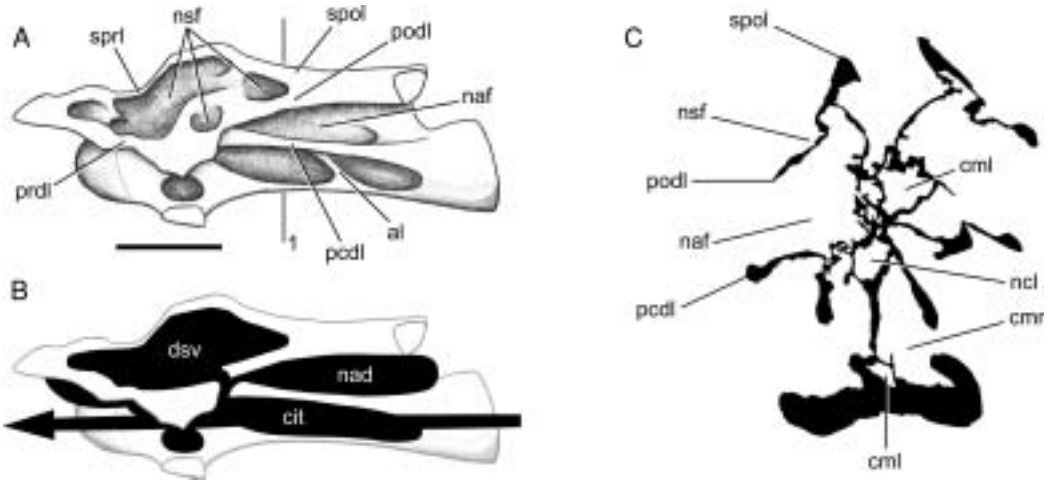

FIGURE 7.2. A cervical vertebra of *Brachiosaurus* and a hypothetical reconstruction of the pneumatic diverticula. A, BYU 12866, a midcervical vertebra of *Brachiosaurus*, in left lateral view. The neural spine fossae are bounded on all sides by the four laminae that connect the pre- and postzygapophyses to the neurapophysis and diapophysis. Some of the neural spine fossae contain large, sharp-lipped foramina. B, Possible appearance of the pneumatic diverticula, shown in black. We can be fairly certain that pneumatic diverticula occupied the fossae on the neural arch, neural spine, and centrum, but the connections between various diverticula and their order of appearance during ontogeny remain speculative. Here the diverticula have been restored based on those of birds, with the canalis intertransversarius running alongside the centrum and the diverticulum supervertebrale occupying the neural spine fossae (see Müller [1907:figs. 3–5, 7, 11, 12] for the appearance of these diverticula in the pigeon). Any connections between the canalis intertransversarius and the diverticulum supervertebrale probably passed intermuscularly, because the laminae bounding the neural spine fossae are uninterrupted by tracks or grooves. C, A transverse section through the midcentrum (A, position 1) traced from a CT image (Wedel et al. 2000:fig. 12C) and corrected for distortion. The volume of air filling the fossae and camellae in the neural arch and spine is unknown, but it may have equaled or exceeded the volume of air in the centrum. Lamina terminology after Wilson (1999). Scale bar equals 20 cm.

The best case for a pneumatic fossa is a fossa that contains pneumatic foramina within its boundaries. The *Brachiosaurus* vertebra shown in figure 7.2 has large, sharply lipped pneumatic foramina in most of the fossae on the lateral sides of the centrum and neural spine (see also Janensch 1950; Wilson 1999). Similar foramina-within-fossae are present in the vertebrae of many other neosauropods, including *Diplodocus* (Hatcher 1901:pl. 3, 7), *Tendaguria* (Bonaparte et al. 2000:fig. 17, pl. 8), and *Sauroposeidon* (Wedel et al. 2000:fig. 8b). The inference that these fossae are pneumatic relies on the presence of unequivocally pneumatic features within the fossae. The inferred presence of pneumaticity is less supported in the case of blind fossae that contain no foramina, such as the large fossae on the dorsal centra of *Barapasaurus* (fig. 7.1).

Wilson (1999) proposed that "subfossae," or fossae-within-fossae, might further support the inference of pneumaticity. "These well defined, smooth-walled depressions are present in many sauropods and seem to be analogous to the more pronounced coels [foramina] that characterize *Brachiosaurus*. Like the coels, these depressions may have housed smaller pneumatic diverticuli [*sic*] in life" (Wilson 1999:651). This hypothesis is supported by the complex morphology of some pneumatic diverticula in birds. In the ostrich, the large diverticula that lay alongside the cervical vertebrae consist of bundles of smaller diverticula (Wedel 2003a:fig. 2). It seems reasonable to expect that when such a bundle comes into contact with a bone, the aggregate would produce a fossa, within which each diverticulum would produce a subfossa. This hypothesis can and should be tested in future computed tomography (CT) studies. Gower (2001:121) argued that the "multipartite fossae" and "deep multi-chambered concavities" in the dorsal vertebrae of *Erythrosuchus*

were more consistent with pneumaticity than with muscular or vascular structures (but see O'Connor 2002).

Britt (1993) proposed that crenulate texture of the external bone is evidence that some fossae are pneumatic. In *Sauroposeidon* the difference in texture between the pneumatic fossae and the adjacent bone is striking, and this allows the boundaries of the fossae to be precisely plotted (Wedel et al. 2000:fig. 7). However, there is little doubt that the fossae of *Sauroposeidon* are pneumatic, because they contain pneumatic foramina. The inference that a blind fossa is pneumatic based on texture alone is less certain. Blind fossae can also contain muscles or adipose tissue (O'Connor 2002). It is not known if these three kinds of fossae can be reliably distinguished on the basis of bone texture. Until this is tested, inferring pneumaticity on the basis of bone texture alone may not be warranted.

For the time being, I know of no test that can definitively determine whether a blind fossa housed a pneumatic diverticulum or some other soft tissue. Pneumatic diverticula often induce bone resorption when they come into contact with the skeleton, and it is possible that external pneumatic features might be recognized by some distinctive aspect of cortical bone histology. I do not suggest that this must be the case, but it is worth investigating.

To determine if a fossa is pneumatic or not, it is worthwhile to consider other potentially pneumatic features on or in the same bone. Consider the fossa bounded by the *podl*, *prdl*, *spol*, and *sprl* in *Haplocanthosaurus* (fig. 7.3). At least in the cervical vertebrae, these fossae do not contain any pneumatic foramina or subfossae, they do not lead to any obvious pneumatic tracks, and the bone texture is smooth rather than crenulate (pers. obs.). In other words, nothing about the fossae themselves indicates that they were pneumatic (as opposed to containing adipose deposits or other soft tissues). However, the centra of the same vertebrae contain deep, sharp-lipped cavities that penetrate to a narrow median septum. By the criteria discussed herein, the cavities in the centra are unequivocally pneumatic. Their presence demonstrates that pneumatic diverticula were in close contact with all of the preserved cervical vertebrae. Because we already know that pneumatic diverticula contacted the cervical vertebrae, it seems safe to infer that the neural spine fossae are pneumatic in origin. At least, the inference of pneumaticity is better founded than it would be based on the neural spine fossae alone.

(As an aside, the nomenclature for vertebral laminae has been thoroughly reviewed and standardized [Wilson 1999], but no standard nomenclature for vertebral fossae exists. It is tempting to propose such a nomenclature, if only to avoid circumlocutions like that used above ["the fossae bounded by the *podl, prdl, spol*, and *sprl*"]. However, a separate nomenclature for fossae is unnecessary and could be misleading. Hatcher [1901] named several fossae, such as the "infraprezygapophyseal cavity," using the same spatial orientation terms that were commonly used for naming laminae [e.g., Osborn 1899]. Such a position-based nomenclature for fossae shares all of the faults of the old orientation-based systems for naming laminae [for further discussion see Wilson 1999]. Laminae should be defined by the structures they connect [Wilson 1999]. Similarly, I think that fossae should be defined by the laminae that bound them. To list all of the bounding laminae when referring to a fossa may be awkward, but it is also precise.)

VERTEBRAL LAMINAE, HOMOLOGY, AND THE ORIGINS OF POSTCRANIAL SKELETAL PNEUMATICITY

It is tempting to assume that the fossae of basal sauropods are pneumatic because they are homologous to the unequivocally pneumatic features of later sauropods. For example, in *Brachiosaurus* the fossa bounded by the *podl*, *prdl*, *spol*, and *sprl* is clearly pneumatic because it contains pneumatic foramina (fig. 7.2). Does this mean that the equivalent fossa in *Barapasaurus* is also pneumatic? After all, phylogenetic analysis indicates that the bounding laminae are homologous in *Barapasaurus* and *Brachiosaurus* (Wilson 1999, 2002). The answer seems to be

