

AN ABSTRACT OF THE DISSERTATION OF

Amy E. Harwell for the degree of Doctor of Philosophy in Zoology presented on September 25, 2009.

Title: New perspectives in archosaur biology

Abstract approved:

John A. Ruben

The respiratory and metabolic biology of dinosaurs is poorly, if at all, reflected in the fossil record. By comparing anatomical features of modern taxa that are functionally linked to specific biology with the remains of theropod dinosaurs (Archosauria: Theropoda) and early birds, we may reasonably infer the physiology of long extinct taxa. This dissertation uses comparative anatomy and experiments with living crocodylians to investigate dinosaur respiratory biology.

Modern crocodylians ventilate a relatively unspecialized lung using both costal action as well as fore-aft movement of the transversely oriented liver. During inhalation, the diaphragmaticus muscles, which attach to the pubis and invest the digestive viscera, pull the liver caudally. Interestingly, the unique crocodylian pubis is mobile at its articulation with the pelvic girdle and is capable of dorso-ventral movement. In my experiments, I surgically fixed the pubis and found that this decreased the movement of the liver and tidal volume but did not increase intrabdominal pressure. Thus I infer that theropod dinosaurs with immobile pubes could have utilized a crocodylian-like ventilatory mechanism without suffering excessively high intrabdominal pressure that would limit venous return. Furthermore,

the skeleton of theropod dinosaurs strongly suggests the presence of crocodylian-like ventilatory mechanisms.

Modern birds ventilate a highly derived lung air-sac system using movements of a specialized thoracic skeleton. Requisite to the proper function of this system are their voluminous, thin-walled abdominal air-sacs that are supported by a specialized synsacrum, pubes and femoral-thigh complex. This lung air-sac system facilitates increased oxygen delivery to serve the demands of highly active tissues characteristic of endothermy. The earliest bird, *Archaeopteryx*, lacked the skeletal modifications indicative of a modern bird-like lung air-sac system and therefore was likely not endothermic, yet may have been capable of powered flight. Endothermy likely did not evolve in birds until the mid-Cretaceous ornithiurine birds *Hesperornis* and *Ichthyornis*.

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New Perspectives in Archosaur Biology

By
Amy E. Harwell

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented September 25, 2009
Commencement June 2010

Doctor of Philosophy dissertation of Amy E. Harwell presented September 25, 2009.

APPROVED:

Major Professor, representing Zoology

Chair of the Department of Zoology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Amy E. Harwell, Author

ACKNOWLEDGEMENTS

It is with the most sincere gratitude that I thank John A. Ruben for his creative & inspirational guidance, unending support, encouragement, enthusiasm and understanding. Dr. Ruben has been an extremely dedicated mentor and has always treated me with the utmost respect as a valued peer. He has provided me with many incredible opportunities and experiences with research, travel for research & conferences, teaching opportunities and service opportunities to Oregon State University. Dr. Devon Quick has been a steadfast ally and supporter for me throughout this entire process, without her this would not be possible. I am also grateful for the continuous support and encouragement of Dr. Arthur Boucot. He always saw what I was capable of and always encouraged me to broaden my knowledge and experiences. Dr. Terry D. Jones, Dr. Nick Geist and Dr. W. Jaap Hillenius have been a continuous source of guidance, creative inspiration and support.

I am grateful for the continuous and unfaltering support of Dr. Joseph Beatty who always made sure that I had incredible teaching opportunities. Dr. Beatty has always been a strong advocate for me and an invaluable mentor. During my time at Oregon State University, I have had the opportunity to interact with many incredible faculty members who have offered support and counsel such as, Dr. Thomas Roberts, Dr. Virginia Weiss, Dr. John Howieson, Dr. Robert Mason and Dr. Douglas Warrick.

I am grateful for the generous support, guidance, dedication, encouragement, patience and understanding of my graduate committee – Dr. John Ruben, Dr. Art Boucot, Dr. Joe Beatty, Dr. Roberta Hall, Dr. Timothy Cowles and to Dr. George Poinar and Dr. Fred Menino for coming to my aid and joining my committee at the last minute.

This research would not have been possible without the assistance of Dr. John Howieson, Dr. Art Boucot and ZoRF (Zoology Research Fund – Oregon State University).

CONTRIBUTION OF AUTHORS

Devon E. Quick was actively involved with data collection and data analysis and Methea Sapp assisted with data collection for Chapter 1. Frank E. Nelson, Annette M. Gabaldón, Thomas J. Roberts, Michael A. Llewellyn and Brian K. Higginson also assisted with experimental design and setup and use of physiological recording equipment for Chapter 1. Devon E. Quick was involved with the design of Chapters 1, 2 and 3. W. Jaap Hillenius generously provided photographs for Chapter 3.

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DEDICATION

I dedicate this dissertation to my family and friends. Without their undying love and support, none of this would have been possible.

Chapter One: General Introduction

In terms of their ecological diversity and highly sophisticated physiology, birds are arguably the most impressive of all vertebrates. Their evolution and phylogenetics have interested scientists since before Charles Darwin, but despite a long history of investigation, little has been resolved (James and Poutles IV 2009). Furthermore, conclusions about the anatomy and biology of these long extinct forms remains highly debated, ranging from considerations of whether feathers were present in fossil forms to the earliest appearance of endothermy (Hillenius and Ruben 2004; Lingham-Soliar 2009).

Reconstructing early bird biology and that of their closest purported relatives, theropod dinosaurs, is only possible using evidence from extant taxa. By examining living forms to identify anatomical characters that are functionally necessary to an animal's unique biology, we can attempt to reconstruct the biology of extinct taxa. In my work, I have examined the anatomy and physiology of birds and crocodylians so that I may draw conclusions about the biology of the related early birds and theropod dinosaurs.

In my first chapter I experimentally investigated the function of the pelvic skeleton to the ventilatory apparatus of crocodylians. The ilia and ischia in modern crocodylians join firmly to contribute to the majority of the pelvic girdle and acetabulum (hip socket). The pubes articulate with the anterior, inferior ischia about a joint that permits movement in the dorso/ventral plane. Large diaphragmaticus muscles surround the abdominal viscera and run caudally from

the ventral pubis to the anterior liver that subdivides the body cavity transversely. During inhalation, intercostal muscles elevate the rib cage while the diaphragmaticus muscles pull the liver caudally, thereby inflating the lungs. I investigated the contribution of pubic movement to liver movement and tidal volume during rest and exercise by surgically fixing the pubes in American alligators (*Alligator mississippiensis*). I was able to quantify liver and pubic movement using Sonomicrometry crystals while also investigating the changes in intrabdominal pressure (using pressure probes) associated with pubic fixation. From my data I was then able to draw conclusions about the likely respiratory anatomy and biology of theropod dinosaurs who share a similar pelvic anatomy to that of modern crocodylians.

Distinctly unlike the diaphragmaticus and liver driven ventilatory mechanism of crocodylians, birds utilize a highly derived and elegant system of thin walled, non-vascularized air-sacs to ventilate their efficient lung. This lung air-sac system facilitates increased oxygen delivery to serve the demands of highly active tissues characteristic of endothermy. Endotherms (birds and mammals) have field metabolic rates that exceed those of similar massed ectotherms by some 15-20 fold (Bennett 1991; Bennett, Hicks et al. 2000) and require substantially more oxygen and nutrients to be delivered to body tissues.

Endothermy can only exist in those taxa capable of accelerated rates of oxygen acquisition and delivery and it is an important specialization that allowed animals increased aerobic capacity over ectotherms and the ability to maintain a

stable internal body temperature. Over time, the advantages of endothermy allowed birds to become independent of niche climate and thus increase ecological occupation. The evolution of endothermy in birds has long been a neglected topic and in my second study I explore the skeletal evidence in the bird fossil record that lead to the development of this important physiological adaptation.

The possible metabolic status of the first known bird, *Archaeopteryx lithographica*, provides clues as to the evolution of avian endothermy and avian powered flight. In my last chapter I examine the skeleton of *Archaeopteryx*, and the pubis in particular, not only for characteristics indicative of endothermy but also for evidence of the respiratory system that may suggest its habits as either a tree dweller or ground runner.

Reconstructing the biology of extinct forms is only possible using evidence from extant taxa. By examining living forms to identify anatomical characters that are functionally necessary to birds' or crocodilians' unique biology, I attempt to reconstruct the metabolic and respiratory biology of early birds and theropod dinosaurs.

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Chapter 2:
Lung ventilation in *Alligator*: new evidence in support of diaphragm-aided
breathing in theropod dinosaurs

Amy E Harwell

John A. Ruben

Introduction

Speculation about the respiratory physiology of theropod dinosaurs began with their description in the mid-1800s, but the intensity and controversy surrounding the topic has dramatically increased over the last several decades (Owen 1842; Ostrom 1974). Dinosaurs (Archosauria: Dinosauria) belonged to the dominant tetrapods, the Amniota, which includes all synapsids and sauropsids, the latter of which encompasses the archosaurs. In turn, the Archosauria is comprised of the dinosaurs, pterosaurs and basal “thecodonts,” as well as two extant taxa, crocodylians and birds (Carroll 1988). The universal presence of aspiration breathing (i.e., generation of negative intrapleural pressure by thoracic expansion and drawing air into the lungs) in all extant amniotes implies that extinct amniotes were also aspiration breathers. Living amniotes employ a variety of mechanisms to accomplish aspiration breathing (Brainerd 1999).

Recent conventional wisdom holds that birds are “living dinosaurs” and that these two groups must, therefore, have shared similar patterns of respiratory and metabolic physiology (Padian 2004). Extant birds utilize a complex lung air-sac system optimized to support the high rates of gas exchange requisite to meet the energetic demands of powered flight (Duncker 1971; Schmidt-Nielsen 1971). In this system, specialized skeletal elements (e.g., enlarged sternum, specialized costal articulations, relatively immobilized femora, etc.) assist in ventilation of a series of non-vascularized air-sacs which create a one-way flow of air across the highly vascularized, dorsally situated lung (Fig. 2.1)

(Duncker 1971; Proctor and Lynch 1993; Ruben, Jones et al. 1997; Perry 2001; Quick and Ruben 2009).

In contrast, crocodilian lungs are ventilated via a “hepatic piston” diaphragm mechanism, broadly analogous to mammalian diaphragm breathing (Boelaert 1942; Naifeh, Huggins et al. 1970; Gans and Clark 1976). The “piston” in this system is the liver which (i) extends completely from the dorsal to the ventral body walls and (ii) creates an air-tight, fore/aft subdivision of the visceral cavity (Ruben, Dal Sasso et al. 1999). Aspiration breathing occurs as the liver is pulled caudally by diaphragmatic muscles which originate on the pelvis and gastralia (Fig. 2.2), thereby increasing pleural cavity volume and ventilating the lungs.

Surprisingly, theropod dinosaurs apparently possessed a variety of anatomical specializations strikingly like those causally linked to hepatic-piston diaphragm breathing in extant crocodilians (Ruben, Dal Sasso et al. 1999). Ruben *et. al.* described the visceral and skeletal anatomy associated with respiration in an exceptionally well preserved specimen of the theropod, *Scipionyx samniticus* (Ruben, Dal Sasso et al. 1999). This theropod possessed skeletal attributes linked to the presence of diaphragmatic muscles (e.g., elongate pubis, robust gastralia) and a crocodilian-like, distinct fore-aft subdivision of the visceral cavity (Ruben, Dal Sasso et al. 1999; Quick 2008). Clearly, theropods seem to have possessed a crocodilian-like, not bird-like, visceral geography (Ruben, Dal Sasso et al. 1999; Quick 2008). Thus, conventional wisdom notwithstanding, it is reasonable to hypothesize that theropods were likely to have utilized a crocodile-like, rather

than bird-like (i.e., air-sac), pattern of lung ventilation (Osborn 1900; Broom 1913; Heilmann 1927).

Despite the marked uniformity of crocodylian and theropod dinosaur respiratory anatomy, some authors have recently suggested that the fixed pubis of theropods was inconsistent with hepatic-piston breathing (Farmer and Carrier 2000). Rather, these authors assert that gator-like, postero-ventral rotation of the pubis (which is mobile in living crocodylians) (Romer and Parsons 1977) is required to prevent elevation of intra-abdominal pressure (IAP) that would otherwise be caused by squeezing of the viscera as the liver is pulled caudally during inhalation. Therefore, they assert, theropods, with their fixed pubes could not have been diaphragm breathers because the IAPs generated during “fixed-pubis” diaphragm breathing would have blocked venous return from the lower extremities.

To evaluate these latter assertions, we surgically immobilized the pubes in four juvenile American alligators (approx. 1 m in total length), thus rendering them functionally theropod-like. The impact of pubis immobilization on hepatic piston lung ventilation in alligators was then evaluated. In the following pages, I describe the outcome of these procedures and their implications for understanding mechanisms of lung ventilation in theropod dinosaurs.

Materials and Methods

I. Anatomical observations

Dissection of several previously preserved American alligators (*Alligator mississippiensis*) ranging in snout-vent length from 0.5-1.5m was performed to

observe and describe functions of muscular, skeletal and visceral components associated with hepatic piston diaphragm breathing.

Experimental Animals

We obtained five healthy juvenile American alligators (*Alligator mississippiensis*), mass = 1.93-4.01 kg from Rockefeller Wildlife Refuge in Grand Chenier, LA, USA. The animals were housed in stock tanks (Newell Rubbermaid, Inc., Freeport, IL, USA) at an ambient temperature of 30°C with basking platforms and full-spectrum lighting/radiant heat source (Zoo Med, San Luis Obispo, CA, USA). They were exposed to a photoperiod of 12L: 12D and fed a diet of chicken, quail, beef and rats. All animal experimentation was performed under the Oregon State University Institutional Animal Care and Use Committee's approval (ACUP CP185) in accordance with federal and institutional guidelines.

II. Surgery

Sonomicrometry:

To measure the extent of the movement of the liver and pubis during lung ventilation, individually wired piezo electric transducer crystals (Sonometrics, Inc., London, ON, Canada) were surgically implanted both in and near these organs in all experimental animals. These crystals exchange ultrasonic pulses with one another and can be used to determine fluctuation in absolute distances between structures over time.

Animals were fasted for at least 72 hours prior to surgery. Three distinct procedures were performed on each experimental subject: (i) placement of

sonomicrometry crystals; (ii) immobilization of the pubis; (iii) reversal of these procedures. Inhaled isoflurane anesthesia (1-2.5%) was mixed with oxygen used to sedate and maintain animals during the surgical procedures.

Liver and pubic bone displacement during lung ventilation was measured using two sets of 2 mm diameter sonomicrometry crystals. For hepatic movement analysis, a crystal was fixed to the cranio-lateral edge of the liver and its “partner” crystal was attached to the distal (external) surface of the immediately adjacent rib (Fig. 2.3).

For the pelvic pair of crystals, an incision was made cranial to the cloaca in the region of the pubis and cranial ischium. One crystal was then fixed to the ventral surface of the distal, bony portion of the pubis and the other placed on the ossified, ventro-cranial edge of the ischium in approximately the same plane.

