

## Vertebral pneumaticity, air sacs, and the physiology of 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 a system of air sacs and pneumatic diverticula similar to that of birds. In extant birds, diverticula of the cervical air sacs pneumatize the cervical and anterior thoracic vertebrae. Diverticula of the abdominal air sacs pneumatize the posterior thoracic vertebrae and sacrum later in ontogeny. This ontogenetic sequence in birds parallels the evolution of vertebral pneumaticity in sauropods. In basal sauropods, only the presacral vertebrae were pneumatized, presumably by diverticula of cervical air sacs similar to those of birds. The sacrum was also pneumatized in most neosauropods, and pneumatization of the proximal caudal vertebrae was achieved independently in Diplodocidae and Titanosauria. Pneumatization of the sacral and caudal vertebrae in neosauropods may indicate the presence of abdominal air sacs. Air sacs and skeletal pneumaticity probably facilitated the evolution of extremely long necks in some sauropod lineages by overcoming respiratory dead space and reducing mass. In addition, pulmonary air sacs may have conveyed to sauropods some of the respiratory and thermoregulatory advantages enjoyed by birds, a possibility that is consistent with the observed rapid growth rates of sauropods.

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### Introduction

The excavations and internal cavities of sauropod vertebrae were recognized as pneumatic structures from the earliest discoveries of sauropods (Seeley 1870; Cope 1877; Marsh 1877). Although many authors subsequently recognized the weight-saving features of sauropod vertebrae (e.g., Osborn 1899; Hatcher 1901; Gilmore 1925), the pneumatic hypothesis fell into disfavor (Britt 1997) and received only infrequent acknowledgment (Janensch 1947; Romer 1966) before the “Dinosaur Renaissance” of the 1970s. Renewed interest in the morphology and implications of skeletal pneumaticity in dinosaurs developed contemporaneously with, and perhaps because of, the attention focused on dinosaur metabolism and the dinosaurian origin of birds (Bakker 1972; Witmer 1987; Britt 1997). The pneumatic vertebrae of sauropods and other saurischians are very similar to those of birds and have been considered evidence for the early evolution of the avian respiratory system (Bakker 1972; Reid 1997; Britt et al. 1998).

The hypothesis that sauropods had a lung/air sac system similar to that of birds (Bakker 1972; Daniels and Pratt 1992; Paladino et al. 1997) or structurally intermediate between the lungs of crocodiles and birds (Perry and Reuter 1999) is not new. My purpose herein is to discuss recent empirical work that supports the air sac hypothesis. The pattern of vertebral pneumatization during sauropod evolution mirrors the ontogenetic development of vertebral pneumaticity in extant birds and may indicate the specific air sacs involved in the pneumatization of the vertebral column. The paleobiological implications of pulmonary air sacs in sauropods are still largely unexplored, because most published studies have assumed that the respiratory systems of sauropods were essentially identical to those of extant chelonians (Spotila et al. 1991), crocodylians (Hengst and Rigby 1994), or squamates (Gale 1997, 1998). Herein I use extant birds as models for interpreting the postcranial pneumaticity of sauropods and discuss the implications of air sacs for our understanding of sauropod physiology.

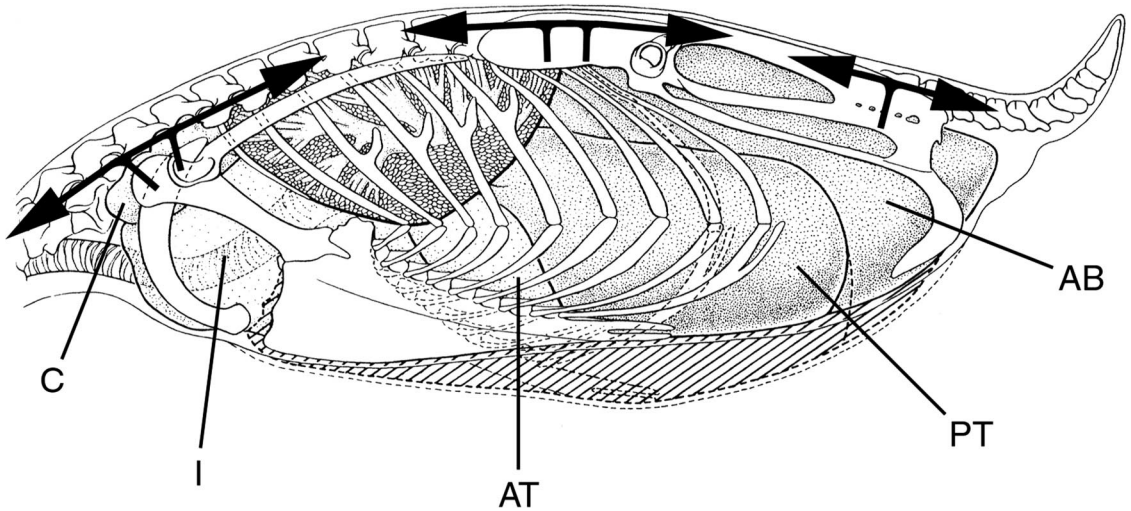


FIGURE 1. Air sacs and axial pneumatization in an extant avian. The body of bird in left lateral view, showing the cervical (C), interclavicular (I), anterior thoracic (AT), posterior thoracic (PT), and abdominal (AB) air sacs. The hatched area shows the volume change during exhalation. The cervical and anterior thoracic vertebrae are pneumatized by diverticula of the cervical air sacs. The posterior thoracic vertebrae and synsacrum are pneumatized by the abdominal air sacs in most taxa (see text for details and an exception). 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.