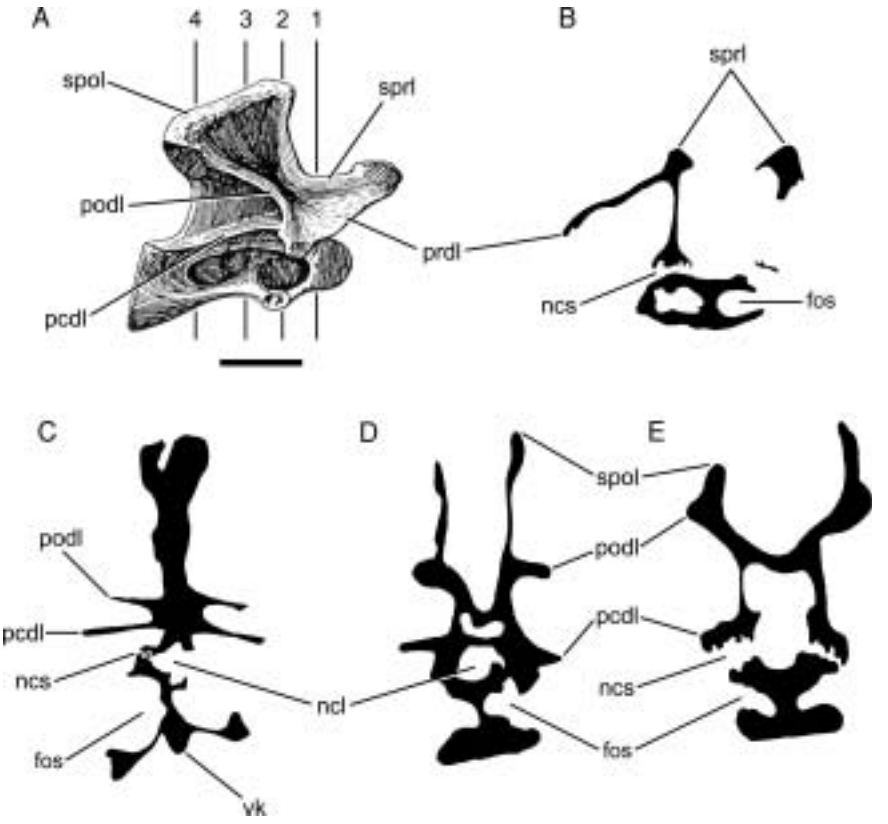

FIGURE 7.3. Pneumatic features in a cervical vertebra of *Haplocanthosaurus*. A, A posterior cervical of *Haplocanthosaurus* in right lateral view (CM 879-7; this specimen was erroneously referred to as CM 572 in Upchurch [1998:fig. 8], and as CM 897-7 in Wedel et al. [2000:fig. 2], Wedel [2003a:fig. 3], and Wedel [2003b:fig. 1]). (Modified from Hatcher (1903:pl. 2.) B–E, Cross sections traced from CT slices. B, Section at A, position 1. C, Section at A, position 2. The opening of the neural canal and the absence of the neurocentral suture on one side are due to a break in the specimen. D, Section at A, position 3. E, Section at A, position 4. The neurocentral sutures are unfused over most of their length, indicating that this animal was not fully mature. Scale bar equals 5 cm.

that the fossae may be homologous, but that is no guarantee that they were produced by the same morphogenetic process. Ontogenetic pathways are themselves subject to evolutionary change. As Hall (1999:347) stated, "A limb built upon one set of rules does not lose its homology with limbs built upon different rules." Conversely, homology does not necessarily indicate identical morphogenetic pathways. The shallow fossae of basal sauropods may have contained deposits of fat such as those identified in birds by O'Connor (2001). It is possible that such adipose deposits were replaced by pneumatic diverticula later in sauropod evolution. In that case, the laminae that bound the fossae would have remained the same, but the tissue that filled the fossae would have changed. The same replacement may also have occurred during ontogeny.

If we order archosaur vertebrae in terms of putatively pneumatic features, the resulting arrangement has no obvious gaps and is roughly congruent with current phylogenies (i.e., Sereno 1991; Wilson 2002). At one end of the spectrum are vertebrae that lack laminae, such as those of extant crocodilians. Very shallow depressions may be present on the neural spines or centra, but these depressions are not bounded by an obvious lip and do not contain subfossae or large foramina. The next grade

of vertebral construction is represented by *Marasuchus*, which has low ridges below some of the presacral diapophyses (Sereno and Arcucci 1994); these ridges may represent rudimentary laminae (Wilson 1999). At the next level, a series of diapophyseal and zygapophyseal laminae is primitive for Saurischia (Wilson 1999). These laminae are present in *Herrerasaurus* and prosauropods (Sereno and Novas 1994; Bonaparte 1986), but the fossae they enclose are blind, lack subfossae, and have no obvious textural differences from the adjacent bone (Wedel, pers. obs.). Vertebral centra of these taxa lack fossae. Shallow fossae are present on the centra of early sauropods such as *Isanosaurus*, *Shunosaurus*, and *Barapasaurus*, and neural chambers may be present in the arch and spine (Jain et al. 1979; Zhang 1988; Buffetaut et al. 2000). In *Jobaria* and *Haplocanthosaurus* the central fossae are bounded by a sharp lip and penetrate to a median septum (Sereno et al. 1999; Wedel 2003b, pers. obs.). Finally, most neosauropods have prominent pneumatic foramina that open into chambers that ramify within the centrum, and the fossae of the neural arches and spines contain subfossae or pneumatic foramina.

It is not clear where pneumaticity first appears in the preceding series. At one end of the scale are the vertebrae of crocodiles, which are known to be apneumatic. At the other end are the vertebrae of neosauropods, the pneumatic features of which are virtually identical to those of birds (Janensch 1947). In between, the inference of pneumaticity receives more support as we approach Neosauropoda, but the "break point" between apneumatic and pneumatic morphologies is debatable. The primitive saurischian complex of laminae first appears in small dinosaurs and seems to be structural overkill if pneumatic diverticula were absent (Wilson 1999). An apneumatic interpretation of these laminae requires that a large number of structures that are clearly related to pneumatization in later forms be primitively present for other reasons, and leaves us (at least for now) without a satisfying hypothesis to explain the origin of vertebral laminae. The blind fossae of early saurischians are, at best, equivocal evidence of pneumaticity. However, any explanation that pushes the origin of PSP forward in time will accumulate a corresponding number of ad hoc hypotheses to explain the early appearance of laminae and fossae. For these reasons, I favor Wilson's (1999) hypothesis that laminae are pneumatic in origin and that the appearance of laminae marks the appearance of PSP, although as Wilson (1999:651) pointed out, more work is needed.

Gower (2001) posited widespread pneumaticity in Archosauria based on vertebral fossae. If he is right, PSP originated before the divergence between crocodile- and bird-line archosaurs and was present in virtually all of the noncrocodilian taxa in the series discussed above. O'Connor (2002) questioned the reliability of blind fossae as indicators of pneumaticity, but he did not present evidence to falsify Gower's hypothesis. Indeed, hypotheses of pneumaticity are difficult to falsify; although it is often easy to demonstrate that a bone has been pneumatized, it is difficult to demonstrate that it has not (Hogg 1980). For now, the possibility that the fossae described by Gower are pneumatic cannot be ruled out, but neither can less radical alternative hypotheses.

OTHER OSTEOLOGICAL CORRELATES OF PNEUMATICITY

Pneumatic tracks, thin outer walls, and large foramina are not likely to be falsely interpreted as pneumatic features in sauropods. External tracks are only rarely identified in sauropods. Wedel et al. (2000:fig. 7) illustrated a pneumatic track in *Sauroposeidon*, but the track was not the basis for the pneumatic interpretation; rather, the track was identified as pneumatic because it led away from a deep, sharply lipped pneumatic fossa. Many sauropod vertebrae have thin outer walls, especially those of the aforementioned *Sauroposeidon* (fig. 7.4). However, the thin outer walls of sauropod vertebrae invariably bound large internal chambers that are clearly pneumatic,

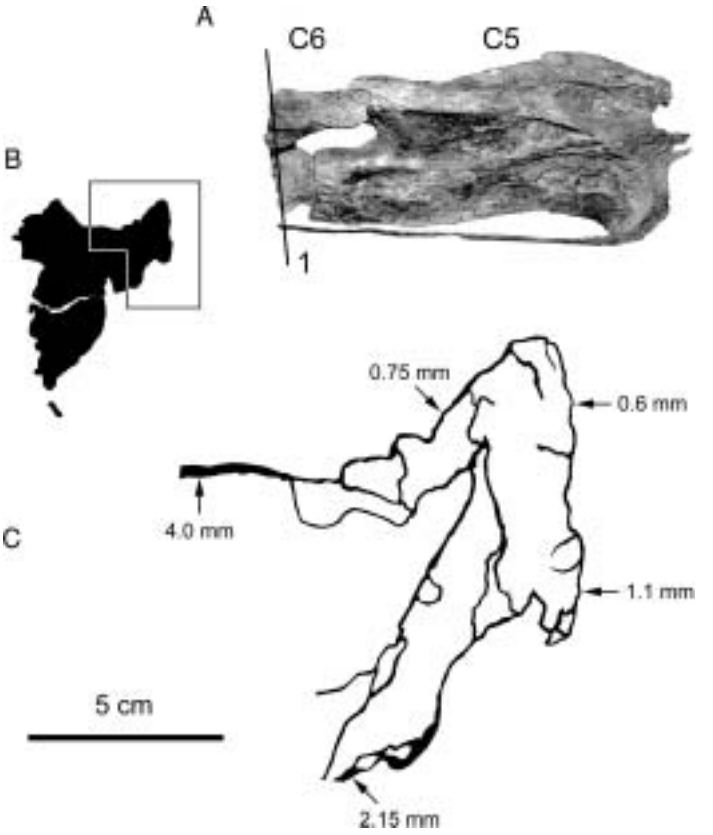

FIGURE 7.4. Internal structure of a cervical vertebra of *Sauroposeidon*, OMNH 53062. A, The posterior two-thirds of C5 and the condyle and prezygapophysis of C6 in right lateral view. The field crew cut though C6 to divide the specimen into manageable pieces. B, Cross section of C6 at the level of the break, traced from a CT image (A, position 1) and photographs of the broken end. The left side of the specimen was facing up in the field and the bone on that side is badly weathered. Over most of the broken surface the internal structure is obscured by plaster or too damaged to trace, but it is cleanly exposed in the ramus of the right prezygapophysis (outlined). C, The internal structure of the prezygapophyseal ramus, traced from a photograph. The arrows indicate the thickness of the bone at several points, as measured with a pair of digital calipers. The camellae are filled with sandstone.

so, again, the inference of pneumaticity does not rest on the equivocal feature. Finally, there is the question of foramina that are not pneumatic, such as nutrient or nervous foramina. Britt et al. (1998) proposed that pneumatic foramina could be distinguished from nutrient foramina on the basis of relative size, with pneumatic foramina typically being about an order of magnitude larger, relative to the length of the centrum. The two kinds of foramina could also be distinguished based on the internal structure of the vertebrae. Pneumatic vertebrae typically lack trabecular bone (Bremer 1940; Schepelmann 1990) and have compact bone in their outer walls and in the septa between pneumatic cavities (Reid 1996). The presence of trabecular bone inside a vertebra is evidence that it is either apneumatic or, at least, incompletely pneumatized (King 1957). Distinguishing pneumatic foramina from nutrient foramina is a potential problem in studies of birds and other small theropods, but most sauropods are simply so large that pneumatic and nutrient foramina are unlikely to be confused. Even juvenile sauropods tend to have large pneumatic fossae rather than small foramina (see Wedel et al. 2000:fig. 14).

