Evolution of the Respiratory System in Nonavian Theropods: Evidence from Rib and Vertebral Morphology

EMMA R. SCHACHNER,[1,2*] TYLER R. LYSON,[2,3] AND PETER DODSON[1,4]

[1]Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, Pennsylvania
[2]Marmarth Research Foundation, Marmarth, North Dakota
[3]Department of Geology and Geophysics, Yale University, New Haven, Connecticut
[4]School of Veterinary Medicine, University of Pennsylvania, Philadelphia, Pennsylvania

ABSTRACT

Recent reports of region-specific vertebral pneumaticity in nonavian theropod dinosaurs have brought attention to the hypothesis that these animals possessed an avian-style respiratory system with flow-through ventilation. This study explores the thoracic rib and vertebral anatomy of *Sinraptor, Allosaurus, Tyrannosaurus*, and *Deinonychus*; four nonavian theropods that all show well-preserved thoracic vertebrae and ribs. Comparisons to the osteology and soft tissue anatomy of extant saurians provide new evidence supporting the hypothesis of flow-through ventilation in nonavian theropods. Analyses of diapophyseal and parapophyseal position and thoracic rib morphology suggest that most nonavian theropods possessed lungs that were deeply incised by the adjacent bicapitate thoracic ribs. This functionally constrains the lungs as rigid nonexpansive organs that were likely ventilated by accessory nonvascularized air sacs. The axial anatomy of this group also reveals that a crocodilian-like hepatic-piston lung would be functionally and biomechanically untenable. Taken together with the evidence that avian-like air sacs were present in basal theropods, these data lead us to conclude that an avian-style pulmonary system was likely a universal theropod trait. Anat Rec, 292:1501–1513, 2009. © 2009 Wiley-Liss, Inc.

Key words: axial skeleton; respiration; theropod dinosaur; avian; lung

Several recent studies on the evolutionary history of the avian respiratory system have indicated that several characters that define modern avian respiration extend back into the nonavian theropod lineage, possibly indicating the group had a more avian-like respiratory system (O'Connor, 2004, 2006; O'Connor and Claessens, 2005). Given the strong support for the placement of theropod dinosaurs between modern birds and crocodilians, the extant phylogenetic bracket (EPB) method (Witmer, 1995a) could potentially be used to provide further support for a more avian-like respiratory system in nonavian theropods. However, while this method has provided reliable reconstructions of theropod soft tissue anatomy, including aspects of tyrannosaur myology (e.g., Carrano and Hutchinson, 2002) and craniofacial morphology (Witmer, 1995b, 1997), the method's reliability is constrained by the number of homologous characters identified in the morphology of the bracketing extant taxa. Unfortunately the respiratory biology, and indeed specific lung morphology of extant birds and crocodilians

is highly divergent from one another, likely reflecting very different evolutionary pressures upon each lineage; thus, based on the EPB alone, it is impossible to determine whether nonavian theropods possessed a more bird-like or crocodilian-like pulmonary anatomy. Nonetheless, there have been numerous attempts to impart nonavian theropods with either a more crocodilian-style hepatic-piston pulmonary system (e.g., Ruben et al., 1997, 1999, 2003; Chinsamy and Hillenius, 2004) or an avian-like lung-air sac respiratory system (e.g., Paul, 2001; O'Connor and Claessens, 2005; O'Connor, 2006).

The hepatic-piston hypothesis posits that theropod dinosaurs possessed septate crocodilian-like lungs that were ventilated by the diaphragmaticus muscle, which runs from the pubes to the liver. When this muscle contracts, it shifts the abdominal viscera caudally, decreasing the pressure within the thoracic cavity, resulting in inspiration (Gans and Clark, 1976; Farmer and Carrier, 2000). Relaxation of this muscle returns the abdominal viscera to their former positions, forcing the air out of the lungs. The hepatic-piston hypothesis is based upon an EPB level II inference, negative evidence, and putative osteological similarities between theropods and extant crocodilians (e.g., Ruben et al., 2003), as well as the untested assumption that the crocodilian lung is plesiomorphic for Archosauria.

The main competing hypothesis proposes that theropod dinosaurs possessed a more avian-like respiratory system with rigid dorsally adhered lungs that are ventilated by cranial and caudal air sacs that variably pneumatize the postcranial skeleton (e.g., Britt et al., 1998; O'Connor and Claessens, 2005; O'Connor, 2006). Using rigorous methods to differentiate pulmonary pneumaticity from fossae and vascular foramina in the axial skeleton, O'Connor (2006) argued that the extensive vertebral pneumaticity in the axial skeleton of theropods is homologous to that seen in extant birds. The region-specific pneumaticity in the postcranial skeleton of *Majungatholus atopus* (and other theropods—see O'Connor and Claessens, 2005 supplemental materials) has been unequivocally correlated with diverticula from the lungs and cranial and caudal air sacs of extant birds (O'Connor and Claessens, 2005). The avian hypothesis has been further supported by Klein and Owerkowicz (2006) study demonstrating that the complex septal coelomic division of the avian thorax is homologous to, and likely derived from, the postpulmonary septum that supports the saccular lung chambers of lizards. Other key osteological characters (e.g., hypapophyses and uncinate processes) have been used as evidence for at least a protoavian respiratory system in nonavian theropods (Klein and Owerkowicz, 2006; Codd et al., 2007).

Alternatively, it is possible that both avian and crocodilian pulmonary anatomies are highly derived, with neither representing the basal archosaurian state. Perhaps, theropod lungs were morphologically similar to or evolved from an animal possessing the saccular multicameral lungs of lizards (e.g., *Varanus* sp.) as proposed by Perry (1992). The lung morphology for each of these hypotheses is very distinct: the varanid lung is multichambered and elastic; the crocodilian lung is similar but also includes the hepatic-piston accessory ventilation mechanism; and the avian lung is small, rigid, and nonexpansive, and has associated nonvascularized air sacs. Furthermore, the craniodorsal surface of the lungs in all

extant archosaurs and lizards are attached to the adjacent vertebral bodies and to varying degrees (depending on the taxon) to the associated rib heads (Perry, 1988; McLelland, 1989; pers. obs. 2007). This close relationship between the lung and the axial skeleton affects the gross morphology of the lung surface in all diapsids, and all three groups possess specific skeletal adaptations that assist in the ventilation of the lungs. Thus, the anatomy of the vertebral column and ribs appear to be reliable indicators of lung morphology in extant diapsids, providing osteological correlates to help reconstruct the respiratory system in extinct diapsids, including nonavian theropods.

Previous reconstructions of nonavian theropod respiratory anatomy focus primarily on the air sac system or pelvic and abdominal morphology, as opposed to the actual pulmonary morphology (although see Perry, 2001; O'Connor, 2006, pp.1216-1219 and Figs. 3D, 8A, and 8B). While these anatomical characteristics correlate with respiratory anatomy, they do not necessarily directly reflect the gross anatomy of the lung. In this study, we test the hypothesis that theropod dinosaurs possessed avian-like rigid nonexpansive lungs that were dorsally attached to the vertebral column and were incised by adjacent bicapitate thoracic ribs. Paul (2001, 2002) presented a generalized review of the anatomical characters of the theropod rib cage that supported the inference of an avian lung in Theropoda. We present additional evidence supporting this hypothesis by analyzing vertebral and rib morphology and positions of the articulation points between the ribs and vertebrae from individual theropod specimens with a well-preserved vertebral series. Our data indicate that rigid, dorsally anchored, nonexpansive lungs were present in Neotetanurae (*sensu* Sereno, 1999 and Avetheropoda of Paul, 1988 and Padian et al., 1999).

RESPIRATORY ANATOMY OF EXTANT SQUAMATES AND ARCHOSAURS
Respiration in Basal Amniotes

Aspiration breathing is plesiomorphic in extant amniotes, derived from a buccal pump respiratory mechanism that is still present in many extant taxa (e.g., Brainerd, 1999; Klein and Owerkowicz, 2006). Inspiration results from negative internal pressure generated by expansion of the thoracic cavity (except in Testudines) (Brainerd, 1999). In modern lepidosaurs, aspiration is primarily driven by rotation of the ribs, which provides the negative pressure in the lungs required to force air into the thoracic cavity (Brainerd, 1999; Carrier and Farmer, 2000b). Expiration results from contraction of the axial muscles, which rotates the ribs in the reverse direction and forces the air out of the pleural cavity (Brainerd, 1999; Carrier and Farmer, 2000b).

Two major complications are associated with costal aspiration that all amniotes counteract to varying degrees using different anatomical adaptations. The first problem is the movement of the abdominal viscera in association with the decrease in internal pressure produced by costal aspiration, resulting in a diminished pleural cavity available for ventilation (Perry, 1985; Brainerd, 1999). To circumvent this potential problem, many animals have either a muscular or membranous

septum separating the pleural cavity from the abdominal cavity (Klein and Owerkowicz, 2006).