*Institutional Abbreviations.*—CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma; PVL, Paleontología de Vertebrados de la Fundación Miguel Lillo, Argentina.

### Postcranial Skeletal Pneumaticity in Birds

Birds are the only extant vertebrates with extensively pneumatized postcranial skeletons. Understanding the morphology and development of postcranial skeletal pneumaticity (PSP) in birds is therefore fundamental to any discussion of PSP in dinosaurs. I emphasize PSP as separate from both cranial pneumaticity and the extraskeletal system of pulmonary air sacs and diverticula. The evolution of cranial pneumaticity in archosaurs, including birds, has been thoroughly reviewed by Witmer (1997) and is not relevant to the hypotheses discussed herein. Air sacs and diverticula are prerequisites for the ontogenetic development of PSP in birds, but they can be present without pneumatizing the skeleton. Also, it is important to remember that PSP can be observed directly in fossil remains, but the presence of the soft-tissue correlates must be

inferred, except in cases of exceptional preservation.

*Skeletal Pneumatization in Birds.*—All birds have an extensive air sac system in the thorax and abdomen (Fig. 1). The pulmonary air sacs of birds arise directly from the bronchi within the lungs (Duncker 1971, 1972). There are typically nine air sacs, including one interclavicular air sac and paired cervical, anterior thoracic, posterior thoracic, and abdominal air sacs (King 1966; Duncker 1974). The air sacs are present throughout the body cavity and enclose the viscera like a nut-shell (Wetherbee 1951). The primary function of the avian pulmonary air sac system is lung ventilation. The air sac system allows ventilation and gas exchange to be decoupled physically; the relatively inflexible lungs are ventilated by changes in air sac volume. The mechanics of avian respiration are discussed further under "Air Sacs and Metabolism."

The postcranial skeletons of most birds are pneumatized by diverticula of the 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

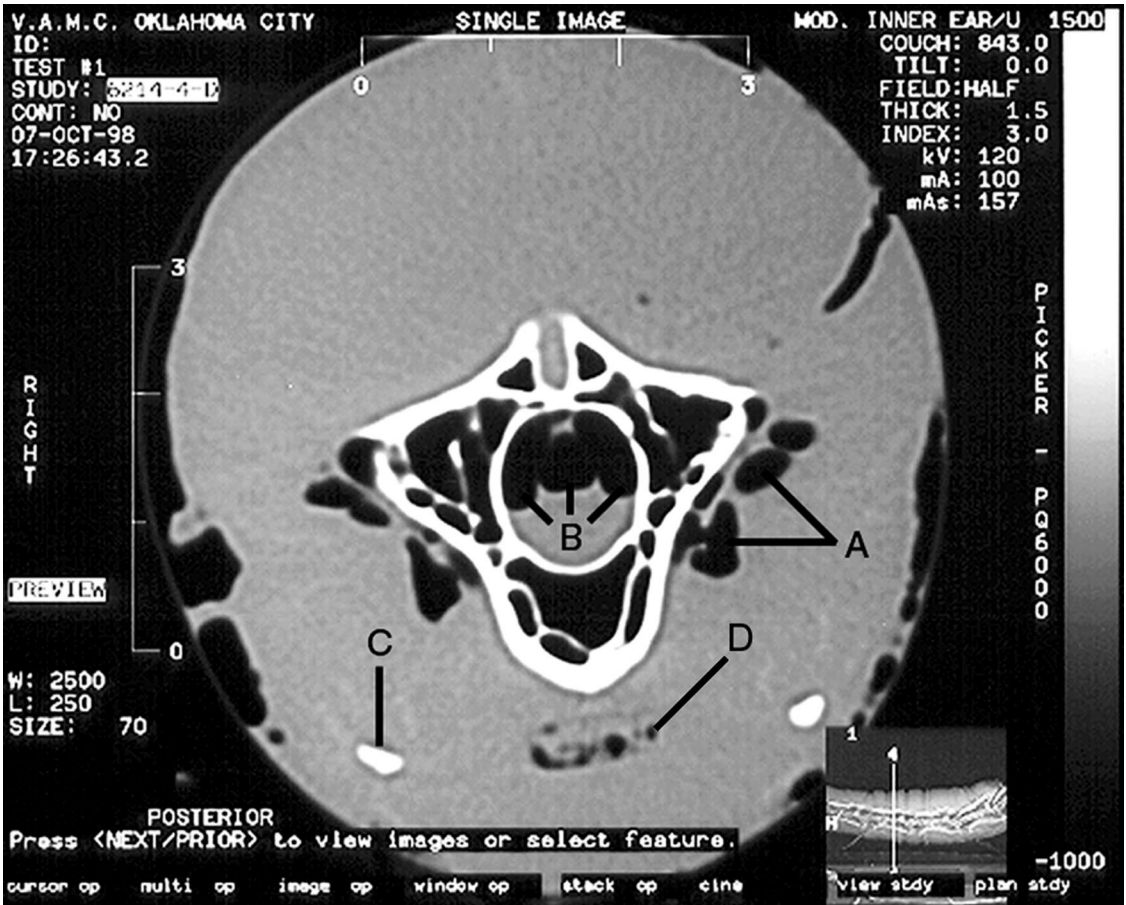


FIGURE 2. CT sections through the neck of an ostrich. The neck section was sealed with surgical gloves and cannulated with an air tube to reinflate the pneumatic diverticula. In this image, air is black, bone is white, and soft tissues are gray. A, Note the essentially camellate nature of the external diverticula, which form aggregates of narrow tubes rather than large, simple sacs. B, Within the neural canal, 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. D, The trachea, which has mostly collapsed, is the black oblong below the centrum and between the cervical ribs. Scale bars are in cm.

