WHAT PNEUMATICITY TELLS US ABOUT 'PROSAUROPODS', AND VICE VERSA

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Abstract: Pneumatic (air-filled) bones are an important feature of the postcranial skeleton in pterosaurs, theropods and sauropods. However, there is no unambiguous evidence for postcranial pneumaticity in basal sauropodomorphs and even the ambiguous evidence is scant. Patterns of skeletal pneumatization in early sauropods and theropods suggest that basal saurischians had cervical air sacs like those of birds. Furthermore, patterns of pneumaticity in most pterosaurs, theropods and sauropods are diagnostic for abdominal air sacs. The air sacs necessary for flow-through lung ventilation like that of birds may have evolved once (at the base of Ornithodira), twice (independently in pterosaurs and saurischians) or three times (independently in pterosaurs, theropods and sauropods). Skeletal pneumaticity appears to be more evolutionarily malleable than the air sacs and diverticula that produce it. The evolution of air sacs probably pre-dated the appearance of skeletal pneumaticity in ornithodirans.

Key words: Prosauropoda, Sauropodomorpha, Saurischia, Ornithodira, pneumaticity, air sacs, diverticula.

PNEUMATICITY is a prominent feature of the postcranial skeleton in theropod and sauropod dinosaurs. In contrast, there is little evidence for postcranial pneumaticity in basal sauropodomorphs (informally referred to as 'prosauropods' in this paper), although from time to time some aspects of prosauropod osteology have been posited as evidence of pneumaticity (Britt 1997) or compared with unequivocal pneumatic structures in sauropods (Yates 2003; Galton and Upchurch 2004). My goals in this paper are to review the evidence for postcranial skeletal pneumaticity (PSP) in prosauropods and to discuss the origin of air sacs and pneumaticity in early dinosaurs and their relatives.

Prosauropod taxonomy is currently in a state of flux, as other papers in this volume attest (Sereno 2007; Upchurch *et al.* 2007; Yates 2007). Prosauropods were traditionally considered a paraphyletic assemblage that gave rise to sauropods. Sereno (1998) recovered a monophyletic Prosauropoda, defined this clade (anchored upon *Plateosaurus*) as a monophyletic sister taxon to Sauropoda and united the two in a node-based Sauropodomorpha. A similar phylogenetic hypothesis was described by Galton and Upchurch (2004). However, other recent phylogenetic analyses (Yates 2003, 2004; Yates and Kitching 2003) have found that some prosauropods are closer to *Saltasaurus* than to *Plateosaurus*; thus, under current phylogenetic definitions they should be regarded as basal sauropods. Some other taxa (e.g. *Saturnalia*) lie outside Sauropodomorpha as defined by Sereno (1998) altogether (Yates 2003, 2004; Yates and Kitching 2003; Langer 2004).

However, the monophyly or paraphyly of the group of taxa traditionally called prosauropods is not critical to the purposes of this paper. What is important is that all traditional 'prosauropods' have two things in common: they lack unequivocal evidence of pneumatic cavities in their vertebrae and ribs, and they are phylogenetically bracketed by sauropods and theropods (Text-fig. 1).

Institutional abbreviations. BMNH, The Natural History Museum, London; CM, Carnegie Museum of Natural History, Pittsburgh, USA; FMNH, Field Museum of Natural History, Chicago, USA; MSM, Mesa Southwest Museum, Mesa, USA; OMNH, Oklahoma Museum of Natural History, Norman, USA; SMNS, Staatliches Museum fur Natürkunde, Stuttgart, Germany.

Anatomical abbreviations. ACDL, anterior centrodiapophyseal lamina; AL, accessory lamina; AVF, anteroventral fossa; NAF, neural arch fossa; PCDL, posterior centrodiapophyseal lamina; PDF, posterodorsal fossa; PODL, postzygodiapophyseal lamina; PPDL, paradiapophyseal lamina; PRDL, prezygodiapophyseal lamina; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina (lamina abbreviations after Wilson 1999).

POSTCRANIAL PNEUMATICITY IN THEROPOD AND SAUROPOD DINOSAURS

Before examining the evidence for PSP in 'prosauropods', I will review the conditions present in other saurischian
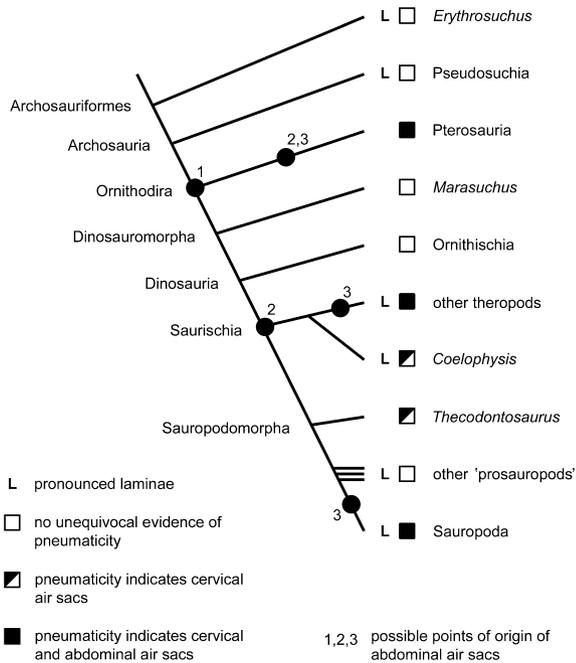
TEXT-FIG. 1. A phylogeny of archosaurs showing the evolution of postcranial skeletal pneumaticity and air sacs. *Thecodontosaurus* is shown as having limited postcranial pneumaticity. The evidence for this is ambiguous; see text for discussion. Based on the phylogenetic framework of Brochu (2001) and Yates (2003).

dinosaurs. The sister taxon of Sauropodomorpha is Theropoda; consequently, 'prosauropods' are phylogenetically bracketed in part by birds, the only clade of extant vertebrates with extensive PSP. The relationship between the respiratory system and pneumatic postcranial bones in birds has been described many times (e.g. Müller 1908; King 1966; Duncker 1971; O'Connor 2004), and is briefly summarized here. The relatively small, constant-volume, unidirectional flow-through lungs of birds are ventilated by the attached air sacs, which are large, flexible and devoid of parenchymal tissue. The lungs and air sacs also produce air-filled tubes called diverticula that pass between the viscera, between the muscles, and under the

skin. Where a diverticulum comes into contact with a bone, it may (but does not always) induce bone resorption, which can produce pneumatic tracks, fossae or foramina. If resorption of the cortex produces a foramen, the diverticulum may enter the medullary space and replace the existing internal structure with a series of air-filled chambers of varying complexity. The best description of this process is provided by Bremer (1940).

The extent of PSP varies in different avian clades. Almost any postcranial bones can become pneumatized; in large soaring birds such as pelicans, almost the entire skeleton is pneumatic, including the distal limb elements (O'Connor 2004). Although many large volant and flightless birds have highly pneumatic skeletons, the correlation between body size and the extent of PSP in birds is weak (O'Connor 2004). PSP tends to be reduced or absent in diving birds (Gier 1952; O'Connor 2004). Different parts of the skeleton become pneumatized by diverticula of different air sacs in extant birds (Table 1); this is important because it allows us to make inferences regarding the evolution of air sacs in fossil taxa. PSP in non-avian theropods generally follows the avian model (Britt 1993, 1997; O'Connor and Claessens 2005; O'Connor 2006). Patterns of pneumatization along the vertebral column indicate that both anterior and posterior air sacs (presumably cervical and abdominal) had evolved by the time of the ceratosaur-tetanuran divergence (O'Connor and Claessens 2005).

Fossae are present in the presacral vertebrae of basal sauropods such as *Shunosaurus* and *Barapasaurus* (Britt 1993; Wilson and Sereno 1998). These fossae are similar to the unequivocally pneumatic foramina and camerae of more derived sauropods, both in their position on individual vertebrae and in their distribution along the vertebral column, and because of these similarities they have usually been regarded as pneumatic in origin (Britt 1993, 1997; Wedel 2003a). However, similar fossae are present in other tetrapods that lack PSP, so the presence of fossae alone is at best equivocal evidence for PSP (O'Connor 2006; see below). The vertebrae of more derived sauropods have foramina that communicate with large internal

TABLE 1. Parts of the postcranial skeleton that are pneumatized by diverticula of different parts of the respiratory system in extant birds. Pneumaticity varies widely within populations and clades, and not all elements are pneumatized in all taxa (based on Duncker 1971 and O'Connor 2004).

