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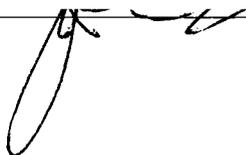
Methea Sapp for the degree of Masters of Science in Zoology presented on

Defense Date. August 24th, 2004

Title: Dinosaur Lung Structure and Ventilation of the Abdominal Air Sacs in Birds.

Redacted for Privacy

Abstract approved:



John A. Ruben

The purpose of this study was to identify any osteological features which might prevent paradoxical movement (=lateral collapse) of the abdominal air sacs in birds during inhalation. A combination of 26 fresh and frozen adult bird carcasses representing 10 avian orders were procured from local sources. Dissections of each specimen first entailed the inflation of the respiratory system via a tracheal tube. The trachea was then sealed off to prevent deflation of the air sacs. Next, the abdominal and thoracic cavities were carefully dissected to expose the inflated air sacs. Using a set of Whitworth electronic digital calipers, a series of two measurements were taken on each carcass: 1. from the posterior sternal tip to the posterior end of the abdominal air sacs, and 2. from the posterior sternal tip to the tip of the pubic bone. Results indicated a strong correlation between the post-sternal length and position of the abdominal air sacs and the post-sternal extension of the pubic bones, such that lateral support of the abdominal air sacs was provided by the pubic bones. These data suggest that during inhalation the pubic bones probably serve to prevent the lateral collapse of these air sacs. The pubic bones of theropod dinosaurs, and even *Archaeopteryx*, were vertically orientated and distally fused. Therefore, it is unlikely that these taxa ventilated a set of abdominal air sacs and where unlikely to have possessed an avian lung-air sac system.

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Dinosaur Lung Structure and Ventilation of the Abdominal Air Sacs in Birds

by
Methea Sapp

A THESIS

submitted to

Oregon State University

In partial fulfillment of
the requirement for the
degree of

Master of Science

Presented August 24th, 2004
Commencement June 2005

Master of Science thesis of Methea Sapp presented on August 24th, 2004

APPROVED,

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Major Professor, representing Zoology

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Chair of the Department of Zoology

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Dean of the Graduate School

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Methea Sapp, Author

ACKNOWLEDGEMENTS

I thank my advisor, John Ruben for challenging me to pursue this body of work. I also wish to thank the members of my committee, Art Boucot, George Poinar, and Mark Harmon for their time and expertise. I am also deeply indebted to both Amy Harwell and Devon Quick for the collegiate spirit with which they so freely gave me both their time and resources. Jaap Hillenius and Michael Cassanego also freely gave their time and expertise with numerous edits and suggestions for improvement. Frank Nelson also has my thanks for his continuous encouragement during the writing process. I am also thankful to Bob Mason for his assistance and support during the long process of securing salvage permits. Many other individuals contributed both their time, expertise and resources in an effort to make this thesis a success, they are; Jim Glick of Backacres Farm, and Fritz Gottfried of Hawthorn Emu Ranch, both of whom donated Emu carcasses, Chintimini Wildlife Rescue for the donation of numerous avian wildlife specimens, and Oregon State University Poultry Barns for their donation of poultry carcasses. Finally I would like to extend my gratitude to Brett Gartrell of Massey University for the kiwi CT scans and to Judy and Joe Passentino for the tinamou specimen.

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DEDICATION

To Mom, Dad, Lysandra, and John C., who sustain me with their everlasting love and support,
and to the late Dr. Howard Towner who ignited my passion for birds.

DINOSAUR LUNG STRUCTURE AND VENTILATION OF THE ABDOMINAL AIR SACS IN BIRDS

INTRODUCTION

Birds are supposedly derived directly from the theropod dinosaurs. This current dogma originated in the mid-1970's with Ostrom's descriptions of the similarities between *Deinonychus* and *Archaeopteryx* (Ostrom 1976) and has since progressed to volumes of works not only supporting the theropod-bird lineage, (Currie 1985, Novas & Puerta 1998, Forster et al. 1998, Xu et al. 1999, Gauthier 1986, Norell et al. 2001, Prum 2002, Padian and Chiappe 1998), but in fact claiming that birds *are* dinosaurs (Dingus and Rowe 1998; Paul 1988, 2002).