Both crystal pairs were sufficiently distant from one another that “cross-talk” between the thoracic (liver) and pelvic (pubic) crystal pairs was not possible.

Crystals were attached using Vetbond tissue adhesive (3M, St. Paul, MN, USA) to either the liver or regions of bone mechanically debrided of periosteum and defatted with chloroform. For recording purposes, a small amount of wire slack was left inside the animal and the wire leads associated with each crystal were routed through the incision site and sutured to the skin at the incision site using 4-0 silk suture. Animals were bandaged with Vetrap (3M, St. Paul, MN, USA) to protect the incision site and the sonomicrometry crystal wires. The animals

were isolated and allowed to recover from surgery in temperature controlled environments for 24–48 h before data recording.

Pubic bone Immobilization:

A second surgery was performed on each animal to immobilize the pubes. A fabricated metal plate was secured between the pubis and ischium using orthopedic screws to prevent caudo-ventral movement of the pubis (Fig. 2.3). Previous crystal placement was maintained and the incision site was sutured.

Recovery Surgery:

After all the data collection was complete, we performed a final surgery to “normalize” the animals. Sonomicrometry crystal placement was inspected to confirm that the crystals had remained in their initial positions. Both sets of crystals as well as the pelvic plate were then removed. All animals recovered quickly.

III. Intra-Abdominal Pressure and Tidal Volume:

Intra-abdominal pressure (IAP) during breathing was measured using a Millar Mikro-tip catheter pressure transducer system (Millar Instruments, Houston, TX, USA). Calibrated catheters were introduced orally into each animal’s stomach prior to each experimental session; the catheter was secured to the animal’s head where it exited the mouth. The catheter was removed immediately after each experiment and the calibration was confirmed.

Tidal Volume:

To measure mean tidal volume, a flexible, gas-tight rubber mask was constructed from a plastic sphere modified to conform to the shape of the animal's rostrum and accommodate two ports. A small, one-way valve (Hans Rudolph, Inc., Kansas City, MO, USA) was placed on the upstream port of the mask allowing intake of ambient air and a second one-way valve was placed on the downstream port of the mask feeding into flexible natural latex rubber tubing (New Age Industries, Southampton, PA, USA). A sealed Mylar balloon fitted with a Mohr's pinchcock tubing clamp (United Scientific Supplies, Inc., Gurnee, IL, USA) collected expired air from the tubing. The mask was adapted to fit each animal and was sealed over the nares with a generous layer of petroleum jelly to prevent air from entering the mask at the animal-mask junction; the mask was secured in place. Mean tidal volume was measured during rest and exercise in both unfixed and fixed pubis conditions.

Collection of sonomicrometry data:

To establish base line (normal) liver and pubic movements during breathing, data were collected from animals after the implantation of sonomicrometry crystals before and after pubic fixation. The data recording laboratory was maintained at $30 \pm 1^\circ\text{C}$ and animals were given adequate time in an undisturbed environment to allow measurement of "resting" activities. The distance observed between each crystal of the thoracic and pelvic crystal pairs were measured simultaneously with intra-abdominal pressure and tidal volume. The animal were then exercised vigorously for 5 minutes (or until it displayed the

inability to right itself) and all measurements were repeated. Two minutes of data were collected for both the resting and exercise conditions.

Hepatic displacement detected by thoracic and pelvic crystal pairs were recorded at 992 Hz using SonoLAB software (Sonometrics, London, Ontario, Canada). Data from the sonomicrometry crystals and from the pressure transducer were collected to a Macintosh computer using the software program IGOR Pro (Wavemetrics, Inc., Lake Oswego, OR, USA). Wave analysis was conducted using IGOR Pro software. For each animal, data from the first 6 breaths from the crystal pairs and the pressure transducer were averaged for analysis. Differences between values obtained during rest and exercise as well as treatment effects were compared for significance at the 5% level using two-sample *t*-tests. To assess the possible effects of body size on liver excursion distance, snout vent length (SVL) was included as an explanatory factor.

Results

Anatomy

Crocodylian visceral anatomy observed here confirmed that previously described by numerous authors (Boelaert 1942; Chiasson 1962; Naifeh, Huggins et al. 1970; Gans and Clark 1976). Thus, only structures and functions associated with hepatic piston diaphragm breathing will be discussed here (Boelaert 1942; Chiasson 1962; Naifeh, Huggins et al. 1970; Gans and Clark 1976). Visceral morphology associated with hepatic piston diaphragm breathing includes especially the relative positions of the liver and lungs and the distinct fore-aft

subdivision of the thoracic and abdominal cavities by the liver. The anterior thoracic compartment houses paired lungs, each of which is enveloped in independent pleural cavities. The liver is immediately caudal to the lungs and subdivides the fore and aft visceral compartments by completely extending between the dorsal, ventral and lateral body walls.

The lateral diaphragmatic muscles originate on the proximal pubis and antero-ventral ischium. The more robust ventral diaphragmatic muscles originate on the last gastrula/cranial edge of the cartilaginous distal portion of the pubis (Gans and Clark 1976, pers. obs.). Diaphragmatic muscles entirely invest the bulk of the digestive viscera and insert ventrally and laterally onto the posterior margin of the liver at the posthepatic septum and less extensively on the ventral pericardium (Chiasson 1962; Duncker 1979, pers. obs.). Although traditionally described as “thin” (Boelaert 1942; Farmer and Carrier 2000), the lateral diaphragmaticus was markedly robust in the larger specimens examined.

In extant crocodylians, the pubes do not participate in the acetabula and are caudo-ventrally mobile about the pubo-ischiac joint (Claessens 2004).

Experimental Data

Figure 2.4 illustrates relative hepatic and pubic movement during lung ventilation. Distance between the crystal placed on the rib and the crystal placed on the liver increases with inspiration as the liver is pulled caudally by the diaphragmaticus (Fig. 2.4, middle trace). Additionally, as the mobile pubis is pulled postero-ventrally by the ischiotruncus muscles (Fig. 2.4, top trace) during

inspiration, there is a marked decrease in the distance between the crystal on the ischium and the crystal on the pubis. During inspiration, intraabdominal pressure (IAP) increases slowly reaching its maximum at full liver caudal excursion and minimum during expiration (Fig. 2.4, bottom trace).

During expiration, these parameters reverse as the liver crystals move closer to one another and pubic crystal move further apart (Fig. 2.3). In addition, IAP decreases. For each animal, total excursion values for the liver and pubis were collected and compared between resting and exercise conditions in both the control and experimental treatments as well as among treatment effects for resting or exercising animals.

After the pubes were surgically fixed to the ischium, all animals exhibited a statistically significant reduction in pubic movement (Fig. 2.5).

Liver excursion typically increases from rest to exercise regardless of the treatment effect. However, during exercise there was no significant difference in the magnitude of liver movement between the normal and fixed pubic conditions (p -value = 0.1431, Fig. 2.7). Also, during exercise, while there was no statistically significant difference in tidal volume between the normal and experimentally fixed pubic condition, tidal volume did generally decline (p -value = 0.789, Fig. 2.8).

Maximal IAP values were compared between treatments and among animals. During exercise, there was no significant difference in maximal intra-

abdominal pressures generated in animals with normal vs. fixed pubes (p -value = 0.7626, Fig. 2.6).

Discussion

Recent assertions that mobile pubes are requisite to minimize IAP during crocodilian hepatic piston diaphragm breathing are not supported. Data reported here (Figs. 2.5 & 2.6) suggest that although extant alligators utilize their mobile pubes during pulmonary ventilation, fixation of the pubes does not result in significantly altered intra-abdominal pressure (IAP) during either rest or exercise. Although venous return from the caudal limbs was not directly measured in these experiments, the association between elevated IAP and decreased venous return during inspiration has been previously recognized (Munns, Hartzler et al. 2005). However, in the absence of a significant increase in IAP associated with experimentally fixed pubes, there is little reason to suggest that rigid pubes in *Alligator* would necessarily be linked to excessively inhibited venous return in animals utilizing hepatic piston lung ventilation or that fixed pubes would necessarily preclude hepatic piston lung ventilation in other taxa with rigid pubic bones.

That IAP is unaffected by mobile vs. fixed pubes is not surprising: for pubic rotation to result in decreased IAP during inspiration, the liver must remain in a fixed position (Fig. 2.9). However, in modern hepatic piston diaphragm breathers, the liver is not anteriorly fixed to any rigid structures (Fig. 2.9). Thus, as the pubis rotates postero-ventrally, the liver is necessarily pulled caudally, along with the

contracted diaphragmatic muscles (Fig. 2.9). As a consequence, retraction of the pubis very likely results in an equivalent posterior migration of the entire abdominal viscera. In any case, as in mammals, inhalatory expansion of the lateral abdominal walls (pers. obs.) probably accommodates otherwise compressed abdominal contents and would serve to mitigate excessive IAP. Thus, while the geometry of the crocodilian abdominal space may change during the ventilatory cycle, overall abdominal volume and IAP remain relatively stable, even with fixed pubic bones (Fig. 2.8).

If not reduction of IAP, what factor(s) might account for the mobile pubis of crocodilians? We suggest that their semi-aquatic mode of life may have influenced pelvic anatomy. Like many semiaquatic taxa, extant crocodilians are dorsoventrally flattened (Fig. 2.2). Simple observation suggests that, compared to animals with broad, slab-aided thoracic regions, crocodilian body shape undoubtedly results in reduced capacity for costally-generated tidal volume (Fig. 2.11). Thus, pubic mobility in crocodilians may help to compensate for otherwise reduced tidal volume by increasing caudal displacement of the liver during the ventilatory cycle. Indeed, data presented here do suggest that pubic flexion in *Alligator* might result in enhanced tidal volume, at least in larger individuals. (Fig. 2.3)

Significantly, some early terrestrial crocodylomorphs, such as *Terristrisuchus*, as well as most theropod dinosaurs, possessed fixed pubic bones and a laterally compressed body wall lacking lateral bony reinforcement in the

abdominal regions (Carroll 1988; Carroll 1988) (Figs. 2.10 & 2.11). This body shape may have facilitated costally-generated tidal volume and obviated the need for mobile pubes in these taxa (Fig. 2.12).

Data presented here are inconsistent with recent assertions that a mobile pubis is requisite for diaphragm breathing in crocodylians. Rather, it seems more likely that (i) the origin of the specialized pubis in modern crocodylians may be related to their dorso-ventrally flattened torso and that (ii) early crocodylians and theropod dinosaurs, both of whom possessed laterally compressed bodies and pubic bones firmly fixed to the pelvis, may well have utilized hepatic-piston diaphragm lung ventilation.

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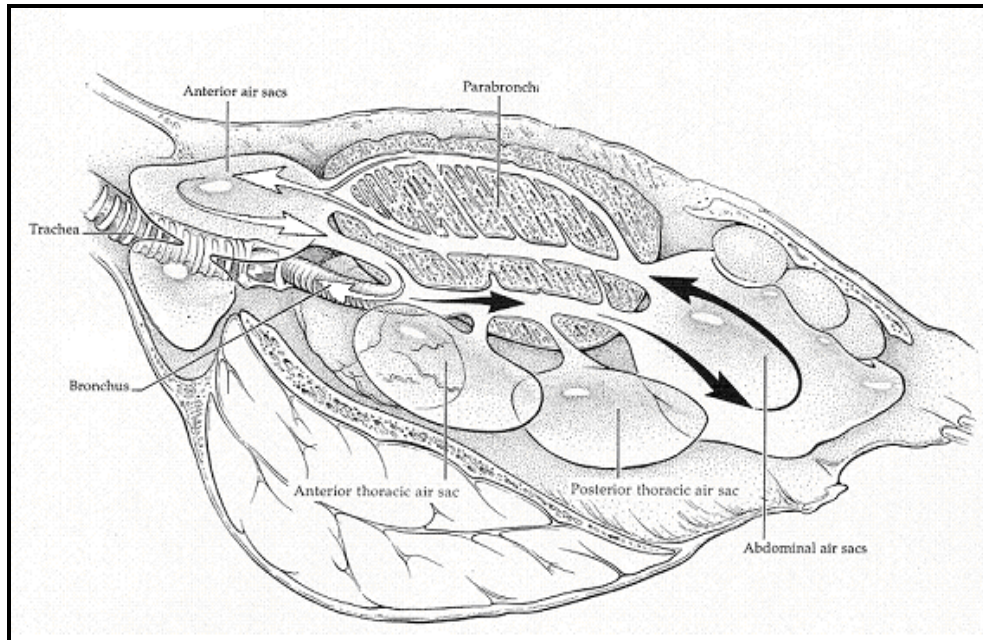


Fig. 2.1: Diagram of the lung-air-sac system of extant birds. The arrows indicate the unidirectional flow of air through a series of non-vascular air-sacs which ultimately pass new air with every breath across the highly vascularized, dorsally positioned lung (parabronchi). (Image modified from Proctor and Lynch, 1993)

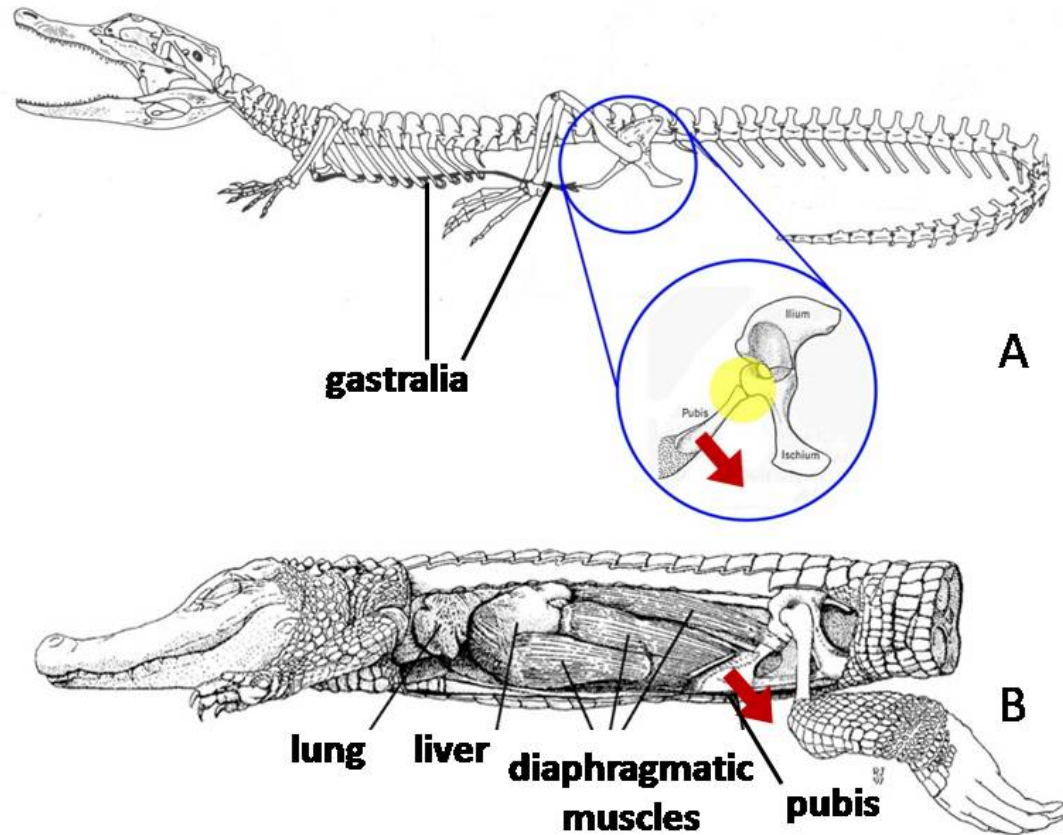


Figure 2.2: In all extant crocodilians, the pubes are excluded from the acetabulae and are mobile at the pubo-ischiac joints. Pubic mobility is in the caudo-ventral axis (A). Crocodilians have a distinctive fore-aft subdivision of the thoracic and abdominal cavities that is created by the liver (B). The diaphragmatic muscles take their origins on the pubis/ischium and the pubis/gastralia and insert onto the liver. When diaphragmatic muscles contract, the liver is pulled caudally which increases the volume in the thoracic cavity, causing inspiration. One should note that caudo-ventral rotation of the pubes would also cause an essentially equivalent caudal shift of the liver due to their attachment by the diaphragmatic muscles. (Image modified from Ruben et al, 1997 and Chiasson, 1962).

