

Cardio-Pulmonary Anatomy in Theropod Dinosaurs: Implications From Extant Archosaurs

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ABSTRACT Although crocodylian lung and cardiovascular organs are markedly less specialized than the avian heart and lung air-sac system, all living archosaurs possess four-chambered hearts and heterogeneously vascularized, faveolar lungs. In birds, normal lung function requires extensive, dorsally situated nonvascularized abdominal air-sacs ventilated by an expansive sternum and specially hinged costal ribs. The thin walled and voluminous abdominal air-sacs are supported laterally and caudally to prevent inward (paradoxical) collapse during generation of negative (inhalatory) pressure: the synsacrum, posteriorly directed, laterally open pubes and specialized femoral-thigh complex provide requisite support and largely prevent inhalatory collapse. In comparison, theropod dinosaurs probably lacked similarly enlarged abdominal air-sacs, and skel-eto-muscular modifications consistent with their ventilation. In the absence of enlarged, functional abdominal air-sacs, theropods were unlikely to have possessed a specialized bird-like, air-sac lung. The likely absence of bird-like pulmonary function in theropods is inconsistent with suggestions of cardiovascular anatomy more sophisticated than that of modern crocodylians. *J. Morphol.* 270:1232–1246, 2009. © 2009 Wiley-Liss, Inc.

KEY WORDS: theropod heart; theropod lung; bird lung

INTRODUCTION

There exists a diversity of vertebrate cardiovascular morphologies ranging from the incompletely divided heart and dual aortic arches of the lower tetrapods to the fully partitioned heart and single aortic arch of birds and mammals. In all cases, the cardiovascular system delivers nutrients and oxygen to tissues while simultaneously removing metabolic wastes including carbon dioxide. The range of vertebrate cardiovascular designs reflects, in part, varied metabolic demands in endotherms and ectotherms. Endotherms, whose field metabolic rates exceed those in similar-mass ectotherms by some 15–20 fold (Bennett, 1991; Bennett et al., 2000), require substantially more oxygen and nutrients per unit time. Accordingly, in birds and mammals, the cardiovascular and respiratory systems are likely to have evolved largely in response to selection for enhanced exchange, transport and delivery of respiratory gases.

Specialized features which developed independently in both birds and mammals include

increased pulmonary surface area, more efficient gas diffusion at the lungs, greatly expanded oxygen carrying capacity of the blood, and increased maximal cardiac output (Bennett, 1991; Ruben, 1995). Furthermore, in birds and mammals there is no mixing of deoxygenated systemic venous (pulmonary arterial) blood with oxygenated systemic arterial (pulmonary venous) blood (see Fig. 1). Complete separation of pulmonary and systemic circulations is achieved initially where interatrial and interventricular septa divide the heart into four chambers. This separation is maintained by two distinct great vessels which emerge from the heart: the pulmonary artery (trunk) from the right ventricle and the single, systemic aortic arch from the left ventricle. During fetal development there is communication between the two circuits via the truncus arteriosus and the foramen ovale and both passages normally close at or before hatching or birth. Should there be incomplete closure, systemic oxygen delivery capacity and stamina can be reduced significantly (Oelberg et al., 1998; Brickner et al., 2000; Hicks, 2002; Suchon et al., 2005). Importantly, oxygen delivery modifications associated with endothermy are most critical not at rest but during bouts of routine or accelerated levels of activity (Bennett and Ruben, 1979).

In addition to the separation of oxygenated and deoxygenated blood in endotherm cardiovascular systems, differential pressures are maintained in the pulmonary and systemic vascular circuits. Mean systolic pressures in the systemic circulations of diverse endotherms vary between 87 and 216 cm H₂O, while the resting pulmonary circulations of men, ducks and chickens are considerably lower, typically achieving less than 30 cm H₂O

Additional Supporting Information may be found in the online version of this article.

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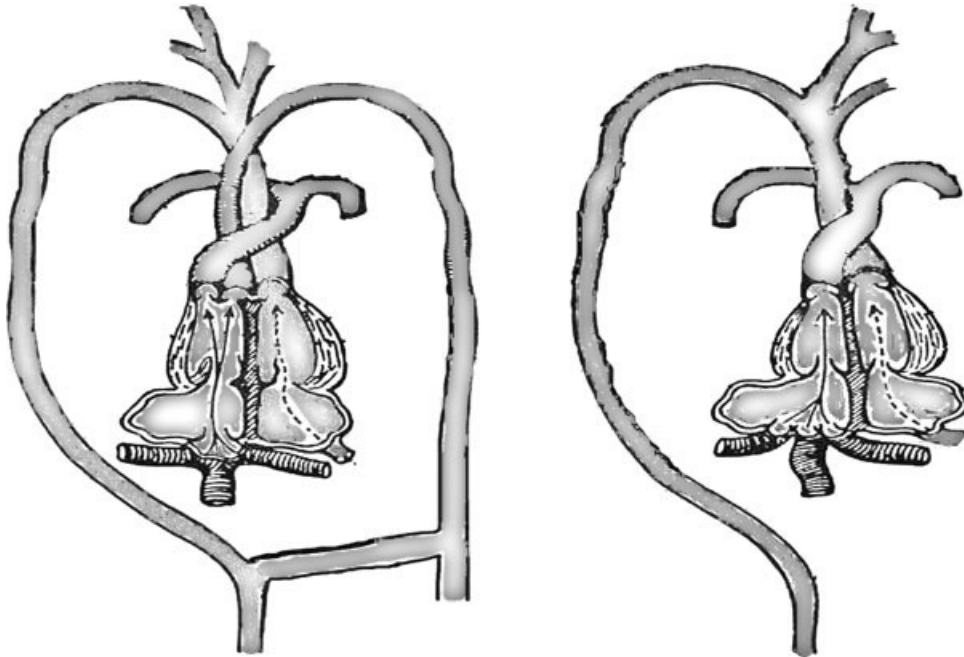


Fig. 1. Diagrams of the heart and great vessels in crocodilians (left) and birds (right). Both possess fully subdivided, four-chambered hearts. Crocodilians, like many sauropsids, retain paired aortae which allow mixing of oxygenated and deoxygenated blood (modified from Goodrich, 1930).

(Johansen, 1972; Seymour and Blaylock, 2000; Weidong et al., 2002). High systemic arterial pressures must be maintained in endotherms to overcome elevated total peripheral resistance in densely vascularized tissues. Similarly elevated pulmonary pressures are untenable due to the necessarily thin respiratory membrane in the lung. Of all the air breathing vertebrates, endotherms have evolved the thinnest respiratory membranes which facilitate faster blood oxygen loading (Maina, 2002). However, the thinner the respiratory membrane, the more susceptible respiratory membranes are to pulmonary edema, effusion or parenchymal structural damage if perfused at elevated pressures. Significantly, similar adverse effects have been recorded in diverse animals during maximal exercise (West and Mathieu-Costello, 1995; Wang et al., 2003; Ware and Matthay, 2005). Even in the most extreme example, the giraffe maintains the highest recorded systemic arterial pressure (>325 cm H_2O) to allow adequate brain perfusion, but laboratory pulmonary arterial pressures peak at 65 cm H_2O (Goetz et al., 1960), i.e., some 20% of systemic pressures. Thus, as endothermy developed along with elevated cardiac output to serve increased systemic tissue demands, so too did the fully partitioned four-chambered heart and physically separate arterial systems with markedly different vascular resistances and pressures.

Most ectotherms have incompletely divided five-chambered hearts and paired systemic aortic arches. Upon contraction, the single ventricle (sub-

divided into three functional chambers) acts as a single pressure pump, synchronously ejecting blood into two systemic aortic arches and the pulmonary trunk; widely disparate pressures in systemic and pulmonary circulations are not possible (Hicks, 1998). Thus, among several turtles and nonvaranid lizards, systemic peak systolic pressures vary between 30 and 80 cm H_2O but pulmonary peak systolic pressures average only $\sim 30\%$ lower at 20–55 cm H_2O (Hicks, 1998). The consequence of elevated pulmonary pressures, which can be $\sim 5\times$ those of mammals, in combination with particularly leaky capillary walls, is that ectotherms produce 10–20 \times more plasma filtrate at the respiratory membrane (Burggren, 1982; Wang et al., 1998). This “wet lung” state increases the barrier to gas exchange in the lung and may contribute to the relatively lower oxygen extraction capacity of reptilian lungs when compared to those of birds, although it does not explain similar oxygen extraction values to those of mammals with dry lungs (Bennett, 1973; Geist, 2000).

