

AN ABSTRACT OF THE DISSERTATION OF

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Abstract approved:



John A. Ruben

Inferences regarding the biology of extinct taxa are often founded primarily on cladistically-based phylogenetic hypotheses. However, these inferences are frequently inconsistent with the morphology and physiology of modern animals. I suggest that reference to the biology of modern animals might be a more appropriate tool to aid in the reconstruction of the morphology and physiology of extinct animals. Here, this methodology is applied to: (1) reconstruction of the respiratory anatomy and physiology of some Paleozoic archosaurs (dinosaurs, early birds, pterosaurs, and early crocodilians), (2) understanding cursorial locomotion in birds and bipedal dinosaurs, and (3) a reinterpretation of an enigmatic archosaur, *Longisquama*. The conclusions drawn from these data raise questions regarding current thinking regarding relationships between birds and dinosaurs.

NEW INSIGHT INTO THE MORPHOLOGY AND PHYSIOLOGY OF  
MESOZOIC ARCHOSAURS

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Terry D. Jones, Author

## ACKNOWLEDGEMENTS

I thank my advisor, John Ruben, without whose guidance, encouragement, and financial and intellectual support, this work would never have been completed. I also thank my committee members, Joseph Beatty, Art Boucot, Charlie Miller, and Karen Timm, the faculty, staff, and current and former graduate students (particularly Emma Coddington, Nick Geist, John Melville, and Sara Tallorovic) of the Zoology Department. Additionally, I thank my colleagues and/or collaborators Jim Farlow, Alan Feduccia, Nick Geist, Don Henderson, Jaap Hillenius, Evgeny Kurochkin, Paul Maderson, Larry Martin, and Storrs Olson for their invaluable input and discussion regarding the biology of extinct and/or extant animals. Finally, I thank the curators in natural history museums in the United States (American Museum of Natural History, Harvard Museum of Comparative Zoology, University of Kansas Museum of natural History, and Yale Peabody Museum) and Europe (British Museum of Natural History, Bergermeister Museum, Eichstätt Museum, Humboldt Museum of Natural History, and Museum of Geology and Paleontology) for allowing me access to specimens for study.

## **CONTRIBUTION OF AUTHORS**

This research for this dissertation was funded by research grants to John Ruben and Jaap Hillenius.

Centers of mass in chapter 3 were calculated using D. Henderson's equations for calculation of centers of mass for fossil specimens. The manuscript was greatly improved by the input of the co-authors.

Chapter 4 resulted from an informal conference at the University of Kansas Museum of Natural History hosted by L. Martin, and is based on fossil specimens that are housed at the Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia. These were brought to the United States by E. Kurochkin and V. Alifanov. Each of the co-authors was offered (and accepted) a co-authorship in recognition of their invaluable input during the study of the specimens.

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## **DEDICATION**

This dissertation is dedicated to my wife, Kim, and my daughters, Kayla, Mallory, and Sydney, for the love and support they have given me during the seeming interminable time spent working toward my graduate degrees.

# **NEW INSIGHTS INTO THE MORPHOLOGY AND PHYSIOLOGY OF MESOZOIC ARCHOSAURS**

## **CHAPTER 1: INTRODUCTION**

Reconstructions of the biology of extinct animals are often based exclusively on cladistically-based assumptions about their affinities to extant groups. The result of this simplistic approach is that long-extinct organisms are frequently assumed to have been biologically similar to their extant relatives. However, in many cases, the physiology of extinct taxa cannot necessarily be deduced from their phylogenetic history. This is especially true when lineages assume novel adaptations, or when phylogeny is poorly understood. In these cases, interpretations regarding the physiology of extinct animals are more robust if based on the physiology of extant animals.

In the following three chapters I draw inferences about some critical biological attributes in long extinct taxa. Accordingly, I have relied on the preservation of unique morphological attributes whose presence is causally-linked to distinct physiological mechanisms in living species. In Chapter 2, aspects of metabolic physiology in dinosaurs, early birds, pterosaurs, and early crocodilians are reconstructed using a number of previously ignored links between distinct morphological attributes and respiratory physiology in living species.

Chapter 3 focuses on morphological features whose presence is tightly linked to specialized modes of cursorial locomotion in bipedal archosaurs—birds,

ornithomimid dinosaurs, and theropod dinosaurs. I then use this data to test whether *Caudipteryx* was a cursorial, secondarily flightless bird or the only truly feathered “theropod dinosaur.”

Chapter 4 centers on a new interpretation of a fossil that was described as “enigmatic” by its discoverer and has remained as such since. Given the presumed ancestor-descendant relationship of dinosaurs and birds, it has been suggested that, although no dinosaur is currently known to have possessed feathers, or feather-like structures, feathers originated within the Dinosauria. However, *Longisquama insignis*, an archosaur that lived 75 million years before the first known bird *Archaeopteryx*, and co-existed with the earliest dinosaurs, had integumentary structures that have unique morphological and developmental characteristics of modern avian feathers.