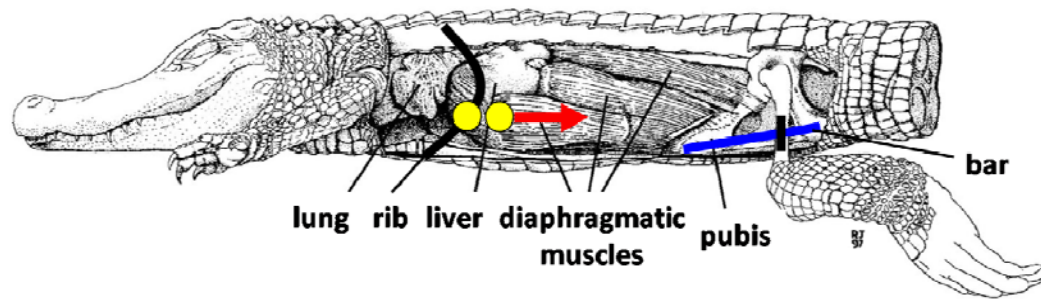
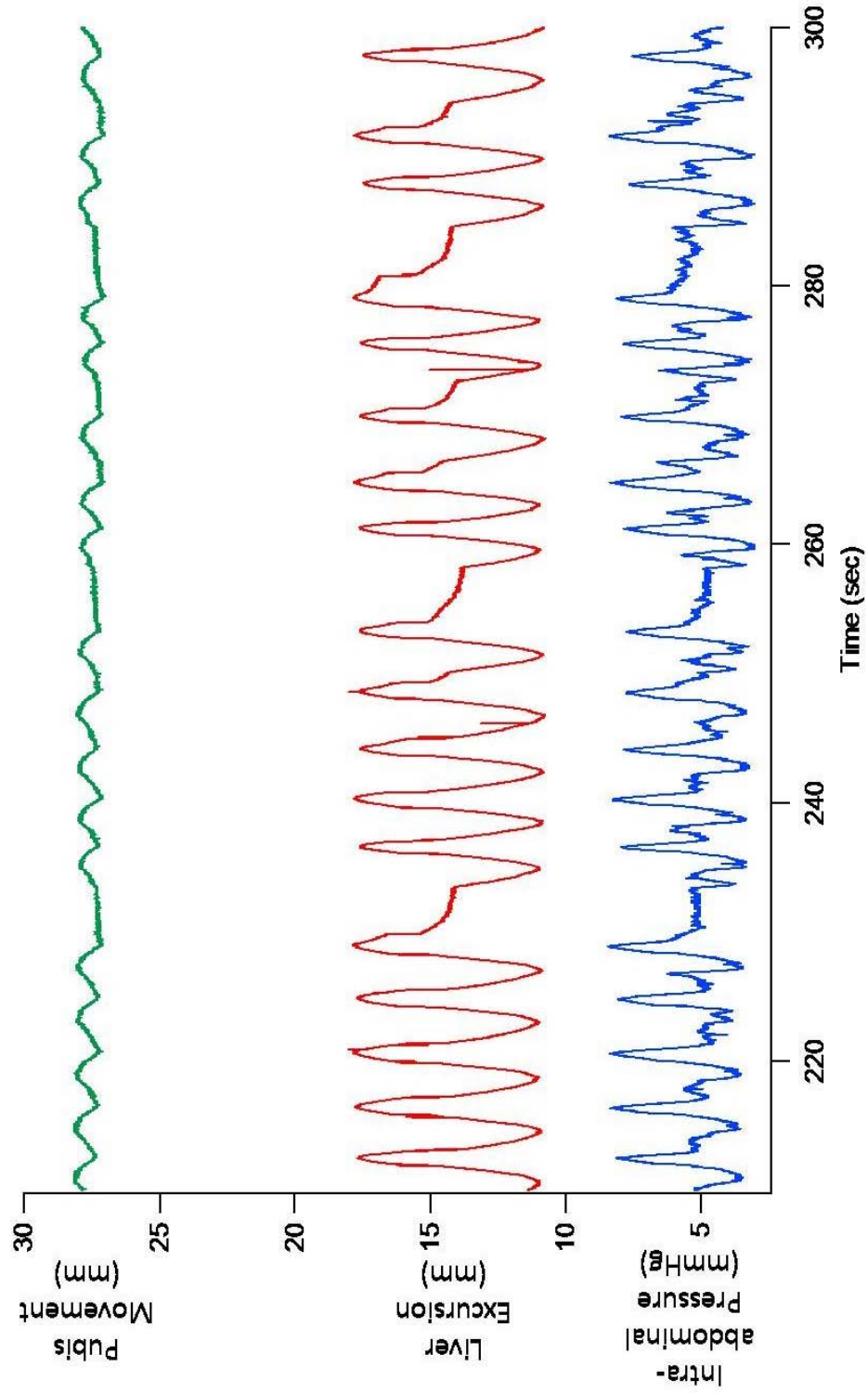


Fig. 2.3: Piezoelectric transducer crystals were surgically implanted on the liver and on an adjacent rib in the same plane (indicated by the yellow circles). When the diaphragmatic muscles contract during inspiration, the crystal on the liver is pulled caudally and farther away from the crystal in its fixed position on the rib (as indicated by red arrow). After recordings were made with the normal pubis condition, a metal plate (indicated by the blue bar) was secured between the ischium and the distal pubis to immobilize the pubis. Crystals were also placed on the pubis and ischium to insure reduction of pubic movement. (Image modified from Ruben et al, 1997).

Fig. 2.4: Sample recording of the changes in pubis movement (top trace), liver excursion (middle trace) and intra-abdominal pressure (bottom trace) during exercise in the un-fixed pubis condition. Inspiration occurs as the liver trace increases in magnitude from the baseline level. Intra-abdominal pressure begins to increase when the liver reaches its full caudal excursion. The pubes are pulled caudally at the same time as the diaphragmatic muscles are pulling the liver caudally. When the pubis is fixed, the patterns are the same with the exception being a dramatic reduction in pubis movement.

Fig. 2.4:



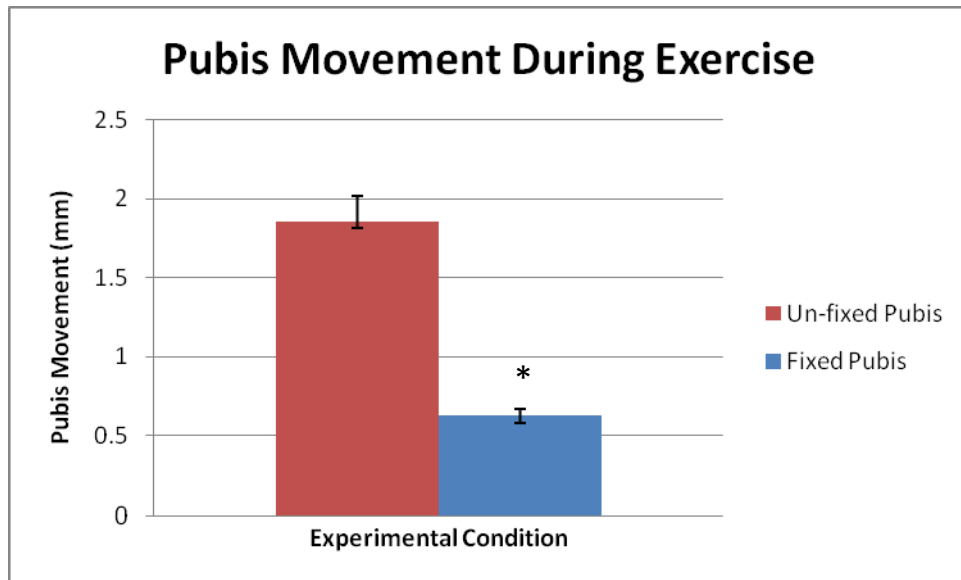


Fig. 2.5: Caudo-ventral pubis movement in the un-fixed pubis condition and fixed pubis condition during exercise. * indicates a statistically significant reduction in pubic movement relative to the un-fixed pubis condition (two-sided, *t*-test *p*-value < 0.0001).

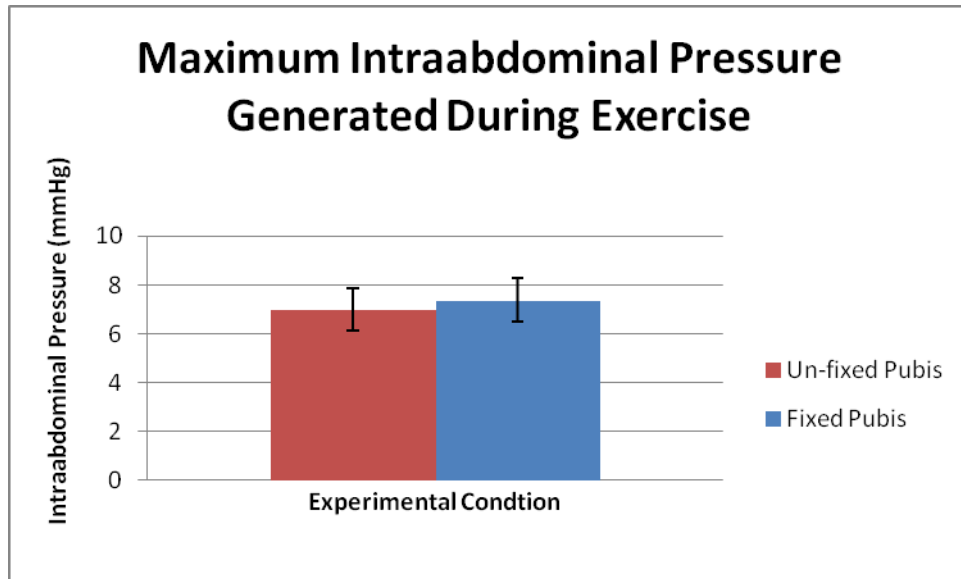


Fig. 2.6: Maximum intra-abdominal pressures generated in the un-fixed pubis condition and fixed pubis condition during exercise. There was no statistically significant difference in maximum intra-abdominal pressure between the un-fixed pubis condition to the fixed pubis condition during exercise (two-sided, *t*-test *p*-value = 0.7626).

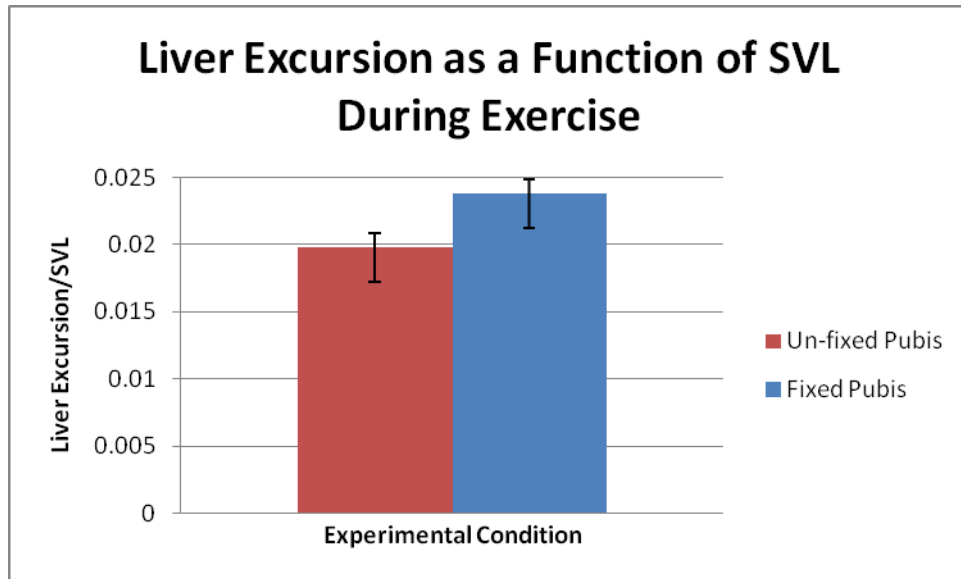


Fig. 2.7: Liver excursion as a function of SVL in the un-fixed pubis condition and fixed pubis condition during exercise. There was no significant difference in liver movement from the un-fixed pubis condition to the fixed pubis condition during exercise (two-sided, t -test p -value = 0.1431).