Fully partitioned four-chambered hearts and/or intermediate systemic vascular pressure differences also occur in certain ectothermic animals. Crocodilians maintain systemic pressures some threefold those of the pulmonary circulatory pressures by utilizing a fully partitioned four-chambered heart (see Fig. 1), while *Varanus* and *Python* manage to do so with a five-chambered heart. Under resting laboratory conditions, the left ventricle and right aorta of crocodilians develop mean

systolic pressures of 104 cm H₂O; the right ventricle develops only 63 cm H₂O pressure and the pulmonary trunk can be an even lower 21 cm H₂O (Shelton and Jones, 1991). In the five-chambered hearts of *Varanus* and *Python*, differential, crocodylian-like pressures may also develop due to the presence of an almost complete muscular ridge that effectively creates a temporary, four-chambered condition during systole (Wang et al., 2003). As such, these seemingly endotherm-like cardiovascular features (four-chambered hearts, differential systemic/pulmonary pressures) are not exclusive to birds and mammals. It has been previously argued that these shared characters may be beneficial to an ectothermic lifestyle to aid in increased systemic oxygen delivery during egg incubation or exercise without debilitating high pulmonary filtration or edema (Burggren and Johansen, 1982; Wang et al., 2003; Hillenius and Ruben, 2004b).

Regardless of some noteworthy cardiovascular similarities between endotherms and some ectotherms, all ectotherms allow deoxygenated and oxygenated blood to mix. Even in crocodylians where the fully divided ventricle separates right-side deoxygenated blood from left-side oxygenated blood, the left aortic arch emerging from the right ventricle communicates with the right aortic arch from the left ventricle (see Fig. 1). Blood may pass between the aortic arches at their bases (after the bicuspid valves, through the foramen of Panizza) or in the abdomen (through anastomoses; Hicks, 2002).

The degree and direction of shunting in ectotherms is controlled by factors that affect pulmonary and systemic vascular resistance, just as all blood flow in the cardiovascular system is ultimately controlled by changes in vascular resistance in response to tissue demands (Hicks, 2002). Generally, increased parasympathetic tone during apnea increases pulmonary resistance and thus the right to left shunt while decreased pulmonary resistance reduces the right to left shunt (Hicks, 1998).

Regardless of the specific mechanism(s), pulmonary bypass in all ectotherms allows deoxygenated systemic venous blood to be recirculated to the tissues, thus reducing systemic oxygen delivery. Ectotherms with their much lower metabolic demands (than endotherms) can tolerate the reduction in systemic arterial blood oxygen generated during shunting, even during exercise. Moreover, widespread shunting in extant reptiles has led to suggestions that this is a highly derived trait with certain distinct advantages (e.g., as an aid to digestion or in maintaining pressure balances; see references in Hicks, 1998; Farmer et al., 2008; e.g., as an aid to digestion or in maintaining pressure balances; see references in Hicks, 2002; Seymour et al., 2004). While many compelling arguments are made for the adaptive significance of shunting, given its phylogenetic distribution and the pres-

ence of central vascular shunts during the embryonic stages of all vertebrates, it is possible that shunting is a plesiomorphic vertebrate character lost in adult endotherms (Hicks, 2002). In endotherms, as evolutionary pressures selected for increased oxygen delivery (increased cardiac output) to meet the elevated demands of the tissues, those characters reducing oxygen delivery (shunting) were lost, and others favoring increased oxygen extraction were acquired (thin respiratory membrane, low pulmonary pressure), perhaps resulting in the character states observed in modern endotherms and ectotherms.

What evidence exists for the cardiovascular anatomy and function in theropod dinosaurs? Rarely are cardiac chambers and/or the aortae preserved in the fossil record. Recent assertions notwithstanding, they remain unknown in any dinosaurs (Fisher et al., 2000; Rowe et al., 2001). However, the exact number of chambers that theropod dinosaur hearts possessed is somewhat irrelevant, their closest living relatives (i.e., crocodylians and birds) possess four-chambered hearts and, by itself, this factor would provide no real insight into their cardiovascular capacities. Arguments have been made that some Permian crocodylomorphs may have required a four-chambered heart (Fisher et al., 2000; Seymour et al., 2004; Hillenius and Ruben, 2004b) and similar arguments may be applied to the Dinosauria. But previous discussions have not addressed the essential question of one vs. two systemic aortic arches and theropods' abilities to tolerate recirculation of deoxygenated blood. Given the almost ubiquitous absence of fossilized soft tissues, cardiovascular morphology in theropod dinosaurs is difficult to interpret. However, indirect but reliable indicators of theropod cardiovascular anatomy may be found in the evidence for avian or crocodylian-like aerobic capacities in these animals, and, by extension, the cardiovascular anatomy requisite for its support and maintenance.

Definitive anatomic features functionally linked to the aerobic capacity of modern animals are unlikely to be preserved in the fossil record. Blood oxygen carrying capacities, blood oxygen affinity and tissue mitochondrial volumes are characters of the soft tissue and have not been described in any fossilized remains. Nasal respiratory turbinates, which are respiratory water and heat conserving mechanisms associated with elevated avian and mammalian rates of pulmonary ventilation have been discussed at length in other publications (Ruben et al., 1996; Ruben et al., 2003; Hillenius and Ruben, 2004a) and are unknown in any theropod remains. However, there exists further evidence in the skeletal and soft tissue remains of theropod dinosaurs that provides insight to their respiratory apparatus and their bird-like or crocodylian-like aerobic capacities.