In the summary chapter, Chapter 5, I discuss biological and phylogenetic implications of the preceding chapters.

**CHAPTER 2: RESPIRATORY STRUCTURE AND FUNCTION IN  
THEROPODS AND SOME RELATED TAXA**

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## ABSTRACT

Respiratory turbinates exist in the nasal passages of all extant terrestrial endotherms. They minimize respiratory water and heat loss that would otherwise result from the high lung ventilation rates of birds and mammals. Respiratory turbinates are absent in all extant ectotherms. Reduced nasal passage cross sectional area, the relative brevity of the nasal passage, and/or the presence of extensive paranasal sinuses in theropods, pterosaurs, and early birds are inconsistent with the presence of respiratory turbinates. The absence of respiratory turbinates indicate that these taxa probably had resting or routine metabolic rates similar to those of modern ectotherms, but reveal little about their capacity for activity.

Anatomical features of the septate lung of modern reptiles probably limited its capacity to support rates of oxygen consumption during sustained activity. Only the mammalian alveolar lung and the highly modified avian “air sac” septate lungs are capable of  $O_2$ - $CO_2$  exchange rates consistent with the stamina of most modern endotherms. Fossilized soft tissue and skeletal evidence indicate that theropod dinosaurs and pterosaurs, like crocodilians, likely possessed reptilian septate lungs that were ventilated with a hepatic piston-diaphragm mechanism. Perhaps this ventilatory mechanism allowed theropods, early crocodilians, and pterosaurs, to circumvent some of the constraints of the septate lung, and may have resulted in oxygen consumption rates during activity that approached those of some extant endotherms.

Axial skeletal morphology of *Archaeopteryx* and the enantiornithine birds indicates that, although both groups probably possessed incipient nonvascularized abdominal air sacs, they lacked the highly derived flow-through lung and the enhanced aerobic capacities of modern birds. Additionally, their pelvic morphology is consistent with the presence of suprapubic musculature similar to those that ventilate the posterior air sacs in modern arboreally roosting birds. These latter features are consistent with an arboreal origin for birds.

## METABOLIC STATUS

Previous work addressing metabolic status and respiration in extinct archosaurs has frequently been based largely on phylogenetic constructs. Often there has been little, if any, comparison with appropriate anatomical structures in living animals that were functionally linked to their metabolic and/or respiratory physiology. For example, it has been assumed that since modern birds are endothermic, then their ancestors must also have been endothermic (Paul 1988; Ostrom 1976). Reliable evidence of metabolic status in extinct taxa requires investigation of anatomical features that are functionally linked to metabolism in extant animals, preservable in fossils, and exclusive to either endotherms or ectotherms.

### Extant taxa

Modern birds and mammals have resting or routine metabolic rates that are about an order of magnitude greater than those of equivalently sized ectotherms (Bennett and Ruben 1979; Nagy 1987). Since ambient air temperatures and/or relative humidity are generally lower than deep body temperatures and relative humidity, and elevated resting metabolic rates require increased lung ventilation rates, this can result in broadly accelerated rates of respiratory heat and water loss (Geist, in press). To ameliorate this situation, terrestrial endotherms, including those inhabiting particularly warm and/or humid environments, possess nasal respiratory turbinates—epithelially covered, complex cartilaginous or osseous

structures located in the nasal passage proper—that increase surface area and serve to significantly reduce respiratory heat and water loss (Figure 1) (Ruben *et al.* 1997a, b; Hillenius 1992, 1994; Geist, in press). The relatively low routine metabolic rates and associated low lung ventilation rates of modern ectotherms render respiratory heat and water loss in modern reptiles inconsequential (Geist, in press). Accordingly, nasal respiratory turbinates are not found in any extant ectotherm (Ruben *et al.* 1997a, b).

Embryological data indicates that the respiratory turbinates in birds and mammals are independently derived neomorphs (Witmer 1995). Importantly, in both groups respiratory turbinates have virtually identical locations and positions—they are situated directly in, and lie parallel to, the path of airflow in the nasal passage proper (Figure 1). Positioning these structures in any other portion of the respiratory tree (*e.g.*, trachea or chest) would result in fluctuations in deep body and/or brain temperatures (Ruben *et al.* 1997b). Additionally, only the geometry and position of the nasal passage proper allow for the low-turbulent, laminar airflow necessary for an efficient, intermittent counter-current heat and water exchange between respired air and turbinate surfaces (Hillenius 1994; Ruben *et al.* 1997a, b). The similar position of respiratory turbinates in extant birds and mammals facilitates optimal efficiency and is unlikely to be coincidental.

