

Evidence for Bird-Like Air Sacs in Saurischian Dinosaurs

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ABSTRACT Among extant tetrapods, pneumatic postcranial bones are only present in birds, and they are osteological correlates of the diverticular lungs and pulmonary air sacs. The presence of postcranial pneumaticity in sauropod and theropod dinosaurs suggests that some form of air sac system was also present in the dinosaurian ancestors of birds. In particular, anatomical and evolutionary patterns of pneumatization in nonavian saurischian dinosaurs are diagnostic for specific air sacs, including the cervical, clavicular, and abdominal air sacs. Pneumatic hiatuses are gaps in the pneumatization of the vertebral column and indicate pneumatization from multiple sources. A pneumatic hiatus in *Haplocanthosaurus* provides additional support for the presence of abdominal air sacs in sauropods. The origins of postcranial pneumaticity in archosaurs are enigmatic because the earliest putative traces of pneumaticity are difficult to distinguish from skeletal imprints of other soft tissues. Nevertheless, several lines of evidence suggest that air sac-driven lung ventilation was primitive for Saurischia. *J. Exp. Zool.* 311A, 2009. © 2009 Wiley-Liss, Inc.

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Among extant tetrapods, air-filled bones posterior to the skull are present only in birds. Postcranial skeletal pneumaticity (PSP) is also present in most saurischian dinosaurs and pterosaurs and was recognized in these animals from very early discoveries (Owen, 1857; Seeley, 1870). After a century of infrequent study (Janensch, '47), PSP in fossil archosaurs has received increasing attention in the past decade and a half (Britt, '97; Britt et al., '98; Christiansen and Bonde, 2000; Wedel et al., 2000; Bonde and Christiansen, 2003; Wedel, 2003a,b, 2005, 2006, 2007; O'Connor and Claessens, 2005; O'Connor, 2006; Schwarz and Fritsch, 2006; Schwarz et al., 2007; Sereno et al., 2008).

Pneumaticity in saurischian dinosaurs is particularly interesting in light of the evolutionary history and fate of the group. One lineage of saurischians, sauropodomorphs, gave rise to the largest terrestrial animals of all time. The other lineage, theropods, produced such well-known carnivores as *Velociraptor* and *Tyrannosaurus* during the Mesozoic Era, and today is represented by 10,000 or more species of birds. Postcranial pneumaticity may have facilitated the evolution of

unprecedented body sizes in saurischians by lightening the postcranial skeleton. It also serves as the osteological footprint of the respiratory system. If nonavian saurischians had lungs and air sacs like those of birds, they might have enjoyed some of the same physiological advantages as birds.

My goals in this article are to present new evidence for bird-like air sacs in dinosaurs, especially sauropods, and to discuss the origin of the avian lung-air sac system in a comparative framework.

CT protocols follow Wedel et al. (2000).

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Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; BYU, Earth Sciences Museum, Brigham Young University, Provo, USA; CCG, Chengdu College of Geology, Chengdu, China; CM, Carnegie Museum of Natural History, Pittsburgh, USA; FMNH, Field Museum of Natural History, Chicago, USA; HM, Humboldt Museum für Naturkunde, Berlin, Germany; MAL, Malawi Department of Antiquities Collection, Lilongwe and Nguludi, Malawi; OMNH, Oklahoma Museum of Natural History, Norman, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA.

AVIAN RESPIRATION AND POSTCRANIAL PNEUMATICITY

Birds are unique among extant animals in having a respiratory system that uses flow-through ventilation with air as the respiratory medium. The lungs of birds consist of minute, parallel tubes called parabronchi that are surrounded by dense networks of even smaller passages called air capillaries (Duncker, '71). Air is forced through the parabronchi on both inspiration and expiration by air sacs, which are attached to the lungs both anteriorly and posteriorly. The lung may be divided into a paleopulmo, which is present in all birds, and in which airflow is unidirectional, and a neopulmo with bidirectional airflow, which is variably developed among avian clades and absent in some (e.g., *Dromaius*, Spheniscidae) (Duncker, '71). Blood flow in the vascular capillaries of the lungs is at right angles to the direction of airflow in the parabronchi (Scheid, '79). This combination of flow-through ventilation (uni- and bidirectional) and cross-current exchange allows birds to extract up to 160% more oxygen from the air than mammals can (i.e., up to 260% of mammalian levels; Brown et al., '97).

The lungs and air sacs of birds also give rise to a network of blind, air-filled tubes of epithelium known as pneumatic diverticula. These diverticula may be present throughout the body, among the viscera, between muscles, and under the skin (King, '66; Duncker, '71). Some diverticula invade the bones of the postcranial skeleton. The marrow of these bones is resorbed and replaced with air spaces, the dense trabeculae are reorganized into an interconnected network of larger air cells, and the walls of the bones typically become thinner as the inner layers of bone are resorbed (Bremer,

'40a,b). These changes reduce the density of the pneumatic bones, which in birds are typically only half as dense as apneumatic bones (see Appendix). Pneumatization of the postcranial skeleton is an epiphenomenon of the formation of lung and air sac diverticula. Gas exchange outside of the lungs accounts for less than 5% of the total respiratory gas exchange, and takes place mostly in the posterior air sacs (Magnussen et al., '76). These data suggest that essentially no respiratory gas exchange takes place in the pneumatic bones.

In extant birds, the cervical and anterior dorsal vertebrae are pneumatized by diverticula of cervical air sacs; the sternum, pectoral girdle, and humeri are pneumatized by diverticula of the clavicular air sacs; dorsal vertebrae and ribs adjacent to the lungs are pneumatized by diverticula of the lungs; sternal ribs are pneumatized by diverticula of the anterior thoracic air sacs; and posterior dorsal, synsacral, and caudal vertebrae, femora, and pelvic girdle elements are pneumatized by diverticula of abdominal air sacs (Duncker, '71; O'Connor, 2006). Distal limb elements are pneumatized by subcutaneous diverticula (O'Connor, 2006). Not all elements are pneumatic in all taxa, and in some birds PSP is entirely absent (e.g., *Apteryx*, *Gavia*; Owen, 1841; Gier, '52).

The relationships among the different parts of the pulmonary system and their respective skeletal "domains" are invariant in all birds that have been studied to date. Diverticula of cervical air sacs never pneumatize elements posterior to the middle of the dorsal series, diverticula of abdominal air sacs never penetrate anterior to the middle of the dorsal series, and cervical and synsacral vertebrae are never pneumatized by diverticula of the lungs (O'Connor and Claessens, 2005; O'Connor, 2006; contra Sereno et al., 2008). The invariant relationships among components of the respiratory system and the regions of the skeleton that they pneumatize form the basis for inferences about the pulmonary anatomy of extinct taxa.

Is postcranial pneumaticity informative?

Farmer (2006, p 91–92) argued that PSP does not provide information about the structure of the respiratory system:

“Without integrating functional data into the study, the most that can be inferred from postcranial pneumaticity in extinct animals is that, as pointed out by Owen (1857), the pneumatized

bones received parts of the lung in the living animal... Because pneumaticity has no known functional role in ventilation or thermoregulation or metabolic rates, its usefulness as a hard-part correlate for lung structure and metabolism is, unfortunately, questionable.”

Inferences based on the *presence* of PSP and inferences based on the *distribution* of PSP must be distinguished. If all that is known about a postcranial element is that it is pneumatic, then Farmer is correct in stating that the most that can be concluded is that it was connected to the respiratory system. (The thermoregulatory function of pneumaticity discussed by Seeley (1870) has been demonstrated for cranial pneumaticity (Warncke and Stork, '77) but has not been experimentally tested for PSP (Witmer, '97).) However, the inference of cervical and abdominal air sacs in nonavian dinosaurs does not depend simply on the existence of PSP. Rather, these inferences are based on patterns of PSP that are diagnostic for specific air sacs. Similarly, the paleobiological implications of PSP are not based on its mere presence, but rather on the probable capabilities of the air sac system, of which PSP is an indicator.

These inferences are asymmetric; the presence of PSP in a fossil taxon shows that diverticula of lungs or air sacs were present, but the absence of PSP does not mean that air sacs were absent. Similarly, pneumatization of the dorsal vertebrae shows that the lungs were attached (O'Connor 2006), but dorsally attached lungs can be present without pneumatizing the vertebral column (Perry, 2001).