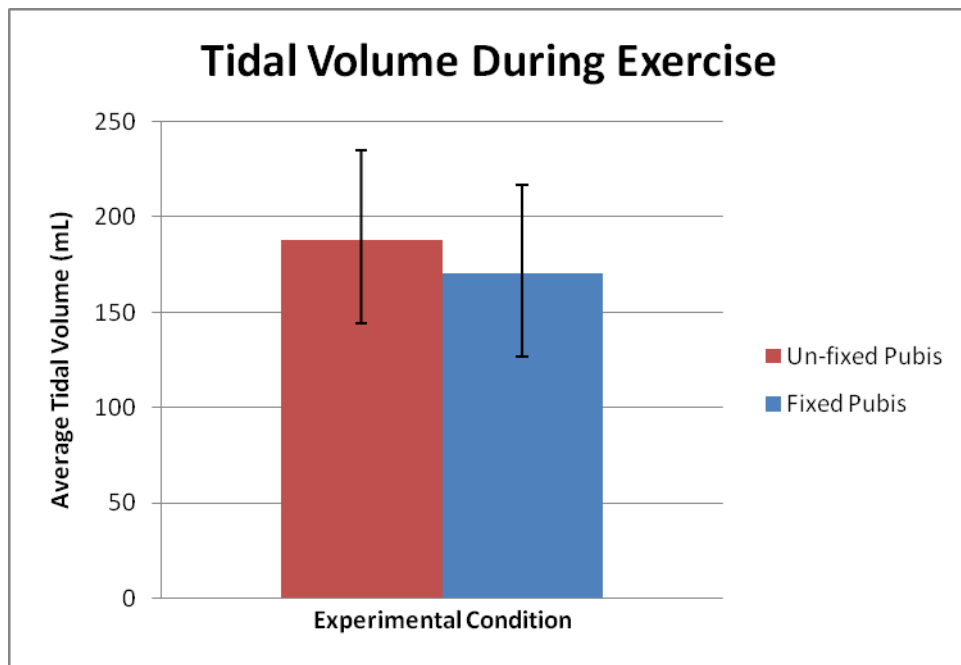
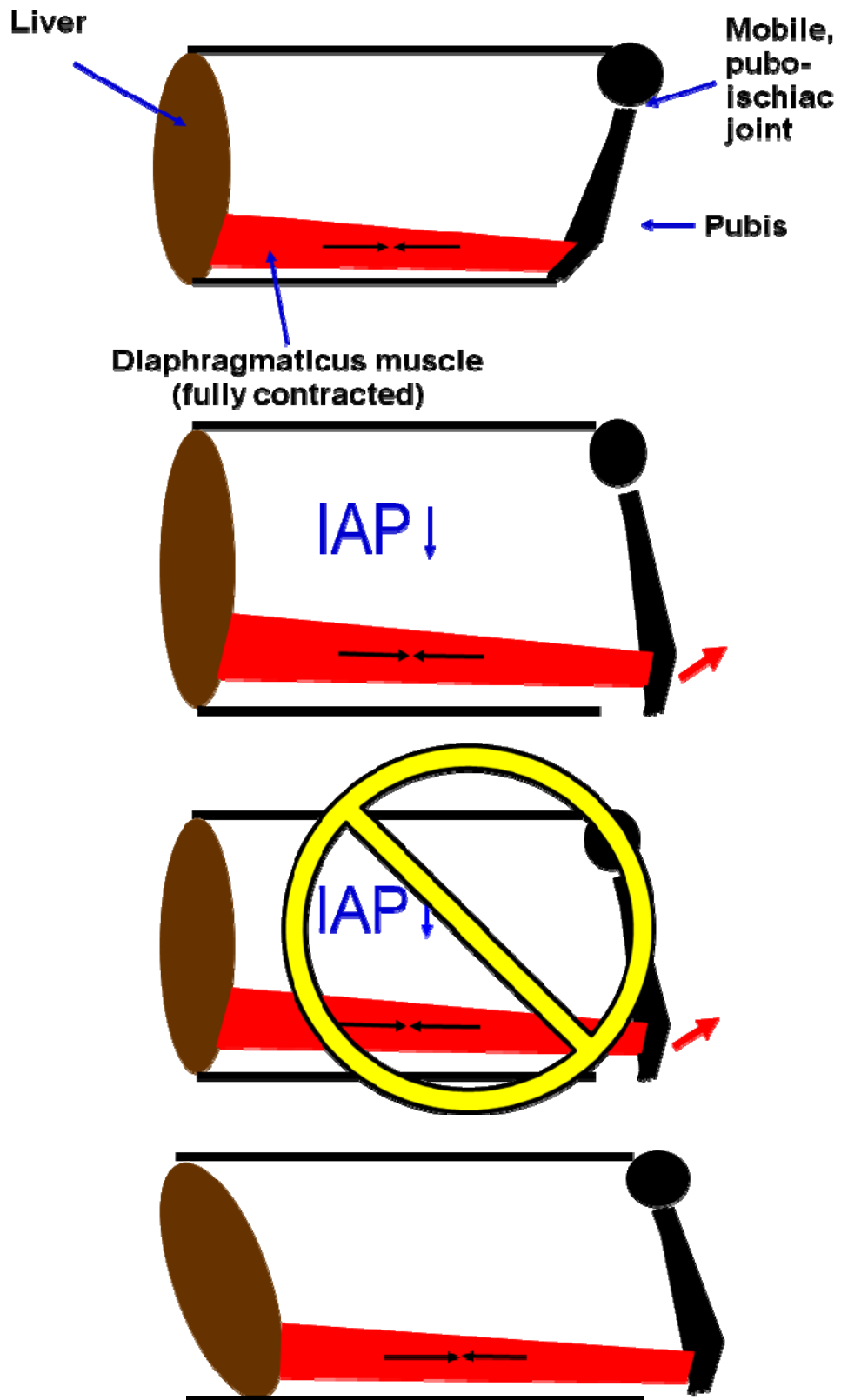


Fig. 2.8: Average tidal volume in the un-fixed pubis condition and fixed pubis condition during exercise. There was no significant difference in tidal volume from the un-fixed pubis condition to the fixed pubis condition during exercise (two-sided, t -test p -value = 0.789).

Fig. 2.9: It has been recently suggested that theropod dinosaurs, with their fixed pubes, would not have been able to utilize a hepatic piston mechanism for lung ventilation because the IAP generated would have blocked venous return from the lower extremities. This schematic illustrates: (A) fully contracted crocodilian diaphragmatic muscles at the end of inspiration cycle but prior to the pubis being pulled caudally. (B) In the recently suggested scenario, the liver would need to remain in a fixed position, and when the pubis rotates caudo-ventrally, the IAP would drop. (C) However, as illustrated here, the crocodilian liver is not rigidly fixed and this scenario is physically impossible. (D) Because the liver is not fixed, when the pubis is rotated caudo-ventrally the liver is pulled caudally along with the pubic bones. Thus, as illustrated by data in Figure 5, regardless of pubic rotation, pelvic volume remains unchanged and IAP is unaffected.

Fig. 2.9



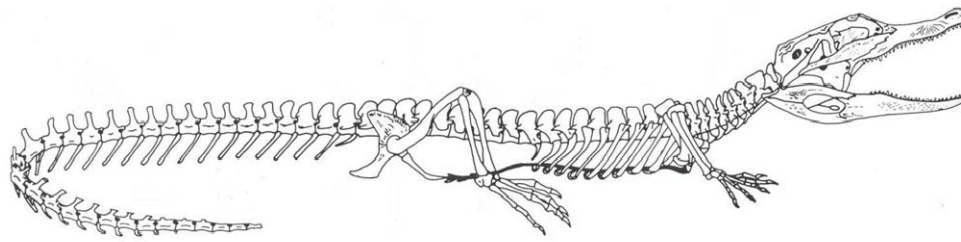
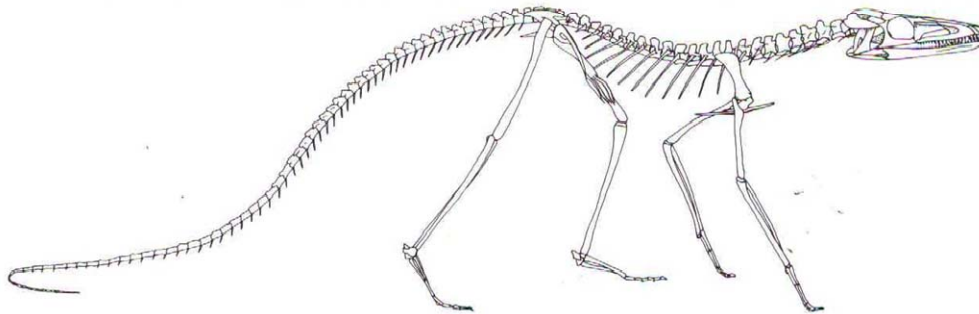
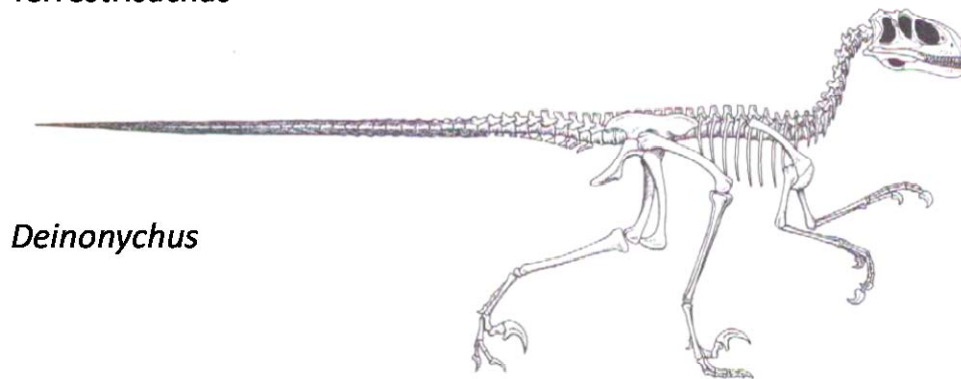
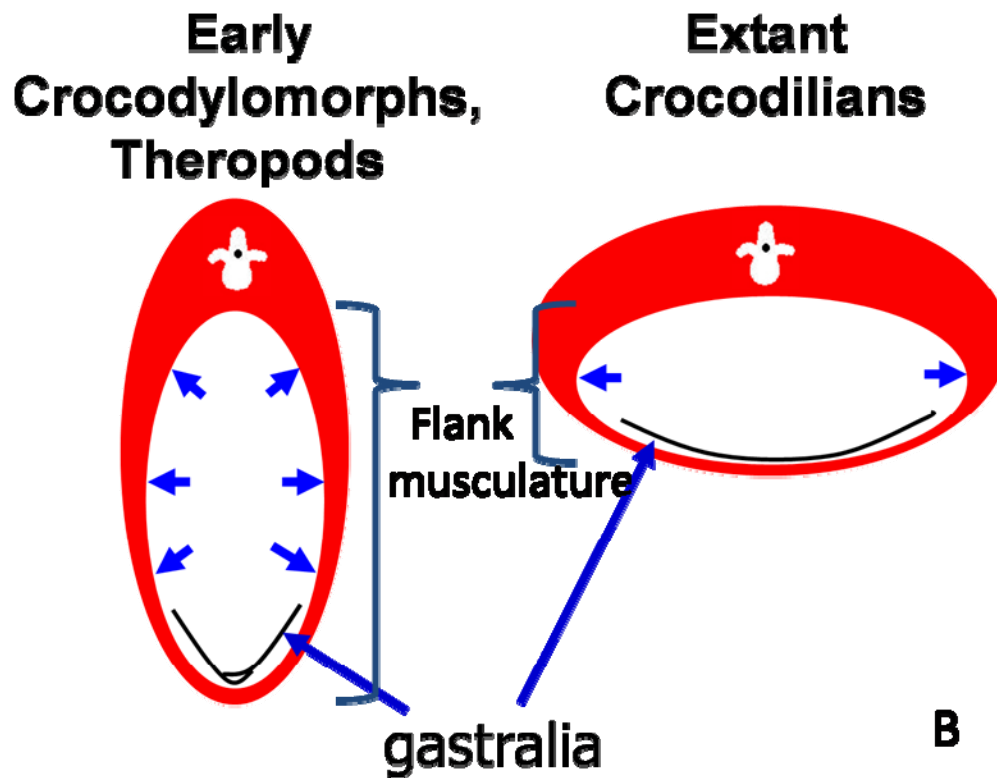
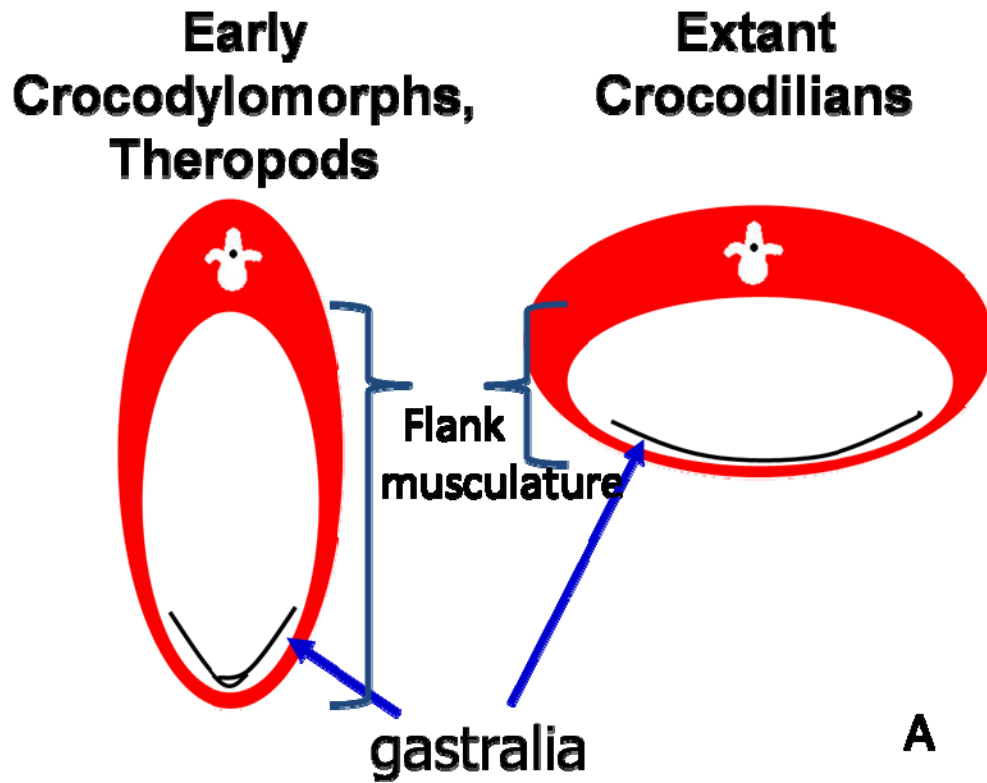
*Alligator**Terrestriisuchus**Deinonychus*

Fig. 2.10: A few variations in archosaurian body shape. All extant crocodylians, such as *Alligator*, are aquatic and dorsoventrally flattened with mobile pubes. A noticeably significant difference in crocodylians is seen comparing the aquatic, dorsoventrally flattened *Alligator* to the extinct, agile, terrestrial, sphenosuchid crocodile, *Terristrisuchus*. *Terristrisuchus* and other basal archosaurs had fixed pubes and laterally compressed body walls with little or no bony support. Similarly, in theropod dinosaurs, such as *Deinonychus*, the pubis was fixed and the body was compressed laterally with little or no bony support of the lateral body wall. (Images modified from Carroll, 1988 and Chiasson, 1962).

Fig. 2.11: Schematic x-sectional representations of the mid-abdominal regions of early crocodylomorphs or theropods and extant crocodylians. (A) All extant crocodylians are dorsoventrally flattened with mobile pubes. Early crocodylomorphs and theropods, were “slab sided” (laterally compressed) with fixed pubes. The “slab sided” body shape of early crocodylomorphs and theropods would have left dramatically more room for lateral expansion of the body wall than extant crocodylians. This extra room for expansion accommodates the caudally displaced viscera that migrate to this region during inspiration.