Since the presence or absence of respiratory turbinates is apparently correlated with lung ventilation rates in extant terrestrial vertebrates, their presence or absence is a reliable indicator of metabolic status of extinct taxa. Unfortunately,

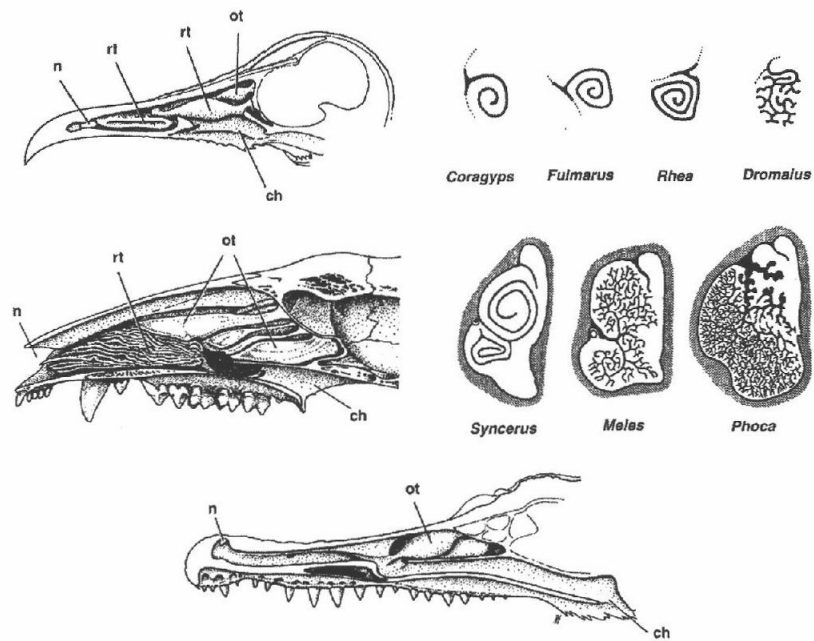


Figure 1. Morphology of nasal passages in extant birds (top left), mammals (middle left), and crocodilians (bottom center) and cross sections of nasal respiratory turbinates in extant birds (top right) and mammals (middle right). Abbreviations: n., external naris; rt, respiratory turbinate; ot, olfactory turbinate; ch, choana (internal nares). Modified from Hillenius 1994.

