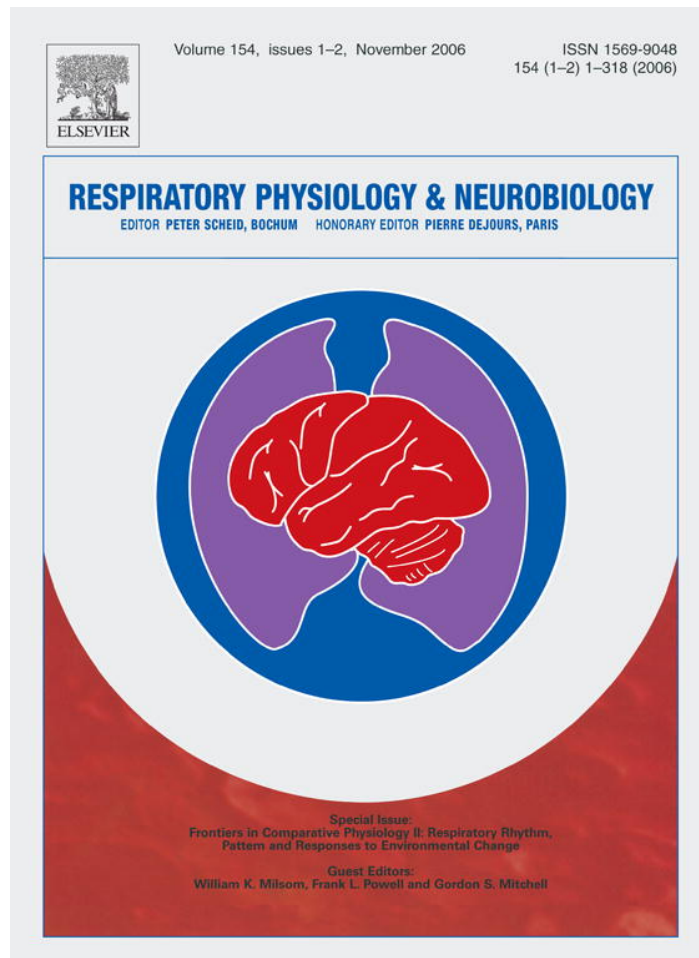


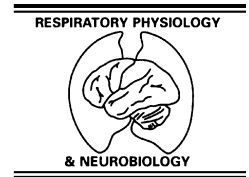
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On the origin of avian air sacs[☆]

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Abstract

For many vertebrates the lung is the largest and lightest organ in the body cavity and for these reasons can greatly affect an organism's shape, density, and its distribution of mass; characters that are important to locomotion. In this paper non-respiratory functions of the lung are considered along with data on the respiratory capacities and gas exchange abilities of birds and crocodylians to infer the evolutionary history of the respiratory systems of dinosaurs, including birds. From a quadrupedal ancestry theropod dinosaurs evolved a bipedal posture. Bipedalism is an impressive balancing act, especially for tall animals with massive heads. During this transition selection for good balance and agility may have helped shape pulmonary morphology. Respiratory adaptations arising for bipedalism are suggested to include a reduction in costal ventilation and the use of cuirassal ventilation with a caudad expansion of the lung into the dorsal abdominal cavity. The evolution of volant animals from bipeds required yet again a major reorganization in body form. With this transition avian air sacs may have been favored because they enhanced balance and agility in flight. Finally, I propose that these hypotheses can be tested by examining the importance of the air sacs to balance and agility in extant animals and that these data will enhance our understanding of the evolution of the respiratory system in archosaurs.

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Keywords: Avian air sacs; Evolution; Dinosaur; Crocodile; Reptile; Bird lungs; Pneumaticity; Agility; Cuirassal breathing; Alligator; Ventilation

1. Introduction

The abilities of birds to sustain flight and to fly in the thin air of high altitude are striking evolutionary accomplishments. The respiratory system is vital to these strenuous feats and thus most research on the form,

function, and adaptive significance of the avian lung has rightly focused on adaptations that enable rapid rates of gas exchange (reviewed in Maina (1989)). The avian respiratory system consists of a compact lung nestled dorsally amongst and immediately ventrad to the thoracic ribs and connected to a number of sacs distributed literally from head to tail throughout the body. While volume changes of the sacs cause air to flow in one direction through the parabronchial part of the lungs where gas exchange occurs, the sacs themselves do not exchange gases with the blood (Magnussen et al., 1979).

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When and how did the avian respiratory system evolve? The roots of both the avian and mammalian lung lie in an ancient reptilian ancestor from which the extant pulmonary architecture is derived. From this ancestral form the lungs evolved in very divergent courses into the alveolar morphology in mammals and the air sac–lung system in birds. What factors influenced the course of this evolution? A number of creative and sometimes provocative articles have addressed the question of the origin of the avian lung (Duncker, 1989; Perry, 1989, 1992; Ruben et al., 1997, 1999; Jones and Ruben, 2001; Paul, 2001; Perry, 2001; Sander and Perry, 2004; O'Connor and Claessens, 2005). Traditionally, the key selective factors shaping the lung have been thought to relate to gas-exchange. However, the differences in the efficacy of the mammalian and avian systems are quite small and probably not a significant determinant in the evolutionary history of the organs (Scheid, 1982). Furthermore, a model of the gas exchange potential of the cardiorespiratory systems of ectothermic reptiles suggests that factors beside gas exchange played critical roles in the evolutionary history of these lungs (Hicks and Farmer, 1998, 1999). In this model key elements of the oxygen transport capacity of extant reptiles were considered in detail, such as the volume of lung devoted to gas exchange (parenchymal volume), the fraction of this volume involved in gas exchange, the barrier to diffusion between the air and capillaries, etc. The results indicate that the lungs of extant reptiles contain all the elements requisite to the rates of gas exchange of many extant endotherms. To expand this gas exchange capacity to the high rates typical of volant forms (birds and bats) would require only a few modifications, primarily an increase in the gas-exchange surface area and some thinning of the barrier to diffusion between air and blood. Adaptations of the avian and mammalian lung that facilitate the rapid exchange of gases between blood and air and therefore support the aerobic demands of sustained flight have been reviewed elsewhere (Maina, 1989). The point I want to make here is that because the alveolar morphology is as capable of gas exchange as the parabronchial lung (see discussion of bats in Maina (1989)), selective factors other than gas-exchange per se may have influenced these divergent evolutionary courses.

For many vertebrates the inflated lung is the largest and lightest organ in the body and in consequence

affects the shape of the body, the manner in which mass is distributed, the density, and the center of mass; these characters are important to locomotion. Recognition of the importance of the lungs to locomotion dates back to the time of Darwin who suggested the original adaptive significance of this structure was its role as a flotation device and that only later in the course of vertebrate evolution did the lung (gas bladder) evolve functions as an accessory to auditory organs and as a gas exchanger (Darwin, 1859). A better understanding of the phylogeny of fishes indicates that lungs originated in osteichthyan fishes some 450 million years or more ago, and that they originally served in gas-exchange (reviewed in Farmer (1999)). However, the importance of the lung to balance, density, and locomotion in fishes is undisputed (Webb, 2002). To understand the evolutionary history and adaptive significance of this organ, its function in both locomotion and in gas-exchange needs to be considered. The relative importance of these functions will of course depend on a variety of ecological, morphological, behavioral, and historical factors that will differ between lineages. For example, amongst Euteleost fishes the importance of the lung to agility and buoyancy predominated over its role in gas-exchange, which has been lost in most groups of these fishes. In the plethodontid salamanders the lungs have been entirely lost and thus serve neither locomotion nor gas-exchange. Numerous features of the respiratory system of manatees (Sirenia) serve locomotion (Rommel and Reynolds, 2000) and below are discussed in detail. In summary, for many vertebrates the lungs serve gas-exchange and locomotion and considering both functions provides a more integrated view of the history of this organ than focusing on gas-exchange alone. This broader perspective may provide a foundation to explain many of the divergences seen amongst vertebrate lineages in pulmonary morphologies and ventilatory mechanics.