There are three principle adaptations which define the general anatomical plan of modern birds. These include skeletal rigidity, skeletal reduction, and redistribution of mass (Proctor and Lynch 1993). Other attributes of modern Aves include, but are not limited to, the presence of a furcula, feathers, long forearms in which the ulna and third metacarpal are bowed, fused carpometacarpus, laterally flexing wrists, pneumaticized bones, retroverted pubis, a reversed first toe called the hallux, and the synsacrum. Theropods also possessed some of these attributes. For example, the small dromaeosaurid, *Deinonychus*, possessed elongate forearms, bowed ulna and metacarpal, and the semilunate carpal, all of which are essential components of the avian wing (Dingus and Rowe 1998). Furthermore, comparative analyses of *Velociraptor*, *Compsognathus*, *Coelurus*, *Microvenator*, and *Struthiomimus* with *Archaeopteryx* have revealed a considerable number of supposed synapomorphies between the theropods and primitive bird (Ostrom 1976).

Proponents of the theropod ancestry of birds have recognized that osteological features alone do not define a bird. Thus, based on a supposedly close theropod-bird relationship, many also assume that theropods possessed a "high performance," avian-like lung-air sac

respiratory system and, therefore, might have been endothermic (Paul 1988; 2000, Claussens 1998, Dingus and Rowe 1998). However, phylogenetically-based interpretation of paleoanatomy has often proven to be broadly misguided and frequently incorrect (Ruben, et al., 2003). Clearly, *a priori*, cladistically-based assumptions regarding an avian-like structure for theropod lungs should be regarded cautiously. Rather, a more powerful argument for bird-like lungs in dinosaurs must necessarily be based on theropods having possessed specialized skeletal attributes which are also present in living birds and which are essential to the function of the avian air sac lung. Alternately, the absence of such skeletal specializations in dinosaurs might serve to falsify assumptions that theropod dinosaurs possessed avian-style lungs.

Birds are unique among all extant air-breathing vertebrates in that the avian lung is ventilated both continuously and unidirectionally, so that air flows *ad infinitum* through the highly compartmentalized parenchyma and air sacs (Figure 1). The vascularized region of the lung (= parenchyma), in combination with a total of nine air sacs (interclavicular and the paired cervical, anterior thoracic, posterior thoracic, and abdominal) occupies 20% of the total body volume in birds. This volume is three to five times greater than in mammals and twice that in reptiles (Maina, 2002). The unidirectional air flow pattern of the avian lung allows for varying PO_2 and PCO_2 within the air sacs. Since they receive gas from the parabronchi, the cranial air sacs, (cervical, and interclavicular) contain relatively high PCO_2 levels, and low PO_2 . In contrast, the caudal air sacs (posterior thoracic, and abdominal sacs) receive a combination of re-inhaled and fresh air which elevates their PO_2 and lowers their PCO_2 . Upon exhalation it is this O_2 rich volume of air that exits the caudal air sacs to ventilate the parabronchi (Powell, 2000). It has long been recognized that the flow-through avian lung cannot fully function in the absence of well-developed abdominal air sacs (Brackenbury 1990).