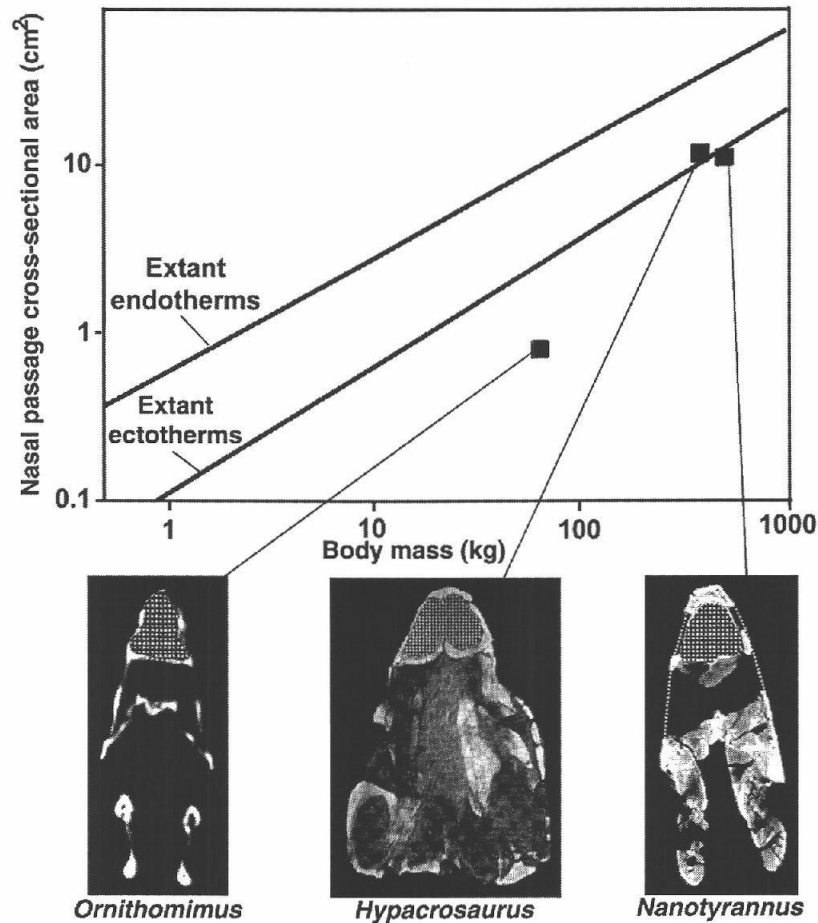


Figure 2. The relation of nasal passage proper cross-sectional area to body mass ( $M$ ) in extant endotherms (birds and mammals; nasal passage cross-sectional area equals  $0.57 M^{0.68}$ ) and ectotherms (lizards and crocodilians; nasal passage cross-sectional area equals  $0.11 M^{0.76}$ ), and three genera of Late Cretaceous dinosaurs: *Hypacrosaurus* (AMNH 5461), *Ornithomimus* (TMP 95.110.1), and *Nanotyrannus* (*Tyrannosaurus*) (CMNH 7541). The checkered areas in the inset CT pictures indicate the cross-sections of the nasal passages. The dinosaurs were not used in regression calculations. Modified from Ruben *et al.* 1996.

respiratory turbinates are delicate and rarely fossilized. However, to accommodate respiratory turbinates, the cross-sectional area of the nasal passage proper in modern endotherms is about fourfold that in equivalently sized ectotherms (Ruben *et al.* 1996) (Figure 2).

### Extinct taxa

#### *Theropods and early birds*

Significantly, nasal cross-sectional areas in the theropods *Nanotyrannus* (*Tyrannosaurus*) and *Ornithomimus*, and the ornithopod *Hypacrosaurus* scale with those of modern ectotherms (Figure 2). The nasal passages of these dinosaurs, like those of modern ectotherms, appear to have been too narrow to have housed respiratory turbinates. Accordingly, dinosaurs were unlikely to have achieved avian or mammalian metabolic status (Ruben *et al.* 1996).

Unfortunately, nasal passage cross-sectional area can only be accurately quantified in three-dimensionally preserved skulls and, therefore, this parameter offers little insight into the metabolic status of many archosaurians, especially early birds. However, pneumatization of the skull, and in particular, the morphology of the paranasal sinuses makes it possible to confidently infer nasal passage dimensions and, consequently, the presence or absence of respiratory turbinates, in many less well-preserved specimens. In advanced theropods (tetanurans) and *Archaeopteryx*, the maxillary and/or promaxillary fenestrae—apertures in the

rostral portion of the antorbital fossa—always open into an expansive maxillary antrum and promaxillary sinus, respectively, and are not part of the nasal passage (Witmer 1997) (Figure 3). The ceilings of one or both of these sinuses form much of the floor of the nasal passage. Conversely, in modern birds, these sinuses have been pushed caudally and their fenestrae are obliterated (Witmer 1997). This results, at least in part, from the expansion of the nasal passage to accommodate respiratory turbinates (Witmer 1997). Therefore, the occurrence of either of these fenestrae signals the likely presence of extensive paranasal sinuses that would have restricted the volume of the nasal passage in many theropods and in *Archaeopteryx*. Accordingly, it is highly unlikely that respiratory turbinates occurred in any theropods or *Archaeopteryx*.

Since the nasal passage proper of theropods was too narrow to have accommodated respiratory turbinates, it has been suggested that nasal respiratory turbinates in theropods may have been located in the vertical prechoanal region of the nasal passage (Paul 1996). In theropods that have a well-developed secondary palate, the only ones where such a scenario is even remotely possible, this region includes a subvertical, ventral flexure. The turbulence resulting from the sharp angulation of the prechoanal flexure would likely have resulted in non-laminar airflow and an inefficient heat and water exchange system, thus rendering the hypothetical “prechoanal” respiratory turbinates virtually useless.

### *Pterosaurs*

Little is known regarding the nasal passages of pterosaurs. Our attempts to quantify nasal passage diameters using CT scans have thus far been unsuccessful. However, it appears that, as in some theropods and extant lepidosaurs (Ruben *et al.* 1996), the nasal passages of pterosaurs were too short to have been able to accommodate respiratory turbinates (Figure 4). This, coupled with the likely ectothermic status of dinosaurs and early birds and the lack of insulatory coverings (contra Wellnhofer 1991, see Unwin and Bakhurina 1994), is suggestive of an ectothermic status in pterosaurs as well.

### INDICATORS OF ACTIVITY CAPACITY

Although evidence of the presence or absence of respiratory turbinates provides some insight into the resting or routine lung ventilation and metabolic rates in both extant and extinct taxa, these data do not provide information into metabolic capacities of these animals during periods of exercise. However, paleontological and neontological evidence of lung morphology and ventilatory mechanisms in theropod dinosaurs, early birds, and pterosaurs allow hypotheses regarding their activity capacities to be proposed.