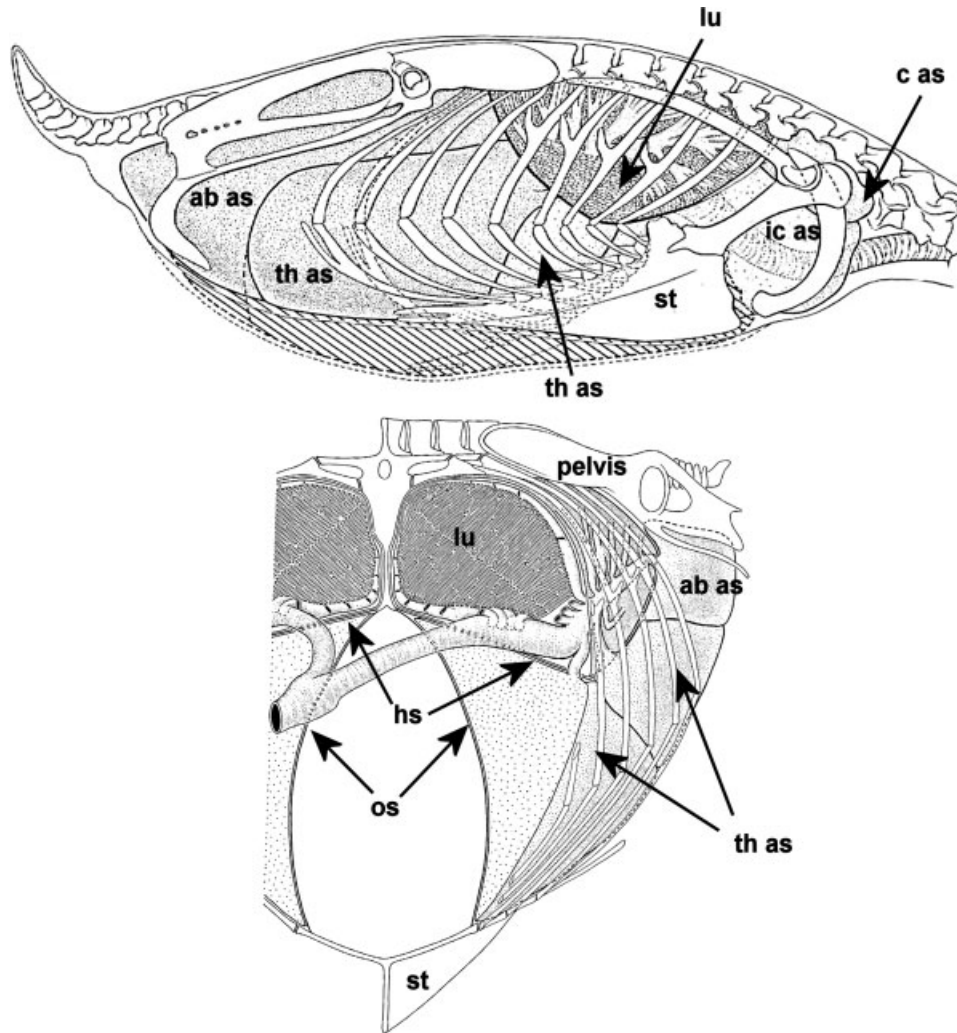


Fig. 2. Longitudinal (above) and cross-sectional (below) diagrams of the lung air-sac system in modern birds. The fixed-volume, vascularized portion of the lung (lu) is ventilated by unidirectional air flow generated by nonvascularized abdominal (ab as), thoracic (th as), clavicular (ic as) and cervical air-sacs (c as). The horizontal septum (hs) underlies the vascularized portion of the lung and the oblique septum (os) surrounds digestive viscera (not depicted), separating them from the air-sacs. St, sternum (modified from Duncker, 1971).

To serve their markedly different metabolic demands, modern birds and crocodylians vary not only in their cardiovascular anatomy, but also in their respiratory apparatus and associated ventilatory mechanisms. Birds utilize a specialized, markedly heterogeneous faveolar lung air-sac system in which nonvascularized air-sacs act as ventilatory bellows to move air continuously and unidirectionally across a fixed volume, vascularized parabronchial lung (Fig. 2; Duncker, 1979; Perry, 1989). The various air-sacs (cervical, clavicular, thoracic, and abdominal) are positioned throughout the body cavity and the lung is firmly attached to the dorsal, thoracic body wall. Movements of the ribs, sternum and/or pelvic apparatus generate intracelomic pressure changes which in turn drive volumetric changes of the air-sacs and thus inspiration and expiration (Scheid and Piiper, 1989). In

crocodylians, the m. diaphragmaticus together with intercostal and abdominal muscles bidirectionally drive inspiration and expiration through a markedly less heterogeneous but multichambered lung (Gans and Clark, 1976; Farmer and Carrier, 2000). Although the crocodylian lung is relatively larger, the avian parabronchial lung has both the greatest known relative gas exchange surface area and thinnest barrier to oxygen diffusion (Perry, 1989), and in combination with its vascular, anatomic and ventilatory features, is the most efficient lung of all air-breathing vertebrates at oxygen extraction (Schmidt-Nielsen, 1997; Maina, 2002).

Requisite to the function of the bird lung air-sac system are the caudal air-sacs and in particular, the large, paired abdominal air-sacs which receive inspired air from the main bronchus before passing it across the lung (Fig. 2; Schmidt-Nielsen,

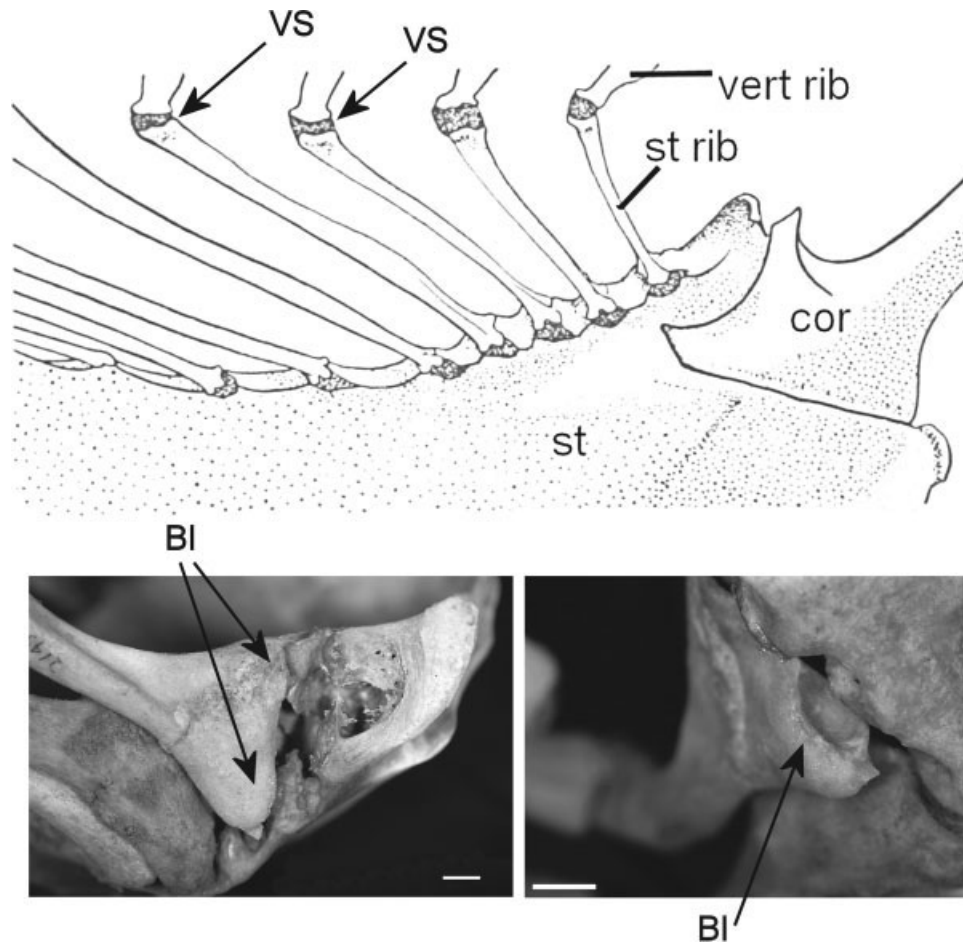


Fig. 3. Specialized articulations in vertebral and sternal ribs of modern birds (vert rib and st rib, respectively). Note the socket-like articulations at the highly mobile vertebral-sternal (intravertebral) costal joints (VS) as well the bifurcate costal processes at their points of contact with the sternum (BI; example from *Struthio*). These features facilitate dorso-ventral movement of posterior sternum during lung ventilation (st, sternum; cor, coracoid). Scale bars = 1 cm, figure modified from Zimmer, 1935.

1997). Experimental occlusion of the abdominal air-sacs in domestic fowl decreases lung ventilation, greatly reducing arterial blood oxygen tension (by about 20%) and diminishing endurance during even minimal exercise (factorial aerobic scope ~ 3) (Brackenbury and Amaku, 1990). Similar procedures that incapacitated only the caudal thoracic air-sacs did not produce significantly reduced blood oxygen tension or diminished endurance (Brackenbury et al., 1989). In the absence of functional abdominal air-sacs, hypoxaemic animals seem unlikely to maintain capacities for more demanding routine daily activities (Nagy, 1987; Bishop, 1999). Similarly, had theropods utilized a modern bird like lung air-sac system to fuel markedly elevated aerobic capacities, functional abdominal air-sacs would likely have been requisite.