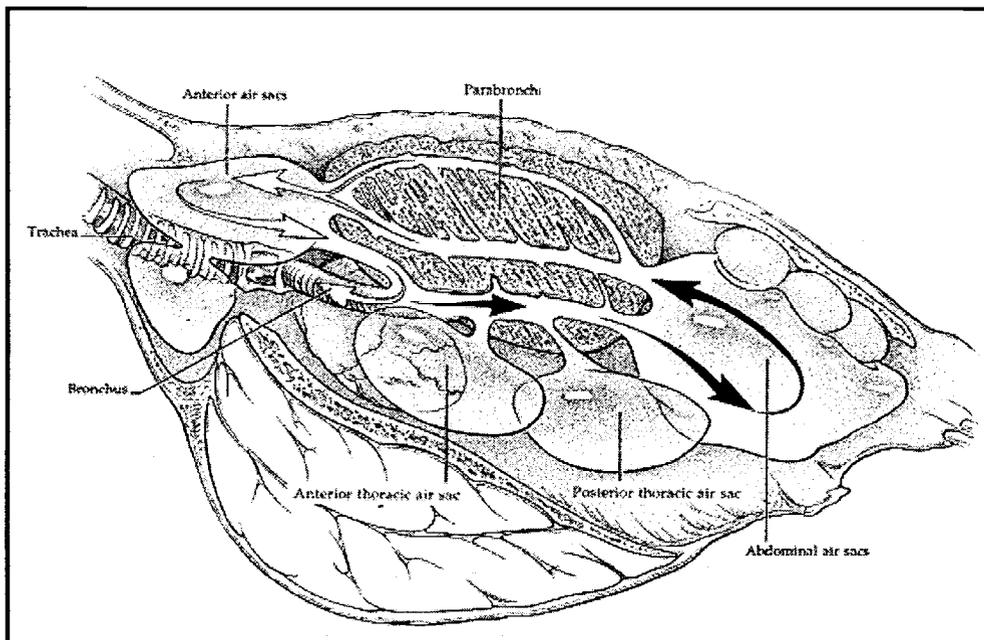


Figure1: The avian respiratory system. Arrows indicate the pathway of a single breath of air. The first inhalation (posteriorly directed black arrows), pulls air past the lung and into the abdominal air sacs. Upon the first exhalation (anteriorly directed black arrow), the air is pushed from the abdominal air sacs into the parabronchi. Upon the second inhalation (anteriorly directed white arrow), air is pulled from the lungs and into the anterior air sacs. Finally, the second exhalation (last two white arrows), pushes air out of the anterior air sacs and into the trachea. It is important to note that during the two-part respiratory cycle, the thoracic volume is increasing and decreasing as a result of skeletal movements (adapted from Proctor and Lynch 1993).

Ventilation of the avian lung/air sac system results from a series of changes in the functional position of the thoracic skeleton during inspiration and expiration (Figure 2). During inspiration the sternum is rotated both cranially and ventrally while the thoraco-abdominal cavity and the sternal ribs are expanded laterally via cranial movement of the vertebral ribs. This skeletal shift increases the volume of the thoracic and abdominal cavities and creates negative internal pressure which results in filling of the respiratory system.

However, under conditions of negative thoracic and abdominal pressures, any unsupported, soft internal structures not held in place or maintained in an open

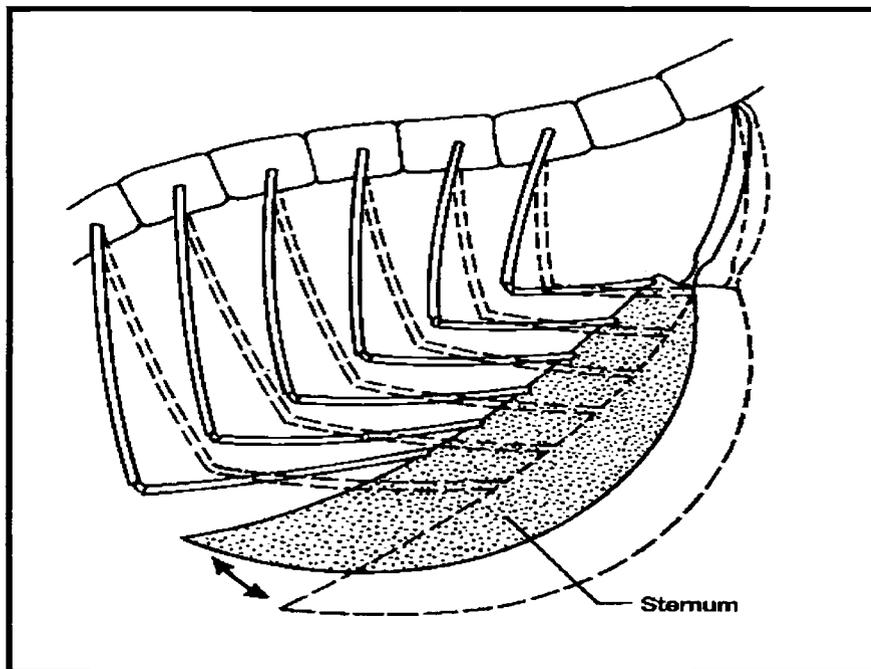


Figure 2: Avian thoracic skeletal changes during respiration. Dashed lines indicate skeletal position during inhalation; while the solid lines depict skeletal orientation during exhalation. These skeletal shifts change both thoracic and abdominal pressures and are essential to avian respiration (adapted from Kardong 2002).

position, (e.g., the air sacs) are subject to shift and/or collapse. This phenomenon, termed “paradoxical movement,” is of particular significance, especially as it pertains to the voluminous abdominal air sacs. These are paired, dorsally situated “air bladders” which are located in the abdominal cavity, largely posterior to the costal skeleton, which is well suited only to prevent paradoxical movements of the clavicular and thoracic air sacs. Curiously, even though abdominal air sacs are essential components of the avian lung, there are no previously described osteological features linked to their skeletal support during avian lung ventilation.