The second issue resulting from costal aspiration is the potential asymmetrical inflation of the lungs, which can lead to lung collapse (Klein and Owerkowicz, 2006). Mammals solve this dilemma by having homogenously structured lungs that are completely encased by a fluid lined pleural cavity (Klein and Owerkowicz, 2006). In contrast, in Reptilia, the lungs are attached to the dorsal surface of the body cavity (Perry, 1992) and attached to a series of pulmonary septa, which prevent the multiple bellows-like septate chambers from collapsing (Perry, 1988).

Respiration in Varanids

Lung morphology. Varanids (and helodermatids) are the only lizards that possess multichambered lungs (Perry, 1998). They are generally large and heterogeneously subdivided into various chambers, with the apical chambers supplied with inspired air through a cartilage-reinforced secondary bronchus (Perry, 1998). The dorsomedial region of the varanid lung is where the majority of gas exchange occurs via dense parenchyma, while the caudal sacculated sections are poorly vascularized, highly compliant (Perry, 1998, 1983), and are believed to serve as ventilatory bellows (Klein and Owerkowicz, 2006). The dorsal and medial chambers of the lungs in varanids are essentially immobile due to the tight attachment of the dorsal lung surface to the body wall (Perry, 1992; pers. obs. 2009). In addition, a complete nonmuscular postpulmonary septum (PPS) that lies caudal to the lungs and cranial to the liver has evolved in varanids (Klein and Owerkowicz, 2006).

The lungs are primarily ventilated by costal aspiration; the craniolateral movement of the ribs is assisted by the PPS, which prevents the caudal regions of the lung from collapsing (Klein and Owerkowicz, 2006). The saccular caudal regions of the varanid lung are poorly vascularized (Perry, 1998) and generally do not participate in gas exchange; however, they are thought to aid in the ventilation of the immobile cranial portion of the lung that contains the dense respiratory parenchyma (Klein and Owerkowicz, 2006). Costal aspiration, however, is only completely effective when the animal is immobile (Owerkowicz et al., 1999). During locomotion, the intercostal muscles, M. external oblique and M. rectus abdominis actively produce lateral undulations of the trunk, diminishing their capacity to help ventilate the lungs (Ritter, 1996; Owerkowicz et al., 1999). This results in a reduced capacity to maintain the necessary blood oxygen concentrations required for intense activity; however, some derived lizards (i.e., *Varanus exanthematicus*) mitigate this axial constraint by using a gular pump in association with costal-driven respiration (Owerkowicz et al., 1999). Nevertheless, the lateral undulations associated with locomotion restrict squamate aerobic activity to short infrequent bursts (Carrier and Farmer, 2000a). Interestingly, varanids possess a cardiopulmonary system that permits oxygen uptake comparable to that of some mammals of similar size (Hicks and Farmer, 1999); however, their ability to ventilate the lung is greatly constrained by their axial morphology (Owerkowicz et al., 1999).

Osteology. Varanids generally have 21–22 procoelous dorsal (=thoracic) vertebrae, with short and broad centra (Romer, 1956). The thoracic ribs are holocephalous, as in other lizards, and articulate with the thoracic vertebrae via a single synapophysis (fused parapophysis and diapophysis) (Hoffstetter and Gasc, 1969). This single articular site permits a flexible rib cage, which facilitates costal aspiration. The interior ceiling of the thoracic cavity is relatively smooth, allowing the caudal compliant portion of the lungs that is not attached to the vertebral column to expand unencumbered during inhalation.

Respiration in Crocodilians

Lung morphology. Crocodilians possess the most complex lung of any extant nonavian reptile (Fig. 1A); they are completely enclosed in a separate pleural cavity and frequently attached to the dorsal parietal pleura (Perry, 1988). The multicameral pattern is comparable to the sacculated multichambered lung of varanids; however, the crocodilian lung is composed of multiple tubular monopodial branching chambers that are connected by intrapulmonary bronchi and lined with perforated interedicular septa (Perry, 1988). The monopodial branching pattern and low number of cranial chambers are similar to the structure found in embryonic avian lungs (Perry, 1988). Crocodilians possess a PPS (like varanids) as well as a posthepatic septum (PHS) that augment the effectiveness of costal aspiration (Perry, 1998). The lungs of crocodilians are partially adhered to the thoracic body wall along their craniodorsal surfaces (as opposed to the entire surface as in varanids) as well as to the viscera along their caudal surfaces, which prevents lung collapse during expiration (Perry, 1998).

Lung ventilation is achieved by costal aspiration in association with a hepatic piston pump, a derived mechanism utilizing a novel respiratory muscle, the diaphragmaticus (Fig. 1A) (Brainerd, 1999; Carrier and Farmer, 2000a,b; Claessens, 2004a). This muscle takes its origin from the caudal gastralia and cranial surface of the pubes and inserts on a collagenous fascia on the caudal surface of the liver; contraction of this muscle pulls the liver and viscera caudally, thus decreasing the pressure within the thoracic cavity (Carrier and Farmer, 2000b; Farmer and Carrier, 2000). The pelvis of crocodilians is highly derived and modified relative to the basal archosaurian condition in that the pubis articulates only with the ischium, forming a mobile joint (Farmer and Carrier, 2000). This mobile pubis of extant crocodilians is a synapomorphy of Crocodyliformes (Claessens, 2004a). In addition to the movement of the liver by the diaphragmaticus, two other muscles (the ischiopubic and ischiotruncus muscles) assist in respiration by rotating the pubic bones ventrally, thus decreasing the pressure within the body cavity initiating inspiration (Carrier and Farmer, 2000b). Relaxation of the diaphragmaticus, ischiopubic, and ischiotruncus muscles, in conjunction with contraction of the rectus abdominus and transversalis muscles, returns the liver and pubic bones to their more cranial orientation commencing expiration (Carrier and Farmer, 2000b).
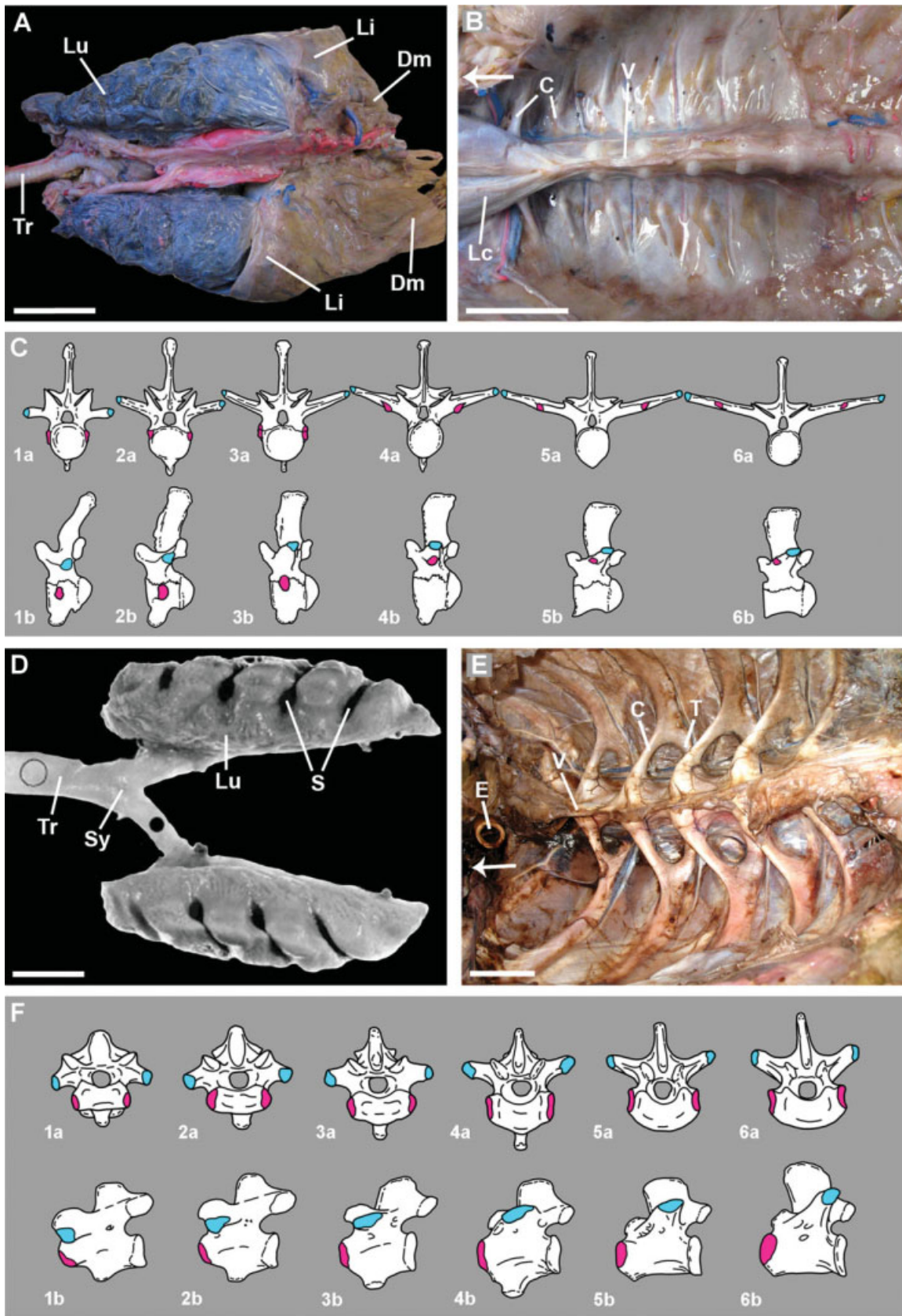
Figure 1.

