Evolution of the Dinosauriform Respiratory Apparatus: New Evidence from the Postcranial Axial Skeleton

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ABSTRACT

Examination of the thoracic rib and vertebral anatomy of extant archosaurs indicates a relationship between the postcranial axial skeleton and pulmonary anatomy. Lung ventilation in extant crocodilians is primarily achieved with a hepatic piston pump and costal rotation. The tubercula and capitula of the ribs lie on the horizontal plane, forming a smooth thoracic "ceiling" facilitating movement of the viscera. Although the parietal pleura is anchored to the dorsal thoracic wall, the dorsal visceral pleura exhibits a greater freedom of movement. The air sac system and lungs of birds are associated with bicapitate ribs with a ventrally positioned capitular articulation, generating a rigid and furrowed rib cage that minimizes dorsoventral changes in volume in the dorsal thorax. The thin walled bronchi are kept from collapsing by fusion of the lung to the thorax on all sides. Data from this study suggest a progression from a dorsally rigid, heterogeneously partitioned, multichambered lung in basal dinosauriform archosaurs towards the small entirely rigid avian-style lung that was likely present in saurischian dinosaurs, consistent with a constant volume cavum pulmonale, thin walled parabronchi, and distinct air sacs. There is no vertebral evidence for a crocodilian hepatic piston pump in any of the taxa reviewed. The evidence for both a rigid lung and unidirectional airflow in dinosauriformes raises the possibility that these animals had a highly efficient lung relative to other Mesozoic vertebrates, which may have contributed to their successful radiation during this time period. Anat Rec, 294:1532–1547, 2011. © 2011 Wiley-Liss, Inc.

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As the sole surviving members of Archosauria, crocodilians and birds are the best extant models for reconstructing the soft tissue anatomy and physiological state of their extinct relatives. However, for features that are disparate in these terminal taxa, it is difficult to infer their evolutionary history in extinct archosaurs, a problem compounded by the lack of a fossil record for many of these features. The interesting questions of the origin of endothermy, aerobic capacity, and the evolution of the avian respiratory system have been particularly troublesome in this regard and addressing these questions necessitates the use of extant phylogenetic

bracketing (EPB) (Witmer, 1995), functional morphological studies (Perry and Sander, 2004), and theoretical models (e.g., Perry et al., 2009). Reconstructing these characters would be greatly aided by unambiguous osteological correlates; however, these have proved illusive. Pneumaticity, or the invasion of bone by air cavities, is a good example of a tempting but equivocal correlate of pulmonary form and function. Pneumaticity is very common in birds, and in the postcranial skeleton, it is caused by diverticula of the respiratory system (e.g., Duncker, 1971; O'Connor, 2004, 2006). Importantly, specific regions of the avian skeleton are pneumatized by distinct parts of the respiratory system; for example, the cervical air sacs typically invade the cervical vertebrae, although this is not a universal feature (e.g., O'Connor, 2004, 2006). Furthermore, the evidence of pneumaticity is preserved in the fossil record, and so this character might provide excellent insight into the unpreserved soft anatomy of the respiratory system (e.g., O'Connor and Claessens, 2005, O'Connor, 2006; Wedel, 2006, 2009). This would be especially interesting if the presence of air sacs was linked to other pulmonary features, such as unidirectional airflow through tubular gas-exchange structures (parabronchi). On the other hand, the use of fossil evidence of pneumaticity to reconstruct respiratory anatomy has been criticized because pneumaticity plays no known role in respiration or gas exchange, and the preponderance of the data indicates its function is lightening the skeleton to aid flight or reduce rotational inertia (Farmer, 2006). In this view, the fact that cervical air sacs pneumatize the cervical vertebrae is simply a consequence of proximity; this part of the respiratory system is nearest at hand, and, therefore, cervical pneumaticity may provide more information about the need to reduce rotational inertia of the neck than it does about the presence or topography of air sacs or about patterns of air flow or gas exchange (Farmer, 2006). Thus, while pneumaticity is consistent with the presence of air sacs, it is not necessarily evidence for air sacs, and additional data are required to shore up or refute hypotheses of bird-like respiratory systems in extinct archosaurs.

Skeletal evidence of a minimally dorsoventrally compressible thorax in fossil taxa might be functionally correlated with two distinct features of the extant avian respiratory system: 1) that the lungs do not change volume significantly with respiration, and 2) the blood-gas barrier (BGB) is extraordinarily thin and the air capillaries are very small in diameter (Duncker, 1971; Perry, 1989; Maina, 2005; Maina and West, 2005). These features are functionally related and place special demands on the axial skeleton. The relationship of the transverse processes of the thoracic vertebrae and the widely separated rib capitula restrict the axis for rib motion (Zimmer, 1935; Duncker, 1971). Ventrally, the lungs are bounded by the horizontal septum (also known as the diaphragm or the pulmonary aponeurosis), which attaches laterally a little dorsal to the intercostal joints and medially to either hypapophyses or a median perpendicular septum that extends ventrally from narrow high vertebral bodies, so that the enclosed space, the cavum pulmonale, undergoes minimal volume changes during breathing and the volume changes that do occur are largely in the ventrolateral portions (Duncker, 1971). The construction of the thorax, therefore, limits the amount of movement of the lung, particularly in the dorsomedial regions, where most of the tubular gas-exchange structures, the parabronchi, are located. The near constant volume of the cavum pulmonale is believed to reduce the mechanical stress on the pulmonary capillaries and enable selection for a very thin, but fragile, blood-gas barrier and very small diameter air capillaries, as they never collapse and therefore require to be reinflated. Until recently, it was thought that, among extant animals, unidirectional airflow was also unique to birds, but the discovery of this character in alligators suggests that it was indeed plesiomorphic for Archosauria (Farmer and Sanders, 2010). Thus, it is necessary to revise what is meant by the phrase "avian-style" features. A constant volume lung might be a true avian synapomorphy, or it may have been present in less derived archosaurs. Here, we analyze the axial skeleton of a phylogenetically broad range of archosaurs to gain insight into the evolution of the rigidity in the thoracic skeleton that is expected to be functionally correlated with the evolution of a lung with near constant volume.

Both the avian and crocodilian respiratory systems are highly derived and modified relative to the pulmonary morphology of lizards and other squamates (e.g., Perry, 1998; Maina, 2002). They are also correspondingly associated with specific anatomical adaptations on the axial skeleton, particularly the vertebral and rib morphology. Based on comparisons between the axial skeleton of extinct archosaurs and their living relatives, revised hypotheses on their pulmonary anatomy and functional morphology can be generated and tested.

RESPIRATION IN EXTANT TAXA

Varanids and other squamates primarily ventilate their large, elastic, heterogeneously partitioned lungs (Fig. 1A) via costal aspiration (e.g., Perry, 1983). All of the thoracic ribs of squamates are holocephalous (Fig. 2A) and articulate with each dorsal vertebra through a synapophysis (the diapophysis and parapophysis are fused; Fig. 1B). The result is a flexible rib cage, which allows the lungs to expand and contract inside the thoracic cavity relatively unencumbered (Table 1).

Crocodilians possess large elastic lungs with multiple tubular monopodial branching chambers that are all connected via intrapulmonary bronchi. Airflow in the lungs of alligators is unidirectional like that of birds (Farmer and Sanders, 2010), and the valving mechanisms appear very similar (Farmer, personal observation). Ventilation is costally driven in association with a hepatic piston pump which functions by shifting the viscera fore and aft with the diaphragmaticus (Carrier and Farmer, 2000a; Claessens, 2004a; Uriona and Farmer, 2008; Claessens, 2009a). The crocodilian respiratory system is associated with a very distinct axial morphology (Table 1), in which the transverse processes progressively flatten and elongate producing a smooth thoracic ceiling (Fig. 1D). There is also a corresponding migration of the parapophyses up from the dorsal centra out onto the transverse processes starting at the third or fourth dorsal vertebra.

