# Postcranial Pneumaticity: An Evaluation of Soft-Tissue Influences on the Postcranial Skeleton and the Reconstruction of Pulmonary Anatomy in Archosaurs

Patrick M. O'Connor*

*Department of Biomedical Sciences, Ohio University, College of Osteopathic Medicine, Athens, Ohio 45701*

ABSTRACT    Postcranial pneumaticity has been reported in numerous extinct sauropsid groups including pterosaurs, birds, saurischian dinosaurs, and, most recently, both crurotarsan and basal archosauriform taxa. By comparison with extant birds, pneumatic features in fossils have formed the basis for anatomical inferences concerning pulmonary structure and function, in addition to higher-level inferences related to growth, metabolic rate, and thermoregulation. In this study, gross dissection, vascular and pulmonary injection, and serial sectioning were employed to assess the manner in which different soft tissues impart their signature on the axial skeleton in a sample of birds, crocodylians, and lizards. Results from this study indicate that only cortical foramina or communicating fossae connected with large internal chambers are reliable and consistent indicators of pneumatic invasion of bone. As both vasculature and pneumatic diverticula may produce foramina of similar sizes and shapes, cortical features alone do not necessarily indicate pneumaticity. Noncommunicating (blind) vertebral fossae prove least useful, as these structures are associated with many different soft-tissue systems. This Pneumaticity Profile (PP) was used to evaluate the major clades of extinct archosauriform taxa with purported postcranial pneumaticity. Unambiguous indicators of pneumaticity are present only in certain ornithodiran archosaurs (e.g., sauropod and theropod dinosaurs, pterosaurs). In contrast, the basal archosauriform *Erythrosuchus africanus* and other nonornithodiran archosaurs (e.g., parasuchians) fail to satisfy morphological criteria of the PP, namely, that internal cavities are absent within bone, even though blind fossae and/or cortical foramina are present on vertebral neural arches. An examination of regional pneumaticity in extant avians reveals remarkably consistent patterns of diverticular invasion of bone, and thus provides increased resolution for inferring specific components of the pulmonary air sac system in their nonavian theropod ancestors. By comparison with well-preserved exemplars from within Neotheropoda (e.g., Abelisauridae, Allosauroidea), the following pattern emerges: pneumaticity of cervical vertebrae and ribs suggests pneumatization by lateral vertebral diverticula of a cervical air sac system, with sacral pneumaticity indicating the presence of caudally expanding air sacs and/or diverticula. The identification of postcranial pneumaticity in extinct taxa minimally forms the basis for inferring a heterogeneous pulmonary system with distinct exchange and nonexchange (i.e., air sacs) regions. Combined with inferences supporting a rigid, dorsally fixed lung, osteological indicators of cervical and abdominal air sacs highlight the fundamental layout of a flow-through pulmonary apparatus in nonavian theropods. J. Morphol. 267:1199–1226, 2006. © 2006 Wiley-Liss, Inc.

KEY WORDS: pneumaticity; air sacs; postcranial skeleton; Archosauria; Dinosauria

Osteological features preserved in the postcranium of fossil archosaurs, particularly saurischian dinosaurs, have been interpreted as pneumatic, with implied causal relationships between this morphology and a pulmonary air sac system similar to the one in extant birds (von Meyer, 1837; Owen, 1856; Seeley, 1870; Janensch, 1947; Romer, 1966; Britt, 1993, 1997; Britt et al., 1998; Gower, 2001; O'Connor, 2003; Wedel, 2003b). In contrast, recently discovered theropod dinosaurs with preserved soft tissues (e.g., Chen et al., 1998; Ji et al., 1998) have led to reconstructions of pulmonary anatomy that drastically differ from those proposed by pneumaticity advocates. In two different theropods, *Sinosauropteryx prima* and *Scipionyx samniticus*, Ruben et al. (1997, 1999, 2003) postulated the existence of a hepatic-piston ventilatory system, based on inferred similarities of body cavity organization with the condition observed in extant crocodylians. They furthermore propose that this system would have prevented the development of an air sac-based ventilatory mode as in extant birds. Notably, these studies fail to address the significance of postcranial pneuma-

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ticity and its bearing on reconstructions of pulmonary anatomy.

As an anatomical condition, pneumaticity refers to the air-filled nature of certain structures or compartments of the body. Pneumatic features typically consist of foramina in cortical bone, often leading to internal chambers in vertebral neural arches and centra. Other traits such as osseous fossae and differential surface texture also have been used as indicators of pneumaticity in fossil groups.

Whereas some employ pneumatic features as characters in phylogenetic analyses (e.g., Gauthier, 1986; Rowe and Gauthier, 1990; Wilson and Sereno, 1999; Carrano et al., 2002), others use them to model respiratory structure–function relationships and as the basis for higher-level physiological inferences related to thermoregulatory ability (Madsen, 1976; Colbert, 1989; Perry, 1992, 2001; Britt, 1993; Perry and Reuter, 1999; Wedel, 2003b; O'Connor and Claessens, 2005). Yet others merely cite the necessity of large animals to reduce body mass, as large fossae and internal cavities within bone (regardless of whether or not the author promoted an air sac origin for them) provide a means of maintaining strength with minimizing materials (Cope, 1877; Marsh, 1877; Osborn, 1899; Romer, 1966; Carrano and O'Connor, 2005).

Generally, pneumatic spaces in bones of extant amniotes are lined by epithelium and communicate with the external environment via pneumatic foramina along the length of the respiratory tract. Many amniote groups exhibit cranial pneumaticity via communications with: 1) the nasal cavity—as in paranasal sinuses, and 2) the pharynx—as in tympanic pneumaticity. These two systems can pneumatize much of the cranial skeleton in different groups (e.g., avian and nonavian dinosaurs; see Witmer, 1990, 1995b, 1997).

Postcranial pneumaticity in extant amniotes is restricted to birds (Fig. 1) and originates from the lung–air sac system (Müller, 1908; King, 1966; Duncker, 1971, 1983; O'Connor, 2004). Whereas main air sacs reside within the body cavity, finger-like projections (i.e., *pneumatic* or *pulmonary* diverticula) originate from air sacs and lungs, and extend throughout both soft and skeletal tissues of the body wall. A pulmonary-injection preparation of a duck (Fig. 2A) illustrates the extensive nature of the air sac system and pneumatic diverticula in birds. A variety of morphologies are associated with air sac invasion of bone, ranging from discreet, simple foramina to complex networks of irregularly shaped openings in the cortical surface (Fig. 2B–D). Although postcranial pneumaticity is generally present in vertebrae, ribs, girdles, and proximal limb elements, there is considerable variation in the relative extent of postcranial pneumaticity among different avian taxa (Crisp, 1857; Campana, 1875; Bignon, 1889; Müller, 1908; Groebbels, 1932; King
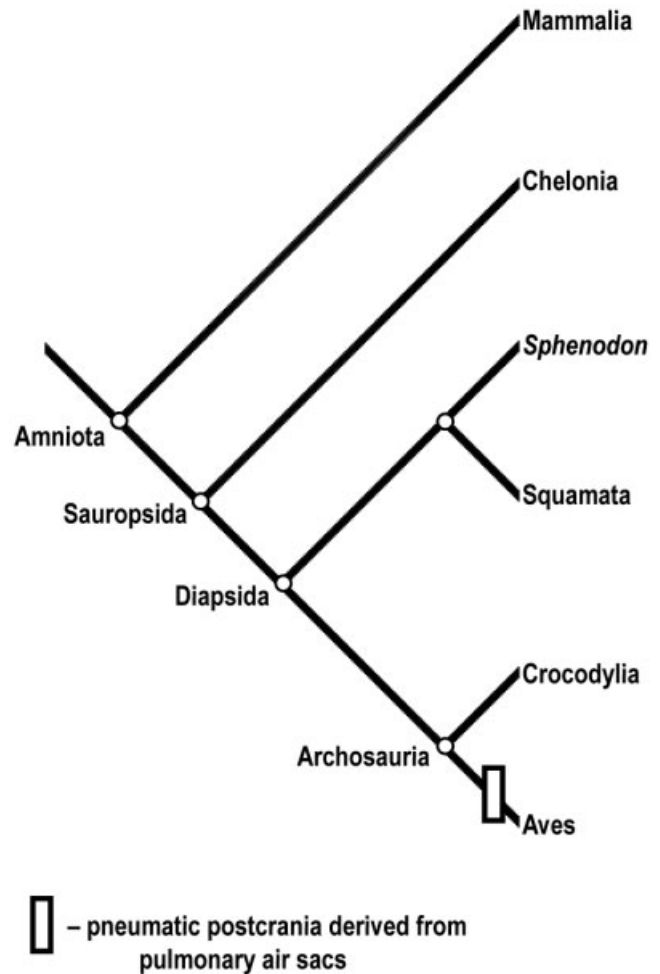


Fig. 1. Phylogenetic hypothesis of extant amniote relationships based on Gauthier (1994)—birds (Aves) are the only extant amniote group possessing pneumaticity of the postcranial skeleton derived from pulmonary air sacs.

and Kelly, 1956; King, 1957, 1966; Hogg, 1984b; McLelland, 1989; O'Connor, 2004).

Crocodylians do not have pulmonary diverticula, but do exhibit areas of reduced parenchymal density in the cranial, caudal, and ventral regions of the lung (Duncker, 1978, 1979; Perry, 1983, 1989, 1992, 2001). These sac-like regions remain entirely within the body cavity and do not penetrate the postcranial skeleton. All other extant nonarchosaurian sauropsid groups (lizards, snakes, turtles) include species that also possess sac-like regions of the lung (Wood and Lenfant, 1976; Duncker, 1978, 1979, 1989; Perry, 1983, 1998), and these also do not pneumatize the postcranial skeleton. Such specializations in sauropsids are the basis for the concept of a heterogeneous pulmonary system, whereby parenchymal density, and thus gas exchange potential, varies throughout the system (e.g., see Duncker, 1978, 1989; Perry, 1983).

Among extinct sauropsids, putative pneumatic features have been identified in a variety of fossil
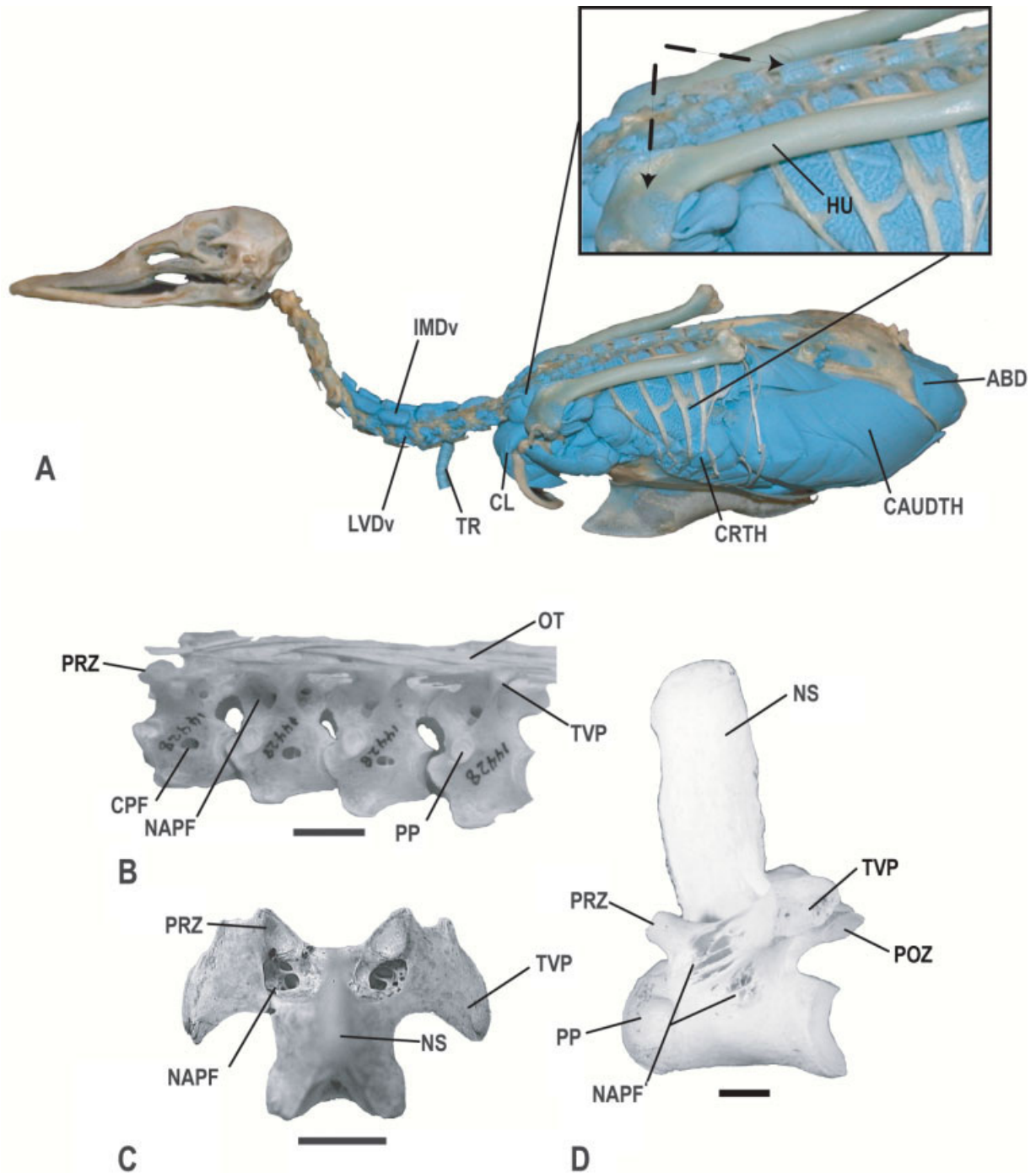
Fig. 2. The pulmonary air sac system (**A**) and osteological correlates (**B–D**) of pneumatic invasion of bone in birds. Scale bars = 1 cm. **A:** Green-winged teal (*Anas crecca*, JLUG 1). Skeletal-latex preparation to demonstrate the extent of the pulmonary-air sac system: note intermuscular (IMDv) and lateral vertebral (LVDv) diverticula along the cervical vertebral series. Dashed arrows in inset indicate injected latex (blue) within humerus and thoracic vertebrae. **B:** Hawaiian goose (*Branta sandvicensis*, CM 14428). Thoracic vertebral series, left lateral view. **C:** Southern ground hornbill (*Bucorvus leadbeateri*, TM 76018). Thoracic vertebra—dorsal view, cranial end facing toward top of image. **D:** Ostrich (*Struthio camelus*, FMNH 222324). Thoracic vertebra, left lateral view. ABD, abdominal air sac; CAUDTH, caudal thoracic air sac; CL, clavicular (interclavicular) air sac; CPF, central pneumatic foramen; CRTH, cranial thoracic air sac; HU, humerus; IMDv, intermuscular diverticulum; LVDv, lateral vertebral diverticulum; NAPF, neural arch pneumatic foramen/fossa; NS, neural spine; OT, ossified tendons; POZ, postzygapophysis; PP, parapophysis; PRZ, prezygapophysis; TR, trachea; TVP, transverse process.

archosaurs including pterosaurs, theropod and sauropod dinosaurs, and basal birds (e.g., Owen, 1856; Seeley, 1870, 1901; Janensch, 1947; Romer, 1966; Bennett, 1991; Britt, 1993; Britt et al., 1998; Forster et al., 1998; O'Connor, 2003; Wedel, 2003a). Osteological features described as pneumatic in fossil specimens include cortical foramina as well as various forms of fossae associated with both vertebral centra and neural arches (Fig. 3). Whereas postcranial pneumaticity is generally restricted to the axial skeleton in nonavian dinosaurs (Romer, 1966; Britt, 1993; Wilson, 1999; O'Connor, 2003; Wedel, 2003a), it has been identified in both axial and appendicular elements of pterosaurs (Seeley, 1901; Bennett, 1991; O'Connor, 2002). Pneumatic features have even been identified in embryonic vertebrae of troodontid (Varricchio et al., 2002) and oviraptorid (Norell et al., 2001) theropods. Finally, both axial and appendicular pneumaticity have been described in the postcranial skeleton of basal avians (e.g., *Archaeopteryx, Rahonavis*; Britt et al., 1998; Forster et al., 1998; Christiansen and Bonde, 2000).

## Taxonomic Distribution of Postcranial Pneumaticity: Archosauriformes

Previous interpretations of postcranial pneumaticity in fossil archosaurs suggest a variable distribution among ornithodiran taxa including examples within both Pterosauria and Saurischia (Fig. 4). Although crurotarsan, ornithischian dinosaur, and basal archosauriform groups are generally regarded as lacking pneumatic postcrania (Romer, 1956; Britt, 1993; Gauthier, 1986), Gower (2001) described pneumatic vertebrae in the basal archosauriform *Erythrosuchus africanus* and certain crurotarsan taxa (e.g., parasuchians), thereby significantly expanding the distribution of postcranial pneumaticity among Archosauriformes (Fig. 4). As interpreted, postcranial pneumaticity may represent a primitive condition for the archosauriform clade and its absence in extant crocodylians, and presumably any other taxa lacking pneumaticity (e.g., ornithischian dinosaurs, etc.), is a derived trait (see Gower, 2001).

Although postcranial pneumaticity appears to have a much broader distribution among fossil groups than living forms, pneumaticity research in extinct groups often lacks direct comparisons with soft-tissue data derived from extant taxa. Most studies rely on comparisons between the fossils of interest and avian skeletons (e.g., Britt, 1993; Christiansen and Bonde, 2000). Moreover, even the critical assessment of pneumaticity in living birds often lacks direct corroboration through the study of the variety of soft tissues that influence vertebral morphology.