Osteology. In extant crocodilians, the 15 procoelous dorsal vertebrae can be subdivided into thoracic and lumbar (rib free) vertebrae (Hoffstetter and Gasc, 1969). The first three (and sometimes four) dorsal centra possess hypapophyses, which serve as the origin sites for the M. longus colli muscles that run cranially. The first two thoracic vertebrae (like the cervical vertebrae) articulate with their corresponding ribs via two distinct costal processes, the ventral capitulum and the dorsal tuberculum (Fig. 2A). The parapophyses in both vertebrae are located on the body of the centrum, beneath the neurocentral suture, while the diapophyses are located on the distal ends of the transverse processes (Fig. 1C). The ribs that articulate with the first two vertebrae are strongly bicapitate with the capitulum located directly ventrally to the tuberculum, with a deep notch separating the two rib heads. The third thoracic vertebra is transitional; the parapophysis is located above (or directly on in some specimens) the neurocentral suture. The capitulum is reduced in this rib and the tuberculum becomes the primary articular process (Fig. 3A). In the remaining vertebrae the transverse processes are very broad and thin, each with two articular surfaces, the craniomedial surface for the capitulum and the caudolateral one for the tuberculum. In each of the successive vertebrae, the parapophyses shift further out on the transverse process toward the diapophysis until they become almost one articular surface (Fig. 1C). The result of this shift in rib articulation is a thoracic cavity with a very flat and smooth ceiling caudal to the first two ribs (Fig. 1B). This facilitates the cranial and caudal movement of the lungs when inflated and deflated by the hepatic-piston pump. The cranial portion of the thoracic cavity is furrowed by the capitula of the first two ribs, which leave impressions on the craniodorsal surface of the lungs (Perry, 1988; pers. obs. 2008). The ribs that articulate only with the transverse processes of their corresponding vertebrae (dorsals 4–15) are generally much more mobile than the preceding ribs because the two articulations lie on the same plane horizontally, allowing the ribs to rotate laterally during costal aspiration.

Respiration in Extant Birds

Lung morphology. The avian respiratory tract is composed of two main components: the rigid gas exchanging bronchial lungs and the nonvascularized ventilatory air sacs (Duncker, 1972, 1974). The air sac system permits unidirectional airflow over the paleopulmonic parabronchi during both inspiration and expiration (Maina, 2005). This system, enabled by the rigid structure of the lung, provides birds with the most efficient respiratory apparatus of any air-breathing vertebrates (Maina, 2002). The rigidity of the avian lung and constant volume throughout the respiratory cycle provide the mechanical foundation for an enlargement of the oxygen exchange surfaces into a three-dimensional mesh network of blood capillaries ∼10 times larger than the gas exchange surfaces found in mammalian lungs (Duncker, 1974).

The body of the lung is positioned in the craniodorsal region of the thoracic cavity; the costal surface is tightly attached to the costal wall and the vertebral (medial) surface of the lung adheres to the adjacent vertebral bodies (Duncker, 1972). The vertebral and costal surfaces of the lung are deeply incised by the proximal section of each bicapitate rib (Fig. 1D), so that approximately one-fifth to one-third of the lung tissue is located in between the neighboring thoracic ribs (Duncker, 1972; Maina and Nathaniel, 2001; Maina, 2005). Respired air enters the lung through the primary bronchus, which gives off four ventrobronchi and 7–10 dorsobronchi; both the ventro and dorsobronchi further subdivide into the smaller parabronchi and capillaries which anastomose with one another and are the primary site for gas exchange (Duncker, 1972). The lungs are bordered ventrally by a horizontal septum that separates the pleural cavity from the abdominal viscera (Duncker, 1972), and an oblique septum dividing the peritoneal cavity into two separate regions (Klein and Owerkowicz, 2006). During both inspiration and expiration the avian lung remains rigid, changing in volume by, at the most, ∼1.4% (Jones et al., 1985). The horizontal septum arises from the hypapophyses of the thoracic vertebrae to insert on the lateral thoracic wall forming the floor of the pleural cavity (Duncker, 1972), and the ceiling of the subpulmonary cavity, which houses most of the air sacs in extant birds (except for *Apteryx*) (Klein and Owerkowicz, 2006). This series of septa is likely homologous to the reptilian PPS that assists the multicameral lungs during respiration, and it is believed to have a similar function in birds (Klein and Owerkowicz, 2006).

The system of air sacs in the avian lung was likely modified from the nonvascularized caudal chambers of the sacculated reptilian lung (Perry, 1992; Ruben et al., 1997; Maina, 2002) into the unpaired cervical, and paired interclavicular, cranial thoracic, caudal thoracic, and abdominal sacs found in extant birds (Duncker, 1972, 1974; Kürtül et al., 2004; Çevik-Demirkan et al., 2006). The air sacs serve as air storage chambers and ventilatory bellows, generating airflow through the lungs (Scheid and Piiper, 1989; Heard, 1997; Powell, 2000). Extrapulmonary diverticulae from the air sac system invade the postcranial skeleton resulting in the pneumaticity of variable

Fig. 1. **A:** Dorsal view of the lungs, trachea, liver, and diaphragmaticus muscles (cut) of an alligator. Scale bar = 5 cm. **B:** Interior of the thoracic cavity of an alligator (*Alligator mississippiensis*) with the viscera removed. Arrow points cranially. Scale bar = 5 cm. **C:** Diagrammatic images of the first six dorsal vertebrae of an American crocodile (*Crocodylus acutus*) redrawn and modified from Mook (1921). The diapophyses are indicated in blue and the parapophyses are indicated in pink. 1a–6a = dorsals 1–6 in cranial view, 1b–6b = dorsals 1–6 in left lateral view. **D:** Dorsal view of the lungs, trachea, and extrapulmonary bronchi of an ostrich (*Struthio camelus*). Image reproduced/adapted with permission from Maina and Nathaniel (2001). Scale bar = 2 cm.

E: Interior of the thoracic cavity of an ostrich (*Struthio camelus*) with the thoracic and abdominal viscera removed and trachea and esophagus cut. Arrow indicates direction of the head. Scale bar = 5 cm. **F:** Diagrammatic image of the first six dorsal vertebrae of an ostrich (*S. camelus*). The diapophyses are indicated in blue and the parapophyses are indicated in pink. 1a–6a = dorsals 1–6 in cranial view, 1b–6b = dorsals 1–6 in left lateral view. C = capitulum; Dm = diaphragmaticus muscle (cut); E = esophagus (cut); Lc = longus coli muscle; Li = liver; Lu = lung; S = costal sulci; Sy = syrinx; T = tuberculum; Tr = trachea; V = ventral surface of the dorsal centra.
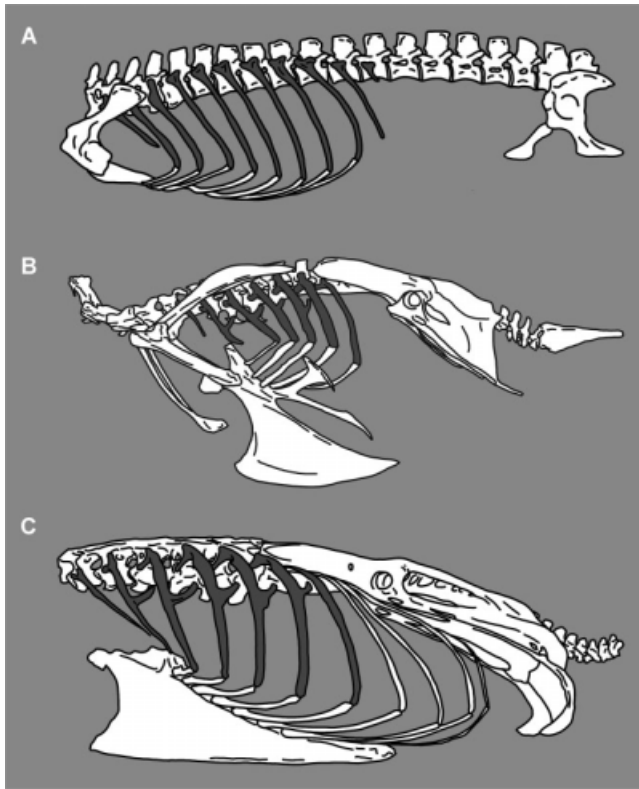
Fig. 2. Diagrammatic images demonstrating the differences in rib morphology and articulation in an alligator (**A**) and two extant birds (**B**, **C**). Dorsal ribs are indicated in gray, images are not to scale. A: Left lateral view of the thoracic skeleton of the American alligator (*A. mississippiensis*) with the forelimbs, hindlimbs, and gastralia removed. B: Left lateral view of the thoracic skeleton of the Argus pheasant (*Argus giganteus*) with the forelimbs removed. Redrawn from Shufeldt (1909). C: Left lateral view of the thoracic skeleton of the Trumpeter swan (*Olor columbianus*) redrawn from Shufeldt (1909) with the forelimb and shoulder girdle removed.

portions of both the axial and appendicular skeleton (e.g., Hogg, 1984; O'Connor, 2004, 2006).