Respiratory structure	Skeletal elements
Lung (parenchymal portion)	Adjacent thoracic vertebrae and ribs
Clavicular air sac	Sternum, sternal ribs, pectoral girdle and humerus
Cervical air sac	Cervical and anterior thoracic vertebrae and associated ribs
Anterior thoracic air sac	Sternal ribs
Posterior thoracic air sac	(none reported)
Abdominal air sac	Posterior thoracic, synsacral and caudal vertebrae, pelvic girdle and femur
Subcutaneous diverticula	Distal limb elements

chambers; the combination of foramina and large internal chambers is an unambiguous indicator of PSP (O'Connor 2006). There is a general trend in sauropod evolution for PSP to spread posteriorly along the vertebral column, albeit to different extents in different clades and with a few reversals (Wedel 2003*b*; Text-fig. 2). In both sauropods and theropods, fossae in basal forms were replaced by large-chambered (camerate) vertebrae and eventually small-chambered (camellate) vertebrae in more derived taxa (Britt 1993, 1997; Wedel 2003*a*).

The evolution of PSP in sauropods mirrors in detail that of non-avian theropods. At the level of individual elements (e.g. vertebrae and ribs), pneumatic features in sauropods compare very closely with those of both avian and non-avian theropods (Text-fig. 3). In terms of the ratio of bony tissue to air space within a pneumatic element, sauropod vertebrae are, on average, comparable with the limb bones of many extant birds: about 60 per cent air by volume (Wedel 2004, 2005; Woodward 2005; Schwarz and Fritsch 2006). At the level of the skeleton, osteological indicators of pneumaticity spread as far back as the mid-caudal vertebrae in at least two groups of sauropods, the diplodocines and saltasaurines (Osborn 1899; Powell 1992). Among non-avian theropods, extensive pneumatization of the caudal series evolved only in oviraptorosaurs (Osmólska *et al.* 2004). Finally, limited appendicular pneumaticity was probably present in both sauropods and non-avian theropods. The dromaeosaur *Buitreraptor* has a pneumatic furcula (Makovicky *et al.* 2005), and a large foramen in the proximal femur of the oviraptorid *Shixinggia* is probably also pneumatic in origin (Lü and Zhang 2005). Large chambers have been reported in the ilia of the basal diplodocoid *Amazonsaurus* (Carvalho *et al.* 2003) and in several titanosaurs (Powell 1992; Sanz *et al.* 1999; Xu *et al.* 2006). Although these chambers are similar to unequivocally pneumatic spaces in the other saurischians, it has not yet been

shown that the ilial chambers are connected to foramina, which are necessary for pneumatization to occur (see O'Connor 2006).

EVIDENCE OF PNEUMATICITY IN 'PROSAUROPODS'

Historically, postcranial pneumaticity in 'prosauropods' has received little attention, which is to be expected given the paucity of available evidence. Janensch (1947) posited that a foramen in a dorsal vertebra of *Plateosaurus* might have been pneumatic, but he attached no great weight to this hypothesis. Britt (1997) considered vertebral laminae evidence of pneumaticity in 'prosauropods'. Most recently, Yates (2003, p. 14, fig. 12) identified 'pleurocoel-like pits' in the mid-cervical vertebrae of *Thecodontosaurus caducus*, and Galton and Upchurch (2004, p. 245) referred to fossae in the posterior dorsals of some prosauropods as 'pleurocoelar indentations'. The 'pleurocoel-like' structures were not explicitly described as pneumatic in either work. Although fossae are not unambiguous indicators of pneumaticity (O'Connor 2006), vertebral fossae seem to be an early step toward full pneumatization, both ontogenetically and phylogenetically (Wedel 2003*a*). Putative pneumatic characters in 'prosauropods' can be divided into three categories: vertebral laminae, foramina and fossae, which will be discussed in this order, below.

Vertebral laminae. Vertebral laminae are struts or plates of bone that connect the various apophyses of a vertebra to each other and to the centrum. The landmarks that are usually connected in this way are the pre- and postzygapophyses, the diapophyses and parapophyses, and the neurapophysis. The form and occurrence of the major laminae in saurischian dinosaurs were reviewed by Wilson

TEXT-FIG. 2. A diagram showing the distribution of fossae and pneumatic chambers (black boxes) along the vertebral column in sauropods. Only the lineage leading to diplodocines is shown here. The same caudal extension of pneumatic features also occurred independently in macronarian sauropods, culminating in saltasaurines, and several times in theropods. The format of the diagram is based on Wilson and Sereno (1998, fig. 47). Phylogeny based on Wilson (2002), Yates (2003) and Upchurch *et al.* (2004).
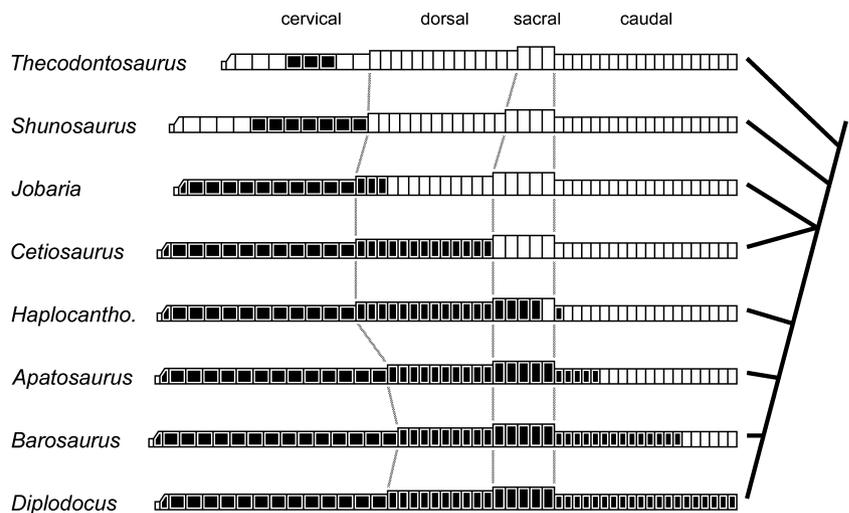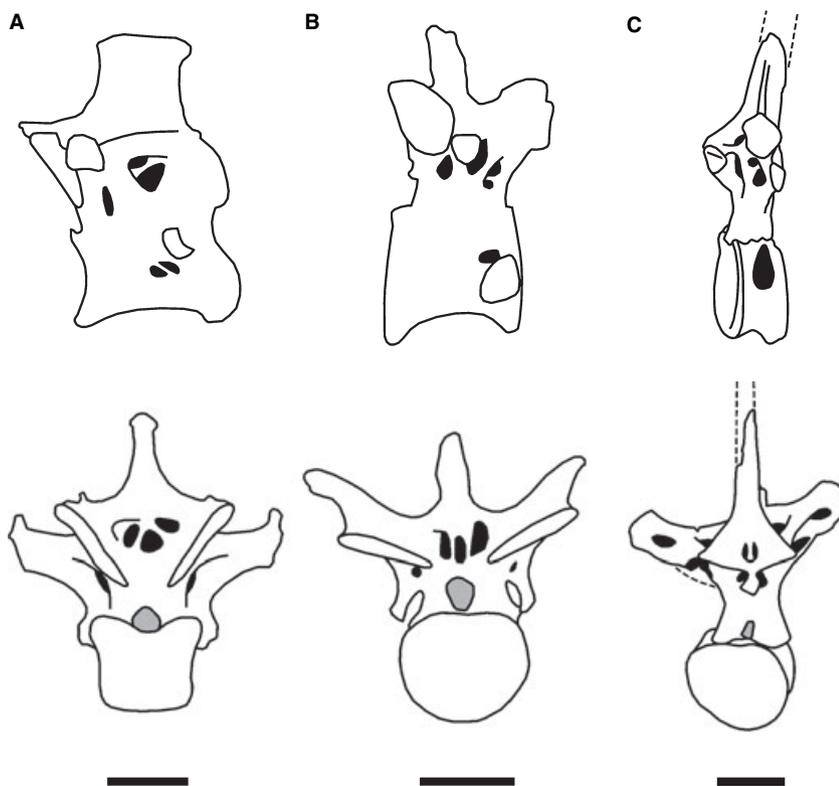
TEXT-FIG. 3. Pneumatic foramina (black) in thoracic or dorsal vertebrae of an extant bird, a non-avian theropod and a sauropod, in right lateral view (above) and posterior view (below). A, a crane, *Grus*. B, an abelisaurid, *Majungatholus*. C, a diplodocid, *Apatosaurus*. A and B traced from O'Connor and Claessens (2005, fig. 3); C traced from a photograph of OMNH 1382. Scale bars represent 1 cm in A, 3 cm in B and 20 cm in C.