Subjective interpretations of morphology combined with imprecise terminology (e.g., excavation, fossa, foramen, pneumatopore, pleurocoel) have hindered the identification of unambiguous pneumatic
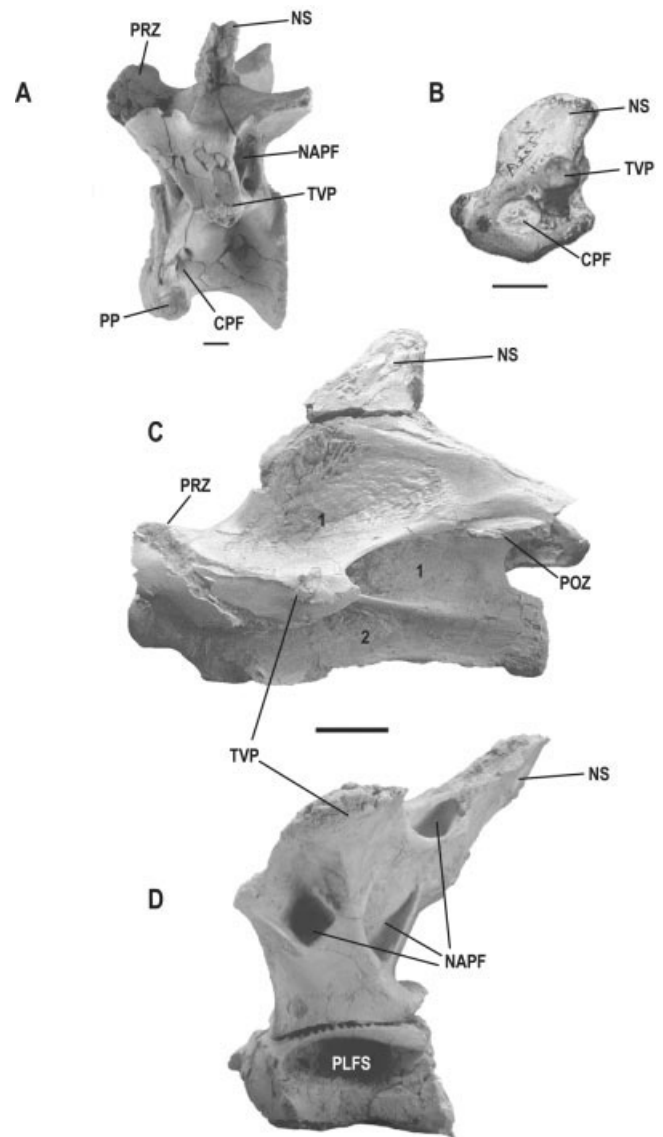


Fig. 3. Inferred pneumatic features in fossil archosaur specimens. Scale bars = 1 cm in **A,B;** 5 cm in **C,D. A:** Theropod dinosaur (*Majungasaurus crenatissimus*, UA 8678). Caudal cervical vertebra, left lateral view. **B:** Ornithocheirid pterosaur (*Ornithocheirus* sp., SM B54.302). Fused atlas-axis complex, left lateral view. **C:** Sauropod dinosaur (*Rapetosaurus krausei*, FMNH PR 2209). Caudal cervical vertebra, left lateral view; note large fossae on both neural arch (1) and centrum (2). **D:** Sauropod dinosaur (*Rapetosaurus krausei*, FMNH PR 2209). Cranial thoracic (dorsal) vertebra, left lateral view. CPF, central pneumatic foramen; NAPF, neural arch pneumatic foramen/fossa; NS, neural spine; PLFS, pulmonary fossa; POZ, postzygapophysis; PP, parapophysis; PRZ, prezygapophysis; TVP, transverse process.

structures. Until rigorous criteria are established for recognizing pneumatic features, reconstructions of pulmonary structure and higher-level inferences related to function (e.g., ventilatory and/or thermoregulatory potential) are unreliable at best. Recent anatomical studies of extant sauropsids (e.g., O'Connor, 2003) indicate that a number of other soft-tissue systems influence vertebral morphology
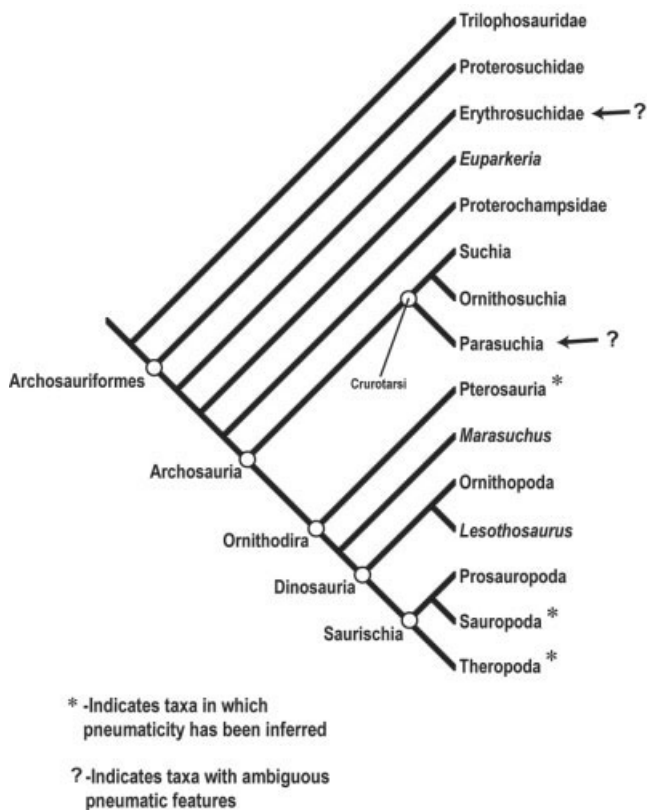
Fig. 4. Phylogenetic hypothesis of Archosauriformes based on Sereno (1991), Gower and Wilkinson (1996), and Brochu (2001) showing the distribution of taxa with inferred postcranial pneumaticity (*), traditionally limited to the Ornithodiran archosaurs. A recent study (Gower, 2001) suggested the presence of pneumatic vertebrae in the basal archosauriform *Erythrosuchus africanus* and other nonornithodiran taxa (e.g., parasuchians; indicated by ? on the diagram).

by the formation of similarly shaped foramina and fossae; hence, reliable indicators of pneumaticity in fossil specimens often remain ambiguous and subjective. The goal of this contribution is to examine putative pneumatic features in the postcranial skeleton of archosauriform taxa and to discuss implications of using such features for reconstructing pulmonary anatomy.

### Objectives

This study evaluates pneumatic features in saurischian dinosaurs, pterosaurs, parasuchians, and the basal archosauriform *Erythrosuchus* by first examining causal relationships between different soft-tissue systems and skeletal morphology in both groups of extant archosaurs (birds and crocodylians). It then assesses the influence of various soft tissues (e.g., pulmonary, neurovascular, muscular) on vertebral morphology, and contrasts osteological correlates of different systems with regard to *system specificity* and *reliability* for interpreting fos-

sil specimens. Finally, this study addresses the fundamental issue of pneumaticity versus apneumaticity in fossil taxa with reference to reconstructing pulmonary anatomy in extinct taxa, and thereby provides a framework for constraining functional inferences related to the evolution of the archosaurian respiratory apparatus.

## MATERIALS AND METHODS

Primary data were collected from extant crocodylians (*Alligator, Caiman, Crocodylus, Melanosuchus, Tomistoma*) and birds (96 species representing most traditional ordinal groupings) (Appendix A) and applied to fossil archosauriform specimens (Appendix B), with lizards and turtles used as outgroup reference taxa. Osteological studies were combined with gross dissection of whole specimens, corrosion casting of vascular and pulmonary systems, and serial sectioning to assess causal relationships between different soft tissues and bony morphologies of the postcranial axial skeleton. Animals used in this study were salvage specimens provided by wildlife rehabilitators, museums, and zoos. Two hundred thirty-four avian specimens that had undergone pulmonary injection preparations were used in this study. The majority of these are housed in the collections of H.-R. Duncker at the University of Giessen, Germany (denoted with the prefix JLUG in Appendix A). Other specimens were prepared in the Department of Biomedical Sciences at Ohio University (OUVC) and the Department of Anatomical Sciences at Stony Brook University (SBU), Long Island, NY. Additional avian specimens were used for both muscular and vascular preparations. The use of crocodylian and nonarchosaurian sauropsids provides additional comparative data for other (nonpulmonary) soft tissues including musculature and neurovasculature. See Appendix A for a complete list of species used and the type(s) of preparations for each.

The Extant Phylogenetic Bracket (EPB) method (Witmer, 1995a) was used to establish the choice of extant reference taxa (Fig. 5). The EPB constrains fundamental inferences regarding potential tissue types in fossil groups, and is a necessary prerequisite before higher-level inferences concerning functional attributes or behavioral characteristics of fossil organisms may be assessed (Witmer, 1995a, 1997). Postcranial pneumaticity in fossil archosaurs represents a Level II inference, as only one of the extant sister groups (Avians) have the soft-tissue system of interest (Fig. 5; Witmer, 1995a). See Perry and Sander (2004) for an alternative approach for inferring respiratory structure/function relationships in tetrapods.

Laboratory studies of extant taxa utilized standard gross anatomical techniques, including serial sectioning, vascular and pulmonary injection protocols, and anatomical dissection. Only special predissection preparation techniques are highlighted here.

### Pulmonary Injection Preparations

Latex or polyester resin (Batson's No. 17 Anatomical Corrosion Kit, Polysciences, Warrington, PA) injection of the pulmonary apparatus was used to identify the extent of the respiratory system throughout the body (Figs. 2A, 11). This method allows not only a direct assessment of bones pneumatized by diverticula, but perhaps more important, causally associates bony morphologies with the pulmonary system, thereby establishing osteological correlates (Witmer, 1995a) for use with examining fossils. Avian specimens were prepared in a hypobaric chamber specifically designed for injection of the pulmonary system. Pulmonary injection protocols were modified from Duncker and colleagues (Duncker and Schlüter, 1964; Duncker et al., 1964) and the modified version is briefly reviewed here (see O'Connor, 2004, for a more detailed description of the procedure).

Frozen specimens were thawed and placed in a hypobaric chamber. One vacuum line was attached to the trachea (through a slip-valve on the chamber) and another to the chamber itself.
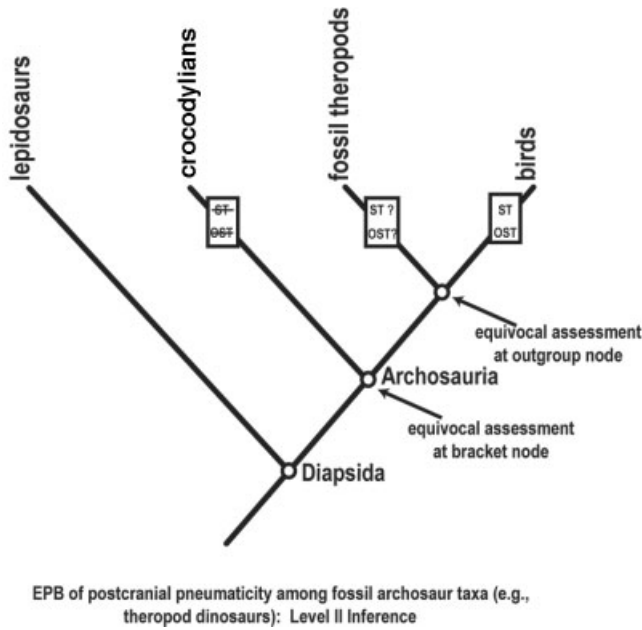
Fig. 5. Postcranial pneumaticity in fossil archosaurs examined within the context of the Extant Phylogenetic Bracket approach (Witmer, 1995a). In this diagram, theropod dinosaurs are used as an example of a fossil archosaur taxon bracketed by their extant sister groups (i.e., birds and crocodylians). In this case, postcranial pneumaticity in fossil archosaurs represents a Level II inference, as only one (birds) of the extant sister groups possess the soft tissue and osteological correlate of interest. Modified from Witmer (1995a). OST, osteological correlate present; OST?, osteological correlate unknown; ~~OST~~, osteological correlate absent; ST, soft tissue present; ST?, soft tissue unknown; ~~ST~~, soft tissue absent.

Following evacuation of both specimen and chamber, latex was allowed to slowly enter the pulmonary system via the line attached to the trachea. Subsequent to infilling, the specimen was refrigerated in a 15% solution of acetic acid to decrease the curing time of the latex. Specimens were then either dissected or subjected to whole-body maceration in order to examine the relationship of pneumatic diverticula to osteological features.

## Vascular Preparations

Standard laboratory latex, Microfil, or polyester resin (Batson's No. 17 Anatomical Corrosion Kit) was used to inject arteries and veins. Arterial preparations were performed by injecting casting medium into either the carotid system or caudal artery, and the venous network was accessed via the jugular system. Whole-body preparations of birds and crocodylians were used in order to identify vascular relationships along the entire length of the vertebral column. After injection, latex specimens were dissected and polyester resin preparations were chemically corroded using 15% sodium hydroxide solution (e.g., see Fig. 9F).

## Anatomical Nomenclature

The basic anatomy of an archosaurian vertebra is summarized in Figure 6. Soft tissues are divided into those related to either fossae or foramina. A "fossa" is any concavity positioned in an anatomical surface (Donath, 1969) and lacking a distinct rim of cortical bone. An "osseous foramen" sensu lato is any hole or opening passing through cortical bone (Donath, 1969). For the purposes of this study, foramina sensu stricto are restricted to those identifiable at gross anatomical level (>0.5 mm) and do not include microscopic canals within cortical bone. Terminology pertaining to different types of internal pneumatic morphology (camerate, camellate, etc.; see Britt, 1993; Wedel et al., 2000), although potentially useful to differentiate among clades of saurischian dinosaurs, will not be used in this study. Table 1 lists anatomical terms and abbreviations used throughout the article, with novel items indicated by an asterisk.

Specimens were examined at the following institutions: American Museum of Natural History, New York (AMNH); the Natural
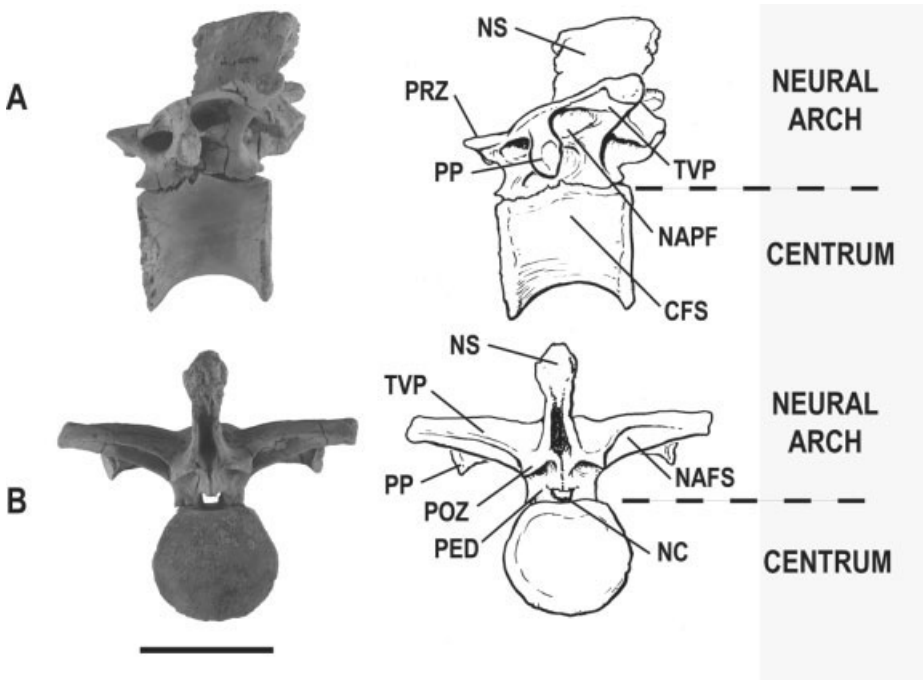


Fig. 6. Generalized archosaurian vertebra represented by a dorsal (thoracic) vertebra of a theropod dinosaur (*Majungasaurus crenatissimus*, UA 8678). Scale bar = 5 cm. **A:** Left lateral view. **B:** Caudal view. CFS, nonspecific central fossa; NAFS, nonspecific neural arch fossa; NAPF, neural arch pneumatic foramen/fossa; NC, neural canal; NS, neural spine; PED, pedicle; POZ, postzygapophysis; PP, parapophysis; PRZ, prezygapophysis; TVP, transverse process. Dashed line indicates division between centrum and neural arch.

**OSSEOUS STRUCTURES**

General descriptors traditionally used to describe osseous pneumatic features include the following terms: chamber, excavation, foramen, fossa, groove, hole, hollow, pit, pleurocoel, pneumatopore, recess, and sulcus. Except for pleurocoel and pneumatopore, the above terms are typically modified with the adjective *pneumatic*.

*Noncommunicating (Blind) Fossae:* any of the variably shaped external osseous concavities on bony surfaces that do not connect with the intraosseous space.

*Communicating Fossa:* any of the variably shaped external osseous concavities that directly connect with large, cavernous spaces within pneumatic bone via foramina.

*Pulmonary Fossa:* laterally facing concavities on thoracic vertebrae casually associated with dorsomedial projections of lung (Fig. 8A).

Pneumatic bone is lined by air-cells (Hunter, 1774) or pneumatic cells (*Cellulae pneumaticae* sensu Baumel and Witmer, 1993). These are made up of epithelial expansions originating from the respiratory tract (e.g., air sacs, diverticula) that expand within bone. Also, see Britt (1993) and Witmer (1997) for a history of bony pneumatic features.

**SOFT-TISSUE STRUCTURES**

*Pneumatic diverticulum (pl. diverticula)*: any epithelial outpocketing that originates directly from pulmonary air sacs or other diverticula, but not the lung itself (Figs. 2A, 11). For both historical and current nomenclature related to pulmonary morphology, see Hunter (1774), Campana (1875), Müller (1908), Locy and Larsell (1916a,b), Groebbels (1932), King (1966, 1993), McLelland (1989), and O'Connor (2004).