The respiratory system of extant birds is composed of a pair of volume–constant, rigid, gas-exchanging bronchial lungs (Fig. 1F), and a collection of nonvascularized air sacs that effect ventilation (Duncker, 1972, 1974;
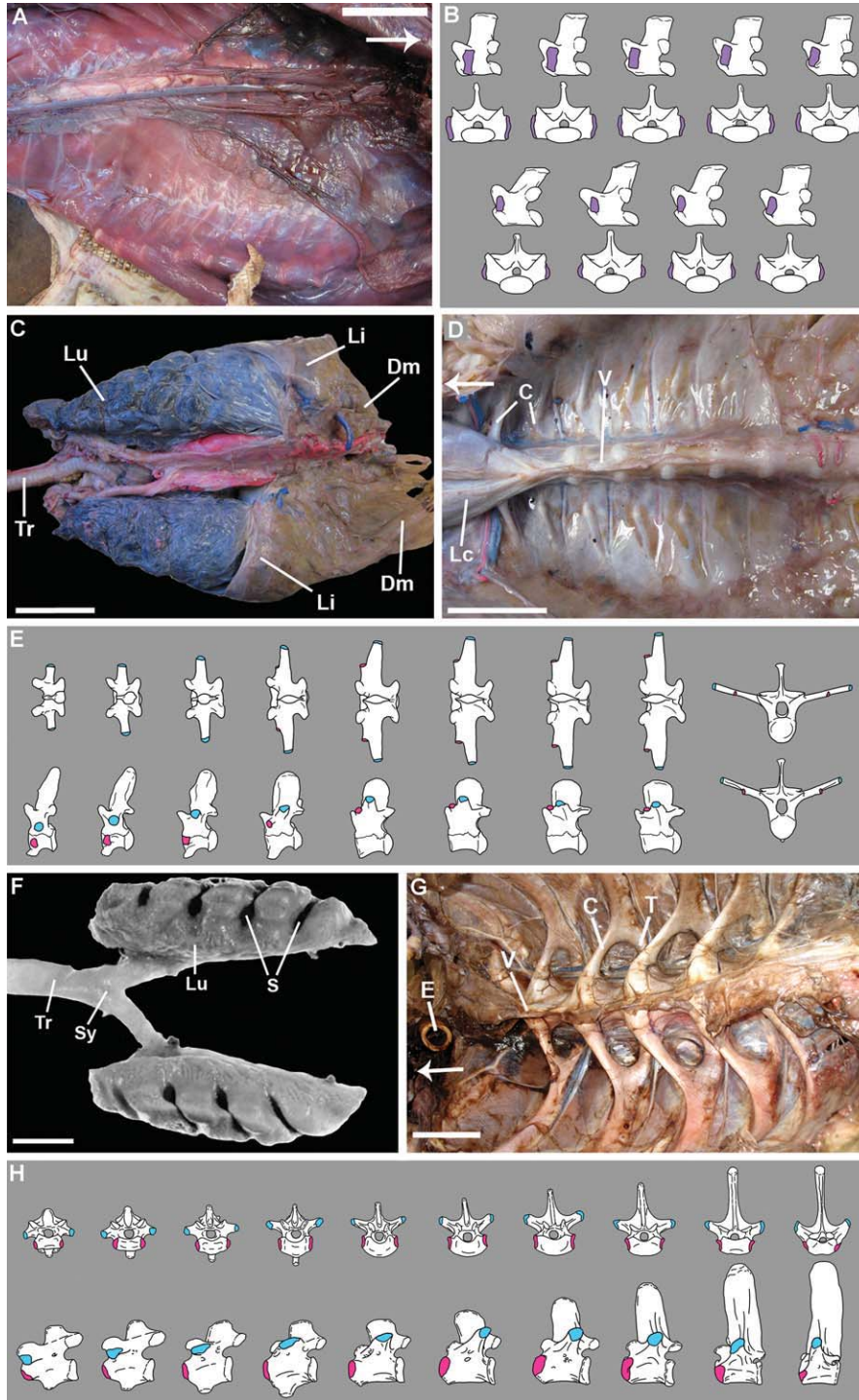
Fig. 1. **A**) Interior view of the thoracic cavity of a white-throated monitor lizard (*V. a. albigularis*) with most of the viscera removed. Arrow points cranially. Scale bar = 10 cm. **B**) Diagrammatic images of the first nine dorsal vertebrae in lateral view (top and third rows) and cranial view (second and fourth rows). The synapophyses are indicated in purple. **C**) Ventral view of the lungs, trachea, liver, and diaphragmaticus muscles (cut) of an alligator. Scale bar = 5 cm. **D**) Interior of the thoracic cavity of an alligator (*A. mississippiensis*) with the viscera removed. Arrow points cranially. Scale bar = 5 cm. **E**) Diagrammatic images of the first eight dorsal vertebrae of an alligator (*A. mississippiensis*) shown in dorsal view (top row) and lateral view (bottom row), and dorsals 7 and 8 in cranial view (far right). The diapophy-

ses are indicated in blue, and the parapophyses are indicated in pink. **F**) Dorsal view of the lungs, trachea, and extrapulmonary bronchi of an ostrich (*S. camelus*). Image modified with permission from Maina and Nathaniel (2001). Scale bar = 2 cm. **G**) Interior of the thoracic cavity of an ostrich (*S. camelus*) with the viscera removed. Arrow points cranially. Scale bar = 5 cm; **H**) Diagrammatic image of the first 10 dorsal vertebrae of an ostrich (*S. camelus*) in cranial view (top row) and lateral view (bottom row). The diapophyses are indicated in blue, and the parapophyses are indicated in pink. C, capitulum; Dm, M. diaphragmaticus; E, esophagus (cut); Li, liver; Lu, lung; S, costal sulci; Sy, syrinx; T, tuberculum; Tr, trachea; V, ventral surface of the dorsal vertebral centra.
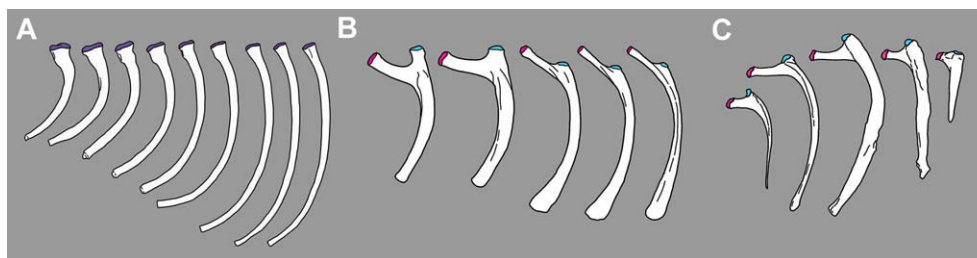
Fig. 2. Diagrammatic images of select dorsal ribs in cranial view of select extant archosaurs and squamates with the parapophyses indicated in pink, diapophyses indicated in blue, and synapophysis indicated in purple. Drawings are not to scale. **A)** Left dorsal ribs one to nine of *V. a. albigularis*. **B)** Left dorsal ribs 1, 3, 5, 7, and 9 of *Crocodylus acutus*; redrawn from Mook (1921). **C)** Left dorsal ribs 1, 3, 5, 7, and 8 of *Rhea americana*.

TABLE 1. Osteological characters in the axial skeleton of extant squamates and archosaurs associated with pulmonary morphology

Taxonomic groups	Transverse processes	Parapophyseal locations	Rib morphology	Rib-free lumbar region	Pulmonary morphology
Squamata	Short; little morphological variation along the dorsal series	Single synapophysis	Unicapitate (holocephalous) ribs	Yes	Sacculated multi-chambered lungs; tidally ventilated by costal aspiration, often in association with a buccal pump
Crocodylia	Short and rounded in the first dorsals; the subsequent processes become progressively elongated, thinner and broader	Located on the centrum, below the neurocentral suture on the first two dorsals; shifts to the transverse process by the fourth dorsal; as an accessory surface migrating towards the diapophysis in the successive vertebrae	The first three thoracic ribs are strongly bicapitate; the subsequent ribs articulate primarily via the tuberculum; the capitulum becomes an accessory notch on the rib shaft	Yes	Flexible sacculated lungs with unidirectional airflow; ventilated by a hepatic piston pump in association with costal aspiration
Aves	Very short and robust, slightly longer in the caudal dorsals, but no significant morphological change along the dorsal series	On the centrum for the entire dorsal series	All of the thoracic ribs are bicapitate and strongly forked	No	Small rigid flow-through lungs ventilated unidirectionally by a series non-vascularized air sacs

This table is modified from Schachner et al. (2009).

Perry, 1989; Maina, 2005). The small dorsally positioned lungs are tightly attached to both the ventral surface of the vertebral column and the adjacent ribs; the capitula of the thoracic ribs incise the dorsal surface of the lungs (Fig. 1F), locking them in place (Maina and Nathaniel, 2001; Maina, 2005). This specialized respiratory system is coupled with strongly bicapitate dorsal ribs (Fig. 2C) that articulate with their corresponding vertebrae so that the rib cage is dorsoventrally (Table 1) incompressible, creating a rigid cavum pulmonale. Unlike crocodilians, there is no parapophyseal shift onto the transverse process; this results in a furrowed or corrugated thoracic ceiling (Fig. 1G,H).

MATERIALS AND METHODS

Data on the pulmonary and skeletal anatomy of the extant taxa are derived from examination of specimens from collections at the ANSP and the University of Pennsylvania, dissections of fresh and preserved specimens, as well as descriptions in the literature. For institutional abbreviations see Table 2. Dissections were completed on multiple specimens of American alligators (*A. mississippiensis*), an ostrich (*Struthio camelus*), an emu (*Dromaius novaehollandiae*), a white-throated monitor lizard (*Varanus albigularis albigularis*), and a Nile monitor lizard (*V. niloticus*). In order to obtain the most parsimonious reconstruction of archosaur pulmonary anatomy, we follow the methodology of Witmer (1995).

The extinct archosaurs that were selected for this study are known from either multiple specimens or single taxa with well-preserved dorsal vertebrae. The various taxa are represented by detailed photographs and illustrations in the literature or were examined directly. For a summary of the taxa included in this study, see Table 3.

RESULTS

Basal Dinosauriformes

The vertebral series from most dinosauriforms are either unknown or very fragmentary for this study; however, *Silesaurus* is represented by multiple well-preserved articulated specimens that were found together in a single bone bed (Dzik, 2003) allowing for clear identification of patterns in vertebral morphology. Although the exact phylogenetic position of *Silesaurus* is still unre-

solved, it is generally accepted that it represents an early dinosauriform that is closely related to dinosaurs (Ezcurra, 2006; Nesbitt et al., 2009). The vertebral-rib articulatory processes in *Silesaurus* closely resemble those of dinosaurs. The transverse processes become more elongate from the first to the sixth dorsal, and then progressively shorter from the mid dorsals to the caudal dorsals (Fig. 3A,B). The parapophysis and diapophysis are distinctly separate until approximately the 13th dorsal vertebra. The parapophysis does not migrate out on the transverse process like it does in crocodilians; it is positioned on an elongated process that shifts dorsally, meeting the cranioventral aspect of the transverse process and diapophysis by the 13th dorsal vertebra. The transverse processes shorten after the mid dorsals so that when the two processes meet, they are of almost the same length, each supported by a thin lamina. The dorsal ribs of *Silesaurus* are not well known, but it is clear from their corresponding vertebral articular processes that the first 12 were bicapitate and forked.