Ventilation of the avian lung is functionally very different from that of other vertebrates and has been well summarized in the literature (e.g., Duncker, 1971; Scheid and Piiper, 1989; Powell, 2000; Maina, 2005; Claessens, 2008). Inspiration results from a ventral shift of the sternum, which decreases the internal thoracic pressure drawing air in through the trachea. The inspired air flows to the abdominal air sacs and the caudal thoracic sacs via the laterobronchus of the lung (Powell, 2000). Air also flows through the lung, across the gas exchange surfaces of the ventrobronchi and parabronchi, to the cranial sacs due to the decrease in thoracic pressure (Scheid and Piiper, 1989). During expiration, the sternum returns to its original position through a hinge-like motion against the intracostal articulations, and the resulting increase in thoracic pressure causes the air in the cranial sacs to be exhaled through the trachea (Claessens, 2008). Also, the air in the abdominal sacs flows through the dorsobronchi, parabronchi, and ventrobronchi of the lungs to the cranial sacs and then out through the trachea as well, thus pro-

viding unidirectional and near-continuous ventilation of the avian lung (Duncker, 1971).

Osteology. The avian lung is structurally and functionally different from that of other extant archosaurs, and as a result is associated with different axial skeletal morphology (Fig. 2B,C). Unlike costal aspirators with elastic inflatable lungs, which require a flexible rib cage, the rigid avian lung requires an equally rigid dorsoventrally incompressible thoracic cavity. It has been proposed that the biomechanics and architecture of the avian rib cage and lung exist in a tensegrity (tensional integrity) state, which allowed for the decoupling of the rigid lung and the ventilatory air sacs (Maina, 2007). The rigidity and volume-constant state of the avian lung is a prerequisite for the extreme subdivision of the parabronchial tissue, which would not be possible if the lung were compliant since surface tension would have to be overcome (Duncker, 2004; Maina, 2007). To support the lung structure, the thoracic ribs articulate with the dorsal vertebrae in a manner so that rib rotation during inspiration is uniform and restricted by an axis of rotation that near vertically through both the parapophysis and diapophysis (Claessens, 2008). As in crocodilians, the tuberculum articulates with the diapophysis on the transverse process; however, the diapophysial surface is located slightly more ventrally than in the crocodilian vertebrae. The transverse processes are generally short and subtriangular in cross section (Fig. 1F). The capitulum is offset and ventral to the tuberculum (Figs. 2B,C and 3B), articulating with its corresponding parapophysis, which is located on the centrum and below the neurocentral suture for the entire dorsal series (Fig. 1F) (King, 1993). The ventrally located capitular articulations produce a deeply furrowed thoracic ceiling (Fig. 1E), with the capitula themselves incising the dorsally adhered lungs (resulting in grooves in the lung tissue (Fig. 1D), or costal sulci), further reducing pulmonary movement or volumetric change.

MATERIALS AND METHODS

This study describes the vertebral anatomy of extant birds, crocodilians, and varanids, as well as specimens of nonavian theropods. Complete vertebral series in theropod dinosaurs are limited; however, there are a few taxa that are either represented by multiple specimens or are complete enough for this study. These taxa include the following: *Sinraptor dongi* (IVPP 10600), *Allosaurus fragilis* (UUVP 6000), *Tyrannosaurus rex* (FMNH PR 2081), and *Deinonychus antirrhopus* (YPM 5204, YPM 5210). All of the nonavian theropods selected for this study are represented by detailed photographs and illustrations in the literature (IVPP 10600, UUVP 6000, FMNH PR 2081) (Madsen, 1976; Currie and Zhao, 1993; Brochu, 2003) or were examined directly (YPM 5204, YPM 5210). Data on the pulmonary anatomy of the extant taxa are derived from dissections of fresh and preserved specimens, as well as descriptions in the literature. Dissections were completed on two alligators (*Alligator mississippiensis*), an ostrich (*Struthio camelus*), a white-throated monitor lizard (*Varanus albigularis albigularis*), and a Nile monitor lizard (*Varanus niloticus*).

To obtain the most parsimonious reconstruction of theropodan pulmonary anatomy, we follow the methodology of Bryant and Russell (1992) and Witmer (1995a).
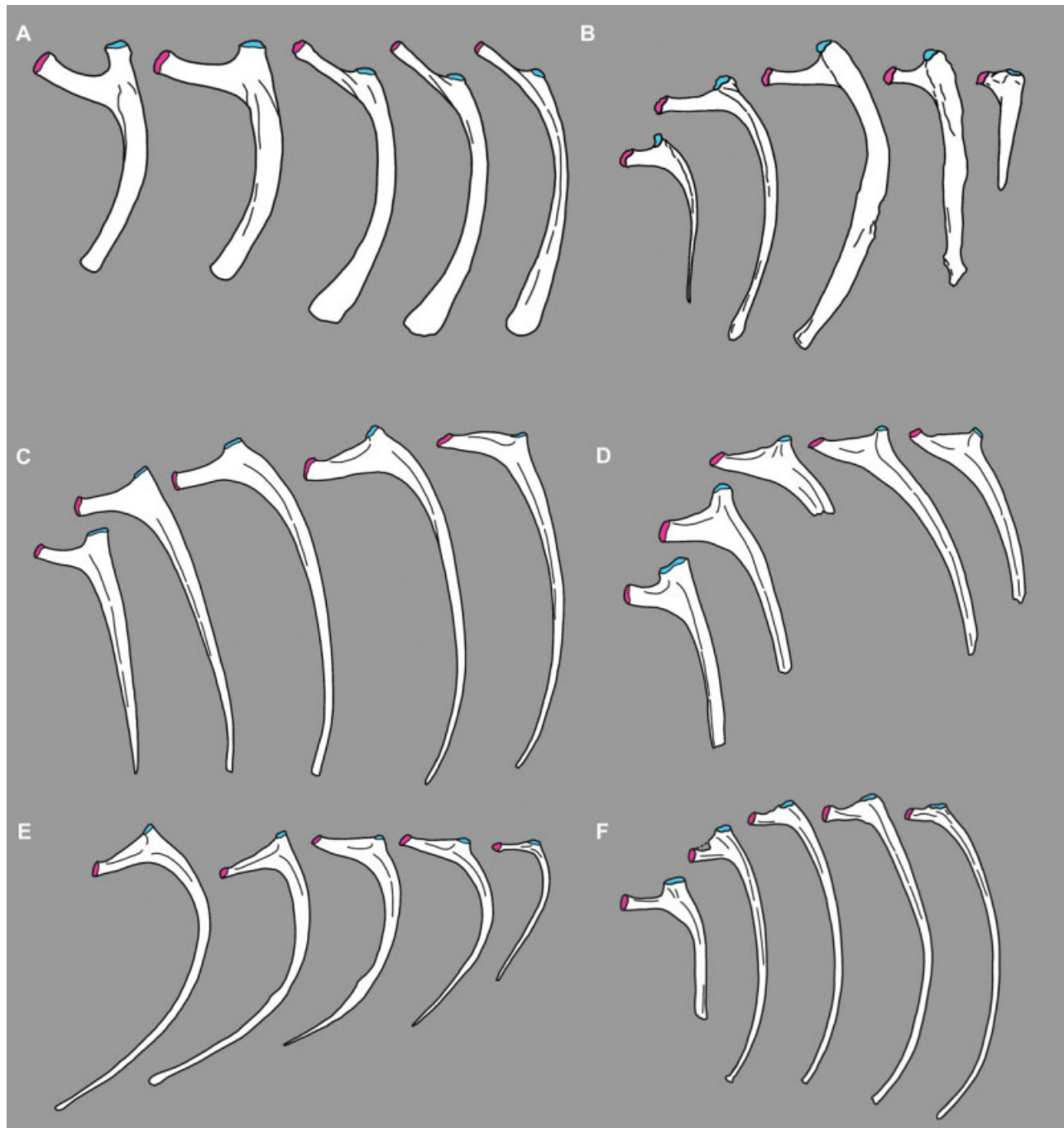
Fig. 3. Diagrammatic images of select dorsal ribs of living and extinct archosaurs with the capitulum indicated in pink and the tuberculum indicated in blue. Drawings are not to scale. **A**: Illustration of left dorsal ribs 1, 3, 5, 7, and 9 in cranial view of *Crocodylus acutus* redrawn from Mook (1921). **B:** Illustration of left dorsal ribs 1, 3, 5, 7, and 8 in cranial view from a *Rhea americana* specimen provided by Peter Dodson. **C:** Illustration of left dorsal ribs 1, 3, 5, 7, and 9 in cranial view of *Allosaurus fragilis* redrawn from Madsen (1976). **D:** Illustration of left dorsal ribs 1, 3, 5, 7, and 9 in cranial view of *Sinraptor dongi* redrawn from Currie and Zhao (1993). **E:** Illustration of left dorsal ribs 1, 3, 5, 7, and 9 in cranial view of *Tyrannosaurus rex* redrawn from Brochu (2003). **F:** Idealized composite illustration of select dorsal ribs in cranial view of two different specimens of *Deinonychus antirrhopus*.