Note: craniocervical pneumatic diverticula originate from the upper respiratory tract (e.g., nasal, pharyngeal, laryngeal, and tympanic cavities), often pneumatizing elements of the cranial skeleton (see Witmer, 1997).

Specific named diverticula used include:

- AnDv—anastomosing diverticulum: short, segmental connections between two or more longitudinal diverticular networks (e.g., between the LVDv and SMDv).
- IMDv—intermuscular diverticulum: short, dorsally-directed outpocketing originating from supramedullary or supravertebral diverticula and expanding within epaxial musculature (note: intermuscular diverticula are also associated with other components of the axial and appendicular musculature (e.g., pectoral diverticulum).
- LVDv—lateral vertebral diverticulum: longitudinal system passing cranially through the vertebrarterial canal, occupying a position on the lateral surface of cervical vertebral centra. The LVDv originates from the cervical air sac at the cervicothoracic junction.
- SMDv—supramedullary diverticulum: longitudinal system variably occupying the extradural space within the vertebral canal. The SMDv is made up of contributions from (1) the cervical air sac, (2) pulmonary diverticula of the lung, and (3) perirenal diverticula of the abdominal air sac.
- SVDv—supravertebral diverticulum: short, segmental expansions from the SMDv that occupy a position on the dorsal surface of vertebral neural arches

*Pulmonary diverticulum:* an epithelial outpocketing originating directly from the lung surface, extending medially to (1) directly pneumatize thoracic vertebral centra and (2) contribute to the formation of the supramedullary diverticulum.

*Pulmonary protuberance:* dorsomedially directed portions of lung parenchyma (Fig. 8B) that occupy fossae in thoracic vertebrae of some bird groups (e.g., procellarids, larids).

Novel terms introduced in this study indicated with an asterisk.

History Museum, London, UK (BMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Canadian National Museum, Ottawa, Canada (CNM); Field Museum of Natural History, Chicago (FMNH); Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (MB); Justus-Liebig Universität, Giessen, Germany (JLUG); Namibian Geological Survey, Namibia (NGS); National Museum of Natural History, Washington D.C. (USNM); Ohio University Vertebrate Collections, Athens (OUVC); Transvaal Museum, Pretoria, South Africa (TM); Stony Brook University, New York (SBU); Sedgewick Museum, University of Cambridge, UK (SM); Université d'Antananarivo, Madagascar (UA); and the University of California Museum of Paleontology, Berkeley (UCMP).

## RESULTS

### Osteological Correlates of Different Soft-Tissue Systems

**Vertebral fossae.** Fossae in archosaurian vertebrae are typically positioned on the lateral or ventrolateral aspect of the vertebral centrum and virtually any surface of the neural arch (Figs. 3, 6). Extant crocodylians have vertebral centra with fossae of variable shape and size, similar in general morphology to those identified as pneumatic in many fossil archosaurs. Such fossae are associated with a variety of soft tissues, depending on their position on the vertebra itself and location within the vertebral series. For example, dorsal vertebral centra of extant crocodylians exhibit fossae of variable depth on the lateral central surface (Fig. 7A, CFS). Within the depth of these fossae, a foramen (or foramina) often penetrates the cortical bone, allowing vasculature to access the medullary cavity (see next section on vasculature). Gross dissection of *Alligator mississippiensis* reveals a layer of fat (perivertebral adipose) contained within these fossae (Fig. 7D, FD).

Crocodylian proximal caudal vertebrae also exhibit concavities on the lateral surface of the centrum (Fig. 7B, CFS). In some cases the fossae are so deep that only thin, bony laminae separate the right and left compartments. Dissection reveals caudofemoralis musculature and fat deposits associated with these features (Fig. 7E,F, CFM, FD). Such excavations increase surface area for attachment of musculature used in femoral retraction during terrestrial locomotion. Similar lateral excavations are found within caudal vertebral centra of many fossil archosaurs, notably among the large theropod and sauropod dinosaurs (e.g., Wilson, 1999, fig. 4). Vertebrae within the cervical region have variably shaped concavities. As in the tail, these excavations are associated with the attachment areas of deep axial musculature and fat.

Crocodylian vertebrae also exhibit a wide variety of fossae on neural arches, particularly on the craniolateral and caudolateral aspects of the neural spine (Fig. 7B, SPFS). The cortical bone within these features is relatively smooth when compared to adjacent areas of the neural arch. In some fossil archosaurs (e.g., saurischian dinosaurs) similar textural
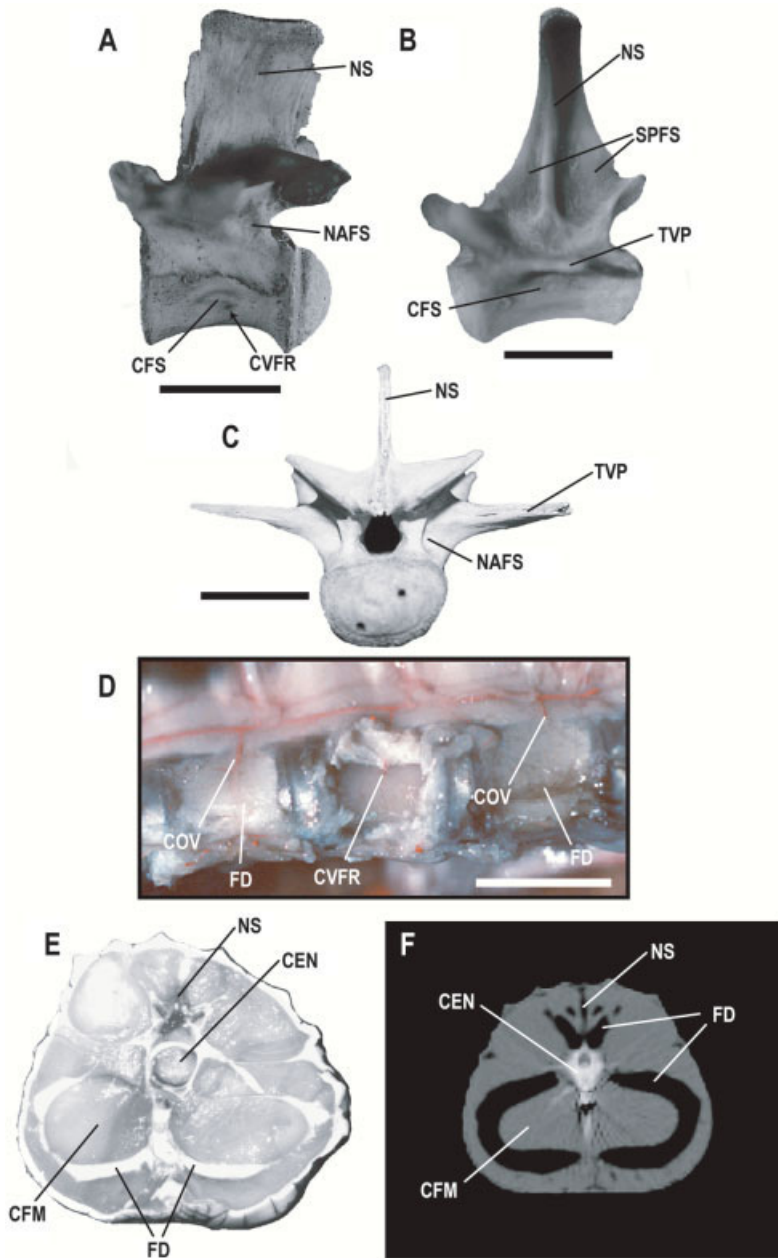
Fig. 7. Crocodylian vertebrae (**A–C**) illustrating fossae in both centrum and neural arch components along with dissections (**D,E**) and a computed tomography (CT) scan (**F**) to demonstrate soft-tissue structures associated with bony features. **A:** American crocodile (*Crocodylus acutus*, FMNH 5157). Lumbar vertebra, left lateral view. Note the central vascular foramen (CVFR) located within the fossa. Scale bar = 5 cm. **B:** American alligator (*Alligator mississippiensis*, AMNH 43314). Proximal caudal vertebra, left lateral view. Scale bar = 2 cm. **C:** Crocodile (*Crocodylus* sp., CM 6450). Lumbar vertebra, caudal view. Scale bar = 2 cm. **D:** American alligator (*A. mississippiensis*, OUVC 9659). Thoracic vertebral series, ventrolateral view illustrating fat deposits (FD) occupying fossae within the lateral surface of vertebral centra. Similar fat deposits are associated with fossae within both vertebral centra (e.g., **A,** CFS) and neural arches (e.g., **B,C,** SPFS, NAFS). The fat adjacent to the middle vertebra has been reflected dorsally to expose the nutrient foramen within the centrum (CVFR). Also visible are corporal (nutrient) vessels supplying vertebral centra (injected orange latex); this vasculature is causally associated with foramina like those in Figures 7A and 9A,C. Scale bar = 2 cm. **E:** American alligator (*A. mississippiensis*, OUVC 9657). Tail, axial cross-section. **F:** American alligator (*A. mississippiensis,* OUVC 9760). Tail, computed tomography axial cross-section to highlight caudofemoralis musculature and fat deposits. Note: Fat appears as radiolucent regions (i.e., black) adjacent to the neural spine and forming a boundary layer peripheral to the caudofemoralis muscle mass. The musculature originates (at least in part) from the fossa (CFS) on the vertebral centrum illustrated in **B,** whereas fat is associated with neural arch fossae as in **B,C.** CEN, centrum; CFM, caudofemoralis musculature; CFS, central fossa; COV, corporeal (nutrient) vessel; CVFR, central vascular (nutrient) foramen; FD, fat deposit; NAFS, neural arch fossa; NS, neural spine; SPFS, spinous fossa; TVP, transverse process.

differences are also observed on neural arches, particularly adjacent to large foramina in the cortical surface (Fig. 3C). Fossae are also commonly located adjacent to pre- and postzygapophyses and near the base of the transverse process (Fig. 7A–C, NAFS). Similar to those on vertebral centra, neural arch fossae are associated with fat deposits (Fig. 7F, FD). In lepidosaurs, similar fat deposits are also found in association with fossae on vertebral centra and neural arches.

Among birds, expansive lateral fossae are particularly well developed in thoracic vertebrae of charadriiform and some procellariform birds. These are relatively shallow and occupy only a small proportion of the lateral surface of the centrum in gulls.

In petrels, however, fossae (*pulmonary fossae*) occupy the entire lateral surface of the centrum and are so deep that the centrum consists of two intervertebral articular facets connected by a thin, midline lamina (Fig. 8A, PLFS). Set within the pulmonary fossae (see Table 1) are medially directed parabronchial protuberances extending from the dorsomedial aspect of the lung (Fig. 8B, PLPR). In this case, the vertebrae are not "pneumatized," as the medullary space is not lined by pneumatic epithelium. Rather, the fossae subdivide portions of the dorsomedial lung parenchyma at the expense of the centrum. This form of vertebral modification is distinguished from that caused by the pneumatization process, whereby pneumatic epithelium invades and

expands throughout the medullary space (e.g., Bremer, 1940a,b; Schepelmann, 1990; Witmer, 1995b). In contrast to the condition in crocodylians and lizards, none of the birds examined in this study exhibits significant amounts of perivertebral fat associated with vertebral fossae.

All fossae described thus far are examples of non-communicating, or *blind fossae*: concavities of variable depth and area that do not communicate with



the medullary cavity through the cortical surface. Birds, however, have vertebral fossae that are pierced by a foramen or multiple foramina at their deepest points, thereby providing continuity between extraosseous and medullary spaces. These communicating fossae are particularly well developed on the ventrolateral and dorsal aspects of the neural arches in many avian taxa (Figs. 2B–D, 8A–F, NAPF), with large-scale trabecular architecture often visible through the openings (e.g., Fig. 2C). One extreme example of this morphology is present within the basal anseriform anhimids, where laminar cortical bone is virtually absent and vertebrae consist of a series of struts connecting articular facets (Fig. 8D). Prominent vertebral fossae pierced by foramina result from invasion of bone by pneumatic diverticula. Diverticula, lined with simple cuboidal to columnar epithelium, pass through the cortical surface and spread throughout the medullary space (Bremer, 1940b; Hogg, 1984a). The bony morphology resulting from diverticular invasion varies enormously in shape, size, and texture (Fig. 2B–D). It is also common in birds for distinct diverticular networks to anastomose with one another, such that those pneumatizing neural arches are continuous with those of the centra. The exact mechanism by which pneumatic diverticula induce bone resorption and interact with one another within a given bone requires further study (e.g., Bremer, 1940b; Ikarashi et al., 1996; Hönig et al., 2002).

**Vascular foramina.** Foramina are typically positioned on lateral and ventrolateral surfaces of the centrum. Extant crocodylians also possess paired foramina on the dorsal surface of the centrum just medial to the neurocentral sutures. Extant birds do not typically have the dorsal pair, but do exhibit foramina of variable size and number on the lateral surface of the centrum. Vascular injection studies in crocodylians and avians reveal that most foramina are causally associated with nutrient vessels supply-
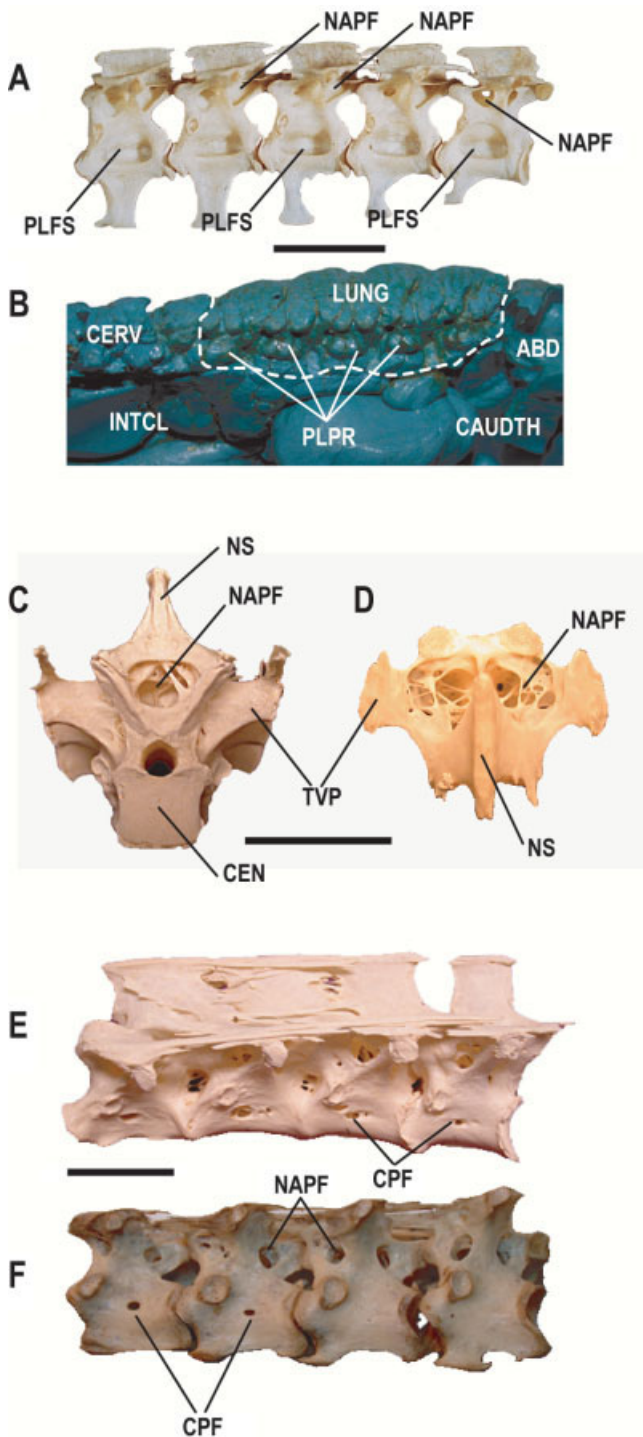
Fig. 8. Osteological features related to the pulmonary system in extant birds. Scale bars = 2 cm. **A:** Dark-rumped petrel (*Pterodroma phaeopygia*, FMNH 313946). Thoracic vertebral series, left lateral view. **B:** Latex cast of petrel lung (right) in dorsomedial view illustrating pulmonary protuberances (PLPR) that are positioned within pulmonary fossae (PLFS) shown in **A.** Dashed white line on latex cast indicates separation between the lung and air sacs. **C:** Sarus crane (*Grus antigone*, SBU AV104063). Thoracic vertebra, caudal view. **D:** Horned screamer (*Anhima cornuta*, NMNH 345217). Thoracic vertebra, dorsal view—cranial end facing the top of image. **E:** Sarus crane (*Grus antigone*, SBU AV104063). Thoracic vertebral series, left lateral view. **F:** Snow goose (*Chen caerulescens*, CM 15047). Thoracic vertebral series, left ventrolateral view. ABD, cast of abdominal air sac; CAUDTH, cast of caudal thoracic air sac; CEN, centrum; CERV, cast of cervical air sac; CPF, central pneumatic foramen; INTCL, cast of interclavicular (clavicular) air sac; NAPF, neural arch pneumatic foramen/fossa; NS, neural spine; PLFS, pulmonary fossa; PLPR, pulmonary protuberance; TVP, transverse process.

ing the medullary tissues. Since nerves supplying the inner regions of bone tend to travel as part of a perivascular plexus (Williams, 1999), no distinction will be made between nutrient and nervous foramina in this study.