(Fig. 2). 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 do not pneumatize any bones because they 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). Despite these generalities, the extent of diverticula and pneumatization is quite variable in different lineages (King 1966). For example, diving birds such as the loon lack pneumati-

zation of the postcranial skeleton altogether (Gier 1952).

The ontogenetic sequence of vertebral pneumatization (as described by Hogg 1984b) is as follows. The diverticula of the cervical air sacs initially pneumatize the vertebrae at the base of the neck. From there, the diverticula spread in both directions to pneumatize the cervical series and the anterior and middle thoracic vertebrae. The abdominal air sacs pneumatize the posterior thoracic vertebrae and synsacrum later in ontogeny, after the cervical diverticula have stopped spreading (Hogg 1984b). If the cervical and abdominal diverticula meet, they may anastomose to form a con-

tinuous airway extending the entire length of the vertebral column (Cover 1953). Because of this dual pneumatization of the thoracic series from two different directions, the middle thoracic vertebrae are occasionally incompletely pneumatized or not pneumatized at all (King and Kelly 1956; Hogg 1984a).

*Skeletal Pneumatization in the Turkey.*—The turkey, *Meleagris gallopavo*, may represent an exception to the developmental sequence described above. Citing King (1975) as their source, Britt et al. (1998: p. 376) stated that, “in turkeys the cervical air sac extends all the way to the free coccygeal vertebrae.” If this statement is accurate, it is important, because it indicates that the posterior thoracic and synsacral vertebrae can be pneumatized in the absence of diverticula from the abdominal air sac (the implications of this for the interpretation of fossil forms are discussed below). Britt et al. (1998) cited King (1975) accurately. “Tubelike cervical diverticula, slightly more elaborate than in the chicken, pass cranially along the cervical vertebrae, and are said also to extend caudally along the vertebral column as far as the fourth caudal vertebra (Cover 1953c); these apparently aerate the cervical, thoracic, synsacral, and caudal vertebrae, and every vertebral rib” (King 1975: p. 1913). It is clear from this passage that King (1975) was not reporting the results of his own research on *Meleagris*, but merely passing on data from Cover (1953).

According to Cover (1953: p. 241), “A continuation of the posterior part of the cervical extension passes caudally along the sides of the vertebrae as far as the fourth coccygeal.” By itself, this statement apparently agrees with the later formulations of King (1975) and Britt et al. (1998). Cover (1953: p. 242) went on to say that “in the region of the synsacrum, there is a suprarenal diverticulum which communicates with the posterior vertebral continuation at every vertebral segment.” This communication between the suprarenal diverticulum and the cervical diverticulum by way of the vertebral airways is the anastomosis described above. Cover (1953) may have believed that the vertebral airways were produced ontogenetically by the cervical air sac alone, and that the connection with the abdominal air sac

was an entirely secondary phenomenon. However, he provided no evidence to support this interpretation over an alternative possibility, which is that the vertebral diverticulum is formed by the cervical and abdominal air sacs in equal measure, and that the posterior thoracic and synsacral vertebrae are pneumatized by the abdominal air sac, as in *Gallus* (King and Kelly 1956; Hogg 1984b) and *Struthio* (Bezuidenhout et al. 1999).

Alternately, Cover (1953) may have intended a purely descriptive account, without favoring any particular ontogenetic scenario. Cover (1953: p. 241) said that “a continuation of the cervical extension,” not the cervical diverticulum proper, “passes caudally . . . as far as the fourth coccygeal.” Cover clearly recognized the difference between the cervical diverticulum proper and its posterior continuation as the vertebral diverticulum, a subtlety that does not survive in the formulations of King (1975) and Britt et al. (1998). Furthermore, Cover may have intended to use the verb “passes” in an achronic, purely descriptive sense, as a synonym for “exists linearly.” King (1975) evidently read this as a statement about ontogeny and interpreted “passes” as “progresses developmentally.” In the paper’s conclusion, Cover (1953: p. 245) stated that “an air-sac diverticulum (vertebral) extends from the second cervical to the fourth free coccygeal vertebra, lateral to the vertebral column. Three connections are made, . . . from the aggregate sac [a collective term for the five anterior air sacs, including the paired cervical sacs], and . . . from the suprarenal diverticulum of the greater abdominal air sac.” Again, although this could be interpreted as an ontogenetic statement (“connections are made”), such an interpretation would imply that the vertebral diverticulum existed as a separate structure before it connected with either the cervical or the abdominal air sacs, a developmental impossibility that Cover (1953) clearly did not intend, judging from the remainder of the paper.