(1999). In addition to a basic set of laminae common to all saurischians, many sauropods and theropods have other irregularly developed laminae that are usually not named but are collectively called accessory laminae. Laminae tend to be more numerous and more sharply defined in camerate than camellate vertebrae (Wilson and Sereno 1998; Wedel 2003a). Camellate vertebrae evolved relatively early in the radiation of non-avian theropods (Britt 1993, 1997), and most derived theropods have less elaborate systems of laminae than neosauropods. This may explain why the literature on laminae has tended to focus on sauropods (e.g. Osborn 1899; Osborn and Mook 1921; Janensch 1929, 1950; Wilson 1999).

Two problems with the identification of laminae that are relevant to the question of pneumaticity are how well developed a ridge of bone must be before we call it a lamina, and whether laminae are primarily additive structures formed by the deposition of new bone, or are simply bone that is left over following the formation of fossae. The first problem is important because, as shown below, incipient laminae are broadly distributed among archosaurs. To what extent are the distinct laminae of saurischian dinosaurs new (= apomorphic) structures, rather than modifications of pre-existing ones? This question has ramifications for the evolution of laminae and for coding of laminae as characters in phylogenetic analyses.

The second question can be stated: do laminae grow out from the corpus of the vertebra to define the fossae that they bound, or do we only recognize laminae as distinct structures because the bone between them has been removed? For example, the cervical vertebra of *Nigersaurus* illustrated by Sereno and Wilson (2005, fig. 5.8) has on the lateral face of the neural spine two fossae divided by an accessory lamina (Text-fig. 4). At its edges, the anteroventral fossa approaches both the prezygapophysis and the diapophysis. This region is flat or convex in most other neosauropods, which have a lateral fossa in roughly the same position as the posterodorsal fossa in *Nigersaurus*. It seems likely therefore that the anteroventral fossa in *Nigersaurus* is a new morphological feature, and that the accessory lamina can only be recognized as a lamina because a fossa has been excavated below it. Conversely, the vertebrae of most tetrapods do not have straight bars of bone that connect the zygapophyses to the neurapophysis, but this is exactly what the spinopre- and spinopostzygapophyseal laminae of some sauropods do (Text-fig. 4). In comparison with the condition in other tetrapods, including prosauropods, these laminae appear to be additive structures. These potentially opposing processes of lamina formation should be kept in mind while reading the following descriptions.

The laminae of sauropods often form the boundaries of fossae that have been interpreted as pneumatic, either

TEXT-FIG. 4. Laminae, fossae and foramina in cervical vertebrae of *Nigersaurus* and *Apatosaurus*. A, fifth cervical vertebra of *Nigersaurus*, traced from Sereno and Wilson (2005, fig. 5.8). B, tenth cervical vertebra of *Apatosaurus*, traced from Gilmore (1936, pl. 24). Scale bars represent 5 cm in A and 20 cm in B.
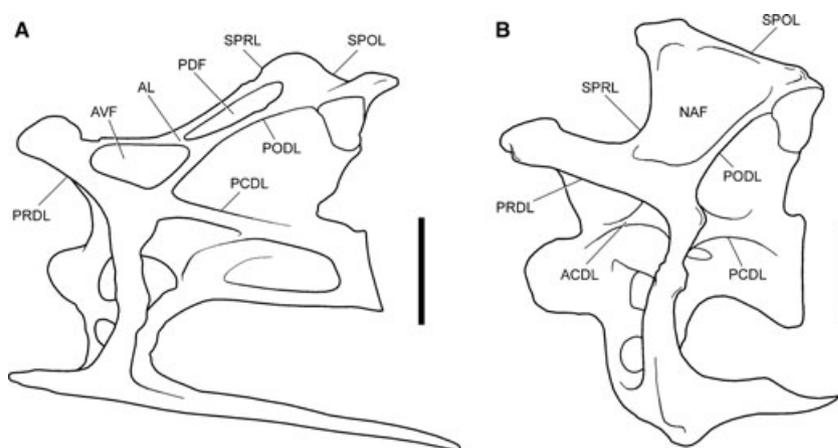
because they contain foramina that lead to internal chambers or because they are heavily sculpted, with numerous subfossae (*sensu* Wilson 1999) and a distinct bony texture (although texture alone is not necessarily a good indicator of pneumaticity; see O'Connor 2006). Wilson (1999) considered whether sauropod laminae existed to provide mechanical support or to subdivide pneumatic diverticula, and concluded that they probably served both functions simultaneously. Following from the aforementioned discussion, we might also ask if sauropod laminae exist because the pneumatic diverticula are subdivided, as they often are in birds (e.g. Wedel 2003*b*, fig. 2), and these subdivisions are impressed into the bone, leaving laminae between them. Rather than try to determine which structure has morphogenetic precedence, it may be more useful to view sauropod vertebrae in light of Witmer's (1997) hypothesis that the form of a pneumatic bone can be viewed as the outcome of a struggle between bone tissue, which grows partly in response to biomechanical stress, and pneumatic diverticula, which are opportunistic and invasive and spread wherever possible (see Sadler *et al.* 1996 and Anorbe *et al.* 2000 for examples of proliferating diverticula).

The laminae of 'prosauropods' differ from those of sauropods in three important ways. The first is that prosauropods have fewer laminae. The laminae that connect the diapophysis to the centrum, parapophysis and zygapophyses are usually present (Wilson 1999), but those that connect the neurapophysis to other landmarks are absent (Text-fig. 5; but see Bonaparte 1999, figs 13–16 on *Lessemsaurus*). The second is that laminae are confined to the presacral vertebrae in 'prosauropods', whereas the sacral vertebrae of neosauropods and the caudal vertebrae of diplodocids also bear laminae.

The third and most important difference between the laminae of sauropods and 'prosauropods' is that the fossae bounded by the latter are blind. These fossae do not contain foramina or subfossae and they do not have a distinctive bone texture. Consequently, there is no strong reason to suspect that they contained pneumatic diverticula. O'Connor (2006) found that similar fossae in extant crocodilians and birds may contain cartilage or adipose tissue. Considering whether the laminae are additive structures or remnants of fossa formation sheds little light on the problem. Some laminae, such as the PRDLs of *Plateosaurus* cervicals, are straight-line structures that
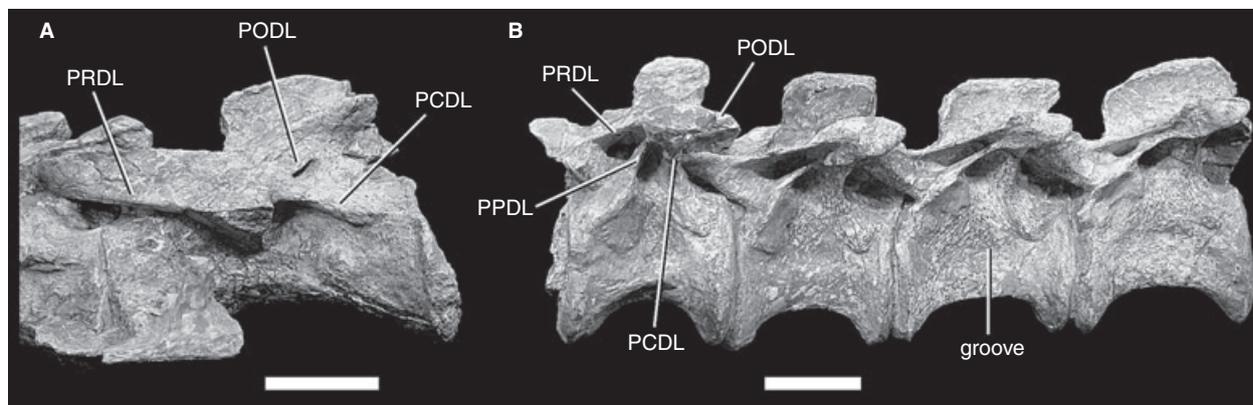
TEXT-FIG. 5. Vertebrae of *Plateosaurus trossingensis* (SMNS 13200) in left lateral view. A, the eighth cervical vertebra. B, dorsal vertebrae 1–4. Scale bars represent 5 cm.

appear to have been added, compared with the condition in vertebrae that lack laminae (Text-fig. 5). Others, such as the PODLs in the same vertebrae, are only detectable because they have been undercut by a fossa. The form of the fossae themselves provides no obvious clues to their contents *in vivo*.