Fig. 2.11



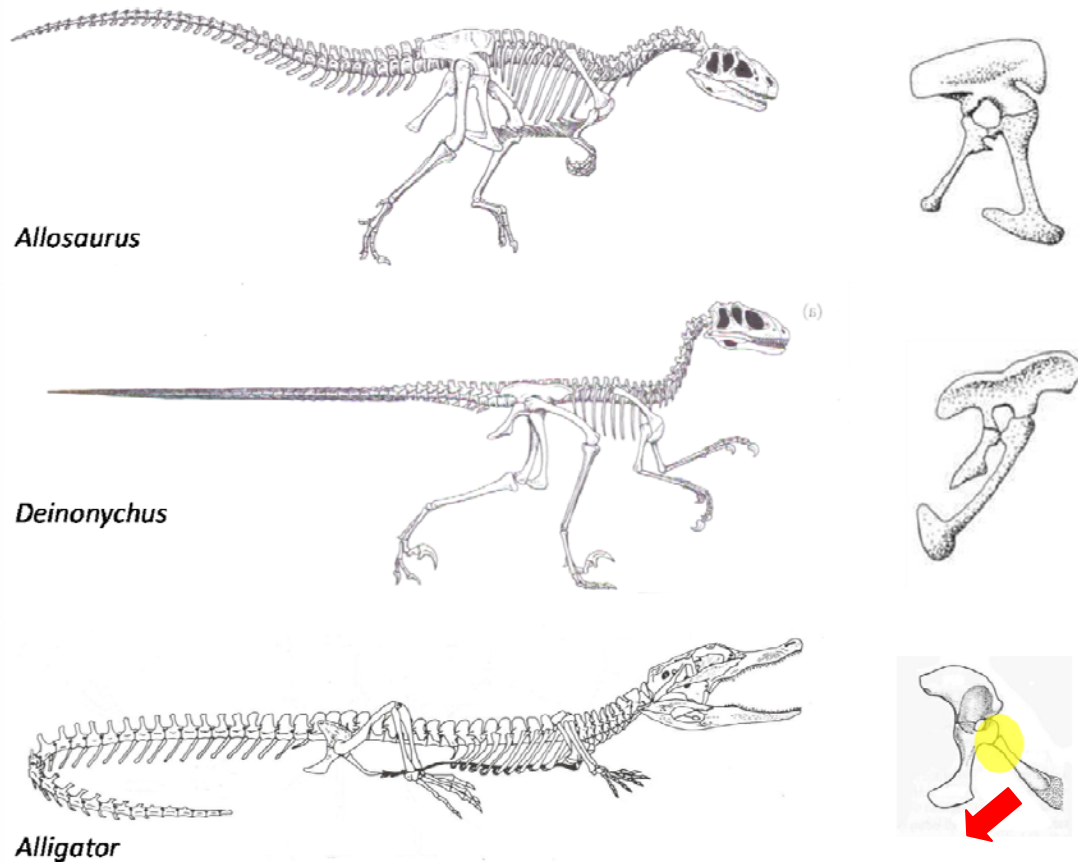


Fig. 2.12: The body shape of extant crocodylians, such as *Alligator*, leaves relatively less room for lateral expansion of the body wall upon inspiration. These animals have mobile pubes which allows for backward as well as lateral movement of the viscera when the liver moves posteriorly during inspiration. In addition to allowing for lateral expansion, the mobile pubis in crocodylians may act to increase tidal volume in a dorso-ventrally flattened animal. This posterior deflection of the mobile pubis in crocodylians sheds light on a possible function of the dramatic opisthopy in small, active theropods, like dromaeosaurs, such as *Deinonychus*. Even though their pubes are fixed, they could be somewhat analogous in function to the mobile pubes of modern crocodylians in that it would facilitate an increased tidal volume, in this case, by allowing a longer muscle length from the liver to the pubis thereby providing greater posterior movement of the liver. When compared to the typical propubic condition of the tri-radiate pelvis of some theropods that are thought to be less active than dromaeosaurs, such as *Allosaurus*, we see that there is less room for diaphragmatic muscle length, therefore less posterior movement of the liver and therefore a relative decrease in tidal volume. (Images modified from Carroll, 1988, Chiasson, 1962 and Romer and Parsons, 1977).

Chapter 3:
The evolution of avian endothermy

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Avian and mammalian endothermy

Endothermy is a highly derived physiological status resulting from chronically elevated resting metabolic rate. Among vertebrate tetrapods, it is attained only by extant birds and mammals. It allows these taxa to maintain stable body temperatures (homeothermy), often in the presence of markedly depressed or elevated ambient temperatures. Clearly, endothermy is one of the most important features of these two successful groups of animals and it is reasonable, therefore, to seek a deeper understanding of not only the physiology of endothermy in these taxa but also how this complex physiological process might have evolved in their ancestors.

Metabolism refers to a series of well defined physiological “cycles,” that result in the formation of biologically useful energy (primarily ATP) and heat. In its absence, processes fundamental to the physiology of all organisms, including growth, reproduction and activity are impossible. Of all environmental variables, ambient temperature has the greatest potential effect on metabolic rate because increasing or lowering body temperature generally accelerates or reduces rates of all physiological processes (Schmidt-Nielsen 1997; Sapp 2004).

Almost all biochemical reactions, including the complex suite of reactions involved in metabolism, are catalyzed by enzymes that generally operate most efficiently within a fairly narrow range of temperatures (Voet, Voet et al. 1999). When an enzyme functions outside of this preferred thermal range, its rate of reactivity changes (“ Q_{10} ” effect), slowing when colder, speeding when warmer. As

a consequence, the ability to maintain a “preferred” stable and elevated body temperature not only allows an organism’s enzymes to operate at accelerated rates, but also with increased efficiencies (i.e., minimal Michaelis constants [K_M]) (Schmidt-Nielsen 1997). Thus, any animal capable of maintaining its body temperature even modestly constant in the face of fluctuating environmental temperatures can minimize or eliminate deleterious Q_{10} effects on enzymatic rate processes. Moreover, such a condition allows for the evolutionary selection of enzyme systems that function most optimally at the homeostatically stabilized body temperature (Hainsworth 1981). Accordingly, almost all tetrapods utilize variations in behavior and/or physiology in order to maintain at least transiently stable internal temperatures, despite fluctuations in environmental temperature.

Extant terrestrial endothermic and ectothermic amniotes employ very different thermoregulatory strategies to acquire (and shed) sufficient body heat to allow constancy of body temperature. Endothermic animals (i.e., birds and mammals) produce their own body heat internally through chronically elevated rates of aerobic metabolism; ectotherms (including especially reptiles) rely primarily on behavioral thermoregulation and access to external sources of heat from the environment (Feduccia 1974; Schmidt-Nielsen 1997).

Endothermic homeothermy is a tightly regulated balance between heat gains and losses, but most body heat is supplied by internal cellular metabolism (Sherwood, Klandorf et al. 2005). Both birds and mammals minimize heat exchange with the environment through the use of insulatory integumentary

structures, feathers in birds and fur in mammals (McNab 1978; Bennett and Ruben 1979; Ruben 1995; Schmidt-Nielsen 1997). Additionally, many extant endotherms reduce heat loss by maintaining stores of subcutaneous fat which act as an insulatory layer; in contrast ectotherms store fat intracoelomically (i.e., in the “deep” body) (Ruben 1995). Elevation of metabolic heat production combined with the low thermal conductance afforded by fur, feathers and fat is the foundation of endothermy (Bennett and Ruben 1979). Consequently, endotherms are often warmer than ambient temperatures and are frequently more active than ectotherms (Bennett and Ruben 1979).

Birds and mammals maintain their internal core body temperature within a narrow temperature span that varies for each group, but most fall generally within the overall range of 35-42°C, with birds usually operating at the higher end of this range (Hainsworth 1981; Schmidt-Nielsen 1997). Significantly, avian and mammalian endothermy evolved independently from one another (Kemp 1988; Hillenius and Ruben 2004; Sherwood, Klandorf et al. 2005).

Advantages and disadvantages of endothermy

Due to the physiological and ecological benefits afforded by endothermy, birds and mammals have succeeded in and even dominate a wide variety of aerial, aquatic and terrestrial environments generally unavailable to ectothermic vertebrates, including arctic regions, high elevations and the nocturnal realm, (Feduccia 1974; McNab 1978). Many travel seemingly effortlessly over great

distances for foraging or migratory purposes (Bennett and Ruben 1979; Ruben 1995; McNab 2002).

In contrast, in the absence of significant external heat sources, most ectotherms frequently experience depressed metabolic rates and often appear slow moving and lethargic (Ruben, Jones et al. 2003). Their abundance and diversity decreases dramatically at the higher latitudes

Increased rates of lung ventilation, improved gas exchange capabilities, enhanced cardiovascular performance as well as extensive cellular and biochemical changes in birds and mammals facilitate maintenance of constant body temperature over a broad range of environmental temperatures (Bennett and Ruben 1979; Bennett 1987). This suite of physiological and anatomical enhancements requisite for endothermic metabolic rates also provides birds and mammals with aerobic capacities that far exceed those of most ectotherms. Observed lab resting metabolic rates of birds and mammals are 5 to 15 times those of similar sized ectotherms, and avian and mammalian field metabolic rates are even higher, some 12 to 20 times greater and even up to 30 times higher than reptiles of similar mass (Bennett and Ruben 1979; Schmidt-Nielsen 1984; Nagy 1987; Bennett 1991; Schmidt-Nielsen 1997; Nagy 2005). Most importantly, avian and mammalian oxygen consumption rates during activity can expand some 5-50X over resting rates (Bennett and Ruben 1979), thus enabling birds and mammals to maintain higher levels of sustainable activity than ectothermic amniotes (e.g., mammals generally are capable of 6-7X greater maximal

sustainable locomotory speeds than equivalent sized reptiles) (Bennett 1991).

This allows endotherms to utilize elevated levels of activity for lengthy periods of time, thus facilitating prey capture, grazing, mate selection, escaping predators and local and long distance migrations (Bennett and Ruben 1979; Ruben 1995).

Although reptiles may achieve high levels of activity and are often capable of producing impressive bursts of activity, they generally do so utilizing less efficient anaerobic metabolism and fatigue quickly due to nutrient depletion and lactic acid accumulation (Ruben 1991). Furthermore, while overall energy requirements of ectotherms are lower due to minimal resting metabolic rates, ectotherms are unable to maintain high levels of aerobic activity and even routine, limited levels of activity typically exceed the aerobic ability of these animals (Bennett and Ruben 1979).

Significantly, some particularly large extant reptiles, such as *Varanus*, living in warm, equable climates are capable of maintaining high and stable body temperatures and thereby remain relatively active over extended periods of time (Ruben, Jones et al. 2003). With their low surface-area-to-volume ratios *Varanus* have little heat loss to the environment and experience only small diurnal fluctuations in internal core body temperature (Frair, Ackman et al. 1972; McNab and Auffenberg 1976; Standora, Spotila et al. 1984; Paladino, O'Connor et al. 1990).

Despite the advantages afforded by endothermy there are significant disadvantages associated with its energetic requirements (Bennett and Ruben

1979). Because the enzymes of endotherms are optimized to function at relatively high and narrow temperature regimes, mammals and birds necessarily maintain elevated metabolic rates and thermoregulatory stability even when resting or otherwise inactive. Therefore, over time, endotherms in the field generally require 15-20X more calories (and food) than equivalent sized ectotherms (McNab 1963; Bennett and Ruben 1979). This increased demand for food often puts endotherms at risk because animals must forage more extensively than an equivalent sized ectotherms and are therefore potentially exposed to greater dangers of predation. Additionally, to prevent torpor and death when ambient temperature drops well below an endotherm's body temperature, energetically costly shivering and fat burning are relied upon to compensate for accelerated rates of heat loss to the environment (Schmidt-Nielsen 1997). Lastly, the warm, stable body temperature of an endotherm provides an ideal environment for parasites (Willmer, Stone et al. 2000).

Physiological bases of endothermy

The foundations of endothermy are defined by many derived physiological and anatomical features not found in ectothermic vertebrates. As noted above, the most notable physiological feature that separates endotherms from ectotherms is significantly elevated rate of aerobic metabolism and associated increased rates of oxygen consumption (Bennett and Ruben 1979; Ruben 1995). Essentially, every aspect of oxygen uptake, transport and delivery has been enhanced in endotherms (Bennett 1991; Ruben, Jones et al. 2003).

The anatomy and physiology of endothermy is almost entirely housed in the soft tissues of extant birds and mammals. Increased cellular oxygen demands of endothermy necessitate major modifications of enzyme systems, organelles, plasma membranes, cells, organs and organ systems to facilitate the delivery, transport and uptake of oxygen to meet the increased demands of the tissues (Ruben, Jones et al. 2003; Seebacher, Schwartz et al. 2006).

The cardiovascular systems of birds and mammals are modified from their ectothermic ancestors to enhance cardiovascular function. In order to increase oxygen delivery to meet the cellular demands of endothermy, there was strong selection for increased cardiac output by the development of a completely partitioned four-chambered heart that allows for widely separated pressures in the pulmonary and systemic vascular circuits (Bennett 1991; Ruben 1995; Hicks 1998; Hicks 2002; Quick and Ruben 2009). Furthermore, the development of fully separated pulmonary and systemic circulation in endotherms prevents the mixing of deoxygenated systemic venous blood with oxygenated systemic arterial blood, dramatically increasing the efficiency of oxygen delivery to the tissues (Hicks 1998; Hicks 2002; Quick and Ruben 2009).

To maximize oxygen acquisition from the environment, extensive pulmonary modifications have occurred in both birds and mammals. Ventilatory rates in birds and mammals have greatly expanded relative to their ectothermic counterparts (Withers 1992; Ruben 1995; Ruben, Jones et al. 2003). Avian and mammalian lungs are much more complex in their structure and are more highly

vascularized than ectothermic amniotes (Bennett 1991; Withers 1992; Ruben 1995; Mania 2002; Ruben, Jones et al. 2003).

In mammals, the lung is a highly compartmentalized structure containing an extensive set of tubes, or bronchi/bronchioles, that deliver air to the 150 million terminal alveoli, the sites of gas exchange (Withers 1992). This arrangement increases the lung surface area relative to body size significantly over that in ectotherms (Perry 1989). In terms of lung ventilatory mechanisms, reptiles utilize primarily costal movements, with exceptions noted for crocodylians and testudines (Kardong 2006), while ventilation of the mammalian lung is accomplished by intercostal muscles supplemented by a muscular diaphragm. The specialized mammalian diaphragm, derived from body wall musculature (Keith 1905), acts as a piston when it contracts, forcing the contents of the abdominal cavity caudally and increasing the volume of the thoracic cavity. This volumetric increase creates negative pressure within the lungs and draws ambient air in.

In birds, there is no mammal-like diaphragm but instead a unique, highly derived system that is surely the most efficient and specialized respiratory system of any extant vertebrate (Duncker 1971; Perry 1989; Withers 1992; Mania 2002). The avian lung consists of a series of nonvascularized air sacs that continuously channel air unidirectionally across the vascularized parabronchi and air capillaries of the lung (Fig 3.1) . The vascular portion of the lung has the largest surface area for gas exchange and the thinnest barrier to oxygen diffusion of any known

vertebrate (Perry 1989; Mania 2002; Quick and Ruben 2009). In order to ventilate this specialized lung, birds have a unique skeletal system designed to create pressure changes within the non-vascularized air sacs while at the same time holding the air sacs open and preventing paradoxical inward inhalatory collapse during generation of negative intramural pulmonary pressure (Quick and Ruben 2009). Extant birds have specialized “ball-and-socket” joints between the vertebral and sternal ribs and between the sternal ribs and the sternum (Zimmer 1935; Sapp 2004). This highly mobile ribcage allows for especially marked expansive movement of the ribs and enlarged sternum during inspiration (Scheid and Piiper 1989). In addition, the avian ventilatory system utilizes a series of disparate skeletal elements (ribs, sternum, synsacrum, pubis and femur) to prevent the paradoxical collapse of the extremely thin walled air sacs, all of which would become dysfunctional if collapsed (Sapp 2004; Quick and Ruben 2009).