It is my contention that King (1975) subtly misinterpreted Cover (1953). King’s statement that the cervical diverticula “aerate the cervical, thoracic, synsacral, and caudal vertebrae”—an ontogenetic hypothesis—goes fur-

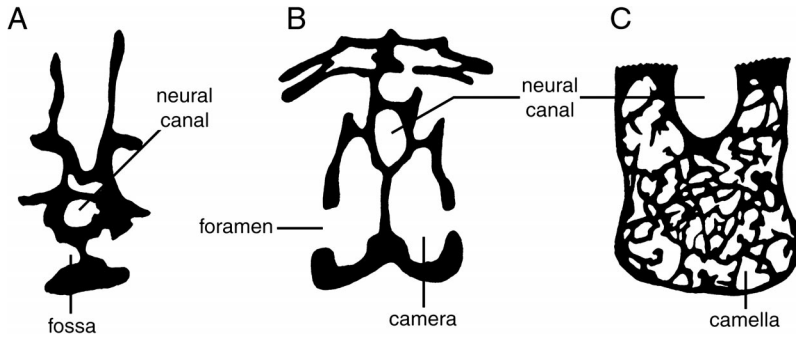


FIGURE 3. Axial sections of sauropod vertebrae showing pneumatic features. A, *Haplocanthosaurus priscus* (CM 897-7). B, *Camarasaurus* sp. (OMNH 01313). C, *Saltasaurus loricatus* (PVL 4017-137). From Wedel et al. 2000: Fig. 2.

ther than Cover's descriptive account, which only specifies the topology of the diverticular system in the adult turkey and does not clearly favor a particular ontogenetic hypothesis. In summation, diverticula of the abdominal air sac pneumatize the posterior thoracic and synsacral vertebrae in *Gallus* (King and Kelly 1956; Hogg 1984a,b) and *Struthio* (Bezuidenhout et al. 1999). In *Meleagris*, diverticula of the abdominal air sac are certainly connected to the vertebral diverticula (Cover 1953), but whether the posterior thoracic and synsacral vertebrae are pneumatized by the cervical or the abdominal diverticula is unclear, and resolution must await further empirical work.

Chasing this particular paper trail back half a century is not an empty exercise in textual analysis. In all but the most extraordinary conditions, pneumatized bones are the only traces of the respiratory system that fossilize. PSP therefore becomes our primary source of evidence regarding the existence and identity of the air sacs of extinct taxa (Britt 1997; Britt et al. 1998; Christiansen and Bonde 2000; Wedel et al. 2000). Because hypotheses regarding air sacs and respiratory physiology depend on inferences derived from PSP, it is crucial that we understand the morphology and ontogeny of the avian air sac system—our only extant model—in detail.

*Osteological Correlates of Pneumaticity.*—The morphology of a pneumatized bone is partly a result of the competing mandates of pneumatic epithelium and developing bone. The pneumatic epithelium advances opportunistically and induces bone resorption, while at the same time, bone grows partly in reaction

to biomechanical stress (Witmer 1997). This "competition" between bone and air sac produces distinct morphological features. Britt (1997) and Britt et al. (1998) listed five osteological correlates of pneumaticity: large foramina, fossae with crenulate texture, bones with thin outer walls, smooth or crenulate tracks, and internal chambers with foramina. These features are all present in the pneumatized bones of extant birds and constitute the compelling morphological evidence by which potentially pneumatic features of fossil taxa may be evaluated.

#### Vertebral Pneumaticity and Air Sacs in Sauropods

*Pneumatized Vertebrae of Sauropods.*—Pneumatic features are present in the presacral vertebrae of all sauropods and include vertebral laminae and the products of invasive pneumatic diverticula. Aside from laminae, which have been described in detail by Wilson (1999), four kinds of pneumatic structures are found on and in sauropod vertebrae: external fossae and foramina, and internal camerae and camellae (Fig. 3). Detailed definitions of these structures are presented by Wedel et al. (2000) and Wedel (in press). I provide brief descriptions here to facilitate the following discussion. Pneumatic fossae are excavations that are broad in contour and are not enclosed by osteal margins to form a foramen. Camerae are large internal cavities separated by thick bony septa, and camellae are small internal cavities separated by very thin bony septa. Camerae and camellae communicate with foramina, either directly or indirectly by inter-

nal connections to other cavities. Small camerae and large camellae can be differentiated on the basis of shape, septal thickness, and presence or absence of an identifiable branching pattern (Wedel et al. 2000). Differentiating fossae and camerae is more problematic, as discussed below.

The pneumatic morphologies described above not only represent different "grades" of evolutionary advancement, they also represent different ontogenetic stages within particular taxa. For example, vertebrae of juvenile *Camarasaurus* and *Apatosaurus* are characterized by large, simple fossae, whereas adults have camerate vertebrae, so there is clearly no barrier to the ontogenetic derivation of camerae from fossae. Indeed, at an even earlier ontogenetic stage the vertebrae of the youngest individuals must have lacked any pneumatic features. 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 represented different strategies for lightening the centrum. However, given that fossae may grade into camerae in an individual, either ontogenetically or serially, it is clear that fossae and camerae are not fundamentally different, but merely two points in a morphological continuum.