Foramina in vertebral centra vary tremendously in relative size, number, and position among taxa studied, in addition to exhibiting regional variation along the vertebral column within a given species. Among crocodylians these features (Fig. 9A–C, CVFR) are related to both arteries and veins supplying the interior of vertebral centra (Fig. 7D, COV). Whereas arteries and veins often utilize a single nutrient foramen within a given vertebra, occasionally there are separate foramina for each. In birds that lack vertebral pneumaticity (e.g., loons and other diving forms), it is common to observe similarly placed nutrient foramina in the lateral surface of vertebral centra. Vascular foramina comparable to those described for crocodylians characterize the condition in many lizard groups (e.g., varanids, *Varanus* sp., CM 118507), where they also exhibit a wide range of relative sizes and positions.

Paired foramina (Figs. 9C, 10B) on the dorsal surface of crocodylian vertebral centra are related to the basivertebral system of veins, which are themselves tributaries of the internal vertebral venous sinus (Fig. 9D–F, IVVS). The IVVS is a longitudinal venous channel occupying the dorsal half of the vertebral canal in extant archosaurs (although its development in extant birds is variable; e.g., Baumel, 1988, 1993; Baumel et al., 1983). Numerous venous tributaries from the dorsal body wall, including the tissues of the vertebral column and spinal cord, drain into the sinus. Basivertebral foramina, through which the basivertebral veins traverse, are ubiquitous both among living (e.g., *Alligator mississippiensis*, OUVC 9657) and fossil (e.g., *Mahajangasuchus insignis*, UA 8654) crocodyliform taxa. Although basivertebral foramina do exhibit regional variation, they are consistently well developed in cervical, thoracic, and lumbar vertebrae. And whereas extant birds (i.e., avian theropods) lack basivertebral foramina, the structures show a variable distribution among nonavian theropods. For example, the abelisaurid theropod *Majungasaurus crenatissimus* (UA 8678) does not have basivertebral foramina in any region of the vertebral column (O'Connor, in press), whereas the allosauroid *Carcharodontosaurus saharicus* (CNM 41774) exhibits large foramina, particularly in the cervical region. The distribution of these features in other extinct archosaurs (or even other theropod dinosaurs) is unknown, but may prove useful for systematic studies of these groups.

Neural arch foramina are rare in crocodylians, occurring only as aberrant nutrient canals adjacent to transverse processes in the caudal series (e.g., *Caiman yacare*, AMNH 97304). Vascular injection
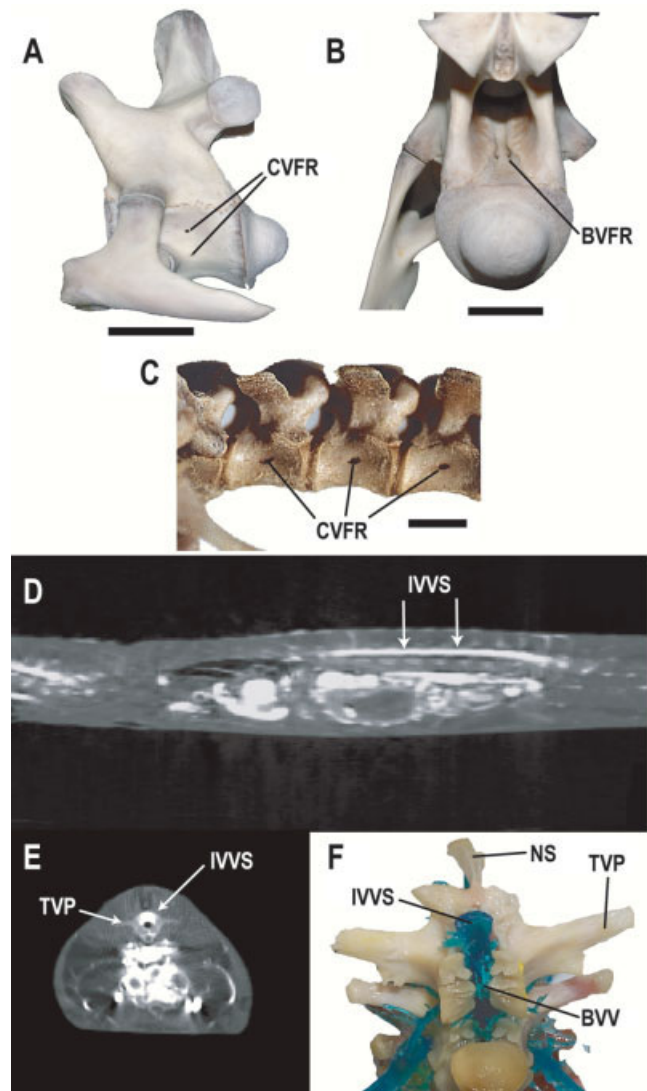


Fig. 9. Vertebral foramina in crocodylians (**A–C**) and computed tomography (CT) images (**D,E**) and polyester resin preparation (**F**) to highlight vascular structures related to these features. **D** and **E** were prepared as barium-latex preparations (modified protocol from Sedlmayr and Witmer, 2002) prior to CT scanning. Scale bars = 2 cm in **A,B**; 1 cm in **C. A:** American alligator (*Alligator mississippiensis*, OUVC 9412). Cervical vertebra, left lateral view. **B:** American alligator (*A. mississippiensis*, OUVC 9412). Cervical vertebra, caudodorsal view. **C:** Caiman (*Caiman* sp., FNNH 250822). Dorsal vertebral series, right lateral view. **D:** American alligator (*A. mississippiensis*, OUVC 9757). Sagittal CT section, cranial to the left of image; illustrating extent of the IVVS (longitudinal radio-opaque feature within the vertebral canal); **E:** American alligator (*A. mississippiensis*, OUVC 9757). Axial cross-section CT in mid-dorsal region (dorsal to the top of image) highlighting IVVS positioned in the dorsal half of the vertebral canal. **F:** American alligator (*A. mississippiensis*, OUVC 9657). Dorsal vertebral neural arch, caudoventral view. Polyester-resin cast of venous system (blue) highlights the IVVS and its tributaries, the basivertebral veins responsible for foramina in dorsal surface of vertebral centra in crocodylians (e.g., **B,** BVFR). BVV, basivertebral veins; BVFR, basivertebral foramina; CVFR, central vascular foramen; IVVS, internal vertebral venous sinus; NS, neural spine; TVP, transverse process.
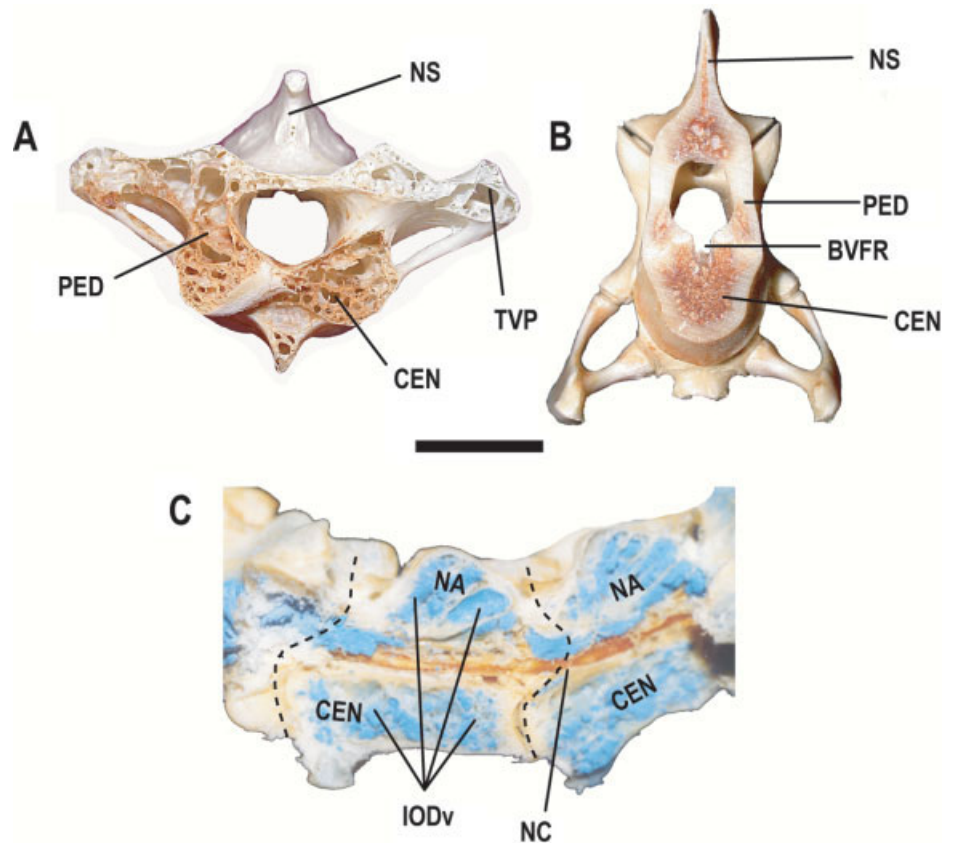
Fig. 10. Comparative cross-sections of crocodylian and avian vertebrae. Scale bar = 1 cm. **A:** Brown pelican (*Pelecanus occidentalis*, SBU AV 103985). Cervical vertebra, cranial view illustrating internal structure of pneumatic bone. **B:** American alligator (*Alligator mississippiensis*, OUVC 9401). Cervical vertebra, cranial view illustrating internal structure of a nonpneumatic bone. **C:** Mute swan (*Cygnus olor*, JLUG 2). Cervical vertebra, cranial view illustrating internal structure of an apneumatic bone. Dashed lines indicate separation between adjacent vertebrae. BVFR, basivertebral foramina; CEN, centrum; IODv, intraosseous diverticula; NA, neural arch; NC, neural canal; NS, neural spine; PED, pedicle; TVP, transverse process.

studies on birds with pneumatic postcrania reveal that nutrient vessels share (i.e., co-occupy) foramina with pneumatic diverticula to gain access to the medullary space (e.g., *Gallus gallus*, OUVC 9419, 9420; *Stuthio camelus*, OUVC 9665). This is consistent with observations that diverticula of the pulmonary system first gain access to the interior of bones by utilizing preexisting vascular foramina (e.g., Bremer, 1940b).

**Pneumatic foramina.** Whereas a range of osteological features can be associated with the pulmonary diverticular system (e.g., Figs. 2D, 8C,D), the most commonly observed are simple foramina (Figs. 2B, 8E,F). These vary not only in relative size, but also position, number, bilateral symmetry, and serially within the vertebral column (e.g., Fig. 8E,F). For example, a series of four thoracic vertebrae of a snow goose (Fig. 8F) illustrate both size (e.g., between the first two vertebrae) and serial variation along the column. Furthermore, it is not uncommon to find one or two variably sized pneumatic foramina on one side of a vertebral centrum with none present on the other side. Birds also exhibit variable pneumatization of vertebral, sternal, and cervical ribs. Vertebral ribs are typically pneumatized at the proximal end between capitular and tubercular processes, whereas sternal ribs receive diverticula near the sternal end of each element. In some "hyperpneumatic" avian species (e.g., storks), even uncinate processes are pneumatized. Avian cervical ribs are pneumatized either directly by diverticula within the vertebrarterial canal (Fig. 11) or extramurally (see Witmer, 1990) by intraosseous diverticula passing through the fused capitular and tubercular articulations. In the former case, ribs have pneumatic foramina on the dorsomedial aspect of the rib body (i.e., that portion of the rib forming the ventrolateral border of the vertebrarterial canal). Finally, both ribs and vertebrae may exhibit pneumatic foramina, with the diverticular network continuous throughout the fused vertebra–rib complex.

**Contrasting vascular and pneumatic foramina.** As vascular and pulmonary tissues may result in superficially similar cortical features (compare Figs. 8F and 9C), an examination restricted solely to the external surface of bone (as is often the case with fossils) is necessarily limited in its ability to assign a causally related soft tissue to a given feature. By examining cross-sections of representative archosaurian vertebrae (Fig. 10), it is clear that pneumatic bone is composed of large, irregular, smooth-walled cavities deep to the cortical surface. Furthermore, this morphology is not limited to select portions of a vertebra (e.g., just the centrum), but rather includes all major structural components of the centrum and neural arch (i.e., pedicles, laminae, transverse process, neural spine). These spaces are lined by pneumatic epithelium that gains access
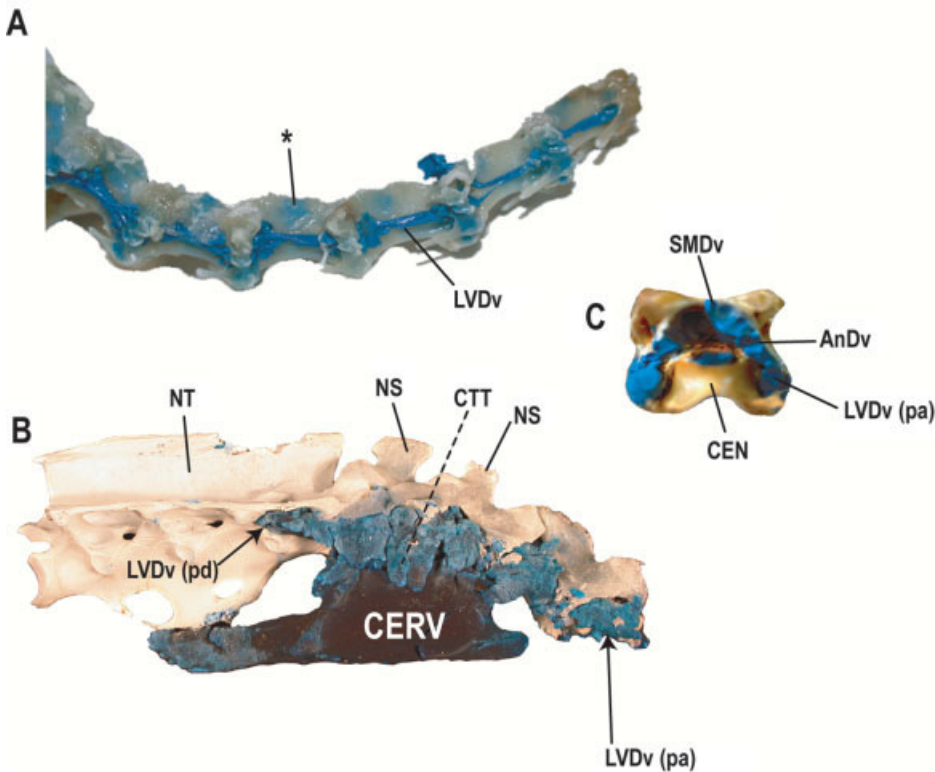
Fig. 11. Pulmonary injection of avian air sac system to highlight cervical air sac and diverticula responsible for pneumatization of the cervical vertebral column. **A:** Ring-necked pheasant (*Phasianus colchicus*, OUVC 9664). Cervical vertebral series, right lateral view. Asterisk indicates intraosseous diverticula (blue) deep to cortical surface within neural arch. **B:** Ring-necked pheasant (*Phasianus colchicus*, OUVC 9664). Cervico-thoracic vertebral transition, right lateral view. **C:** Common rhea (*Rhea Americana*, JLUG 15). Middle cervical vertebra, caudal view. AnDv, anastomotic diverticulum; CEN, centrum; CERV, cervical air sac; CTT, cervicothoracic transition (dashed line); LVDv (pa), lateral vertebral diverticulum pars ascendens; LVDv (pd), lateral vertebral diverticulum pars descendens; NS, neural spine; NT, notarium; SMDv, supramedullary diverticulum.

to the medullary space via foramina in the cortical surface (Fig. 8C–F). Figure 10C illustrates the extent of intraosseous diverticula (IODv) within cervical vertebrae of a swan. Note that virtually the entire volume of the vertebra deep to the cortical surface is pneumatized, as evidenced by infilled latex. Vertebrae are typically reduced to thin shells of cortical bone with large (macroscopic) support trabeculae reinforcing them internally (Fig. 10A,C). Moreover, marrow is reduced or absent in pneumatic bone and the internal cortical surface is quite smooth. In contrast, the cross-section of a typical crocodylian vertebra (Fig. 10B) reveals the absence of large internal cavities. Trabecular bone is more dense than in birds, and cortical bone is relatively thick. Even when sizable cortical foramina are present (see Fig. 10B, BVFR), the macroscopic canal ends abruptly when it reaches the trabecular bone. In birds that lack pneumatic bones (e.g., penguins), as in crocodylians, trabecular bone is dense and the cortices are relatively thick.

## Regional Pneumaticity of the Avian Postcranial Skeleton

As the avian lung is fixed in the dorsal portion of the body cavity (Fig. 2), tightly packed against thoracic vertebrae and vertebral ribs, potentially pneumatizing soft tissues are in direct association with many of the bones of the thoracic skeleton. Whereas a detailed anatomical description of the many diverticular networks is beyond the scope of this article, this contribution will highlight those associated pneumatization of the vertebral column and rib series. See McLelland (1989), O'Connor (2004), and O'Connor and Duncker (in prep) for overviews on the other facets of air sac diverticula in birds.

**Cervical air sac diverticula.** Two interconnected longitudinal systems variably span the craniocaudal extent of the cervical vertebral column and are generally referred to as *diverticula vertebralia* (King, 1993). Originating from cervical air sacs (*Saccus cervicales*) in the craniodorsal thoracic cavity, vertebral diverticula pass through the dorsal body wall musculature to occupy positions along and within the cervical vertebral column (Fig. 11; also see Müller, 1908; King, 1966). Lateral vertebral diverticula (*canalis intertransversarius* of Müller, 1908) enter the vertebrarterial canal near the cervicothoracic junction, passing cranially into the neck and caudally into the thorax (Fig. 11, LVDv). Supramedullary diverticula (*diverticula medullaria* of Müller, 1908) enter the vertebral canal near the cervicothoracic junction, and similar to lateral cervical diverticula, pass both cranially and caudally within the dorsal half of the vertebral canal (Fig. 11C, SMDv). Some species (e.g., ostriches) partition the supramedullary system into a series of parallel diverticula, whereas others (e.g., ducks) retain a single, simple diverticulum. Still others (e.g., storks, pelicans) have an "expanded" supramedullary diverticulum that completely envelops the meninges on

all sides, thereby forming a complete peridural diverticulum. In addition to their circumferential distribution around the spinal cord and meninges, supramedullary diverticula give rise to segmental, dorsally projecting extensions that occupy the space on the dorsal surface of neural arches (e.g., supravertebral diverticula, SVDv), some of which even expand between portions of the epaxial musculature (e.g., intermuscular diverticula; also see Fig. 2A, IMDv) in certain species.