Laminae like those of 'prosauropods' occur in many other archosaurs. Desojo *et al.* (2002) and Parker (2003) recognized that many of the laminae described by Wilson (1999) for saurischian dinosaurs are also present in basal archosaurs and pseudosuchians. The full complement of diapophyseal laminae is present in dorsal vertebrae of the basal archosauriform *Erythrosuchus* and in those of popo-saurs such as *Sillosuchus* and *Arizonasaurus*, including the PCDL, PODL, PPDL and PRDL (Text-fig. 6; see Alcober and Parrish 1997; Nesbitt 2005). At least in *Erythrosuchus*, the fossae bounded by these laminae contain aggregates of vascular foramina; obvious foramina like these are not present or at least not common in the interlaminar fossae of 'prosauropods' (pers. obs.). Incipient laminae are also present in some neosuchian crocodyliforms. Most dorsal vertebrae of *Goniopholis stovalli* have rudimentary PCDLs and PODLs (Text-fig. 7). The PODL is bounded dorsally by a shallow fossa on the lateral face of the neural spine and ventrally by a deep infrapostzygapophyseal fossa. In at least some of the vertebrae, the fossa on the side of the neural spine has a distinct margin (Text-fig. 7B). Although most neosuchian crocodyliforms have extensive skull pneumatization (Witmer 1997; Tykoski *et al.* 2002), PSP is absent in the clade (O'Connor 2006).

Vertebral laminae also occur in non-amniotes. The best example is probably the plethodontid salamander *Aneides lugubris*, in which plate-like shelves of bone connect the parapophyses of dorsal vertebrae to the ventrolateral margins of the centra (Wake 1963). These shelves of bone are absent in other species of *Aneides* and in other pletho-dontid genera, and they are thus additive structures that are apomorphic for *A. lugubris* (compare Wake 1963, fig. 9 with Wake and Lawson 1973, fig. 6). *A. lugubris* has the most prolonged ontogeny of any plethodontid, and it is peramorphic relative to other species in the genus, with a more extensively ossified skeleton (Wake 1963; Wake *et al.* 1983). The development of laminae in the species is probably an epiphenomenon of the extensive ossification of the skeleton, which in turn is related to adaptations for arboreality and feeding (Larson *et al.* 1981). As such, the laminae of *A. lugubris* are not homologous with those of archosaurs in a taxic sense, and they are probably produced by different developmental processes. Still, *A. lugu-bris* demonstrates that laminae can evolve in vertebrates that are far removed from basal dinosaurs in both gene-alogy and body size, and it provides a potential system in which to investigate the development of laminae in an extant tetrapod.

On one hand, it is possible that the laminae and fossae of basal archosauriform and pseudosuchian vertebrae appear pneumatic because they are pneumatic (Gower 2001), but the morphology is not compelling. Like the fossae of 'prosauropod' neural spines, those of *Erythrosu-chus* and *Arizonasaurus* lack subfossae, foramina that lead to large internal chambers, or altered texture. The pres-ence of similar features in crocodyliforms and salaman-ders is strong evidence that the morphologies in question can be produced in the absence of pneumaticity. Unlike 'prosauropods', basal archosauriforms and pseudosuchi-ans are not bracketed by taxa with unequivocal evidence of pneumaticity, so inferring that they had pneumatic vertebrae would require pulmonary diverticula and poss-ibly also air sacs to have evolved much earlier than other-wise supposed (see 'Palaeobiological implications' below).

Regardless of when the capacity for PSP evolved, the laminae of 'prosauropods' bound fossae that are not unequivocally pneumatic. Similar laminae are present in crocodilians, a group in which postcranial pneumaticity is entirely absent. Some of the osteological traces of diverti-cula are subtle, and the possibility that the neural arch fossae of 'prosauropods' accommodated pneumatic diver-ticula cannot be ruled out, but there is no strong evidence for it.

Foramina. The only putative pneumatic foramen in a 'prosauropod' is that described by Janensch (1947) in a cervical vertebra of *Plateosaurus*. Janensch argued that the size (11 × 4 mm) and form of the foramen were more consistent with a pneumatic than a vascular interpret-ation. The identity of the foramen can only be settled by first-hand observation, preferably with a computed tomo-graphic (CT) scan to determine if the foramen leads to any large internal chambers. Unfortunately, such an examination has yet to be conducted. However, the cau-dal vertebrae of some whales are similar in size to *Plateo-saurus* dorsal vertebrae (*c.* 20 cm in maximum linear dimension) and have vascular foramina up to 30 mm in diameter (pers. obs.), so large foramina do not necessarily indicate the presence of pneumaticity. In general, the prominent foramina and internal chambers that are typ-ical of sauropod vertebrae are absent in the vertebrae of 'prosauropods'.

Fossae. The first step in recognizing pneumatic fossae is to distinguish between vertebrae that have distinct fossae and those that are merely waisted (narrower in the mid-dle than at the ends). The vertebrae of most vertebrates are waisted to some extent. In humans the effect is barely noticeable, but in some archosaurs the 'waist' of the ver-tebra may be only half the diameter of the ends of the centrum (e.g. Nesbitt 2005, fig. 16). Some degree of waisting is to be expected based on the early development

TEXT-FIG. 6. Dorsal vertebrae of *Erythrosuchus africanus* (BMNH R533). A, right lateral and B, ventrolateral views. Scale bar represents 5 cm.
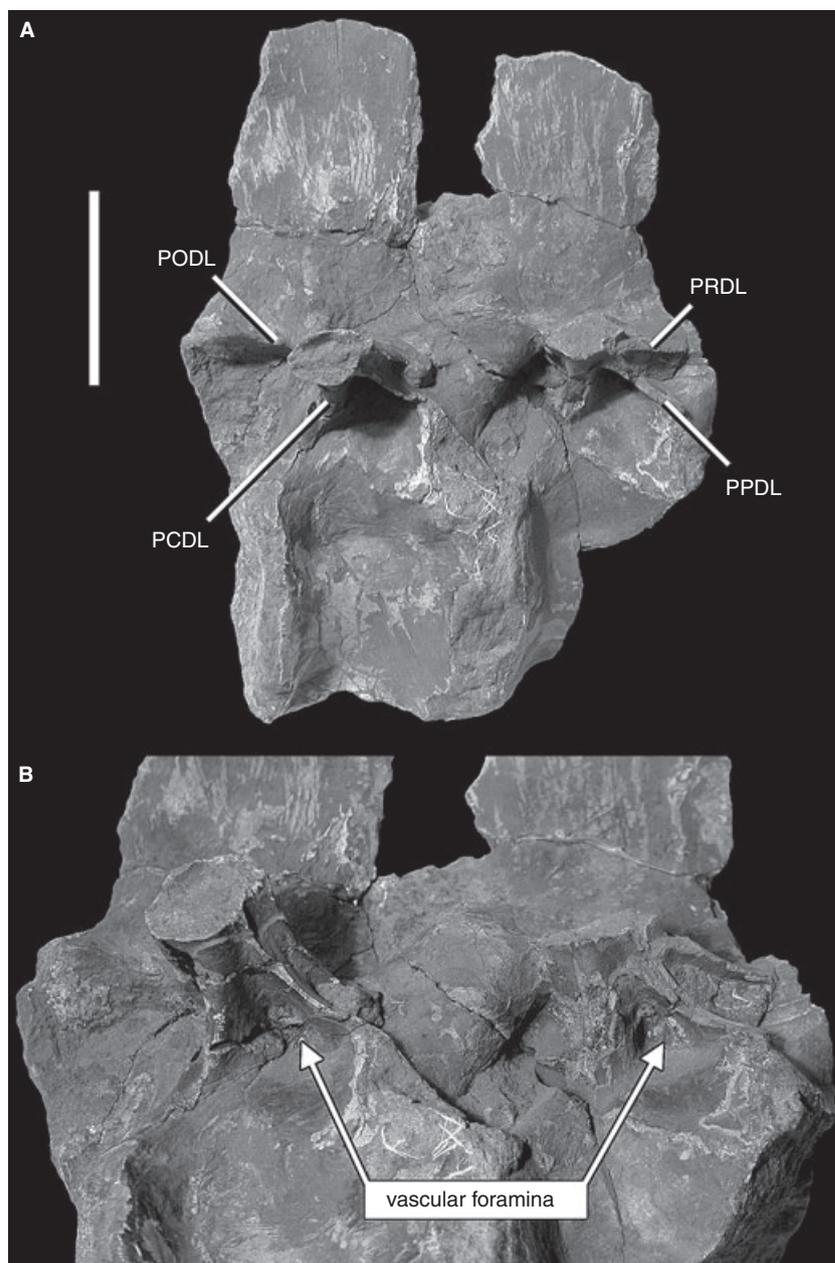
of vertebrae. Cell-dense regions of the embryonic axial column become intervertebral discs, and lower-density regions become vertebral bodies. This produces centra that are inherently waisted (Verbout 1985, pl. 10; Wake 1992, figs 6.5, 6.7). The degree of waisting has occasionally been used as a taxonomic character (Case 1907), but to date there is no clear explanation of why some vertebrae are more waisted than others. Regardless, vertebral waisting is widespread in vertebrates and is not evidence for pneumaticity.