DESCRIPTION OF PNEUMATIC ELEMENTS

At least four aspects of skeletal pneumaticity can be described: the external traces of pneumaticity (discussed above), the internal complexity of an element, the ratio of bone to airspace within an element, and the distribution of pneumatic features along the vertebral column.

INTERNAL COMPLEXITY OF PNEUMATIC BONES

This variable has received the most attention in previous studies and is only briefly reviewed here. Longman (1933) recognized that sauropod

TABLE 7.1

Classification of Sauropod Vertebrae into Morphologic Categories Based on Pneumatic Characters

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 has an inflated appearance.

NOTE: After Wedel et al. (2000:table 3).

vertebrae with internal chambers fall into two broad types, those with a few large chambers and those with many small chambers. Longman called the first type phanerocamerate and the second cryptocamerillan (although he did not explicitly discuss them as products of skeletal pneumatization). Britt (1993, 1997) independently made the same observation and used the terms camerate and camellate to describe large-chambered and small-chambered vertebrae, respectively. Wedel et al. (2000) expanded this terminology to include categories for vertebrae with fossae only and vertebrae with combinations of large and small chambers (table 7.1). Wedel et al. (2000) and Wedel (2003b) also discussed the phylogenetic distribution of different internal structure types. In general, the vertebrae of early diverging sauropods such as *Shunosaurus* and *Barapasaurus* have external fossae but lack internal chambers. Camerae are present in the vertebrae of diplodocids, *Camarasaurus*, and *Brachiosaurus*. Presacral vertebrae of *Brachiosaurus* also have camellae in the condyles and cotyles, and camellae are variably present in the neural spine and apophyses. The vertebrae of *Sauroposeidon* and most titanosaurs lack camerae and are entirely filled with camellae, although some titanosaurs may have vertebral camerae. From published descriptions (Young and Zhao 1972; Russell and Zheng 1994), the vertebrae of *Mamenchisaurus* appear to be camellate.

From the foregoing, it might appear that the internal structures of sauropod vertebrae, their evolution, and their phylogenetic distribution are all well understood. In fact, vertebral internal structure is only known for a small minority of sauropods. Even in those taxa for which the internal structure is known, this knowledge is usually limited to a handful of vertebrae or even a single element, which severely limits our ability to assess serial, ontogenetic, and population-level variation. Despite these limitations, three broad generalizations can be made. First, the vertebrae of very young sauropods tend to have a simple I-beam shape in cross section, with large lateral fossae separated by a median septum (Wedel 2003b). This is true even for taxa in which the vertebrae of adults are highly subdivided, such as *Apatosaurus*. In these taxa the internal complexity of the vertebrae increased during ontogeny. The second generalization is that complex internal structures evolved independently in *Mamenchisaurus* and diplodocids and one or more times in Titanosauriformes (Wedel 2003b). This suggests

a general evolutionary trend toward increasing complexity of vertebral internal structure in sauropods, albeit one that took different forms in different lineages (i.e., polycamerate vertebrae in Diplodocidae and somphospondylous vertebrae in Somphospondyli) and that may have been subject to reversals (i.e, camerate vertebrae in some titanosaurs [see Wedel 2003b]). Finally, the largest and longest- necked sauropods, such as *Mamenchisaurus*, the diplodocines, brachiosaurids, *Euhelopus*, and titanosaurs such as *Argentinosaurus* and the unnamed taxon represented by DGM Serie A, all have polycamerate, semicamellate, or fully camellate internal structures. I have previously stated that the complex internal structures were correlated with increasing size and neck length (Wedel 2003a, 2003b). This may or may not be true; I have not performed any phylogenetic tests of character correlation. Nevertheless, the presence of complex internal structures in the vertebrae of the largest and longest-necked sauropods suggests that size, neck length, and internal structure are related.

VOLUME OF AIR WITHIN A PNEUMATIC BONE

The aspect of skeletal pneumaticity that has probably received the least attention to date is the ratio of bone tissue to empty space inside a pneumatic bone. Although many authors have commented on the weight-saving design of sauropod vertebrae (Osborn 1899; Hatcher 1901; Gilmore 1925), no one has quantified just how much mass was saved. The savings in mass could have important paleobiological implications, for example, in determining how much mass to subtract from volumetric mass estimates.

Currey and Alexander (1985) and Cubo and Casinos (2000) reported relevant data on the long bones of birds, which are tubular and may be filled with marrow or air. In both studies, the variable of interest was *K*, the inner diameter of the element divided by its outer diameter. Both studies found mean values of *K* between 0.77 and 0.80 for pneumatic bones. The mean for marrow-filled bird bones is 0.65 (Cubo and Casinos 2000), and the mean for terrestrial mammals is 0.53 (calculated from Currey and Alexander 1985:table 1).

The *K* value is a parameter of tubular bones; it is meaningless when applied to bones with more complex shapes or internal structures, such as sauropod vertebrae. I propose the *airspace proportion* (ASP), or the proportion of the volume of a bone—or the area of a bone section—that is occupied by air spaces, as a variable that can be applied to both tubular and nontubular bones. One problem is that measuring the volumes of objects is difficult and often imprecise. It is usually easier to measure the relevant surface areas of a cross section, but any one cross section may not be representative of the entire bone. For example, the long bones of birds and mammals are usually tubular at midshaft, but the epiphyses mostly consist of marrow-filled trabecular bone or pneumatic camellate bone. Nevertheless, it may be easier to take the mean of several cross sections as an approximation of volume than to directly measure volume, especially in the case of large, fragile, matrix-filled sauropod vertebrae.

For the avian long bones described above, data were only presented for a single cross section located at midshaft. Therefore, the ASP values I am about to discuss may not be representative of the entire bones, but they probably approximate the volumes (total and air) of the diaphyses. For tubular bones, ASP may be determined by squaring *K* (if *r* is the inner diameter and *R* the outer, then *K* is r/R, ASP is $\pi r^2/\pi R^2$ or simply r^2/R^2, and ASP = K^2). For the *K* of pneumatic bones, Currey and Alexander (1985) report lower and upper bounds of 0.69 and 0.86, and I calculate a mean of 0.80 from the data presented in their table 1. Using a larger sample size, Cubo and Casinos (2000) found a slightly lower mean *K* of 0.77. The equivalent values of ASP are 0.48 and 0.74, with a mean of 0.64, or 0.59 for the mean of Cubo and Casinos (2000). This means that, on average, the diaphysis of a pneumatic avian long bone is 59%–64% air, by volume.

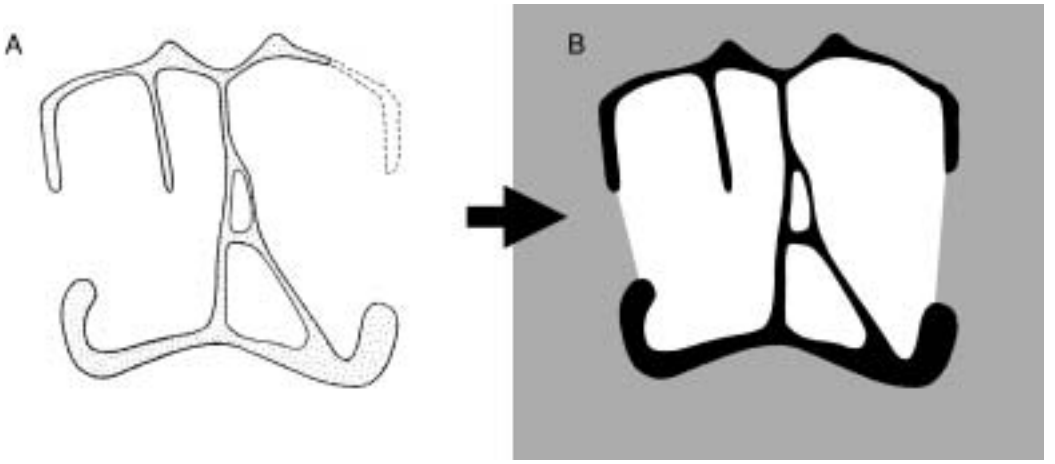

FIGURE 7.5. How to determine the airspace proportion (ASP) of a bone section. (A) A section is traced from a photograph, CT image, or published illustration; in this case, a transverse section of a *Barosaurus africanus* cervical vertebra from Janensch (1947:fig. 3). (B) Imaging software is used to fill the bone, airspace, and background with different colors. The number of pixels of each color can then be counted using Image J (or any program with a pixel count function) and used to compute the ASP. In this case, bone is black and air is white, so the ASP is (white pixels)/(black pixels + white pixels).

How do these numbers compare with the ASPs of sauropod vertebrae? To find out, I measured the area occupied by bone and the total area for several cross sections of sauropod vertebrae (see fig. 7.5 for an example). I obtained the cross-sectional images from CT scans, published cross sections, and photographs of broken or cut vertebrae. For image analysis I used Image J, a free program available online from the National Institutes of Health (Rasband 2003). Some results are presented in table 7.2 (this research is in progress and I will present more complete results elsewhere). The results should be approached with caution: I have only analyzed a few vertebrae from a handful of taxa, and only one or a few cross sections for each bone, so the results may not be representative of either the vertebrae, the regions of the vertebral column, or the taxa to which they belong. The sample is strongly biased toward cervical vertebrae simply because cervicals are roughly cylindrical and fit through CT scanners better than dorsal or sacral vertebrae. Despite these caveats, some regularities emerge.

First, ASP values range from 0.32 to 0.89, with a mean of 0.60. Even though the data may not be truly representative, it seems reasonable to conclude that most sauropod vertebrae contained at least 50% air, by volume, and probably somewhat more. This assumes that the cavities in sauropod vertebrae were entirely filled with air and the amount of soft tissue was negligible. Chandra Pal and Bharadwaj (1971) found that the air spaces in pneumatic bird bones are lined with simple squamous epithelium, so the assumption is probably valid. The ASP values presented here for sauropod vertebrae are similar to the range and mean found for pneumatic long bones of birds (or at least their diaphyses).