Herein lies the problem mentioned above: given that fossae and camerae grade into each other, how are they to be differentiated? Wedel et al. (2000) and Wedel (in press) used an arbitrary measure of enclosure—an opening 50% or less of the diameter of the cavity—to separate camerae from partially enclosed fossae. Other authors have used the depth of the cavity (Upchurch 1998) or the presence of a sharp lip bounding the cavity (Wilson and Sereno 1998) to parse the evolution of pneumatic characters in sauropods. These alternative formulations mean that the evolutionary changes tracked by each study are not necessarily comparable, because each author is using different character states (I am grateful to J. A. Wilson for bringing this previously ne-

glected point to my attention in his review comments). I do not advocate any of the three approaches listed above to the exclusion of the others, because each describes a different kind of change. Readers should keep the above distinctions in mind when comparing between studies.

From a functional standpoint, the complex morphologies described by Wedel et al. (2000) are probably oversplit. Although polycamerate and semicamellate vertebrae can be distinguished on the basis of discrete criteria, both morphologies involve filling the condyles, cotyles, and epiphyses with networks of small pneumatic chambers. Both types are "complex," using the criteria established by Britt (1997). These complex morphologies evolved at least three times, in *Mamenchisaurus*, diplodocids, and titanosauriforms. These taxa were all relatively long-necked (see Powell 1987; Wilson and Sereno 1998). The presence of complex internal structures in these taxa is thus strongly correlated with neck elongation. Although it has not yet been tested, it is possible that "honeycombed" camellate structures are biomechanically more effective than "I-beam" camerate structures, and that acquisition of the more complex morphologies facilitated the evolution of the spectacularly long necks observed in some sauropod lineages.

*The Air Sacs of Sauropods.*—The presence of PSP in sauropods indicates a physical connection between the pulmonary system and the vertebral column. Some basic features of the sauropod pulmonary system can be deduced from the presence of pneumatized vertebrae. The lungs must have been dorsally attached (Perry and Reuter 1999), and the portions of the pulmonary system responsible for pneumatization could not have been excluded from the vertebral column by a diaphragmatic muscle (Christiansen and Bonde 2000).

The pattern of vertebral pneumatization in sauropod evolution parallels that seen during avian ontogeny. In primitive sauropods such as *Jobaria*, pneumatic fossae occur only in the cervical and anterior thoracic vertebrae (Sereno et al. 1999). In most neosauropods, the posterior thoracic and sacral vertebrae are also pneumatized. Derived diplodocoids and

titanosaurians independently acquired pneumatized caudal vertebrae (Britt 1997; 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, by diverticula of the cervical air sacs (Cover 1953; Hogg 1984b; Bezuidenhout et al. 1999). In most birds, diverticula of the abdominal air sacs pneumatize the posterior thoracic vertebrae and synsacrum later in ontogeny. A similar caudad progression of pneumatized vertebrae also occurred in the evolution of theropods (Britt 1997).

I have previously assumed from comparisons to *Gallus* (King and Kelly 1956; Hogg 1984a,b), *Meleagris* (Cover 1953), and *Struthio* (Bezuidenhout et al. 1999), that pneumatization of the posterior thoracic, sacral, and caudal vertebrae in neosauropods unequivocally indicated the presence of abdominal air sacs (Wedel et al. 2000, Wedel in press). However, this is not necessarily so, because the posterior thoracic, sacral, and caudal vertebrae of sauropods could have been pneumatized by posterior extensions of the cervical diverticula, as King (1975) described for *Meleagris*. Even if further empirical work demonstrates that the abdominal air sacs of birds pneumatize the posterior portion of the vertebral column more commonly than do the cervical diverticula alone, there is still no reason in principle why the same vertebrae in sauropods could not have been pneumatized by diverticula of cervical air sacs. The posterior extension of the cervical diverticula over the course of sauropod evolution would produce the same trend described above, in which vertebral pneumaticity extends farther posteriorly in increasingly derived sauropods.

The presence of abdominal air sacs in sauropods (or non-avian theropods) could be confirmed under the right conditions. In adult individuals of *Gallus*, the middle thoracic vertebrae are occasionally apneumatic, because the posteriorly advancing diverticula of the cervical air sacs and the anteriorly advancing diverticula of the abdominal air sacs fail to meet. This failure of the two systems of diverticula to meet and anastomose is described by

King and Kelly (1956), and osteological documentation is also provided by Hogg (1984a). All individuals of *Gallus* have apneumatic thoracic vertebrae early in ontogeny, before the anastomosis of the cervical and abdominal diverticula, so a pneumatic hiatus in the middle thoracic vertebrae of an adult is a retained juvenile character. The presence of abdominal air sacs in sauropods would be confirmed by the discovery of a similar pneumatic hiatus in a sauropod, because pneumatized vertebrae posterior to the apneumatic vertebrae would have to have been pneumatized separately, by the abdominal air sacs (Fig. 4). I am unaware of any sauropod skeletons that have a pneumatic hiatus. It is possible that such specimens have already been discovered, and that the pneumatic hiatus was not reported because its significance was not recognized. It is also possible that no sauropods with a hiatus have been discovered, either because the pneumatic hiatus is only expressed infrequently, as in *Gallus*, or because sauropod vertebrae were exclusively pneumatized by cervical air sacs (Fig. 4B) and the pneumatic hiatus never existed. If skeletal pneumatization in sauropods followed the same ontogenetic sequence as in birds, then our best chance to find a pneumatic hiatus, if it exists, is in a juvenile sauropod. Failure to find a pneumatic hiatus in a sauropod does not mean that sauropods did not have abdominal air sacs, only that the presence of abdominal air sacs cannot be deduced from a continuously pneumatized vertebral column.