Avian ancestry nests within bipedal theropod dinosaurs (Huxley, 1870; Gauthier, 1986). Bipedalism is an impressive balancing act; the taller and more top-heavy the animal the more difficult it is to balance. Evolving bipedalism from a quadrupedal ancestry mandates many changes in the body plan and even greater changes are required to adapt a terrestrial animal to flight. In these new forms the mechanics of ventilation and the size, shape, and position of the lung would have been significant determinants in the center of mass,

body-shape, and the distribution of mass. I hypothesize that many features of the avian respiratory system are a result of selection that facilitated the balancing acts required by bipedalism and flight rather than resulting solely from selection for gas-exchange requirements. For example, I suggest that a dorsal location of the lung served to stabilize terrestrial theropod dinosaurs by moving the center of mass ventrad while an expansion of the lung into the abdominal cavity facilitated turning. Similarly, volant animals are more stable when the center of mass is ventrad to the center of lift. I hypothesize that the use of air sacs for ventilation was favored in Aves because this mechanism facilitated stability and agility in flight. Fore and aft movements of the center of mass impact angle of attack stability; lateral shifts affect roll. Ventilation of cranially and caudally located air sacs with a dorsoventral rocking of the sternum minimizes fore and aft shifts in the center of mass. In distinction to most vertebrates in which costal ventilation shifts the heavy viscera fore and aft, in birds the costal contribution to ventilation can empty and fill the laterally positioned air sacs leaving the center of mass undisturbed. Thus the respiratory system of birds may have undergone selection in ways that facilitated better control of the center of mass.

2. How did dinosaurs breathe?

2.1. Combining functional and historical data: lessons from pneumaticity

Integrating mechanistic with historical data can greatly strengthen inferences regarding the evolutionary history of characters and their adaptive significance (Autumn et al., 2002). It is especially important to include a mechanistic dimension to the study of the evolution of correlated characters to distinguish between spurious and causative correlations. The use of correlations is very common and important in paleontology where the lack of extant animals precludes the direct study of many characters (e.g., ventilation, metabolism, thermoregulation). This point is well illustrated by the study of pneumaticity of the bones of extinct organisms. Pneumaticity is the presence of air-filled cavities within bone. In the head these cavities (sinuses) are formed as epithelial outgrowths (diverticula) of other air-filled cavities, e.g., arising from the nasal or tym-

panic cavity (reviewed in Witmer (1997)). In birds the post-cranial skeleton is pneumatized by diverticula of the air sacs, which are themselves diverticula of the lung (Duncker, 1971). The idea that post-cranial pneumaticity was also present in extinct archosaurs, such as pterosaurs and dinosaurs, dates back to the early 1800s. Pneumaticity was suggested to be an adaptation for flight (pterosaurs) and evidence that the bones received parts of the lungs in the living animal (Von Meyer, 1837; Owen, 1856; reviewed in Britt (1997)). It has also been suggested that because post-cranial pneumaticity in extant birds is correlated with the air sac–lung system and endothermy, that pneumaticity in extinct dinosaurs is therefore evidence of an avian style lung (Seeley, 1870; reviewed in Britt (1997) and O'Connor and Claessens (2005)) and also the elevated metabolic rates of endothermy (O'Connor and Claessens, 2005). However, without integrating functional data into the study, the most that can be inferred from post-cranial pneumaticity in extinct animals is that, as pointed out by Owen (1856), the pneumatized bones received parts of the lung in the living animal. In contrast, inclusion of functional data enables much stronger inferences to be made about the adaptive significance and the history of pneumaticity than hypotheses that are based on correlates.

What is the function of pneumaticity? One of the most robust lines of evidence of the adaptive significance of a trait is the convergent evolution of the character in distantly related lineages. Thus the pneumaticity of the vertebral column of the osteoglossomorph fish *Pantodon* (Fig. 1) by the respiratory gas bladder (Nysten, 1962; Poll and Nysten, 1962; Liem, 1989) is compelling support for the hypothesis that pneumaticity functions to reduce mass and density (Nysten, 1962). *Pantodon* are surface dwellers capable of leaping out of the water and gliding through the air. The reduction of bone density increases the buoyancy of the animal while in the water and the reduction in mass probably serves to facilitate this aerial locomotion (Liem, 1989). The gas-bladders of the flying fish of the family Exocoetidae are reported to have diverticula far back into the haemopoyses of the caudal vertebrae, although it is unclear from this description whether the diverticula penetrate the bones as they do in *Pantodon* (Fowler, 1936). Land tortoises also have dorsal diverticula of the lung that impinge on the sides of the central and rib heads and are associated with lightening the

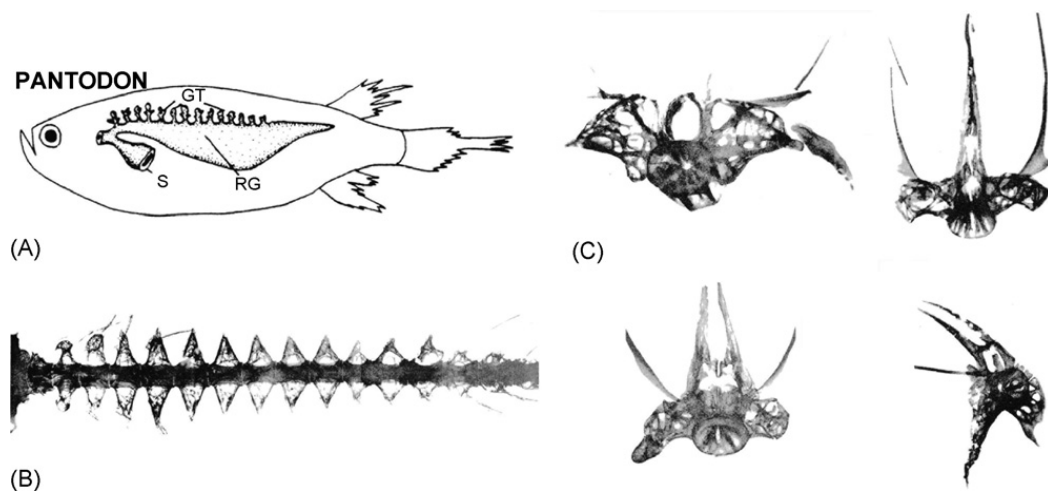


Fig. 1. Pneumaticity in *Pantodon*, an osteoglossomorph fish. (A) Illustration of multiple dorsal diverticula of the gas-bladder into the vertebral column; s = stomach, rg = respiratory gas bladder; gt = diverticula of gas bladder that penetrate the vertebrae (from Liem (1989); reproduced with permission of the author and publisher). (B) Photograph of the vertebral column illustrating the extent of pneumaticity throughout the column (Nysten, 1962). (C) Photograph of individual vertebrae illustrating the degree to which the bone has been hollowed including the centra and transverse processes (Nysten, 1962).

carapace (D.M. Bramble, unpublished observation). The originating spinal nerves are surrounded by these pneumatic diverticula, and Duncker (1989) has suggested that the diverticula increase the flexibility of the carapace (Duncker, 1989). Empirical studies are needed to investigate this interesting suggestion. While the flying ectothermic fish *Pantodon* has acquired pneumaticity of the bones, penguins and many other diving birds have lost or greatly reduced this character, apparently as a mechanism to decrease buoyancy (reviewed in Duncker (2004) and Meister (2005)), but these birds have maintained both the avian lung and their endothermic physiology. Because pneumaticity has no known functional role in ventilation or thermoregulation or metabolic rates, its usefulness as a hard-part correlate for lung structure and metabolism is, unfortunately, questionable. On the other hand, avian pneumaticity is positively correlated with soaring flight and size but negatively correlated with diving (O'Connor, 2004), consistent with the hypothesis that pneumaticity serves the function of reduction in mass and density. Historical data further corroborate this function in the convergent evolution four times of post-cranial pneumaticity (pleurocoelous presacral vertebrae) in (1) an early suchian (*Effigia okeeffeae*), (2) pterosaurs, (3) sauropod dinosaurs, and (4) theropod dinosaurs (Gauthier, 1986; Nesbitt and Norell, 2006). The adaptive advantage of having strong light bones for flying animals, such as

pterosaurs, and for the massive skeletons of sauropods is immediately apparent, but the adaptive advantage of lightening the skeleton is less obvious for the theropod dinosaurs (reviewed in Britt (1997)) and for *Effigia*, yet this is the function for pneumaticity supported by the data. Hypotheses for the importance of pneumaticity to these latter lineages that are consistent with these data from fish and birds are more plausible than those based on correlations with gas-exchange, because pneumaticity has no known function in gas-exchange in extant lineages.