Second, although only a handful of measurements are available for each taxon, it is already clear that ASP can vary widely from slice to slice within a single vertebra and probably also between vertebrae of different regions of the skeleton and between individuals of the same species. As we collect more data we may find more predictable relationships, for example, between the ASP values of cervical and dorsal vertebrae or between certain taxa. The system may also be so variable that such relationships will be impossible to detect, if they even exist. Rampant variation seems to be the rule for skeletal pneumaticity in general (e.g., King 1957; Cranford et al. 1996; Weiglein 1999), and it would be surprising if ASP were not also highly variable.

TABLE 7.2

The Airspace Proportion (ASP) of Transverse Sections through Vertebrae of Sauropods and Other Saurischians

	REGION	ASP	SOURCE
Apatosaurus	Cervical condyle	0.69	Wedel (2003b:fig. 6b)
	Cervical midcentrum	0.52	Wedel (2003b:fig. 6c)
	Cervical cotyle	0.32	Wedel (2003b:fig. 6d)
Barosaurus	Cervical midcentrum	0.56	Janensch (1947:fig. 8)
	Cervical, near cotyle	0.77	Janensch (1947:fig. 3)
	Caudal midcentrum	0.47	Janensch (1947:fig. 9)
Brachiosaurus	Cervical condyle	0.73	Janensch (1950:fig. 70)
	Cervical midcentrum	0.67	Wedel et al. (2000:fig. 12c)
	Cervical cotyle	0.39	Wedel et al. (2000:fig.12d)
	Dorsal midcentrum	0.59	Janensch (1947:fig. 2)
Camarasaurus	Cervical condyle	0.49	Wedel (2003b:fig. 9b)
	Cervical midcentrum	0.52	Wedel (2003b:fig. 9c)
	Cervical, near cotyle	0.50	Wedel (2003b:fig. 9d)
	Dorsal midcentrum	0.63	Ostrom and McIntosh (1966:pl. 23)
	Dorsal midcentrum	0.58	Ostrom and McIntosh (1966:pl. 24)
	Dorsal midcentrum	0.71	Ostrom and McIntosh (1966:pl. 25)
Phuwiangosaurus	Cervical midcentrum	0.55	Martin (1994:fig. 2)
Pleurocoelus	Cervical midcentrum	0.55	Lull (1911:pl. 15)
Saltasaurus	Dorsal midcentrum	0.55	Powell (1992:fig. 16)
Sauroposeidon	Cervical prezygapophyseal ramus	0.89	Fig. 7.4
	Cervical midcentrum	0.74	Wedel et al. (2000:fig. 12g)
	Cervical postzygapophysis	0.75	Wedel et al. (2000:fig. 12h)
Theropoda	Cervical prezygapophysis	0.48	Janensch (1947:fig. 16)
	Dorsal midcentrum	0.50	Janensch (1947:fig. 15)

NOTE: Only values for published sections are presented. Much more work will be required to determine norms for different taxa and different regions of the vertebral column, and the values presented here may not be representative of either. Nevertheless, these values suggest that pneumatic sauropod vertebrae were often 50%–60% air, by volume. The mean of these 22 measurements is 0.60.

Third, the lowest ASP values—0.32 in *Apatosaurus* and 0.39 in *Brachiosaurus*—are for slices through the cotyle, or bony cup, at the posterior end of the centrum. Here the cortical bone is doubled back on itself to form the cup, and the wall of the cotyle itself is at an angle to the slice and appears wider in cross section. The cotyle is surrounded by pneumatic chambers in both *Apatosaurus* and *Brachiosaurus*, but these become smaller and eventually disappear toward the end of the vertebra. For these reasons, the cotyle is expected to have a lower ASP than the rest of the vertebra.

Fourth, *Sauroposeidon* has the highest values of ASP, up to a remarkable 0.89. The values for *Sauroposeidon* are even higher than those for the closely related *Brachiosaurus*, and the ranges for the two taxa do not overlap (although they may come to when a larger sample is considered). A very high ASP is probably an autapomorphy of *Sauroposeidon* and may have evolved to help lighten its extremely long (~12-m) neck.

Finally, ASP appears to be independent of the internal complexity of the vertebrae. The *Saltasaurus* vertebra is the most highly subdivided of

the sample. The I-beam-like vertebrae of the juvenile *Pleurocoelus* and *Phuwiangosaurus* are the least subdivided; the other taxa fall somewhere in the middle. Nevertheless, most values in the table 7.2, including those for *Saltasaurus*, *Pleurocoelus*, and *Phuwiangosaurus*, fall between 0.50 and 0.60. The means for all taxa other than *Sauroposeidon* also fall within the same range, so there is no apparent trend that relates ASP to internal complexity. Cast in evolutionary terms, this indicates that the evolution of complex internal structures from simple ones involved a redistribution rather than a reduction of bony tissue within the vertebrae. The ASP values of the juvenile *Pleurocoelus* and *Phuwiangosaurus* imply that a similar redistribution was involved in the ontogenetic derivation of complex chambers from juvenile fossae.

The results presented here are preliminary, and the available data are better suited for suggesting hypotheses than for testing them. Much work remains to be done, both in gathering comparative data from extant forms and in exploring the implications of pneumaticity for sauropod biomechanics.

DISTRIBUTION OF PNEUMATICITY ALONG THE VERTEBRAL COLUMN

The two previous sections dealt with the characteristics of a single pneumatic bone. We must also consider the location of pneumatic features in the skeleton, because these features constrain the minimum extent of the diverticular system. For example, in the USNM 10865 skeleton of *Diplodocus*, pneumatic foramina are present on every vertebra between the axis and the nineteenth caudal ([Gilmore 1932; foramina are only present on caudals 1–18 in the skeleton of *Diplodocus* described by Osborn [1899] and on caudals 1–16 in the mounted DMNS skeleton [Wedel, pers. obs.]). This means that in life the pneumatic diverticula reached at least as far anteriorly as the axis and as far posteriorly as caudal vertebra 19 (fig. 7.6). The diverticular system may have been more extensive and simply failed to pneumatize any more bones, but it could not have been any less extensive.

In mapping the distribution of pneumaticity along the vertebral column, it is important to consider where on the vertebrae the pneumatic features are located. In the co-ossified block of *Diplodocus* caudal vertebrae illustrated by Gilmore (1932:fig. 3), the centra of caudals 15–19 bear large pneumatic foramina, but the neural spines lack laminae and do not appear to have been pneumatic. This is in contrast to the presacral, sacral, and anterior caudal vertebrae, which have heavily sculpted neural spines with deep fossae and scattered foramina (see Osborn 1899:figs. 7, 13). In the opposite condition, the neural spines bear laminae and fossae and may have been pneumatic, but the centra lack pneumatic features. Examples include the middle and posterior dorsal vertebrae of *Jobaria* (see Sereno et al. 1999:fig. 3). Sauropod vertebrae can therefore exist in one of four states: (1) both centrum and neural spine pneumatic, as in the presacral vertebrae of most neosauropods; (2) centrum pneumatic but neural spine apneumatic, as in the middle caudals of *Diplodocus*; (3) neural spine pneumatic but centrum apneumatic, as in the posterior dorsals of *Jobaria* (assuming that the laminate neural spines are pneumatic); or (4) no signs of pneumaticity in the centrum or neural spine, as in the distal caudals of most sauropods. Pneumatization of the centrum typically results in large internal cavities with prominent foramina, so the inference of pneumaticity is well supported in conditions 1 and 2. In condition 3 the situation may be less clear. In derived neosauropods such as *Brachiosaurus* and the diplodocids, the neural spine fossae often bear small subfossae and foramina, which indicate that these fossae are pneumatic (see Janensch 1950; Curtice and Stadtman 2001). In more basal sauropods such as *Haplocanthosaurus*, the neural spine fossae are often blind and lack the heavily sculpted texture seen in later forms. The neural spines of these basal sauropods may have been pneumatic, but the inference is less well founded.

The earliest sauropodomorph with distinctly emarginated pneumatic fossae is *Thecodontosaurus caducus* (Yates 2003). In

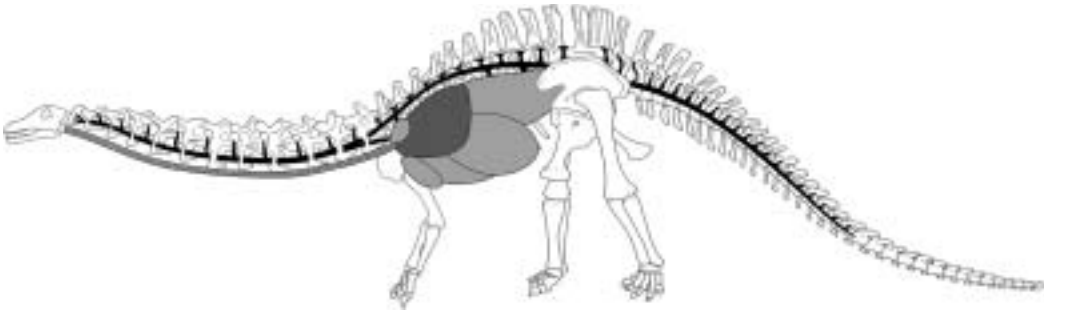

FIGURE 7.6. Hypothetical conformation of the respiratory system of a diplodocid sauropod. The left forelimb, pectoral girdle, and ribs have been removed for clarity. The lung is shown in dark gray, air sacs are light gray, and pneumatic diverticula are black. Only some of the elements shown in this illustration can be determined with certainty: the minimum length of the trachea, the presence of at least some air sacs, and the minimum extent of the pneumatic diverticula. The rest of the respiratory system has been restored based on that of birds, but this remains speculative. The skeleton is modified from Norman (1985:83).

T. caducus, pneumatic fossae are only present on the middle cervical vertebrae. This means that the fossae must have been produced by diverticula of cervical air sacs similar to those of birds (as opposed to diverticula of the lungs proper). A similar pattern of pneumatization in *Coelophysis* indicates that cervical air sacs were present in both sauropodomorphs and theropods by the Norian (Late Triassic), and cervical air sacs are probably primitive for saurischians (Wedel 2004).