Waisting aside, fossae still suffer from a problem of definition. Consider a spectrum of morphological possibilities (Text-fig. 8). At one end is a vertebra that is waisted but lacks distinct fossae: for example, a thoracic vertebra of an artiodactyl. At the other end is a vertebra with large foramina that open into internal chambers, such as a dorsal vertebra of *Saltasaurus*. The 'chamber morphospace' between these endpoints is filled with a continuum of deeper and more distinct fossae and camerae. Adjacent to the artiodactyl vertebra we might put a vertebra that has fossae with a distinct margin on one side but not the other, like those in the cervical centra of *Arizonasaurus*, which are bounded dorsally by the PCDL; next, a fossa that has a distinct bony rim on all sides, but that is not enclosed by a bony lip, like those in dorsal centra of adult *Barapasaurus* or juvenile *Apatosaurus*. The
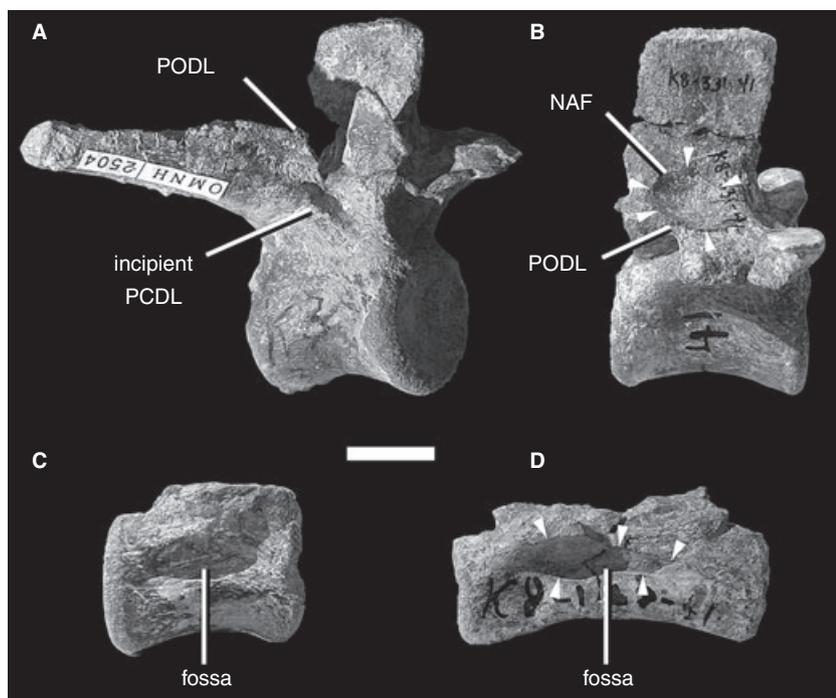
TEXT-FIG. 7. Dorsal and caudal vertebrae of *Goniopholis stovalli*. These vertebrae are part of an associated collection of several individuals from the type locality of the species. A, a dorsal vertebra (OMNH 2504) in left posterolateral view. B, a dorsal vertebra (OMNH 2470) in right lateral view. C, a middle caudal centrum (OMNH 2448) in right lateral view. D, a distal caudal centrum (OMNH 2454) in left lateral view. White arrows in B and D highlight the margins of fossae. Scale bar represents 1 cm.

penultimate example is a fossa that is enclosed by a bony lip, but that is little expanded beyond the boundaries of the opening, such as the fossae in presacral centra of *Haplocanthosaurus* [Britt (1993) referred to these chambers as camerae, whereas Wedel termed them fossae (Wedel *et al.* 2000; Wedel 2003*a*). The morphology of these features is intermediate between that of fossae and camerae, and either term could reasonably be applied]. Finally, in neosauropods such as *Camarasaurus* and *Saltasaurus* the space beyond the bony lip is greatly expanded, so that the result is a foramen that leads to camerae or camellae.

The fossae along this spectrum vary in geometry and they are not all pneumatic. Although *Goniopholis* is extinct and not part of the crown-group Crocodylia, it is highly unlikely that the caudal vertebrae of this semi-aquatic neosuchian were pneumatic. Nevertheless, they bear lateral fossae with distinct margins that are very similar to structures that are sometimes interpreted as pneumatic in dinosaurs, such as the sacral 'pleurocoels' of ornithomimosaurs. However, distinct margins alone are not compelling evidence of pneumaticity. Conversely, truly pneumatic fossae need not have distinct margins. For example, the fossae behind the prezygapophyses of ratites lack clear margins, but CT scans show that they house pneumatic diverticula, and they sometimes contain pneumatic foramina (Text-fig. 9). In extant birds, the pneumatic canalis intertransversarius lies alongside the centrum (Müller 1908), but many birds have cervical centra that are laterally convex and lack any fossae (the

pneumatic foramina are usually located inside the cervical rib loop or ansa costotransversaria).

The foregoing discussion implies that where chambers lack a distinct lip of bone, geometry alone is a poor clue to whether or not a given fossa has a pneumatic origin. Other lines of evidence must be used, such as position in the body, the presence or absence of adjacent pneumatic foramina, subfossae, or textural differences (and even the last two may be misleading; see O'Connor 2006).

Vertebral centra of 'prosauropods' can be quite narrow-waisted, and some have lateral grooves or fossae that are bounded on one side by a lamina. As with neural arch laminae, these features are sometimes associated with pneumaticity but they are not diagnostic for it. The 'pleurocoelar indentations' mentioned by Galton and Upchurch (2004) do not have a distinct boundary or lip in any of the specimens that I have examined (e.g. Moser 2003, pl. 16). The only known 'prosauropod' with distinctly emarginated lateral fossae is *Thecodontosaurus caducus* (Yates 2003). Cervical vertebrae 6–8 of BMNH P24, the holotype of *T. caducus*, have small, distinct fossae just behind the diapophyses (Text-fig. 10). The fossae are high on the centra and may have crossed the neurocentral sutures, which are open. The fossa on the eighth cervical looks darker than it should because it is coated with glue. The ninth cervical has a very shallow, teardrop-shaped hollow in the same region of the centrum. The bone texture in this hollow is noticeably smoother than on the rest of the centrum (this is especially apparent under low-angle lighting). That the fossa on the ninth