POSTCRANIAL PNEUMATICITY AND THE AIR SACS OF NONAVIAN DINOSAURS

Contributions of this study in the context of previous work

The study of soft tissues in fossil taxa depends on the ability to recognize osteological correlates of those soft tissues, and to infer likely ancestral states using phylogenetic bracketing. This mode of phylogenetic inference was developed by Bryant and Russell ('92) and Witmer ('95, '97).

The most important works to date on PSP in nonavian dinosaurs and birds are those of O'Connor and Claessens (2005) and O'Connor (2006). The major contributions of these studies have been (1) to establish the relationships among pulmonary components and regions of the skeleton in birds, (2) to show that patterns of PSP

present in nonavian theropods enable the inference of the presence and relative positions of the lungs, cervical air sacs, and abdominal air sacs in these animals, and (3) to show that most nonavian theropods had all of the pulmonary components necessary for flow-through lung ventilation.

In this article, I build on the results of O'Connor and Claessens (2005) and O'Connor (2006). In particular, this study focuses on the evidence for air sacs in sauropodomorph dinosaurs. Sauropodomorpha is the sister group to Theropoda within Saurischia, and sauropodomorphs are the only other clade of dinosaurs with extensive PSP (although PSP is also present and extensive in pterosaurs, and absent in most basal sauropodomorphs). Documenting the origin and evolution of PSP in sauropodomorphs provides new information that helps to phylogenetically constrain inferences about the evolution of PSP and the presence of pulmonary air sacs in Saurischia (Fig. 1).

Some authors have posited the presence of an air sac system in sauropodomorphs based on physiological modeling (Daniels and Pratt, '92; Paladino et al., '97; Perry and Reuter, '99). Although such models can explore the utility of air sac breathing in dinosaurs, the question of whether air sacs were actually present must be decided on anatomical grounds.

Evidence for cervical air sacs

The cervical vertebrae of almost all sauropods and theropods have invasive pneumatic features (Britt, '97; Wedel et al., 2000; Wedel, 2003a,b; O'Connor and Claessens, 2005; O'Connor, 2006; Schwarz and Fritsch, 2006; Schwarz et al., 2007). Furthermore, putative PSP in basal sauropodomorphs and theropods is confined to cervical vertebrae that are not adjacent to the lungs, so the pneumatic diverticula that pneumatized the neck must have originated from another source. The only hypothesis that is consistent with the available evidence is that the cervical vertebrae of sauropodomorphs and theropods were pneumatized by diverticula of cervical air sacs (Wedel, 2006).

Evidence for clavicular air sacs

In extant birds, diverticula of the clavicular air sac pneumatize the furcula, sternum, pectoral girdle elements, and humerus (Duncker, '71; O'Connor, 2006). Pneumatization of any of these elements in a nonavian dinosaur suggests that a clavicular air sac was present. Pneumatic

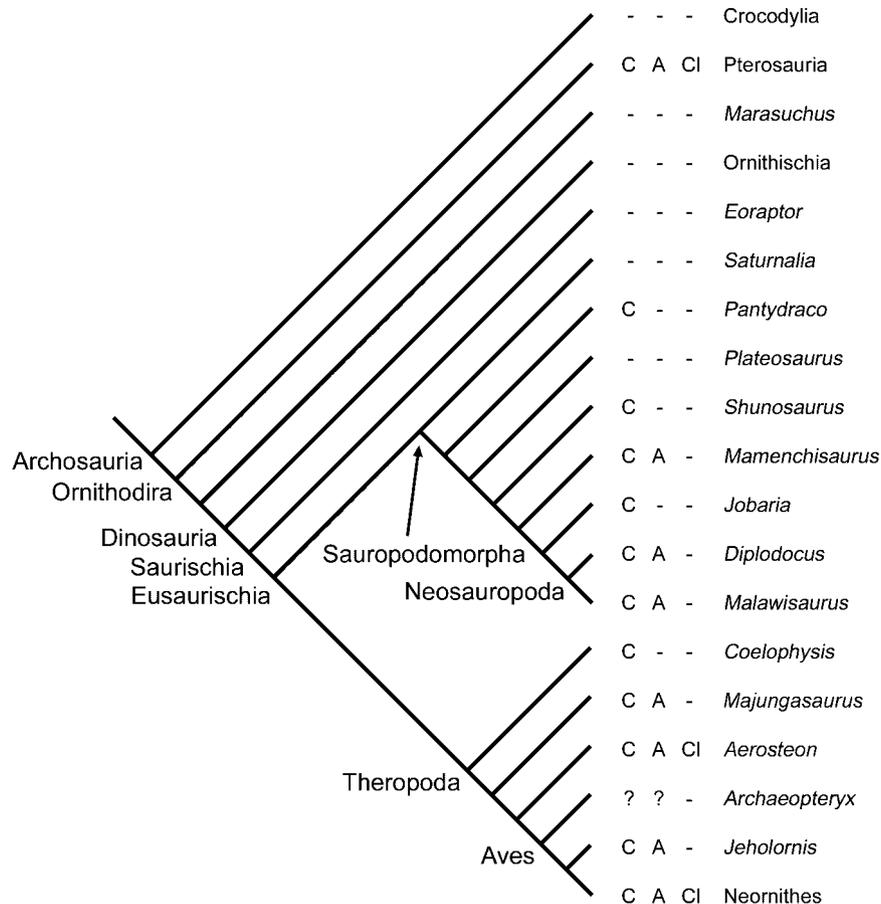


Fig. 1. Evidence for air sacs in fossil archosaurs. Letters next to each taxon indicate that they have patterns of PSP that are diagnostic for certain air sacs: C, cervical air sacs; A, abdominal air sacs; Cl, clavicular air sacs. See text for diagnostic criteria. In both sauropodomorphs and theropods, cervical air sacs pneumatized the skeleton before abdominal air sacs. Morphological evidence for PSP in *Archaeopteryx* is equivocal (O'Connor, 2006). A naïve reading of the fossil record would suggest that different air sacs evolved independently several times—for example, independent origins of abdominal air sacs in *Mamenchisaurus* and Neosauropoda. However, it is more parsimonious to infer that cervical and abdominal air sacs, at least, were present in all members of Eusaurischia, and simply failed to pneumatize the postcranial skeleton in some taxa (e.g., most basal sauropodomorphs). It is possible that an air sac system is primitive for Ornithodira, but the total absence of PSP in Ornithischia, a diverse and long-lived clade, is problematic (see Wedel, 2007). Phylogeny based on Gauthier ('86), Wilson (2002), Zhou and Zhang (2002), Upchurch et al. (2004, 2007), and Yates (2007).

furculae are present in the dromaeosaur *Buitreraptor* (Makovicky et al., 2005) and in the basal tetanuran *Aerosteon* (Serenó et al., 2008). This suggests that either the clavicular air sac evolved at or before the diversification of tetanuran theropods, or that several clades evolved clavicular air sacs in parallel.

A broken humerus of the basal tyrannosauroid *Eotyrannus* shows several large, irregular chambers. Although the form of the chambers is reminiscent of pneumatic internal structure, the proximal part of the humerus is crushed and it is not clear if any pneumatic foramina are present (Hutt et al., 2001). Hollow appendicular elements,

presumably filled with marrow in life, are ubiquitous in theropods (Gauthier, '86; Colbert, '89), so it is not surprising that the humerus of *Eotyrannus* is hollow. The question is, are the chambers pneumatic or not? From the evidence in hand, both hypotheses are viable. If *Eotyrannus* had a pneumatic humerus, it was the only known nonavian dinosaur that did because pneumatic humeri have not been reported in taxa that are closer to the origin of birds (e.g., *Caudipteryx*, *Sinornithosaurus*: Ji et al., '98; Xu et al., '99). Those facts weigh against the pneumatic interpretation for *Eotyrannus*, but it cannot be ruled out on the basis of available evidence. New and

better specimens will be required to resolve this problem.

No other pneumatic furculae, sterna, pectoral girdle elements, or humeri have been reported in nonavian dinosaurs.