#### Evolution of Air Sacs and Postcranial Pneumaticity within Archosauria

Sauropods are not the only fossil archosaurs with pneumatic postcranial skeletons. PSP is also present in pterosaurs, theropods, and at least some prosauropods (see Yates 2001), but lacking in ornithischians and most prosauropods (Fig. 5). Furthermore, recent work by Gower (2001) indicates that vertebral pneumaticity may have been present even in basal archosaurs such as *Erythrosuchus*, albeit in a cryptic and rudimentary form. This distribution of postcranial pneumaticity requires either multiple origins or multiple losses. Sauropods and theropods show similar trends in

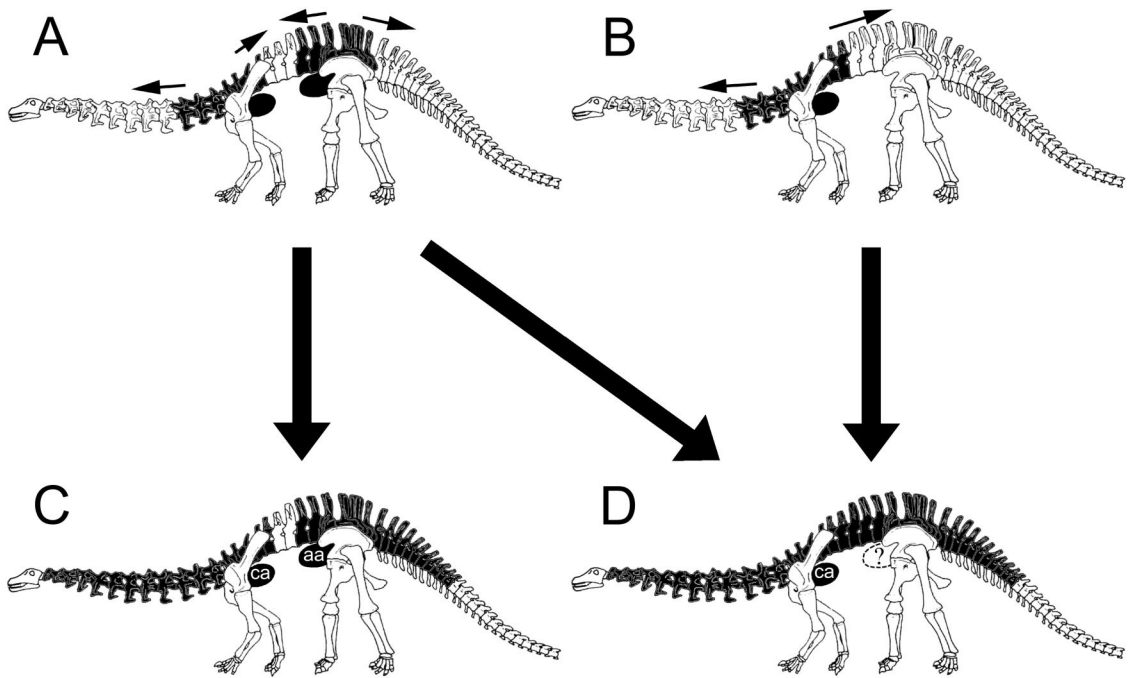


FIGURE 4. Criteria for inferring the presence of abdominal air sacs in a sauropod. Air sacs and pneumatized vertebrae are shown in black. Small arrows show the spread of pneumatic diverticula, and large arrows represent ontogenetic trajectories. A, Pneumatization of the vertebrae by diverticula of cervical and abdominal air sacs. B, Pneumatization of the vertebrae by diverticula of cervical air sacs alone. C, A hypothetical sauropod with a "pneumatization hiatus" in the mid-dorsal vertebrae. This pattern could only be produced if both cervical (ca) and abdominal (aa) air sacs were present. D, Pneumatization of the posterior dorsal, sacral, and caudal vertebrae does not necessarily indicate the presence of abdominal air sacs, because continuous pneumatization of the vertebral column could be produced by anastomosing diverticula of the cervical and abdominal air sacs (as in A) or by cervical air sacs alone (as in B). The *Apatosaurus* skeleton is modified from Norman 1985: p. 83.

both the extent of pneumatization along the vertebral column (discussed above) and the internal complexity of the pneumatized vertebrae (Britt 1997; Wedel in press), demonstrating substantial parallelism in the evolution of PSP in the two groups.

Although the pulmonary air sacs of extinct taxa cannot be observed directly, their presence can be inferred from osteological correlates and by comparative studies with birds. The postcrania of birds are pneumatized by diverticula of the pulmonary air sacs, not by the air sacs themselves. This topology is dictated by ontogeny: air sacs form first, diverticula grow out from the air sacs later, and skeletal pneumatization occurs last (Müller 1907; Bremer 1940). A complete and functional system of air sacs can be present without pneumatizing the skeleton, as in the loon (Gier 1952). Loss of PSP in the loon was apparently

accomplished by the deletion of terminal steps from the sequence described above.