In general, more derived sauropods tended to pneumatize more of the vertebral column. Except for the atlas, which is always apneumatic, pneumatic chambers (or prominent fossae) are present in the cervical vertebrae of *Shunosaurus*; in the cervical and anterior dorsal vertebrae of *Jobaria*; in all of the presacral vertebrae of *Cetiosaurus*; in the presacral and sacral vertebrae of most neosauropods; and in the presacral, sacral, and caudal vertebrae of diplodocids and saltasaurids (Wedel 2003a, 2003b, pers. obs.). This caudad progression of vertebral pneumaticity also occurred in the evolution of theropods (Britt 1993) and occurs ontogenetically in extant birds (Cover 1953; Hogg 1984b). At a gross level, the system is both homoplastic and recapitulatory.

In extant birds, diverticula of the cervical air sacs do not extend farther posteriorly than the anterior thoracic vertebrae. If the diverticula of sauropods followed the same pattern of development as those of birds, then the presence of pneumatic sacral vertebrae in most neosauropods indicates the presence of abdominal air sacs (Wedel et al. 2000). There are no strong reasons to doubt that neosauropods had abdominal air sacs. However, the future discovery of a sauropod with a pneumatic hiatus—a gap in the pneumatization of the dorsal vertebrae—would unequivocally demonstrate the presence of abdominal air sacs and their diverticula (Wedel 2003a).

APPLICATION TO A PALEOBIOLOGICAL PROBLEM: MASS ESTIMATES

The implications of PSP for sauropod paleobiology are only beginning to be explored. In particular, skeletal pneumaticity may be an important factor in future studies of the biomechanics and respiratory physiology of sauropods. The most obvious implication of extensive PSP in sauropods is that they may have weighed less than is commonly thought. In this section, the problem of estimating the masses of sauropods is used as an example of how information about PSP may be applied to a paleobiological question.

Two distinct questions proceed from the observation that most sauropod skeletons were highly pneumatic. The first is purely

methodological: (How) Should we take pneumaticity into account in estimating the masses of sauropods? The second question is paleobiological: If we find that pneumaticity significantly lightened sauropods, how does that affect our understanding of sauropods as living animals? If pneumaticity did not significantly lighten sauropods, then the second question is moot, so I consider the methodological question first.

METHODS

The masses of dinosaurs are generally estimated using allometric equations based on limb bone dimensions (Russell et al. 1980; Anderson et al. 1985) or volumetric measurements using physical or computer models (Colbert 1962; Paul 1988, 1997; Henderson 1999). If allometric equations are used, then pneumaticity need not be taken into account; the limb bones are assumed to have been as circumferentially robust as they needed to be to support the animal's mass, regardless of how the body was constituted. If an animal with a pneumatic skeleton was lighter than it would have been otherwise, this should already be reflected in its limb bone morphology, and no correction is necessary. On the other hand, if volumetric measurements are used, then it is possible to take skeletal pneumaticity into account and failure to do so may result in mass estimates that are too high.

Volumetric mass estimation is performed in three steps (Alexander 1989). First, the volume of a scale model of the organism is measured. Next, the volume of the model is multiplied by the scale factor to obtain the volume of the organism in life. Finally, the volume of the organism is multiplied by the estimated density to obtain its mass. The presence of air in the respiratory system and pneumatic diverticula can be accounted for in the first two steps, by reducing the estimated volume of model or the organism, or in the third step, by adjusting the density used in the mass calculation. Both methods have been used in published mass estimates of dinosaurs. Alexander (1989) used plastic models in his volumetric study, and he drilled holes to represent the lungs before estimating the center of mass of each model and the proportion of mass supported by the fore- and hindlimbs (see Alexander 1989:figs. 4.6, 5.3). Curiously, he does not seem to have drilled the holes before performing his mass estimates; at least, the holes are only mentioned in conjunction with the center of mass and limb support studies. Henderson (1999) included lung spaces in his digital models for mass estimation purposes and, later, included air sacs and diverticula in a buoyancy study (Henderson 2004). Paul (1988, 1997) used the alternative method of adjusting the density values for the mass calculations. He assigned a specific gravity (SG) of 0.9 to the trunk to account for lungs and air sacs, and an SG of 0.6 to the neck to account for pneumatization of the vertebrae.

Before attempting to estimate the volume of air in a sauropod, it is important to recognize that the air was distributed among four separate regions: (1) the trachea, (2) the "core" respiratory system of lungs and, possibly, pulmonary air sacs, (3) the extraskeletal (i.e., visceral, intermuscular, and subcutaneous) diverticula, and (4) the pneumatic bones. These divisions are important for two reasons. First, the volumes of each region are differently constrained by skeletal remains. The volume of air in the skeleton can be estimated with a high degree of confidence because the sizes of the airspaces can be measured from fossils. In contrast, the volume of the trachea is not constrained by skeletal remains and must be estimated by comparison to extant taxa. The lung/air sac system and extraskeletal diverticula are only partly constrained by the skeleton (see below). This leads to the second point, which is that estimates of all four regions can be made independently, so that skeletal pneumaticity can be taken into account regardless of conformation (birdlike, crocodile-like, etc.) and volume of the core respiratory system.

AN EXAMPLE USING *DIPLODOCUS*

Consider the volume of air present inside a living *Diplodocus*. Practically all available mass

TABLE 7.3
The Volume of Air in Diplodocus

	AIR VOLUME (L)	MASS SAVINGS (KG)
Trachea	104	104
Lungs and air sacs	1,500	1,500
Extraskeletal diverticula	?	?
Pneumatic vertebrae		
Centra		
Cervicals 2–15	136	82
Dorsals 1–10	208	125
Sacrals 1–5	75	45
Caudals 1–19	329	198
Subtotal for centra	748	450
Neural spines		
Cervicals 2–15	136	82
Dorsals 1–10	416	250
Sacrals 1–5	150	90
Caudals 1–19	165	99
Subtotal for spines	867	520
Subtotal for vertebrae	970	1,455
Total	2,574	3,059

NOTE: See the text for methods of estimation. The total volume for vertebrae is 1,615.

estimates for *Diplodocus* (Colbert 1962; Alexander 1985; Paul 1997; Henderson 1999) are based on CM 84, the nearly complete skeleton described by Hatcher (1901). Uncorrected volumetric mass estimates—i.e., those that do not include lungs, air sacs, or diverticula—for this individual range from 11,700 kg (Colbert 1962; as modified by Alexander 1989:table 2.2) to 18,500 kg (Alexander 1985). Paul (1997) calculated a mass of 11,400 kg using the corrected SGs cited above, and Henderson (1999) estimated 14,912 kg, or 13,421 kg after deducting 10% to represent the lungs. For the purposes of this example, the volume of the animal is assumed to have been 15,000 liters. The estimated volumes of various air reservoirs and their effects on body mass are listed in table 7.3.

Estimating the volume of air in the vertebral centra is the most straightforward. I used published measurements of centrum length and diameter from Hatcher (1901) and Gilmore (1932) and treated the centra as cylinders. The caudal series of CM 84 is incomplete, so I substituted the measurements for USNM 1065 from Gilmore (1932); comparison of the measurements of the elements common to both skeletons indicates that the two animals were roughly the same size. I multiplied the volumes obtained by 0.60, the mean ASP of the sauropod vertebrae listed in table 7.2, to obtain the total volume of air in the centra.

The volume of air in the neural spines is harder to calculate. The neural spines are complex shapes and are not easily approximated with simple geometric models. Furthermore, the fossae on the neural arches and spines only partially enclosed the diverticula that occupied them. Did the diverticula completely fill the space between adjacent laminae, did they bulge outward into the surrounding tissues, or did surrounding tissues bulge inward? In the complete absence of in vivo measurements of diverticulum volume in birds, it is impossible to say. Based on the size of the neural spine relative to the centrum in most sauropods (see fig. 7.2), it seems reasonable to assume that in the cervical vertebrae, at least as much air was present in the arch and spine as in the centrum, if not more. In the high-spined dorsal and sacral vertebrae (see fig. 7.1), the volume of air in the neural arch and spine may have been twice that in the centrum. Finally, proximal caudal vertebrae have large neural spines but the size of the spines decreases rapidly in successive vertebrae. On average, the caudal neural spines of *Diplodocus* may have contained only half as much air as their associated centra. These estimates are admittedly rough, but they are probably conservative and so they will suffice for this example.

As they developed, the intraosseous diverticula replaced bony tissue, and the density of that tissue must be taken into account in estimating how much mass was saved by pneumatization of the skeleton. In apneumatic sauropod vertebrae the internal structure is filled with cancellous bone and presumably supported red (erythropoeitic) bone marrow (fig. 7.7). Distal

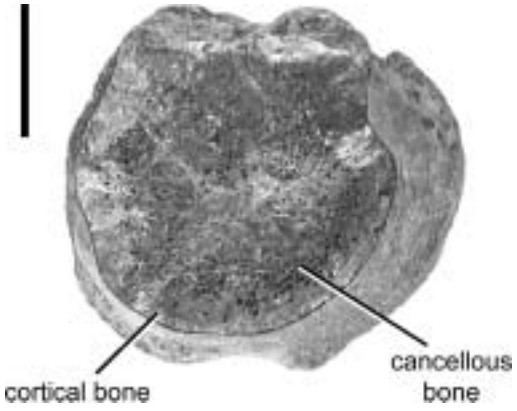

FIGURE 7.7. Internal structure of OMNH 27794, a partial distal caudal vertebra of a titanosauriform. The internal structure is composed of apneumatic cancellous bone, and no medullary cavity is present. Scale bar equals 1 cm.

caudal vertebrae of the theropod *Ceratosaurus* have a large central chamber or centrocoel (Madsen and Welles 2000:fig. 6). This cavity lacks large foramina that would connect it to the outside, so it cannot be pneumatic in origin. The medullary cavities of apneumatic avian and mammalian long bones are filled with adipose tissue that acts as lightweight packing material (Currey and Alexander 1985), and the same may have been true of the centrocoels in *Ceratosaurus* caudals. The presence of a similar marrow cavity in sauropod vertebrae prior to pneumatization cannot be ruled out, but to my knowledge no such cavities have been reported. In birds, the intraosseous diverticula erode the inner surfaces of the cortical bone in addition to replacing the cancellous bone (Bremer 1940), so pneumatic bones tend to have thinner walls than apneumatic bones (Currey and Alexander 1985; Cubo and Casinos 2000). The tissues that may have been replaced by intraosseous diverticula have SGs that range from 0.9 for some fats and oils to 3.2 for apatite (Schmidt-Nielsen 1983:451, table 11.5). For this example, I estimated that the tissue replaced by the intraosseous diverticula had an average SG of 1.5 (calculated from data presented in Cubo and Casinos 2000), so air cavities that total 970 liters replace 1,455 kg of tissue. The extraskeletal diverticula, trachea, lungs, and air sacs did not replace bony tissue in the body. They are assumed to replace soft tissues (density of 1 g/cm^3) in the solid model.