Necessarily elevated rates of lung ventilation in endotherms might be expected to incur substantial and hazardous losses of respiratory water and heat. (Jackson and Schmidt-Neilsen 1964; Hillenius 1994; Ruben 1995; Hillenius and Ruben 2004). Indeed, without a mechanism to prevent dangerous rates of respiratory water and heat loss, endotherms could well be in chronic negative water and heat balance, which, if not controlled, would have made the evolution of endothermic metabolism highly problematic and most likely improbable (Hillenius and Ruben 2004). All terrestrial birds and mammals compensate for this potential hazard by employing respiratory turbinates which act to recover the

water vapor and heat contained in expired air (Hillenius 1992; Ruben 1995; Geist 2000; Hillenius and Ruben 2004). Respiratory turbinates are cartilaginous or bony structures that curl inward to varying complexities from the nasal passage wall and are covered by a moist, mucus producing epithelium. A highly vascular layer deep to the epithelium acts to absorb heat and water from the expired air using a countercurrent exchange mechanism (Jackson and Schmidt-Neilsen 1964; Hillenius and Ruben 2004). Significantly, respiratory turbinates are found in all extant terrestrial birds and mammals, but are completely absent in all extant ectotherms (Hillenius and Ruben 2004).

Selective factors in the evolution of endothermy in mammals.

The evolution of endothermy is the culmination of both subtle and dramatic anatomical and physiological changes allowing the shift to endothermic thermoregulation from an ancestral ectothermic state. Anatomical and physiological specializations that evolved in birds and mammals allowed both groups to achieve endothermic status, although endothermy in birds and mammals evolved independently and at different times in geological history (Kemp 1988).

Currently there are two primary hypotheses for selective factors involved in the evolution of avian and mammalian endothermy. In the thermoregulatory model, it is hypothesized that there was initial selection for increasing resting metabolic rate to enhance thermoregulatory capacity (Ruben, Jones et al. 2003; Hillenius and Ruben 2004). The alternate, the aerobic capacity model, proposes

that instead of selection per se for thermoregulation and increased resting metabolic rate, there was initial selection for elevation of aerobic capacity. In this scenario, increased resting metabolic rate and thermoregulatory capacities were beneficial by-products of enhanced aerobic capacities (Bennett and Ruben 1979; Ruben 1995; Hillenius and Ruben 2004).

It is likely that at least incipient endothermy in the mammalian lineage appeared initially in their immediate ancestor, the therapsids (Bennett and Ruben 1979; Bennett, Hicks et al. 2000). Thus, the first evidence of elevated metabolic rates in the mammalian lineage is seen in large wolf- to bear-sized therapsid predators of the late Paleozoic (Ruben 1995). More specifically, theriodont therapsids living in equable subtropical regions of the late Permian possessed rudimentary respiratory turbinates consistent with the early stages of the evolution of endothermy (Ruben 1995). As in some large extant ectotherms discussed above (e.g., *Varanus*), these large “proto-mammals” were most likely already de facto “inertial” homeotherms that have relatively stable body temperatures due to their low surface-area-to-volume ratios and the warm, equable ambient temperatures of the subtropical late Paleozoic (Ruben 1995; Ruben, Jones et al. 2003). Rather, there would likely have been strong selection for an increased ability to increase their aerobic capacity to facilitate greater endurance and aerobically sustainable speeds. Thus the gradual anatomical and physiological changes that occurred in these ancestral taxa to support increased aerobic capacity would have yielded diverse advantages of increased predatory

efficiency and an increased ability to escape predation. These ultimately represent a gradual shift toward complete endothermic homeothermy. Together, these attributes would have increased their capacities for sustainable activities even at low temperatures, thus expanding their utilizable niches and supporting the evolution of the complex behavior patterns of extant birds and mammals.

Despite the vast amount of literature published on the evolution of mammalian endothermy, there is little published on the evolution of avian endothermy.

Metabolic status of Archaeopteryx

The late Jurassic *Archaeopteryx* is the earliest known true bird. There are 10 more-or-less complete specimens and one fossilized feather from the Solnhofen limestone of Bavaria, Germany (Ostrom 1985; Feduccia 1999; Padian 2004; Mayr, Pohl et al. 2007). This small, pigeon-sized bird, which internally bore striking similarities to coelurosaurian theropods, appears to have had an extraordinary combination of both avian and reptilian anatomy. The skeleton was essentially reptilian yet it was completely covered in feathers that were remarkably similar to those of extant birds (Ruben 1991; Ruben 1995; Feduccia 1999).

Much speculation has been devoted to deciphering the metabolic status and lifestyle of *Archaeopteryx* since its discovery almost 150 years ago, and dramatically varied hypotheses on the subject have generated great and often contentious debate (Feduccia 1999). The prevailing model for the lifestyle of

Archaeopteryx prior to the 1970's was that it was bipedal, arboreal and a relatively unskilled flyer that was most likely endothermic (Bock 1965). Today there are two primary prevailing theories of the lifestyle of *Archaeopteryx*. The cursorial theory of the origin of flight proposed that *Archaeopteryx* was a bipedal predator using wing movements to gain lift and ultimately achieving flight from the "ground up" (Williston 1879; Ostrom 1974; Ostrom 1976; Ostrom 1979; Feduccia 1999). The arboreal theory of the origin of flight proposed that *Archaeopteryx* was bipedal and terrestrial, but took to the trees using the claws on its forelimb like that of extant juvenile hoatzins and hopped from perch to perch and glided from tree to tree and/or tree to ground (Bock 1985; Bock 1986; Feduccia 1999). Based on popular wisdom that dinosaurs were endothermic and that *Archaeopteryx* is the direct descendent of the derived theropods of the Cretaceous, both the cursorial and arboreal theories include *a priori* assumptions of an endothermic status for *Archaeopteryx* (Ostrom 1974; Bakker 1975; Ostrom 1976; Ostrom 1979; Bock 1985; Bock 1986; Feduccia 1999). Nevertheless, objective evidence for the metabolic status of *Archaeopteryx* remains, at this time, largely undescribed.

All extant birds are, of course, consummate endotherms that possess especially efficient lungs, the highest body temperatures, and the highest resting metabolic rates of all vertebrates (Sherwood, Klandorf et al. 2005). However, the vast majority of anatomical parameters linked to avian endothermy are

associated with the soft tissues and interpretation of metabolic rates in extinct taxa is therefore problematic.

Of the anatomical and physiological attributes of endothermic metabolism discussed earlier, there is little to no soft tissue evidence of endothermy preserved in known *Archaeopteryx* specimens. There are, however, several skeletal attributes preserved in *Archaeopteryx* that might provide previously unrecognized insights into its metabolic status.

Some of these skeletal features are linked to the presence or absence of enhanced lung ventilation and the presence of air-sac lungs. As discussed above, in extant birds, specialized portions of axial and appendicular skeleton help to ventilate the air-sac lung. In part, these features include the requisite, highly modified rib cage with mobile, jointed intracostal and sterno-costal articulations (Quick and Ruben 2009). In addition, during lung ventilation in modern birds, paradoxical collapse of the extensive posterior non-vascularized air sacs is prevented by caudally expanded ribs, enlarged sternum and, especially, by a highly modified synsacral-femoral complex (Quick and Ruben 2009) (Fig. 3.1 and 3.2). In the latter, the femur has been incorporated into the body wall and remains relatively static during locomotion (Quick and Ruben 2009) (Fig. 3.2). Significantly, the modern avian pelvis, the “synsacrum” includes a specialized antitrochanter process which helps to restrict movement of the femur during locomotion, thus helping to prevent paradoxical collapse of the posterior air sacs during ventilation (Hertel and Campbell 2007) (Fig. 3.2). Without these requisite

skeletal structures, a highly efficient lung air sac respiratory system could not have functioned as it does today (Quick and Ruben 2009) and an endothermic metabolic status could not be inferred.

Fossil specimens of *Archaeopteryx* inevitably possess a simple and unjointed ribcage, a small, flat sternum and a relatively unmodified pelvis (Feduccia 1999; Padian 2004). Most significantly, the absence of an antitrochanter process in the pelvis indicates that incorporation of the femur into the posterior body wall was unlikely and, therefore, it is unlikely that there was a mechanism to prevent paradoxical collapse of posterior non-vascularized air sacs had they been present. The lack of skeletal features in *Archaeopteryx* requisite for ventilating a modern avian lung air sac respiratory system imply that *Archaeopteryx* most likely retained the ventilatory mechanism and therefore metabolic capacity of its ectothermic ancestor.

If *Archaeopteryx* had somehow been able to ventilate an avian lung air sac respiratory system consistent with an endothermic metabolic status, as in modern mammals and birds, it would also necessarily have possessed a mechanism to prevent excessive respiratory water and heat loss which would otherwise have been linked to high pulmonary ventilation rates. Respiratory turbinates, which are found in the nasal cavities of all extant terrestrial endotherms, function to prevent accelerated rates of respiratory water and heat loss, but these structures are either very thin, bony structures or they are cartilaginous. Such structures are rarely preserved in the fossil record (Hillenius

and Ruben 2004). Fortunately, there is a strong correlation between nasal cavity cross-sectional area and the presence of respiratory turbinates in extant endotherms (Ruben, Hillenius et al. 1996; Hillenius and Ruben 2004).

Significantly, *Archaeopteryx*, like theropod dinosaurs, possessed extensive maxillary and promaxillary fenestrae as well as paranasal sinuses that markedly restricted the diameter of the nasal passage. Thus, the presence of respiratory turbinates is highly unlikely (Ruben, Jones et al. 2003; Hillenius and Ruben 2004). Without the presence of skeletal structures requisite to ventilating an avian style lung air sac system and without requisite mechanisms associated with endothermic lung ventilation rates, it is most likely that *Archaeopteryx* did not possess an air sac lung and did not have pulmonary ventilation rates similar to those in modern endotherms. These data suggest that *Archaeopteryx* was unlikely to have attained, or perhaps even approached an endothermic metabolic status.

An alternate theory to conventional cursorial or arboreal theories for avian flight origins is that *Archaeopteryx* lived both a cursorial (terrestrial) lifestyle combined with an arboreal lifestyle and was capable of powered flight from both the “ground up” and the “trees down,” while nevertheless retaining ectothermic metabolic status (Ruben 1991). As discussed earlier, a number of extant reptiles, such as *Varanus*, have somewhat expanded aerobic metabolic capacities and many extant reptiles are capable of maintaining extremely intense burst levels of exercise for several minutes (Bennett and Ruben 1979; Ruben and

Battalia 1979; Bennett 1991). Indeed, during anaerobically-supported, burst level activity, locomotory muscles in many extant reptiles generate power sufficient to support powered (flapping) flight in birds (Ruben 1991). Thus, endothermic metabolic status would not have been requisite for short distance powered flight in early birds; even an ectothermic *Archaeopteryx* would have been capable of short distance powered flight and a ground upward “takeoff” (Ruben 1991). Although it seems highly likely that *Archaeopteryx* was capable of short distance powered flight and possibly even takeoff, its ectothermic status did not afford it the aerobic capacity necessary to support the long distance powered flight of extant, endothermic birds (Bennett 1991; Ruben 1991).

When did birds become endothermic and why?

When and why, then, did birds attain endothermic metabolic status? To answer these questions, it is helpful to review some of the requisite anatomical and physiological characteristics that are necessary to maintain an endothermic metabolism in extant taxa.

Endothermic metabolism is characterized by high resting metabolic rates tightly linked to high rates of oxygen consumption and lung ventilation. To deliver sufficient oxygen an efficient respiratory system is a necessity. In modern birds this consists of a highly derived lung air sac complex. Significantly, *Archaeopteryx* did not have the requisite skeletal modifications required to have ventilated a lung air sac system. In addition it lacked a mechanism to reduce elevated rates of respiratory heat/water loss that would otherwise have been associated with

endothermic lung ventilation rates. It almost certainly had not attained an endothermic metabolic status.

The only known bird of the Jurassic is *Archaeopteryx*, but by the mid-Cretaceous, at least two groups of ornithiurine (i.e., modern-like) birds had emerged, the Hesperornithiformes (*Hesperornis*) and Ichthyornithiformes (*Ichthyornis*) (Carroll 1988). Both *Hesperornis* and *Ichthyornis* lived in marine habitats. *Hesperornis* was a large flightless, diving bird but *Ichthyornis* was a gull-like sea bird apparently capable of sophisticated and perhaps long distance flight, (Carroll 1988; Feduccia 1999). Both groups possessed highly mobile, ball-and-socket jointed ribcages, and relatively large sterna that would have allowed for ventilation of a lung air sac system (Carroll 1988; Feduccia 1999). Also, both groups possessed structures requisite to prevent paradoxical collapse of the posterior air sacs, including caudally projected ribs, expansive synsacrum, elongate pubis and relatively immobile femora which were apparently embedded within the body wall. Additionally, nasal cavity volume and cross-sectional areas in *Hesperornis* and *Ichthyornis* were expanded and nearly identical to those attributes in modern birds. These features are consistent with the presence of respiratory turbinates and imply that lung ventilation rates in these taxa approached, or were perhaps equal to those in modern birds (Hillenius and Ruben 2004). Taken together, these data strongly imply that by the mid-Cretaceous (i.e., 35 MY post-*Archaeopteryx*) at least some birds had approximated, or perhaps had even attained, endothermic metabolic status.

Somewhere in time between *Archaeopteryx* and the appearance of *Hesperornis* and *Ichthyornis* there was a shift from avian ectothermy to endothermy, or near endothermy. *Archaeopteryx* was probably capable of little more than short distance powered flight (i.e., less than 1 km), while increased capacity for longer distance flight would have expanded niches available to early birds. In this regard, it is reasonable to suggest that endothermy and the increased aerobic capacity that accompanies it would have been requisite for longer distance powered flight capacity.

Finally, since *Archaeopteryx* was most likely ectothermic there was a ~35 MY gap between the appearance of early birds and the development of avian endothermy. Further investigation into the intermediate stages in the evolution of avian endothermy might provide key insights into this timescale and the selection pressures associated with the appearance of modern avian physiology.