2.2. Cervical pneumaticity reduces rotational inertia, decreases torque, and improves agility

The idea that pneumaticity served the function of reducing mass of theropods is strengthened by the co-evolution of numerous other characters in this lineage with the same apparent adaptive significance. For example the forearms of many theropods (e.g., *Allosaurus*, *Albertosaurus*, *Tyrannosaurus*) were greatly reduced in mass and size (Molnar et al., 1990; Bakker et al., 1992), the hands were lightened by reduction of the number of digits, and the head was lightened in several lineages by the loss of teeth, e.g., ornithomimosaurs, oviraptorosaurs, and several lineages of Aves (Gauthier, 1986; Carrier et al., 2001). The adaptive advantage of these changes has been hypothesized to

be improved agility (Carrier et al., 2001). To turn an animal must overcome rotational inertia, which is a function of mass multiplied by the square of the distance between the mass and the axis of rotation. Thus rotational inertia of a body depends upon the axis about which it is rotating, on the shape of the body as well as the manner in which the mass is distributed (Halliday and Resnick, 1978). The fact that rotational inertia is a function of the distance squared means that small masses if located far from the axis of rotation will make very large contributions to rotational inertia. Non-avian theropod dinosaurs were terrestrial bipeds; their axis of rotation was therefore the pelvic girdle and the mass of the head and the distal tail would make much greater contributions to their rotational inertia than an equivalent mass located close to the pelvic girdle. Thus, to reduce rotational inertia the mass furthest from the axis of rotation would have experienced the most intense selection to be either lost or redistributed closer to the pelvic girdle. This prediction is supported nicely by the fossil record. For example, pneumaticity in theropod dinosaurs is most extensively found in the bones of the head, neck, and anterior thorax (Carrier et al., 2001). The evolution of the strong light bones of the neck produced by pneumaticity and reduction in mass through the loss of teeth have also been proposed to decrease torque of the long necks of theropods (Büller, 1992).

Theropod dinosaurs were not alone in evolving this suite of characters. Although the archosaurian group that gave rise to extant crocodylians (suchians) is generally considered to have had a more conservative body plan than the dinosaurs (Nesbitt and Norell, 2006), a recently prepared specimen of a suchian archosaur, *Effigia okeefeae*, is exceptional in showing a large number of specialized features that are convergent with theropod dinosaurs, particularly the ornithomimids (Nesbitt and Norell, 2006). This suchian may be the exception that proves the rule. It was a biped (reduced arm/leg length ratio) with an elongated pubis and an expanded pubic boot (discussed below), its forearms were greatly reduced in mass and size, the hands were lightened by reduction of the number of digits, and the head was lightened by the loss of teeth. Importantly, it had pleurocoelous cervical vertebrae (pneumaticity). These iterative patterns of morphological evolution in distantly related archosaurs suggest selective forces directed this evolution (Nesbitt and Norell, 2006). This

suite of character changes makes sense from the perspective of selection for increased agility in a bipedal animal.

2.3. Sacral pneumaticity lowers the center of mass and improves balance

In some dinosaurs pneumaticity extends beyond the cervical and thoracic vertebra into the sacral region (abelisauroid, spinosauroid, allosauroid, ornithomimid, tyrannosauroid and maniraptoran clades; O'Connor and Claessens, 2005 and references therein). Pneumaticity of sacral bones indicates that there was selection for lightening the sacral skeleton in this region. This would have been of little importance to rotational inertia about the vertical axis of the pelvic girdle, but it would have served to move the center of mass ventrad, as did the evolution of a large heavy boot on the distal end of the long pubes. Just as the keel of a ship lowers its center of mass and improves its stability, a lower (ventrad) center of mass caused by these changes was undoubtedly a more stable situation for a biped.

2.4. From pectoral to pelvic girdles: the decline of costal and rise of cuirassal breathing

Was the respiratory system affected by the many changes of the trunk entailed in the evolution of an agile biped? The answer to this question is almost certainly yes, if changes in shape entailed decreases in thoracic volumes and if lung volumes and capacities scaled similarly amongst the Archosauria. Data on pulmonary volumes and capacities of extant crocodylians and birds (Table 1 and Fig. 2) suggest these traits have been well conserved amongst the Archosauria. These data indicate that compared to mammals both crocodylians and birds have very large lungs (+air sacs) for their body mass (about 150 ml kg⁻¹); mammals have lungs about a third or quarter of this volume. Pulmonary capacities of birds and alligators are also similar. The avian relationship between tidal volume (ml) and body mass (kg) is $V_T = 20.3M^{1.06}$ (Frappell et al., 2001). Tidal volumes of American alligators fit this avian scaling relationship remarkably well: $V_T = 20.7M^{1.06}$ (Fig. 2). The similarity in lung volumes and tidal volumes is intriguing in and of itself because the underlying physiological reasons for these relationships are not yet clear.

Table 1
Respiratory capacities of extant archosaurs and an outgroup (mammals)

	Specific volume (ml kg ⁻¹)	Functional residual capacity (ml kg ⁻¹)	Vital capacity (ml kg ⁻¹)	Source
Birds (air sac + lung)	100–200			Reviewed in Scheid and Piiper (1989)
Pigeon (air sac + lung)	140 ^a	19	139	Perry (1983)
Crocodile	140 ^a	20	136	Perry (1983)
Mammals (0.020–100 kg)	34–37			Based on 20 terrestrial species with similar weight range to birds (Maina, 1989)
	42–71	14–44	48–68	Based on humans, cats, rats, dogs (Stahl, 1967)
Bats (0.02–0.2 kg)	45–53			Maina (1989)

Birds and crocodiles have very similar functional residual capacities and vital capacities.

^a For pigeon and the crocodile the lung volumes were estimated by the following: lung volume = vital capacity + functional residual capacity – tidal volume. Tidal volumes were computed from scaling relationships (Frappell et al., 2001; Fig. 3). The lungs of crocodiles and the lung + air sacs of birds are very similar and are large compared to mammals. Respiratory capacities of extant archosaurs are also remarkably similar.

Thus a very fruitful area of experimental research may lie in studies designed to illuminate the mechanistic basis of these relationships. Furthermore, additional data are wanted relating lung volume to body mass and studies of pulmonary capacities in a broader range of suchian species (e.g. caiman, more crocodiles, gavials) to shore up these trends. Nevertheless, even if not fully

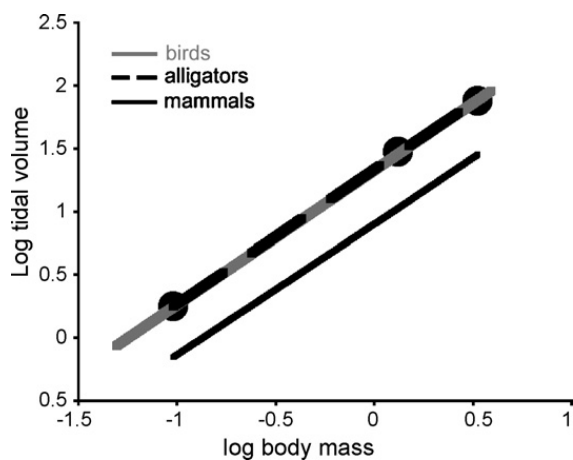


Fig. 2. Scaling of tidal volume (V_T) with body mass (M) for extant archosaurs and mammals. The solid grey line is the avian scaling relationship between tidal volume (ml) and body mass (kg), $V_T = 20.3M^{1.06}$, which is based on data from 50 species of birds (Frappell et al., 2001). The black dots indicate mean tidal volumes measured for American alligators from three different studies. The scaling equation of the alligators is given by $V_T = 20.7M^{1.06}$. The data for the largest mass ($N=4$) are from Hicks and White (1992). The data for the intermediate mass ($N=5$) are from Farmer and Carrier (2000b). The data for smallest mass ($N=10$) are computed from unpublished observations of vital capacities, T.J. Uriona and C.G. Farmer. The solid black line is the mammalian relationship $V_T = 7.7M^{1.04}$ (Stahl, 1967).

understood, these data on lung volumes and pulmonary capacities suggest that amongst the archosaurs phylogenetically bracketed by crocodylians and birds, lung volumes and pulmonary capacities scaled comparably. Certainly there is no basis to assume extinct archosaurs had diminutive respiratory systems compared to the extant taxa.