I investigated whether there is an unrecognized combination of skeletal attributes that prevent paradoxical inhalatory movements of the abdominal air sacs in birds. More specifically, I hypothesize that during inhalation, specialized pelvic skeletal elements,

especially the synsacrum and the fully retroverted and unfused pubic bones, act in concert to stabilize these air sacs and prevent their collapse. Abdominal air sacs are located in close proximity to these axial skeletal structures and might reasonably be expected to derive ventilatory support from them. Furthermore, if my hypothesis is correct, the presence or absence of similar skeletal attributes in theropod dinosaurs might provide evidence for, or against, the former existence of abdominal air sacs in theropods and, by extension, the presence of an avian-style lung air sac system in those animals.

MATERIALS AND METHODS

I investigated (via simple dissection) the structure and placement of abdominal air sacs and their closely associated axial skeletal elements (i.e., synsacrum, and pubic bones) in a combination of 26 fresh and frozen adult bird carcasses from 10 distinct avian orders. These included: Anseriformes: Northern Shoveler, Green-winged Teal; Passeriformes: Stellers Jay, Barn Swallow, American Robin; Columbiformes: Rock Dove; Falconiformes: Sharp-shinned Hawk, Merlin, Red-tailed Hawk, American Kestrel; Strigiformes: Western Screech Owl, Barn Owl, Great Horned Owl; Tinamiformes: Chilean Tinamou; Struthioniformes: Emu; Picciformes: Sapsucker; Pelicaniformes: Double-crested Cormorant, Brown Pelican; Galliformes: domestic Chicken.

All non-domesticated specimens were donated from Chintimini Wildlife Rescue Center and registered under Federal and State Salvage permits. Poultry were donated by Oregon State University's Department of Animal Sciences; Emu specimens came from Backacres Emu Ranch of Olympia, Washington and Hawthorn Emu Ranch in Tacoma, Washington.

To insure anatomical accuracy, no bird which had suffered thoracic or abdominal trauma was included in this study. All dissections were performed from the ventral side with birds prone (Figure 3). Abdominal air sacs in dead specimens are inevitably collapsed with little indication of their true anatomy and function. Therefore, for these studies it was necessary to artificially inflate the respiratory system to accurately define its true anatomical relationship to the axial skeleton. To facilitate inflation of the respiratory system, an incision was made in the lower trachea. A section of plastic tubing was then fitted to closely match the diameter of each specimen's trachea; this was then inserted into the tracheal slit. The respiratory system was then fully inflated by gently blowing into the tube; this was subsequently sealed using a pair of forceps. To reduce the chance of

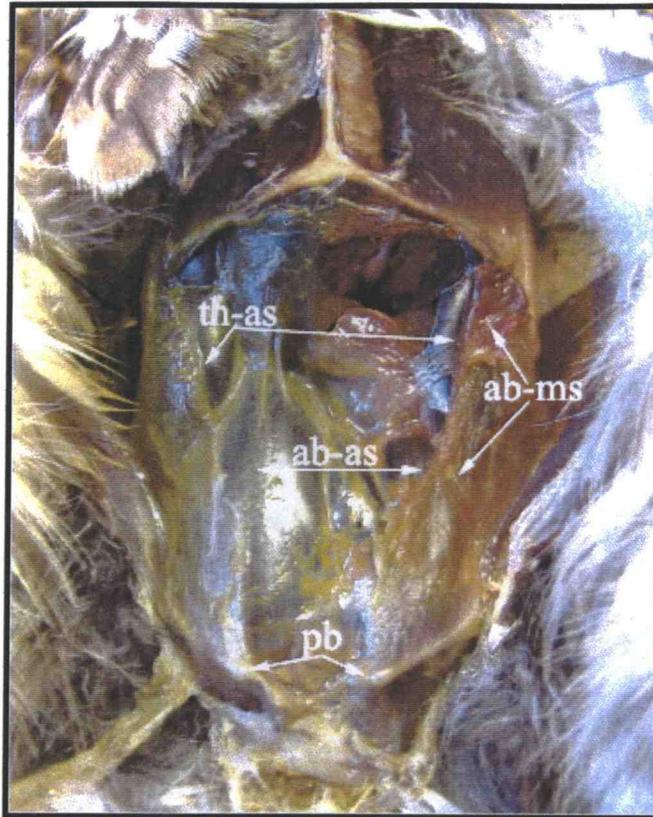


Figure 3: Abdominal cavity of an adult Merlin. Note the extensive occupation by the thoracic and abdominal air sacs (**th-as** and **ab-as**, respectively). Since the caudal air sacs exist in pairs, arrows point to the corresponding air sac situated on the opposite side of the body. A thin sheet of abdominal muscle has been left partially intact on the animals left side (**ab-ms**). The medial tip of both the left and right pubic bones are indicated by (**pb**).

distending or overfilling of the air sacs beyond expected “in situ” capacity, the abdomen was kept intact prior to dissection of the abdominal air sacs.