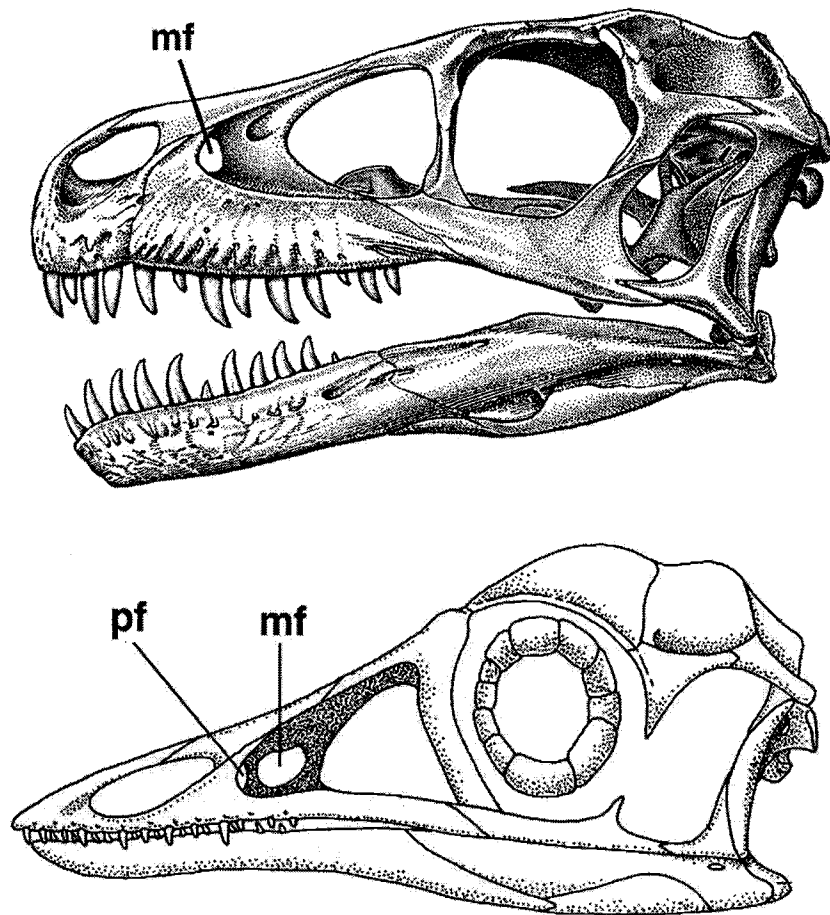


Figure 3. The promaxillary and/or maxillary fenestrae in *Dromaeosaurus* (top) and the Eichstätt specimen of *Archaeopteryx* (bottom) that open into paranasal sinuses, which are causally linked to narrow nasal passages and likely absence of nasal respiratory turbinates. Modified from Chatterjee 1997 and Currie 1995. Abbreviations: mf, maxillary foramen; pf, promaxillary foramen.

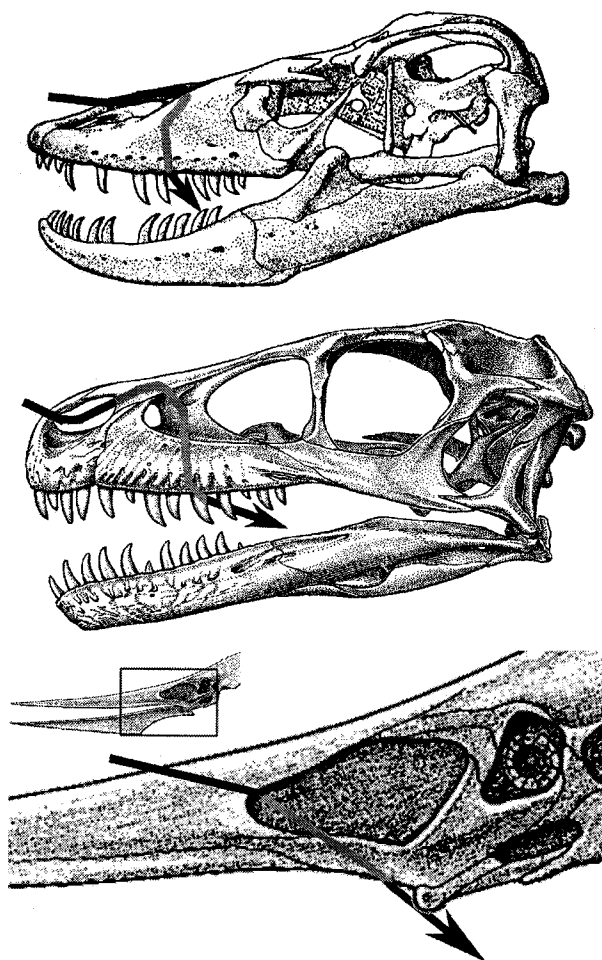


Figure 4. Lateral views of the skulls of a monitor lizard *Varanus* (top), the theropod dinosaur *Dromaeosaurus* (middle), and the pterosaur *Pteranodon* (bottom). The arrows approximate the path of airflow through the nasal passage into the oral cavity. The short, direct path of airflow in pterosaurs and some theropods is similar to that of varanids and other extant lizards and almost certainly precluded sufficient space to have housed nasal respiratory turbinates. Modified from Currie 1995, Romer 1956, Ruben *et al.* 1996, and Wellnofer 1991.