Both longitudinal systems (i.e., lateral vertebral and supramedullary) may extend as far cranially as the atlas, although there is considerable interspecific variation in the extent of this cranial elongation. Supramedullary and lateral vertebral systems interconnect with one another at intervertebral joints via small, anastomosing diverticula (Fig. 11C, AnDv). It is unclear how far caudally the two systems extend, but in some taxa (e.g., hornbills, pelicans, storks) supramedullary diverticula anastomose with a cranially projecting counterpart derived from the abdominal air sac system (see below). Therefore, cranial (cervical air sac diverticula) and caudal (abdominal air sac diverticula) components of the air sac system can communicate with one another via the vertebral canal. It is significant that none of the birds examined showed caudal extension of cervical air sac diverticula to pneumatize post-midthoracic regions of the vertebral column. Due to the close approximation of the medial border of the avian lung to the thoracic vertebral series, the descending portion of the lateral vertebral diverticulum (LVDv .) terminates at the cranial end of the notarium (see Fig. 11B).

Any of the above-mentioned diverticula (i.e., SMDv, LVDv, and SVDv), when adjacent to bone, can pneumatize vertebrae and ribs in the cervical and thoracic regions. More specifically, cervical vertebrae and ribs are pneumatized by lateral vertebral diverticula, usually around the periphery of the vertebrarterial canal. Extensions from lateral vertebral diverticula also pneumatize neural arches via foramina on the cranial and caudal aspects of transverse processes. Typically located near the base of the transverse process, such foramina occupy positions ventral to the zygapophyses, thereby forming infrapre- and infrapostzygapophyseal foramina. In contrast, it is rare that supramedullary diverticula directly pneumatize bone forming the periphery of the neural canal. However, in some taxa (e.g., bucerotids, gruids, anhimids), this system does have intraosseous connections indirectly via its supravertebral extensions. Supravertebral diverticula gain access to vertebrae via foramina on the dorsal surface of the neural arch (e.g., Fig. 2C, NAPF) and by openings on both the pre- and postspinal surfaces of the neural spine (e.g., Fig. 8C, NAPF). Finally, cranial thoracic vertebrae and ribs are also pneumatized by diverticula originating from cervical air sacs (Fig. 11B, LVDv .).

**Lung diverticula.** Whereas caudally projecting diverticula from the cervical system may pneumatize the cranialmost thoracic vertebrae, it is typically the case that the dorsomedially positioned avian lung directly pneumatizes adjacent vertebrae and ribs, in some cases as far caudally as the last free thoracic vertebra (e.g., Fig. 8E,F, CPF). The overall distribution of this characteristic among extant birds (e.g., Tinamidae, Anseriformes, Galliformes, Falconiformes, Strigiformes, Pelecaniformes, Ciconiiformes, Gruiformes, Charadriiformes, Picaformes) indicates that this is a very common mode of pneumatizing the thoracic vertebral series. Pneumatic foramina in vertebral centra typically decrease in size or are absent altogether in more caudal portions of the thoracic series (Fig. 8F); this general pattern is also observed in nonavian theropods (see below). Although resulting in an air-filled bone (similar to pneumaticity derived from air sac diverticula), it seems prudent to differentiate the anatomical soft tissues responsible for inducing pneumaticity in each case on whether the epithelium originates from the lung directly or via the air sacs. The term pneumatic diverticulum (diverticula, pl.) will be retained in the case of the latter, whereas pulmonary diverticula will be restricted to epithelial projections originating directly from the lung surface.

**Abdominal air sac diverticula.** Abdominal air sac diverticula responsible for osseous pneumaticity are, generally speaking, much simpler than those of the cervical system. Originating from the dorsal aspect of abdominal air sacs (*Saccus abdominalis*; e.g., O'Connor, 2004, fig. 2), small perirenal diverticula (*diverticula pelvica* of Müller, 1908) intercalate into the space between the kidneys and the pelvic girdle, variably pneumatizing coxal elements and post-midthoracic regions of the vertebral column. Concerning the axial skeleton, the most commonly pneumatized elements are synsacral and caudal thoracic vertebrae, with only very rare pneumatization of free caudal vertebrae and the pygostyle (O'Connor, 2004). As with pneumatization of the cervical series, extensions from perirenal diverticula occupy a dorsal position within the vertebral canal (i.e., forming a supramedullary diverticulum), and give rise to both cranially and caudally directed extensions. The cranially directed supramedullary diverticulum of the abdominal air sac may anastomose with its caudally directed counterpart derived from cervical air sacs. In these cases, abdominal air sac diverticula unambiguously pneumatize the pelvic girdle and post-midthoracic regions of the vertebral column (e.g., synsacrum, caudal thoracic vertebrae), only secondarily anastomosing with caudally projecting components of the cervical air sac system. Significantly, the supramedullary diverticula of cervical air sacs were not observed to pneumatize regions of the post-midthoracic vertebral column and pelvic girdle. In other words, if pelvic girdle elements and caudal thoracic/synsacral portions of the vertebral
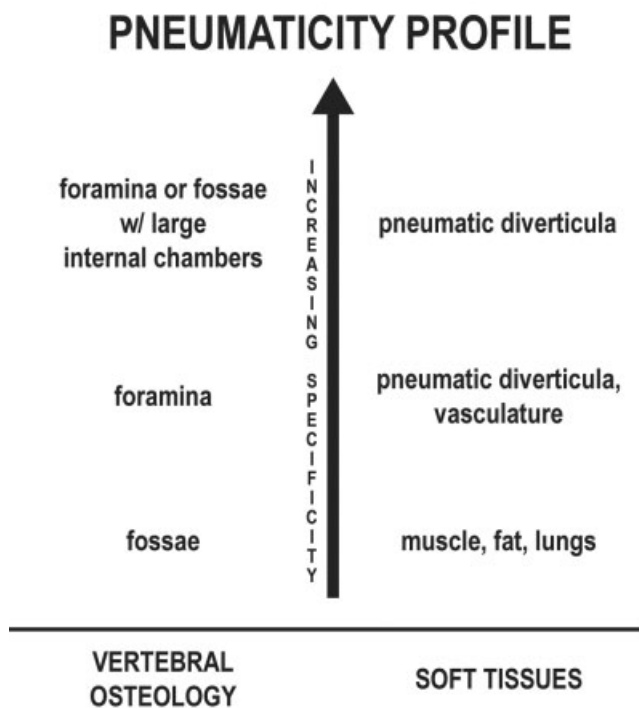
# PNEUMATICITY PROFILE



Fig. 12. Pneumaticity Profile illustrating correlation and relative specificity of osteological features as a function of different soft-tissue systems. Vertebral fossae are causally associated with many soft-tissue systems, thus their reliability as specific indicators of pneumaticity remains ambiguous. Vertebral foramina are better indicators of pneumaticity, but only when combined with the presence of large internal cavities within the bone. In order to justify a positive pneumaticity assessment, these cavities must demonstrate clear continuity with the extraosseous space (i.e., cortical foramina) as pneumatic diverticula originate within the body cavity (i.e., from the air sacs/lungs) and must traverse cortical bone in order to gain access to the interior of bones.

column are pneumatized in extant birds, this is achieved by the abdominal air sac system. (For a discussion of pneumaticity in other portions of the avian skeleton, see Müller, 1908; Groebbels, 1932; King, 1966; Witmer, 1995b, 1997; O'Connor, 2004.)

## Postcranial Pneumaticity in Fossil Archosauriform Groups: Application of the Pneumaticity Profile

The anatomical data presented above are here used to establish a *Pneumaticity Profile* (PP) by which osteological features in fossils may be examined in order to determine the relative specificity of their soft-tissue associations (Fig. 12). The following case studies use the PP to reevaluate purported postcranial pneumatic features in representative ornithodiran and nonornithodiran archosauriform taxa.

**Nonornithodiran archosauriformes.** Putative pneumatic features in basal archosauriforms and certain crurotarsans (Gower, 2001) consist of fossae

on the ventral surface of the neural arch and foramina on the dorsal arch surface adjacent to the base of the neural spine (Fig. 13A,B). An examination of *Erythrosuchus africanus* (BMNH R8667, BMNH R3592, NGS F377) shows that although vertebral fossae are superficially similar to many features identified as pneumatic in other fossil specimens, the features do not communicate with large internal chambers within the vertebrae. Due to fortuitous breaks in BMNH R8667, it is also possible to examine cross-sectional views of all components of vertebral centra and neural arches, including both transverse processes and neural spines adjacent to the inferred "pneumatic" features (Fig. 13A–C). These views reveal thick cortices surrounding densely packed trabecular architecture void of the large internal cavities that characterize pneumatic bone. The soft-tissue system likely responsible for the dorsally positioned neural arch foramina is vasculature, as these openings lead directly into densely packed trabecular bone, similar to vascular foramina in extant crocodylians (e.g., Fig. 10B). A larger and more complete specimen of *Erythrosuchus* (NGS F377) also exhibits similar neural arch fossae, with no apparent sign of internal cavity formation.

An examination of representative parasuchians (e.g., *Phytosaurus kapfi* [BMNH R38071], *Rutiodon adamanensis* [UCMP 26699], and *R. zunii* [UCMP 27036]) also reveals similar noncommunicating fossae on dorsal neural arches (Fig. 13C). However, such features are morphologically consistent with neural arch fossae found in extant crocodylians (e.g., Fig. 7C) and other nonavian sauropsids that house adipose deposits, and have no relationship to any portion of the respiratory system. Other parasuchians (e.g., *Rutiodon* [*Angistorhinopsis*] sp., MB 1922.23.342) exhibit generally similar neural arch fossae with no internal cavity formation, as indicated by an examination of cross-sectional views of specimens.

**Ornithodira: Pterosauria.** Examination of pterosaur specimens reveals that vertebral pneumaticity is morphologically similar to that of extant birds, particularly with regard to the position, size, and number of foramina in both central and neural arch components (Figs. 3B, 14A). These in turn lead to spacious internal chambers within vertebrae. Appendicular elements of pterosaurs, particularly long bones, are characterized by extremely thin cortices, with the placement of pneumatic foramina in positions similar to those found in birds (Fig. 14B,C). See O'Connor (2003) for additional information on postcranial pneumaticity in pterosaurs.

**Ornithodira: Saurischia.** Numerous workers have commented on the pneumatic postcranial skeletons of both sauropod and nonavian theropod dinosaurs (e.g., Owen, 1856; Janensch, 1947; Romer, 1956, 1966; Britt, 1993; Wilson, 1999; Wedel, 2003a; O'Connor and Claessens, 2005). This study confirms morphology consistent with pneumatic invasion of
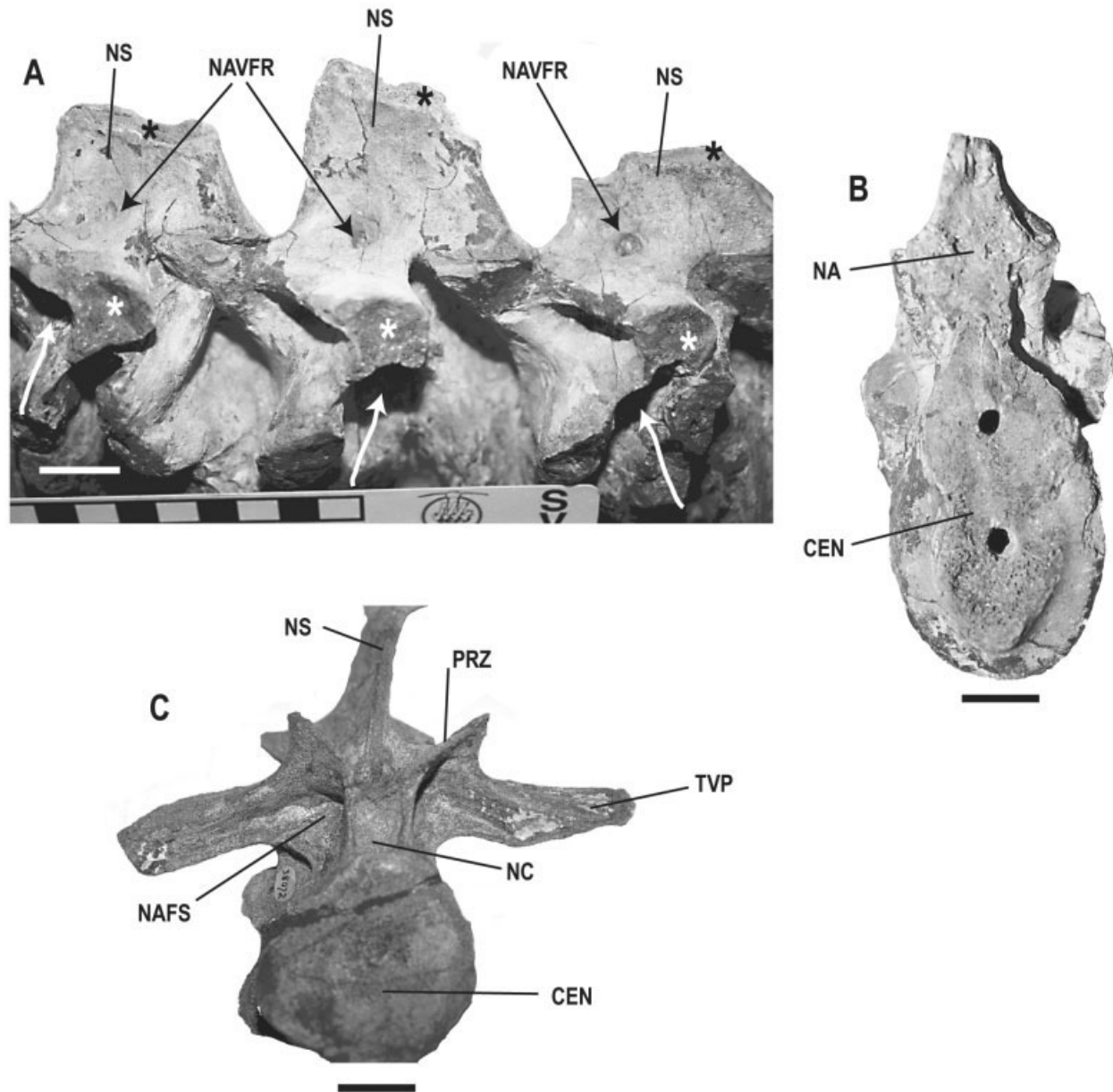
Fig. 13. Inferred pneumatic features in nonornithodiran archosauriforms. Scale bars = 2 cm. **A:** *Erythrosuchus africanus* (BMNH R8667). Dorsal vertebral series, left lateral view. White arrows indicate neural arch fossae; black arrows indicate foramina in the base of the neural spine; white asterisks indicate cross-sectional views of transverse processes; black asterisks indicate cross-sectional views of neural spines. **B:** *Erythrosuchus africanus* (BMNH R8667). Cranial view of **A** highlighting cross-section of centrum and neural arch with thick cortices and dense trabecular architecture (similar to asterisked regions in **A**). Note: The two midline circular holes represent drill cores from when the specimen was mounted in the museum. **C:** Representative parasuchid (*Phytosaurus kapfi*, BMNH R38072). Dorsal vertebra, cranial view. Note similarity of neural arch fossae in this figure and the apneumatic arch fossae in crocodylians (e.g., Fig. 7C). CEN, centrum; NA, neural arch; NAFS, nonspecific neural arch fossa; NAVFR, neural arch vascular foramen; NC, neural canal; NS, neural spine; PRZ, prezygapophysis; TVP, transverse process.

bone within both major saurischian clades (Figs. 3A,C,D, 15A,B). As previous work has focused on the systematic variability of pneumatic features within Sauropoda (see Janensch, 1947; Wedel, 2003a), the remainder of this section will highlight patterns of region-specific pneumaticity in theropod dinosaurs and inferences related to higher-level pulmonary organization with the clade.