Once the respiratory system was inflated the superficial abdominal tissues were carefully removed to the extent that both the lateral and caudal edges of the abdominal air sacs and pubic bones were observed. The abdominal air sacs were observed to invariably extend posteriorly from the ribcage into the abdominal region and to be located dorsally within the synsacrum and laterally to be bounded by the pubic bones. Removal of the infrapubic and suprapubic abdominal musculature revealed extensive connective tissue which tightly fused the air sacs to the aforementioned musculature as well as to the medial

aspects of the pubic bones, synsacrum and, in some cases, the gizzard. A series of two measurements were then recorded for each specimen (Figure 4). Distances were recorded in millimeters using a pair of Whitworth electronic digital calipers. These measurements included: The length from the posterior tip of the sternum to the end of the abdominal air-sacs **st-as**; and the length from the posterior tip of the sternum to the tip of the pubis **st-pb**. The proportion of longitudinal abdominal air sac length supported by the pubic bones and synsacrum ($=[\text{st-pb}/\text{st-as}]$) was then calculated.

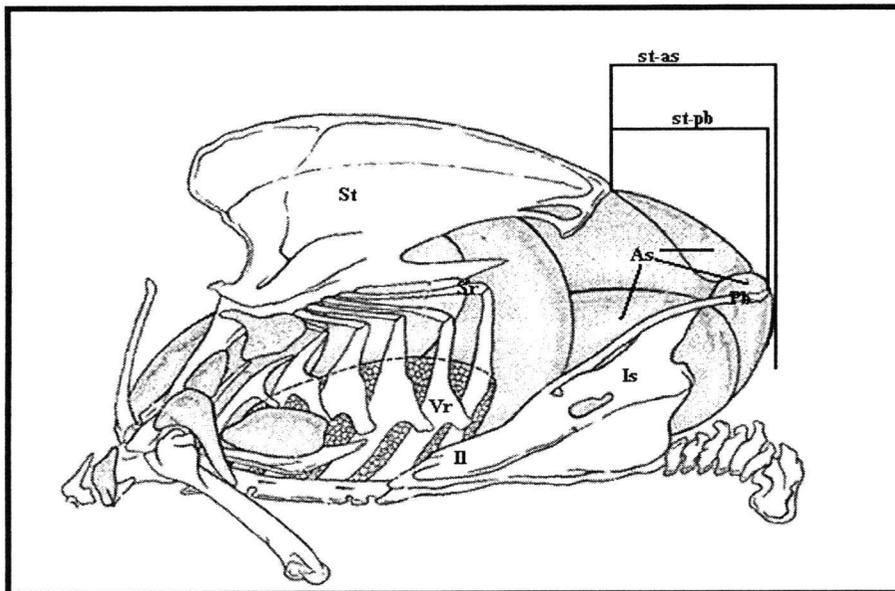


Figure 4: Lateral aspect of the thoracic skeleton and pelvis of a Rock Dove (*Columba livia*). Illustrates skeletal structures and distances measured. Sternum (**St**); Sternal rib (**Sr**); Vertebral rib (**Vr**); Abdominal air sacs (**As**); Ischium (**Is**); Ilium (**Ii**); Pubis (**Pb**); The length from the posterior tip of the sternum to the end of the abdominal air-sacs (**st-as**); Length from the posterior tip of the sternum to the tip of the pubis (**st-pb**). (adapted from Proctor and Lynch 1993).

Data was compiled using a simple Microsoft Excel spread sheet so that ratios of the distance between structural markers were then calculated.

RESULTS

Primary findings from dissection measurements indicate that, in every specimen in this study, the lateral post-sternal extension of the synsacrum+pubic bones coincides closely with the post-sternal extension of the abdominal air sacs. In fact, the percent of dorso-lateral "coverage" of the abdominal air sacs by the combination of synsacrum and pubic bones was 79% or greater in every case (Table 1).

Visual inspection and dissection revealed that the dorsal surfaces of the abdominal air sacs are tightly fused to the ventral surface of the synsacrum and the medial aspects of the pubic bones via the parietal peritoneum. Ventrally, the abdominal air sacs adhere tightly (via connective tissue) to both the suprapubic and infrapubic abdominal musculature. Additionally, as is true for Aves in general, pubic bones in every specimen in this study were widely separated and lack a symphysis. Therefore, the unfused and broadly spaced pubic bones allowed for the requisite space for the voluminous abdominal air sacs.