Extraskeletal diverticula include visceral, intermuscular, and subcutaneous diverticula. None of these leave traces that are likely to be fossilized. The bony skeleton places only two constraints on the extraskeletal diverticula. First, as previously discussed, the distribution of pneumatic bones in the skeleton limits the minimum extent of the diverticular system. Thus, we can infer that the vertebral diverticula in *Diplodocus* must have extended from the axis to the nineteenth caudal vertebra (at least in USNM 1065), but the course and diameter of the diverticula are unknown. The second constraint imposed by the skeleton is that the canalis intertransversarius, if it existed, could not have been larger than the transverse foramina where it passed through them, although it may have been smaller or increased in diameter on either side. I am unaware of any studies in which the in vivo volume of the avian diverticular system is measured. This information vacuum prevents me from including a volume estimate for the diverticular system in table 7.3.

To estimate the volume of the trachea, I used the allometric equations presented by Hinds and Calder (1971) for birds. The length equation, $L = 16.77M^{0.394}$, where L is the length of the trachea (cm) and M is the mass of the animal (kg), yielded a predicted tracheal length of 6.8 m for a 12-ton animal. The cervical series of *Diplodocus* CM 84 is 6.7 m long and the trachea may have been somewhat longer, and I judged the correspondence between the neck length and the predicted tracheal length to be close enough to justify using the equations, especially for the coarse level of detail needed in this example. The volume equation, $V = 3.724M^{1.090}$, yields a volume of 104 liters.

Finally, the volume of the lungs and air sacs must be taken into account. The lungs and air sacs are only constrained by the skeleton in that they must fit inside the ribcage and share space with the viscera. Based on measurements from caimans and large ungulates, Alexander (1989) subtracted 8% from the volume of each of his

models to account for lungs. Data presented by King (1966:table 3) indicate that the lungs and air sacs of birds may occupy 10%–20% of the volume of the body. Hazlehurst and Rayner (1992) found an average SG of 0.73 in a sample of 25 birds from 12 unspecified species. On this basis, they concluded that the lungs and air sacs occupy about a quarter of the volume of the body in birds. However, some of the air in their birds probably resided in extraskeletal diverticula or pneumatic bones, so the volume of the lungs and air sacs may have been somewhat lower. In the interests of erring conservatively, I put the volume of the lungs and air sacs at 10% of the body volume.

The results of these calculations are necessarily tentative. The lungs and air sacs were probably not much smaller than estimated here, but they may have been much larger; the trachea could not have been much shorter but may have been much longer, or it may have been of a different or an irregular diameter (see McClelland [1989a] for tracheal convolutions and bulbous expansions in birds); the neural spines may have contained much more or somewhat less air; the ASP of *Diplodocus* vertebrae may be higher or lower; and the tissue replaced by the intraosseous diverticula may have been more or less dense. The extraskeletal diverticula have not been accounted for at all, although they were certainly extensive in linear terms and were probably voluminous as well. Uncertainties aside, it seems likely that the vertebrae contained a large volume of air, possibly 1,000 liters or more if the very tall neural spines are taken into account. This air mainly replaced dense bony tissue, so skeletal pneumatization may have lightened the animal by up to 10%—and that does not include the extraskeletal diverticula or pulmonary air sacs. In the example presented here, the volume of air in the body of *Diplodocus* is calculated to have replaced about 3,000 kg of tissue that would have been present if the animal were solid. If the total volume of the body was 15,000 liters and the density of the remaining tissue was 1 g/cm^3, the body mass would have been about 12 metric tons and the SG of the entire body would have been 0.8. This is lower than the SGs of squamates and crocodilians (0.81–0.89) found by Colbert (1962), higher than the SGs of birds (0.73) found by Hazlehurst and Rayner (1992), and about the same as the SGs (0.79–0.82) used by Henderson (2004) in his study of sauropod buoyancy. Note that the amount of mass saved by skeletal pneumatization is independent of the estimated volume of the body, but the proportion of mass saved is not. Thus if we start with Alexander's (1985) 18,500-liter estimate for the body volume of *Diplodocus*, the mass saved is still 1,455 kg, but this is only 8% of the solid mass, not 10% as in the previous example.

It could be argued that adjusting the estimated mass of a sauropod by a mere 8%–10% is pointless. The mass of the living animal may have periodically fluctuated by that amount or more, depending on the amount of fat it carried and how much food it held in its gut (Paul 1997). Further, the proposed correction is tiny compared to the range of mass estimates produced by different studies, from 11,700 kg (Paul 1997) to 18,500 kg (Alexander 1985). However, there are several reasons for taking into account the mass saved by skeletal pneumatization. The first is that estimating the mass of extinct animals is fraught with uncertainty, but we should account for as many sources of error as possible, and PSP is a particularly large source of error if it is not considered. Also, the range of mass estimates for certain taxa may be very wide, but 8%–10% of the body mass is still a sizable fraction when applied to any one estimate. The entire neck and head account for about the same percentage of mass in volumetric studies (Alexander 1989; Paul 1997), so failing to account for PSP may be as gross an error as omitting the neck and head from the volumetric model. These are the purely methodological reasons for considering the effect of PSP on body mass. There is also the paleobiological consideration, which is that the living animal was 8%–10% lighter because of PSP than it would have been without. Mass reduction of this

magnitude almost certainly carries a selective advantage (Currey and Alexander 1985), and this may explain the presence of extensive PSP in many sauropods.

An alternative possibility is that sauropod skeletons weighed as much as they would have in the absence of PSP but that pneumatization allowed the elements to be larger and stronger for the same mass. This hypothesis was first articulated by Hunter (1774) to explain skeletal pneumatization in birds. It is supported by the observation that the skeletons of birds are not significantly lighter than the skeletons of comparably sized mammals (Prange et al. 1979). If this hypothesis is correct, pneumatic elements should be noticeably larger and more voluminous than nonpneumatic elements. The transitions from pneumatic to apneumatic regions of the vertebral column in *Jobaria* (Sereno et al. 1999:fig. 3) and *Diplodocus* (Osborn 1899:fig. 13; Gilmore 1932:fig. 3, pl. 6) are not marked by obvious changes in size or form of the vertebrae. This supports the hypotheses that pneumatic vertebrae were lighter than apneumatic vertebrae and that PSP really did lighten sauropod skeletons.

PALEOBIOLOGICAL IMPLICATIONS

The importance of PSP for sauropod paleobiology is still largely unexplored. To date, Henderson's (2004) study of sauropod buoyancy is the only investigation of the biomechanical effects of PSP. Henderson included pneumatic diverticula in and around the vertebrae in his computer models of sauropods, and found that floating sauropods were both highly buoyant and highly unstable. Pneumaticity may also be important in future studies of neck support in sauropods. Alexander (1985, 1989) calculated that a large elastin ligament would be better suited than muscles to holding up the neck of *Diplodocus*. His calculations were based on a volumetric estimate of 1,340 liters (and, thus, 1,340 kg) for the neck and head. Using the values in table 7.3, one fifth of that volume, or 268 liters, was occupied by airspaces. If Paul (1997) and Henderson (2004) are correct, the SG of the neck may have been as low as 0.6, which would bring the mass of the neck down to about 800 kg (the same result could be obtained by applying the air volumes in table 7.3 to a more slender neck model than that used by Alexander). As the mass of the neck goes down, so to does the perceived need for a large "nuchal" ligament, the existence of which is controversial (see Wedel et al. 2000; Dodson and Harris 2001; Tsuihiji 2004).

Recognition of skeletal pneumaticity in sauropods may also affect physiological calculations. For example, most published studies of thermal conductance in dinosaurs (e.g., Spotila et al. 1973, 1991) have modeled dinosaur bodies using solid cylinders. Air is a better insulator than conductor, but moving bodies of air may cool adjacent tissues by convection or evaporation. The pneumatic diverticula of birds tend to be blind-ended tubes except where they anastomose (Cover 1953), and most are poorly vascularized (Duncker 1971), so there appears to be little potential for evaporative cooling. On the other hand, thermal panting is an important homeostatic mechanism for controlling body temperature in birds and depends on evaporation from nasal, buccopharyngeal, and upper tracheal regions (Lasiewski 1972; Menaum and Richards 1975). At the very least, the inclusion of tracheae, lungs and pneumatic diverticula in thermal conductance models would decrease the effective radius of some of the constituent cylinders. What effect, if any, this would have on the results of thermal conductance studies is unknown, which is precisely the point: it has not been tested.

PROBLEMS AND PROSPECTS FOR FURTHER RESEARCH

Despite a long history of study, research on PSP is, in many ways, still in its infancy. Anyone who doubts the accuracy of this statement is directed to Hunter (1774). In the first published study of PSP, Hunter developed two of the major functional hypotheses entertained today: pneumaticity may lighten the skeleton, or it

may strengthen the skeleton by allowing bones of larger diameter for the same mass as marrow-filled bones (see Witmer [1997], for a historical perspective on these and other hypotheses). Although many later authors have documented the presence and extent of PSP in certain birds (e.g., Crisp 1857; King 1957), most have focused on one or a few species (but see O'Connor 2004), some have produced conflicting accounts (reviewed by King 1957), and few have attempted to test functional hypotheses (but see Warncke and Stork 1977; Currey and Alexander 1985; Cubo and Casinos 2000; O'Connor 2004). Evolutionary patterns of PSP in birds are difficult to discern because few species have been studied (King, 1966), usually with little or no phylogenetic context (O'Connor 2002, 2004). Limits of knowledge of PSP in extant vertebrates necessarily limit what can be inferred from the fossil record. For example, disagreements between various published accounts of the development of pneumatization in birds frustrate attempts to infer the ontogenetic development of PSP in sauropods (Wedel 2003a).