These observations of extant taxa have important implications for fossil forms. First, if the ontogeny of extant birds accurately reflects the evolution of the air sac/diverticula system—air sacs first, then diverticula, and finally skeletal pneumatization—then the evolution of the dorsally attached lung/air sac system must predate the first appearance in the fossil record of a taxon with pneumatic postcranial bones. Second, if pulmonary air sacs originated before the evolution of PSP, they must have initially evolved for some purpose other than pneumatizing the skeleton. This other purpose was probably not mass reduction. Pulmonary air sacs alone merely displace soft tissues outward; mass reduction is achieved by the diverticula invading the skeleton and actively replacing tissue, which



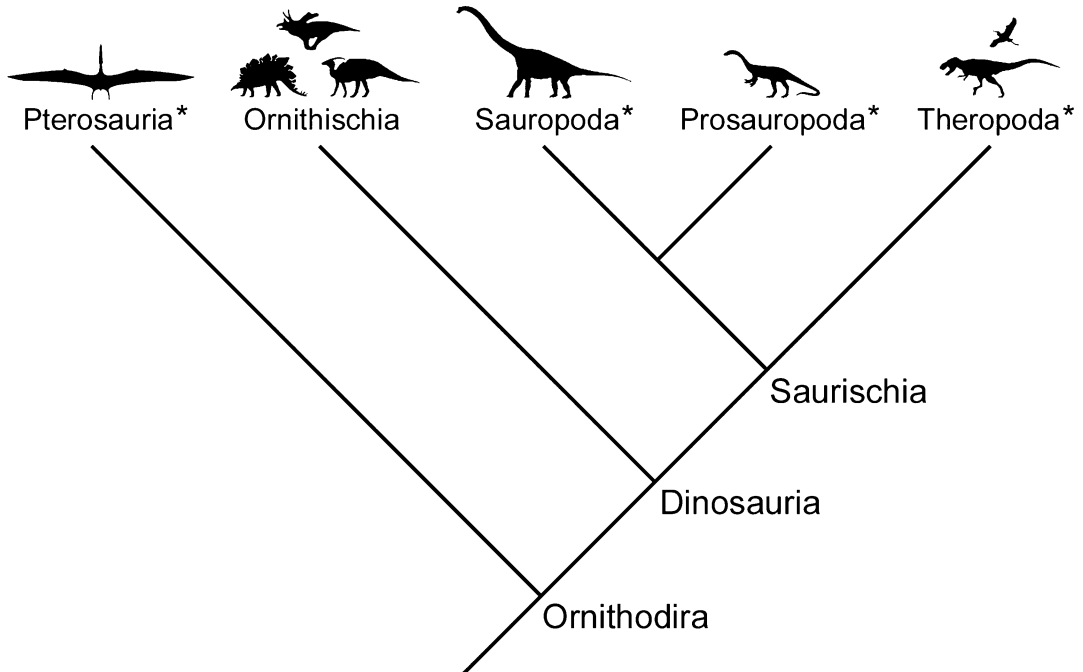


FIGURE 5. Postcranial skeletal pneumaticity in Ornithodira. General tree topology and node terminology after Sereno 1991, 1999. Clades with PSP are denoted with asterisks. Either PSP is primitive for Ornithodira and secondarily lost in some dinosaurs, or it evolved independently more than once. Most prosauropods lack PSP, but recent work (see Yates 2001) indicates that it may have been present in *Thecodontosaurus*. Icons after Sereno 1999.

could only have happened later. Air sacs probably initially evolved to fulfill the same purpose they serve in extant birds: to ventilate the lungs. Between the septate lungs of extant “reptiles” and the derived air sac system of extant birds, there must have existed an entire spectrum of intermediates (Perry and Reuter 1999; Perry 2001). Although the air sac systems of basal archosaurs would not have been as complex or efficient as those of birds, there is no logical reason why they could not have become so in the course of the ornithodiran radiation. And obviously, in time, they did.

Ornithodirans, saurischians, and sauropods are all characterized by having longer necks than their immediate outgroups (Gauthier 1986; Sereno 1991; Wilson and Sereno 1998). The continuing trend toward neck elongation in these nested clades may have been related to the progressive evolution of pulmonary air sacs in the same groups. Air sac systems would have facilitated the evolution of progressively longer necks, first by overcoming tracheal dead space (see below), and later by

pneumatizing the axial skeleton, thereby reducing mass.

#### Air Sacs and Metabolism

The lung/air sac system of birds profoundly affects their physiology. If sauropods and other fossil archosaurs had air sac systems, they may have enjoyed some of the same advantages that air sacs convey to birds. Therefore, I will briefly review the physiological functions of avian air sacs before considering their possible effects on sauropod metabolism.

*Avian Respiration and Physiology.*—Avian respiration is complex but now quite well understood (see Brackenbury 1971; Bouverot and Dejours 1971; Duncker 1971, 1972, 1974; Scheid et al. 1972; Kuethe 1988), and merits only a brief description here. Inhalation is accomplished by expanding the air sacs, which draws air through the parabronchi of the lungs and into the air sacs. During exhalation, the air sacs are compressed and air also flows through the parabronchi. Airflow through the parabronchi is unidirectional during both in-

spiration and expiration. Cross-current gas exchange occurs between the air capillaries of the parabronchi and the capillaries of the circulatory system.