Was there enough space for the respiratory system within the thorax to house these large lungs and could costal ventilation alone power similar pulmonary capacities in extinct archosaurs? Perhaps not in the bipedal forms. The Ornithodira (Fig. 3) evolved shorter trunks than those in outgroup taxa (reviewed in Padian (1997)). Short trunks reduce the distance between the pelvic and pectoral girdles and thus reduce rotational inertia of the trunk (Carrier et al., 2001). However, if the reduction in the length of the trunk was not fully compensated by increased height and breadth, then this trend reduced thoracic volume. To preserve lung volume, the lungs would have had to expand beyond the bounds of the thorax into the abdominal cavity. Smaller thoraxes also would have reduced the costal contribution to tidal volumes and the retention of pulmonary capacities would have mandated compensation through the active expansion and contraction of the abdominal volume. This hypothesis makes two predictions that can be tested with the fossil record. First, fossil indicators of a reduced thoracic volume (a relatively smaller ribcage) will be mirrored by indicators of an increased abdominal volume, such as elongation of the pubes and elaboration of the cuirassal basket. Second, pneumaticity of the sacral region of the body will be found most often in lineages with a small thorax and large abdomen

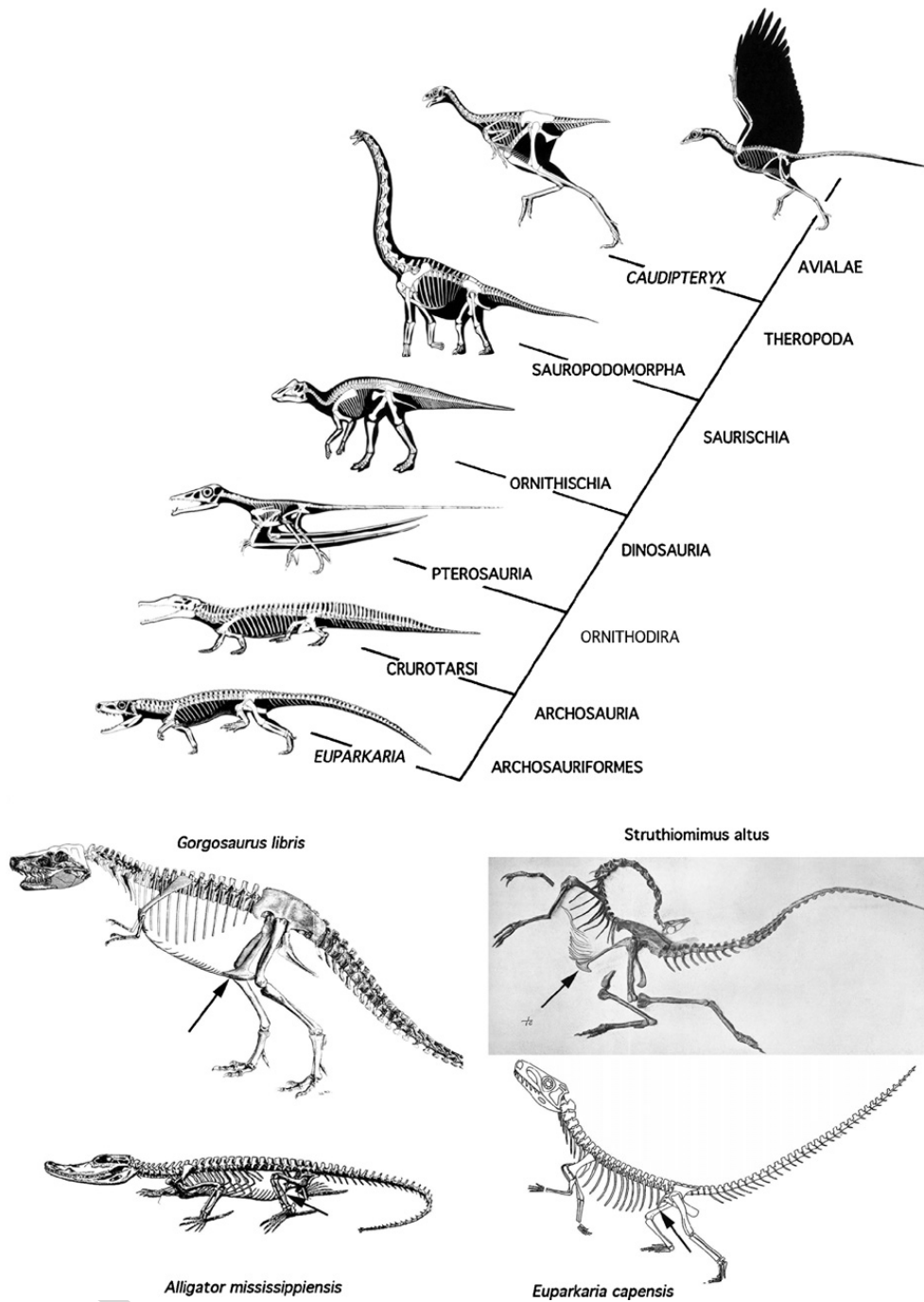


Fig. 3. Relationship of the Ornithodira and outgroup taxa (top panel). The bottom panel illustrates typical body-shape differences between theropods such as *Gorgosaurus* and *Struthiomimus* and non-ornithodiran archosaurs such as *Alligator* and *Euparkaria*. The illustrations were taken from scaled reconstructions. The photograph (*Struthiomimus*) is from a panel mount of a specimen placed approximately as found. These specimens illustrate several of the changes in morphology that accompanied bipedalism in theropods compared to their quadrupedal ancestors that are discussed in the text. Pubic bones are marked with arrows. Compared to the basal archosaurian pattern the theropod pubes are elongated relative to the trunk lengths. The shoulder girdle is reduced in the theropods with small forelimbs and loss of digits (*Gorgosaurus*) and/or through the thinning the glenoid and other bones (*Struthiomimus*). *Euparkaria* was found with gastralia but they were not included in the reconstruction (Ewer, 1965, reproduced with permission of the publisher). *Gorgosaurus* (Lambe, 1917); *Struthiomimus* (Osborn, 1916); *Alligator* (Reese, 1915).



Fig. 4. Photograph of holotype *Ornithomimus edmontonicus* (CMNFV 8632) reproduced courtesy of the Canadian Museum of Nature, Ottawa, Canada. The specimen was not greatly distorted by overburden and the entire set of gastralia is preserved (Sternberg, 1933). These bones meet at the midline in a simple V much as the gastralia of American alligators do. The elements close to the pelvic girdle are more robust than those near the pectoral girdle, suggesting these elements may have experienced more mechanical stress in the living animal than the more cranial elements. The distal ribs are very slender and appear not much more robust than the gastralia. The volume of the thorax appears small compared to the abdomen, as is the case for other specimens of ornithomimids.

(large pubis to trunk length ratio) because caudally located respiratory structures are more likely to have been present. The reader is also referred to Paul (2001, 2002) for an interesting perspective of how changes in trunk design may have affected the positions of air sacs and lungs in archosaurs.

Quantification of changes in thoracic and abdominal volumes in fossils is problematic on a number of accounts. The accuracy of measurements of trunk dimensions can be hampered by distortion of the fossils from overburden, disarticulation of the skeletal elements, incomplete skeletons, omission of information in descriptions of the fossil, and the worldwide geographic distribution of specimens that make direct measurements of a large number by a single group of researchers using a consistent methodology quite difficult. Nevertheless, the case is not hopeless and there are a number of well articulated specimens that do not appear to have been greatly distorted during fossilization and that are either complete or near enough to characterize these changes in body shape. Such a specimen is illustrated in Fig. 4, a photograph of an articulated skeleton of the theropod dinosaur *Ornithomimus*

edmontonicus. The specimen consists of the distal portions of most of the left thoracic ribs and portions from the right as well, a complete set of gastralia, most of the pubes, a complete right forelimb, etc. The dorsal ribs, gastralia, and pubes are preserved very close to their natural positions (Sternberg, 1933). Several characters of this specimen are consistent with the hypothesis of a decrease in reliance on costal ventilation and an increase in reliance on cuirassal ventilation in this lineage. The thoracic ribs are very slender relative to the cuirassal basket, which becomes increasing robust close to the pubes where more mechanical stress would have occurred with cuirassal breathing. Furthermore, the curvature of the ribs and cuirassal basket suggest this animal had a very small thoracic volume relative to its abdominal volume. Other ornithomimids have a similar shape.