Table 1: Attributes of skeletal and soft tissues associated with the abdominal air-sacs in 10 avian orders. Dissection measurements in millimeters, include the lengths between the sternal tip and the posterior extremity of the abdominal air sacs (**st-as**), and the length between the sternal tip and tip of the pubic bone (**st-pb**); The percentage of abdominal air sac support dorsally and laterally by the pubic bones and synsacrum is expressed as the ratio of st-pb to st-as (see third data column). These data reveal a strong correlation between the length of the pubis and the extent of the abdominal air sacs.

Bird	st-as (mm)	st-pb (mm)	Percent of abd. air sac length supported dorsally and laterally by the synsacral/pubic complex (=st-pb/st-as)
Anseriformes			
Northern Shoveler 1	67.79	55.42	82
Northern Shoveler 2	67.30	60.32	90
Green-winged Teal	23.86	18.92	79
Passeriformes			
Stellars Jay	30.73	29.14	95
Barn Swallow	10.83	9.26	85
American Robin 1	19.17	16.28	85
American Robin 2	23.91	20.24	85
American Robin 3	20.86	19.61	94
Columbiformes			
Rock Dove	18.06	16.46	91
Falconiformes			
Sharp Shinned Hawk	23.00	22.88	99
Merlin	34.68	36.75	100
Red-tailed Hawk	52.06	48.29	93
American Kestral	29.61	30.43	100
Stringiformes			
Western Screech Owl 1	23.86	27.04	100
Western Screech Owl 2	22.48	26.29	100
Barn Owl	52.56	51.86	99
Great Horned Owl	64.89	58.43	90
Tinamiformes			
Tinamou 1	20.67	16.46	80
Tinamou 2	13.18	14.25	100
Struthioniformes			
Emu	378.00	387.00	100
Picciformes			
Sapsucker	13.40	12.26	91
Pelicaniformes			
Pelican	120.27	125.36	100
Cormorant (dbl crested)	107.22	93.05	87
Galliformes			
Chicken 1	33.10	31.73	96
Chicken 2	23.81	24.18	100
Chicken 3	20.17	27.82	100

DISCUSSION

For a large fraction of their antero-posterior length, the abdominal air-sacs are fused tightly to, and supported dorsally and laterally by the synsacrum and pubic bones in every bird included in this study (Table 1: st-as/st-pb). Of the 26 specimens examined here, all possessed pubic bones which “covered” at least 79% of the length of the abdominal air sacs. Thus, there exists a strong relation between the caudal extent of the abdominal air sacs and the degree of dorsal and lateral support provided by the synsacrum and pubic bones.

In addition to the lateral support of the abdominal air sacs provided by the pubic bones, paradoxical inhalatory movement of these air sacs is undoubtedly prevented by the infrapubic and suprapubic musculature ventrally (Figure 5). The abdominal air-sacs adhere to the ventral and lateral sides of the synsacrum via fusion of the parietal peritoneum of the body wall to the peritoneal coverings of the air-sacs, thereby securing them both dorsally and dorso-laterally (McLelland 1989). Ventral support is provided by infrapubic musculature, which is fused to the peritoneal coverings of the air-sacs.

Although air sac support by pubic musculature has not been noted previously, Baumel reports that contraction of this musculature coincides with inhalation. Consequently, fusion between the fascia of the suprapubic abdominal muscles and ventral portions of the abdominal air-sacs probably prevent the ventral paradoxical movement of these air sacs during inhalation.

These parameters provide evidence that in extant birds, resistance of the abdominal air sacs to lateral, dorsal, and ventral inhalatory paradoxical movement is provided by the pubic bones, synsacrum, and abdominal musculature. Extinct taxa with avian style, air sac lungs would therefore, be expected to have exhibited similar osteological attributes to those described here.