Evidence for abdominal air sacs I. Pneumatization of the posterior vertebral column

Wedel et al. (2000) hypothesized that pneumatization of postdorsal vertebrae in nonavian dinosaurs implied the presence of abdominal air sacs. The posterior dorsal vertebrae and synsacrum of birds are pneumatized by diverticula of the abdominal air sacs (Duncker, '71). The posterior dorsal, sacral, and anterior caudal vertebrae are pneumatic in many sauropods (Table 1) and nonavian theropods. Therefore, it seems likely that these taxa had abdominal air sacs. All of those statements are still accurate, but further work has clarified several important points. (For the sake of simplicity, the term “posterior compartment” is used herein to refer to the portions of the vertebral column that are pneumatized by diverticula of the abdominal air sacs.)

The crucial inference, that posterior compartment PSP implies the presence of abdominal air

sacs, has been obscured by inconsistency in published accounts. Diverticula of the cervical air sacs, lungs, and abdominal air sacs have been described as anastomosing to produce a continuous network of diverticula that spans most or all of the vertebral column (Müller, '08, p 377; Cover, '53, p 241). In some older accounts (e.g., Cover, '53), the entire network of vertebral diverticula is called an extension of the cervical diverticulum, and so some authors have inferred that diverticula of the cervical air sacs alone can pneumatize the entire vertebral column (King, '75; Britt et al., '98; Sereno et al., 2008). If that were true, then it would not be possible to infer the presence of abdominal air sacs based on postdorsal PSP (Britt et al., '98; Sereno et al., 2008).

The uncertainties and contrary claims listed above have been dispelled or falsified by O'Connor and Claessens (2005) and O'Connor (2006). Diverticula of the cervical vertebrae never pass farther posteriorly than the middle dorsal vertebrae, diverticula of the lungs pneumatize only the dorsal vertebrae and vertebral ribs immediately adjacent to the lungs, and the posterior compartment is only pneumatized by diverticula of abdominal air sacs. These relationships were found to be invariant in more than 200 individual birds representing 19 extant higher clades, and they support the hypothesis that posterior compartment PSP in sauropods and theropods indicates the presence of abdominal air sacs. No other hypothesis is consistent with known patterns of pneumatization in extant tetrapods.

Examples

In theropods, pneumatization of the posterior compartment is present in at least some taxa in Abelisauroidea, Spinosauroidea, Allosauroidea, Tyrannosauroidea, Oviraptorosauria, and Dromaeosauridae (O'Connor and Claessens, 2005).

Among sauropods, posterior compartment pneumaticity was recognized very early. Marsh (1878, 1879, 1881, 1884) described and figured cavities in the sacral vertebrae of many sauropods, and he considered hollow sacral vertebrae a diagnostic character of Sauropoda. Pneumatic caudal vertebrae were first illustrated by Marsh (1890) for *Barosaurus*. Osborn (1899), Hatcher ('01), and Gilmore ('32) also illustrated pneumatic caudal vertebrae in *Diplodocus*. Although Marsh described the sacral vertebrae of *Morosaurus* (*Camarasaurus*) as hollow, the evidence for sacral pneumaticity in *Camarasaurus* is equivocal

TABLE 1. Vertebral pneumaticity in the posterior compartment in sauropods

Taxon	PD	S	AC	MC	Source or specimen
<i>Omeisaurus tianfuensis</i>	X	-	-	-	He et al. ('88)
<i>Mamenchisaurus youngi</i>	X	-	-	-	Pi et al. ('96)
<i>M. hochuanensis</i>	X	-	-	-	CCG V 20401
<i>Apatosaurus louisae</i>	X	X	-	-	CM 3018
<i>Apatosaurus</i> sp.	na	na	X	na	OMNH 1436
<i>Diplodocus carnegii</i>	X	X	X	X	CM 84
<i>Barosaurus lentus</i>	X	X	X	X	AMNH 6341
<i>Camarasaurus supremus</i>	X	-	-	-	AMNH 5761
<i>Camarasaurus lewisi</i>	X	-	-	-	BYU 9047
<i>Haplocanthosaurus priscus</i>	X	X	X	-	CM 572, 879
<i>Brachiosaurus altithorax</i>	X	X	-	na	FMNH P 25701
<i>Brachiosaurus brancai</i>	X	X	X	X	HM Fund no
<i>Euhelopus zdanskyi</i>	X	X	na	na	Wiman ('29)
<i>Malawisaurus dixeyi</i>	X	X	X	-	MAL holotype series

An X indicates that pneumaticity is present, a dash indicates that it is absent, and na (not applicable) indicates that the elements in question are not preserved. Abbreviations: PD, posterior dorsal vertebrae; S, sacral vertebrae; AC, anterior caudal vertebrae; MC, middle caudal

(McIntosh et al., '96). In *C. lewisi* (BYU 9047), the sacral vertebrae have large lateral fossae but no foramina, and the internal structure of the vertebrae is composed of apneumatic spongiosa (personal observation). However, unequivocally pneumatic sacral vertebrae are present in *Brachiosaurus altithorax* (Riggs, '04) and *B. brancai* (Janensch, '50). Pneumatic foramina are present in the caudal vertebrae of *B. brancai* HM "Fund no" and will be described elsewhere. In *Malawisaurus dixeyi*, the neural spine of the first caudal vertebra is pneumatic but the centrum is not (Fig. 2). Posterior compartment pneumaticity is, therefore, present in both lineages of Neosauropoda (Diplodocoidea and Macronaria) and in some nonneosauro-pods, such as *Mamenchisaurus youngi* (Pi et al., '96).

Evidence for abdominal air sacs II. Pneumatization of the pelvic girdle and hindlimb

Pneumatization of the pelvic girdle and hindlimb in birds is accomplished by diverticula of the abdominal air sacs (Müller, '07; Cover, '53; King, '66, '75; Duncker, '71; Hogg, '84a,b; Bezuidenhout et al., '99; O'Connor and Claessens, 2005; O'Connor, 2006). Pneumatization of the pelvic girdle and hindlimb elements in nonavian dinosaurs would be further evidence for the presence of abdominal air sacs.

Examples

Among sauropods, large chambers have been reported in the ilia of the diplodocoid *Amazon-saurus* (Carvalho et al., 2003), the titanosaur *Sonidosaurus* (Xu et al., 2006), and the saltasaurine titanosaurs *Saltasaurus* and *Neuquensaurus* (Powell, '92; Sanz et al., '99). From published descriptions, these internal chambers appear to have the same morphology as those in the pneumatic vertebrae of sauropods, and some authors (e.g., Carvalho et al., 2003; Xu et al., 2006) have interpreted the chambers as pneumatic. However, the case would be stronger if the pathways by which the air got into the bones were known. Pneumatization cannot take place and pneumatic chambers cannot persist without a patent (open) foramen (Ojala, '57; Witmer, '97). The case for appendicular pneumaticity in sauropods would be strengthened by the discovery of pneumatic foramina on the outside of the ilium, or a series of chambers connecting the ilium to the sacral vertebrae.

Keeping that caveat in mind, there is no strong reason to doubt that the chambers reported in the ilia of the sauropods listed above are pneumatic. Compelling evidence of sacral pneumaticity in both Diplodocoidea and Macronaria (the sister clade to Diplodocoidea, and a clade that contains, among other taxa, the Titanosauria) already exists. Iliac chambers are so far only found in clades in which sacral pneumatization is known, so the phylogenetic distribution of iliac chambers is consistent with the hypothesis that they are pneumatic. At the very least, broken specimens (e.g., *Camarasaurus* BYU 9047, Jensen, '88) demonstrate that iliac chambers are absent in most sauropods, so the presence of iliac chambers is a derived character that was independently acquired in Diplodocoidea and Macronaria in taxa for which sacral pneumaticity was also present.