Ventilation of the modern bird lung air-sac system relies on specialized synovial articulations between vertebral and sternal ribs and the sternum and sternal ribs (Fig. 3; Hillenius and Ruben, 2004a). At the sternocostal joint, the sternal ribs

are distally expanded into two fossae that articulate with the thickened, dorsally oriented posterolateral border of the sternum which bears two paired articular convexities (i.e., internal and external condyles, Zimmer, 1935; Fig. 3). A single facet exists on the distal vertebral rib forming a modest hinge joint with the proximal sternal rib at the intracostal joint. Contractions of several intercostal and trunk muscles during inspiration increase the intracostal angle at the joint, rotating the ribs cranially and forcing the sternum ventrally (Fig. 4; Zimmer, 1935; Fedde, 1987; Hillenius and Ruben, 2004a; Codd et al., 2005). Distal coracoids form a saddle joint with the coracoid sulcus of the cranial sternum and the coracoids act as a strut during inhalation: when the sternum is depressed, the caudal end moves further ventrally than the cranial end (Fig. 4; Jenkins et al., 1988; Baumel and Raikow, 1993; O'Connor and Claessens, 2005). This sternal motion accounts for at least half of total tidal volume in many, if not all birds (Fedde, 1987). The effect of these skeleto-

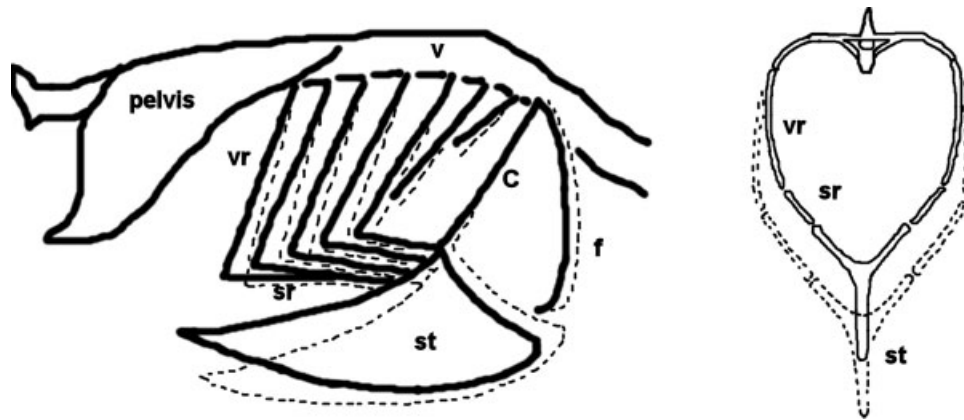


Fig. 4. Longitudinal (left) and anterior (right) avian ribcage/sternum movement during lung ventilation. During inhalation (dashed lines), the posterior sternum moves ventrally and the ribs flare laterally (c, coracoid; f, furcula; sr, sternal rib; st, sternum; v, vertebral column; vr, vertebral rib). Figure modified from Zimmer, 1935.

muscular actions during inspiration is primarily to generate ventral and lateral expansion of the torso, especially toward the abdominal body cavity (see Fig. 4). When normal ribcage motions are limited due to roosting or resting on the sternum, birds can still ventilate the abdominal air-sacs using costal musculature to laterally flare the rib cage or via pelvic rocking to effect pressure changes in the caudal cavity, or both together (Baumel et al., 1990; Codd, 2004; Codd et al., 2005). Recent experiments demonstrate that the muscles inserting on the uncinatous processes (bony, posteriorly projected processes of vertebral ribs) in Canada geese are particularly active while sitting and as such, these costal projections may be important to rib cage movements when sternal depression is unavailable (Codd et al., 2005). This specialized costosternal anatomy and action is unique to birds although other air breathing vertebrates certainly possess sternocostal articulations and uncinatous processes. However, in nonavians, sternocostal articulations are flat wherein the distal sternal ribs abut the lateral edges of the sternum to form gliding, synovial joints or firmer, cartilaginous articulations and bird-like motion of the sternum is not permitted (Hillenius and Ruben, 2004b).

Air movement in and out of the thin walled, nonvascularized air-sacs is driven by changes in transmural air-sac pressure. Energy must be expended during all stages of ventilation because the flimsy air-sac walls possess no significant number of elastic fibers capable of recoil (Duncker, 1971). While flying at their preferred speeds in a wind tunnel, black-billed magpies (*Pica pica*) generate peak expiratory pressures of roughly 2 cm H₂O in their anterior clavicular air-sac and 8 cm H₂O in posterior thoracic air-sacs, about a 6× increase over those observed at rest (Boggs et al., 1997). Mean inhalatory pressures achieved

roughly equivalent negative pressures (Boggs et al., 1997). Brackenbury (1986) observed slightly higher clavicular air-sac pressures (2–5 cm H₂O) among domestic fowl running on the treadmill at a factorial aerobic scope of ~3×. Either at rest or while flying, Boggs et al. (1997) consistently measured a significantly elevated posterior air-sac pressure compared to that of the clavicular air-sac which they attributed to the greater volume of the posterior sacs. Although abdominal air-sac pressures have yet to be measured directly during activity, it is reasonable to infer that pressures in the more voluminous abdominal air-sacs probably also exceed pressures in the smaller thoracic air-sacs. Accordingly, birds are likely to subject their thin walled, compliant air-sacs to significant transmural pressures during the course of routine and accelerated activity levels. Using their body wall and skeletal anatomy, birds must generate and then translate these negative inhalatory pressures to their compliant respiratory structures while also preventing inward collapse or translation of the viscera/body wall into the air-sacs thereby negating air-sac filling and function (so called paradoxical collapse).

Paradoxical collapse in the anterior air-sacs is undoubtedly prevented by the indirect fusion of the air-sacs with the costally-reinforced thoracic body wall (see Fig. 2). Although ribs and sternum move significantly during ventilation, the avian rib cage maintains a minimum volume below which the thoracic wall cannot collapse. The viscera are separated from the compliant air-sacs in the thoracoabdominal cavity where inelastic oblique and horizontal septa divide the cavity into two subpulmonary cavities and one peritoneal cavity (Duncker, 1971). Paired subpulmonary cavities are bounded dorsally by the horizontal septum (dorsal to which is found the lung), medially and caudally by the oblique septa (which spans from vertebral column to the

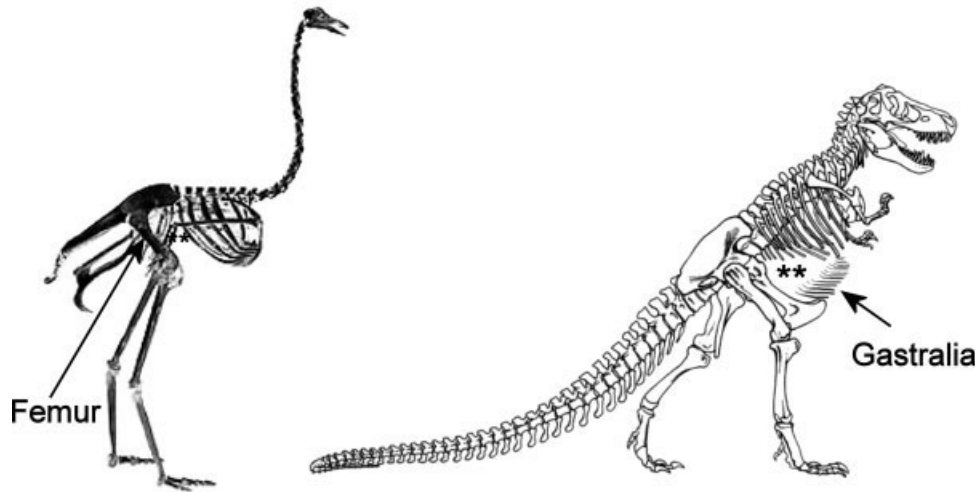


Fig. 5. Ostrich (*Struthio*) and *Tyrannosaurus rex*. Note the broadly open abdominal lumbar regions in both taxa (asterisks). In the ostrich, the semihorizontal femoral complex is incorporated into the lateral body wall and helps prevent paradoxical ventilatory collapse of the large abdominal air sacs. No such collapse-preventing mechanism existed in *Tyrannosaurus*: during locomotion in theropods, the distal femur rotated freely and the femoral complex was not incorporated into the abdominal wall. (Figures modified from Bolzan, 2001; Figures modified from Osborn, 1916).

sternum and caudal, lateral body wall) and laterally and ventrally by the rib bearing body wall (Fig. 2; Duncker, 1971). The clavicular and cervical air-sacs are found cranially in these cavities while the thoracic air-sacs are positioned caudally; the air-sac walls fuse with the surrounding tissues (Duncker, 1979). During inspiration the air-sacs are pulled open ventrally and laterally as the ribs flare laterally and sternum pulls ventrally on the ventral oblique septum. Thoracic cavity and air-sac volume is thereby directly affected by movements of bony or inflexible structures on all sides.