To assess the relationship between thoracic and abdominal volumes, I quantified the length of the thoracic vertebral column and the length of the pubis on a number of fossils and one recent taxon (Table 2). I measured these lengths directly on an articulated skeleton of a juvenile American alligator. The rest of the data, however, were culled from the literature and although the measurements will inherently have a lot of variation that reflects measurement inaccuracies rather than real variations in the animals' proportions (e.g., noise), if the signal is large enough, real trends may still be recognized. The length of the thorax was estimated in two ways: If the lengths of the dorsal vertebrae were reported in the literature, then these lengths were simply summed. If this information was not available, then for articulated and nearly complete skeletons, measurements were made on photographs of the specimen. Measurements were also made on illustrations if they had been drawn to scale. These entailed measurement of the length (usually a straight line) through the center of vertebral column from the cranial edge of the first dorsal vertebra to the caudal edge of the last dorsal vertebra. Measurements of the photographs and illustrations were made using calipers that are accurate to 0.01 mm. Pubic length was either taken from the reported values or measured from these same photographs or illustrations. The measurement was the distance from the distal pubis to the cranial edge of the symphysis of the pubis and ilium. If the symphysis was not discernable from the photograph then the pubic length was determined to the center of

Table 2
The ratio of the length of the pubis to the length of the trunk

Non-ornithodirans	Pubis trunk ⁻¹	Source	Non-ornithodirans	Pubis trunk ⁻¹	Source
<i>Alligator mississippiensis</i>	0.3	Personal observation	Megalancosaurus	0.1	Paul (2002)
<i>Euparkaria</i>	0.2	Ewer (1965)	<i>Euparkaria</i>	0.2	Paul (2002)
<i>Terrestrisuchus</i>	0.3	Crush (1984)	<i>Terrestrisuchus</i>	0.2	Paul (2002)
			Postosuchus	0.4	Paul (2002)
			Riojasuchus	0.3	Paul (2002)
Mean ± S.E.	0.27 ± 0.03			0.24 ± 0.05	
Ornithodirans ^a	Pubis trunk ⁻¹	Source	Ornithodirans	Pubis trunk ⁻¹	Source
			Eoraptor	0.4	Paul (2002)
			Herrerasaurus	0.5	Paul (2002)
			Syntarsus	0.4	Paul (2002)
<i>Carnotaurus sastrei</i>	0.7	Bonaparte et al. (1990)	Allosaurus	0.6	Paul (2002)
<i>Gorgosaurus libris</i>	0.6	Lambe (1917)	Gorgosaurus	0.5	Paul (2002)
<i>Compsognathids</i>			Compsognathus	0.4	Paul (2002)
<i>Huaxiagnathus orientalis</i>	0.6	Hwang et al. (2004)			Paul (2002)
<i>Sinosauropterus prima</i>	0.6	Chen et al. (1998)			Paul (2002)
Ornitholestes	0.5	Osborn (1916)	Ornitholestes	0.5	Paul (2002)
<i>Scipionix samniticus</i> (juvenile specimen)	0.4	Del Sasso and Signore (1998)	Scipionix	0.4	Paul (2002)
<i>Struthiomimus altus</i> (no. 5339)	0.9	Osborn (1916)	Gallimimus	0.6	Paul (2002)
			Alxasaurus	0.4	Paul (2002)
<i>Archaeopteryx lithographica</i>	0.6	Wellnhofer (1992)	Archaeopteryx	0.5	Paul (2002)
			Deinonychus	0.6	Paul (2002)
			Caudipteryx	0.7	Paul (2002)
			Oviraptor	0.5	Paul (2002)
<i>Sinornithoides youngi</i>	0.5	Russell and Dong (1993)	Troodont	0.5	Paul (2002)
			Mononykus	0.4	Paul (2002)
			Avimimus	0.6	Paul (2002)
			Confuciusornis	0.5	Paul (2002)
			Cathayornis	0.6	Paul (2002)
			Messelornis	0.5	Paul (2002)
Mean ± S.E.	0.6 ± 0.05			0.5 ± 0.02	

^a This ratio was significantly greater in the ornithodirans ($p < 0.05$ unpaired t -test).

the acetabulum. The ratio of the lengths of the pubis to the thoracic vertebral column was rounded to the nearest tenth. The data were then binned into two groups: Group A composed of archosaurs excluding the Ornithodira, and group B composed of members of the Dinosauria (Fig. 3). The length of the pubes with respect to the dorsal vertebral column is significantly greater in the Ornithodira compared to the outgroup taxa ($p < 0.05$; unpaired t -test; Table 2). Proportions obtained from these measurements made on articulated and well-preserved specimens described in the primary literature are close to those obtained by making the same measurements on illustrations of these or closely related species found in Paul (2002). If these ratios indi-

cate changes in trunk shape, then as the trunk shortened and the thorax became smaller relative to the mass of the animal, the respiratory system would have had to expand caudad or diminished in volume.

If the respiratory system expanded beyond the bounds of the ribs into the abdominal cavity, the ribs would have been incapable of ventilating this portion of the lung (or air sac). Thus to preserve pulmonary capacities and ventilate lung tissue outside the bounds of the ribs these animal would have needed a mechanism to actively expand and contract the abdominal cavity. Lambe (1917) proposed that the rugosities of the gastralia (Fig. 5) of a theropod dinosaur, *Gorgosaurus libris*, indicate that there was considerable play between

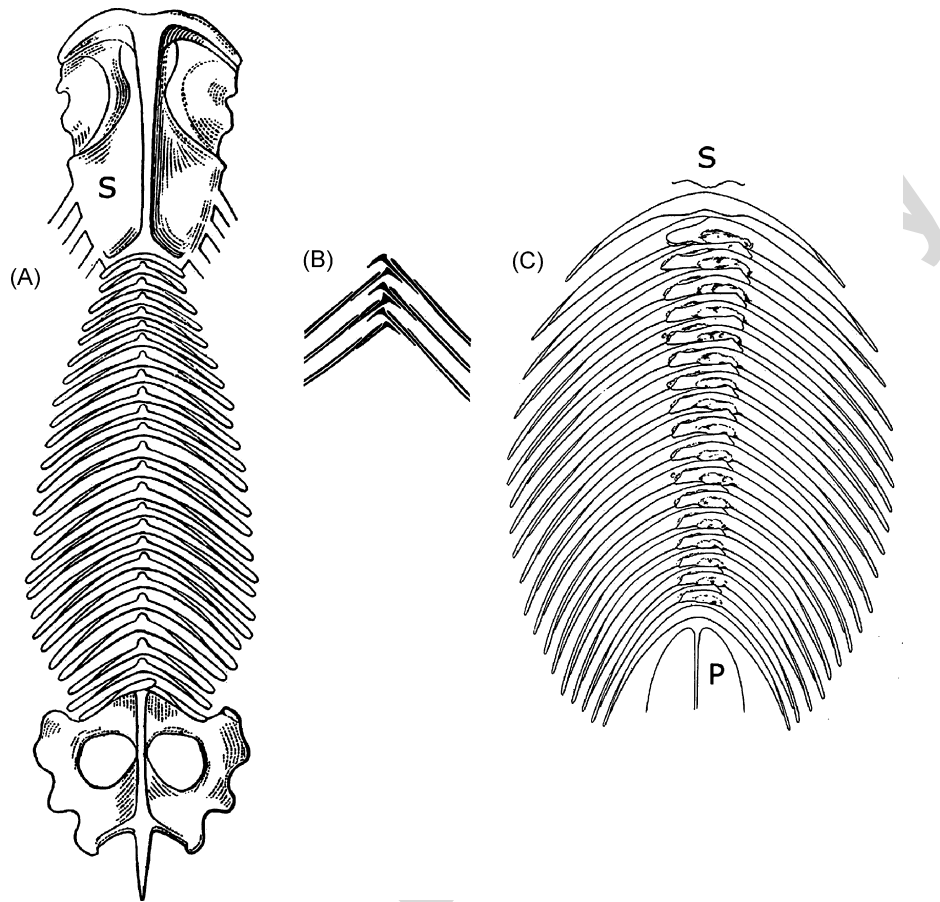


Fig. 5. Ventral view of the cuirassal baskets in several groups of tetrapods illustrating the v-shaped elements that may have served in ventilation. (A) An outgroup to archosaurs, *Sphenodon*, where the elements at the midline are fused (illustration from Lambe (1917)). (B) Gastralia of the basal archosaur *Euparkaria* with goosenecks and a herring bone orientation (based on Ewer (1965)). (C) Complete cuirassal basket of a theropod dinosaur *Gorgosaurus libris* (Lambe, 1917). S = sternum; P = pubes.

the elements and that this flexibility evolved in connection with the animals breathing. Other authors have subsequently also proposed a role in ventilation for gastralia (Perry, 1983; Claessens, 1997; Carrier and Farmer, 2000a).