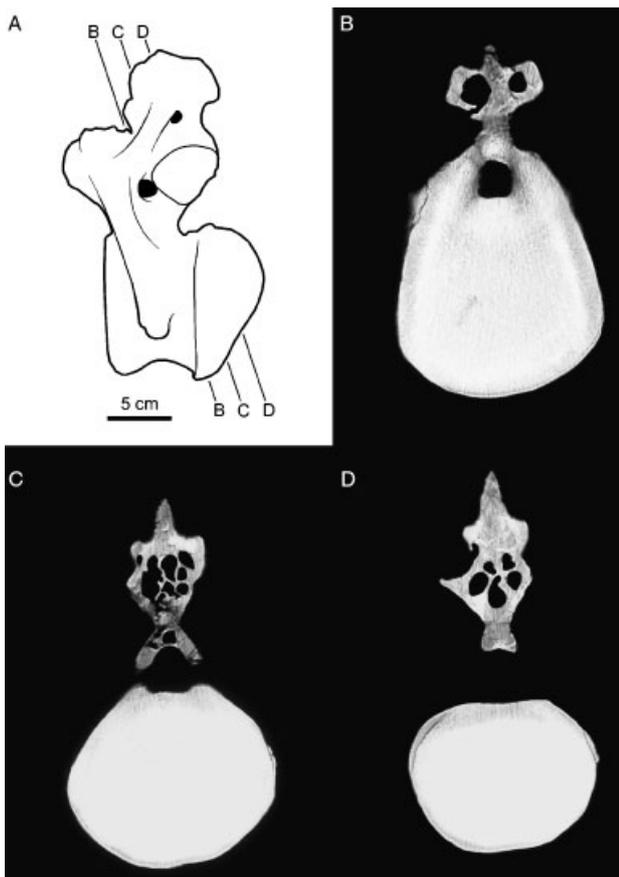


Fig. 2. MAL-200, an anterior caudal vertebra of *Malawisaurus dixeyi*. (A) The vertebra in left lateral view showing the position of CT slices. (B–D) CT cross sections. Matrix was erased from the internal chambers using Photoshop 5.5. Pneumatic foramina on the neural arch and spine are connected to a network of internal chambers, but the centrum is apneumatic.

In theropods, the ilium of the basal tetanuran *Aerosteon* is highly pneumatic, with numerous foramina that communicate with an extensive complex of internal chambers (Sereno et al., 2008). A large foramen is present in the proximal femur of the oviraptorosaur *Shixinggia* (Lü and Zhang, 2005). In its size and location, this foramen is similar to pneumatic foramina in the femora of extant birds. It would be helpful to know what connections, if any, this foramen shares with spaces inside the femur. If this foramen is pneumatic, then femoral pneumaticity evolved independently within oviraptorosaurs and birds (although femoral diverticula may have been present in the common ancestor of both clades). Note that Maryanska et al. (2002) recovered oviraptorosaurs as basal birds, but this has not been supported by subsequent phylogenetic analyses using larger datasets (e.g., Hwang et al., 2004; Senter, 2007).

Evidence for abdominal air sacs III. Recapitulatory development of PSP in extant birds

The cervical and anterior dorsal vertebrae are the first parts of the axial skeleton to be pneumatized during the ontogeny of birds, and they are pneumatized by diverticula of the cervical air sacs (Fig. 3; Cover, '53; Hogg, '84b). Later in ontogeny, diverticula of the abdominal air sacs pneumatize the posterior dorsal vertebrae and synsacrum. The sequence of pneumatization of the vertebral column in avian ontogeny closely parallels the evolutionary sequence of vertebral pneumatization in both sauropodomorphs (Wedel, 2007, Text-Fig. 2) and theropods. PSP is present

only in the cervical series in basal members of both saurischian lineages. Dorsal, sacral, and caudal vertebrae become pneumatized in successively more derived taxa (Wedel, 2007). Thus, the spread of pneumaticity posteriorly along the vertebral column in the ontogeny of birds recapitulates the evolution of pneumaticity in theropods and sauropodomorphs (Wedel, 2003a, 2005).

The posterior progression of vertebral pneumatization in birds is not caused by diverticula developing from a single, anteriorly located source (contra Ruben et al., 2003; Chinsamy and Hillenius, 2004; Hillenius and Ruben, 2004; Sereno et al., 2008). Rather, diverticula of different sources (cervical air sacs, lungs, abdominal air sacs) pneumatize their respective skeletal domains at different times. It is not clear why vertebral pneumatization in birds proceeds front-to-back, as opposed to back-to-front or in both directions starting from the middle, or why this pattern is so highly conserved. Nevertheless, the identical sequence of pneumatization in avian ontogeny and saurischian phylogeny supports the hypothesis that extinct saurischian dinosaurs had bird-like respiratory systems.

Evidence for abdominal air sacs IV. Pneumatic hiatuses

Definition and occurrence in birds

Diverticula of cervical air sacs, lungs, and abdominal air sacs invade the vertebral column at different points. Diverticula of the cervical air sacs first contact the posterior cervical and anterior dorsal vertebrae; diverticula of the lungs may invade the vertebrae adjacent to the lungs;

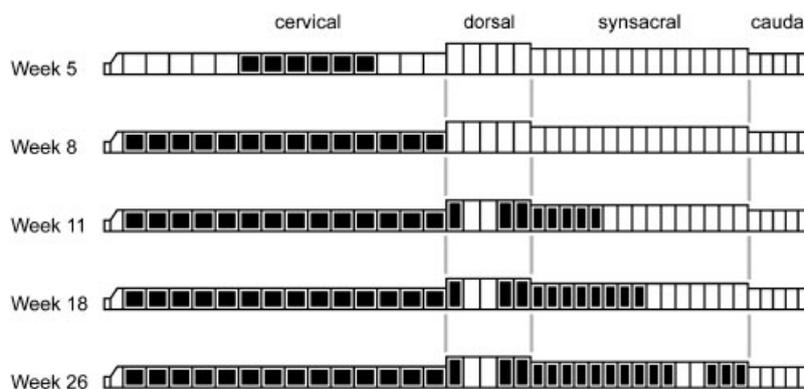


Fig. 3. Pneumatization of the vertebral column in the chicken, *Gallus gallus*. Pneumatic vertebrae are shown in black. Data are from Hogg ('84b); vertebrae are shown at earliest date of complete pneumatization. Some rare variations are not shown; for example, the second and third dorsal vertebrae were pneumatized in one individual (from a total of 44) examined by Hogg ('84b). The spread of PSP along the vertebral column in the chicken parallels the evolution of PSP in nonavian theropods and sauropods; compare to Wedel (2007, Text-Fig. 2).

and diverticula of the abdominal air sacs may invade the synsacrum at several points (King, '57; Duncker, '71; O'Connor, 2006). Paravertebral diverticula derived from these sources may grow along the column until they contact each other and anastomose. The growth and anastomosis of the paravertebral diverticula may produce an uninterrupted pattern of vertebral pneumatization, so that every vertebra from the second or third cervical back to the free caudals is pneumatic.

However, in some cases the vertebral column is not continuously pneumatized. One or more pneumatic hiatuses may be produced as a result. A pneumatic hiatus is an apneumatic portion of the vertebral column that is bordered by pneumatic vertebrae both anteriorly and posteriorly (Fig. 4; Wedel, 2003a). There are at least three kinds of pneumatic hiatus, which I define here based on their positions. A cervicodorsal hiatus (CvD) is a gap in pneumatization between diverticula of the cervical air sacs and lungs, and it appears in the most posterior cervical vertebrae or the most anterior dorsal vertebrae. A caudal dorsal hiatus (CaD) is a gap in pneumatization between diverticula of the cervical air sacs or lungs and diverticula of the abdominal air sacs. It

may occur in the middle or posterior dorsal vertebrae (Fig. 5). Finally, a caudosacral hiatus (CaS) is a gap in pneumatization between different diverticula of the abdominal air sac, and it may occur in the (syn)sacrum or caudal vertebrae.

King ('57) and Hogg ('84a) described the distribution of PSP in chickens, *Gallus gallus*. Although neither author used the term "pneumatic hiatus," both studies documented the presence of all three types of pneumatic hiatus (Table 2). In both studies, the majority of the birds examined had caudal dorsal hiatuses; cervicodorsal and caudosacral hiatuses were rare. King ('57) found no cervicodorsal hiatuses, but his study had a much smaller sample size (six birds) than Hogg's ('84a) study (51 birds). The two authors also found differences in the location of the hiatuses in different breeds. In his study of Rhode Island Reds, King ('57) found that the fourth dorsal vertebra was infrequently pneumatized and the fifth dorsal vertebra was never pneumatized. King and Kelly ('56) obtained similar results in a study of 50 chickens of unknown breed. In contrast, Hogg ('84a) found that, in Golden Comets, the fourth and fifth dorsal vertebrae were almost always pneumatized, and the second and third dorsal vertebrae were frequently apneumatic.