The abelisaurid theropod *Majungasaurus crenatissimus* not only exhibits extensive vertebral and costal pneumaticity, but is represented by multiple, exceptionally well-preserved specimens. As such, it will be used as a case study for reconstructing different components of the pulmonary air sac system in nonavian theropod dinosaurs. Although *Majungasaurus* is the focal taxon for this contribution, the
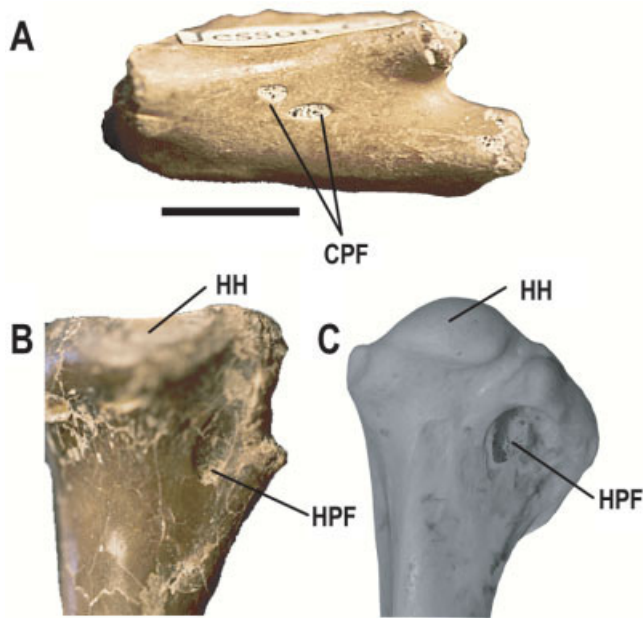
Fig. 14. Pneumatic postcranial elements in a pterosaur (**A,B**), with an extant bird (**C**) for comparison. **A:** Ornithocheirid pterosaur (*Ornithocheirus* sp., SM B54.320). Middle cervical vertebra, left lateral view. **B:** Ornithocheirid pterosaur (*Ornithocheirus* sp., BMNH R558). Proximal left humerus, caudal view. **C:** Black-necked swan (*Cygnus melancoryphus*, CM S-201). Proximal left humerus, caudal view. Scale bar = 2 cm in **A**; **B** and **C** are scaled to the same size in image. CPF, central pneumatic foramen; HH, humeral head; HPF, humeral pneumatic foramen.

second cervical centrum relative to the rest of the cervical series (e.g., Fig. 16A). A similar serial pattern (i.e., pneumatic foramina present on vertebral centra between C2 and D4) characterizes many other nonavian theropods including *Allosaurus fragilis* (Madsen, 1976) and *Sinraptor dongi* (Currie and Zhao, 1993). The largest pneumatic foramina on vertebral centra are typically located at the cervicodorsal transition, establishing a common pattern of relatively larger pneumatic features in vertebrae at the cranial end of the thorax; other theropods showing this trait include *Spinostropheus gautieri* [MNN TIG6], *Allosaurus* (Madsen, 1976), *Sinraptor* (Currie and Zhao, 1993), and *Monolophosaurus* (Zhao and Currie, 1993) and numerous groups of extant birds.

*Majungasaurus* also exhibits pneumatic sacral neural arches (Fig. 16C), with apneumatic sacral centra, a characteristic poorly known within Theropoda. Whereas other theropods have been identified with sacral pneumaticity, pneumatic foramina are usually restricted to sacral centra (e.g., ornithomimids: Gilmore, 1920; allosauroids: Harris, 1998; tyrannosaurids: Brochu, 2003). *Majungasaurus* does not exhibit pneumaticity in the caudal vertebral series, although it has been identified in other nona-
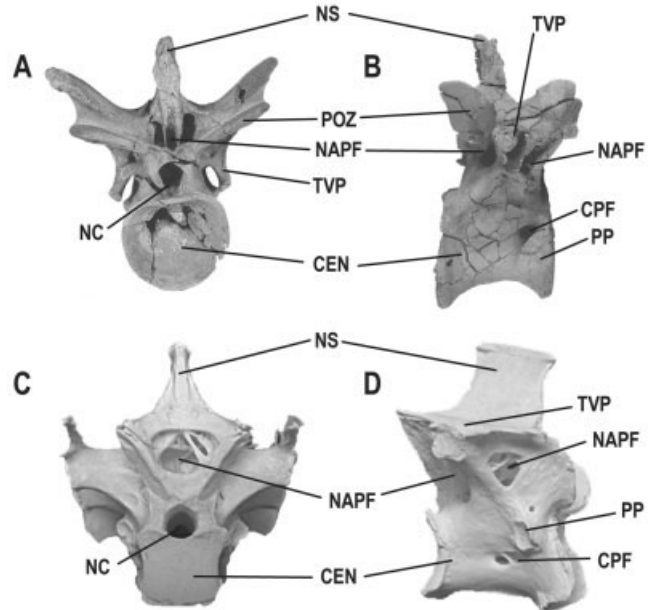
patterns highlighted here are also found in numerous other clades of neotheropods (O'Connor and Claessens, 2005; O'Connor, in press). Vertebrae throughout the entire postatlantal, precaudal series (UA 8678) exhibit pneumatic morphology consistent with that of extant birds, namely, cortical foramina that communicate with large, internal chambers within both centra and neural arches (Figs. 15, 16). Pneumaticity of the centrum and neural arch is present in the postatlantal cervical series and the cranial four dorsal vertebrae. The remainder of the dorsal series exhibits pneumatic features solely within the neural arch, with the caudal two dorsal arches (i.e., D12–13) showing a reduction in both size and number of pneumatic foramina and chambers. Pneumatic foramina are restricted to the lateral surface of the centrum, typically located just caudal to the parapophysis. In contrast, pneumatic features are found on virtually all components of the neural arch, including the pedicle, lamina, and transverse processes, in addition to the neural spine (Figs. 15, 16) (O'Connor, in press). UA 8678 exhibits the largest pneumatic foramina (4–11 mm diameter) in vertebral centra between cervical vertebra 9 and dorsal vertebra 4 (Figs. 3A, 15B, 16B), with foramina of more cranial vertebrae being much smaller in size (~1–2 mm diameter). Most neotheropods exhibit an enlarged pneumatic foramen on the



Fig. 15. Comparison of pneumatic features in vertebrae of a nonavian theropod dinosaur (**A,B**) and an extant bird (**C,D**). **A:** Theropod dinosaur (*Majungasaurus crenatissimus*, UA 8678). Third cervical vertebra, caudal view. **B:** Theropod dinosaur (*Majungasaurus crenatissimus*, UA 8678). Tenth cervical vertebra, right lateral view. **C:** Sarus crane (*Grus antigone*, SBU AV104063). Thoracic vertebra, caudal view. **D:** Sarus crane (*G. antigone*, SBU AV104063). Thoracic vertebra, right lateral view. Images not to scale. CEN, centrum; CPF, central pneumatic foramen; NAPF, neural arch pneumatic foramen; NC, neural canal; NS, neural spine; POZ, postzygapophysis; PP, parapophysis; TVP, transverse process.
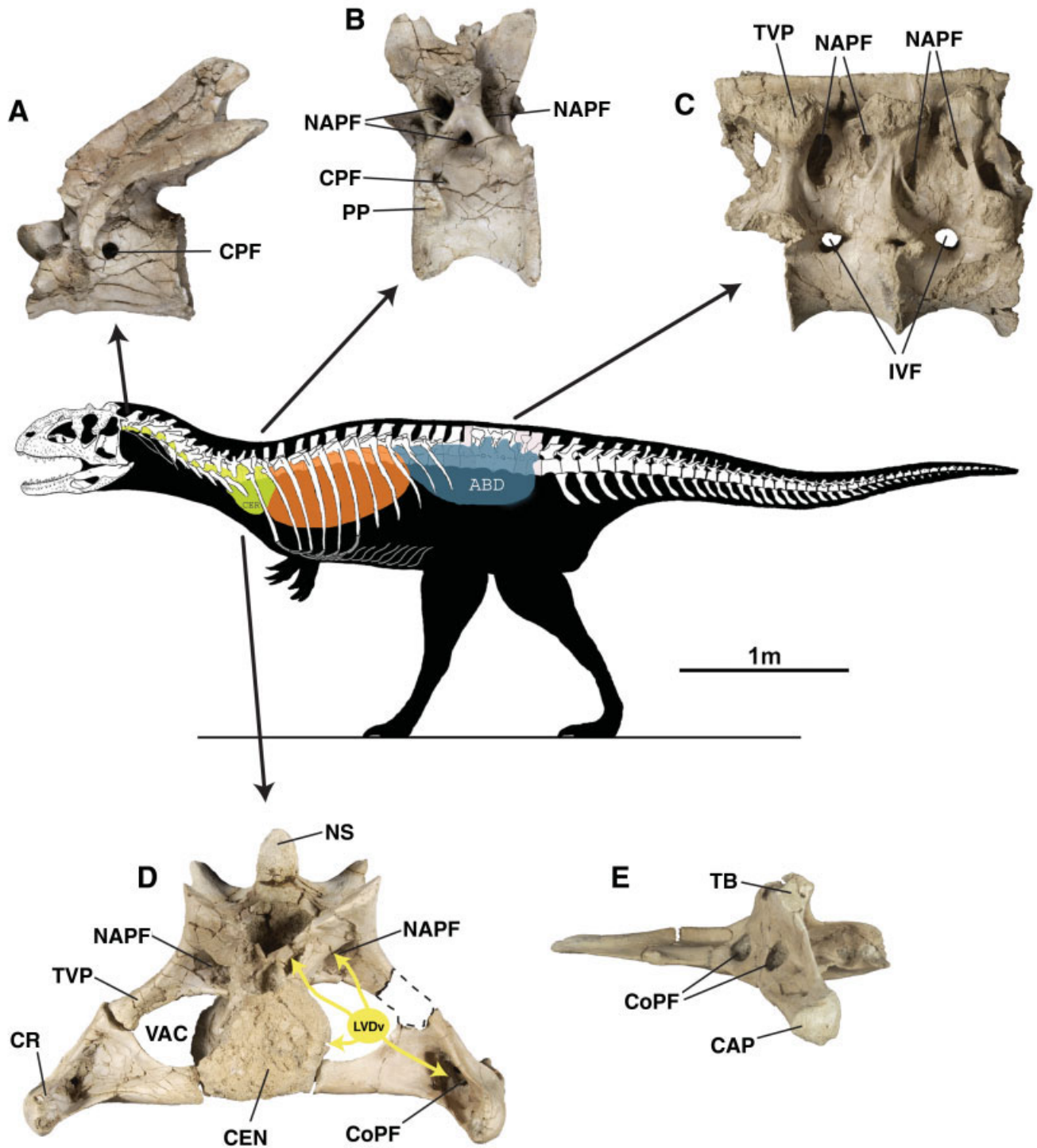
Fig. 16. Axial skeletal reconstruction of *Majungasaurus crenatissimus* in left lateral view (based on UA 8678), with inferred components of pulmonary air sac system based on site-specific pneumaticity of the axial skeleton. **A–E:** Vertebrae and rib specimens of theropod dinosaur (*Majungasaurus crenatissimus*, UA 8678) illustrating pneumatic features. **A:** Second cervical vertebra, left lateral view. **B:** Tenth cervical vertebra, ventrolateral view. **C:** Sacral complex, left lateral view. **D:** Ninth cervical vertebra with articulated cervical ribs, cranial view. Yellow oval indicates position of lateral vertebral diverticulum of the cervical air sac; arrows indicate locations of pneumatic foramina around the periphery of the vertebrarterial canal (VAC). **E:** Ninth cervical rib, medial view. Colors indicate the following structures: orange, inferred position of lung; yellow, cervical air sac and lateral vertebral diverticulum; blue, abdominal air sac. ABD, inferred position of abdominal air sac; CAP, capitulum; CEN, centrum; CER, inferred position of cervical air sac; CoPF, costal pneumatic foramina; CPF, central pneumatic foramen; IVF, intervertebral foramen; LVDv, inferred position of lateral vertebral diverticulum; NAPF, neural arch pneumatic foramen/fossa; NS, neural spine; PP, parapophysis; TB, tuberculum; TVP, transverse process; VAC, vertebrarterial canal.

vian saurischian taxa (e.g., oviraptorid theropods: Barsbold et al., 2000; diplodocid sauropods: Wedel, 2003a). See Britt (1993), O'Connor and Claessens (2005), and O'Connor (in press) for a more comprehensive analysis of the distribution of vertebral pneumaticity in nonavian theropods.

Cervical ribs of *Majungasaurus* demonstrate extensive pneumaticity that is unparalleled in other nonavian theropod taxa. Large pneumatic foramina (5–12 mm diameter) are found bilaterally on cervical ribs 4–10, many with multiple foramina (Fig. 16D,E). Costal foramina are located on both the dorsomedial surface of the rib shaft in addition to the cranial and caudal surfaces of the capitulotubercular lamina (Fig. 16, CoPF). These parts of the rib form the lateral and ventral boundaries of the vertebrarterial canal (i.e., transverse foramen), whereas the cervical centrum and transverse process form the medial and dorsal boundaries of the canal, respectively (Fig. 16D, VAC). Cervical transverse processes often exhibit accessory pneumatic foramina on their ventral surfaces. The morphology and position of these features in cervical vertebrae and ribs of *Majungasaurus* are consistent with pneumatic foramina in the cervical vertebral column of extant birds. The dorsal ribs of *Majungasaurus* are apneumatic.

**Pulmonary fossae in Saurischian dinosaurs.** Large, laterally directed fossae in dorsal vertebral centra of sauropod (e.g., Fig. 3D; also see *Diplodocus carnegie*, CM 84; *Apatosaurus louisae*, CM 3018; *Camarasaurus* sp., CM 11338) and larger-bodied theropod (*Tyrannosaurus*, FMNH PR 2081; *Allosaurus*, CM 11844) dinosaurs are nearly identical in shape and position to pulmonary fossae observed in some extant birds (e.g., procellarids: Fig. 8A). In birds, medial projections of the dorsally positioned, rigid lung occupy the fossae. As such, these fossae are indicative of two aspects of pulmonary morphology in birds; the first conveys topological information (i.e., the dorsomedial position of the lung within the thorax), with the second relating compositional information (i.e., densely packed parenchyma occupying a fossa within a bone). Pulmonary fossae in extinct groups then represent unambiguous osteological correlates of the actual lung within the thoracic cavity, rather than a seemingly general inference related to the presence of pulmonary air sacs (as has been done previously).

**Pneumaticity in basal avians.** As part of this study, both London and Berlin specimens of *Archaeopteryx lithographica* were examined. The Berlin specimen (MB 1880.81.4598) preserves a portion of the vertebral column in right lateral view. Cervical vertebra 5 possesses a partially preserved foramen on the craniolateral margin of the centrum. Whereas it appears that the caudoventral rim of this foramen has an intact ostial margin, the cranial and craniodorsal rim of the foramen does not. Accordingly, it is difficult to assess the actual size and

shape of the foramen on this vertebra. Foramina on adjacent vertebral centra are ambiguously defined, particularly under microscopic examination, contrary to diagrams provided by Britt et al. (1998, fig. 1). A section of the dorsal vertebral column is also exposed in right lateral view. The caudalmost dorsal vertebrae exhibit shallow fossae on the lateral surface of the centra ("pleurocoels" of Ostrom, 1976); however, consistent with statements by Britt et al. (1998), they do not have foramina piercing the cortical surface. Exposed appendicular elements of MB 1880.81.4598 do not exhibit any features indicative of pneumaticity.

Putative pneumatic features recently identified (Christiansen and Bonde, 2000) on axial and appendicular elements of the London specimen of *Archaeopteryx* (BMNH 37001: main slab) were also examined. The vertebral features (thoracic vertebrae 1–2) are rough-edged depressions located at the junction of the pedicle and transverse process. Within each fossa are 1–2 small (<1 mm) foramina, also with rough edges. Notably, the position of these features would allow continuity of soft-tissue structures between the lateral surface of the neural arch and the neural canal, and not into the medullary cavity. Moreover, rough edges on the surrounding bone suggest that the structures are an artifact (of either preservation or preparation) and do not represent intact bone surfaces.

A large, rough-edged "fossa" on the caudodorsal aspect of the proximal left pubis has been interpreted as pneumatic, and used to infer the existence of abdominal air sacs in this taxon (Christiansen and Bonde, 2000). This opening leads to a short canal directed cranially into the body of the pubis. It is unilateral in its development, as a similar fossa is not visible on the right pubis (although a complete examination of the right pubis is prevented in part by the overlying, displaced, scapula). Pneumatic pubes are known in a variety of basal extant avian taxa (e.g., *Struthio, Rhea, Anser*: O'Connor, 2004). However, in contrast to the orientation of the opening in BMNH 37001, pubic pneumatic foramina are directed caudoventrally down the pubic shaft. Finally, similar to the condition in thoracic vertebrae, the edges of this structure are rough and appear to consist of broken bone, and may pertain to artifact rather than invasion by air sac diverticula.

## DISCUSSION

Based on the relationship between specific skeletal morphologies and different soft-tissue systems identified in extant sauropsids, results from this study indicate that the vast range of features previously used to infer pneumaticity in extinct taxa overestimate pneumatic invasion by pulmonary air sacs. The only reliable and consistent indicators of pneumaticity are cortical openings (i.e., foramina or communicating fossae) connected directly with large

internal cavities within the bone (Figs. 12, 15, 16). In contrast, other osteological features such as vertebral fossae and cortical foramina alone are causally related to many different types of soft tissues (e.g., vascular, muscular, etc.), indicating a lower degree of system specificity, and ultimately, providing much less discriminating value for interpreting soft-tissue associations when examined in extinct taxa. Application of the Pneumaticity Profile (PP) derived in this study to fossil archosauriform taxa reveals the following: 1) that the ornithodiran clades Saurischia and Pterosauria include members with unambiguous pneumatic features, thereby supporting historical interpretations of these structures; and 2) that recently inferred pneumatic structures in nonornithodiran archosauriforms (e.g., *Erythrosuchus*, parasuchians) are not consistent with known pneumatic morphology and likely relate to other causal factors (e.g., vasculature). Finally, based on an analysis of region-specific pneumaticity in extant birds, it is possible to constrain inferences related to the identification of specific components of the pulmonary system responsible for pneumatizing the axial skeleton in saurischian dinosaurs.

Other osteological characteristics have been used as indicators of pneumaticity in saurischian dinosaurs. For example, noncommunicating fossae on the dorsal aspect of sauropod neural arches have been characterized as pneumatic (Fig. 3C-1; also see Wilson, 1999). Bone within these fossae may either be rugose ("crenulate" texture: Britt, 1993) or smooth relative to adjacent cortical bone, and both textural categories have been used to identify pneumaticity in fossils (e.g., Britt, 1993; Wedel et al., 2000; Wedel, 2003a). However, an examination of extant crocodylians reveals that neural arch fossae associated with adipose deposits are lined by cortical bone that is relatively smooth when compared to adjacent bone (e.g., Fig. 7B). Minimally, this suggests that nonpulmonary soft tissues may result in cortical bone that is smooth in appearance and located in similar positions as putative "pneumatic" fossae in fossil taxa. From this observation, causal relationships between surface morphology and associated soft tissues may not be system specific, underscoring the necessity for a reevaluation of textural characteristics used for identifying pneumaticity in fossils.