Another problem for studies of PSP in fossil organisms is small sample sizes. As mentioned above, few taxa have been intensively studied and the importance of serial, ontogenetic, and intraspecific variation is difficult to assess. Sample sizes are mainly limited by the inherent attributes of the fossils: fossilized bones are rare, at least compared to the bones of extant vertebrates; they may be crushed or distorted; and they are often too large, too heavy, or too fragile to be easily manipulated. Even if these difficulties are overcome, most of the pneumatic morphology is still inaccessible, locked inside the bones.

SOURCES OF DATA

Information on the internal structure of fossil bones comes from three sources: CT studies, cut sections of bones, and broken bones. Although CT studies of fossils are becoming more common, access to scanners is very limited and can be prohibitively expensive. Large fossils, such as sauropod vertebrae, cause logistical problems. Most medical CT scanners have apertures 50 cm or less in diameter, and many sauropod vertebrae are simply too big to fit through the scanners. Furthermore, medical scanners are not designed to image large, dense objects like sauropod bones. The relatively low-energy X rays employed by medical scanners may fail to penetrate large bones, and this can produce artifacts in the resulting images (Wedel et al. 2000). Industrial CT scanners can image denser materials, but the rotating platforms used in many industrial scanners are too small to accept most sauropod vertebrae. For the near-future, CT will likely remain a tool of great promise but limited application.

Cut sections of bones can yield valuable information about pneumatic internal structures. The cuts may be made in the field to break aggregates of bones into manageable pieces, as in the cut *Sauroposeidon* vertebra shown in fig. 7.4. Less commonly, bones may be deliberately cut to expose their cross sections or internal structures, such as the cut specimens illustrated by Janensch (1947:fig. 5) and Martill and Naish (2001:pl. 32). Cutting into specimens is invasive and potentially dangerous to both researchers and fossils. Although cut specimens will continue to appear from time to time, they are unlikely to become a major source of data. In contrast, broken bones are ubiquitous. The delicate structure of pneumatic bones, even large sauropod vertebrae, may make them more prone to breakage than apneumatic bones. For these reasons broken bones are an important resource in studies of PSP and could be exploited more in the future. Published illustrations of broken sauropod vertebrae are numerous; notable examples include Cope (1878:fig. 5), Hatcher (1901:pl. 7), Longman (1933:pl. 16, fig. 3), and Dalla Vecchia (1999:figs. 2, 19). A beautiful example from outside Sauropoda is the broken transverse process of *Tyrannosaurus* illustrated by Brochu (2003:fig. 75).

DIRECTIONS FOR FUTURE RESEARCH

Four attributes of pneumatic bones are listed above under "Description of Pneumatic Elements":

(1) external pneumatic features, (2) internal structure, (3) ASP, and (4) distribution of pneumaticity in the skeleton. Only the second attribute has been systematically surveyed in sauropods (Wedel 2003b), although aspects of the first are treated by Wilson (1999). Knowledge of the fourth is mainly limited to the observation that diplodocines and saltasaurines have pneumatic caudal vertebrae and other sauropods do not (Wedel 2003b). All existing data on the ASPs of sauropod vertebrae are presented in table 7.2. Not only do all four attributes need further study, but the levels of serial, ontogenetic, and intraspecific variation should be assessed whenever possible. Similar data on PSP in pterosaurs, nonavian theropods, and birds are needed to test phylogenetic and functional hypotheses.

The pneumatic diverticula of birds are morphologically and morphogenetically intermediate between the core respiratory system of lungs and air sacs and the pneumatic bones. Understanding the development, evolution, and possible functions of diverticula is therefore crucial for interpreting patterns of PSP in fossil vertebrates. Müller (1907), Richardson (1939), Cover (1953), King (1966), Duncker (1971) and a few others described the form and extent of the diverticular network in the few birds for which they are known, but information on many bird species is lacking or has been inadequately documented (King 1966). The ontogenetic development of the diverticula is very poorly understood; most of what we think we know is based on inferences derived from patterns of skeletal pneumatization (Hogg 1984a; McClelland 1989b). Such inferences tell us nothing about the development of the many visceral, intermuscular, and subcutaneous diverticula that do not contact the skeleton or pneumatize any bones. These diverticula could not have evolved to pneumatize the skeleton. Most diverticula that pneumatize the skeleton must grow out from the core respiratory system before they reach their "target" bones, so they probably also evolved for reasons other than skeletal pneumatization (Wedel 2003a). Those reasons are unknown, in part because the physiological functions—or exaptive effects (*sensu* Gould and Vrba 1982)—of diverticula remain obscure. Three important physiological questions that could be answered with existing methods are: (1) What volume of air is contained in the diverticula in life? (2) What is the rate of diffusion of air into and out of blind-ended diverticula? and (3) In cases where diverticula of different air sacs anastomose, is air actively circulated through the resulting loops?

Finally, more work is needed on the origins of PSP; if nothing else, Gower's (2001) unconventional hypothesis has drawn attention to this need. Potential projects include histological and biomechanical studies to assess the structure and functions of vertebral laminae (Wilson 1999). In addition, criteria for distinguishing the osteological traces of adipose deposits, muscles, vascular structures, and pneumatic diverticula are badly needed for the interpretation of potentially pneumatic features in fossil bones. This problem is the subject of ongoing research by O'Connor (1999, 2001, 2002).

CONCLUSIONS

The best evidence for pneumaticity in a fossil element is the presence of large foramina that lead to internal chambers. Based on this criterion, pneumatic diverticula were present in the vertebrae of most sauropods and in the ribs of some. Vertebral laminae and fossae were clearly associated with pneumatic diverticula in most eusauropods, but it is not clear whether this was the case in more basal forms. Measurements of vertebral cross sections indicate that, on average, pneumatic sauropod vertebrae were 50%–60% air, by volume. Taking skeletal pneumaticity into account may reduce mass estimates of sauropods by up to 10%. Although the functional and physiological implications of pneumaticity in sauropods and other archosaurs remain largely unexplored, most of the outstanding problems appear tractable, and there is great potential for progress in future studies of pneumaticity.

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ERRATUM

to

Wedel (2005) Table 7.3, The volume of air in *Diplodocus*

Dear reader,

In my chapter in the UC Press book, The Sauropods: Evolution and Paleobiology, Table 7.3 was formatted incorrectly. The leftmost column heading was deleted, so all of the values were transposed to incorrect columns, except for some of the totals, which now make no sense. This is as much my fault as anyone else's: the error happened before the proofs were set, and I codified it into a mistake by failing to catch it. Here is the corrected table.

I am sorry for the inconvenience. Thank you for your interest in my work.

All the best,

Matt Wedel

TABLE 7.3. The volume of air in *Diplodocus*. See the text for methods of estimation.

System	Total Volume (L)	Air Volume (L)	Mass Savings (kg)
Trachea	104	104	104
Lungs and air sacs		1500	1500
Extraskeletal diverticula	?	?	
Pneumatic vertebrae			
Centra			
Cervicals 2-15	136	82	
Dorsals 1-10	208	125	
Sacrals 1-5	75	45	
Caudals 1-19	329	198	
Subtotal for centra	748	450	
Neural spines			
Cervicals 2-15	136	82	
Dorsals 1-10	416	250	
Sacrals 1-5	150	90	
Caudals 1-19	165	99	
Subtotal for spines	867	520	
Subtotal for vertebrae	1615	970	1455
Total volume of air spaces		2574	
Total mass replaced by air spaces			3059

Reference:

Wedel, M.J. 2005. Postcranial skeletal pneumaticity in sauropods and its implications for mass estimates; pp. 201-228 in Wilson, J.A., and Curry-Rogers, K. (eds.), *The Sauropods: Evolution and Paleobiology*. University of California Press, Berkeley.