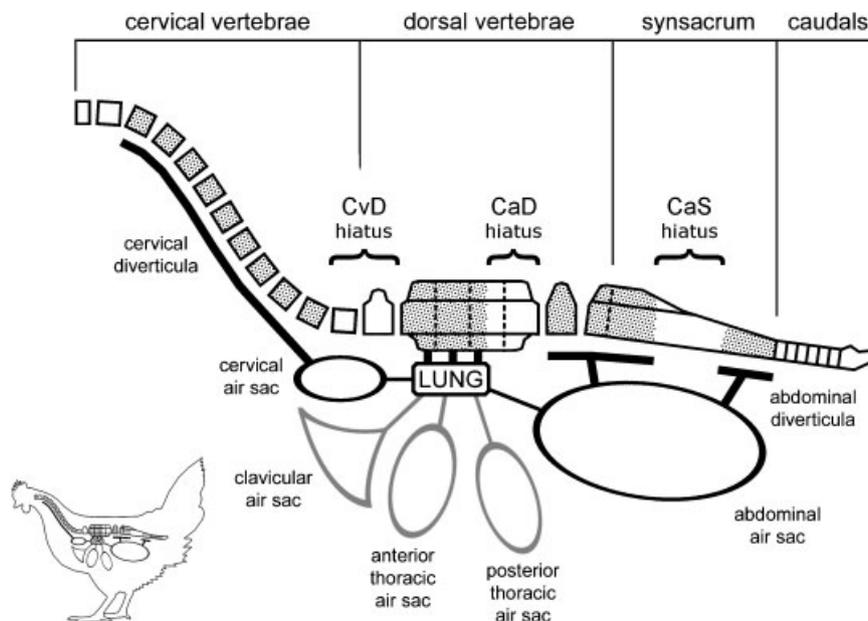


Fig. 4. Pneumatization of the vertebral column in the chicken, *Gallus gallus*. Pneumatic vertebrae are stippled. The vertebral column is pneumatized by diverticula of the cervical air sacs, lungs, and abdominal air sacs. A pneumatic hiatus is one or more apneumatic vertebrae that are bordered anteriorly and posteriorly by pneumatic vertebrae. These hiatuses are produced if the diverticula from the different parts of the respiratory system do not meet. Supporting data come from King ('57), King and Kelly ('56), Hogg ('84a,b), and from personal examination of museum specimens. Inspired by King ('57, Fig. 1). Abbreviations: CaS, caudosacral; CaD, caudal dorsal; CvD, cervicodorsal.

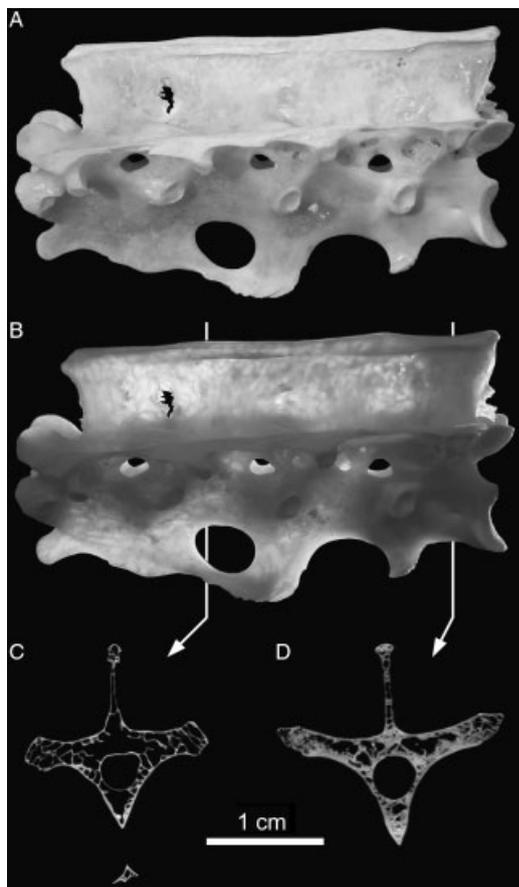


Fig. 5. A pneumatic hiatus in a chicken. The notarium of UCMMP 119225 is composed of four vertebrae. The three anterior vertebrae are pneumatic, but the fourth is not. (A) The specimen in left lateral view under normal lighting. (B) The specimen lit from behind to show the pneumatic (translucent) and apneumatic (opaque) regions. (C) A micro CT slice through a pneumatic vertebra. (D) A micro CT slice through the apneumatic vertebra. Note the density of the trabeculae in D compared to C. The anterior synsacral vertebrae of this individual are pneumatic. The apneumatic vertebra is bordered anteriorly and posteriorly by pneumatic vertebrae, and constitutes a caudal dorsal pneumatic hiatus.

Each type of pneumatic hiatus is informative. The most anterior dorsal vertebrae may be pneumatized by diverticula of cervical air sacs or by diverticula of the lungs. Based on osteological evidence alone, it is impossible to determine whether diverticula of the cervical air sacs or lungs were involved if the posterior cervical and anterior dorsal vertebrae are all pneumatic. However, if a cervicodorsal hiatus is present, then the anterior dorsal vertebrae posterior to the hiatus were most likely pneumatized by diverticula of the lung. Similarly, vertebrae posterior to a caudal dorsal or sacrocaudal hiatus were most likely pneumatized by diverticula of abdominal air sacs.

TABLE 2. Frequencies of pneumatic hiatuses in two breeds of chickens

	Pneumatic hiatuses		
	CvD	CaD	CaS
Rhode Island Red			
Males (1)	0/0%	1/100%	0/0%
Females (5)	0/0%	5/100%	2/40%
Total (6)	0/0%	6/100%	2/33%
Golden Comet			
Males (3)	1/33%	2/67%	0/0%
Females (48)	3/6%	34/71%	2/4%
Total (51)	4/8%	36/71%	2/4%

Data on Rhode Island Reds from King ('57); data on Golden Comets from Hogg ('84a). See text for descriptions of different types of hiatuses. Abbreviations: CaS, caudosacral; CaD, caudal dorsal; CvD, cervicodorsal.

If it is possible for a single diverticulum to span a pneumatic hiatus, then vertebrae on either side of a pneumatic hiatus would not have to be pneumatized by independent sources of diverticula, and pneumatic hiatuses would have little or no diagnostic value. I am not aware of any such cases, and it seems unlikely that such a developmental anomaly would occur bilaterally. Diverticula on the left and right side of the vertebral column are derived from contralateral lungs and air sacs, and they presumably develop independently. Nevertheless, the inferences drawn below can potentially be falsified if future studies show that it is possible for a single diverticulum to span a pneumatic hiatus.

Importance

If the development of pneumaticity in nonavian dinosaurs followed that of birds, then pneumatization of the cervical, dorsal, and sacral vertebrae in some sauropods and theropods shows that they had both cervical and abdominal air sacs—and, therefore, all of the components necessary for flow-through lung ventilation (O'Connor and Claessens, 2005). However, this inference only holds if the development of pneumaticity in nonavian dinosaurs followed that of birds. Although diverticula of the cervical air sacs or lungs never pneumatize the posterior compartment in extant birds, the possibility remains as a hypothesis. The inference that abdominal air sacs were present in sauropods and nonavian theropods is already robust (see above); it would be stronger still if pneumatic hiatuses occur in these groups because the vertebrae posterior to the

hiatus would have to have been pneumatized independently, by diverticula of abdominal air sacs (Wedel, 2003a). One such hiatus is present in the sauropod *Haplocanthosaurus*.

Example: *Haplocanthosaurus*

Haplocanthosaurus is a sauropod from the Upper Jurassic Morrison Formation of western North America (Hatcher, '03). In phylogenetic analyses it has been recovered as a eusauropod basal to Neosauropoda (Upchurch, '98; Rauhut et al., 2005), the most basal diplodocoid (Wilson, 2002, Fig. 13A), the most basal macronarian (Wilson and Sereno, '98), or a macronarian more derived than *Camarasaurus* (Upchurch et al., 2004).