### Extant taxa

Amniote lungs are of two morphologically and ontogenetically distinct types, each of which is derivable from hypothetical ancestral simple sac-like lungs. Extant theropsids (mammals) have alveolar lungs; extant sauropsids (*i.e.*, lepidosaurs, rhychocephalians, crocodilians, and birds) possess septate lungs (Ruben *et al.* 1997b).

Alveolar lungs are composed of millions of highly vascularized, spherical alveoli, in which ventilatory airflow is bi-directional. During inhalation, expansion of the ribcage and/or contraction of the diaphragm increases pleural cavity volume, decreases pleural cavity pressure, and results in the expansion of the alveoli. Exhalation is accomplished, at least in part, by elastic rebound of the alveoli. The unique morphology of this lung, and especially of the alveoli, removes the necessity of high volumes of supporting parenchymal tissues and allows nearly all of the lung parenchyma to function actively in gas exchange (Perry 1983, 1989). These attributes, combined with a thin blood-gas barrier, provide the alveolar lung with a high anatomical diffusion factor (ADF) (Perry 1983, 1992; Duncker 1989), an attribute essential for maintenance of high rates of oxygen consumption during extended periods of intensive activity.

The general lung morphology of extant nonavian sauropsid amniotes (“reptiles”) is distinct from the alveolar lungs of mammals. The generalized sauropsid septate lung (a unicameral lung) is functionally analogous to a single, oversized mammalian alveolus. Septa—vascularized ingrowths—penetrate

medially from the perimeter, forming respiratory units (*i.e.*, ediculae, or faveoli depending on their depth), and are the principle sites of gas exchange (Perry 1983).

Variations from this generalized sauropsid septate lung morphology range from homogeneous to heterogeneous distribution of parenchyma, from one to many chambers, from dorsally attached to unattached, and from possessing no diverticulae to exhibiting many, elaborate diverticulae (Perry 1983; Perry and Duncker 1980). As in the mammalian lung, airflow in the reptilian septate lung during ventilation is bi-directional. However, unlike alveoli, the respiratory units of the reptilian septate lung contribute little to air convection during ventilation. Additionally, the amount of effective parenchymal tissue (parenchymal tissue volume/respiratory surface area)—an indicator of the amount of nonrespiratory, supportive tissues—of the reptilian lung is significantly greater than that of the mammalian lung (Perry 1989). To compensate, the ventral region of the lung in some nonavian sauropsids is often poorly vascularized and functions largely to assist in ventilation of dorsal, vascularized portions of the lung (Perry 1983). The result is a low relative overall ADF in reptiles (Perry 1983). Thus, although maximal oxygen consumption rates ( $\text{VO}_2 \text{ max}$ ) in some varanid lizards are significantly higher than those of other reptiles, nonavian septate lungs in extant taxa are probably constrained from supporting respiratory exchange consistent with aerobic metabolic rates typical of active endotherms (Ruben *et al.* 1997a).

Birds, like all sauropsids, also possess septate lungs, but they have circumvented inherent constraints on respiratory gas exchange rates of the reptilian

septate lung. Unlike reptiles, birds have a particularly high ADF. Additionally, modification of the nonvascularized chambers into a series of extensive, highly compliant air sacs, that extend into the visceral cavity and aid in a specialized cross-current ventilation of the dorsal vascularized parabronchi during both inhalation and exhalation, result in especially high rates of lung ventilation and gas exchange (Maina *et al.* 1989).

The parabronchial lung in modern birds is securely attached to the vertebral column. In some birds—particularly those with notaria—there are distinct, inverted T-shaped hypophyses that serve as additional sites of attachment. Diverticulae from the air sacs invade and pneumatize portions of the skeleton. Pneumatization of the avian skeleton, with the exception of the longbones of the hindlimbs in a small subset of birds, is limited to the axial skeleton and forelimbs, and results from invasion by the anterior (cervical and clavicular) air sacs, but is not linked to respiratory function or specific lung morphology (Duncker 1989; McLelland 1989; Scheid and Piiper 1989).