The constant airflow through the lungs and cross-current gas exchange allow birds to have much higher oxygen extraction than mammals (Bernstein 1976). In addition to their ventilatory function, air sacs overcome the respiratory dead space imposed by the long tracheae of many species (Müller 1907; Duncker 1972). The air sacs are also important in thermoregulation. Birds dump heat through the air sac system by evaporation (Bernstein 1976; Dawson and Whittow 2000). Indeed, in the absence of significant evaporation through the skin, evaporative cooling in the air sac system is the only way for large subtropical birds to maintain stable body temperatures below high ambient temperatures (Schmidt-Nielsen et al. 1969). The complex architecture of the lung/air sac system allows the lungs to be excluded from airflow during thermoregulatory panting to avoid respiratory alkalosis (Schmidt-Nielsen et al. 1969; Fowler 1991; Powell 2000).

*Air Sacs and Sauropod Physiology.*—If sauropods had lung/air sac systems similar to those of extant birds, we might expect to see some evidence that their metabolic rates were elevated above the basal reptilian condition. Sauropods have traditionally been viewed as “gigantotherms,” whose sheer size made elevated metabolic rates unnecessary or impossible (Dodson 1990; Spotila et al. 1991). However, recent discoveries suggest that it is time to rethink sauropod metabolism.

Studies of the bone histology of sauropods indicate that they reached sexual maturity in 8–12 years and attained full adult size in about two decades (Rimblot-Baly et al. 1995; Curry 1999; Sander 2000). These sustained rapid growth rates approach those of extant eutherian mammals (Erickson et al. 2001). If rapid growth rates reflect the basal metabolic rates of sauropods, then these giant dinosaurs can no longer be regarded as “good reptiles.” Generally favorable Mesozoic climates are an insufficient causal explanation, because extant tropical and subtropical ectotherms such as crocodiles have much lower growth rates than

those inferred for sauropods (Bossert et al. 2000; Erickson et al. 2001; Padian et al. 2001). Rather, the sustained rapid growth of sauropods suggests that they had elevated or even endothermic metabolic rates.

The suggestion that sauropods were tachymetabolic is not new (e.g., Bakker 1972). However, it has previously been discounted on the grounds that sauropod respiratory systems were inadequate to support endothermy (Hengst and Rigby 1994; Gale 1997, 1998), and that the endogenous heat loads associated with endothermy were incompatible with sauropod gigantism (Spotila et al. 1991). I discuss each of these points in turn.

The assertion that the respiratory systems of sauropods were inadequate to sustain endothermy is based on the assumption that their lungs were essentially identical to those of modern crocodylians (Hengst and Rigby 1994). No morphological evidence has been cited to support this assumption. On the contrary, the morphology and evolution of vertebral pneumaticity in sauropods suggests that their respiratory systems were more similar to those of birds than to those of crocodiles. Diaphragmatically driven respiratory systems have been postulated for some theropods (Ruben et al. 1999), but this hypothesis lacks empirical support and is contradicted by several lines of evidence (Claessens et al. 1998; Christiansen and Bonde 2000; Hutchinson 2001; Padian 2001).

It has also been argued that the respiratory dead spaces associated with the long necks of sauropods would have prohibited elevated metabolic rates (Gale 1997, 1998). However, the studies in question explicitly assumed that the respiratory systems of sauropods could be approximated by scaling up monitor lizards to dinosaurian proportions. Using the monitor lizard model, Gale concluded that sauropods either had functional pharyngeal slits at the base of their necks (1997) or used 50–100% of their metabolic energy for lung ventilation (1998), neither of which seems possible, let alone likely. The air sac systems of sauropods may not have been as complex as those of extant birds, but the preponderance of osteological evidence suggests that sauropods were more similar to birds than to monitors in their

respiratory anatomy. In birds, the air sacs are sufficient to overcome respiratory dead space (Müller 1907; Duncker 1972). The presence of similar air sacs in sauropods, based on osteological evidence for PSP, provides a far more plausible explanation as to how they were able to breathe through their anomalously long necks.

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

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

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

dothermic or at least intermediate in metabolic strategy. Elevated metabolic rates in sauropods were probably facilitated by pulmonary air sac systems. Rather than being an aberrant feature solely related to mass reduction, the postcranial pneumaticity of sauropods may be one key to understanding their physiology and paleobiology.

### 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 PSP in sauropods. The evolution of extensively subdivided internal structures in the vertebrae of mamenchisaurids, diplodocids, and titanosauriforms is correlated with increasing body size and neck length and suggests that these complex morphologies were mechanically more efficient than the fossae and simple camerae of less derived taxa.

The evolutionary pattern of vertebral pneumatization in sauropods parallels the ontogenetic development of vertebral pneumaticity in extant birds. Although it may have been less complex and extensive than that of birds, a pulmonary air sac system was probably present in sauropods. The irregular distribution of PSP within Archosauria suggests that the evolution of air sacs within the group was complex and may have involved substantial parallelism. It is likely that the air sac systems of ornithomimids evolved primarily for lung ventilation, and this adaptation may have been one of the keys to the success of the group. The potential benefits of a pulmonary air sac system include mass reduction, thermoregulation, and most importantly, efficient lung ventilation.

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