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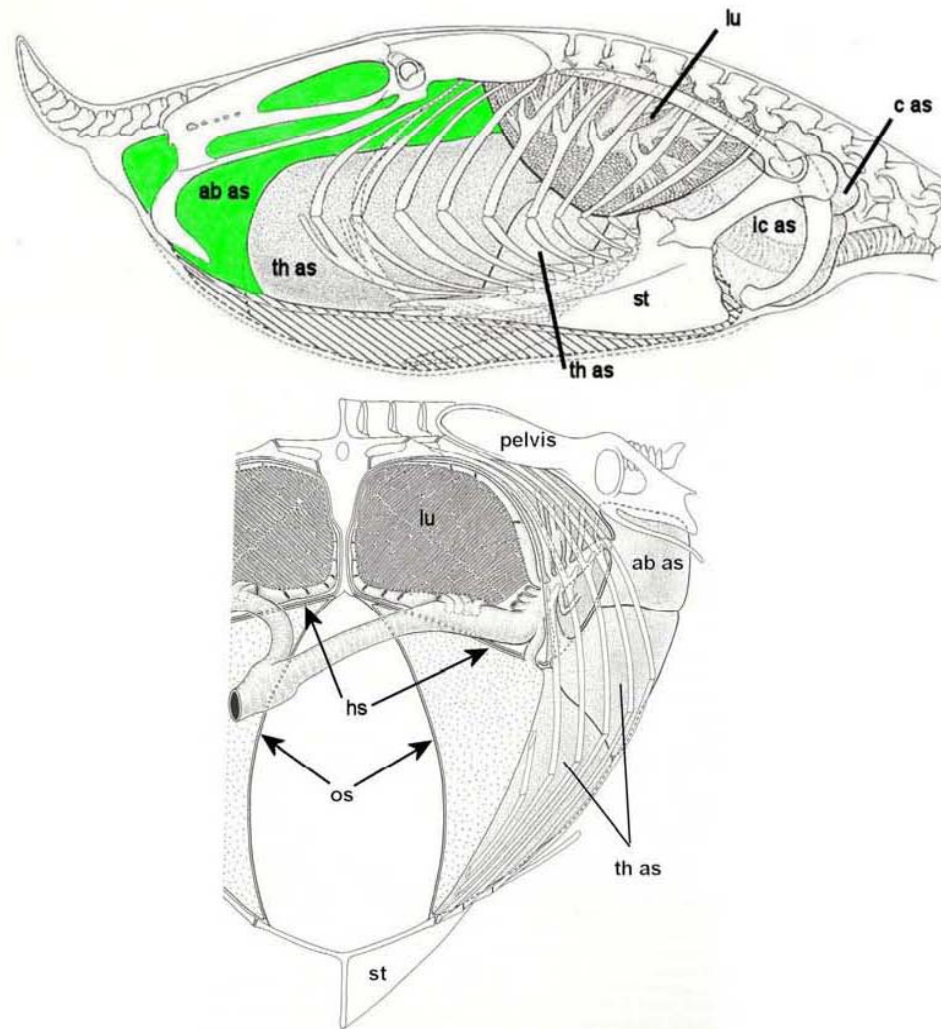


Fig. 3.1. Longitudinal diagram of the extant bird lung-air-sac system. Unidirectional air flow generated by the non-vascularized abdominal (ab as), thoracic (th as), clavicular (ic as) and cervical air sacs (c as) moves new air with every breath across the dorsally positioned lung (lu). The skeletal elements required to hold the thin walled air sacs open, thereby preventing paradoxical collapse, are the sternum (st), pelvis, ribs and femur (not shown). (Image modified from Quick and Ruben, 2009).

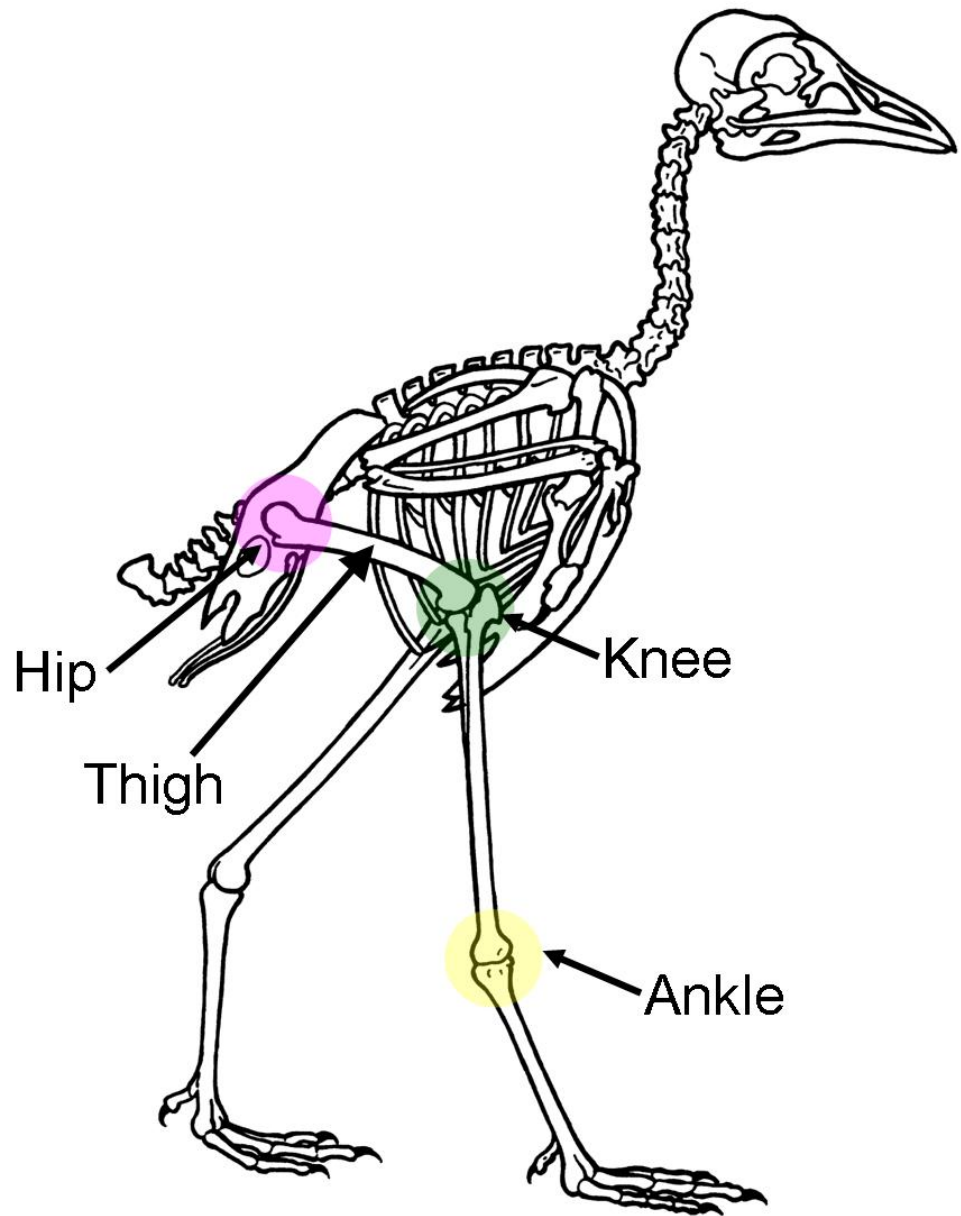


Fig. 3.2: Lateral view of a diagram of a modern bird skeleton indicating the position of the hip, knee and ankle joints. To prevent the paradoxical collapse of the extensive posterior non-vascularized air sacs, the caudally expanded ribs, the enlarged sternum, the highly modified synsacral-femoral complex and the incorporation of the femur into the body wall all act in concert to provide rigid support to hold open the highly collapsible air sacs. (Image modified from Quick and Ruben, 2009).

Chapter 4:
The pelvis of *Archaeopteryx* and the politics of dinosaur biology

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John A. Ruben

Almost as if on cue, just two years after publication of Charles Darwin's *On The Origin of Species*, a nearly complete skeleton of the earliest known bird was unearthed from late Jurassic Solnhofen limestone deposits in southern Germany (Feduccia 1999). *Archaeopteryx lithographica* possessed a reptilian skeleton but was almost fully cloaked in a set of body and flight feathers similar in most respects to those in many extant birds (Ostrom 1985) (Fig. 4.1). To date, ten individuals of the renowned *Archaeopteryx* have been discovered in Germany (Mayr, Pohl et al. 2007) and the specimens have been thoroughly described and redescribed. Understandably, specimens of this iconic "first bird" are arguably the most famous fossils ever found (Feduccia 1999).

From almost their outset, discussions about the paleobiology of *Archaeopteryx* have been contentious. Over the almost 150 years since it was unearthed, descriptions of *Archaeopteryx* have included (but not been limited to) terms such as "reptile," "dinosaur," "bird," "missing link," "Rosetta Stone" and "forgery" (!). To this day it remains an object of controversy and a subject of acrimonious debate(s) on its anatomy, physiology, origins, capacity for powered flight, lifestyle and numerous other aspects of its biology (Feduccia 1999). Part of the difficulty in discussing the paleobiology of *Archaeopteryx* stems from the unusually varied skeletal reconstructions presented by the numerous authors who have studied the fossils. Thus, even slight variations in the placement of skeletal elements can have dramatic effects on the interpretation of the biology of extinct taxa and, moreover, accurate reconstruction of fossilized sauropsids

(i.e., birds or reptiles) is especially problematic because the articular surfaces of their long bones consist of large cartilaginous caps which are most unlikely to fossilize (Haines 1969).

Anatomy of the pelvis in Archaeopteryx

Of all its skeletal elements, perhaps no others have been reconstructed with such variation, or similarly impacted interpretation of its biology as has the pelvis in *Archaeopteryx*. It is generally agreed that *Archaeopteryx's* three part pelvis was composed of paired ischia, ilia and pubes (Fig. 4.2) and was, overall, remarkably similar to the pelvis in many other subsequent Mesozoic birds, including such familiar forms as *Confuciusornis*, *Chaoyangia*, *Sinornis* and many others (Martin 1995; Martin, Zhou et al. 1998; Feduccia 1999; Naples, Martin et al. 2002). The ilia, ischia and pubes all appear to have contributed to the open acetabulae and, unlike modern birds, individual pelvic components appear to have remained unfused and somewhat loosely articulated as in reptiles (Heilmann 1927; Ostrom 1976; Tarsitano 1980; Martin 1991; Feduccia 1999). The ilia were antero-posteriorly elongate with the dorsal edge being slightly convex (Ostrom 1976, Tarsitano Hecht 1980, Wellnhofer 1985) (Fig. 4.2). Postacetabular portions of the ilia were short with tapered posterior processes; the preacetabular ilia were very birdlike with anteriority expanded, rounded cranial edges (Ostrom 1976; Tarsitano 1980; Wellnhofer 1985). The ischia were robust, unusually quadrangularly shaped and converged distally in paired, small, curved, hooked processes (Petronievics and Woodward 1917; Heilmann 1927; Tarsitano

1980; Martin 1991) (Fig. 4.2). The stout ischia were relatively short compared to the elongate, slender pubes (Ostrom 1976; Tarsitano 1980). The pubes were long, narrow, relatively linear bones that expanded medially at approximately the mid-shaft and formed a pubic apron; at their most distal point, there was a spoon-like medial symphysis (Heilmann 1927; Martin 1991; Feduccia 1999) (Fig. 4.2).

History of the description of the pubes in Archaeopteryx and avian origins among theropod dinosaurs

One of the more chronically contentious topics linked to studies of *Archaeopteryx* has been interpretation of the position and function of the pubic bones. More specifically, there remains acrimonious debate about the angle of the pubis relative to the sacral axis and the shape and orientation of the distal symphyseal termini of the pubes (Walker 1980; Feduccia 1999).

From its 19th century discovery until the 1970's, the pubis of *Archaeopteryx* was inevitably reconstructed in a typical modern avian-like, opisthopic position, i.e., with the distal extremity rotated markedly caudally, inferior to the ischium, and at an angle to the vertebral column of approximately 135 degrees (Heilmann 1927; Charig 1972; Walker 1980) (Fig. 4.3). These reconstructions were based primarily on the superbly preserved pelvises of the London and Berlin specimens (Tarsitano 1980; Walker 1980) (Fig. 4.4). In these specimens, not only are the skeletons generally well articulated but many other elements were preserved *in situ* as well, including primary and secondary flight feathers (Tarsitano 1980).

Nevertheless, based largely on many of his observations of the poorly preserved Eichstätt specimen, and two other mostly disarticulated specimens, in 1975, the influential John Ostrom redescribed *Archaeopteryx* and all birds as having been direct descendants of the carnivorous dinosaurs and interpreted its pelvis as having been remarkably like that of typical theropod dinosaurs and not at all bird-like (Ostrom 1975). Thus, despite the unequivocal evidence preserved in the superbly preserved London and Berlin specimens, the pelvis of *Archaeopteryx* has for the last 30+ years been presented as having been more like that of typical theropod dinosaurs (Fig. 4.5), that is with the pubes in a nearly vertical position (approximately 90 degrees relative to the vertebral column) (Wellnhofer 1974; Ostrom 1975; Ostrom 1976; Wellnhofer 1976; Tarsitano 1980; Ostrom 1985; Wellnhofer 1985; Feduccia 1999). Ostrom recognized that the pubis in the Berlin specimen was preserved in the avian position, but he asserted that the Berlin pubis had been shifted by post-mortem displacement and were no longer in their natural position (Ostrom 1973; Ostrom 1975; Ostrom 1976). Ostrom drew much of his evidence not only from the Eichstätt specimen but also from the Haarlem (Teyler) and Maxberg (Solnhofen) specimens. In all three, the pubes are nearly vertical with orientations of about 100 degrees relative to the vertebral column. For Ostrom, these confirmed that the Berlin specimen did not reflect the *in situ* condition (Ostrom 1973; Ostrom 1976).

Based on his own studies of the Eichstätt specimen, Peter Wellnhofer concurred with Ostrom that the pelvis of the Berlin specimen had been rotated

caudally post-mortem to falsely appear bird-like (Wellnhofer 1974; Tarsitano 1980; Walker 1980; Wellnhofer 1985; Feduccia 1999). In describing the Eichstätt specimen, Wellnhofer restored the pubis of *Archaeopteryx* at a 110 degree angle, greater than Ostrom described, but far less than the avian, opisthopubic position of the Berlin specimen (Wellnhofer 1985).

Ostrom went on to describe other evidence from the pubis of *Archaeopteryx* which he claimed to be supportive of its supposedly theropod origins. Thus, he also asserted the existence of a “pubic boot” located at the distal extremity *Archaeopteryx*’ pubic apparatus, and also like that preserved in many theropod dinosaurs (Ostrom 1976; Feduccia 1999).

Together, the observations of Ostrom and Wellnhofer provided strong and long-lasting impetus for the currently popular dogma among most paleontologists that birds are directly derived from the dinosaurs. Furthermore, the anatomy of *Archaeopteryx*’ pelvis as described by Ostrom supposedly provided strong evidence for the lifestyle of *Archaeopteryx* and for the origins of avian flight. Subsequent to Ostrom’s initial work, others have argued that *Archaeopteryx*’ vertical, booted pubis was consistent with its having been a bipedal, theropod-like terrestrial predator using running-related wing movements to gain lift and ultimately achieving flight from the “ground up” (i.e., “cursorial theory” for the evolution of flight) (Williston 1879; Ostrom 1975; Ostrom 1976; Ostrom 1979; Feduccia 1999). These assertions should be regarded with caution.