Mechanisms for powering lung ventilation vary among extant amniotes. Lizards and snakes lack complete transverse subdivision of the body cavity (with partial separation, when present, resulting from the presence of an incomplete postpulmonary septum or, in some cases [*e.g.*, macroteiids], by an incomplete posthepatic septum, but not both [Dunker 1989]) and rely largely on costal ventilation, in which changes of pleural cavity pressure results from lateral expansion and contraction of the ribcage. To some extent, mammals and

crocodilians also use ribcage movements to ventilate the lungs, but they also rely on diaphragm-assisted lung ventilation.

In mammals, the diaphragm consists of an airtight, transversely oriented, muscularized septum that completely subdivides the visceral cavity into anterior pleuro-pericardial and posterior abdominal regions (Figure 5). Muscular contraction of the diaphragm increases the volume of the pleural cavity, which reduces pleural cavity pressure, resulting in filling of the lungs.

In crocodilians, an airtight, transversely oriented diaphragm (composed of the postpulmonary and posthepatic septa [Goodrich 1958]) also completely subdivides the visceral cavity into anterior pleural-pericardial and posterior abdominal regions (Figure 5). Unlike the mammalian diaphragm, the crocodilian diaphragm is nonmuscular and adheres to the anterior surface of the liver. The posterior and lateral aspects of the liver serve as the insertion for the paired diaphragmatic muscles that take origin from the small, preacetabular portion of the ischium, the pubes and the last pair of gastralia (Personal observation; Reese 1915) (Figure 6). Bilateral contraction of the diaphragmatic muscles pulls the liver posteriorly in a piston-like manner, resulting in decreased pleural cavity pressure and filling of the lungs (Gans and Clark 1976).

The triradiate pelvis of extant crocodilians, with its stout, rodlike pubic rami, is ideally suited to accommodate these diaphragmatic muscles (Figure 6 and Figure 7). However, it is important to note that the elongate, distinctly theropod dinosaur-like pubes of early (Triassic) crocodilians (*e.g.*, *Terrestrisuchus* [Crush

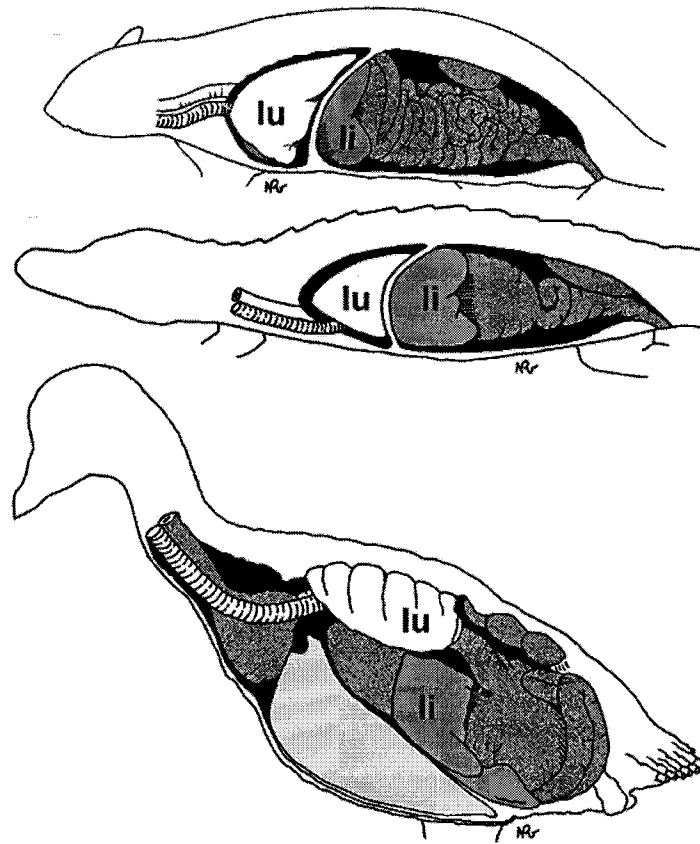


Figure 5. Correlation of body cavity partitioning and lung ventilation mechanism in extant amniotes. Only mammals (top) and crocodilians (middle) utilize active diaphragmatic lung ventilation. This mechanism necessitates a complete, transverse separation of the pleuro-pericardial cavity from the peritoneal (abdominal) cavity. In obligatory costal (rib) breathers—birds (lower) and lepidosaurs (*e.g.*, lizards and snakes)—there is no similar separation of the body cavity. Lepidosaurs are exclusively costal breathers; extant birds possess a unique flow-through lung-air sac system ventilated in large part by flexion and extension of intercostal joints that facilitate elevation and depression of the sternum. Abbreviations: li, liver; lu, lung. Modified from Ruben *et al.* 1997b.