The EPB method (Witmer, 1995a) facilitates the identification of soft tissue anatomical structures in extinct taxa by analyzing homologous tissues present in phylogenetically related extant taxa. Skeletal morphology is used to avoid restoring features that vary greatly from those found in extant relatives (Rowe, 1986). Data on the skeletal anatomy of extant taxa are from direct examination of specimens from the avian collections of the ANSP and descriptions in the literature. See Table 1 for abbreviations.

RESULTS

Respiration in Nonavian Theropods

As the lungs are partially, if not completely dorsally, adhered to the vertebral column in extant archosaurs and lepidosaurs, it is most parsimonious to assume that this was also the anatomical state in nonavian theropods. Because of the intimate relationship between lung morphology, function and axial osteology in all diapsids, predictions of the gross anatomy of the lung in nonavian theropods may be made based upon their vertebral morphology. Specific osteological characters associated with lung type in each of the three extant groups described earlier (Table 2) were used as indicators for lung morphology in extinct theropods.

Sinraptor dongi (IVPP 10600). *Sinraptor dongi* Currie and Zhao, 1993 is a large allosauroid theropod from the Middle to Late Jurassic Shishugou Formation of China, and is known from a mostly complete skeleton with a well-preserved series of dorsal vertebrae (Currie and Zhao, 1993). The transverse processes of the dorsals are subtriangular in cross-section, are connected to the vertebral bodies via the cranial and caudal centrodiapophyseal laminae and to the prezygapophysis by the prezygopophyseal lamina (*sensu* Wilson, 1999). The transverse processes remain relatively short throughout the entire dorsal series without any significant change in length (Fig. 4A1,A2). The parapophyses are located on the body of the centrum in the first four dorsal vertebrae, just cranial to pneumatic openings that invade the body of each centrum. The parapophysis of the fifth dorsal is slightly transitional, shifting further up the centrum to occupy the suture between the centrum and the neural arch, while the remaining dorsals have parapophyses at the bases of their respective neural arches (Fig. 4A1,A2). For the entire dorsal series, the parapophyses and diapophysis remain strongly separated and offset, with the diapophysis located slightly caudal to the parapophysis in the vertical plane (Fig. 4A2). All of the dorsal ribs of *S. dongi* are strongly bicapitate, with the capitulum ventral to and offset from the tuberculum; the two rib heads are connected via a thin lamina (Fig. 3D). Interestingly, only one rib is hollow, demonstrating some of the same variation in postcranial pneumatization seen in some extant birds (Hogg, 1984; O'Connor, 2004). There is no rib-free lumbar region in *S. dongi*. When the thoracic ribs are articulated with their corresponding vertebrae the result is a deeply furrowed ceiling adjacent to the first five dorsals, followed by shallower furrows in the thoracic ceiling associated with D6 and the remaining dorsal vertebrae.

Allosaurus fragilis (UUVP 6000). *Allosaurus fragilis* Marsh 1877 is a well-known theropod from the Late Jurassic Morrison Formation of North America. The transverse processes are generally robust and remain similar in length along the entire dorsal series. In the cranial dorsal vertebrae (D1–D4), they extend out at an ∼90-degree angle to the neural spine; in the more caudal dorsals the transverse processes are elevated to at least 30° above the horizontal axis and 60° caudal to the transverse axis (Fig. 4B1,B2) (Madsen, 1976). The transverse processes in all of the dorsal vertebrae are connected to the prezygapophyses by prezygopophyseal

TABLE 1. Institutional abbreviations

ANSP	Academy of Natural Sciences, Philadelphia, PA
FMNH	Field Museum of Natural History, Chicago, IL
IVPP	Institute of Vertebrae Paleontology and Paleoanthropology, Beijing, China
UUVP	University of Utah Paleontology Collection, Salt Lake City, UT
YPM	Yale Peabody Museum, New Haven, CT

laminae and to the centra by the caudal centrodiapophyseal laminae (as well as the cranial centrodiapophyseal laminae in the second and third dorsals). In the first four dorsal vertebrae, the parapophyses are located on the body of the centrum. In the fifth dorsal it shifts to the suture between the centrum and the neural canal, and in the remaining vertebrae, the parapophyses are located directly on the neural arch (Fig. 4B1,B2). At no point along the dorsal series do the parapophyses move to the transverse processes, remaining distinctly separate and ventral to the diapophysis. Like the cranial dorsals of *S. dongi*, the first four dorsal vertebrae of *A. fragilis* have a small pneumatic foramen on the lateral surface of each centrum caudal to the parapophyseal facet. The dorsal ribs of *A. fragilis* are also morphologically similar to those of *S. dongi*; the first through the seventh are strongly bicapitate with two distinct articular surfaces connected via a thin lamina (Fig. 3C). The thoracic ribs caudal to the seventh remain bicapitate, but the articular surfaces have shifted so that they are on the same horizontal plane. The ribs that articulate with the first seven dorsal vertebrae in *A. fragilis* produce a deeply corrugated thoracic cavity; the costovertebral articulations of the caudal dorsal vertebrae result in a similarly ridged roof but less strongly so.

Tyrannosaurus rex (FMNH PR2081). *Tyrannosaurus rex* Osborn 1905 is represented by multiple skeletons; however, the most complete and best preserved specimen is "Sue" (FMNH PR2081). All of the dorsal vertebrae of *T. rex* are similarly shaped, and contain pneumatic foramina (or pneumatopores) on both sides of the centra (Brochu, 2003). The transverse processes are robust, triangular in cross-section, and flat dorsally with some containing pneumatic openings along their caudoventral surfaces (Fig. 4C1). Like the other theropods described earlier, they are connected to the vertebral body by the cranial and caudal centrodiapophyseal laminae and to the prezygapophyses by the prezygopophyseal lamina, all of which are more strongly developed in the cranial dorsal vertebrae. The parapophyses are located at the craniolateral margin of the neural arch in all of the dorsal vertebrae, exhibiting a very slight upward shift in the caudal dorsals (Fig. 4C1,C2). There is a complete separation of the parapophyses and diapophyses for the entire series of dorsal vertebrae; however, as the transverse processes become more horizontal in the caudal dorsals, the two processes become closer together in the vertical plane (Fig. 4C1). All of the dorsal ribs are deeply curved and bicapitate, with a distinct capitulum and tuberculum (Fig. 3E). A notch in the first rib separates the two processes; the succeeding rib heads are