New evidence for a bird-like pubis in Archaeopteryx

As previously noted, much of the data for a theropod like orientation of the pubes in *Archaeopteryx* is based on the conditions in the Maxberg, Haarlem and, most especially the Eichstätt specimens. However, upon closer inspection, and most especially under UV light, the true condition of the supposedly “pristine” Eichstätt pelvis is evident: all pelvic elements have been severely crushed (Fig. 4.6). Most significantly, distal elements of the ischium and pubis have clearly been fractured and rotated, either immediately post-mortem or during taphonomic processes, to a more theropod-like anterior or vertical position. Moreover, at least to my eye, preservation in the Maxberg and Haarlem specimens is so poor (e.g., the Haarlem specimen was long thought to be a pterosaur!) that any definitive interpretation of pelvic structure based on these fossils was, and remains, unwise.

Rather, I suggest that, as almost all pre-Ostrom authors concluded, it is more appropriate to refer to the specimens with clearly the best preservation of pelvic elements. Together, the relatively pristine London and Berlin specimens can be used to interpret the *in situ* pubic angle to be somewhere between what is observed in the Berlin specimen (135°) and that which is seen in modern birds (150°+).

With respect to the distal pubic symphysis, when viewed anteriorly (London specimen) there existed a very distinct cup-shaped structure called the “hypopubic cup,” dramatically unlike the robust, vertically oriented pubic “foot” or “boot” found in theropod dinosaurs (Martin 1991; Feduccia 1999; Jones and

Ruben 2001). The hypopubic cup is best viewed in UV light in the Berlin specimen, where the two halves have been folded over onto one another (Ruben, Jones et al. 1997) (Fig. 4.2 and 4.4). It has been suggested that the hypopubic cup of *Archaeopteryx* and other early birds was a site of suprapubic musculature which moved the pelvis and the tail assisting in ventilation of non-vascularized air sacs (Ruben et al 1997, Ruben et al New Persp 2001) (Fig. 4.7). This morphology and behavior is also seen in extant, arboreal, perching birds that use pelvic rotation and suprapubic musculature to ventilate their lungs when their primary ventilatory mechanism, their sternum, is unavailable (i.e., when roosting) (Ruben, Jones et al. 1997; Jones and Ruben 2001).

Conclusions

As noted above, the combined presence of the hypopubic cup and an opisthopubic pubis in *Archaeopteryx* and other early birds is unknown in any theropod, but is consistent with a predominantly arboreal lifestyle (Ruben, Jones et al. 1997; Feduccia 1999; Jones and Ruben 2001).

Why then did, and do, Ostrom and others choose to ignore the evidence for pelvic structure in *Archaeopteryx* that is preserved in the magnificent London and Berlin specimens? I cannot say with certainty, but there can be no doubt that Ostrom's interpretation of pelvic structure in *Archaeopteryx* has become a fundamental tenet of the broadly popular notion that birds are little more than flying dinosaurs.

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Fig. 4.1: Berlin specimen of *Archaeopteryx lithographica*. (Image courtesy of W. Hillenius)

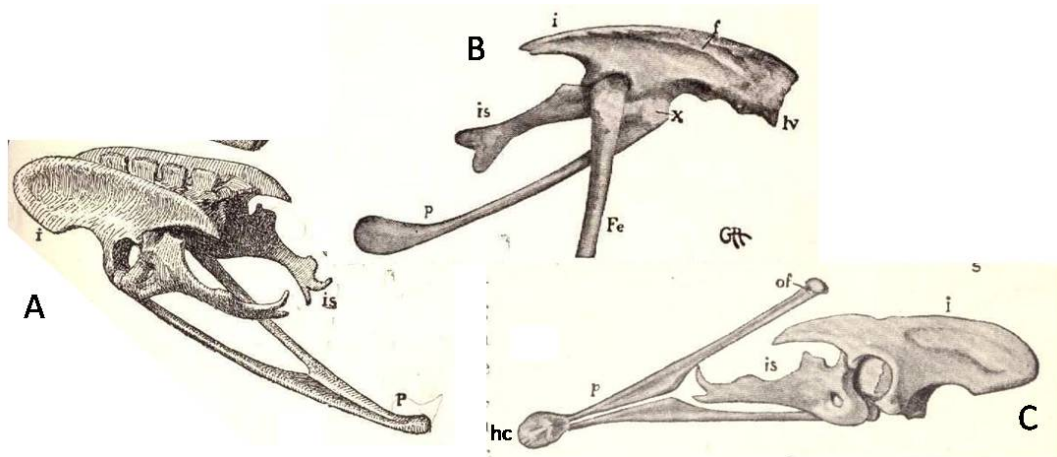


Fig. 4.2: Diagrams of the pelvis of *Archaeopteryx* reconstructed from the London specimen (A and B). The three part pelvis is composed of the long, low, dorsally positioned ischium (i), the posteriorly reflected ischium (is) and pubis (p). A drawing of the pelvis of the fossil specimen (C) shows the actual position of the pelvic elements including the hypopubic cup (hc) at the distal end of the pubis. (Images modified from Heilmann, 1927)

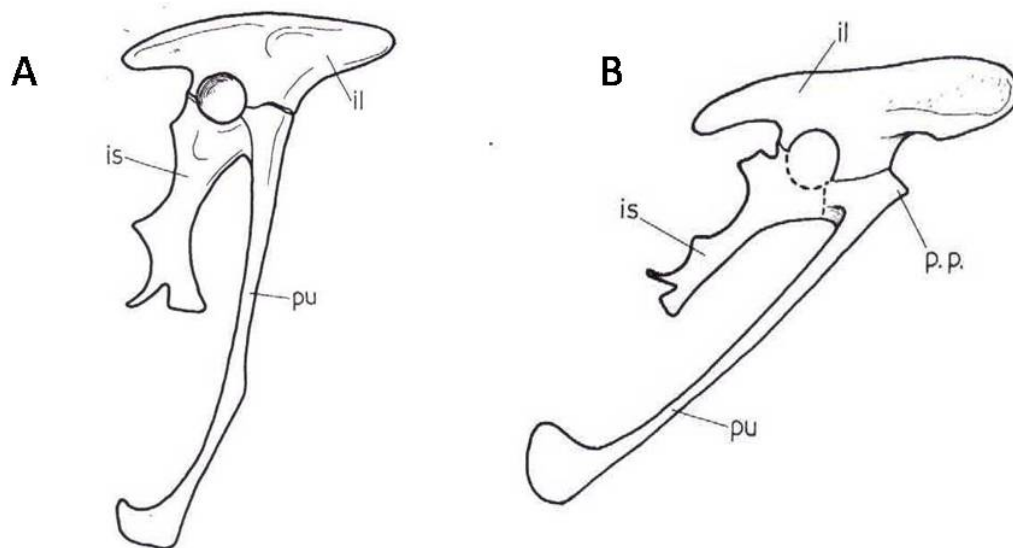


Fig. 4.3: Various reconstructions of the pelvis of *Archaeopteryx* showing the highly varied interpretations of pubic position. The Eichstätt specimen's pubis (A) was preserved in a vertically oriented position of approximately 100 degrees relative to the sacral axis. The Berlin specimen's pubis (B) was preserved in a posteriorly reflected, opisthopic position of approximately 135 degrees relative to the sacral axis. (Image modified from Walker, 1980)

Fig. 4.4: Pelvises of the Berlin (left) and London (right) specimens of *Archaeopteryx*. The Berlin specimen shows the pubis in the likely opisthopic position. Both pelvises show the hypopubic cup at the distal end of the pubis (in the Berlin specimen the two halves of the pubis that form the hypopubic cup have been folded over each other during fossilization as shown in B). (Images courtesy of W. Hillenius)

Fig. 4.4:



Fig. 4.5: Ostrom's reconstructions of *Archaeopteryx* (A) and the theropod dinosaur, *Deinonychus* (B) showing the pubis of *Archaeopteryx* in the vertical position found in many theropod dinosaurs. An alternate, avian reconstruction of *Archaeopteryx* (C). (Images (A and B) modified from Ostrom, 1976 and C from Martin, 1995)

Fig. 4.5:

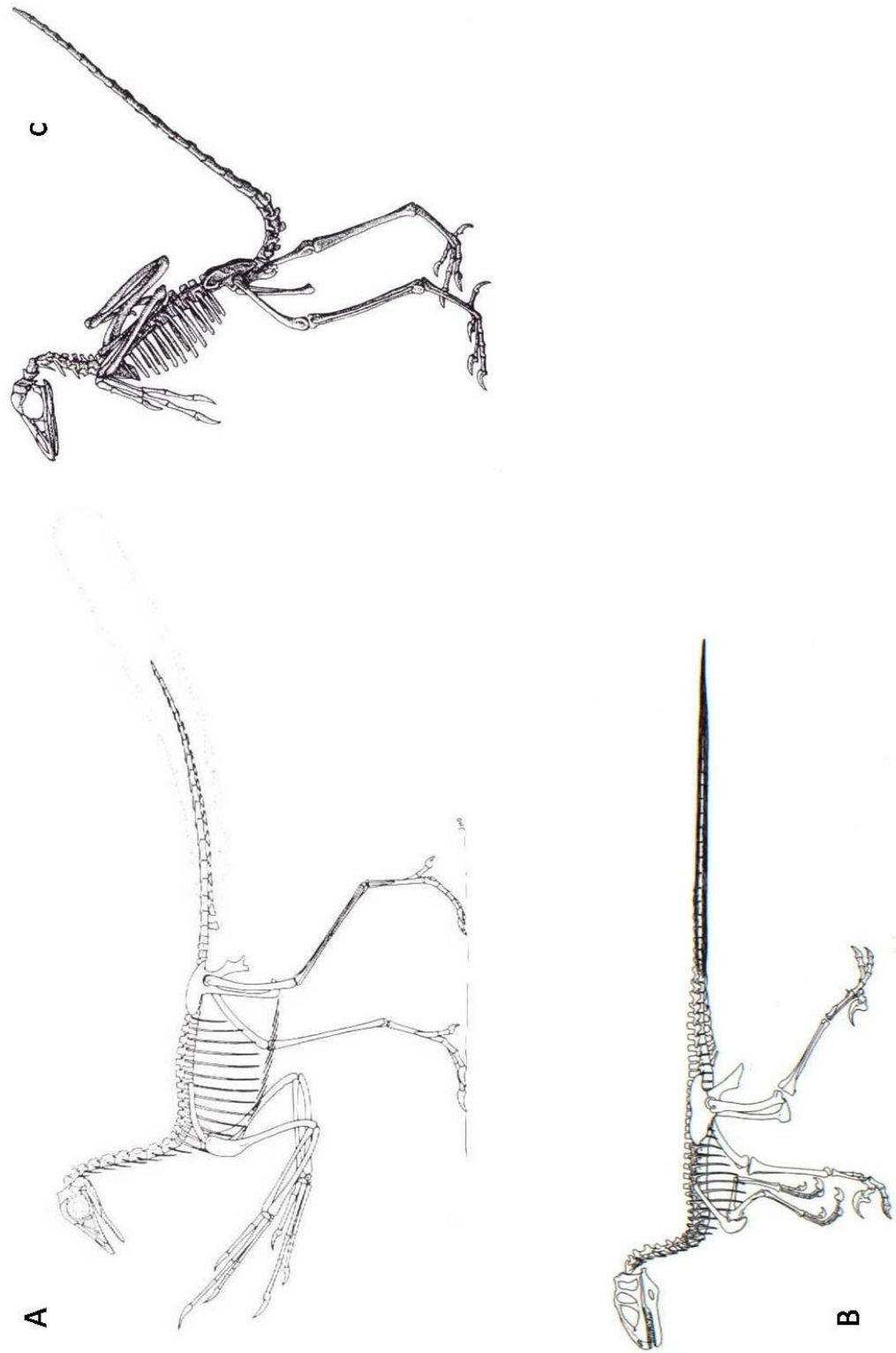




Fig. 4.6: Images of the Eichstätt specimen of *Archaeopteryx* showing the severely crushed and distorted pelvic elements. Abbreviation: p, pubis. (Images courtesy of W. Hillenius)

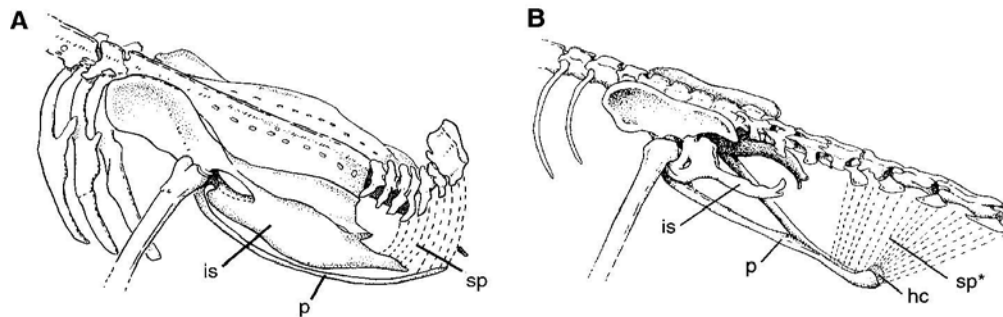


Fig. 4.7: Pelvis of an extant, perching bird (A) showing the pelvis and tail with suprapubic musculature used for ventilating posterior air sacs to assist in lung ventilation while perching. Pelvis of *Archaeopteryx* (B) reconstructed with similar morphology to extant perching birds. Abbreviations: is, ischium; p, pubis; hc, hypopubic cup; sp, suprapubic musculature; sp*, likely suprapubic musculature. (Image modified from Ruben et al, 1997)

Chapter Five: General Conclusion

It is difficult to fully reconstruct the biology of long extinct forms, especially so because of the incomplete nature of the fossil record. Regardless of these limitations, we can use anatomical characters that are functionally linked to specific attributes within living, related forms to attempt at least partial reconstruction of the biology of extinct forms.

The skeletons of early birds like *Archaeopteryx* and other theropod taxa are well known and it has been argued frequently that they utilized modern bird like respiratory systems to support bird like metabolic rates (Ostrom 1974; Bakker 1975; Ostrom 1976; Ostrom 1979). However, I have shown that *Archaeopteryx* and theropod dinosaurs lacked the skeletal components consistent with the support and maintenance of the unique avian style lung air-sac system. In the absence of a high performance avian lung air-sac system adapted for elevated oxygen extraction, there is little reason to reconstruct *Archaeopteryx* or theropods as endotherms. It is more likely that theropods ventilated a relatively non-specific crocodilian-like lung using crocodilian respiratory ventilatory mechanisms to support ectothermic metabolic rates. Although *Archaeopteryx* was likely capable of powered flight, full endothermy was not likely achieved in birds until the mid-Cretaceous birds *Ichthyornis* and *Hesperornis*.

Future study into the evolution of the avian thoracic, pelvic and limb skeleton will provide additional insight into the evolution of avian endothermy and powered flight.

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