TEXT-FIG. 8. Diagram showing the evolution of fossae and pneumatic chambers in sauropodomorphs and their outgroups. Vertebrae are shown in left lateral view with lines marking the position of the cross-sections, and are not to scale. The omission of 'prosauropods' from the figure is deliberate; they have no relevant apomorphic characters and their vertebrae tend to resemble those of many non-dinosaurian archosaurs. Cross-sections are based on first-hand observation (*Giraffa* and *Arizonasaurus*), published sections (*Barapasaurus*, *Camarasaurus* and *Saltasaurus*) or CT scans (*Apatosaurus* and *Haplocanthosaurus*). *Giraffa* based on FMNH 34426. *Arizonasaurus* based on MSM 4590 and Nesbitt (2005, fig. 17). *Barapasaurus* based on Jain *et al.* (1979, pls 101–102). *Apatosaurus* based on CM 11339. *Haplocanthosaurus* based on CM 572. *Camarasaurus* based on Ostrom and McIntosh (1966, pl. 24). *Saltasaurus* modified from Powell (1992, fig. 16).
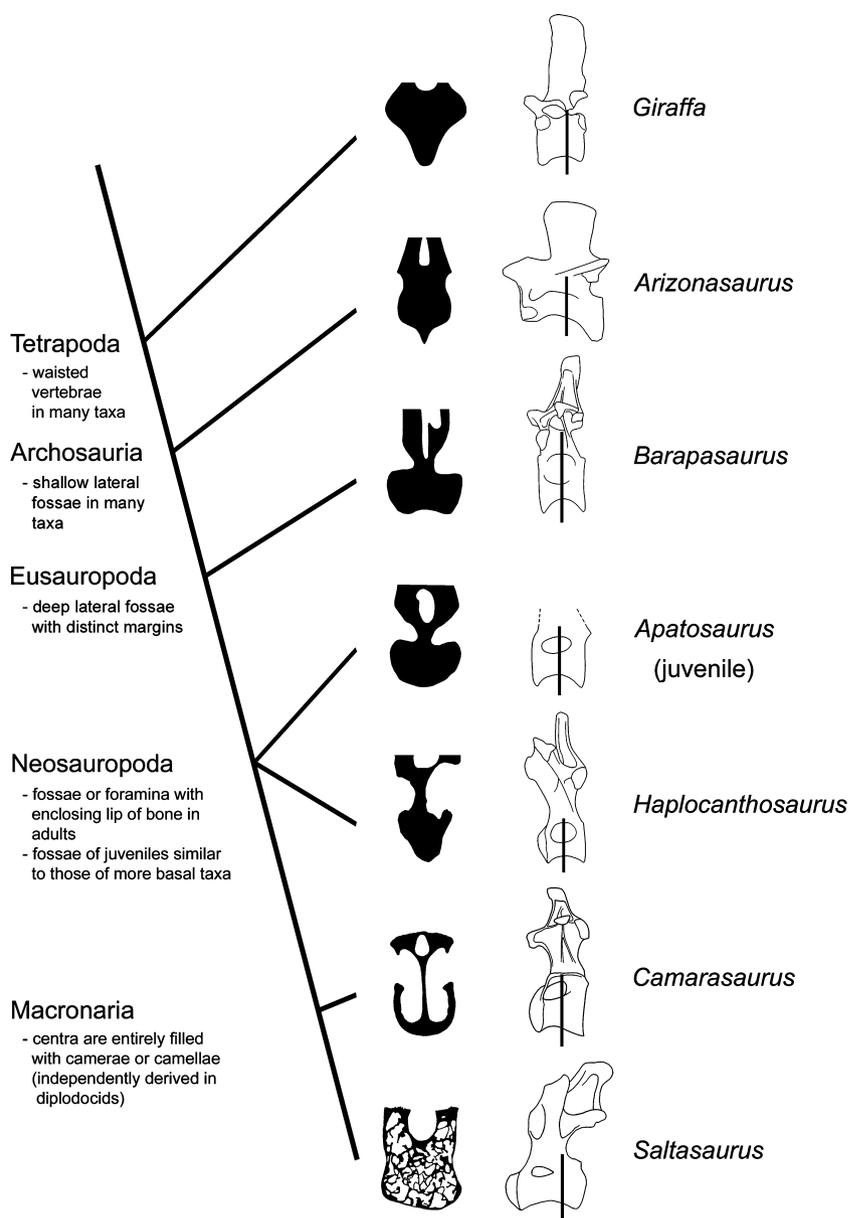
cervical is shallower and less distinct than those on cervicals 6–8 is reminiscent of the diminution of pneumatic features observed at the transition from pneumatic to apneumatic vertebrae, as seen in the anterior dorsal vertebrae of *Jobaria* (Sereno *et al.* 1999, fig. 3) and the middle caudal vertebrae of *Diplodocus* (Osborn 1899, fig. 13). The holotype specimen of *T. caducus* represents an immature individual (Yates 2003), however, so the shallow fossa on the ninth cervical may be incompletely developed.

Are the fossae of *T. caducus* pneumatic? If so, they are the only good evidence for invasive pneumatic features in the postcrania of 'prosauropods'. Previously, I have assumed that they were pneumatic, based in part on the

distinct margins of the fossae in cervicals 6–8, and also on the fact that the fossae only occur on cervicals 6–9 (Wedel 2006). The first line of evidence is inadequate to diagnose pneumaticity unequivocally. The second is also problematic. Cervical vertebrae 5–9 are the only ones that are always pneumatized in the chicken (Hogg 1984a), and the cervical and anterior thoracic vertebrae are the first parts of the axial skeleton to be pneumatized during the ontogeny of birds (Cover 1953; Hogg 1984b). The spread of pneumaticity posteriorly along the vertebral column in the ontogeny of birds appears faithfully to recapitulate the evolution of pneumaticity in theropods and sauropods (Wedel 2003b, 2005). The presence of fossae on the midcervical vertebrae of *T. caducus* is easily explained if
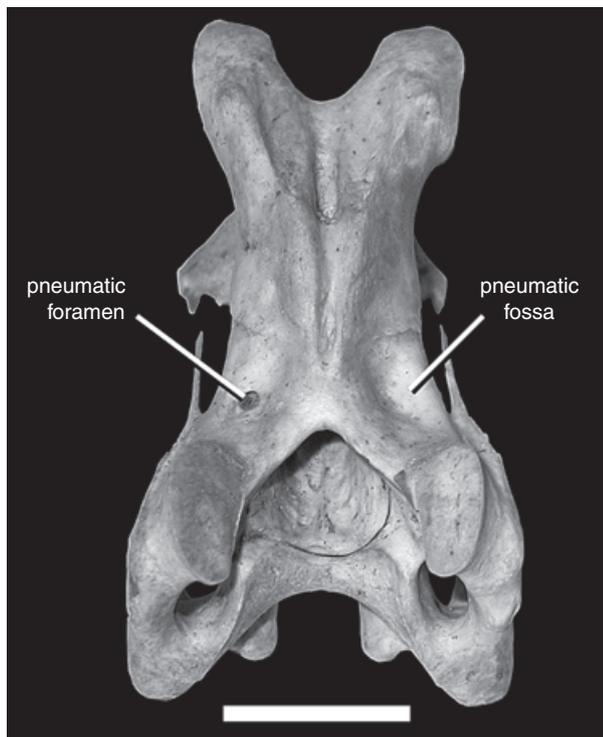
TEXT-FIG. 9. An uncatalogued cervical vertebra of an emu (*Dromaius novaehollandiae*) from the OMNH comparative collection. Scale bar represents 2 cm.

the fossae are pneumatic; their appearance in that part of the skeleton mirrors early ontogeny in birds and is also consistent with later trends in the evolution of PSP in sauropodomorphs (Text-fig. 2). On all four vertebrae, the fossae are not closely associated with laminae and cannot be dismissed as epiphenomena of lamina formation (see O'Connor 2006); a specific soft-tissue influence was causally related to the formation of the fossae. The geometry of the fossae is not sufficient to specify that soft-tissue influence because adipose, muscular and pulmonary tissues have all been found to occupy similar fossae in other tetrapods (O'Connor 2006). On the other hand, the presence of the fossae only on the midcervical vertebrae is difficult to explain if they were not produced by pneumatic diverticula like those of more derived sauropods.

Summary. Vertebral laminae and shallow depressions on the centra are widespread in archosauriforms and not diagnostic of pneumaticity, although it is difficult to rule out the possibility that they may have been associated with pneumatic diverticula. 'Prosauropods' have fewer laminae than most sauropods, fewer vertebrae with laminae, and the fossae adjacent to the laminae are almost always blind (with no large foramina or chambers). A foramen in a vertebra of *Plateosaurus* and distinct fossae in the cervical vertebrae of *Thecodontosaurus caducus* are

the best evidence for potential pneumaticity in 'prosauropods', but neither is an unambiguous indicator of PSP and both would benefit from further study. In any case, the diagnostic osteological correlatives of pneumaticity that are common in sauropods and theropods are absent or extremely rare in 'prosauropods', and the putative pneumatic features that are widespread in 'prosauropods' (laminae and shallow fossae) are not compelling evidence of pneumaticity. To leave aside for a moment the question of 'prosauropod' monophyly, 'prosauropods' are unusual as the only sizeable group (or grade) of saurischian dinosaurs that lack extensive PSP.

PALAEOBIOLOGICAL IMPLICATIONS

Pneumatic bones are of palaeobiological interest in two ways. We may be interested in the bones themselves: in their external and internal morphology, in the ratio of bone to air space, and in the ways that they develop. They are also important, arguably more important, as osteological markers of the pulmonary system. In this section I discuss the origins of pneumaticity and of air sacs, and the implications for the respiratory physiology of sauropodomorphs.

Origin of the diverticular lung and PSP. The first part of the postcranial skeleton to be pneumatized in any saurischian dinosaur is the cervical column. The fossae in the mid-cervical vertebrae of *Thecodontosaurus caducus* are not definitely pneumatic on the basis of geometry alone. However, their placement in the skeleton is suspiciously similar to the early stages of pneumatization in birds. The same is true of fossae in the cervical column of the basal sauropod *Shunosaurus* (Wilson and Sereno 1998). Among basal theropods, *Coelophysis bauri* is the earliest well-represented taxon with evidence of pneumaticity. The postaxial cervical vertebrae of *C. bauri* have pneumatic cavities that occupy most of the neural spine and that communicate with the outside through several large foramina (Colbert 1989).