The CM 879 specimen of *Haplocanthosaurus* has a mostly complete vertebral column. All of the preserved cervical and dorsal centra have prominent lateral cavities that penetrate to a median septum (Fig. 6). A CT scan of a dorsal vertebra of the CM 572 specimen of *Haplocanthosaurus* shows that the lateral fossae do not invade the condyle or the ventral half of the centrum and that they are only partially bounded by a distinct lip of bone. Fossae in the dorsal vertebrae of CM 879 have the

same morphology. In both specimens, the ventral margins of the lateral fossae are more clearly delimited than the dorsal margins, so that the fossae open dorsolaterally.

The sacrum of CM 879 is incomplete, and includes five coossified spines and the fourth and fifth sacral centra. The sacral neural spines have no distinct pneumatic fossae or foramina. The only well-developed laminae are the spinodiapophyseal laminae, which are present only in the first three spines (Fig. 7). In particular, the fossae present on the neural arch and spine of the first caudal vertebra (described below) are absent in the sacral neural spines.

The fourth sacral vertebra of CM 879 is asymmetrically pneumatized. The right side of the centrum bears a large, distinct fossa that extends upward underneath the facet for the sacral rib. This fossa is 78 mm long, 33 mm tall, and 27 mm deep. The fossa differs from the apneumatic fossae of extant crocodylians in being proportionally larger and deeper and in having a distinct margin. The dorsal margin is much more



Fig. 6. Pneumatization of the presacral vertebrae in *Haplocanthosaurus*. (A) X-ray image of a posterior cervical vertebra of CM 879 in right lateral view. (B) A CT slice through the same vertebra. (C) X-ray image of an anterior dorsal vertebra of CM 572 in left lateral view. (D) X-ray image of the same vertebra in anterior view. All of the preserved presacral vertebrae of both specimens have large, sharp-lipped fossae that penetrate to a narrow median septum.

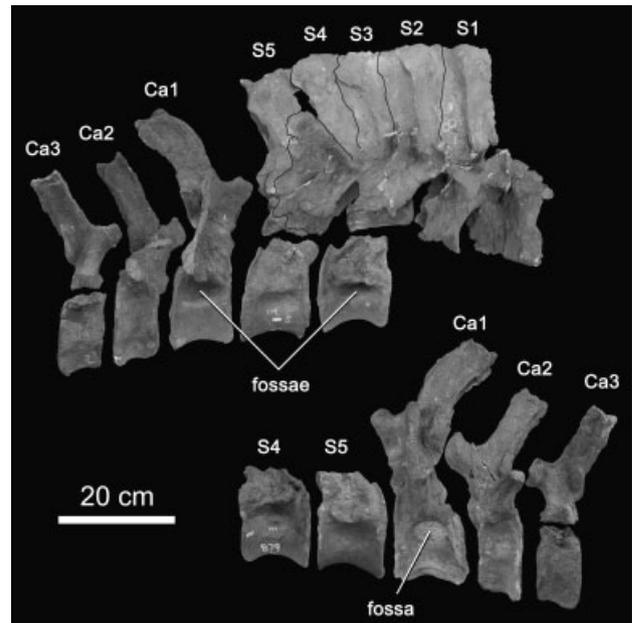


Fig. 7. A pneumatic hiatus in a sauropod dinosaur. The preserved portions of the sacrum (S1–S5) and anterior caudal vertebrae (Ca1–Ca3) of *Haplocanthosaurus* CM 879 are shown in right lateral (top) and left lateral (bottom) views. All of the preserved cervical and dorsal vertebrae have large, distinct fossae. Distinct fossae are also present on the right sides of the fourth sacral and first caudal vertebrae, and on the left side of the first caudal. The left side of the fourth sacral and both sides of the fifth sacral are waisted but lack distinct fossae (see text for discussion), and constitute a caudosacral pneumatic hiatus.

pronounced than the ventral, so in cross section the fossa is similar to the fossae of the dorsal vertebrae, only flipped upside down. The left side of the centrum is strongly waisted (i.e., narrower in the middle than at either end) but has no distinct fossa below the articular surface for the sacral rib.

On both sides of the centrum are smaller cavities above the sacral rib facets (Fig. 8). On each side, this space is bounded ventrally and anteriorly by the sacral rib facet, posteriorly by the rim of the cotyle, and dorsally by a bony lamina. Each space is also divided into anterodorsal and posterodorsal compartments by an accessory lamina. The anterodorsal compartments on both sides consist of shallow fossae only a few millimeters deep. The posterodorsal fossae are much deeper. On the left side, the posterodorsal fossa is conical and 32 mm deep. The fossa on the right side is similar in size and shape, but it still contains some matrix so its depth cannot be determined. Hatcher ('03, Figs. 15 and 20) illustrated both the lateral and dorsal fossae on the right side of the centrum.

The fifth sacral vertebra has no evidence of pneumaticity. The sides of the centrum are shallowly waisted, but there are no invasive fossae anywhere on the element. The facets for the sacral ribs are more dorsally extensive than in the fourth sacral and cover the area occupied by the dorsal fossae in the preceding vertebra. It is possible that

the large sacral rib facets simply left no room for the dorsal fossae to form. However, the sacral rib facets are no more ventrally extensive than those of the fourth sacral. In other words, there is room for lateral fossae on the sides of the centrum, but the fossae are not present.

The first caudal vertebra has deep, distinct fossae on both the centrum (Fig. 7) and the neural spine (Fig. 9). The lateral fossae of the centrum are similar in size and form to the fossa on the right side of the centrum of sacral vertebra four. The fossa on the right side of the centrum is 69 mm long, 41 mm tall, and 31 mm deep. Like the right-hand fossa of the fourth sacral, it extends upward under the attachment of the transverse process and the dorsal margin is more sharply delineated than the ventral. The fossa on the left side of the centrum is 54 mm long, 29 mm tall, and mostly filled with matrix, so its depth cannot be determined.

The neural spine fossae of the first caudal are all located just posterior to the prezygapophyses. The vertebra lacks a true intraprezygapophyseal lamina. Instead, a low rampart of bone connects the prezygapophyseal rami below and behind the prezygapophyses. A bilobate fossa is situated behind this bony rampart at the base of the prespinal ligament scar. The fossa is 17 mm long, 16 mm wide, and at least 17 mm deep. The fossa is too deep and too narrow to accept the postzygapophyses of the preceding vertebra; it is vertically oriented, unlike the pits left on the neural spines of many bird vertebrae by the interspinous ligaments; and it is smooth, unlike the rugose interspinous ligament scar just dorsal to it. These characteristics suggest that the fossa is not related to the interspinous ligaments or to the zygapophyseal articulations. Rather, the form of the fossa is similar to that of the dorsal fossae on the fourth

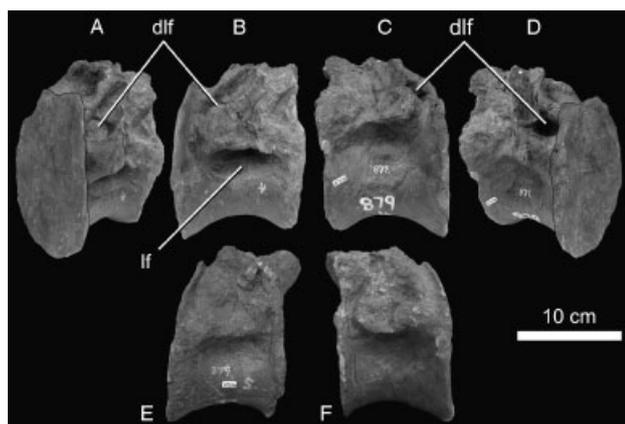


Fig. 8. The fourth and fifth sacral centra of *Haplocanthosaurus* CM 879. Above, the centrum of the fourth sacral vertebra in right posterolateral (A), right lateral (B), left lateral (C), and left posterolateral (D) views. Below, the centrum of the fifth sacral vertebra in right lateral (E) and left lateral (F) views. The centrum of S4 has dorsolateral fossae on both sides and a lateral fossa on the right side. The left side of S4 is waisted but lacks a lateral fossa. The centrum of S5 is waisted and lacks both lateral and dorsolateral fossae. Abbreviations: dlf, dorsolateral fossa; lf, lateral fossa.