TABLE 2. Institutional abbreviations

ANSP	Academy of Natural Sciences, Philadelphia, PA
CEUM	College of Eastern Utah Prehistoric Museum, Price, UT
CM	Carnegie Museum of Natural History, Pittsburgh, PA
YPM	Yale Peabody Museum, New Haven, CT

TABLE 3. Summary of the extinct archosaurs selected for this study

| Taxa	Reference/Collection
Dinosauriformes	
Silesaurus opolensis	Dzik, 2003
Theropoda	
Herrerasaurus ischigualastensis	Novas, 1993
Sinraptor dongi	Currie and Zhao, 1993
Allosaurus fragilis	Madsen, 1976
Tyrannosaurus rex	Brochu, 2003
Unnamed oviraptorid	CM 78001
Deinonychus antirrhopus	YPM 5204; 5210
Sauropoda	
Apatosaurus louisae	Gilmore, 1936
Diplodocus carnegii	Hatcher, 1901
Camarasaurus grandis	McIntosh et al., 1996
Giraffatitan (= "*Brachiosaurus*") *brancai*	Janensch, 1950
Basal Sauropodomorpha	
Plateosaurus sp.	Huene, 1926
Lamplughsaura dharmaramensis	Kutty et al., 2007
Massospondylus carinatus	Galton, 1976; Cooper, 1981
Thyreophora	
Scutellosaurus lawleri	Colbert, 1981
Loricatosaurus priscus	Galton, 1990
Huayangosaurus taibaii	Maidment et al., 2006
Stegosaurus stenops	Ostrom and McIntosh, 1966
Hesperosaurus mjosi	Carpenter et al., 2001
Ankylosaurus magniventris	Brown, 1908; Carpenter, 2004
Saichania chulsanensis	Maryanska, 1977
Marginocephalia	
Homalocephale calathocercos	Maryanska and Osmólska, 1974
Psittacosaurus xinjiangensis	Sereno and Chao, 1988
P. sibiricus	Averianov et al., 2006
Montanoceratops cerorhynchus	Brown and Schlaikjer, 1942
Triceratops prorsus	Hatcher et al., 1907
Styracosaurus albertensis	Holmes et al., 2005
Ornithopoda (and basal ornithischian)	
Stormbergia dangershoeki	Butler, 2005
Hypsilophodon foxii	Galton, 1974
Tenontosaurus tilletti	YPM 5458; Forster, 1990
Dryosaurus altus	CM 3392
Uteodon aphanoecetes	CM 11337; Carpenter and Wilson, 2008; McDonald, 2011
Mantellisaurus (= "*Iguanodon*") *atherfieldensis*	Hooley, 1925; Norman, 1986
Eolambia caroljonesa	CEUM 52053; 52092; 52114; 52173; 52833; 52836
Edmontosaurus annectens	Parks, 1935; Lull and Wright, 1942
Gryposaurus notabilis	Pinna, 1979
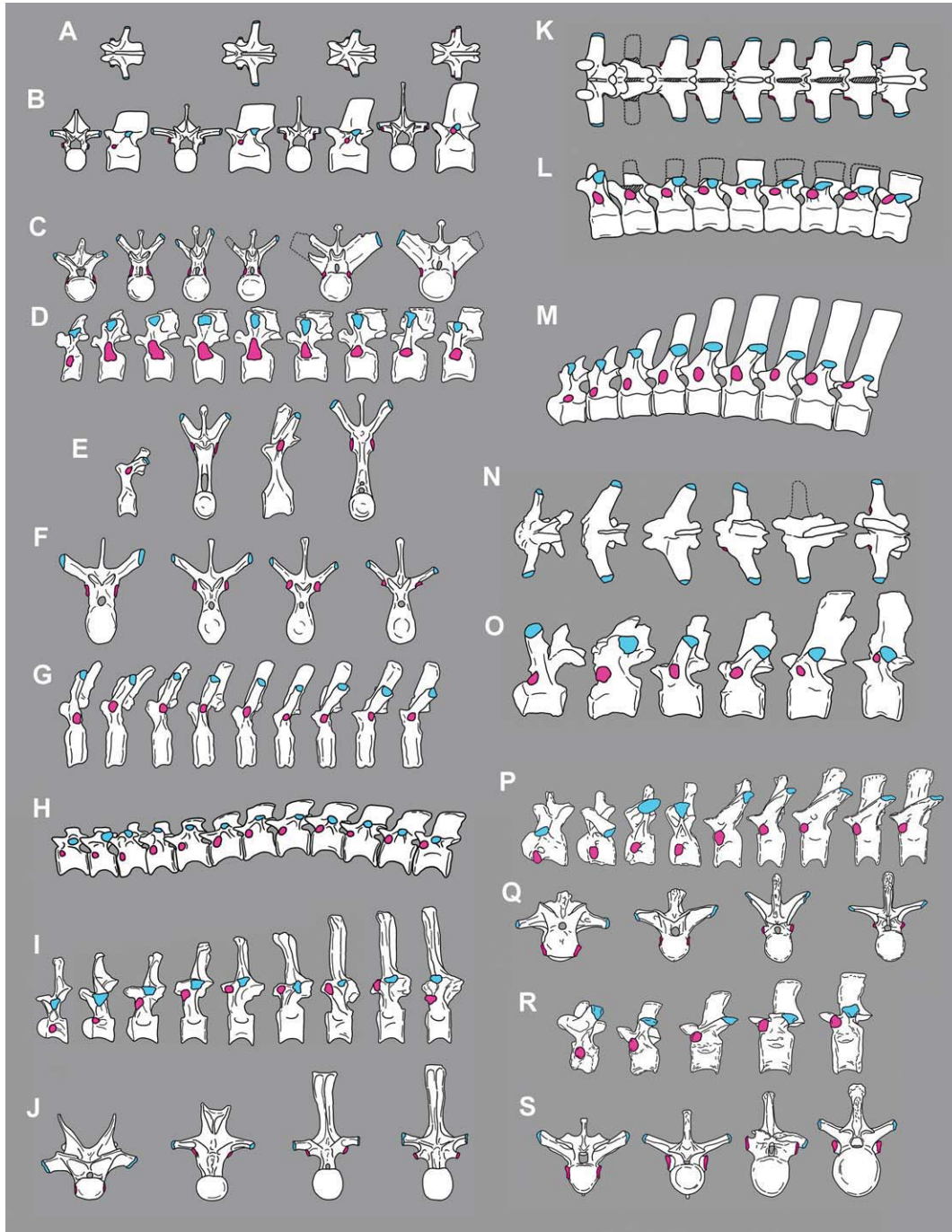
Fig. 3. Diagrammatic images of the dorsal vertebrae of select dinosauriform taxa with the articular processes highlighted. Diapophyses are indicated in blue, parapophyses are indicated in pink. Drawings are not to scale. **A**) Dorsals 1, 6, 10, and 13 of *Silesaurus opolensis* in dorsal view; redrawn from Dzik (2003). **B**) Dorsals 1, 6, 10, and 13 of *S. opolensis* in alternating cranial and left lateral view; redrawn from Dzik (2003). **C**) Dorsals 1, 3, 5, 6, 8, and 9 of *Ankylosaurus magniventris* in cranial view; redrawn from Carpenter (2004). **D**) First nine dorsal vertebrae of *A. magniventris* in left lateral view; redrawn from Carpenter (2004). **E**) Select dorsal vertebrae of *Stegosaurus stenops* (left to right) in alternating left lateral, and cranial views; redrawn from Ostrom and McIntosh (1966). **F**) Dorsals 1, 4, 6, and 9 of *Styracosaurus albertensis* in cranial view; redrawn from Holmes et al. (2005). **G**) The first nine dorsal vertebrae of *S. albertensis* in left lateral view; redrawn from Holmes et al. (2005). **H**) The first 12 dorsal vertebrae of *Plateosaurus* sp. in left lateral view; redrawn from Galton and Upchurch (2004). **I**) The first nine dorsal vertebrae of *Apatosaurus louisae* in left lateral view; redrawn from Gilmore (1936). **J**) Dorsals 1, 4, 7, and 9 of *A. louisae* in cranial view; redrawn from Gilmore (1936). **K**) The first nine dorsal vertebrae of *Hypsilophodon foxii* in dorsal view; redrawn from Galton (1974). **L**) The first nine dorsal vertebrae of *H. foxii* in left lateral view; redrawn from Galton (1974). **M**) The first nine dorsal vertebrae of *Mantellisaurus* (= "*Iguanodon*") *atherfieldensis* in left lateral view; redrawn from Norman (1986). **N**) Select dorsal vertebrae of *Eolambia caroljonesa* in dorsal view (CEUM 52173, 52836, 52092, 52833, 52114, and 52053, in order cranial to caudal). **O**) Select dorsal vertebrae of *E. caroljonesa* in left lateral view. **P**) The first nine dorsal vertebrae of *Allosaurus fragilis* in left lateral view; redrawn from Madsen (1976). **Q**) Dorsals 1, 4, 7, and 9 of *A. fragilis* in cranial view; redrawn from Madsen (1976). **R**) The first, fourth, sixth, seventh, and tenth dorsal vertebrae of *Deinonychus antirrhopus* (YPM 5204, YPM 5210) in left lateral view. **S**) The first, fourth, seventh, and tenth dorsal vertebrae of *D. antirrhopus* (YPM5204, YPM 5210) in cranial view.

Ornithischia

Thyreophora

There is a divergence between the morphology of basal thyreophorans and that of the more derived stegosaurs and ankylosaurs. The basal thyreophoran *Scutellosaurus* is not well known; however, the few dorsal vertebrae that have been found display a partially crocodilian morphology in the location of the parapophyses. The parapophysis shifts to the transverse process and gradually migrates out toward the diapophysis as in extant crocodilians, until the two articular processes merge into one facet. There is also a distinct broadening of the transverse processes in the caudal dorsal vertebrae, although the transverse processes do not lengthen. They remain robust and short for the entire vertebral series. The dorsal ribs of *Scutellosaurus* are known only from fragments, but it is clear that the cranial dorsal ribs are bicapitate with the two heads gradually migrating to one articular surface in the last rib (although it is not clear if they actually become holocephalous).

In stegosaurs, the parapophyses are located on the neural arch; in the cranial dorsal vertebrae, they are positioned at the base of the arch and progressively shift more dorsally in the middle and caudal dorsal vertebrae (Fig. 3E). The parapophyses do not migrate onto the transverse processes as in *Scutellosaurus*. The transverse processes are elevated 50°–60° above the horizontal plane. All of the thoracic ribs are double headed, with a short tuberculum and a large elongated capitulum that projects perpendicular to the rib shaft. When articulated, they produce a narrow, dorsoventrally incompressible rib cage with a corrugated ceiling (albeit less furrowed than in saurischian dinosaurs due to the more elevated position of the parapophyses).