Finally, it is not necessary to invoke a "soft tissue" culprit for every bony feature on the skeleton. Some features may not represent the effect of a specific soft-tissue influence at that particular spot, but the cumulative effect of processes in surrounding areas (see Witmer, 1995a, for a discussion of the "hole-or-doughnut" problem). As an example, transverse processes function to support body wall musculature in addition to serving as an articulation site for ribs. In many cases the transverse process is ventrally buttressed by either a small strut or lamina connecting it to the base of the neural arch. Depending on the form of this strut, variably shaped fossae are positioned ventral to the transverse process. When the ventral buttress consists of a simple, craniocaudally restricted lamina (e.g., parasuchians, Fig. 13C), distinct arch fossa are located along the ventral surface of the process. Instead of assigning specific soft-tissue associations to the fossae, it is reasonable that they merely represent epiphenomena related to the size and shape of the ventral buttressing unit and, ultimately, are dictated by mechanical demands placed on the vertebra.

## Postcranial Pneumaticity in Extinct Archosauriform Taxa

Based on compelling morphological evidence, numerous examples of postcranial pneumaticity exist in many extinct ornithodiran clades, including pterosaurs, and sauropod and nonavian theropod dinosaurs (Figs. 3, 4). Although both the London and the Berlin specimens of *Archaeopteryx* exhibit bony features interpreted as pneumatic (Britt et al., 1998; Christiansen and Bonde, 2000), results from this study indicate that in only one case (i.e., a single foramen on the C5 vertebra of the Berlin specimen) is this morphology consistent with that observed in extant birds. Other putative pneumatic features at best represent equivocal assessments (e.g., foramina on cervical vertebrae other than C5 in the Berlin specimen), or represent preservational or preparation artifact (e.g., "pneumatic" vertebrae in the London specimen). In summary, variable preservation, combined with only limited access to all bony surfaces, likely contributes to the ambiguous assessment of pneumaticity in *Archaeopteryx* (e.g., contrast the studies of Müller, 1908; Swinton, 1960; Ostrom, 1976; Britt et al., 1998; Christiansen and Bonde, 2000; current study). Similarly, evidence in support of pneumatic postcrania in prosauropod dinosaurs remains somewhat ambiguous (e.g., see Britt, 1993, 1997), although recent work has identified possible pneumatic features on vertebrae of *Thecodontosaurus* (Yates, 2003). Additional research is currently under way evaluating pneumaticity in prosauropod dinosaurs (e.g., Wedel, 2005).

Although an extensive survey of nonornithodiran archosauriform taxa was not conducted during this study, the few specific reported examples (e.g., Gower, 2001) of vertebral pneumaticity were included, and in all cases fail to meet morphological criteria consistent with a pneumatic designation. Putative pneumatic features in nonornithodiran archosauriforms (e.g., parasuchians, *Erythrosuchus*) consist of external osteological markers that are at best ambiguous and internal bone characteristics completely unlike pneumatic bone (Fig. 13). Whereas these examples fail to meet explicit criteria of the PP, the taxa included represent a mere fraction of the known diversity within the group. The study of Gower (2001) is significant not only in that it suggests (even tentatively) the presence of postcranial pneumaticity in nonornithodiran archosau-

riforms, but in some of the earliest known (mostly Triassic) members of the group. Notably, other non-ornithodiran archosauriform clades (e.g., rauisuchians, sphenosuchian crocodylomorphs; Gower, 2001) also have vertebrae with features similar to those identified as pneumatic in past studies. The present study, combined with those of Gower (2001) and Yates (2003), indicates that a systematic examination of vertebral morphology is necessary to assess potential pneumatic features within basal archosauriform and basal sauropodomorph archosaurs. Such studies will not only help to evaluate, identify, and elucidate patterns of postcranial pneumaticity within different clades, but will serve to constrain "first-occurrence," both temporally and phylogenetically, of postcranial pneumaticity in the fossil record.

## General Pulmonary Structure in Taxa with Pneumatic Postcrania

Ornithodiran archosaurs identified with unambiguous postcranial pneumaticity include saurischian dinosaurs and pterosaurs. Such features may be used to infer the existence of a heterogeneous pulmonary apparatus in these taxa. In this context, heterogeneous refers to a pulmonary system exhibiting variable parenchymal densities, implying the presence of both gas exchange (i.e., parenchyma-dense) and nonexchange (i.e., air sacs) regions (Duncker, 1978; Perry, 1983, 2001; also see Hunter, 1774). The lungs in all major clades of extant sauropsids exhibit sac-like regions (e.g., Duncker, 1971, 1978, 1989; Wood and Lenfant, 1976; Perry, 1983, 1998). For example, lungs of various chameleonid and varanid species exhibit variably sized and shaped diverticula extending from the caudal surface of the lung (Wolf, 1933; Klaver, 1981; Becker et al., 1989; Perry, 1998, fig. 1.12). Other sauropsid groups such as crocodiles, snakes, and turtles also have lungs that exhibit a large range of parenchymal densities, such that areas of lowest parenchymal density are functionally equivalent (i.e., performing little to no gas exchange) to avian air sacs (Hunter, 1774; Duncker, 1978, 1989; Perry, 1998; Wallach, 1998; Wyneken, 2001). Whereas regions of low parenchymal density (i.e., air sacs) in nonavian sauropsids do not invade the postcranial skeleton, they do provide analogs for air sacs and pneumatic diverticula observed in the avian system. As such, the extant sister taxa of all fossil sauropsids, including dinosaurs and pterosaurs, have the anatomical foundation (i.e., the soft-tissue potential) for pneumatizing the postcranium. Postcranial pneumaticity requires only the presence of a heterogeneously partitioned pulmonary system.

Perry (2001 and references therein) and Perry and Reuter (1999) suggested that theropod and sauropod dinosaurs exhibiting pneumatic postcrania not only possessed a heterogeneous pulmonary system, but

likely possessed dorsally fixed lungs within the thoracic cavity. Such inferences are based on two lines of reasoning. First, and perhaps the stronger of the two points, a dorsally fixed lung places pulmonary tissues in contact with the vertebral column and ribs, thereby providing direct access for pneumatizing components (i.e., diverticula) of the system to bones most commonly pneumatized. Second, a dorsally fixed lung also provides an anchor point for the region of relatively high parenchymal density (i.e., the exchanger) of the heterogeneous system, and prevents collapse of this region into the less dense air sac portions. Data supporting this notion are derived from studies of extant sauropsids exhibiting high levels of pulmonary heterogeneity (e.g., birds, lizards), where less-dense regions are located on the cranial, caudal, and ventral portions of the lung, with parenchyma-dense regions located dorsally, often "attached" to the dorsal body wall (Duncker, 1978, 1989; Perry, 1983, 1998, 2001; Wyneken, 2001).

Results from the current study support these concepts based on the identification of different "types" of osteological correlates from throughout the vertebral column. For example, this study provides new data to discriminate between inferences related to the lung itself, and those related to air sacs and pneumatic diverticula. Pulmonary fossae in vertebrae of saurischian dinosaurs (e.g., Fig. 3D, PLFS) highlight two key features concerning lung structure in the group. First, the lungs occupied a dorsal or dorsomedial position within the thoracic cavity, confirming the theoretical work of others (e.g., Perry and Reuter, 1999). Second, and perhaps more important, lungs were composed of densely packed, rigid parenchyma capable of influencing vertebral morphology, similar to the condition in extant birds. Although the rigid avian lung is always positioned in the dorsal portion of the thoracic cavity (Hunter, 1774; Duncker, 1971), pulmonary fossae in vertebral centra remain taxonomically restricted (e.g., procellarids; Fig. 8). However, when present, they are causally associated with medially directed parabronchial protuberances, and hence, provide robust osteological correlates for both lung position and composition. Comparable vertebral modifications are apparent in many large-bodied saurischians (Fig. 3D; e.g., *Diplodocus*; Hatcher, 1901, pl. 7; *Allosaurus*, CM 11844; *Tyrannosaurus,* FMNH PR 2081). The identification of similar vertebral modifications in fossil archosaurs helps constrain inferences related not only to lung position, but to aspects of the intrapulmonary structure (i.e., rigid architecture = densely packed parenchyma) of the exchanger itself. Pulmonary fossae, combined with the wealth of data on postcranial pneumaticity, support not just the presence of air sacs, but also of a level of pulmonary heterogeneity (i.e., a relatively dense, rigid exchange region vs. relatively less dense, compliant nonexchange regions) approaching that in ex-

tant birds. Finally, whereas specific details regarding the intrapulmonary functional characteristics (e.g., air conduit and vascular capillary architecture) of saurischian dinosaur lungs may prove difficult to discern, region-specific pneumaticity may be used to elucidate other aspects of higher-level pulmonary organization in these groups (see below).

## Pulmonary Heterogeneity in Ornithischian Dinosaurs

Although the presence of postcranial pneumaticity is indicative of pulmonary air sacs and diverticula, the lack of pneumaticity in no way indicates the absence of such pulmonary specializations. The absence of postcranial pneumaticity merely indicates that the pneumatization process is absent, but provides no direct data related to lung structure. For example, although ornithischian dinosaurs lack pneumatic postcrania, phylogenetic inference based on their extant relatives (i.e., the EPB) suggests that they possessed a heterogeneous pulmonary system. This is based not only on the inferred condition of pulmonary structure in their extinct ornithodiran relatives, but the condition in extant sauropsids in general. Exactly why postcranial pneumaticity occurs in some groups (saurischians) and not others (ornithischians) remains unclear; however, similar variability is also found among birds. This is illustrated in a number of taxa (e.g., *Apteryx*, oxyurine Anseriformes, Podicepidiformes, Gaviiformes) that completely lack pneumatic postcrania, although having the typical avian pulmonary air sac system, including diverticula positioned adjacent to the vertebral column (O'Connor, 2004). Importantly, such variation in birds suggests that there is an on-off switch for the pneumatization process, and whereas it is likely that genetic factors determine this trait, specific control mechanisms are far from being understood (or even hypothesized; although see Hönig et al., 2002; Kurbel et al., 2004). Thus, the absence of pneumatic postcranial bones in ornithischians remains intriguing, not only from the perspective of pulmonary organization inferred from outgroup comparison, but also from a developmental perspective of how certain clades of archosaurs (e.g., diving birds) with air sac systems restrict the pneumatization process.

## Anatomical Inferences: Postcranial Pneumaticity and Pulmonary Organization in Theropod Dinosaurs

Based on modeling exercises derived from studies of extant sauropsid lung morphology and osteological studies of select fossil specimens, Paul (2001) and Perry (2001) predicted a cranial-to-caudal progression in the evolutionary acquisition of avian-like air sacs in nonavian theropods. In these scenarios, cervical air sacs are present throughout Neothero-

poda, with abdominal air sacs "appearing" only in derived coelurosaurs (Paul, 2001). It is within such scenarios that functional attributes (e.g., ventilatory dynamics) of the theropod pulmonary apparatus have been hypothesized.

**Cervical air sacs and diverticula in theropod dinosaurs.** Many theropod dinosaurs possess pneumatic foramina that are best-developed (i.e., relatively larger) in the cranial dorsal and caudalmost cervical vertebrae. This is not only evident in *Majungasaurus* (Figs. 3B, 15B, 16), but also in a number of forms throughout the clade (e.g., *Spinostropheus, Allosaurus, Monolophosaurus, Sinraptor*). A similar pattern of pneumaticity is observed in a number of extant birds, with relatively larger pneumatic foramina located at the cervicodorsal transition. Pulmonary injections reveal that cervical air sacs are located adjacent to the vertebral column at this point (Fig. 11B; O'Connor, 2004, fig. 1), suggesting that the proximity of an air sac (and not just its diverticula) to bones may influence the character (e.g., size) of pneumatic features derived from it. A number of diving taxa (e.g., penguins) that typically lack postcranial pneumaticity have large fossae within the lateral surface of vertebral centra at the cervicothoracic junction, with the medial portion of the cervical air sac occupying this space (pers. obs.). Based both on location and relative size, pneumatic foramina at the cervicodorsal transition in nonavian theropods are consistent with the presence of a significant cervical air sac system similar to that in extant birds (Fig. 16). Interestingly, Hatcher (1901) also mentioned the relatively large size of vertebral cavities at the cervicodorsal transition in some sauropods (e.g., *Diplodocus*), thereby providing the initial osteological basis for scenarios (e.g., Janensch, 1947; Wedel, 2003a) hypothesizing cervical air sacs in this saurischian group.

The patterning of foramina on both cervical vertebrae and ribs of theropods is virtually identical to the condition in birds. Variably located around the periphery of the vertebrarterial canal, pneumatic foramina are present on both centra and neural arch components of vertebrae and cervical ribs (Fig. 16D; yellow arrows originating from the LVDv indicate the typical position of foramina in these elements). Whereas the vertebrarterial canal conveys neurovasculature to portions of the cervical vertebral column, spinal cord, and head in all sauropsids, it also transmits the lateral vertebral diverticulum (Fig. 11, LVDv) in birds. This diverticulum originates from cervical air sacs at the base of the neck, passes cranially within the canal, and is responsible for pneumatization of both cervical vertebrae and ribs. Hence, the pattern and relative development of pneumatic features in the cervical vertebral column of *Majungasaurus* (and theropods generally) indicates the presence of a well-developed cervical air sac complex complete with ascending diverticula comparable to that observed in extant birds (Figs.

11, 16). A similar pattern of cervical pneumaticity, along with hypothesized cervical air sac diverticula, has also been suggested for sauropod dinosaurs first by Janensch (1947) and most recently by Wedel (2003b).

**Abdominal air sacs and diverticula in theropod dinosaurs.** Among extant birds, pneumatic caudal, synsacral, and caudal thoracic vertebrae are pneumatized by diverticula of abdominal air sacs (Müller, 1908; Groebbels, 1932; King and Kelly, 1956; King, 1957, 1966; Hogg, 1984b; O'Connor, 2004). By comparison, then, sacral pneumaticity in nonavian theropods provides strong evidence for the presence of abdominal air sacs in these taxa. Interestingly, Britt et al. (1998) and Wedel (2003b) have spent considerable effort to account for the possibility that cervical air sac diverticula may spread caudally along the axial skeleton, pneumatizing the caudal thoracic, sacral, and caudal regions of the vertebral column. Much of this effort stems from ambiguous assertions by Cover (1953), along with additional statements perpetuating the ambiguity by King (1975), that cervical air sac diverticula in the turkey (*Meleagris gallopavo*) pneumatize portions of the post-midthoracic vertebral series. As pointed out in the Results section, pneumaticity of post-midthoracic vertebral elements by components of the cervical air sac system could not be demonstrated in any bird, including the suspect taxon *Meleagris*.

No doubt contributing to Cover's (1953) initial observation is the fact that diverticula of the cervical and abdominal air sac systems often anastomose with one another in the midthoracic region. Sacral pneumaticity, when present in extant birds, results from invasion by diverticula of the abdominal air sac system. Statements by others on this point, particularly with regard to interpreting region-specific pneumaticity in fossil archosaurs (e.g., Britt et al., 1998; Ruben et al., 2003; Wedel, 2003a), not only stem from their interpretations of the ambiguous statements of Cover (1953) and King (1975) specifically, but also from the general lack of empirical data on avian air sac systems and diverticula associated with the vertebral column. In contrast to scenarios based on modeling studies, then (e.g., Paul, 2001; Perry, 2001), the interpretation in this study of an abdominal air sac system in basal neotheropods significantly expands the distribution of this characteristic throughout the clade. Other saurischian taxa with pneumatic sacra (e.g., neosauropods) likely also possessed abdominal air sac systems (see Wedel, 2003a). The observations of actual diverticular morphology highlighted here (rather than reviews of others' work) provide novel data for use in future modeling studies focused on pulmonary evolution in saurischian dinosaurs.

Finally, the strongest evidence for distinct cervical and abdominal air sacs in a fossil specimen would be the presence of both cervical and sacral pneumaticity with an absence of pneumaticity in the dorsal region (i.e., the *pneumatic hiatus* of Wedel, 2003a). However, most fossils are not preserved in enough detail or completeness for such studies. Fortunately, one specimen of *Majungasaurus* (UA 8678) preserves a near-complete vertebral column with pneumatic foramina throughout the precaudal vertebral series. Whereas this specimen does not have a complete absence of pneumaticity at any point along the series, it does show a reduction in pneumaticity in the last two dorsal neural arches, with enhanced pneumaticity in sacral arches (Fig. 16C). While not unequivocal evidence for distinct cervical and abdominal air sac systems, it is suggestive of two focal centers for the origin of pneumatic diverticula. This interpretation is also consistent with results from extant birds that indicate a relationship between the relative size of pneumatic features and the distance of a given bone from the air sac pneumatizing it. As discussed above, relatively larger pneumatic features are found closer to the main air sac giving rise to the pneumatizing diverticula, with smaller features located further away from the air sac.

In summary, the results of this project provide new perspectives regarding not only the presence of pulmonary air sacs in theropod dinosaurs, but also document specific components of the air sac system in basal neotheropods that were generally thought to be present only in derived coelurosaurs. The presence both of cervical and sacral pneumaticity in *Majungasaurus* indicates that abdominal and cervical air sac systems were present in basal neotheropod taxa, and were not restricted to coelurosaurs, as has been predicted by modeling studies. These interpretations, combined with inferences positing a dorsally positioned, rigid lung underscore the anatomical prerequisites for a flow-through ventilatory system relatively early in the evolution of Theropoda (Fig. 16). Results from this study do not constrain specific physiological parameters of the pulmonary system and comments regarding functional attributes (e.g., ventilatory mechanics, uni- vs. bidirectional intrapulmonary air flow) or inferred metabolic consequences of it are beyond the scope of this work. However, studies examining musculoskeletal anatomy and function in both extant and extinct archosaurs (e.g., Carrier and Farmer, 2000; Farmer and Carrier, 2000; Claessens, 2004a,b, 2005) may be combined with pulmonary reconstructions to form more robust hypotheses of pulmonary function in extinct archosaurs (e.g., see O'Connor and Claessens, 2005). Such complementary studies, when combined with data derived from other sources (e.g., growth rates based on histology or the presence of insulatory integumentary structures; Erickson et al., 2001; Ricqlès et al., 2001; Xu et al., 2001, 2004), may provide the basis for paleontologic meta-analyses geared at elucidating metabolic potential and other physiological inferences pertaining to extinct dinosaurs.