Abdominal air-sacs may fill virtually the entire abdominal (peritoneal) cavity (Duncker, 1971). They are apparently firmly supported consistently only at their dorsal and anterior aspects (Duncker, 1971; Sapp, 2004): they are fused above to the rigid vertebral column and expanded synsacrum and cranially to the oblique septum (see Fig. 2). Surprisingly, in many birds, both laterally and ventrally there is no obvious support provided by the compliant body wall or by the surface of the viscera (Duncker, 1971). It would seem then that during negative inhalatory pressure generation, the thin walled abdominal air-sacs would be likely to suffer collapse due to paradoxical movement of the viscera from their unsupported ventro-lateral aspects. That is, without a mechanism to reinforce especially its lateral aspects, the abdominal wall and by extension, the abdominal air-sacs would tend to collapse, rather than inflate, during inhalation. This problem seems especially acute in many cursorial birds where there exists a particularly extensive, unsupported gap between the caudal extent of the rib cage and the craniolateral expansion of the pelvic rami/ala (Duncker, 1971; Codd,

2004). This space is most apparent in the large ratites as these walking birds require room for pronounced leg muscles which can comprise as much as 25–30% of body mass (Fig. 5; Bundle et al., 1999; Ellerby et al., 2003; Fig. 5; Patak and Baldwin, 1993). Perry (1983) suggests that birds escape paradoxical collapse of the body wall in this region by tightly suspending the unsupported lateral abdominal wall between the caudal extent of the ribs and the cranial aspect of the pelvis. However, in all extant tetrapods, ventilation of compliant respiratory structures is inevitably linked to their close proximity to rigid skeletal support capable of resisting negative intramural pressures. Consequently, we suggest it more likely that lateral abdominal collapse resistance in birds is provided by the uniquely subhorizontal femur and its associated musculature (Hertel and Campbell, 2007), both of which have been incorporated into the posterior body wall in this region.

By extension, if theropod dinosaurs were to have possessed an endotherm-like circulatory system consistent with an avian style lung air-sac system, then they too were likely to have required voluminous, functional abdominal air-sacs and a supportive ventilatory mechanism capable of preventing paradoxical collapse of these air-sacs during inhalation. In the following pages, we explore this possibility.

MATERIALS AND METHODS

Measurements of Pelvic Area Used to Assess Relative Pelvic Volume in Birds and Other Amniotes

Avian abdominal air-sacs are fused cranially to the dorsal body wall at the oblique septa and extend caudally to the cloaca

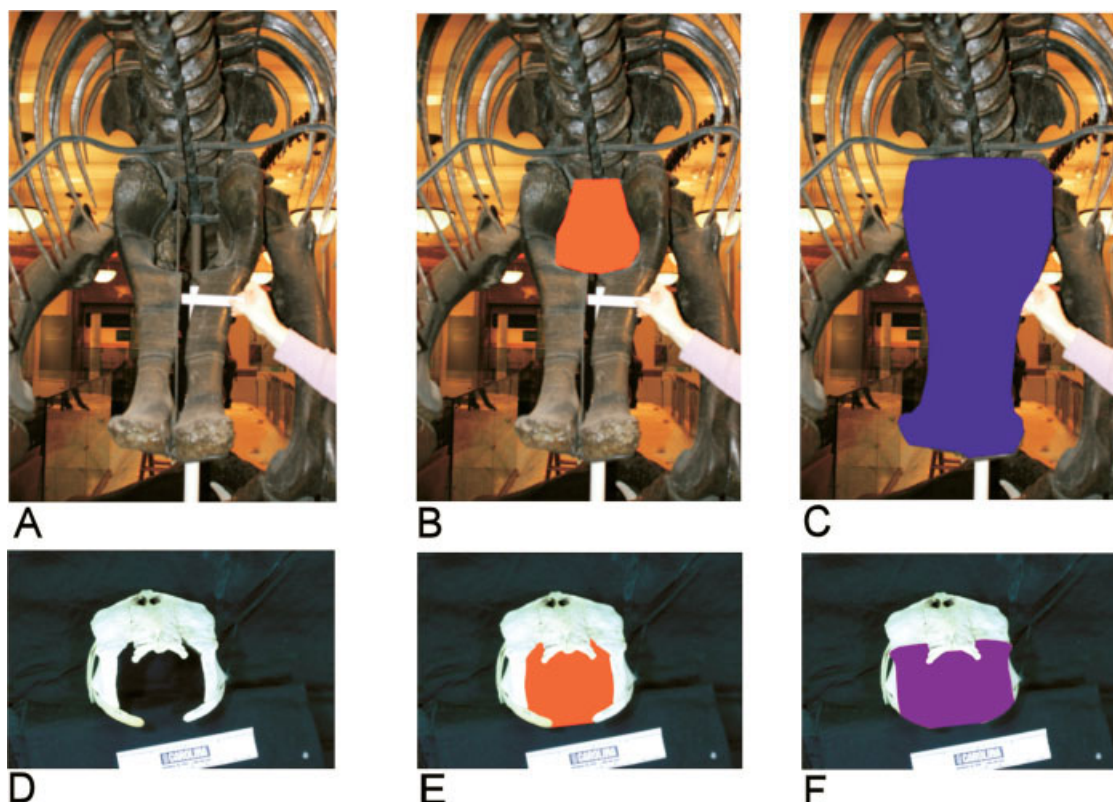


Fig. 6. (A–C) Anterior views of *Allosaurus fragilis* (AMNH 5753). Free pelvic cross sectional area is highlighted in red (B) and total pelvic area is highlighted in blue (C). (D–F) Posterior views of *Melagaris gallopavo* (KU 86024) pelvis. Free pelvic cross sectional area is highlighted in red (E) and total pelvic area is highlighted in blue (F). Measures of free pelvic area as a function of total pelvic area were compared between taxonomic groups.

in most species [exceptions noted for rheas, penguins, and loons (Duncker, 1971)]. They are supported laterally in their course through the pelvis by the synsacrum and unfused pubic rami (Duncker, 1971; Sapp, 2004). Gastral viscera are suspended in the abdominal cavity by the dorsal mesentery and are generally situated between the abdominal air-sacs with most of their mass anterior to the caudal pelvis (Duncker, 1971). In 10 orders of birds employing a wide variety of ecological and locomotor strategies, it has been shown that the synsacral/pubic complex overlaps the length of the abdominal air-sacs by at least 89% in the cranio-caudal plane, often with the fully filled abdominal air-sacs extending posterior to the pelvis itself and always bounded ventrally by the tips of the pubic rami, if not extending further to the ventral margin of the body wall (Duncker, 1971; Sapp, 2004; O'Connor and Claessens, 2005; O'Connor, 2006).

To objectively assess the relative magnitude of free infra-pelvic volume available to accommodate the extensive abdominal air-sacs of modern birds, the internal cross-sectional area of the abdomen beneath the posterior pelvis was calculated (cross-sectional area of pelvic foramen, Fig. 6). Using skeletons of 17 species of modern birds (representing eight families and four orders) the total cross-sectional area of the caudal pelvis (Fig. 6F) and the cross-sectional area of the caudal pelvic foramen were calculated from digital photographs in Adobe Photoshop (Adobe Systems Incorporated) and MVHImageAnalysis software (<http://mvh.sr.unh.edu/index.htm>). The same procedures were then conducted on digital images of skeletal material of 19 species of saurischian dinosaurs, 6 species of modern, nonavian sauropsids and mammals (2 crocodylians, 1 iguana, 1 deer, 1 monkey, 1 cat) and 9 species of early birds (scaled published photographs, published reconstructions of specimens or data collected by the authors; for complete specimen list, see Sup-

porting Information Table 1; the control outgroup of modern, nonavian sauropsids and mammals were selected to include carnivorous “reptiles” and based on availability of skeletal material of fully articulated adult pelvises). In an effort to compare the most restrictive skeletal areas that could support abdominal air-sacs in modern birds to the least restrictive potential infrapelvic skeletal areas available for abdominal air-sac support in other taxa, the pelvic canal was assessed from the posterior aspect in modern birds but from the larger anterior aspect for all dinosaurs, modern, nonavian sauropsids, mammals and early birds (see Fig. 6). Total pelvic area was compared to body mass to confirm it as an acceptable measure of body size.