TABLE 2. Osteological characters in the axial skeleton of extant archosaurs and squamates associated with respiration

| Taxonomic group	Transverse processes	Parapophyseal location	Rib morphology	Rib-free lumbar region	Respiratory mechanism
Lizards	Short, simple and generally similar along the dorsal series	Fused with the diapophysis forming a synapophysis (Hoffstetter and Gasc, 1969)	Simple unicapitate (holocephalous) ribs (Hoffstetter and Gasc, 1969)	Yes	Sacculated lungs ventilated by tidal costal aspiration sometimes accompanied by a buccal pump (Perry, 1998)
Crocodilians (Figs. 1A–C, 2A, and 3A)	Cranial most processes are short and rounded; following processes become progressively longer, thinner and broader	Located below the neurocentral suture on the centrum in the first two dorsals; directly on the neurocentral suture in the third; as an accessory surface on the transverse process in the remaining vertebrae	The first three dorsal ribs are strongly bicapitate; the fourth and subsequent ribs articulate primarily via the tuberculum, the capitulum becomes an accessory notch on the rib shaft	Yes	Flexible sacculated lungs ventilated by a hepatic-piston pump that shifts the viscera fore and aft resulting in changes in thoracic pressure
Birds (Figs. 1D–F, 2B,C, and 3B)	Very short and robust, slightly longer in the caudal dorsal vertebrae, but no significant morphological change along the dorsal series	On the body of the centrum along the entire dorsal series	All of the dorsal ribs are strongly bicapitate	No	Rigid lungs ventilated unidirectionaly by nine nonvascularized air sacs
Theropod Dinosaurs (Figs. 3C–F and 4A1–D2)	Moderately short and robust, no significant change in length along the dorsal series	On the body of the centrum in the cranial dorsals and on the neural arch in the caudal dorsals	All of the ribs are bicapitate; the cranial 3–4 dorsal ribs are more strongly forked than the caudal dorsal ribs	No	Rigid lungs likely ventilated by air sacs
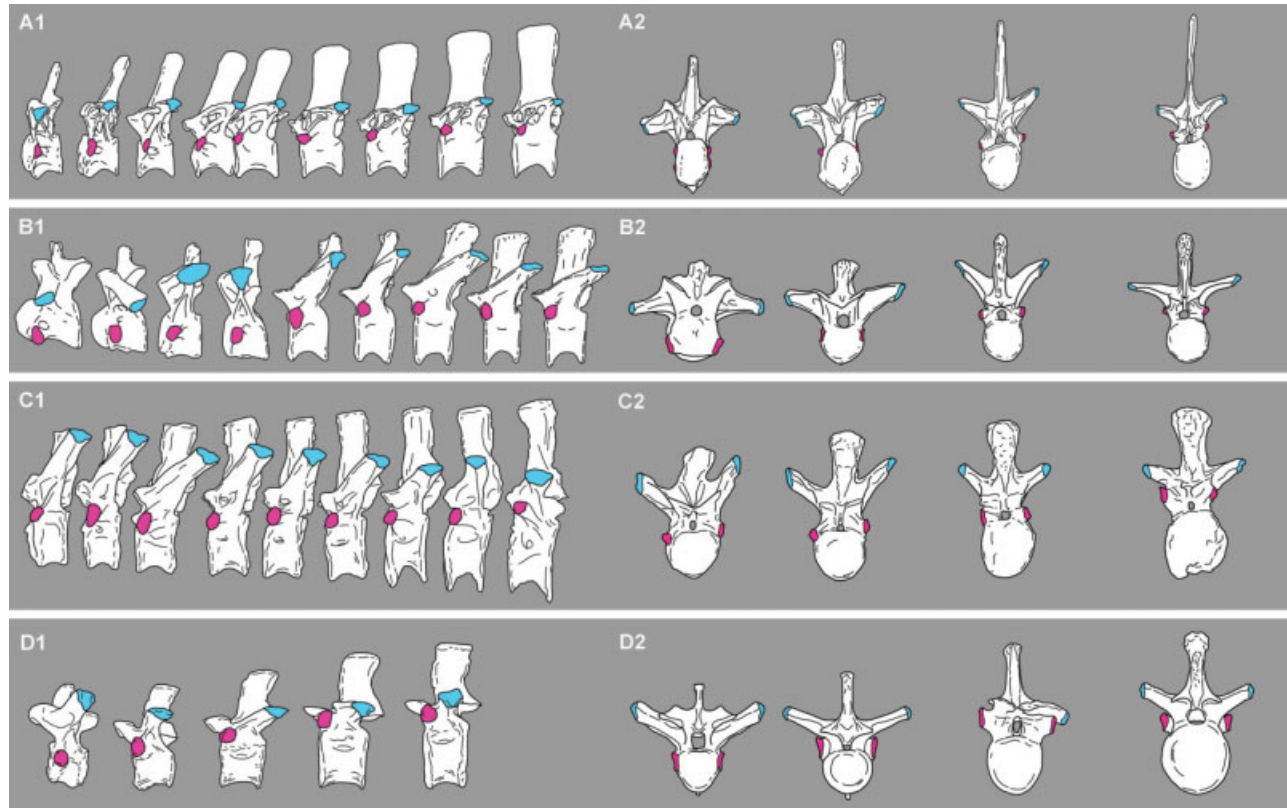
Fig. 4. Diagrammatic images of the dorsal vertebrae of four nonavian theropods with the parapophyses indicated in pink and the diapophyses indicated in blue. Drawings are not to scale. **A1:** Illustration of the first nine dorsal vertebrae of *Sinraptor dongi* in lateral view, redrawn from Currie and Zhao (1993). **A2:** Illustration of the 1st, 2nd, 4th, and 9th dorsal vertebrae (left to right) in cranial view of *S. dongi*, redrawn from Currie and Zhao (1993). **B1:** Illustration of the first nine dorsal vertebrae of *Allosaurus fragilis* in lateral view, redrawn from Madsen (1976). **B2:** Illustration of the 1st, 4th, 7th, and 9th dorsal vertebrae (left to right) of *A. fragilis* in cranial view, redrawn from Madsen (1976). **C1:** Illustration of the 14th through the 22nd presacral vertebrae of *Tyrannosaurus rex* in lateral view, redrawn from Brochu (2003). **C2:** Illustration of the 14th, 17th, 20th, and 22nd presacral vertebrae (left to right) of *T. rex* in lateral view, redrawn from Brochu (2003). **D1:** Illustration of the 1st, 4th, 6th, 7th, and 10th dorsal vertebrae (left to right) of *Deinonychus antirrhopus* in left lateral view. **D2:** Illustration of the 1st, 4th, 7th, and 10th vertebrae of *D. antirrhopus* in cranial view.

separate but connected by a thin lamina. When articulated, the ceiling of the ribcage of *T. rex* is deeply grooved for its entire length, which extends caudally to the sacrum. There is no rib-free "lumbar" region, with last dorsal vertebra (V23) likely possessing a small vestigial rib.

Deinonychus antirrhopus (YPM 5204 and YPM 5210). While *Deinonychus antirrhopus* Ostrom 1969 does not possess a complete dorsal vertebral series, the vertebrae that are present are extremely well preserved and the relevant osteological characters associated with respiratory anatomy are clear. They have been identified as dorsals 1, 4, 6, 7, and 10; however, because a complete vertebral series is not known for *D. antirrhopus* this assignment must be considered tentative. Ostrom (1969) noted that the five vertebrae are likely from two separate individuals; however, there does not seem to be an overlap and a composite can be created from the vertebrae based on the central size, height of the neural spine, parapophyseal location, and shape and orientation of the transverse processes. The transverse processes in

all of the preserved vertebrae are angled slightly caudally and at ~40° above the horizontal plane, except for the 6th vertebra, in which the processes project horizontally (Fig. 4D2). They remain robust and similar in length and morphology in all of the vertebrae. The parapophyses are located on the body of the centrum in the first dorsal, shifting to the junction between the centrum and the neural arch by the fourth, and on to the neural arch in the succeeding three vertebrae (Fig. 4D1,D2). In the caudal most vertebra [identified as either dorsal 10 or dorsal 11 by Ostrom (1969)], the parapophyses are still completely distinct, offset and ventrally positioned relative to the diapophyses, which are (as in all of the archosaurs and lizards described) located on the distal end of the transverse processes. Numerous dorsal rib fragments were found associated with YPM 5204 and YPM 5210; however, the skeletons were completely disarticulated and scattered, thus preventing a complete reconstruction. All of the thoracic ribs are bicapitate, with the capitulum and tuberculum separated by a 30-mm notch in the first rib (Fig. 3F). In the first few dorsal vertebrae, the ribs articulate with the tuberculum directly above the capitulum; there is a rotation the

middle and caudal ribs, articulating with their corresponding vertebrae at a 45-degree angle that reaches closer to horizontal in the caudal most dorsals (Fig. 4D1). Like the other theropods, *D. antirrhopus* possessed a thoracic cavity with a corrugated ceiling, with deeper furrows in the cranial half of the rib cage.

DISCUSSION
Lung Morphology and Its Osteological Correlates in Nonavian Theropod Dinosaurs

Transverse processes. The transverse processes of crocodilians become progressively elongated and flattened in the middle and caudal dorsal vertebrae providing a flat surface for the expansion of the lungs. In birds, the transverse processes remain short and robust for the entire length of the dorsal series; avian lungs are rigid and nonexpansive, and thus do not require a similar flattening of the ceiling of the rib cage. All of the nonavian theropods examined exhibited transverse processes that were morphologically similar to those found in extant birds. In both groups all of the transverse processes were short and rounded, while the parapophyses and diapophyses remained separate and offset for the entire vertebral series. Furthermore, none of the theropods exhibited any kind of flattening or extension of the transverse processes in any of their dorsal vertebrae, with some theropods (e.g., *D. antirrhopus*) even exhibiting a shortening of the processes relative to the centrum in the caudal dorsal vertebrae.