The parapophyses of ankylosaur dorsal vertebrae are different from other dinosaurs in that they are connected with the diapophyses, but in a manner very different from crocodilians. After an initial shift from the body of the centrum in *Ankylosaurus*, the parapophyses remain at the base of the neural arch, directly ventral to the diapophyses for the entire dorsal series (Fig. 3C,D). In the fifth dorsal vertebra, the two processes are merged via an extension of the diapophysis onto the ventral surface of the transverse process (shaped like an upside down teardrop) so that the single articular facet is hourglass shaped. As in stegosaurs, all of the transverse processes are angled above the horizontal plane. In the last few dorsal vertebrae, there is a thin lamina running vertically from the parapophysis up to the diapophysis. The first four dorsal ribs are bicapitate and forked; in the following ribs the capitulum and tuberculum are connected via a lamina eliminating the gap between the two heads and their corresponding vertebrae (Fig. 4B). In the four caudal-most vertebrae of *Ankylosaurus*, the ribs are fused with the transverse processes so that the caudal region of the rib cage is completely immobile. In *Saichania*, this fusion begins at the sixth dorsal so that almost the entire thoracic ribcage is immobile.

Marginocephalia

The axial skeleton of pachycephalosaurs is very poorly known; the most complete axial skeleton consists of 10 caudal dorsal vertebrae of *Homalocephale*. The parapophyses and diapophyses are separate in all of the vertebrae; however, there is a gradual migration of the parapophysis toward the diapophysis caudally. The parapophysis remains directly ventral to the diapophysis and moves dorsally up the ventral aspect of the transverse process, as opposed to a migration onto the cranial aspect of the transverse process as in crocodilians. All of the transverse processes are angled above the horizontal plane. The ribs are all bicapitate, but they are not forked (Fig. 4A). The capitulum is located at the terminal margin of the rib while the tuberculum is located further back on the dorsal surface of the rib so that articulation is along the same line, perpendicular to the corresponding vertebra. This articular morphology precludes any dorsoventral movement of the ribs.

Psittacosaurs possess a vertebral and rib morphology similar to that of pachycephalosaurs (Fig. 4C). The parapophyses and diapophyses are separate in the cranial dorsal vertebrae; however, there is a gradual migration onto the transverse processes so that, by the caudal dorsals, the two articular facets have united into one process. The cranial and middle ribs are double headed, whereas the caudal dorsal ribs are correspondingly holocephalous.

In basal neoceratopsians, the parapophyses and diapophyses are separate and distinct for the entire dorsal series. There is a slight dorsal migration of the parapophysis in the middle and caudal vertebrae from the neural arch to the base of the transverse process, but it never migrates out onto the transverse process toward the diapophysis. All of the thoracic ribs in basal neoceratopsians are correspondingly double headed, and the cranial ribs are strongly forked much like the ribs of saurischian dinosaurs. In the caudal thoracic ribs, the tuberculum is smaller and closer to the capitulum but remains a distinct process. When articulated, the rib cage would be dorsoventrally incompressible.

In all of the dorsal vertebrae of ceratopsid dinosaurs, the parapophyses and diapophyses are separate (Fig. 3F,G). The parapophysis is on the centrum in the first two dorsal vertebrae, shifting to the base of the neural arch in the third, and then up to the base of the transverse process in the fourth. From the fifth dorsal on, the parapophysis migrates out on the ventral surface of the transverse process toward the parapophysis, although the two articular facets do not meet. The transverse processes are oriented dorsally above the horizontal plane by the third dorsal vertebra and decrease slightly in length in the more caudal dorsal vertebrae. The cranial dorsal ribs are strongly forked with a robust tuberculum (Fig. 4D). The middle dorsal ribs show a sequential diminishing of the size of the tuberculum until it is just a small facet on the dorsal aspect of the capitulum in the caudal dorsal ribs.

Ornithopoda

Basal ornithopods exhibit the least avian-like vertebral and rib morphology among the dinosauriform taxa examined. The transverse processes project slightly dorsally in the cranial dorsal vertebrae and shift to project horizontally in the middle and caudal dorsals. They are broad, flat, and short for the entire dorsal vertebral series. The parapophysis begins at the base of the neural
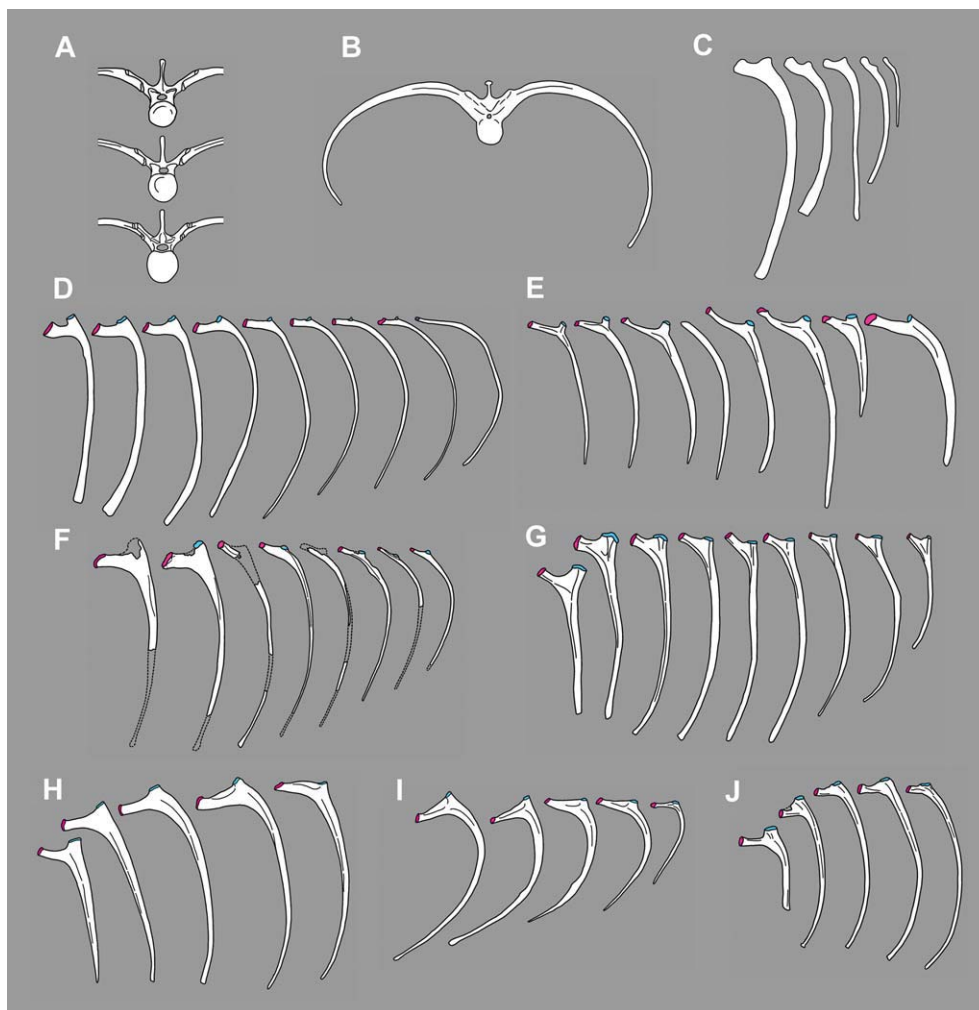
Fig. 4. Diagrammatic images of select dorsal ribs in cranial view of several extinct archosaurs with the parapophyses indicated in pink and the diapophyses indicated in blue. Drawings are not to scale. **A)** Select dorsal vertebrae with corresponding articulated ribs of *Homalocephale calathocercos*; redrawn from Maryanska and Osmólska (1974). **B**) Nineteenth dorsal vertebra and ossified ribs of *Ankylosaurus magniventris*; redrawn from Brown (1908). **C**) Select dorsal ribs of *Psittacosaurus sibiricus*; redrawn from Averianov et al. (2006). **D**) Left dorsal ribs one through nine of *Styracosaurus albertensis*; redrawn from Holmes et al. (2005). **E**) Left dorsal ribs one through eight of *Camarasaurus grandis*; redrawn from McIntosh et al. (1996). **F**) Left dorsal ribs one through eight of *Giraffatitan* (= "*Brachiosaurus*") *brancai*; redrawn from Janensch (1950). **G**) Left dorsal ribs one through nine of *A. louisae*; redrawn from Gilmore (1936). **H**) Left dorsal ribs 1, 3, 5, 7, and 9 of *A. fragilis*; redrawn from Madsen (1976). **I**) Left dorsal ribs 1, 3, 5, 7, and 9 of *T. rex*; redrawn from Brochu (2003). **J**) Idealized composite illustration of select dorsal ribs in cranial view of *D. antirrhopus* (YPM 5204, YPM 5210).

arch in the cranial dorsals (as opposed to on the centrum in other dinosaurs) and shifts to the cranial margin of the transverse process at about the fourth or fifth dorsal vertebra. The parapophysis progressively migrates out toward the diapophysis in the successive vertebrae, remaining on the cranial margin of the transverse process and thus on the same horizontal plane as the diapophysis (Fig. 3K,L). All of the thoracic ribs are bicapitate with the exception of the last two. The capitulum is positioned on the cranial margin of each rib and moves toward the diapophysis in the middle and caudal thoracic ribs.

Basal iguanodontians possess a vertebral and rib morphology similar to that of basal ornithopods. The parapophysis is above the neurocentral suture in the first dorsal vertebra in *Mantellisaurus* and is considered as the indicator of the transition from the cervical to the dorsal vertebrae (Fig. 3M). Along the dorsal series, the parapophysis migrates up and out along the cranial margin of the transverse process as a stepped facet and eventually merging with the diapophysis in most taxa (Fig. 3N,O). The transverse processes are large and angled up above the horizontal plane. Of the 17 dorsal ribs in *Mantellisaurus* and *Tenontosaurus*, all but the last one are bicapitate. The first dorsal rib is forked; however, in the following ribs, the tuberculum is a small process lying on the dorsal aspect of the capitulum that progressively decreases in size.

In hadrosaurs, the shift of the parapophysis from the neural arch to the transverse processes occurs much later in the dorsal series. All of the transverse processes are relatively short and angled dorsally above the

horizontal plane. The dorsal ribs are similar to those of the other ornithopods. The cranial thoracic ribs are forked while the middle and caudal ribs show a progressively diminished tuberculum.