2.5. Cuirassal breathing—a putative mechanism

Gastralia are primitive for amniotes and are probably homologous with the ventral body armor of basal Paleozoic tetrapods (Romer, 1956; reviewed in Carrier and Farmer (2000a)). In early amniotes gastralia have generally been thought to function for mechanical protection of the ventral body wall. They are present as a series of chevrons composed of a variable number of long slender bones and with the apex of the chevron pointing cranial. The central chevrons in ani-

mals such as *Sphenodon* are composed of fused lateral elements that cross the midline of the belly and have uncinat processes (Fig. 5). In other taxa, for example *Alligator mississippiensis*, the central chevrons are composed of two bones that meet at the midline (Fig. 6) and this is also the case in the theropod *O. edmontonicus* (Sternberg, 1933; Fig. 4). In the basal archosauromorpha, *Euparkaria*, the gastralia have goosenecks that are highly variable in shape and form a herringbone pattern at the ventral midline (Fig. 5). A herringbone pattern is also found in *E. okeefeae* (S.J. Nesbitt, unpublished observation). Were these gastralia actively recruited for ventilation and, if so, what sort of mechanics might have been employed? Insight into these questions has come from studies of the role of the pelvic girdle in ventilation in extant archosaurs.

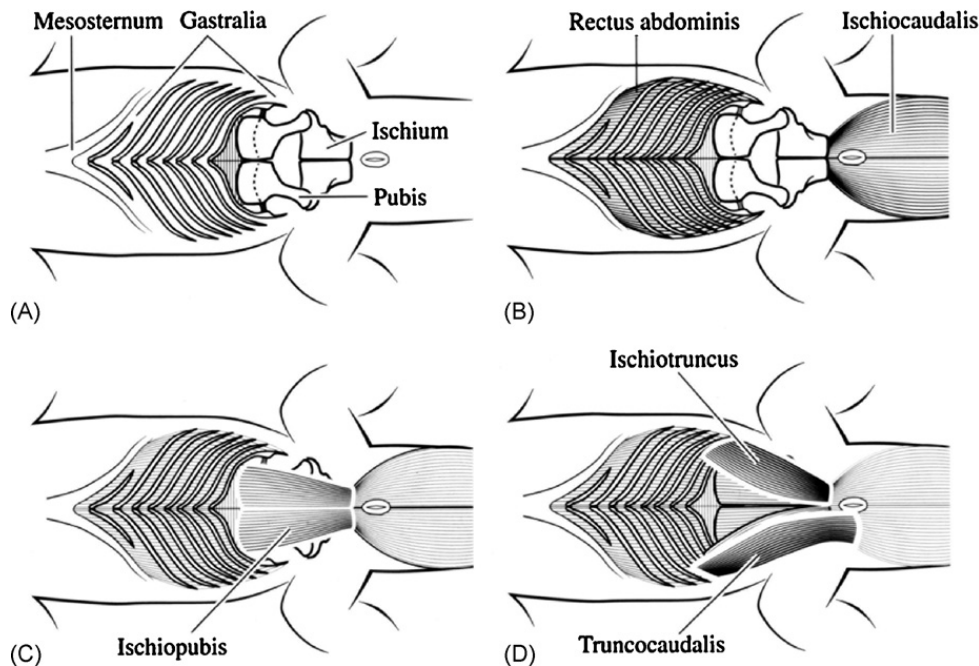


Fig. 6. Ventral view of the musculature and skeletal elements of the American alligator. (A) Skeletal elements showing the gastralia meeting in the midline in a simple V. The symphyses of the pubes and ischia allow mobility. (B) The gastralia are embedded in the rectus abdominis muscles, which are active during exhalation. (C) and (D) show three muscles, the ischiopubis, ischiotruncus, and truncocaudalis, that are active during inspiration and cause the pubes and gastralia to rotate ventrocaudad. From Farmer and Carrier (2000a).

Ventilation in alligators is accomplished by several mechanisms, one entailing the rotation of the gastralia ventrocaudad. Volume changes of the thorax are produced by intercostal muscles that cause the ribs to swing primarily either craniolaterally or caudomedially. This movement should be capable of producing a considerable proportion of the tidal volume because of the elongate body cavity of the animals (Hartzler et al., 2004). However, crocodylians supplement costal inspiration by contraction of the diaphragmaticus muscle (Gans and Clark, 1976) that pulls the liver and lungs primarily caudad. Simultaneously, the volume of the abdomen is expanded by the contraction of the ischiopubic and ischiotruncus muscles that rotate the pubes and gastralia ventrocaudad (Fig. 6) (Farmer and Carrier, 2000). Expiration is produced by the intercostal musculature and by the contraction of the transversus abdominis and the rectus abdominis that push the liver forward and pull the gastralia and pubes dorsocranially (Farmer and Carrier, 2000).

A mechanism for expansion of the cuirassal basket of other archosaurs has been proposed that is based on this anatomy and physiology in the American alligator (Carrier and Farmer, 2000a,b). If archosaurs ancestrally

had an ischiotruncus muscle with the activity pattern of that seen in alligators and a similar orientation, it could have pulled on the gastralia during inspiration, causing the apex of the chevrons to rotate ventrocaudad. This mechanism was proposed to be analogous to expansion of the buccal cavity by the hyoid pulling on the hyobranchials. If such a mechanism existed, the pubes would have served as a fulcrum and their length would have directly impacted the volume of expansion of the abdominal cavity. Thus the longer the pubes, the greater the potential for abdominal volume changes to contribute to pulmonary capacities. The pubes in basal archosaurs (e.g., *Euparkaria*) were slightly elongated compared to outgroup taxa, but not nearly as long as in the theropod dinosaurs (Fig. 3, Table 2). Hence the importance of this putative mechanism for inspiration may have increased in theropods in connection with the body shape changes that accompanied bipedalism.

In alligators the lung occupies the thorax while the liver, stomach and other intestines are positioned in the abdomen dorsad to the gastralia, which are imbedded in the rectus abdominis muscles. Because these viscera are incompressible contraction of the rectus along with the transversus abdominis squeezes the abdominal vis-

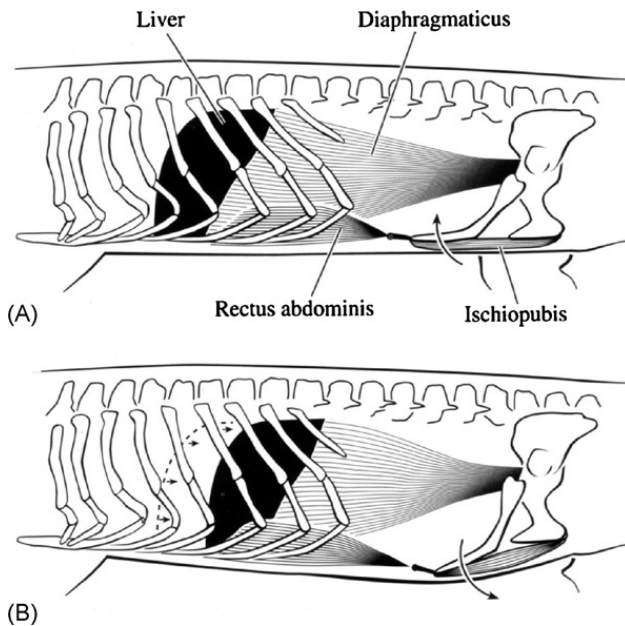


Fig. 7. Lateral view illustrating the mechanisms of ventilation in American alligators. Inspiration is accomplished by the intercostal muscles that rotate the ribs craniolaterally while the diaphragmaticus muscle pulls the liver caudad. The ischiopubis, ischiotruncus, and truncocaudalis pull on the gastralia and pubes to rotate them ventrocaudad and expand the abdominal cavity. Exhalation is accomplished by the rectus abdominis and transversus abdominis (not shown here) that squeeze the viscera craniad to push air out of the lung. Thus the center of mass primarily shifts fore and aft with ventilation. Farmer and Carrier (2000a).

cera causing them to move primarily craniad into the lung during exhalation (Fig. 7). Thus each breath produces primarily a fore and aft shift in center of mass. However, if the lungs were positioned dorsad to the cuirassal basket in theropods, as has been proposed, then cuirassal ventilation would have resulted in the movement of the viscera, and thus the center of mass, in a dorsoventral plane as well. Below the potential impact on locomotion of these movements of center of mass with breathing is discussed.