Parapophyseal location. The shift of the parapophysis from the lateral aspect of the centrum to the transverse process is very distinct and consistent in extant crocodilian taxa in that the shift occurs no later than the fourth dorsal vertebra. The successive movement of the parapophysis out on the lengthening processes toward the diapophysis in crocodilians is coupled with the flattening and elongation of the transverse process, providing a smooth inner surface for contact with the lungs. In contrast to the crocodilian state, the entire parapophysis remains completely on the craniolateral aspect of the centrum in all of the dorsal vertebrae in birds. The parapophyses of the nonavian theropods examined did have a shift in location; however, the articular surface never reaches the transverse processes (Fig. 4) as in crocodilians (Fig. 1C). In all four taxa examined, the cranial dorsal vertebrae possess parapophyses located on the craniolateral surfaces of their centra; the parapophyses shift up to the neural arch at around the fourth dorsal in *D. antirrhopus* and *T. rex*, and the fifth dorsal in *A. fragilis* and *S. dongi*. While the parapophyses do exhibit an upward shift in their location in the nonavian theropods, they do not move to the transverse processes as they do in crocodilians, and remain distinctly separate and ventral to the diapophyses for the entire dorsal series.

Rib morphology. The first two thoracic ribs of crocodilians resemble those of their avian counterparts; they are strongly bicapitate with a large notch between the two heads. The more caudal crocodilian ribs retain both articular surfaces but the ribs become unicipital, with the capitulum migrating closer to the tuberculum in each successive rib (Fig. 3A). In all of the thoracic ribs

caudal to the first four, the capitulum and tuberculum are on the same plane horizontally so that the rib is dorsoventrally flattened, similar to its corresponding transverse process. Avian thoracic ribs are morphologically similar throughout the entire series, with a distinct capitulum and tuberculum separated by a large notch (Fig. 3B). The nonavian theropods observed possess avian-like ribs with distinctly separate capitula and tubercula along the entire thoracic sequence. The capitulum and tuberculum are connected by a thin lamina in the nonavian theropods and are not as distinctly offset as the avian ribs (Fig. 3C–F). However, when articulated the ribs produce a deeply furrowed thoracic cavity, similar to the avian rib cage.

Lung Morphology of Nonavian Theropods

Based on the EPB, nonavian theropods probably had heterogeneously partitioned multichambered lungs. Similarly, nonavian theropods likely had lungs that were dorsally anchored to the vertebral column and whose function was tightly constrained by vertebral and rib morphology. None of the derived crocodilian characters are present, including the pronounced elongation of the transverse processes or parapophyses that migrate progressively toward the diapophyses. The rib-free "lumbar" region of crocodilians is also noticeably absent in both theropods and birds. The manner in which the bicapitate ribs articulate with their corresponding vertebrae in nonavian theropods generates a rigid ribcage around the lungs with limited dorsoventral mobility compared to crocodilians. The corrugated ceiling resulting from this anatomical arrangement (generated by articulation of the capitulum to a parapophysis located on the centrum) would have greatly inhibited the inflation of the lungs by a crocodilian hepatic-piston mechanism. The caudal expansion of the lungs from contraction of the diaphragmaticus is facilitated by the smooth interior of the crocodilian rib cage; this mechanism likely would not function with lungs that were incised and fixed in place by the thoracic ribs. The axial osteology of nonavian theropods contradicts assertions that they may have had a respiratory mechanism similar to that of extant crocodilians.

Another significant flaw in the hepatic-piston hypothesis concerns the basic biomechanics of bipedal locomotion; all theropods are obligate bipeds, whereas all crocodilians are obligate quadrupeds. When the abdominal viscera shift cranially and caudally by action of the diaphragmaticus in crocodilians, the center of mass also shifts (Farmer, 2006). This is not a problem for a quadrupedal sprawling animal with a low center of mass; however, it creates a significant equilibrium problem for a parasagittaly erect biped with, in many cases, an enlarged head. Shifting the center of mass cranially and caudally with every breath would substantially disrupt the balance and agility of any biped, particularly the large theropods for which a fall could be fatal. Despite the arguments for the presence of a hepatic-piston based respiratory apparatus in theropods (e.g., Ruben et al., 2003), both the biomechanics of bipedalism, and the osteology of the theropod axial skeleton make this hypothesis untenable from a functional perspective.

The case for an avian-style respiratory tract in nonavian theropods is argued elsewhere (e.g., O'Connor and Claessens, 2005; O'Connor, 2006), and these results lend

further support to this hypothesis. In the caudal dorsal vertebrae of the four theropods examined, while the parapophyses do not move to the transverse processes, they do shift dorsally, and the ribs associated with these vertebrae are markedly less forked. It is more likely that nonavian theropods had a respiratory system that was similar to that of modern birds, with cranial and caudal air sacs as evidenced by the vertebral pneumaticity (see O'Connor and Claessens, 2005), but was not fully developed into the respiratory apparatus found in extant birds. The main osteological difference between birds and nonavian theropods is the enlarged avian sternum coupled with jointed ribs, which plays a significant role in lung ventilation. The complex avian rib-sternum complex is lacking in nonavian theropods, so the protoavian lungs must have been ventilated in a different manner, possibly by gastralial or pelvic aspiration (see Carrier and Farmer, 2000a; Claessens, 2004a,b). While these results are restricted to theropods, investigation into the vertebral and rib anatomy of other dinosaurian groups and basal archosaurs would provide more information on the evolution of the avian lung and the plesiomorphic pulmonary morphology of archosaurs in general.

Evolution of the Avian Lung

Both crocodilians and birds have very specialized and unique respiratory systems that require certain osteological characteristics to function properly. The extreme subdivision of the avian lung is only possible because it is not compliant, so it seems that it would be highly unlikely for this type of lung to have evolved from one inflated by a hepatic-piston, which would be the case if the crocodilian respiratory system were indeed the basal state for dinosaurs. The argument that crocodilian physiology and anatomy does not represent the plesiomorphic state for all of Archosauria is not new (see Seymour et al., 2004), and is further supported by these results. It is more likely that the derived avian respiratory tract evolved from something similar to that seen in extant varanids. The heterogeneously partitioned multichambered lung of monitor lizards with its dense parenchyma in the cranial region, and poorly vascularized compliant caudal region functioning as ventilatory bellows, represent a possible precursor to the avian air sac system and flow-through lung. The strong attachment of the entire dorsal surface of varanid lungs to the body wall (and resulting immobility) provides a more plausible analogous evolutionary starting point than the more partial craniodorsal attachment of crocodilian lungs. The "varanid hypothesis" is also supported by developmental evidence that indicates that the avian coelomic organization and PPS are homologous to the PPS in varanids and other more basal reptiles (Klein and Owerkowicz, 2006). Perry (1992) proposed an interesting and viable model for the ancestral state of archosaur lungs and the successive steps that led to the evolution of the derived avian and crocodilian conditions similar to the "varanid hypothesis." The basal archosaurian or "euparkerian grade" lung would consist of monopodially branching tubular chambers in the cranial half of the lung, which anastamose with a collection of arching tubular chambers in the caudal portion of the lung, features present in all extant archosaurian lungs. The key evolutionary step from the "euparkerian-grade" lung toward the avian flow-through lung would be the secondary connection between the caudal chambers with the cranial ones.

LITERATURE CITED

Brainerd EL. 1999. New perspectives on the evolution of lung ventilation mechanisms in vertebrates. Exp Biol Online 4:11–28.

Britt BB, Makovicky PJ, Gauthier J, Bonde N. 1998. Postcranial pneumatization in *Archaeopteryx*. Nature 395:374–376.

Brochu CA. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. Soc Vert Paleontol Mem 7:1–138.

Bryant HN, Russell AP. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. Philos Trans R Soc B 337:405–418.

Carrano MT, Hutchinson JR. 2002. Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). J Morphol 253:207–228.

Carrier DR, Farmer CG. 2000a. The integration of ventilation and locomotion in archosaurs. Am Zool 40:87–100.

Carrier DR, Farmer CG. 2000b. The evolution of pelvic aspiration in archosaurs. Paleobiology 26:271–293.

Çevik-Demirkan A, Kürtül I, Haziroglu RM. 2006. Gross morphological features of the lung and air sac in the Japanese quail. J Vet Med Sci 68:909–913.

Chinsamy A, Hillenius WJ. 2004. Physiology of nonavian dinosaurs. In: Weishampel DB, Dodson P, Osmólska H, editors. The dinosaurian. 2nd ed. Berkeley: University of California Press. p 643–659.

Claessens LPAM. 2004a. Archosaurian respiration and the pelvic girdle aspiration breathing of crocodyliforms. Proc R Soc Lond R B 271:1461–1465.

Claessens LPAM. 2004b. Dinosaur gastralia: origin, morphology, and function. J Vertebr Paleontol 24:89–106.