Saurischia

Basal Sauropodomorpha

Basal sauropodomorphs exhibit dorsal vertebrae with distinctly separate diapophyses and parapophyses for the entire series. In *Massospondylus*, the shift of the parapophysis from the body of the centrum to the neural arch occurs by the fourth dorsal vertebrae. All of the transverse processes are short, and, in the third and succeeding vertebrae, the dorsal margins of the parapophyses are connected to the transverse processes by a thin lamina, which when articulated with their corresponding ribs limits costal mobility. In the last dorsal vertebra, the two processes are fused in a manner similar to the sacral vertebrae. *Plateosaurus* (Fig. 3H) and *Lamplughsaura* share a vertebral morphology very similar to *Massospondylus*; by the fourth dorsal vertebra, the parapophysis has shifted to the base of the neural spine and remains ventral and slightly cranial to the diapophysis. The transverse processes in *Plateosaurus* are equally short for the entire dorsal series. In *Lamplughsaura*, the transverse processes of the caudal dorsal vertebrae are angled slightly cranially.

The ribs of *Massospondylus, Plateosaurus*, and *Lamplughsaura* are all bicapitate with a gradual and successive reduction in the size of the tuberculum. The first four are the most strongly forked, although the tuberculum and capitulum remain distinctly separate for the entire series. When articulated, the thoracic ribs provide a rigid and dorsoventrally incompressible rib cage.

Sauropoda

Sauropods possess a vertebral and costal morphology very similar theropods; the parapophyses and diapophyses remain distinctly separate for the entire dorsal series, and all of the dorsal ribs are forked. In all of the sauropods examined, the transverse processes are robust and short, with a slight decrease in length in the caudal dorsal vertebrae. In *Apatosaurus* (Fig. 3H,I), the parapophysis shifts onto the neural arch in the third dorsal and remains there for the entire series. Once on the neural arch, the parapophysis shifts to a position that is slightly cranial and ventral to the diapophysis, at the base of the transverse process. The dorsal vertebrae of *Diplodocus* display a similar morphology to that of *Apatosaurus*. The parapophysis is on the centrum in the first four vertebrae, shifting onto the neural arch in the fifth vertebra. In the succeeding dorsal vertebrae, the parapophysis holds a position cranial and slightly ventral to the diapophysis, remaining separate and distinct for the entire series. In *Apatosaurus*, *Diplodocus* and *Giraffatitan*, the parapophyses in the caudal dorsal vertebrae are at the end of a process or peduncle. In the dorsals of *Camarasaurus* in which the parapophyses are preserved, they are a distinct process on the neural arch. In some of the vertebrae, they are connected to the transverse process by a thin vertically oriented lamina.

All of the thoracic ribs in *Camarasaurus* (Fig. 4E), *Apatosaurus* (Fig. 4G), and *Diplodocus* are strongly bicapitate with no reduction of either articular head. The thoracic ribs in *Giraffatitan* (Fig. 4F) are also all bicapitate, although there is a slight reduction in the size of the tuberculum in the more caudal ribs.

Theropoda

Of all the extinct taxa examined, the vertebrae and ribs of theropods are the most distinctly avian (Schachner et al., 2009). In *Herrerasaurus*, the parapophysis is a distinct process on the centrum in the first two dorsal vertebrae, shifting to sit at the base of the neural arch in dorsals 3–9. The parapophyses and diapophyses are oriented on the vertical plane in the cranial vertebrae of *Sinraptor*, *Allosaurus* (Fig. 3P,Q), *Tyrannosaurus rex*, and *Deinonychus* (Fig. 3R,S) shifting approximately 15° clockwise in the middle and caudal dorsals so that when articulated with their corresponding vertebrae, the tuberculum is slightly caudal to the capitulum on the vertical plane. There is some variation in the angle that the transverse processes project within theropods, although none of the taxa examined exhibit the broadening and lengthening trend seen in crocodilians. All of the theropod ribs are bicapitate and strongly forked (Fig. 4H–J), the cranial ribs more so than the more caudal ribs, generating a rigid rib cage.

DISCUSSION

Pulmonary Anatomy and Corresponding Skeletal Morphology in the Dinosauriformes

Transverse processes

In extant crocodilians, there is a progressive flattening and elongation of the transverse processes in the dorsal vertebrae. This might facilitate the shifting viscera and aid expansion of the lungs within the thoracic cavity. In contrast, avian transverse processes are short and generally uniform throughout the dorsal series. Some basal thyreophorans exhibited a broadening of the transverse processes in the caudal dorsal vertebrae; however, there was not the corresponding lengthening seen in crocodilians. None of the other taxa examined exhibited any kind of lengthening or broadening of the transverse processes similar to that observed in extant crocodilians. Many taxa (e.g., *Silesaurus*, *Hypsilophodon*, *Apatosaurus*, and *Deinonychus*) even displayed a general shortening of the transverse processes in the middle and caudal dorsal vertebrae relative to the overall vertebral size (Fig. 3A,B,J,K,L,S).

Parapophyseal positioning

Extant crocodilians all demonstrate a distinct parapophyseal shift from the centrum to the transverse process by either the third or fourth dorsal vertebra. The parapophysis shifts farther distally onto the transverse process toward the diapophysis with each successive dorsal vertebra until the two processes eventually meet in the caudal dorsals. The avian parapophyses remain on the bodies of the centra for the entire series of dorsal vertebrae. The processes in the dinosauriform *Silesaurus* remain separate for the entire series, although the parapophysis does move toward the diapophysis in the

caudal dorsals (Fig. 3A,B). Unlike crocodilians, however, the parapophysis is located on its own pedicle and does not migrate along the cranial margin of the transverse process. Thus, the thoracic ceiling would have been corrugated in a manner similar to that of extant birds but to a lesser extent. Aside from the partially crocodilian morphology observed in *Scutellosaurus*, the parapophyses are positioned on the neural arch for the entire dorsal series in all of the thyreophorans examined. In ankylosaurs, the parapophyses remain directly ventral to the diapophyses and are often connected via a bony lamina in the more derived taxa (Fig. 3C,D). In pachycephalosaurs and psittacosaurs, the parapophysis migrates out to meet the diapophysis in the caudal dorsal vertebrae; however, in neoceratopsians, the parapophyses and diapophyses adopt a more avian morphology and remain separate for the entire dorsal series (Fig. 3F,G). Ornithopods demonstrated a similar parapophyseal morphology to that of the marginocephalians; the more basal taxa possessed the crocodilian parapophyseal shift toward the diapophysis on the transverse process (Fig. 3K,L), whereas the derived taxa showed a slightly more avian morphology with the two processes remaining separate for the entire series (Fig. 3M,N,O). All of the saurischian taxa examined exhibited a distinctly avian parapophyseal morphology (Fig. 3H,I,J,P,Q,R,S). For a detailed review of nonavian theropod dinosaurs, see Schachner et al. (2009).

Proximal rib morphology

The first two dorsal ribs of crocodilians are bicapitate and strongly forked, with distinctly separate capitula and tubercula (Fig. 2B,C). The middle and caudal thoracic crocodilian ribs retain both their capitula and tubercula, although the capitulum migrates proximally toward to the tuberculum in each successive rib (Fig. 2B) until the two merge into one articular process. The caudal thoracic unicipital ribs have capitula that have shifted to the same horizontal plane as the tuberculum so that the rib is flattened dorsoventrally like its corresponding transverse process. Avian ribs are morphologically similar to the first two crocodilian ribs; all of them are bicapitate and strongly forked for the entire costal series (Fig. 2C). Complete series of ribs in dinosaurs are rare, although there are a few taxa in which enough ribs were preserved to observe morphological trends. All of the ribs of the extinct taxa examined were bicapitate, except for the caudalmost thoracic rib of *Psittacosaurus* and *Styracosaurus* (Fig. 4A,C,D). In many derived thyreophorans, the capitula and tubercula are positioned on the same vertical plane, and some of the caudal dorsal ribs are fused to their corresponding vertebrae creating a deeply furrowed thoracic ceiling for the length of the dorsal series. The fusion of the ribs precludes any form of costal aspiration in these taxa. Saurischian dinosaurs possessed the most distinctly avian-style forked ribs; both the sauropods (Fig. 3H–J) and the theropods (Fig. 3K,L) have capitula and tubercula that project at different angles and are connected via a thin bony lamina. When articulated, saurischian ribs would produce a deeply corrugated thoracic ceiling and a proximally dorsoventrally incompressible ribcage similar to that of extant birds. All taxa, including the ornithischians with a more croco-

dilian-like parapophyseal shift to the neural arch in the middle or caudal dorsals, exhibited a significant portion of their cranial dorsal vertebrae that, when articulated with their corresponding ribs, produced a distinctly furrowed thoracic ceiling. This suggests that the extent of the axial skeleton that shows costal corrugation could be an indicator of either overall lung size or at least the portion of the lung that was immobile, although this hypothesis has yet to be tested and warrants further investigation in fossil taxa and validation in extant taxa.

Pulmonary Morphology of the Dinosauriformes

There are a suite of morphological characters associated with the crocodilian respiratory system, all of which are almost entirely absent from the specimens examined in this study. None of the taxa exhibited a mobile pubic joint (for reviews of pelvic girdle evolution in archosaurs see Carrier and Farmer, 2000a,b; Claessens, 2004a,b), a rib-free lumbar region, or elongated and flattened dorsal transverse processes. A few basal thyreophorans possessed broadened transverse processes, but the majority of dinosaurs exhibited the avian-style parapophyseal–diapophyseal morphology. Taxa that possess the more crocodilian parapophyseal–diapophyseal morphology were the pachycephalosaurs, psittacosaurs, and basal ornithopods, the majority of which were obligate bipeds. Large cranial-caudal movement of the viscera, which occur with the hepatic-piston ventilation of extant crocodilians, are expected to shift the center of mass and could cause equilibrium problems and general instability in a parasagittally erect biped but not in quadrupeds (Farmer, 2006; Uriona and Farmer, 2008; Schachner et al., 2009). The basal dinosauromorph *Marasuchus* (which is more basal than *Silesaurus*; see Nesbitt et al., 2009) is also considered an obligate biped (Sereno and Arcucci, 1994), further reducing the possibility that this respiratory mechanism evolved in basal dinosauromorphs. The probable biomechanical infeasibility of such a respiratory mechanism in a biped, coupled with the lack of supporting osteological correlates, leads to a rejection of the hypothesis of a hepatic piston respiratory system as the plesiomorphic state for all of dinosauriformes.