The pattern of pneumatization in these early diverging saurischians indicates the presence of cervical air sacs like those of birds. It is true that in sauropsids diverticula may develop from practically any portion of the respiratory system. However, it does not follow that the diverticula that pneumatize the skeleton can come from anywhere (contra Hillenius and Ruben 2004), for two reasons. First, in extant birds the cervical vertebrae are only pneumatized by diverticula of cervical air sacs. Diverticula of the cranial air spaces, larynx and trachea are never known to pneumatize the postcranial skeleton (King 1966), and diverticula of the parenchymal portion of the lung only pneumatize the vertebrae and ribs adjacent to
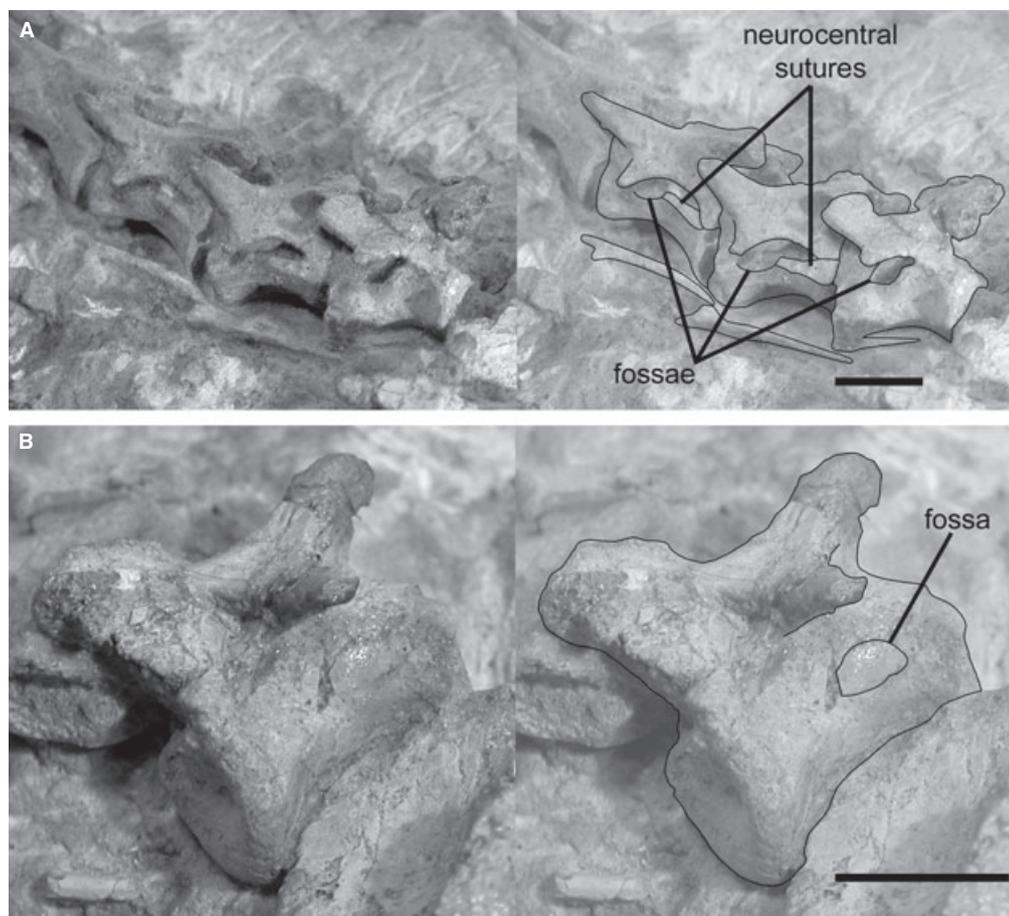
TEXT-FIG. 10. Vertebrae of *Thecodontosaurus caducus*, BMNH P24. A, cervical vertebrae 6–8 in left lateral view. B, cervical vertebra 9 in right lateral view. Scale bars represent 1 cm.

the lungs (O'Connor 2004). Second, as discussed below, pneumatization of the posterior half of the body is accomplished only by diverticula of abdominal air sacs (O'Connor and Claessens 2005). These observations of extant taxa provide valuable guidelines for interpreting patterns of skeletal pneumatization in fossil taxa. Pneumatization by diverticula of cervical air sacs is the only mechanism for pneumatizing the neck that is (1) known to occur in extant taxa and (2) consistent with the pattern of pneumatization found in basal saurischians (Wedel 2006).

Pneumaticity in basal saurischians is extremely limited. The bone removed by pneumatization of the postcranial skeleton (or fossa formation, if the fossae of *Thecodontosaurus* are not pneumatic) accounted for much less than 1 per cent of the total body volume in both *Coelophysis* and *Thecodontosaurus* (see Appendix), compared with several per cent for more derived sauropods and theropods (Wedel 2004, 2005). PSP probably did not evolve as an adaptation for lightening the skeleton, although it seems to have been exapted for that purpose later in saurischian evolution (Wedel 2003b).

Furthermore, diverticula did not evolve to pneumatize the skeleton. In the first place, many of the diverticula of birds are visceral, subcutaneous or intermuscular, and do not pneumatize any bones (Duncker 1971). Skeletal pneumatization cannot be invoked to explain the presence of these diverticula. In the second place, the presence of diverticula is a prerequisite for pneumatization of the skeleton. The immediate ancestors of *Coelophysis* and *Thecodontosaurus* must have already had cervical diverticula (assuming that the fossae of the latter are pneumatic in origin). Pneumatization of the cervical series could not happen until these diverticula were already in place, so the diverticula must have evolved for some other reason.

Alternatively, the origins of paravertebral diverticula and of PSP may have been coincident. The first step may have been a developmental accident that allowed the diverticula to push beyond the coelom and these 'unleashed' diverticula may have pneumatized the vertebral column immediately. This sort of morphogenetic behaviour on the part of diverticula is plausible on the basis of cases in the human clinical literature (e.g. Sadler *et al.* 1996; Anorbe *et al.* 2000). The main argument

against this near-saltational scenario is that the first vertebrae to be pneumatized in both sauropodomorphs (*Thecodontosaurus*, *Shunosaurus*) and theropods (*Coelophysis*) are cervicals that are not adjacent to the lungs (Wedel 2006).

Origin of flow-through ventilation. Flow-through ventilation requires that air sacs be present both anterior and posterior to the parenchymal portion of the lung. Given the pattern of pneumatization found in pterosaurs, sauropods and theropods, we may infer that cervical air sacs were present in the ancestral ornithodiran (or evolved independently in pterosaurs and saurischians). The next problem is to determine when abdominal air sacs originated and how many times.

In extant birds, the posterior thoracic, synsacral and caudal vertebrae, pelvic girdle and hindlimb are only pneumatized by diverticula of abdominal air sacs (O'Connor and Claessens 2005; contra Ruben *et al*. 2003; Chinsamy and Hillenius 2004; Hillenius and Ruben 2004). So if a fossil archosaur is discovered with pneumatic vertebrae posterior to the mid-thorax, we have a compelling case for inferring that the animal had abdominal air sacs. Pneumatic vertebrae in the 'posterior compartment' are present in pterosaurs, diplodocid and macronarian sauropods, and in most clades of neotheropods, but are absent in non-dinosaurian dinosauromorphs, ornithischians, herrerasaurids, 'prosauropods', basal sauropods, dicraeosaurids, and in basal members of most neotheropod clades (e.g. *Baryonyx*, *Ceratosaurus* and *Allosaurus*; pers. obs.).

How many times did abdominal air sacs evolve? Possibly just once, before the ornithodiran divergence; possibly twice, in pterosaurs and saurischians; or possibly three times, in pterosaurs, sauropods and theropods (Text-fig. 1). We could take this to its logical conclusion and assume that abdominal air sacs evolved afresh in every group with posterior compartment pneumaticity; this would require the independent origin of abdominal air sacs in ceratosaurs, allosauroids and coelurosaurs, for example (not to mention several independent derivations within coelurosaurs).

The alternative is that some or all of the groups listed above had abdominal air sacs but failed to pneumatize any elements in the posterior compartment. The same condition pertains in many extant birds (O'Connor 2004, table 2). O'Connor and Claessens (2005) posited an origin of abdominal air sacs by the time of the ceratosaur-tetanuran divergence, based on the presence of posterior compartment pneumatization in *Majungatholus*, and despite its absence in basal ceratosaurs and basal tetanurans.