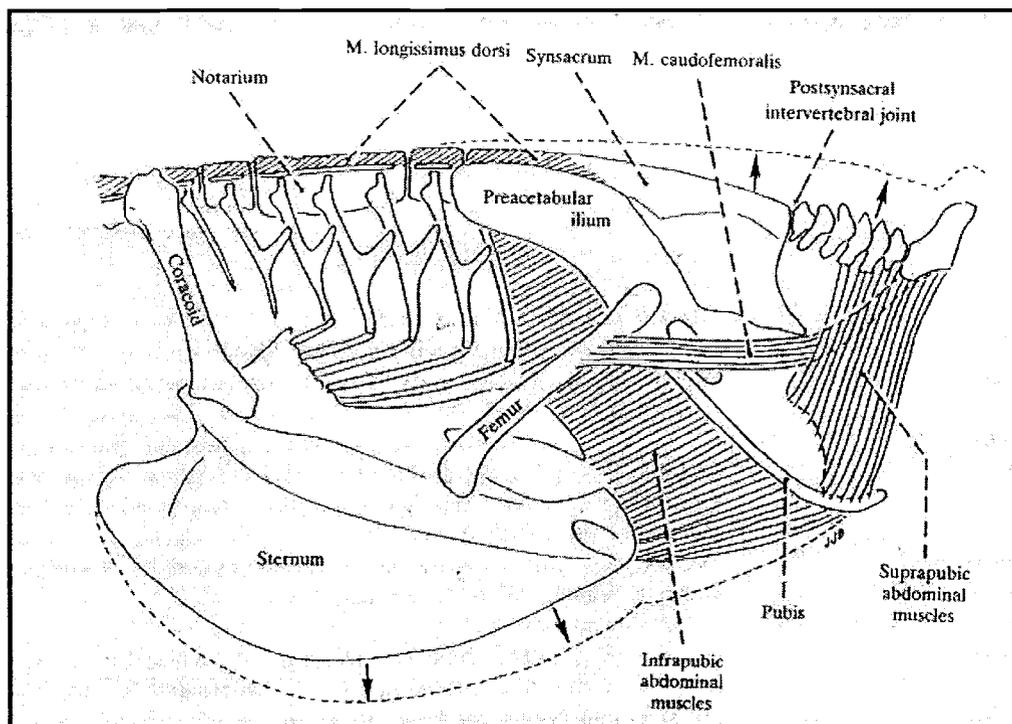


Figure 5. Ventilatory movements of thoracic and abdominal skeletal elements and muscle groups. In addition to aiding in respiration, the infrapubic abdominal muscles and the suprapubic abdominal muscles prevent the ventral and caudal paradoxical movement of the abdominal air sacs via fusion of the peritoneal linings. The air sacs are also supported dorsally by the synsacrum and laterally by the pubic bones. Dashed lines and arrows indicate movement of sternum and pelvis during inspiration. Note that these movements do not occur simultaneously (From Baumel, et.al. 1990).

In sharp contrast to previous assumptions of avian style respiration in some dinosaurs, these data suggest that theropods probably did not possess the essential osteological characteristics necessary to ventilate abdominal air sacs and by extension to support a high performance avian lung air sac system. As described above there are a number of osteological attributes that seem required for the support and ventilation of abdominal air sacs: 1. A fully retroverted pubis whose long axis is orientated essentially parallel to the lateral aspect of the abdominal air sacs; 2. the presence of a synsacrum, and broadly open pubic bones through which abdominal air sacs may extend.

With few exceptions, theropod pubic bones are orientated vertically, relative to the hip joint (Figure 6). Therefore, the right-angle positioning of the pubic bone could not have provided substantial lateral support for avian style abdominal air sacs. Furthermore, within these extinct taxa, the complete absence of a synsacrum is also inconsistent with an ability to have prevented dorsal and dorso-lateral paradoxical movements of abdominal air-sacs

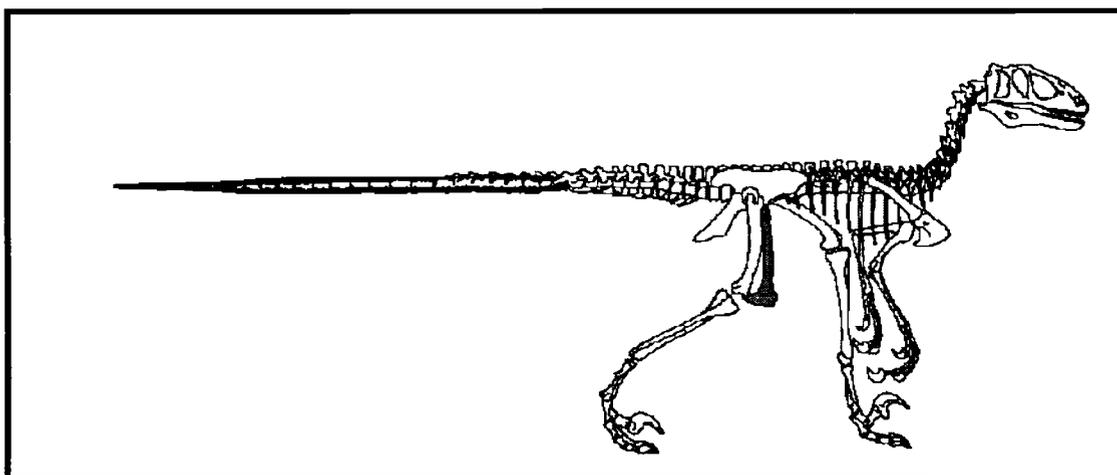


Figure 6. Pubic bone orientation in theropods as exemplified by the dromaeosaurid theropod *Deinonychus*. (Illustration adapted from Carroll 1988) Note the vertical orientation of the pubic bones (Pubic bones are shaded gray).