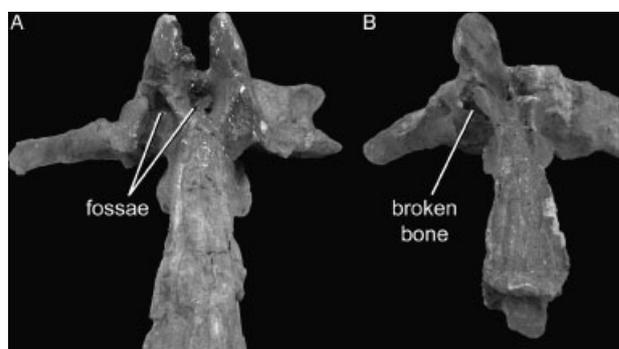


Fig. 9. Anterior caudal vertebrae of *Haplocanthosaurus* CM 879 in dorsal view. (A) The first caudal vertebra. (B) The second caudal vertebra.

sacral vertebra, and the location of the fossa behind the prezygapophyses is similar to the position of pneumatic fossae and foramina in the vertebrae of birds (Wedel, 2007, Text-Fig. 9).

In dorsal view, with anterior to the top, the prezygapophyseal laminae of the first caudal vertebra resemble the letter M. The middle legs of the M are formed by short spinoprezygapophyseal laminae that converge on the lower portion of the neural spine. The bilobate fossa described in the preceding paragraph sits just above the convergence of the middle legs. The lateral legs of the M are formed by posterolaterally directed laminae that connect the prezygapophyses to the transverse processes. On the right side of the vertebra, these laminae are poorly developed, and there is only a shallow depression between the right spinoprezygapophyseal lamina and the posterolateral lamina. On the left side, the laminae are much more pronounced and the same space is occupied by a prominent fossa at least 19 mm deep.

None of the fossae present in the first caudal vertebra are present in the second. The lateral faces of the centra are shallowly waisted but have no distinct fossae. Two small nutrient foramina are present on the right side of the centrum, both less than 2 mm in diameter. Most of the right prezygapophysis is missing. The remainder of the right prezygapophysis, the left prezygapophysis, and the neural spine form three sides of a rectangular trough. This trough does not extend posteriorly or ventrally past the margin of the right prezygapophysis. It is no larger or deeper than needed to accept the postzygapophyses of the first caudal vertebra.

In summary, the fourth sacral and first caudal vertebrae have a variety of large, distinct fossae that compare well to those found on the dorsal vertebrae, and to pneumatic features in the vertebrae of birds. These fossae are compelling evidence of pneumaticity. These fossae are absent in the centra and neural spines of the fifth sacral and second caudal vertebra. The apneumatic fifth sacral vertebra is bordered anteriorly and posteriorly by pneumatic vertebrae, and constitutes a caudosacral pneumatic hiatus. The first caudal vertebra was, therefore, most likely pneumatized by diverticula of abdominal air sacs (Fig. 10).

DISCUSSION

Shared developmental pathways and the origin(s) of air sacs and PSP

Until now, the hypothesis that nonavian saurischian dinosaurs had cervical and abdominal air sacs has been supported by the presence of pneumaticity in the parts of the skeleton that are pneumatized by those air sacs in extant birds. The evidence presented above shows that PSP in nonavian dinosaurs also shared some aspects of development with PSP in birds. In basal theropods and sauropodomorphs, PSP is present only in the cervical vertebrae (if at all). This shows that diverticula of the cervical air sacs must have developed anteriorly from the thorax before they pneumatized the skeleton, just as in extant birds. The pneumatic hiatus in *Haplocanthosaurus* suggests that vertebral diverticula developed from more than one part of the abdominal air sacs. The parallel between the evolution of PSP in nonavian

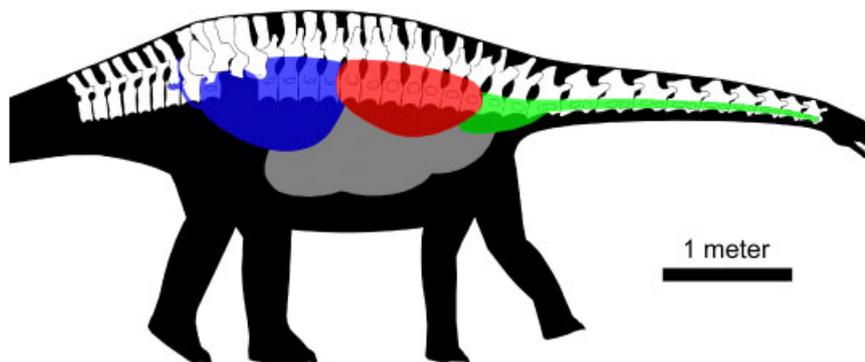


Fig. 10. The air sacs of *Haplocanthosaurus*. Preserved elements of CM 879 are shown in right lateral view. The cervical and anterior dorsal vertebrae were pneumatized by diverticula of cervical air sacs (green). Middle dorsal vertebrae were pneumatized by diverticula of the lung (red). Diverticula of the abdominal air sac (blue) pneumatized the posterior dorsal, sacral, and first caudal vertebrae. Other air sacs may have been present (gray), but their presence is not detectable from the preserved elements.

dinosaurs and its development in birds also suggests that similar generative mechanisms were responsible.

Evidence for PSP in *Archaeopteryx* is equivocal (contra Britt et al., '98; Christiansen and Bonde, 2000; see O'Connor, 2006; Mayr et al., 2007). Foramina in the vertebrae and pelvic elements are not clearly pneumatic. Some may be vascular foramina, and some may be breaks in the specimens (O'Connor, 2006). Furthermore, radiographs of at least one specimen show that the vertebrae are dense and solidly constructed, which is more consistent with apneumatic bone than with pneumaticity (Mayr et al., 2007). However, PSP was present in other basal birds (e.g., *Ichthyornis*, *Jeholornis*; Marsh, 1880; Zhou and Zhang, 2003), and many other basal birds have humeral and vertebral fossae that may have been pneumatic (Sanz et al., '95). Therefore, it is not clear if PSP in nonavian theropods is taxically homologous (sensu Patterson, '82) with that of birds. On the basis of currently available evidence, the absence of unequivocal PSP in *Archaeopteryx* could represent a loss in that taxon alone.

Archaeopteryx is not the only lacuna in the phylogenetic distribution of PSP in Saurischia. Sauropodomorphs evolved PSP independently from theropods; PSP is absent in the most basal known sauropodomorph (*Saturnalia*; Langer et al., '99) and absent or, at least, not clearly present in most basal sauropodomorphs (Wedel, 2007). Furthermore, posterior compartment pneumaticity evolved independently in diplodocoids, titanosauriforms, ceratosaurians, and coelurosaurians. The skeletal traces of abdominal air sacs are not phylogenetically continuous throughout Saurischia.

Although PSP does not have a continuous phylogenetic distribution in Saurischia, it seems to have been produced by similar developmental pathways in sauropodomorphs, nonavian theropods, and birds, and none of the gaps in the phylogenetic distribution of pneumatic characters are very large. It is possible that both cervical and abdominal air sacs were present in the ancestral saurischian, but did not pneumatize the postcranial skeleton in some descendants of that ancestor—for example, most basal sauropodomorphs. A similar situation exists in extant birds, all of which have an air sac system even though PSP has been lost in some clades.

On the other hand, air sacs (and not just PSP) may have evolved independently in sauropodomorphs and theropods. Sac-like regions of the lung

are present in many sauropsids (Wolf, '33; Perry, '83, '98), and these suggest some level plasticity in sauropsid pulmonary systems (O'Connor and Claessens, 2005). If air sacs were absent in the ancestral saurischian, they must have evolved in both lineages very soon after the divergence of theropods and sauropodomorphs because PSP is present in early representatives of both clades. The ancestral saurischian must have had at least the potential to evolve air sacs, but this potential may have been realized independently in theropods and sauropodomorphs. However, the balance of the evidence suggests that air sacs are primitive for Saurischia.