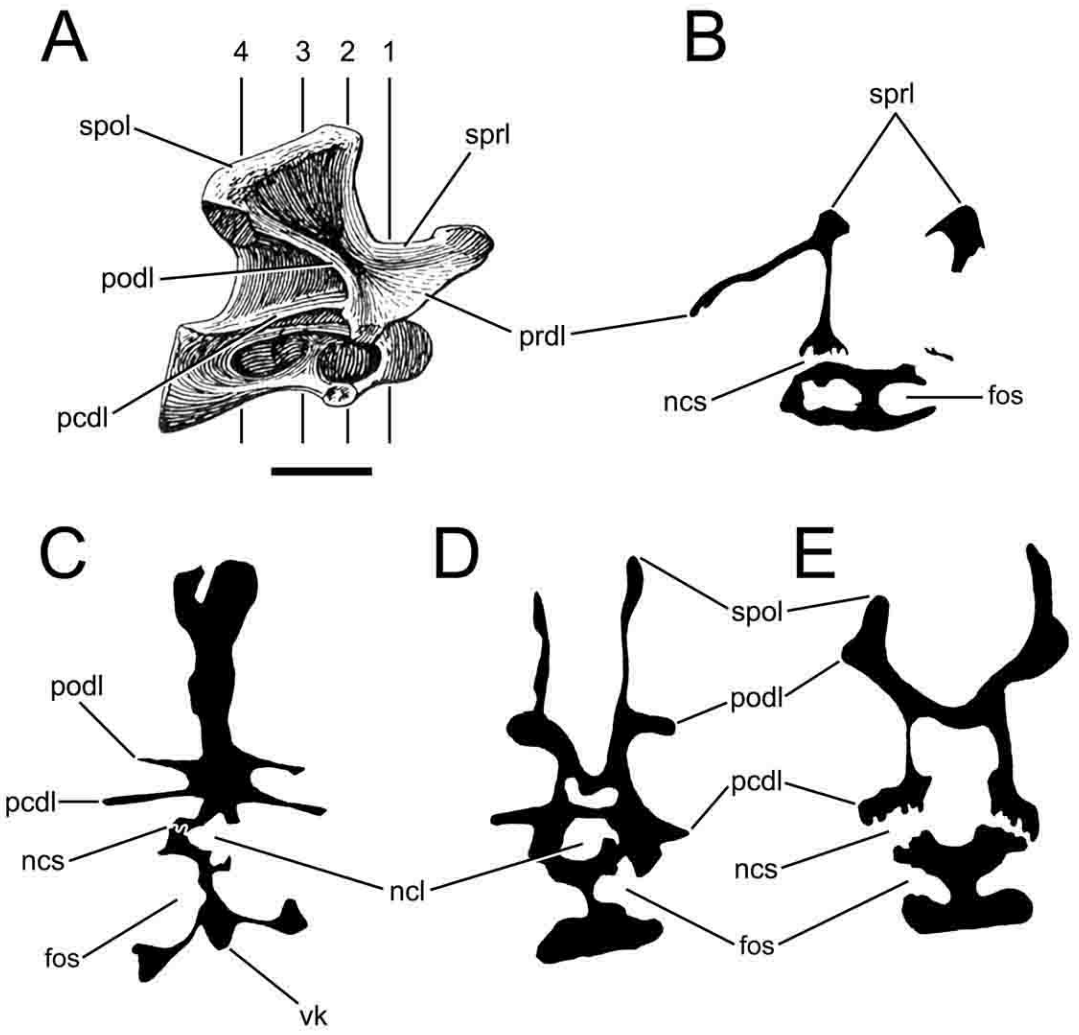

FIGURE 7.3. Pneumatic features in a cervical vertebra of *Haplocanthosaurus*. A, A posterior cervical of *Haplocanthosaurus* in right lateral view (CM 879-7; this specimen was erroneously referred to as CM 572 in Upchurch [1998:fig. 8], and as CM 897-7 in Wedel et al. [2000:fig. 2], Wedel [2003a:fig. 3], and Wedel [2003b:fig. 1]). (Modified from Hatcher (1903:pl. 2.) B–E, Cross sections traced from CT slices. B, Section at A, position 1. C, Section at A, position 2. The opening of the neural canal and the absence of the neurocentral suture on one side are due to a break in the specimen. D, Section at A, position 3. E, Section at A, position 4. The neurocentral sutures are unfused over most of their length, indicating that this animal was not fully mature. Scale bar equals 5 cm.

fos	fossa
ncl	neural canal
ncs	neurocentral suture
pcdl	postcentrodiapophyseal lamina
podl	postzygodiapophyseal lamina
prdl	prezygodiapophyseal lamina
spol	spinopostzygapophyseal lamina
sprl	spinoprezygapophyseal lamina
vk	ventral keel

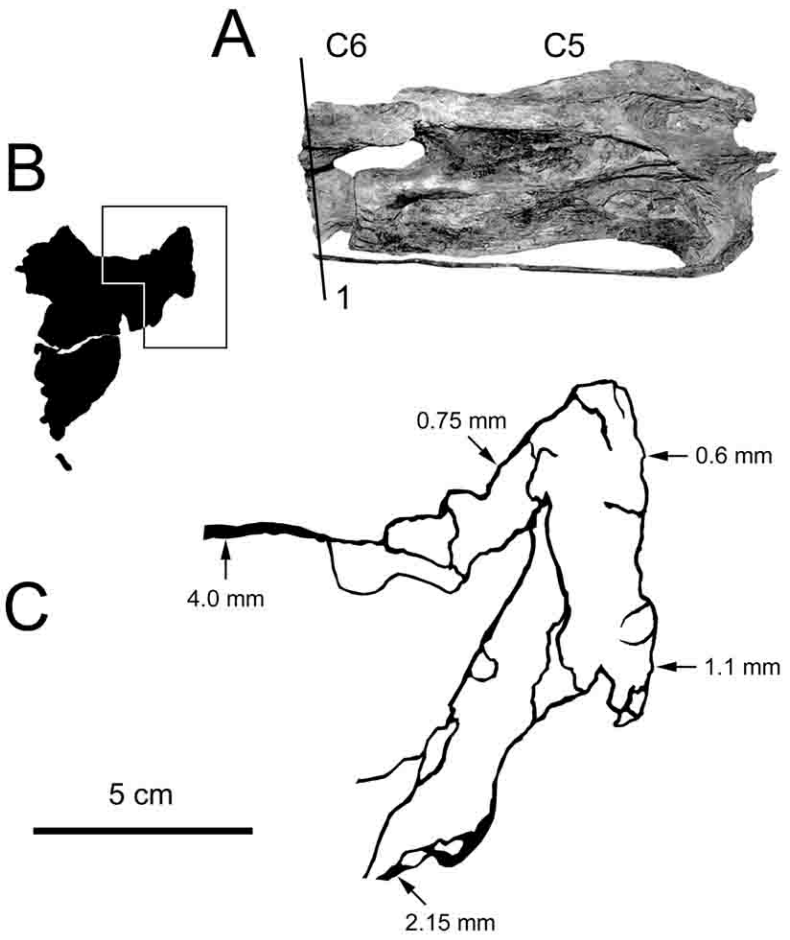

FIGURE 7.4. Internal structure of a cervical vertebra of *Sauroposeidon*, OMNH 53062. A, The posterior two-thirds of C5 and the condyle and prezygapophysis of C6 in right lateral view. The field crew cut though C6 to divide the specimen into manageable pieces. B, Cross section of C6 at the level of the break, traced from a CT image (A, position 1) and photographs of the broken end. The left side of the specimen was facing up in the field and the bone on that side is badly weathered. Over most of the broken surface the internal structure is obscured by plaster or too damaged to trace, but it is cleanly exposed in the ramus of the right prezygapophysis (outlined). C, The internal structure of the prezygapophyseal ramus, traced from a photograph. The arrows indicate the thickness of the bone at several points, as measured with a pair of digital calipers. The camellae are filled with sandstone.

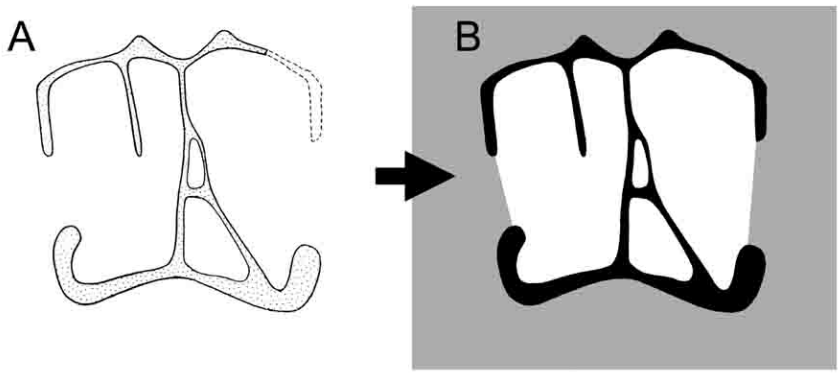

FIGURE 7.5. How to determine the airspace proportion (ASP) of a bone section. (A) A section is traced from a photograph, CT image, or published illustration; in this case, a transverse section of a *Barosaurus africanus* cervical vertebra from Janensch (1947:fig. 3). (B) Imaging software is used to fill the bone, airspace, and background with different colors. The number of pixels of each color can then be counted using Image J (or any program with a pixel count function) and used to compute the ASP. In this case, bone is black and air is white, so the ASP is (white pixels)/(black pixels + white pixels).

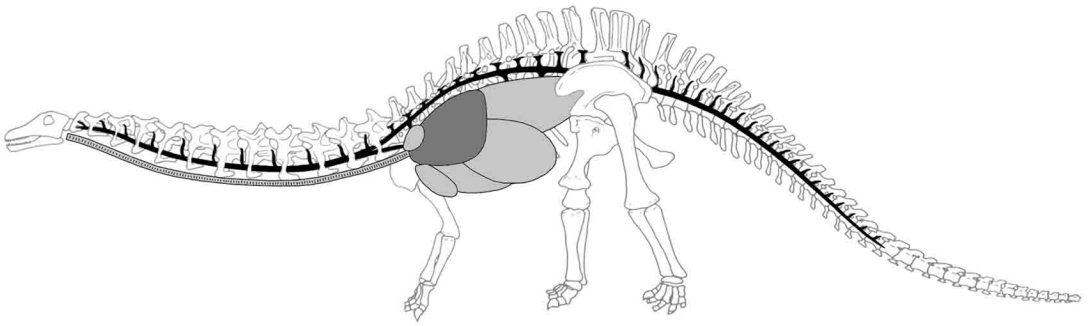

FIGURE 7.6. Hypothetical conformation of the respiratory system of a diplodocid sauropod. The left forelimb, pectoral girdle, and ribs have been removed for clarity. The lung is shown in dark gray, air sacs are light gray, and pneumatic diverticula are black. Only some of the elements shown in this illustration can be determined with certainty: the minimum length of the trachea, the presence of at least some air sacs, and the minimum extent of the pneumatic diverticula. The rest of the respiratory system has been restored based on that of birds, but this remains speculative. The skeleton is modified from Norman (1985:83).

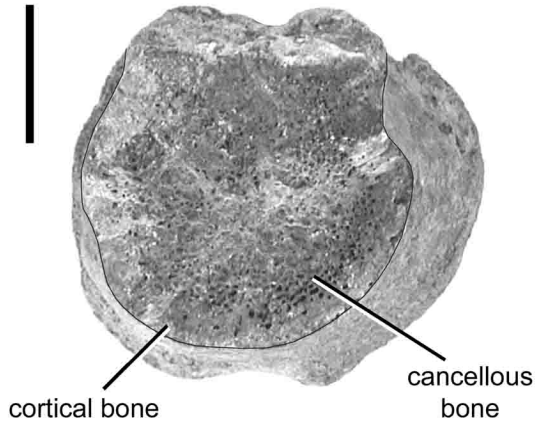

FIGURE 7.7. Internal structure of OMNH 27794, a partial distal caudal vertebra of a titanosauriform. The internal structure is composed of apneumatic cancellous bone, and no medullary cavity is present. Scale bar equals 1 cm.