Basal dinosauriforms

Based on the EPB, all archosaurs likely possessed dorsally attached multichambered unidirectionally ventilated lungs with heterogeneously partitioned parenchyma (Table 4). Despite the lack of basal dinosauriform taxa with dorsal vertebrae preserved, the distinct separation of the articular processes in *Silesaurus* (Fig. 2B) indicates an avian-style dorsoventrally incompressible ribcage. The capitulum remains separate and ventral to the tuberculum as far caudally as the 10th dorsal vertebra; when articulated with their corresponding ribs, the interior ceiling of the thoracic cavity would be corrugated in a manner similar to that observed in extant birds. This suggests a heterogeneously partitioned lung, with a craniodorsal region that was immobile and incised by the capitula of the adjacent ribs. This distinct and rigid cranial region could have contained the majority of the respiratory parenchyma and been ventilated

TABLE 4. Osteological characters in the axial skeleton of extinct archosaurs associated with respiratory anatomy and the predicted pulmonary morphology

Taxonomic groups	Transverse processes	Parapophyseal location	Rib morphology	Rib-free lumbar region	Predicted pulmonary morphology
Basal Dinosauriformes	Increase in length in the middle dorsals, followed by a shortening in the caudal dorsal vertebrae	On a pedicle on the neural arch for the entire dorsal series	Predicted to be bicapitate based upon vertebral morphology	No	Dorsally immobile heterogeneously partitioned multichambered lungs with unidirectional airflow; rigid cranial region, flexible caudal half
Thyreophora	Slight elongation in the caudal vertebrae; project dorsolaterally; in basal taxa, becoming broad and short in the caudal dorsals	In basal taxa the parapophysis merges with the diapophysis in the caudal vertebrae; In derived taxa it's on the centrum in the cranial dorsals and on the neural arch in the middle and caudal dorsal vertebrae	All of the dorsal ribs are bicapitate, with the exception of a few basal taxa	No, although the last dorsal vertebra does not always bear a rib in some taxa	Dorsally immobile heterogeneously partitioned multichambered lungs with unidirectional airflow; rigid cranial highly vascularized region, flexible less vascularized caudal region
Marginocephalia	Project strongly dorsolaterally	On the neural arch for the majority of the dorsal series with a subtle shift to the base of the transverse process in the caudal dorsals	The cranial ribs are strongly forked, although the tuberculum becomes successfully less pronounced in the middle and caudal ribs	No	Dorsally immobile heterogeneously partitioned multichambered lungs with unidirectional airflow; rigid cranial highly vascularized region, flexible less vascularized caudal region
Ornithopoda	Elongated relative to other dinosaurs, but generally maintain a constant length through the series; range from projecting horizontally to dorsolaterally	Dorsal to the neurocentral suture in the cranial dorsals, shifting to the transverse process in the middle dorsals and eventually merging with the diapophysis in the caudal dorsal vertebrae	The cranial ribs are forked; however the capitulum shifts to the transverse process at the middle dorsals	No	Dorsally immobile heterogeneously partitioned multichambered lungs with unidirectional airflow; rigid cranial highly vascularized region, flexible less vascularized caudal region
Basal Sauropodomorpha	Short and robust with little change throughout the series	On the body of the centrum in the cranial dorsals, shifting to the neural arch in the middle and caudal dorsals	All of the ribs are bicapitate; in the first four ribs the tuberculum is a distinct process but becomes a facet on the capitulum on the rest	No	Rigid lungs with unidirectional airflow; possibly ventilated by either an elastic nonvascular caudal section or air sacs
Sauropoda	Short and robust with little change throughout the series; project laterally	On the body of the centrum in the cranial dorsals, shifting to the neural arch in the mid and caudal dorsals	All of the ribs are bicapitate; they are not as forked as theropod ribs but the capitulum and tuberculum are distinctly separate for the entire series	No	Rigid avian style flow-through lungs likely ventilated by air sacs
Theropoda	Moderately short and robust, no significant change in length along the dorsal series; project laterally and dorsally	On the body of the centrum in the cranial dorsals, 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 avian style flow-through lungs likely ventilated by air sacs

by a more flexible and less vascularized caudal region. It is likely that the lungs were subdivided and unidirectionally ventilated by a less vascularized caudal compliant region, if not by a proto avian-style air sac system.

Ornithischian dinosaurs

Of all the taxa examined, the basal ornithischians displayed the most crocodilian-like dorsal vertebrae; however, it is in one character only (the position of the parapophysis), and, in most taxa, it is not significant enough to warrant the reconstruction of a crocodilian respiratory system due to the lack of any of the other corresponding osteological features (e.g., elongated and flattened transverse processes, mobile pubis, rib-free lumbar vertebrae). The more derived ornithischian dinosaurs follow a more avian vertebral pattern (albeit to a lesser degree than observed in saurischian taxa) in having separate parapophyses and diapophyses throughout their dorsal vertebral series. Like basal dinosauriforms, the data suggests that they possessed heterogeneously partitioned unidirectionally ventilated lungs, with a rigid dorsocranial region ventilated by a flexible less vascularized caudal region. Although there is a complete lack of evidence for postcranial pulmonary pneumaticity in ornithischian taxa (see, e.g., O'Connor, 2006), it has been reported in pterosaurs (Claessens et al., 2009). If these structures are homologous to the pneumatic structures found in the axial skeleton of saurischian dinosaurs, then it is possible that an air sac system may have indeed been present in ornithischian dinosaurs, but with a secondary loss of postcranial pulmonary pneumaticity, as suggested by Wedel (2007). This has been found to be the case in numerous extant avian taxa, in which postcranial pulmonary pneumaticity is either reduced (e.g., cormorants and darters) or lost completely (e.g., auks, loons, grebes, and penguins) (Gier, 1952; McLelland, 1989; O'Connor, 2004; O'Connor, 2009). Notably, O'Connor (2009b) observed that in apneumatic avian taxa pneumatic diverticula are still present and positioned directly alongside the axial skeleton but do not invade the bones. This opens up the possibility that the lack of postcranial pulmonary pneumaticity in the axial skeleton of ornithischian dinosaurs and basal dinosauriforms may not necessarily indicate the absence of an avian-style respiratory system in these groups, just an absence of skeletal pneumatization by the adjacent air sacs if present.

Nonavian saurischian dinosaurs

For a detailed review of the lung morphology of nonavian theropod dinosaurs, see Schachner et al. (2009). The morphology of the articular and transverse processes in all of the dorsal vertebrae of nonavian saurischian taxa is markedly avian (Fig. 3H–J,P–S); when articulated, the rib cage has a strongly corrugated ceiling and dorsoventrally limited mobility. None of the derived osteological characters associated with the crocodilian respiratory system are present in any of the saurischian taxa. As in all other archosaurs, these data support the hypothesis that nonavian saurischian dinosaurs had heterogeneously partitioned lungs with an immobile dorsal region that was incised by the adjacent capitula. In conjunction with the extensive evidence for pulmonary pneumaticity in both sauropods and theropods (see e.g., O'Connor and Claessens, 2005; O'Connor, 2006; Wedel, 2006, 2009), these data support previous hypotheses of an avian-style respiratory system in both sauropods and nonavian theropods ventilated by a series of air sacs (e.g., Perry and Reuter, 1999; O'Connor and Claessens, 2005). There is no clear unambiguous evidence for vertebral pneumaticity in basal sauropodomorphs (Wedel, 2007), so a reconstruction of an avian-style respiratory tract for this group is less well supported. However, the presence of strongly forked ribs in the taxa examined, and possible pneumaticity in the cervical region of *Thecodontosaurus* (Wedel, 2007), indicates that this group likely had small rigid dorsally attached lungs with the possibility of cranial air sacs, if not the abdominal air sacs that are reconstructed in the more derived saurischian taxa. As mentioned previously, air sacs do not always pneumatize the adjacent skeletal tissues in extant birds, thus the lack of postcranial pneumatic foramina do not necessarily indicate a lack of air sacs in basal sauropodomorphs.