The origin of flow-through lung ventilation

Flow-through lung ventilation like that of birds minimally requires four things: (1) lungs that function as tubes rather than sacs; (2) air sacs anterior to the lungs; (3) air sacs posterior to the lungs; and (4) a musculoskeletal system capable of driving ventilation. Evidence from the fossil record, particularly PSP, can extend the understanding of the origin of this system, but it may not be sufficient to pinpoint the origin of avian-style lung ventilation.

Fossil evidence and phylogenetic inferences suggest that all of the components necessary for flow-through lung ventilation were present in basal saurischians. But the hypothesis that bird-like lung ventilation was common to all saurischians comes with two important caveats. The first is obvious: at least for now, there is no way of knowing the path of inspired air in nonavian dinosaurs. The fossil evidence can only show that saurischians had the anatomical components necessary for flow-through lung ventilation. It is possible that basal saurischians had air sacs but not flow-through ventilation. However, in crocodylians adjacent lung chambers are often connected by small foramina, which allow the possibility of extra-bronchial airflow (Perry, '88, '91). The presence of these foramina in crocodylians together with the parabronchi of birds shows that some form of extra-bronchial airflow is probably primitive for archosaurs. Nevertheless, the detailed internal structures and airflow patterns of extinct archosaurs are not well constrained by available evidence.

The other caveat extends uncertainty in the opposite direction. PSP is present in pterosaurs (Bonde and Christiansen, 2003; O'Connor, 2006) but absent in the closest outgroups of Saurischia,

which are Ornithischia and nondinosaurian dinosauromorphs. Avian development demonstrates that the air sac system and its diverticula are present before they leave skeletal traces (Locy and Larsell, '16a,b; Hogg, '84a,b), and that the fully avian air sac system can be present without producing PSP, as in loons and penguins. Therefore, the possibility exists that an air sac system, and possibly even flow-through lung ventilation, evolved earlier in archosaurs and only became detectable in the fossil record when it started leaving diagnostic traces in the skeletons of basal saurischians and pterosaurs.

The enigmatic origin of postcranial pneumaticity

The evolution of PSP in saurischians is marked by trends in the invasiveness and physical scale of the pneumatic traces. Pneumatic fossae in the vertebrae of basal sauropods and theropods are antecedent to the simple, camerate (large-chambered) vertebrae of more derived taxa that, in turn, give way to the complex, camellate (small-chambered) vertebrae of the most derived taxa in both lineages. In sauropods, at least, there was also a trend toward increasing pneumatization of individual elements, so that the pneumatic vertebrae of most sauropods were only about half as dense as the apneumatic vertebrae of their basal sauropodomorph ancestors (see Appendix). This trend may also be present in theropods, although it has not yet been documented.

If progressively more basal taxa are examined in the quest to find the origin of PSP, the problem is not that evidence of PSP disappears entirely. It is that the shallow, unbounded fossae of basal dinosaurs are no longer diagnostic for pneumaticity (Wedel, 2007). Similar fossae are present in the vertebrae of many tetrapods, and they may be associated with many soft tissues, including muscles, cartilage, and fat (O'Connor, 2006).

One potential step forward is to search for criteria that would distinguish pneumatic fossae from those associated with other soft tissues. Such criteria might be present in the microscopic surface texture of pneumatic bones, or in their histology, which has been little studied except for a few brief treatments (e.g., Reid, '96; Woodward, 2005). Perhaps the ancestors of Saurischia had air sacs and diverticula but the skeletal traces of the respiratory system are so faint or so nondiagnostic that they have not been recognized. Perhaps they had air sacs but no diverticula, or no air sacs at all.

There is no guarantee that diagnostic criteria for pneumatic fossae exist to be found, or that, if found, they will be present in the outgroups to Saurischia. Nevertheless, to improve the understanding of the origin of the avian air sac system, that is where and how they should be sought.

CONCLUSION: SHIFTING THE NULL HYPOTHESIS OF SAURISCHIAN RESPIRATION

In an article on the antorbital fenestra of archosaurs, Witmer ('87) found that the fenestra probably housed an air sac rather than a muscle or a gland. Witmer argued that because the air sac hypothesis was the best supported of the three, it should become the null hypothesis for the soft-tissue contents of the antorbital fenestra.

A similar turning point is at hand for hypotheses of saurischian respiration. As they diverged from a common ancestor, the linear ancestors of birds and crocodylians must have passed through functionally intermediate stages. Nonavian dinosaurs did not necessarily have the same pulmonary anatomy as crocodylians or extant birds. As hypotheses of pulmonary anatomy in dinosaurs, "croc lungs" versus "bird lungs" is a false dichotomy. It is more informative to identify the derived features that nonavian dinosaurs share with their extant relatives, and to determine the hierarchical distribution of these characters in archosaurian phylogeny. The pulmonary anatomy of nonavian saurischians may not have been exactly like that of extant birds, but the evidence discussed above suggests that both cervical and abdominal air sacs were present in all saurischians. Some form of air sac-driven lung ventilation should be considered the null hypothesis for saurischians.

Some previous studies assumed that sauropods and other saurischians had lungs like those of crocodylians (Hengst and Rigby, '94; Hengst et al., '96; Ruben et al., '97, '99, 2003) or turtles (Spotila et al., '91). Others have located the origin of the air sac system in the first coelurosaurian theropods, without entertaining the possibility that the system might have originated much earlier (Farmer, 2006). It is not beyond the bounds of possibility that sauropods had turtle lungs or that air sac-driven lung ventilation originated in coelurosaurs, but neither of those hypotheses is consistent with the abundant evidence for cervical and abdominal air sacs in all saurischians, and they can no longer be regarded as null.

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APPENDIX

The method of calculating the relative densities of pneumatic and apneumatic bones is given here. The thickness of the walls of tubular bones is typically expressed as the variable K , which is the inner diameter of the bone (r) divided by the outer diameter (R). For a large sample (>150) of avian long bones, Cubo and Casinos (2000) reported average K values of 0.65 for apneumatic bones and 0.77 for pneumatic bones. For tubular bones, the amount of the cross-sectional area that is not occupied by bone can be found by taking the square of K ($\pi r^2/\pi R^2 = r^2/R^2 = K^2$). For the apneumatic bones, this is 0.65^2 or 0.42, and for the pneumatic bones it is 0.77^2 or 0.59. This means that on average, the cross-sectional area of a pneumatic element is 59% air and 41% bone, and the cross-sectional area of an apneumatic element is 42% marrow and 58% bone. The specific gravity of marrow is 0.95 (Currey and Alexander, '85), and that of avian compact bone is 1.8 (Spector, '56). The mass of air is negligible. On average, the density of pneumatic avian long bones is $1.8 \times 0.41 = 0.74 \text{ g/cm}^3$, and the density of apneumatic avian long bones is $(1.8 \times 0.58) + (0.95 \times 0.42) = 1.4 \text{ g/cm}^3$. It may seem surprising that pneumatic bones that differ from apneumatic bones by 10% of K are only half as dense. However, the cross-sectional geometry of the bones is proportional to the square of K , and the diaphyses

of apneumatic bones are filled with marrow that contributes much of the mass of the elements.

Pneumatic sauropod vertebrae were, on average, about 60% air by volume (Wedel, 2005; Schwarz and Fritsch, 2006). Assuming that the compact bone of sauropods was as dense as that of birds, the average density of their pneumatic vertebrae was $1.8 \times 0.4 = 0.72 \text{ g/cm}^3$ —about the same as that of pneumatic long bones in birds. Although quantitative comparisons are lacking, the apneumatic vertebrae of basal sauropodomorphs are similar in cortical thickness and internal structure to those of large extant mammals (personal observation), and were probably about as dense. In *Giraffa* and *Syncerus* the density of the vertebrae is $1.3\text{--}1.4 \text{ g/cm}^3$ (van Schalkwyk et al., 2004), very close to the mean for apneumatic bird bones calculated above. If the vertebrae of basal sauropodomorphs were equally dense, then pneumatization of sauropod vertebrae and avian long bones both produce the same density reduction, about 50%.

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