In terms of evolutionary change, ventilation mechanisms are highly conserved, PSP is highly labile and diverticula seem to lie between these extremes. All birds have essentially the same lung architecture; the biggest difference among living forms is the presence or absence of a neopulmo (Duncker 1971). On the other hand, PSP varies widely within small clades and even within populations (King 1966; Hogg 1984*a*; O'Connor 2004). Diverticula appear to be more conserved than PSP, although a dedicated study comparing the evolution of the two is needed. For example, most birds have femoral and perirenal diverticula, but the femur and pelvis are only pneumatized in a subset of these taxa (Müller 1908; King 1966; Duncker 1971). These observations are necessarily tentative, given the paucity of phylogenetically based comparative studies of pneumatic diverticula and PSP (but see O'Connor 2004). Furthermore, our knowledge of variation in the pulmonary system and its diverticula is based entirely on extant birds, and may not be applicable to other saurischians.

Nevertheless, the evolutionary malleability of lungs, diverticula and PSP in birds should not be ignored in reconstructing the pulmonary systems of fossil archosaurs. The absence of unequivocal PSP in most 'prosauropods' does not mean that they lacked air sacs. Depending on the preferred phylogenetic hypothesis, Sauropodomorpha is only one or two nodes away from Neotheropoda. Most neosauropods have pneumatic vertebrae in the posterior compartment. If these sauropods found some way to pneumatize the posterior compartment without abdominal air sacs, then surely the same could be true of some or all non-avian theropods. Likewise, if posterior compartment pneumaticity is *prima facie* evidence of abdominal air sacs in theropods, then abdominal air sacs must also have been present in sauropods (and, by extension, pterosaurs). What is good for the goose is good for *Gongxianosaurus*. It is more parsimonious to infer that cervical and abdominal air sacs were present in the ancestral saurischian, but did not pneumatize the skeleton in 'prosauropods', than to infer independent origins of air sacs in sauropods and theropods.

Most pterosaurs have extensively pneumatized skeletons, although it is not clear whether pneumaticity is present in any of the Triassic forms (Bonde and Christiansen 2003). The presence of PSP in pterosaurs, sauropodomorphs and theropods suggests that air sacs may have been present in the ancestral ornithodiran. An apparent problem with pushing the origin of air-sac-driven breathing back before the origin of Saurischia is the utter absence of PSP in ornithischians. PSP appeared in pterosaurs, sauropodomorphs and theropods relatively quickly after the divergence of each clade: by the Norian in theropods (Colbert 1989) and no later than the Early Jurassic in pterosaurs and sauropodomorphs (Bonde and Christiansen 2003; Wedel 2005). If ornithischians had air sacs and diverticula

then it is odd that they never evolved PSP during the 160 million years of their existence. However, this problem may be more illusory than real. The invasion of bone by pneumatic epithelium is essentially opportunistic (Witmer 1997). Although pneumatic diverticula may radically remodel both the exterior and the interior of an affected bone, this remodelling cannot occur if the diverticula never come into contact with the bone, and may not occur even if they do. Furthermore, for all of the potential advantages it conveys, PSP is still an exaptation of a pre-existing system: in an adaptive sense, lineages that lack PSP do not know what they are missing. Recall that PSP in basal saurischians did little to lighten the skeleton (see above). Ornithischians may have had air sacs without diverticula, or diverticula without PSP. It is pointless to consider the advantages that ornithischians 'lost' by never evolving PSP, because that evolution would have hinged on the incidental contact of bone and air sac and could not have been anticipated or sought by natural selection.

The problem of determining when abdominal air sacs evolved is challenging because it forces us to decide between events of unknown probability: the possibility that ornithischians had an air sac system and never 'discovered' PSP (if abdominal air sacs are primitive for Ornithodira), vs. the possibility that a system of cervical and abdominal air sacs evolved independently in pterosaurs and saurischians. Currently, available evidence is insufficient to falsify either hypothesis.

Sauropodomorph palaeobiology. It is likely that 'prosauropods' had cervical and abdominal air sacs, given the strong evidence for both in sauropods and theropods. We may not be able to determine for certain whether 'prosauropods' had a bird-like flow-through lung, but the requisite air sacs were almost certainly present. Our null hypothesis for the respiratory physiology of 'prosauropods' should take into account some form of air-sac-driven ventilation.

The air sacs of birds mitigate the problem of tracheal dead space (Schmidt-Nielsen 1972), and some birds have improbably long tracheae (i.e. longer than the entire body of the bird; see McClelland 1989). In addition, birds can ventilate their air sacs without blowing air through the lungs, which allows them to avoid alkalosis during thermoregulatory panting (Schmidt-Nielsen *et al.* 1969). Finally, flow-through breathing allows birds to extract much more oxygen from the air than mammals can (Bernstein 1976). In general, sauropods were larger and longer-necked than 'prosauropods', and the aforementioned capabilities of a bird-like ventilation system may have helped sauropods overcome the physiological challenges imposed by long necks and large

bodies, including tracheal dead space, heat retention and oxygen uptake.

The one obvious advantage that 'prosauropods' did not share with sauropods is the very lightweight skeletal construction afforded by pneumaticity. In life, the average pneumatic sauropod vertebra was approximately 60 per cent air by volume (Wedel 2005; Woodward 2005; Schwarz and Fritsch 2006). All else being equal, a sauropod could have a neck two-thirds longer than that of a prosauropod for the same skeletal mass. Pneumaticity helped sauropods overcome constraints on neck length, and thereby opened feeding opportunities that were not available to 'prosauropods'. How important that difference was is unknown, but it is worth considering in reconstructions of sauropodomorph evolution and palaeobiology.

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APPENDIX

The method of calculating the volumes of bone removed by pneumatization in *Coelophysis* and *Thecondontosaurus* (see 'Palaeobiological implications' above) is provided here. To estimate the whole body volumes of the dinosaurs I used graphic double integration (GDI: Jerison 1973; Hurlburt 1999; Murray and Vickers-Rich 2004). I traced over the skeletal reconstructions of Colbert (1989, fig. 103) and Benton *et al.* (2000, fig. 19) to make lateral view body outlines. Dorsal view body outlines were drawn by hand based on those of Paul (1997) and digitally manipulated to match the dimensions of the skeletal reconstructions. Using GDI, I obtained whole body volumes of 23·5 L for *Coelophysis* and 3·3 L for the holotypic individual of *Thecodontosaurus caducus*; the latter animal is a small juvenile. Adjusted for scale, these results are consistent with previous mass estimates for both taxa (Peczkis 1994).

Pneumaticity is present throughout the cervical series of *Coelophysis*. The total length of the cervical series is *c.* 50 cm, and the vertebral centra have a mean diameter of 1 cm, based on measurements of uncatalogued CM specimens. The neural spines are roughly the same size as the centra. The combined cervical centra are treated as a simple cylinder 50 cm long with a diameter of 1 cm, which yields a volume of 40 cm^3. If the neural spines are assumed to be equal in volume to the centra, the combined volume of the cervical vertebrae is 80 cm^3. The cervical vertebrae of *Coelophysis* are probably not more than 50 per cent air by volume, based on observations of broken specimens, so the volume of bone removed during pneumatization of the cervical vertebrae was *c.* 40 cm^3, or 0·17 per cent of the volume of the body.

For *Thecondontosaurus caducus* it is simpler to calculate the volumes of the individual fossae. The fossae on cervicals 6–8 are each *c.* 5 mm long, 2·5 mm tall and 1·25 mm deep. The paired fossae on each vertebra can be thought of as forming the two halves of an oblate spheroid with x, y and z diameters of 5, 2·5 and 2·5 mm, respectively. The volume of this spheroid, and thus the volume of the paired fossae, is 0·016 cm^3. The fossae on cervicals 6–8 are all roughly the same size, and the visible fossa on the ninth cervical is only about half as deep. The volume of bone removed during fossa formation is therefore 0·057 cm^3, or 0·0017 per cent of the volume of the body.

These calculations are all approximate, but they are sufficient to demonstrate that PSP did not have a noticeable effect on the skeletal mass of basal saurischians. In the case that I have underestimated the volume of the pneumatic chambers in *Coelophysis* relative to the body volume by a factor of six: the volume of these chambers would still only be 1 per cent of the volume of the body. In contrast, the volume of air in the pneumatic vertebrae of *Tyrannosaurus* and *Diplodocus* accounted for 4–6 per cent of the volume of the animals. These air spaces replaced bone, a relatively dense tissue, and lightened the animals by 7–10 per cent (Wedel 2004, 2005).