## Nonpulmonary Roles of Postcranial Pneumaticity

In addition to the role in gas exchange, pulmonary air sacs and diverticula also provide a mechanism for pneumatizing heavy, metabolically expensive skeletal tissues. Previous workers (e.g., Cope, 1877; Marsh, 1877; Seeley, 1901; Müller, 1908; Romer, 1966; Currey and Alexander, 1985; Carrano and O'Connor, 2005) have emphasized the density-reducing effect of skeletal pneumatization in fossil archosaurs. From studies of extant birds, pneumatization proceeds by the replacement of trabecular bone and marrow with air sac diverticula (Bremer, 1940b; King and Kelly, 1956; King, 1957; Schepelmann, 1990; Brackmann, 1991), resulting in a significant reduction in the density of a given bone. From an energetics perspective, then, the cost of transport for a pneumatic bone will be less than for an apneumatic bone of the same volume. Thus, pneumatizing the entire skeleton would prove beneficial as long as the mechanical requirements of bones are not jeopardized. Whereas general scaling arguments for a relationship between large organismal size and postcranial pneumaticity are found throughout the literature on both extant and fossil taxa (e.g., Cope, 1877; Müller, 1908; King, 1966; McLelland, 1989; Carrano and O'Connor, 2005), few studies have actually tested this concept. As one example, anseriform birds ranging in body mass between 0.30–10.65 kg indicate only a very weak relationship between body size and relative pneumaticity (O'Connor, 2004). Instead, clade-specific patterns and eco/functional attributes (e.g., diving behavior) are better predictors of overall pneumaticity. Similar studies examining body size and relative pneumaticity in fossil archosaurian clades are lacking, although such approaches may prove fruitful for establishing general rules of construction (Witmer, 1995a) in groups possessing pneumatic postcrania.

## Thermoregulation and Pulmonary Air Sacs

Numerous studies have suggested that pulmonary air sacs in extinct taxa, inferred on the basis of postcranial pneumaticity, provided sites for evaporative heat loss, which itself has been used to support "high metabolic rates" and/or sustained rapid growth rates in different ornithodiran taxa (e.g., Bakker, 1972; Padian, 1983; Paul, 1988; Reid, 1997; Wedel, 2003a). However, these assertions concerning evaporative heat loss are not warranted based on thermoregulatory experiments conducted on extant birds. Contrary to often-cited thermoregulatory benefits of an air sac system (e.g., "birds can dump heat by evaporation in their air sacs…future studies of sauropod thermal biology should at least acknowledge the possibility of efficient, avian-style thermoregulation" Wedel, 2003b:253), there are in fact no experimental studies to date that have actually demonstrated a heat-exchanging role for air sac portions of the pulmonary apparatus. The studies cited supporting this notion (e.g., Schmidt-Nielson et al., 1969; Bernstein, 1976; Dawson and Whittow, 2000) provide data that are at best equivocal, if not actually documenting a virtual lack of evaporative cooling properties for the posttracheal respiratory system in extant birds. Instead, the richly vascularized trachea represents the only portion of the lower respiratory tract functioning in substantial amounts of heat exchange (e.g., Schmidt-Nielson et al., 1969; Dawson and Whittow, 2000, and references therein). Anatomical characteristics consistent with these experimental results include the low-density vasculature reported for avian air sacs and diverticula (Hunter, 1774; Salt and Zeuthen, 1960; McLelland, 1989). Thus, whereas osteological indicators of pneumaticity in fossil archosaurs do have a solid morphological basis in extant birds, putative thermoregulatory roles for air sacs in fossil organisms should be dismissed until experimental studies on extant species demonstrate a link between pulmonary air sacs and evaporative cooling.

## Lung Ventilation in Taxa with Pneumatic Postcrania

The identification of pneumatic postcrania in pterosaurs, theropods, and sauropods indicates the presence of a heterogeneous pulmonary apparatus, with living birds providing the only extant reference for anatomical and physiological properties of such a system. However, to what extent the specific morphology, and perhaps more important, the functionality of this system were similar to that of modern birds is unclear.

Whereas this study is not a direct test of ventilatory mechanisms in fossil groups, pneumaticity data certainly should be factored into *any* reconstruction of pulmonary anatomy in fossil archosaur groups possessing it. For example, reconstructions of theropod pulmonary morphology and function based solely on extant crocodylians (e.g., Ruben et al., 1997, 1999, 2003) seem logically incomplete, as there are solid morphological grounds for inferring an extremely heterogeneous pulmonary system, complete with air sacs and pneumatic diverticula. Moreover, results from the present study even indicate the presence of individual components of an air sac system in theropod dinosaurs, including distinct cervical and abdominal air sac systems. Admittedly, other aspects of pulmonary organization (e.g., the presence of cranial and caudal thoracic and clavicular air sacs similar to living birds) remain ambiguous due to the absence of site-specific osteological markers for thoracic components of the air sac system. Furcular foramina (see Makovicky et al., 2005) in the new dromaeosaurid, *Buitreraptor,* likely represent osteological evidence for clavicular air sacs in nonavian theropods.

In summary, whereas higher-level inferences (e.g., uni- vs. bidirectional air flow) of pulmonary function in extinct archosaurs may remain chalkboard exercises, the basic anatomical requirements of a flow-through pulmonary apparatus (i.e., a rigid, dorsally fixed exchanger with both cranial and caudal air sac ventilators) were present in basal neotheropod dinosaurs and likely characterize basic pulmonary design throughout the clade.

Whereas the potential skeletal kinematics required for flow-through ventilation have yet to be elucidated in theropods, it minimally involved differential costal movements along the rib series (i.e., relatively larger movements of the caudalmost vertebral ribs) to generate pressure differentials between the cranial and caudal regions of the trunk (see O'Connor and Claessens, 2005). Claessens (2004b) also recently put forth a model of an "accessory aspiration pump" in theropod dinosaurs whereby the gastralial apparatus works to preferentially ventilate the caudal region of the trunk, possibly facilitating air flow into caudal (i.e., abdominal and caudal thoracic) air sacs. Similar to the situation in extant archosaurs, it is likely that multiple musculo-skeletal functional units (e.g., costovertebral and gastralial systems) worked together to coordinate ventilatory air flow in theropod dinosaurs. Future work combining studies of pneumaticity with experimental analyses of the musculoskeletal system in extant archosaurs may well refine models of pulmonary organization and ventilatory potential in theropod dinosaurs.

## CONCLUSIONS

An examination of vertebrae in extant sauropsids indicates that different soft-tissue systems profoundly impact skeletal morphology, sometimes in strikingly similar ways. Vertebral fossae are associated with a variety of tissues including fat and muscle in addition to different components of the pulmonary system, indicating relatively low specificity for causally associating these features with a single soft-tissue system. Vertebral foramina may better predict pneumaticity, but only when combined with knowledge of the internal character of the bone. The most reliable, consistent, and "system-specific" indicators of pneumaticity are cortical foramina that communicate directly with large internal cavities within bones.

Unambiguous examples of postcranial pneumaticity in archosaurs can be found in pterosaurs and theropod and sauropod dinosaurs. Other archosauriform taxa with putative pneumatic features (e.g., *Erythrosuchus africanus*, parasuchians) lack criteria for a positive assessment based on a Pneumaticity Profile developed in this study. Vertebral and costal pneumaticity in neotheropods supports the inference of cervical and abdominal air sacs in this group, in addition to pneumatization directly from the lung, and highlights the anatomical prerequisite for a flow-through lung design. Such a condition in noncoelurosaurs indicates that a highly heterogeneous pulmonary system likely characterized Theropoda (at least Neotheropoda), and was not restricted to avian members of the clade.

Pneumaticity of the postcranial skeleton represents an exaptation founded on the basis of a high degree of pulmonary heterogeneity, this latter characteristic being variably expressed among all extant sauropsids. Whereas its role in the adaptive radiation of different archosaur clades (pterosaurs, theropods, sauropods) remains a point of inquiry, each of these groups likely benefited from the density-reducing effects of skeletal pneumaticity. This may have facilitated not only the rapid exploitation of large body size in some dinosaurian clades, but the attainment of flight in pterosaurs and birds. However, its presence in many small-bodied forms in conjunction with its absence in other large-bodied taxa (e.g., ornithischian dinosaurs) remains puzzling, requiring additional research. Future studies may provide data necessary for exploring possible functional or biomechanical hypotheses testing such as the relationship between relative pneumaticity, locomotor mode, and body size in this diverse assemblage of animals.

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# APPENDIX A

List of extant taxa examined in the study. Numbers in parentheses indicate the type(s) of anatomical preparation(s) for each specimen. See Materials and Methods for list of institutional abbreviations.

Avians: *Accipiter nissus*, JLUG (1,4); *Aix galericulata*, JLUG (1,4); *A. sponsa*, JULG (1,4); OUVC 9421 (1,2,3); OUVC 9663 (2,4); *Alca torda*, JLUG (1,4); *Anas crecca*, JLUG 1 (1,4); *A. platyrhynchos*, JLUG (1,4); *Anhima cornuta*, NMNH 345217 (1); *Anser albifrons*, JLUG (1,4); *A. anser*, JLUG (1,4); *Anthropoides virgo*, JLUG (1,4); *Aptenodytes patagonicus*, JLUG (1,4); *Ardea cinerea*, JLUG (1,4); *Asio otus*, JLUG (1,4); *Athene noctua*, JLUG (1,4); *Aythya ferina*, JLUG (1,4); *A. fuligula*, JLUG (1,4); *Balearica pavonina*, JLUG (1,4); *Branta sandvicensis*, CM 14428 (1); *Bubo virginianus*, JLUG (1,4); OUVC (1); *Bucorvus leadbeateri*, AMNH 3953 (1); TM 76018 (2); *Buteo buteo*, JLUG (1,4); *B. jamaicensis*, OUVC 9788 (1); OUVC 9791 (1); *Cairina moschata*, JLUG (1,4); *Casuarius casuarius*, AMNH 1106 (1); 3870 (1); JLUG (1,4); *Cathartes aura*, OUVC 9648 (1,2); *Chauna chavaria*,JLUG (1,4); *Chen caerulscens*, CM 15047 (1); *Chrysolophus pictus*, JLUG (1,4); *Ciconia ciconia*, JLUG (1,4); *Circus aeruginosus*, JLUG (1,4); *C. cyaneus*, JLUG (1,4); OUVC 9654 (1); *Colaptes auratus*, OUVC 9775 (1); *Columba livia*, JLUG (1,4); *Corvus corone*, JLUG (1,4); *C. monedula*, JLUG (1,4); *Cygnus attratus*, JLUG (1,4); *C. columbianus*, JLUG (1,4); *C. cygnus*, JLUG (1,4); *C. olor*, JLUG 2 (1,4); *C. melancoryphus*, CM S-201 (1); *Dendrocopus major*, JLUG (1,4); *Dromaius novaehollandiae*, JLUG (1,4); *Eudroma elegans*, OUVC 9804 (1); *Eudyptes cristatus*, JLUG

(1,4); *Falco tinnunculus*, JLUG (1,4); *Fratercula arctica*, JLUG (1,4); *Fulica atra*, JLUG (1,4); *Fulmaris glacialis*, JLUG (1,4); *Gallinula chloropus*, JLUG (1,4); *Gallus gallus*, JLUG (4); OUVC 9419 (1,2,3,4,5); OUCV 9420 (1,2,3,4,5); *Garrulus glandarius*, JLUG (1,4); *Gavia arctica*, JLUG (1,4); *Grus antigone*, SBU AV104063 (1); *Larus argentatus*, JLUG (1,4); *L. canus*, JLUG (1,4); *L. marinus*, JLUG (1,4); *L. ridibundus*, JLUG (1,4); *Leptoptilos dubius*, SBU 118743 (1); *Meleagris gallopavo*, JLUG (1,4); *Mergus albellus*, JLUG (1,4); *M. merganser*, JLUG (1,4); *Nucifraga caryocatactes*, JLUG (1,4); *Nycticorax nycticorax*, JLUG (1,4); *Nymphicus hallandicus*, JLUG (1,4); *Otus asio*, OUVC 9778 (1); *Pelecanus erythrorhynchos*, JLUG (1,4); SBU 103985 (1); *P. occidentalis*, AMNH 21610 (2,4); SBU AV103985 (1); *Perdix perdix*, JLUG (1,4); *Phalacrocorax aristotelis*, JLUG (1,4); *Phasianus colchicus*, OUVC 9664 (1,4,5); *Phoenicoparrus ruber*, JLUG 1,4); *Pica pica*, JLUG (1,4); *Platycercus icterotis*, JLUG (1,4); *Podiceps cristatus*, JLUG (1,4); *P. ruficollis*, JULG (1,4); *Porphyrula alleni*, JLUG (1,4); *Psephotus haematonotus*, JLUG (1,4); *Psittacus erithacus*, JLUG (1,4); *Pterodroma phaeopygia*, FMNH 313946 (1); *Puffinus puffinus*, JLUG (1,4); *Rallus aquaticus*, JLUG (1,4); *Ramphastos swainsonii*, JLUG (1,4); *Rhea American*, JLUG 15 (1,4); SBU 131109 (1); *Scolopax rusticola*, JLUG (1,4); *Spheniscus demeris*, JLUG (1,4); *Sterna hirundo*, JLUG (1,4); *Stix aluco*, JLUG (1,4); *Strepopelis decaocta*, JLUG (1,4); *Struthio camelus*, AMNH 1727 (1); AMNH 1821 (1); FMNH 222324 (1); JLUG (1,4); OUVC 9422 (1,2,4); OUVC 9658 (1,2,3,5); OUVC 9665 (2,3); SBU AV20 (1,2,4); *Sula bassana*, CM T-21320 (2); JLUG (1,4); USNM 554787 (1); *S. dactylatra*, JLUG (1,4); *Tadorna tadorna*, JLUG (1,4); *Tringa hypoleucos*, JLUG (1,4); *Uria aalge*, JLUG (1,4); *Vanellus vanellus*, JLUG (1,4).

Crocodylians: *Alligator mississippiensis*, AMNH 43314 (1); AMNH 46842 (1); OUVC 9401 (1); OUVC 9412 (1); OUVC 9657 (1,2,3,4,5); OUVC 9659 (1,2,5); OUVC 9666 (1,2,5); OUVC 9667 (1,2,5); OUVC 9757 (1,2,3,6); OUVC 9760 (1,2,3,6); SBU HP99013 (2,3); SBU HP99014 (2,3,4); *Alligator sinensis*, AMNH R142507 (1); *Caiman* sp., FMNH 250822 (1); *Caiman crocodilus*, AMNH 20584 (1); CM 114437 (1); FMNH 98961 (1); *Caiman yacare*, AMNH 97304 (1); *Crocodylus* sp., CM 6450 (1); *Crocodylus acutus*, FMNH 5157 (1); *Crocodylus rhombifer*, FMNH 34677 (1); *Melanosuchus niger*, CM 55624 (1); *Tomistoma schlegeli*, FMNH 206755 (1);

Nonarchosaurian Sauropsids: *Caretta caretta*, FMNH 218507 (1); *\*C. caretta*, 1 specimen (2,4); *\*Chelonia mydas*, 2 specimens (2,4); *Ctenosaura similes*, CM 144933 (1); *Cyclura cornuta*, CM 144935 (1); *Hydrosaurus* sp., OUVC 9960 (1,2,3,4,5); *Iguana iguana*, CM 144975 (1); CM 114410 (1); *Tupinambis teguixin*, CM 112012 (1); *Varanus* sp., CM 118507 (1).

Key for anatomical preparations: 1, skeletal preparation; 2, gross dissection; 3, vascular injection preparation; 4, pulmonary injection preparation; 5, corrosion cast; 6, computed tomography following vascular injection with barium-latex medium. \*Specimens provided by J. Wyneken, Florida Atlantic University (no accession data available).

## APPENDIX B

List of fossil archosauriform specimens examined in the study.

Ornithodiran Archosaurs: *Allosaurus fragilis*, CM 11844, USNM 8367; *Archaeopteryx lithographica* (London), BMNH 37001; *Archaeopteryx lithographica* (Berlin), MB 1880.81.4598; *Apatosaurus louisae*, CM 3018; *Camarasaurus* sp., CM 11338; *Carcharodontosaurus saharicus*, CNM 41774; *Ceratosaurus nasicornis*, USNM 4735; *Diplodocus carnegii*, CM 84; *Lonchodectes* sp., BMNH R3694; *Majungasaurus crenatissimus*, UA 8678; Ornithocheirus sp., SM B54.302; *Ornithocheirus* sp., BMNH R558; *Rahonavis ostromi*, UA 8656; *Rapetosaurus krausei*, FMNH PR 2209; *Tyrannosaurus rex*, FMNH PR 2081.

Nonornithodiran Archosauriforms: *Erythrosuchus africanus*, BMNH R8667; *Erythrosuchus africanus*, BMNH R3592; *Erythrosuchus africanus*, NGS F377; *Leptosuchus (Rutiodon) adamanensis*, UCMP 26699; *Leptosuchus (Rutiodon) zunii*, UCMP 27036; *Rutiodon (Angistorhinopsis) reutimeyer*, MB 1922.23.342; *Mahajangasuchus insignis*, UA 8654; *Phytosaurus (Nicrosaurus) kapffi*, BMNH R38072.