Pelvic Aspiration and Cuirassal Breathing in Archosaurs

The pelvic girdle and pelvic musculature have a functional role in ventilation in both extant crocodilians and birds (e.g., Boggs et al., 1997; Carrier and Farmer, 2000a,b; Claessens, 2009a;b). Despite functional differences in ventilatory mechanisms in the extant taxa, Carrier and Farmer (2000a,b) suggested that pelvic aspiration was plesiomorphic for Archosauria, and proposed a possible mechanism based on pelvic and gastralial morphology in basal archosaurs. This mechanism, or "cuirassal breathing," would have been driven by the ischiotruncus muscle, which is proposed to have originated from the ventral margin of the ischial boot, and run cranially over the distal boot or tip of the pubis to insert along the medial aspect of the gastralia. When contracted, the ischiotruncus (in association with the abdominal muscles) would rotate the apex of the gastralial chevrons ventrally, expanding the volume of the abdominal cavity (Claessens, 2004b). This mechanism is expected to work best if the dorsal ribs resist dorsoventral compression and therefore the ventral pull of the ischiotruncus. It is possible, contrary to the hypothesis proposed in this study that the dorsoventrally incompressible forked rib morphology found in dinosauriform archosaurs evolved specifically in concert with pelvic aspiration, instead of as a support structure for a rigid lung. The strongly bicapitate and almost vertically oriented articulation of the thoracic ribs in most of the taxa examined indicate that rib rotation and thus costal aspiration was craniocaudally oriented, and minimal compared to that of extant squamates and crocodilians, particularly since none of the extinct animals possess the jointed ribs of extant crocodilians and birds that allow for enhanced costosternal movement to supplement costal lung ventilation. In some ankylosaurs, the caudal dorsal ribs are fused to their corresponding vertebrae, precluding costal aspiration entirely, necessitating some form of pelvic or abdominal aspiration. Clearly, costal aspiration was not the
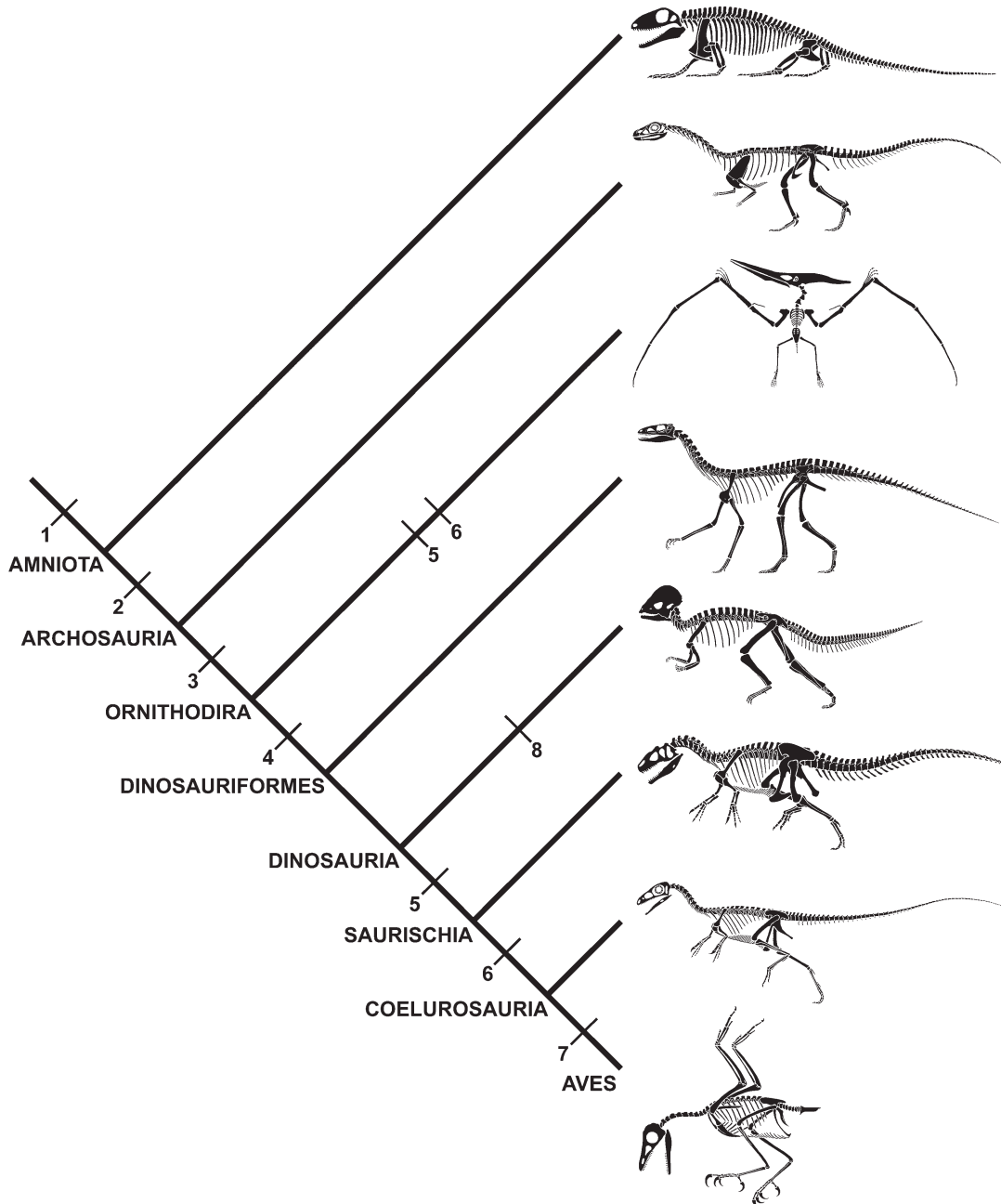
Fig. 5. Phylogeny of Amniota (Gauthier, 1986) demonstrating the key modifications associated with the evolution of an avian respiratory system. Diagrammatic images of (from top to bottom): a generalized amniote skeleton by E. R. Schachner; the archosaur *Effigia okeeffeae* redrawn from Nesbitt (2007); the ornithodiran *Pteranodon longiceps* based on Schiff (2004); the dinosauriform *Silesaurus opolensis* redrawn from Dzik (2003); the dinosaur *Stegoceras validum* by E. R. Schachner; the coelurosaurian theropod *Sinosauropteryx prima* redrawn from Paul (2002); and the bird *Sinornis santensis* redrawn from Sereno and Chenggang (1992). **1**) Costal breathing and septate lungs (Padian and Horner, 2004); **2**) four-chambered heart (Padian and Horner, 2004), unidirectionally ventilated lungs (Farmer and Sanders, 2010); **3**) possible origin of postcranial pneumaticity and hypothesized associated air sacs (Wedel, 2007); **4**) dorsally immobile heterogeneously partitioned multichambered lungs with unidirectional airflow, possible thinning of the blood-gas barrier; **5**) confirmed postcranial pulmonary pneumaticity (Wedel, 2003, 2006, 2007, 2009); **6**) hypothesized caudally positioned abdominal air sacs (O'Connor and Claessens, 2005; O'Connor, 2006; Wedel, 2009); **7**) uncinate processes (Codd et al., 2008); **8**) possible secondary loss of postcranial pulmonary pneumaticity in ornithischians.

primary mechanism for ventilating the lungs in extinct archosaurs, leaving pelvic aspiration as a likely candidate due to its presence in both of the extant bracketing groups, and cuirassal breathing as a viable hypothesis.

Evolution of the Avian Lung

Dorsally attached, heterogeneously partitioned lungs with the respiratory parenchyma limited to the dorsal portion of the rib cage have been proposed for dinosaurs

before (see e.g., Perry, 1992; Perry and Reuter, 1999), and the data presented herein lend further support to this hypothesis. It has frequently been observed that crocodilians possess very efficient cardiorespiratory systems that are greatly underutilized (Perry, 1990; Perry, 1992; Hicks and Famer, 1999; Owerkowicz, 1999; Claessens, 2004a, 2009a). The recent discovery by Farmer and Sanders (2010) of unidirectional airflow in the lungs of alligators demonstrated that the hepatic piston respiratory mechanism of crocodilians and unidirectional airflow in the lungs are not incompatible. They argue that the presence of unidirectionally ventilated lungs in both extant crocodilians and birds suggests that this trait was present in all of Archosauria. Crocodilian-style unidirectionally ventilated lungs in a basal archosaur, ventilated by a system of proto-air sacs or pelvic aspiration (as proposed by Carrier and Farmer, 2000a,b) would have been an effective method of respiration, particularly because these animals possessed parasagittally erect limbs and thus lung inflation was not constrained by lateral axial bending as in lepidosaurs (Carrier, 1987). This hypothesis is the most plausible considering that it allows for the evolution of both the extant crocodilian hepatic piston respiratory system and the extant avian respiratory system from the ancestral state in a stepwise fashion and would explain the underutilization and enhanced potential of the extant crocodilian lung. Claessens et al. (2009) reconstructed flow-through heterogeneously partitioned lungs ventilated by a series of air sacs in pterosaurs analogous to avian lungs, based on vertebral pulmonary pneumaticity in conjunction with various other lines of skeletal evidence. In light of the results presented herein, in association with the presence of unidirectional airflow in the lungs in extant crocodilians (Farmer and Sanders, 2010; Farmer, 2010), it is plausible that this pulmonary morphology is plesiomorphic for Ornithodira (Fig. 5).

Implications of a Rigid Lung in Dinosauriformes

A firm rib cage and rib heads that incise the dorsal surface of the lungs are considered integral features supporting the rigidity of the avian lung (Duncker, 1971; Maina, 2006). This rigidity is probably crucial for the thinning of the blood-gas barrier and air capillaries with a small diameter. As the capillaries are not required to be pliant, they do not need elastin, collagen and other structural elements that increase their strength but also increase their thickness, as is the case in the alveoli of the mammalian lung; thus, the capillaries can have very thin walls (e.g., Maina and West, 2005; Farmer, 2010). Furthermore, parabronchi do not collapse with ventilation, there are no issues with surface tension preventing reinflation, and they can, therefore, have a very small diameter. A thin blood-gas barrier has been purported to be particularly important for oxygen uptake under conditions of environmental hypoxia (Farmer, 2010) and the efficacy of the avian respiratory system under these conditions is dependent on the rigidity of the lung and the adjacent supporting skeletal structures (Duncker, 1971; Maina, 2006). The evidence for unidirectional airflow in the compliant lungs of alligators suggests that this airflow pattern was plesiomorphic for Archosauria and not restricted to the lungs of extant birds (Farmer and

Sanders, 2010). The evidence for both a rigid thorax and unidirectional airflow in dinosauriformes raises the possibility that these animals had a very thin blood-gas barrier relative to other contemporaneous vertebrates, which could have contributed to a great aerobic capacity in a hypoxic world, and contributed to their successful radiation during the Mesozoic.

LITERATURE CITED

Averianov AO, Voronkevich AV, Leshchinskiy SV, Fayngertz AV. 2006. A ceratopsian dinosaur *Psittacosaurus sibiricus* from the Early Cretaceous of West Siberia, Russia and its phylogenetic relationships. J Syst Palaeontol 4:359–395.

Brochu CA. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. J Vertebr Paleontol Mem 7 22:1–138.

Brown B. 1908. The Ankylosauridae, a new family of armored dinosaurs from the Upper Cretaceous. Bull Am Mus Nat Hist 24: 187–201.

Brown B, Schlaikjer EM. 1942. The skeleton of *Leptoceratops* with the description of a new species. Am Mus Novit 1169:1–15.

Boggs DF, Jenkins FA, Dial KP. 1997. The eects of the wingbeat cycle on respiration in black-billed magpies (*Pica pica*). J Exp Biol 200:1403–1412.

Butler RJ. 2005. The 'fabrosaurid' ornithischian dinosaurs of the Upper Elliot Formation (Lower Jurassic) of South Africa and Lesotho. Zool J Linn Soc Lond 145:175–218.

Carpenter K. 2004. Redescription of *Ankylosaurus magniventris* Brown 1908 (Ankylosauridae) from the Upper Cretaceous of the Western Interior of North America. Can J Earth Sci 41:961–986.