Claessens LPAM. 2008. The skeletal kinematics of lung ventilation in three basal bird taxa (emu, tinamou, and guinea fowl). J Exp Zool 309A:1–14.

Codd JR, Manning PL, Norell MA, Perry SF. 2007. Avian-like breathing mechanics in maniraptoran dinosaurs. Proc R Soc B 1233:1–5.

Currie PJ, Zhao X-J. 1993. A new carnosaurs (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Can J Earth Sci 30:2037–2081.

Duncker HR. 1971. The lung air sac system in birds. Adv Anat Embryol Cell Biol 45:1–171.

Duncker HR. 1972. Structure of the avian lungs. Respir Physiol 14:44–63.

Duncker HR. 1974. Structure of the avian respiratory tract. Respir Physiol 22:1–19.

Duncker HR. 2004. Vertebrate lungs: structure, topography and mechanics a comparative perspective of the progressive integration of respiratory system, locomotor apparatus and ontogenetic development. Respir Physiol Neurobiol 144:111–124.

Farmer CG, Carrier DR. 2000. Pelvic aspiration in the American alligator (*Alligator mississippiensis*). J Exp Biol 203:1679–1687.

Farmer CG. 2006. On the origin of avian air sacs. Respir Physiol Neurobiol 154:89–106.

Gans C, Clark B. 1976. Studies on ventilation of Caiman crocodilus (Crocodilia: Reptilia). Respir Physiol 26:285–301.

Heard DJ. 1997. Avian respiratory anatomy and physiology. Semin Avian Exotic Pet Med 6:172–179.

Hicks JW, Farmer CG. 1999. Gas exchange potential in reptilian lugs: implications for the dinosaur-avian connection. Respir Physiol 117:73–83.

Hoffstetter R, Gasc J-P. 1969. Vertebrae and ribs of modern reptiles. In: Gans C, Bellairs A, Parsons TS, editors. Biology of the Reptilia. London: Academic Press.

Hogg DA. 1984. The distribution of pneumatisation in the skeleton of the adult domestic fowl. J Anat 138:617–629.

Jones JH, Effmann EL, Schmidt-Nielsen K. 1985. Lung volume changes during respiration in ducks. Respir Physiol 59:15–25.

King AS. 1993. Apparatus respiratorius (system respiratorium). In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC, editors. Handbook of avian anatomy: nomina anatomica avium. Cambridge, MA: Nuttall Ornithological Club. p 257–299.

Klein W, Owerkowicz T. 2006. Function of intracoelomic septa in lung ventilation of amniotes: lessons from lizards. Physiol Biochem Zool 79:1019–1032.

Kürtül I, Aslan K, Aksoy G, Özcan S. 2004. Morphology of the air sac (Sacci pneumatici) in the rock partridge (Alectoris graeca). Vet Res Commun 28:553–559.

Madsen JHM, Jr. 1976. Allosaurus fragilis: a revised osteology. Bull Utah Geol Survey 109:1–163.

Maina JN, Nathaniel C. 2001. A qualitative and quantitative study of the lung of an ostrich, Struthio camelus. J Exp Biol 204:2313–2330.

Maina JN. 2002. Structure, function and evolution of gas exchangers: comparative perspectives. J Anat 201:281–304.

Maina JN. 2005. The lung-air sac system of birds: development, structure, and function. Berlin: Springer-Verlag.

Maina JN. 2007. Spectacularly robust! Tensegrity principle explains the mechanical principle explains the mechanical strength of the avian lung. Respir Physiol Neurobiol 155:1–10.

Marsh OC. 1877. Notice on new dinosaurian reptiles. Am J Sci 3:514–516.

McLelland J. 1989. Anatomy of the lungs and air sacs. In: King AS, McLelland J, editors. Form and function in birds. London: Academic Press. Vol. 4: p 221–279.

Mook CC. 1921. Notes on the postcranial skeleton in the Crocodilia. Bull Am Mus Nat Hist 44:67–100.

O'Connor PM, Claessens LPAM. 2005. Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. Nature 436:253–256.

O'Connor PM. 2004. Pulmonary pneumaticity in the postcranial skeleton of extant Aves: a case study examining Anseriformes. J Morphol 261:141–161.

O'Connor PM. 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. J Morphol 267:1199–1226.

Osborn HF. 1905. Tyrannosaurus and other Cretaceous carnivorous dinosaurs. Bull Am Mus Nat Hist 21:259–265.

Ostrom JH. 1969. Osteology of Deinonychus antirrhopus, an unusual theropod from the Lower Cretaceous of Montana. Bull Peabody Mus Nat Hist 30:1–165.

Owerkowicz T, Farmer CG, Hicks JW, Brainerd EL. 1999. Contribution of gular pumping to lung ventilation in monitor lizards. Science 284:1661–1663.

Padian K, Hutchinson JR, Holtz TR. 1999. Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria (Theropoda). J Vert Paleontol 19:69–80.

Paul GS. 1988. Predatory dinosaurs of the world. New York: Simon and Schuster.

Paul GS. 2001. Were the respiratory complexes of predatory dinosaurs like crocodilians or birds? In: Gauthier J, Gall LF, editors. Proceedings of the International Symposium in Honor of John H. Ostrom (February 13–14, 1999): New Perspectives on the Origins and Evolution of Birds. Yale Peabody Museum of Natural History, Yale University, New Haven, CT. p 463–482.

Paul GS. 2002. Dinosaurs of the air: the evolution and loss of flight in dinosaurs and birds. Baltimore: The Johns Hopkins University Press.

Perry SF. 1983. Reptilian lungs: functional anatomy and evolution. Adv Anat Embryol Cell Biol 79:1–81.

Perry SF. 1985. Evolution of the mammalian chest wall. In: Roussos C, Macklem PT, editors. The thorax, Part A. New York: Dekker. p 187–198.

Perry SF. 1988. Functional morphology of the lungs of the Nile crocodile, Crocodylus niloticus: non-respiratory parameters. J Exp Biol 134:99–117.

Perry SF. 1992. Gas exchange strategies in reptiles and the origin of the avian lung. In: Wood SC, Weber RE, Hargens AR, Millard RW, editors. Physiological adaptations in vertebrates: respiration, circulation, and metabolism. New York: Marcel Dekker. p 149–167.

Perry SF. 1998. Lungs: comparative anatomy, functional morphology, and evolution. In: Gans C, Gaunt AS, editors. Biology of the Reptilia, Vol. 19: Morphology G visceral organs. St. Louis, MO: Society for the Study of Amphibians and Reptiles. p 1–92.

Perry SF. 2001. Functional morphology of the reptilian and avian respiratory systems and its implications for theropod dinosaurs. In: Gauthier J, Gall LF, editors. New perspectives on the origin and early evolution of birds: proceedings of the international symposium in honor of John H. Ostrom. New Haven, CT: Yale Peabody Museum of Natural History, Yale University. p 429–441.

Powell FL. 2000. Respiration. In: Whittow GC, editor. Sturkie's Avian physiology. 5th ed. New York: Academic Press. p 233–264.

Ritter D. 1996. Axial muscle function during lizard locomotion. J Exp Biol 199:2499–2510.

Romer AS. 1956. Osteology of the reptiles. Chicago: University of Chicago Press.

Rowe T. 1986. Homology and evolution of the deep dorsal thigh musculature in birds and other Reptilia. J Morphol 71:251–298.

Ruben JA, Dal Sasso C, Geist NR, Hillenius WJ, Jones TD, Signore M. 1999. Pulmonary function and metabolic physiology of theropod dinosaurs. Science 283:514–516.

Ruben JA, Jones TD, Geist NR. 2003. Respiratory and reproductive paleophysiology of dinosaurs and early birds. Physiol Biochem Zool 76:141–164.

Ruben JA, Jones TD, Geist NR, Hillenius WJ. 1997. Lung structure and ventilation in theropod dinosaurs and early birds. Science 278:1267–1270.

Scheid P, Piiper J. 1989. Respiratory mechanics and air flow in birds. In: King AS, McLelland J, editors. Form and function in birds. London: Academic Press. Vol. 4: p 369–391.

Sereno P. 1999. The evolution of dinosaurs. Science 284:2137–2147.

Seymour RS, Bennett-Stamper CL, Johnston SD, Carrier DR, Grigg GC. 2004. Evidence for endothermic ancestors of crocodiles at the stem of archosaur evolution. Physiol Biochem Zool 77:1051–1067.

Shufeldt RW. 1909. Osteology of birds. Educ Dept Bull NY State Museum 447:1–381.

Witmer LM. 1995a. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason JJ, editor. Functional morphology in vertebrate paleontology. Cambridge, UK: Cambridge University Press. p 19–33.

Witmer LM. 1995b. Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae. J Morphol 225:269–327.

Witmer LM. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Soc Vert Paleontol Mem 3:1–73.