2.6. The swing of the pendulum: the fall of cuirassal and rise of avian breathing mechanics

Birds are amongst the fastest and most nimble of vertebrates. The evolution of birds entailed a major reorganization in the body plan; many of these changes are elegant solutions to problems of physics imposed by flight. To evolve aerial dexterity from a terrestrial, bipedal ancestry entailed many changes besides

the evolution of wings. For example, mass was lost and/or redistribution closer to the axis of rotation, the wings, by the following mechanisms: (1) reduction of the number of caudal vertebrae (Carrier et al., 2001), (2) in many species the pelvic girdle (synsacrum), caudal vertebrae and hind-limb bones were pneumatized (McLelland, 1989), and (3) the heavy gastrointestinal organs evolved a more craniad location. For example the crop, which is an organ used to store food, evolved and sits craniad to the sternum outside the coelomic cavity (Fig. 8). The liver, one of the heaviest organs of the body evolved a craniad location, closer to the pectoral girdle. All of this reorganization in body form makes sense from the perspective of agile locomotion centered about the wings rather than the pelvis.

The respiratory system was also involved in these changes in trunk design. Although ancestral birds had a cuirassal basket, these bones were reduced and eventually lost in the lineage leading to modern birds (reviewed in Carrier and Farmer (2000a,b)). In extant lineages, the trunk skeleton is a capsule made of rigidly interconnecting and even fused bones (Ruppell, 1975). A large, ventrally located keel provides for the attachment of powerful flight musculature (Figs. 8 and 9). A pendulum like swing of this keel and its attendant ribs in a dorsoventral orientation produces most of the tidal volume; there is very little lateral displacement of the ribs (Zimmer, 1935). Evolutionary biology is preeminently concerned with questions of why. Why was a rocking keel a more favorable mechanism for breathing than rotation of the ribs in a craniolateral and caudo-medial manner?

2.7. Changing directions to understand the adaptive significance of the avian air sacs

Although the avian respiratory system, like that of mammals, is capable of rapid rates of gas exchange, it is clear that there are many alternative ways to evolve such a system (Hicks and Farmer, 1999). Thus factors besides gas exchange may have directed the evolution of the avian air sac system. The idea that pulmonary diverticula serve non-respiratory functions is not new. For example, Duncker (1989) has pointed out that pulmonary diverticula of snakes and lizards may serve the function of enlarging the body for defensive display or play roles in enabling large prey items to be swallowed. The lung and its diverticula can also serve locomotion.

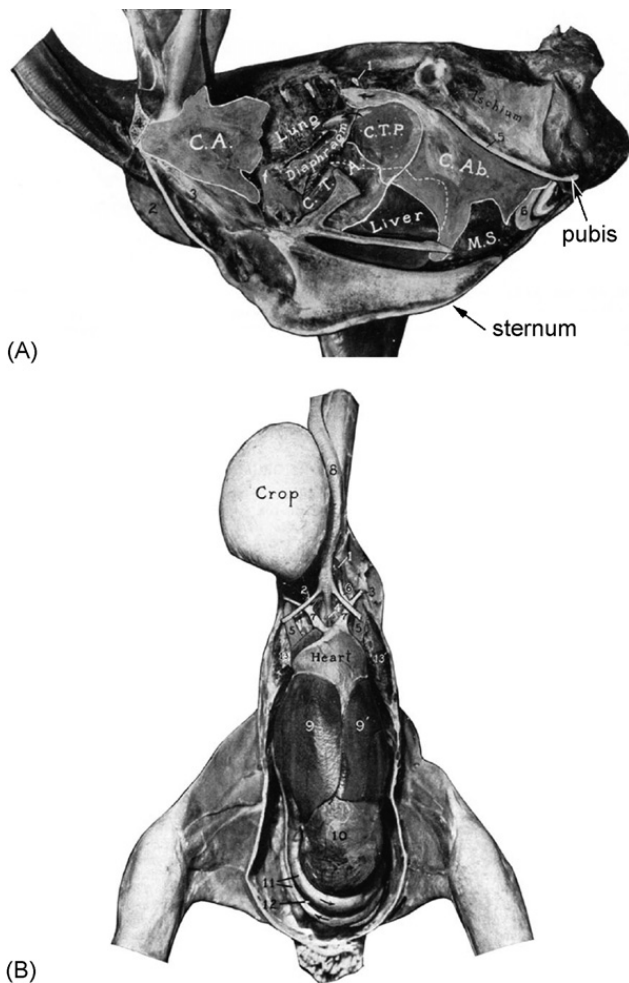


Fig. 8. Anatomy of a chicken. (A) Lateral view showing the position of the lung nestled dorsally amongst the ribs, which can be seen in cross-section (number 1). The lungs are held in this position by a diaphragm. Both the abdominal and cranial air sacs (C) are outlined in white. The crop (2) is exterior to the body cavity and sits on the furcula cranial to the sternum (3). (B) Ventral view illustrating the position of the viscera such as the liver (9) and stomach, which occupy a cranial location compared to the basal condition. M.S. muscular stomach (Sisson and Grossman, 1953).

Terrestrial mammals control their locomotion by pushing against the earth but birds accelerate, decelerate, and many species can turn on a dime without the benefits of an immobile ground upon which to base their movements. Rather than contact with a solid substrate, movement in air involves deflection of airflow, which produces lift and drag. Much of the physics involved with moving through air is similar to movement through water and therefore it is not surprising to find similar adaptations (e.g., airfoils and hydrofoils)

to these physical problems in the design of aquatic and volant organisms (Vogel, 1981). Both lift and drag based maneuvers depend on speed; the slower the speed the less force that is generated through these mechanisms (Alexander, 1990). Thus, stability and maneuverability is most difficult at slow speeds (Alexander, 1990); yet control of pitch, roll, and yaw are essential regardless of the speed the animal is traveling (Dudley, 2002; Webb, 2002). In aquatic animals the lung and its diverticula affect center of mass, center of buoyancy, and the distance between these centers (metacentric height), and appear to be especially important for slower swimmers (Alexander, 1990). This locomotor role of the lungs no doubt underlies much of the variation in lung structure seen amongst aquatic animals. The lung and its diverticula may provide a certain amount of evolutionary flexibility regarding the way mass and air are distributed in the body to facilitate locomotion. For example, in *Luciocephalus*, and all Anabantoid fish, caudal expansions of the gas bladder appear to counteract air that is held in the head during a breath hold (K.F. Liem, unpublished observation). Many other fishes have caudal, cranial, dorsal or ventral diverticula whose functions may well relate to locomotion. Manatees also show specialization of the lungs that appear to serve locomotion.

The organization of the body cavity of manatees is very distinct from all other mammals but markedly similar to birds. In most mammals the body cavity is subdivided at the level of the heart and liver by a musculotendinous diaphragm in a diagonal transverse plane; the thorax (the cranial portion) is bounded by the ribs and contains the lungs (housed in the pleural cavities) and heart (housed in the pericardial cavity) while the abdominal cavity is caudal to the diaphragm and contains most of the other viscera (housed in the peritoneal cavity). Attachment sites for the diaphragm include the sternum, the distal tips of the vertebral ribs, and a small region of the vertebral column. In contrast, manatees have two muscular hemidiaphragms that subdivide the body cavity horizontally nearly its entire length (Fig. 10). Laterally the diaphragms attach to the ribs, extending cranial from the level of the sixth cervical vertebra (affiliated with the first thoracic rib) and caudal to the level of the third post-thoracic vertebra. Medially these diaphragms attach to hypapophyses (bony ventral extensions of the vertebral centra). Nearly the entire volume of the lungs is contained



Fig. 9. Skeleton of a bird and a representative of an outgroup (mammal) illustrating the large sternum that is important for the attachment of flight musculature. Note the small thorax of the mammal, which houses the relatively small lungs (Table 1). Figures from Ruppell (1975).