Carpenter K, Miles CA, Cloward K. 2001. New primitive stegosaur from the Morrison Formation, Wyoming. In: Carpenter K, editor. The armored dinosaurs. Bloomington, IN: Indiana University Press. p 55–75.

Carpenter K, Wilson Y. 2008. A new species of *Camptosaurus* (Ornithopoda: Dinosauria) from the Morrison Formation (Upper Jurassic) of Dinosaur National Monument, Utah, and a biomechanical analysis of its forelimb. Ann Carn Mus 76:227–263.

Carrier DR. 1987. The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. Paleobiology 13:326–341.

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.

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. 2009a. A cineradiographic study of lung ventilation in *Alligator mississippiensis*. J Exp Zool 311A:563–585.

Claessens LPAM. 2009b. The skeletal kinematics of lung ventilation in three basal bird taxa (emu, tinamou, and guinea fowl). J Exp Zool 311A:586–599.

Claessens LPAM, O'Connor PM, Unwin DM. 2009. Respiratory evolution facilitated the origin of pterosaur flight and aerial gigantism. PLoS One 4:1–8.

Codd JR, Manning PL, Norell MA, Perry SF. 2008. Avian-like breathing mechanics in maniraptoran dinosaurs. Proc R Soc B 1233:1–5.

Colbert EH. 1981. A primitive ornithischian dinosaur from the Kayenta Formation of Arizona. Mus Northern Ariz Press Bull Series 53:1–61.

Cooper MR. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. Occas Pap Natl Mus Rhod B Nat sci 6:689–840.

Currie PJ, Zhao X-J. 1993. A new carnosaur (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.

Dzik J. 2003. A beaked herbivorous archosaur with dinosaur anities from the Early Late Triassic of Poland. J Vertebr Paleontol 23:556–574.

Ezcurra MD. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan and Lucas, 1999 from the Upper Triassic of New Mexico, USA. Geodiversitas 28:649–684.

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

Farmer CG. 2010. The provenance of alveolar and parabronchial lungs: insights from paleoecology and the discovery of cardiogenic, unidirectional airflow in the American alligator (*Alligator mississippiensis*). Physiol Biochem Zool 83:1–15.

Farmer CG, Sanders K. 2010. Unidirectional airflow in the lungs of alligators. Science 327:338–340.

Forster CA. 1990. The postcranial skeleton of the ornithopod dinosaur *Tenontosaurus tilletti*. J Vert Paleontol 10:273–294.

Galton PM. 1974. The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. Bull Br Mus (Nat Hist) Geol 25:1–152.

Galton PM. 1976. Prosauropod dinosaur (Reptilia: Saurischia) of North America. Postilla 169 25:1–98.

Galton PM. 1990. A partial skeleton of the stegosaurian dinosaur *Lexovisaurus* from the uppermost Lower Callovian (Middle Jurassic) of Normandy, France. Geologica et Palaeontologica 24:185–199.

Galton PM, Upchurch P. 2004. Prosauropoda. In: Weishampel D, Dodson P, Osmólska H, editors. The Dinosauria, 2nd ed. Berkeley: University of California Press. p 232–258.

Gauthier JA. 1986. Saurischian monophyly and the origin of birds. In: Padian K, editor. The origin of birds and the evolution of flight. Memoirs of the California Academy of Sciences 8:1–55.

Gier HT. 1952. The air sacs of the loon. The Auk 69:40–49.

Gilmore CW. 1936. Osteology of *Apatosaurus* with special reference to specimens in the Carnegie museum. Mem Carnegie Mus 11:175–299.

Hatcher JB. 1901. *Diplodocus* (Marsh): its osteology, taxonomy, and probable habits, with a restoration of the skeleton. Mem Carnegie Mus 1:1–64.

Hatcher JB, Marsh OC, Lull RS. 1907. The Ceratopsia. U.S. Geol Surv Monogr 49:1–300.

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

Holmes RB, Ryan MJ, Murray AM. 2005. Photographic atlas of the postcranial skeleton of the type specimen of *Styracosaurus albertensis* with additional isolated cranial elements from Alberta. Can Mus Nat Syllogeus 75:1–75.

Hooley RW. 1925. On the skeleton of *Iguanodon atherfieldensis* from the Wealden. Q J Geol Soc London 81:1–61f.

Huene FV. 1926. Vollständige osteology eines Plateosauriden aus dem schwäbischen Keuper. Geol Palaeontol Abhandl N F 15:139–179.

Janensch W. 1950. Die Wirbelsäule von *Brachiosaurus brancai*. Palaeontographica 3(Suppl. 7):27–93.

Kutty TS, Chatterjee S, Galton PM, Upchurch P. 2007. Basal sauropodomorphs (Dinosauria: Saurischia) from the lower Jurassic of India: their anatomy and relationships. J Paleontol 81:1218–1240.

Lull RS, Wright NE. 1942. Hadrosaurian dinosaurs of North America. Geol Soc Am Spec Pap 40:1–242.

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

Maidment SCR, Wei G, Norman DB. 2006. Re-description of the postcranial skeleton of the Middle Jurassic stegosaur *Huayangosaurus taibaii*. J Vertebr Paleontol 26:944–956.

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. 2006. Spectacularly robust! Tensegrity principle explains the mechanical strength of the avian lung. Respir Physiol Neurobiol 155:1–10.

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, West JB. 2005. Thin and Strong! The bioengineering dilemma in the structural and functional design of the blood-gas barrier. Physiol Rev 85:811–844.

Maryanska T. 1977. Ankylosauridae (Dinosauria) from Mongolia. Palaeontol Polonica 37:85–151.

Maryanska T, Osmólska H. 1974. Pachycephalosauria, a new suborder of ornithischian dinosaurs. Palaeontol Polonica 30:45–102.

McDonald AT. 2011. The taxonomy of species assigned to *Camptosaurus* (Dinosauria: Ornithopoda). Zootaxa 2783:52–68.

McIntosh JS, Miles CA, Cloward KC, Parker JR. 1996. A new nearly complete skeleton of *Camarasaurus*. Bull Gunma Mus Nat Hist 1:1–87.

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.

Nesbitt S. 2007. The anatomy of *Egia okeeeae* (Archosauria, Suchia), theropod-like convergence, and the distribution of related taxa. Bull Am Mus Nat Hist 302:1–84.

Nesbitt SJ, Irmis RB, Parker WG, Smith ND, Turner AH, Rowe T. 2009. Hindlimb osteology and distribution of basal dinosauromorphs from the Late Triassic of North America. J Vertebr Paleontol 29:498–516.

Norman DB. 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). Bull Inst R Sci Nat Belg Sci Terre 56:281–372.

Novas NE. 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto formation (Upper Triassic) of Argentina. J Vertebr Paleontol 13:400–423.

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.

O'Connor PM. 2009. Evolution of archosaurian body plans: skeletal adaptations of an air-sac-based breathing apparatus in birds and other archosaurs. J Exp Zool 311:629–646.

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

Ostrom JH, McIntosh JS. 1966. Marsh's dinosaurs: The collections from Como Bluff. New Haven: Yale University Press. 388 pp. Reprint, New Haven: Yale University Press, 1999.

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, Horner JR. 2004. Dinosaur physiology. In: Weishampel DB, Dodson P, and Osmólska H, editors. The dinosauria. 2nd ed. Berkeley: University of California Press. p 660–671.

Parks WA. 1935. New species of trachodont dinosaurs from the Cretaceous formations of Alberta with notes on other species. Univ Toronto Stud Geol Ser 37:5–45.

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. 1989. Mainstreams in the evolution of vertebrate respiratory structures. In: King AS, McLelland J, editors. Form and function in birds. London: Academic Press. Vol. 4: p 1–67.

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, NY: 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: morphology G visceral organs. New York: Society for the Study of Amphibians and Reptiles. Vol. 19: p 1–92.

Perry SF, Christian A, Thomas B, Pajor N, Codd JR. 2009. Implications of an avian-style respiratory system for gigantism in sauropod dinosaurs. J Integr Biol 311A.

Perry SF, Reuter C. 1999. Hypothetical lung structure of *Brachiosaurus* (Dinosauria: Sauropoda) based on functional constraints. Mitt Mus Natkd Berl Geowiss Reihe 2:75–79.

Perry SF, Sander M. 2004. Reconstructing the evolution of the respiratory apparatus in tetrapods. Respir Physiol Neurobiol 144: 125–139.

Pinna G. 1979. Osteologia dello scheletro di *Kritosaurus notabilis* (Lambe, 1914) del Museo Civico di Storia Naturale di Milano.

Memorie della societa Italiana di scienze naturali Museo Civico di Storia Naturale di Milano 22:33–55.

Schachner ER, Lyson TR, Dodson P. 2009. Evolution of the respiratory system in nonavaian theropods: evidence from rib and vertebral morphology. Anat Rec 292:1501–1513.

Schiff JA. 2004. Old Yale: what Yale brought to the fair. Yale Alumni Magazine 67:72.

Sereno PC, Arcucci AB. 1994. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. J Vertebr Paleontol 14:53–73.

Sereno PC, Chao S. 1988. *Psittacosaurus meileyingensis* (Ornithischia: Ceratopsia), a new psittacosaur from the Lower Cretaceous of northeastern China. J Vert Paleontol 8:353–365.

Sereno PC, Chenggang R. 1992. Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. Science 255:845–848.

Uriona TJ, Farmer CG. 2008. Recruitment of the diaphragmaticus, ischiopubis and other respiratory muscles to control pitch and roll in the American alligator (*Alligator mississippiensis*). J Exp Biol 211:1141–1147.

Wedel MJ. 2003. Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. Paleobiology 29:243–255.

Wedel MJ. 2006. Origin of postcranial skeletal pneumaticity in dinosaurs. Integrative Zool 2:80–85.

Wedel MJ. 2007. What pneumaticity tell us about 'prosauropods', and vice versa. Palaeontol 77:207–222.

Wedel MJ. 2009. Evidence for bird-like air sacs in saurischian dinosaurs. J Exp Biol 311:611–628.

Witmer LM. 1995. 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.

Zimmer K. 1935. Beitrage zur Mechanik der Atmung bei den Viigeln im Stand und Flug. Auf Grund ana-tomisch-physiologischer und experimenteller Studien. Zoologicu 33 Heft 88:l–69.