Furthermore, the pelvises of most modern birds lack pubic symphyses and the full extent of the abdomen (housing digestive viscera) includes spaces which are not surrounded completely by bony pelvic processes. These extra-osseous spaces were not included in our calculation of avian pelvic cross-sectional space because their extent could not be estimated with certainty from skeletal evidence. However, excluding this measure is not likely to influence the data as the abdominal air-sacs extend ventrally to the body wall margin in this region (Duncker, 1971). All extinct taxa examined, and modern crocodylians and modern mammals have pubic symphyses and in these taxa, the symphyses were considered to be the ventral margins of the body cavities beneath the respective pelvises. Measurements from taxa with pubic symphyses indicate not only the potential amount of space available for abdominal air-sacs, but also other abdomino-pelvic viscera (distal digestive tract, urogenital organs and infrapelvic musculature). However, our measures of avian pelvic cross-sectional areas were limited to only the ventral extent of the pubes and thus areas containing largely air-sacs and not digestive viscera.

We also examined pelvic structure, including especially the pelvic apron and pelvic canal, in a number of theropod dinosaurs and early (i.e., nonornithurine) birds.

By comparing avian pelvic cross-sectional area with those in other taxa, we were able to conservatively assess the possibility that the nonavian pelvic canal might have been sufficiently large to accommodate the presence of both gastrointestinal organs and avian style, fully functional abdominal air-sacs.

Measurements for each taxonomic group were compared using simple linear regression analysis, analysis of covariance and pairwise and group comparisons of reduced means where appropriate. All compared groups were assessed for the influence of body size (as indicated by total pelvic area) on pelvic free space using SAS statistical package (SAS Institute Cary, NC). The PROC MIXED procedure was used to conduct an analysis of variance and to make comparisons of SAS LSMEANS. Homogeneity of slopes was demonstrated using CONTRAST statements in the PROC GLM procedure.

RESULTS

Among modern birds, we found no significant difference in free pelvic cross-sectional area between cursorial and volant taxa ($P = 0.99$, $df = 61$, cursorial = $21.55 \text{ cm}^2 \pm 1.86$, volant = $21.59 \text{ cm}^2 \pm 1.40$, pair-wise t -test of LSMEANS). Significantly, modern birds have considerably more free pelvic cross-sectional area than did the dinosaurs measured here [$P < 0.01$, simple linear regression, birds = $(0.63 \pm 0.010)x + (0.63 \pm 1.12)$; dinosaurs = $(0.20 \pm 0.0065)x + (9.12 \pm 9.14)$. Fig. 7]. Furthermore, modern birds have significantly more relative free pelvic cross-sectional area than do modern, nonavian sauropsids and mammals ($df = 69$, $P < 0.0001$, birds = $0.63 \text{ cm}^2 \pm 0.005$, modern, nonavian sauropsids and mammals = $0.49 \text{ cm}^2 \pm 0.016$, pairwise t -test of log transformed LSMEANS; \pm values are mean standard errors.) These data indicate that the presence of enlarged, functional abdominal air-sacs in modern birds is accompanied by expanded abdominal volume to accommodate these vital pulmonary structures.

DISCUSSION

If theropods possessed modern bird-like cardiovascular and respiratory capacities they would almost surely have utilized a modern avian style lung air-sac system, including an extensive system of functional abdominal air-sacs. We believe that three thoraco-abdominal attributes are tightly linked to normal abdominal air-sac function in modern birds, including (1) mechanisms supporting both lateral and ventral ribcage expansion/contraction, (2) expansion of abdominal cross-sectional area to accommodate voluminous abdominal air-sacs, and (3) specialized abdominal skeletal mechanisms to resist paradoxical collapse of abdominal air-sacs during inhalation.

Hillenius and Ruben (2004a) have argued previously that certain osteological features are tightly linked to ventilation of the modern avian lung air-

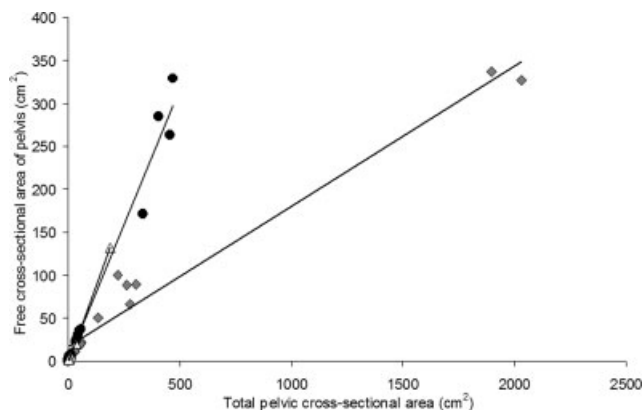


Fig. 7. Free pelvic cross-sectional area as a function of total pelvic cross-sectional area in modern birds, early birds and dinosaurs. Modern birds (Neornithes) have significantly more free pelvic cross-sectional area than all dinosaurs (Dinosauria) measured [$P < 0.01$, simple linear regression; Neornithes = $(0.63 \pm 0.010)x + (0.63 \pm 1.12)$, $r^2 = 0.984$; Dinosauria = $(0.20 \pm 0.0065)x + (9.12 \pm 9.14)$, $r^2 = 0.969$]. Dinosaurian pelvic foramina were significantly smaller than those of modern birds and therefore likely lacked the requisite space capable of supporting modern avian-sized abdominal air-sacs. Early birds (Aves) = $(0.71 \pm 0.0083) - (0.97 \pm 0.529)$, $r^2 = 0.999$. ●, All modern birds (Neornithes) $n = 62$, △, Early Birds (Aves) $n = 9$, ◆, All dinosaurs (Dinosauria) $n = 19$.

sac systems. Specifically, the hinged intracostal joints between vertebral and sternal ribs and the bicondylar articulation between the distal sternal ribs and posterolateral sternum are unique to modern avians and allow sternal movements to generate great changes in intracoelomic pressure (Hillenius and Ruben, 2004a). Significantly, these articulations allow birds with short, but often broad, sterna to generate negative intra-abdominal pressure sufficient to ventilate far placed abdominal air-sacs despite markedly less ventral excursion of the caudal sternum (O'Connor and Claessens, 2005). Ostriches do not differ in their free pelvic area or their abdominal air-sac development (Bezuidenhout et al., 1999) despite their substantially shorter sterna, and it has been suggested that when sterna are unavailable for ventilation, pelvic aspiration may be able to effect the pressure changes required for ventilation (Baumel et al., 1990; Ruben et al., 1997; Ruben et al., 2003). However, cineradiographic evidence of breathing emu while sitting, standing and walking does not show significant pelvic contribution to air-sac ventilation (Claessens, 2004a). Recent evidence has shown that uncinat processes in Canada geese are important to ventilation when sternal movements are restricted during sitting (Codd et al., 2005) and they could also aid ventilation in birds with short sterna. However, not all birds possess uncinat processes and in particular, emus with very short sterna lack them entirely. Rather, we suggest that it is not the

length of the sternum or the presence/absence of uncinata processes that are restrictive or permissive factors in the ability to ventilate abdominal air-sacs but instead the ability to move the sternum and ribs in such a manner that negative intrathoracic pressures are effectively transferred to the compliant abdominal respiratory structures.