Finally, no known theropod possessed the unfused, broadly spaced pubic bones typical of modern birds. In contrast, the pubic bones of theropods were characterized by a lengthy medial fusion of the two pubic halves which resulted in formation of a broad, uninterrupted osseous pubic apron (Figure 7). This elongate pubic symphysis is inconsistent with the presence of an avian style abdominal air sac, which in modern birds inevitably passes between and extends posteriorly through the pubic rami. Thus, even if orientation of the pubic bones were fully retroverted there would likely have been inadequate space between the pubic rami to contain the colon, cloacal structures, and abdominal air-sacs. Based upon these data, it is clear that proper ventilation of abdominal air sacs in the avian lung requires

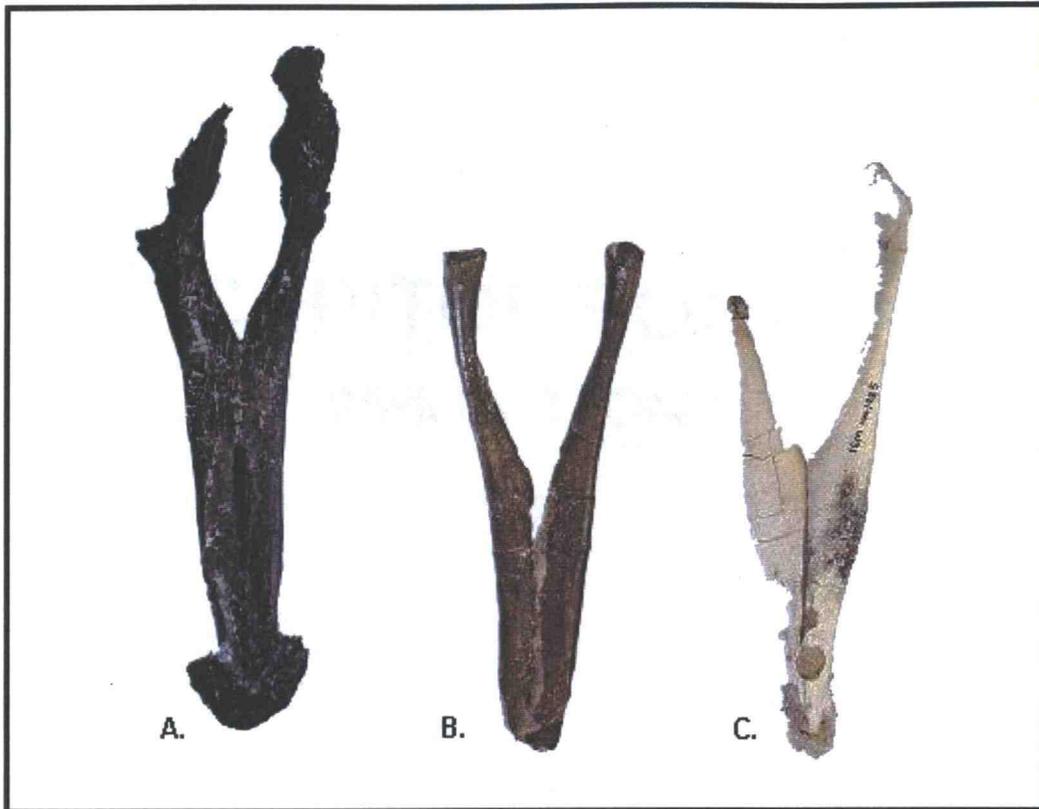


Figure 7. Pubic bones from: A. *Albertasaurus* (photograph courtesy of Jaap Hillenius); B. *Mircovenator*; and C. *Velociraptor*; Note that the fused pubic apron in specimens A-C do not provide space for abdominal air-sacs.

a distinct combination of anatomical features which seem present in all extant birds, but which were apparently absent in all theropods. These data do not support previous assumptions that theropods ventilated an avian-lung air sac system.

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