within the dorsally arched ribs, extending ventrad only to the level of the vertebral bodies. The rest of the rib cage encases not only the heart, but also much of the viscera of the peritoneal cavity (liver, stomach, etc.), which is referred to by Rommel and Reynolds (2000) as the intrathoracic abdominal cavity (Fig. 10). Birds have convergently evolved dorsally located lungs that are supported ventrally by a musculotendinous diaphragm, known as the horizontal septum, that attaches laterally to the ribs and medially to hypapophyses (Duncker, 1971). Other than birds and manatees, I know of no examples of this striking convergent evolution amongst tetrapods. In both birds and manatees the diaphragm is composed primarily of an aponeurosis but has a skirt of muscle (*M. costopulmonalis* and *M. sternopulmonalis* in birds, *pars muscularis* in manatees). In birds the muscular fibers extend about a third of the width of the septum in its middle part (Duncker, 1971); in manatees the fibers extend about a quarter of the transverse extent of the hemidiaphragm (Rommel and Reynolds, 2000). The ostia to the avian air sacs, particularly the posterior thoracic and abdominal air sacs, are surrounded

by the *M. costopulmonales*. Furthermore, in birds as in manatees the liver, stomach, and other peritoneal contents are located cranially, in many species within the bounds of the ribs and sternum, within an intrathoracic abdominal cavity. The reorganization of the viscera, the specialized lungs, and the hemidiaphragms of manatees appear to enable the animals to distribute air within the lungs to affect aspects of their locomotion such as roll and pitch (Rommel and Reynolds, 2000). The extremely dorsal location of the lungs places the center of mass cranioventrad compared to where it would be if the coelomic cavity were partitioned obliquely like it is in other mammals. This organization apparently provides stability. The similarity in the organization of the viscera of birds raises the question of the importance of the dorsal location of the avian lung and its diverticula to balance and stability. In aquatic vertebrates the buoyancy of the lung and its diverticula affect balance and locomotion but how could the respiratory system affect balance and locomotion of volant birds?

Changes in center of mass can greatly affect flight and are not only relevant to agility but also to glid-

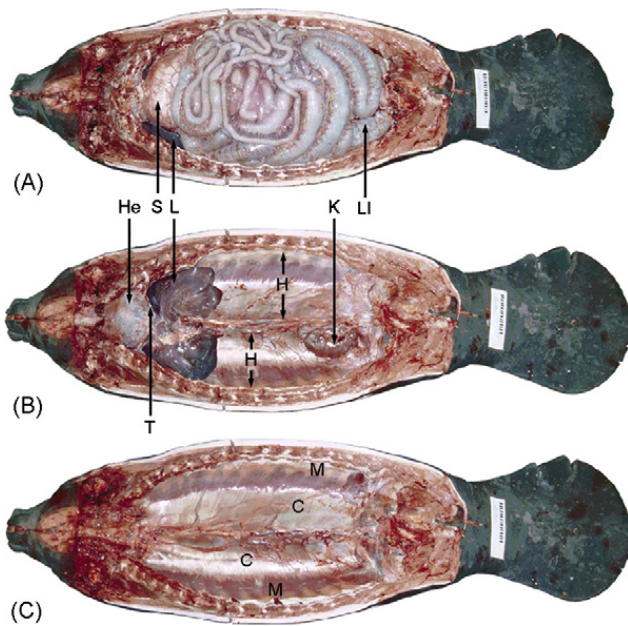


Fig. 10. Photographs of ventral views of a manatee (from Rommel and Reynolds (2000)) illustrating adaptations in the lungs and diaphragms serving posture and locomotion. The basal mammalian condition where the diaphragm separates a cranial thorax from a ventrad abdomen has been lost. The lungs have evolved an extremely dorsal location and extend caudad nearly the full length of the coelomic cavity. The liver and other viscera have shifted cranial. The diaphragm has evolved into two hemidiaphragms that appear to be able to modulate independently the volume of air in the right and left sides of the lung to control roll. (A) Ventral view after removal of the skin, fat and musculature. (B) Photograph after removal of the gastrointestinal tract. (C) Photograph after removal of the heart, liver, and kidney. The two central tendons (C) of the hemidiaphragms attach medially to the hypapophyses. Large intestine (LI), stomach (S), liver (L), heart (He), hemidiaphragms (H), right kidney (K), transverse septum (T).

ing and soaring. For example, a person hanging in a harness at the center of mass of a hang glider can steer it simply by a slight change in position of his or her body (center of mass). Movement of the center of mass cranial decreases pitch and vice versa while a shift to the right or left causes a turn to the right or left. Birds are built a lot like high-wing monoplanes; the body hangs from the wings like a pendulum (Ruppell, 1975). Birds have achieved great stability in flight; changes in speed or direction of the wind do not deflect gliding and soaring birds from their course unless the gust is very strong. This stability is accomplished through the tilt of the wings, but it is not beyond reason to sug-

gest the air sacs facilitate it. Breathing in vertebrates affects the center of mass of the body by the displacement of bones, muscles, and viscera. As previously mentioned, in crocodiles and most mammals inspiration moves the viscera caudoventrad, while expiration moves the mass of the heavy viscera craniodorsad. Thus the center of mass moves primarily in a fore and aft orientation (Farmer, personal observation). In contrast in birds inspiration and expiration increase and decrease respectively the volume of air in the anterior and posterior air sacs fairly similarly (Scheid and Piiper, 1989) and this occurs primarily by the dorso-ventral rocking of the sternum and a smaller contribution from cranio-lateral and caudomedial movements of the ribs (Zimmer, 1935). The lateral and medial movements of ribs would tend to fill and empty the lateral air sacs rather than shift the liver and other viscera. Thus most of the changes in center of mass appear to occur in the dorso-ventral plane with the rocking of the sternum rather than fore and aft or laterally and medially. Breathing in this way would not affect pitch or roll and would facilitate stability.

Alternately, if some air sacs could be preferentially inflated more than others the center of mass could be shifted by displacement of the viscera and muscles and thus have effects on pitch, roll and yaw. For example contraction of the *M. costopulmonales* (also known as the costoseptal muscles) theoretically could alter resistance to flow through the ostia of the air sacs where they pierce the diaphragm (horizontal septum) and thus alter flow to and from the air sacs. It is known that these muscle contract during exhalation, perhaps to prevent narrowing of the ostia or distortion of the lung during breathing (King and McLelland, 1975; Fedde, 1987). However, these muscles appear to be somewhat overbuilt for these purposes alone, it is estimated they generate 300 times more force than is required to prevent lung distortion during quiet breathing (Fedde, 1987). During flight, asymmetrical contractions of these robust muscles could alter airflow and therefore the volumes of the sacs and in this way change center of mass. To my knowledge, these putative locomotor effects of the avian air sacs have never been investigated.

The hypothesis that the system of air sacs that evolved in archosaurs was in response to selection for improved balance and agility is testable in extant animals. There are approximately 9000 species of birds

with diverse lifestyles, modes of locomotion, and body forms. Furthermore, great variation exists in the relative sizes, numbers, and orientations of the air sacs within the thoraco-abdominal cavity (Duncker, 1971; McLelland, 1989). For example, while storks have 11 sacs the domestic turkey has but 7 (King and McLelland, 1975). In some birds the caudal thoracic air sac is the largest (e.g., hummingbirds) while in other birds the abdominal air sac is most capacious (King and McLelland, 1975). The hypothesis that the air sacs serve locomotion is corroborated if this variation makes sense with respect to balance and agility. For example, if improved agility in flying birds by the reduction in mass in the caudal body was a determinant in the evolution of abdominal air sacs, then abdominal air sacs should be larger in agile flyers than they are in flightless forms (e.g., ratites; penguins). Agile runners would be expected to have redistributed the weight from the pectoral girdle toward the pelvic girdle, providing another reason to have a large group of cranial sacs but relatively small abdominal sacs. Another approach to testing these ideas is to experimentally manipulate the air sacs directly (occlude or otherwise impair) and study the consequences of the manipulations on balance and movement.

3. Summary

Most research on the form, function, adaptive significance, and evolutionary history of the avian respiratory system has focused on gas-exchange. However, the differences in the efficacy of the mammalian and avian respiratory systems are quite small and probably not a significant determinant in the evolutionary history of the organs (Scheid, 1982). In this manuscript I have hypothesized that the evolution of bipedal posture of dinosaurs may have initiated selection for a caudal expansion of the respiratory system from the thoracic into the dorsal abdominal cavity to facilitate balance and agility. Pneumatization of the sacrum and vertebral column lowered the center of mass and improved stability whereas a reduction in costal ventilation and an increase in cuirassal ventilation improved agility. Volent theropods may have experienced selection for diverticula of the lungs (air sacs) that facilitated control of the pitch, roll, and yaw so important in this form of locomotion.

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