Abdominal Air-Sacs

To accommodate large abdominal air-sacs, all modern birds have significantly more pelvic cross-sectional area than do modern, nonavian sauropsids and mammals. Even ostriches, which possess the most limited abdominal air-sacs among those examined, have significantly more free pelvic space than the nonavian sauropsids and mammals examined (including mammalian herbivores and at least one primate all of which have expanded pelvic canals). The larger pelvic foramen of birds is often assumed to be correlated to the size of the egg produced (Romer and Parsons, 1977; Carpenter, 2000), and clearly having wider, open pelvises allow for larger eggs (and embryos). However, in many turtles, eggs are significantly smaller than predicted by the pelvic aperture size constraint (Bowden et al., 2004; Hofmeyr et al., 2005) and there are locomotor and postural factors beyond reproduction that influence avian pelvic dimensions (Naples et al., 2002; Hertel and Campbell, 2007). We suggest that in addition to the previously addressed factors, the enlarged pelvic space of modern birds is, in part, tightly linked to the presence of extensive abdominal air-sacs in these taxa. Additionally, modern birds possess a unique, laterally expanded pelvis (synsacrum) with generally unfused pubes and ischia from which the abdominal air-sacs are suspended (Duncker, 1971; Sapp, 2004). Our measurements of the avian pelvic canal only account for space bounded by pelvic bone as it is our contention that the bony features of the pelvis provide a rigid framework to support the abdominal air-sacs and prevent their inward collapse during negative inhalatory intra-abdominal pressures.

The Avian Femoral Skeleto-Muscular Complex

In modern birds, depending on locomotor mode, there is often a significant dearth of supportive axial skeletal- or pelvic girdle structures between the caudal extent of the rib cage and the cranio-ventral extent of the pubis or ischium (i.e., the “lumbar” region). Large terrestrial birds lack ribs in this area although the rib cage may extend this far caudally in diving and swimming forms (Duncker, 1971; Codd, 2004; Fig. 5). How do these birds avoid collapse of unsupported compliant respiratory structures (e.g., abdominal air-sacs) in this region? We suggest that the subhorizontal

femoral complex of modern (ornithurine) birds provides the requisite resistance and support. During the course of avian evolution, the progressive migration of the long axis of the femur, from vertical in early forms to an almost horizontal position adjacent to the flank, has long been recognized (Gatesy, 1995; Hertel and Campbell, 2007; Fig. 5). Significantly, in modern birds, the subhorizontal femoral/thigh muscle complex is functionally incorporated into the body wall and invested by the trunk integument. This “migration” of the distal femur (probably in response to a cranially displaced center of mass) is coupled with the thigh’s relatively minor contribution to stride generation during cursorial locomotion (replaced by substantial contributions from knee and ankle movements). In kinematic studies of walking guinea fowl, the femur retracted little, only 5–15° compared with 60–80° retraction observed in the vertically oriented femur of walking alligators, while the avian knee moved through a 50–70° arc (Gatesy, 1995). Even during running the femur never passed vertical in birds, achieving a maximal 40° hip extension relative to the vertebral column (Gatesy, 1995, 1999).

Together these femoral features create a lateral, rigid skeleto-muscular framework around the compliant abdominal respiratory structures that not only physically supports air-sacs, but also allows negative pressures to be developed at a distance from the air-sacs and then translated efficiently to the abdomen. In lieu of this arrangement, any unsupported compliant structure of the body would move inward in response to a negative pressure, not outward to effect an increase in volume. Thus, even birds with reduced rib cages but femoral support can still fully ventilate their abdominal air-sacs provided that they have the means by which to generate negative intra-abdominal pressures somewhere in the rigid thoracic frame.

Comparison With Extinct Forms

Specialized articulations of the ribs and sternum allow modern birds to generate negative inhalatory pressures and the compound, rigid skeleto-muscular framework that surrounds posterior respiratory structures acts to prevent inward collapse of the air-sacs during inspiration. Many of these skeletal specializations are not apparent in the earliest birds, including *Archaeopteryx*, confuciusornithine or enantiornithine birds (Hillenius and Ruben, 2004a). Their presence is also questionable in even Early Cretaceous ornithurines but well developed in the Late Cretaceous hesperornithiform birds (Hillenius and Ruben, 2004a). The femur most likely did not attain its subhorizontal position until the Late Cretaceous in ornithurines as indicated by the presence of the antitrochanter, although some enantiornithine birds may have

achieved this femoral orientation (Hertel and Campbell, 2007). Our data indicate that the earliest avian forms (*Archaeopteryx*, confuciusornithine and some enantiornithine birds) may have had pelvic volume similar to ostriches; however, it seems unlikely that they were able to have efficiently prevented abdominal air-sacs from paradoxical collapse due to their short postacetabular ilia and ischia (Naples et al., 2002) and vertical femur. It was not until the appearance of Late Cretaceous ornithurines (e.g., *Ichthyornis*) that the postacetabular ilium expanded, the pubic rami lost midline fusion and the specialized ventilatory features of the sternum and ribs first appeared (Naples et al., 2002; Hillenius and Ruben, 2004a). Perhaps adaptations for long-distance flight (sternal adaptations for increased pectoral muscle mass, change in position of center of mass, adoption of a fusiform body shape) facilitated development and support of abdominal air-sacs and a modern avian flow-through style lung (Ruben, 1991).

Theropods examined in this study uniformly lacked the specialized sternal and costal features of modern birds (Hillenius and Ruben, 2004a). Theropods also exhibited significantly less pelvic cross-sectional space with which to have accommodated abdominal air-sacs similar in development to those in modern birds. In addition, the deep, vertically-oriented lateral body wall of theropods apparently lacked lateral skeletal support for caudally positioned (e.g., abdominal) air-sacs: the theropod "lumbar" rib cage was reduced and the vertical, free-swinging femur almost surely could not have contributed to a rigid lateral abdominal wall (see Fig. 5). Notably, the gastralia (imbriating slender "belly ribs," Fig. 5) do not articulate solidly with other bony elements nor do they significantly invest the lateral body wall (Claessens, 2004b). Thus, in the absence of a bird-like ribcage, a dearth of space to accommodate fully avian sized abdominal air-sacs in the caudal body cavity or a skeletal mechanism to resist their paradoxical collapse, theropods were unlikely to have possessed functional bird-like abdominal air-sacs.

Postcranial Pneumatization: Evidence for an Avian Lung in Theropod Dinosaurs?

It has been previously argued that postcranial pneumatization signals the existence of functional abdominal air-sacs in theropods. Supposedly, these air-sacs could have been ventilated via relatively unmodified rib cages with well developed gastralia or uncinat processes or a combination of both (Carrier and Farmer, 2000a; O'Connor and Claessens, 2005; Tickle et al., 2007; Codd et al., 2008). However, there are several reasons to question these arguments.

Skeletal pneumatization is well documented in pterosaurs, sauropods, some early birds, numerous

theropods and possibly even the Late Triassic archosauriforms *Erythrosuchus* and *Effigia* (Nesbitt and Norell, 2006; O'Connor, 2006). Given so wide a phylogenetic distribution, postcranial pneumatization is likely plesiomorphic for Ornithodira (birds, dinosaurs and pterosaurs) and possibly as ancient as basal Archosauria (O'Connor, 2006). Nevertheless, birds are the only extant animals with postcranial pneumatization and their pneumatization patterns are linked to specific structures of the avian lung air-sac system: anterior thoracic vertebral pneumatization is linked to the fixed parabronchial lung while caudal thoracic (dorsal) and sacral vertebral pneumatization is associated with the presence of abdominal air-sacs (O'Connor and Claessens, 2005). Accordingly, some have concluded that several theropod clades with thoracic and sacral vertebral pneumatization (including Abelisauroidae, Spinosauroidae, Allosauroidae, Ornithimimidae, and Tyrannosauroidae) possessed an avian flow through style lung replete with abdominal air-sacs (O'Connor and Claessens, 2005). However, it must be stressed that postcranial pneumatization is solely a function of the presence of a heterogeneously partitioned pulmonary system (O'Connor, 2006). By itself, vertebral pneumatization need not imply the presence of a ventilation-capable, nonvascularized avian style air-sac but simply posterior air-sacs, a bewildering variety of which are found in many lizards, snakes, turtles (Duncker, 2004; Farmer, 2006) and even the fish *Pantodon* (Farmer, 2006).

Moreover, while postcranial pneumatization is associated with the avian style respiratory system, skeletal pneumatization does not serve a pulmonary function per se: many modern birds with fully developed lung air-sac systems entirely lack postcranial pneumatization (*Apteryx*, and certain diving birds in the families Sphenisciformes, Podicipediformes, Gaviiformes, Pelecaniformes, Charadriiformes) or have reduced postcranial pneumatization (other partially diving forms of Charadriiformes, Procellariiformes, Anseriformes and some terrestrial forms of Gruiformes and Galliformes; O'Connor and Claessens, 2005). Some of these absences or reductions most likely represent a secondary loss in the diving relatives of once flighted forms because although postcranial pneumatization can lighten the skeleton for flight without sacrificing structural strength, it confers unwanted buoyancy during submerged swimming (O'Connor, 2004). It has also been suggested that pneumatization may act to remove metabolically expensive cortical bone from total energetic costs of an animal without reducing trabecular bone volume and therefore strength (O'Connor, 2006; Fajardo et al., 2007).

The presence of ornithodiran pneumatization may simply be linked to skeletal weight reduction. Among nondiving Anseriformes there is a positive relationship between increased body mass and

increased pneumatization (O'Connor, 2004) which may explain postcranial pneumatization in extinct large flying animals (pterosaurs) and very large bodied sauropods (Bühler, 1992). Furthermore, among the Ornithodira in general, the pattern of postcranial pneumatization is variable: some Jurassic and Cretaceous flying forms clearly do not show pneumatic evidence of a parabronchial lung or its requisite caudally positioned air-sacs while other terrestrial (large and small) Jurassic and Cretaceous forms do. Moreover, the presence of abdominal air-sacs as indicated by vertebral pneumatization is questionable in some smaller early theropods (Coelophysoidea) but is known in later and very large forms (Allosauroidea, Spinosauroida, Abelisauroida, Tyrannosauroida). Also, while pneumatic trunk (thoracic and dorsal) and sacral vertebrae are reported in the Dromaeosaurs *Velociraptor*, *Deinonychus*, *Saurornitholestes*, and *Unenlagia* they are absent in the early birds *Archaeopteryx*, *Sapeornis*, *Yixianornis*, and *Asparavis*, the troodontids *Mei* and *Sinovenator* and the Dromaeosaurs *Microraptor* and *Mahakala* (Clarke and Norell, 2002; Hwang et al., 2002; Zhou and Zhang, 2002; Xu et al., 2004; Clarke et al., 2006; O'Connor, 2006; Turner et al., 2007). Accordingly, these data are more indicative of a pattern of skeletal weight reduction, whether in large forms and their descendents or volant species.

Reduction of the skeletal mass serves obvious roles for large sauropods and flying birds and might have benefited bipedal theropods as they shifted their center of mass caudally and ventrad to improve stability during turning (Carrier et al., 2001; Farmer, 2006). Several other features consistent with skeletal mass reorganization for improved turning agility accompany pneumatization in these groups including retroverted pubes, cranial body mass reduction (loss of teeth, increased pneumatization of skull, digit and forelimb reduction) and tail reduction (Carrier et al., 2001).

Interpretation of vertebral pneumatization as a lock-step indicator for the presence of a fully functional avian style lung air-sac system ignores the widespread distribution of posterior, nonvascularized air sacs in many living reptiles and undoubted selective pressures for skeletal mass reduction. Furthermore, as discussed earlier, reconstruction of theropods with modern avian lung air-sac anatomy and function neglects the absence of requisite skeletal morphology necessary for its ventilation in modern forms.

Cuirassal Ventilation in Theropod Dinosaurs

Recently, a means of "cuirassal" ventilation for dromaeosaurid theropods with a presumed early bird lung air-sac system has been proposed by several authors (Carrier and Farmer, 2000a; 2000b;

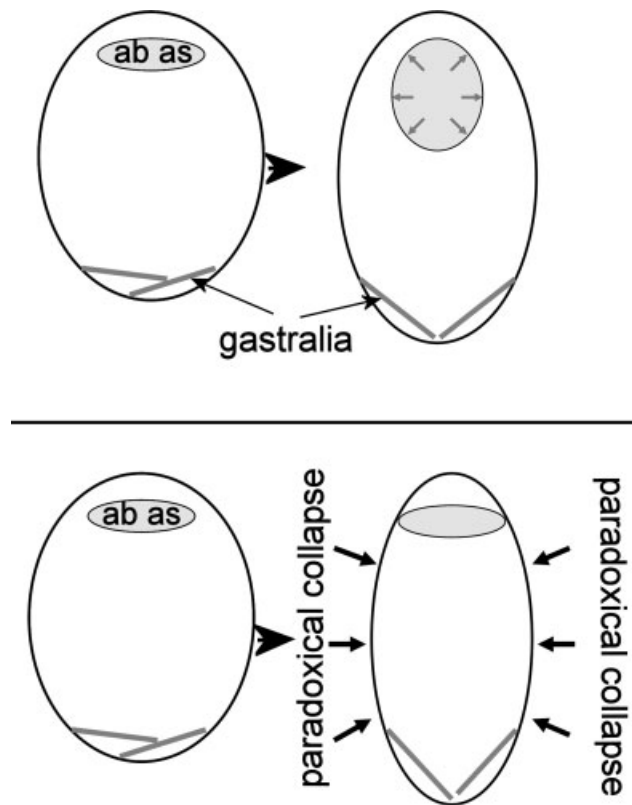


Fig. 8. Cross-sectional cartoon of proposed mechanism for inhalatory expansion of abdominal air-sacs in theropod dinosaurs (as proposed in Carrier and Farmer, 2000a; as proposed in Claessens, 2004b): expansion of abdominal air-sacs (ab as) followed generation of negative pressure by ventral and lateral rotation of the gastralia (upper diagrams). However, without reinforcing mechanisms for the lateral abdominal wall, inward paradoxical movement of the flank would have been a more likely result (below).

Claessens, 2004b; Codd et al., 2008). Supposedly, muscle-driven, horizontal rotation of the gastralia (imbricating slender "belly ribs," Fig. 5) effected ventral and lateral movement of the abdominal cavity and its viscera (Carrier and Farmer, 2000a); expansion of the abdominal cavity followed (see Fig. 8). This mechanism would have relied upon two features of gastralia: their supposed ability to pivot on one another and the action of the ischio-truncus musculature pulling medially on the gastralia. However, numerous examples of broadly fused gastral elements exist in the theropod fossil record including tyrannosaurids, carnosaurids and dromaeosaurs (Lambe, 1917; Bonaparte et al., 1990; Currie and Zhao, 1993; Claessens, 2004b; Grellet-Tinner and Makovicky, 2006).

Romer (1956) suggested that theropod gastralia reinforced the belly wall and supported overlying viscera, their sole function in extant crocodylians and *Sphenodon*. Even if the gastralia were to function as proposed, it is unlikely that negative (expansory) pressure generated by them could

have been efficiently transmitted to the dorsally-situated abdominal air-sacs. Theropod flanks were broadly open (see Fig. 5) and unsupported (e.g., long ribs, gastralia, and pelvic and/or pelvic limb elements were absent) and negative intrabdominal pressures generated by gastralia would likely have dissipated between the source of negative pressure generation and the compliant dorsally-situated air-sacs (see Fig. 8). As noted earlier, inward paradoxical collapse of the lateral belly wall would likely have occurred.

CONCLUSIONS

Many modern "reptiles" possess well defined abdominal air-sacs whose functions have nothing to do with an avian style, air-sac lung. Similarly, although theropod dinosaurs may well have possessed abdominal air-sacs linked to vertebral pneumatization, there is little evidence that they could have functioned in a manner consistent with the modern avian-style air-sac system: abdominal air-sacs in theropods seems to have been far smaller than in modern birds and mechanisms for their ventilation were absent.

We conclude that there are few data supportive of there having been an avian style lung air-sac system in theropods or that these dinosaurs necessarily possessed cardiovascular structure significantly different from that of crocodylians. These conclusions are reinforced by previously cited evidence for crocodylian-like lung ventilation in theropod dinosaurs (Ruben et al., 2003).

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