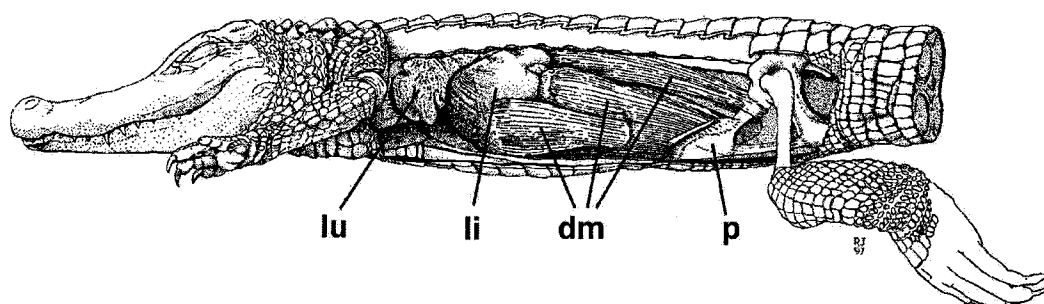


Figure 6. The hepatic-piston lung ventilatory mechanism of crocodilians. Extensive diaphragmatic muscles insert on the liver and take origin from the small preacetabular process of the ilium, the shaft of the pubis, and the distal, curved extremity of the pubis of living crocodilians (along with the distal cartilaginous portion of the pubis and the last pair of gastralia). Upon contraction, these muscles pull the liver posteriorly thus producing negative intrapleural pressure and filling of the lungs. Abbreviations: dm, diaphragmatic muscles; li, liver; lu, lung; p, pubis. From Ruben *et al.* 1997b.

1984]) probably represent the pleisiomorphic pelvic morphology for this group (Figure 7). Additionally, as in mammals, crocodilian lumbar ribs are reduced to allow lateral expansion of the viscera when the liver is pulled caudally during inhalation (Hengst 1998).

In most tetrapods, rectus abdominus musculature functions to support the abdominal viscera. However, in crocodilians much of the rectus abdominus appears to have contributed to formation of diaphragmatic muscles. Consequently, in crocodilians, the gastralia, as well as passively aiding in lung ventilation by

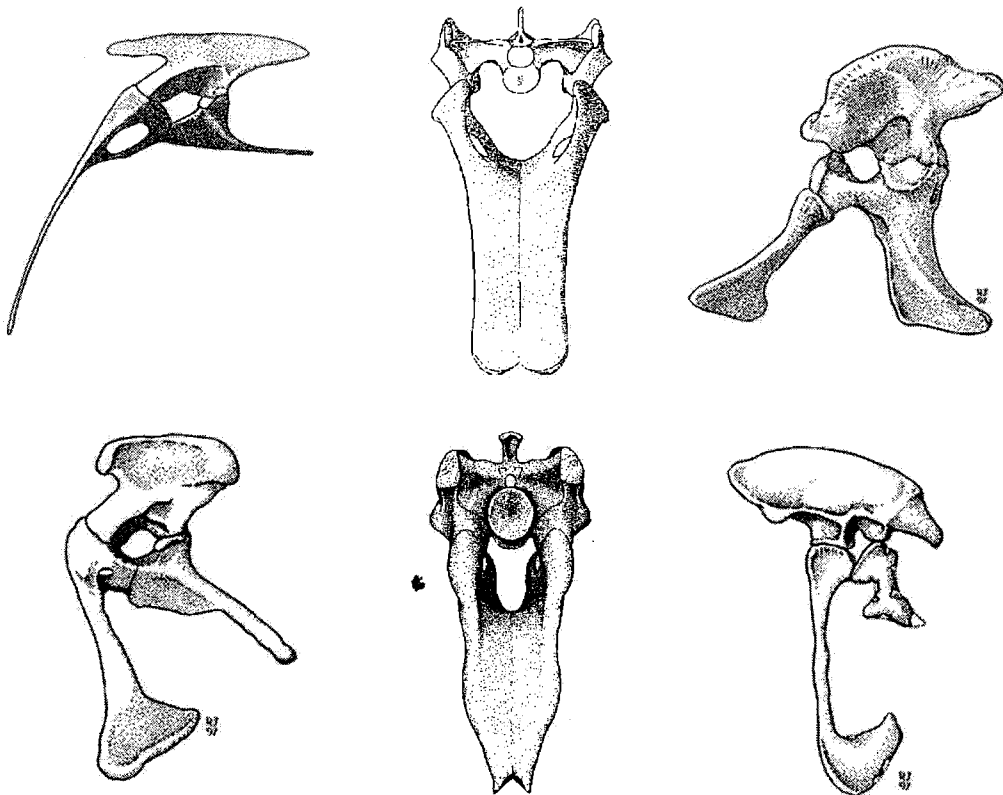


Figure 7. Left lateral and anterior views of the pelves of crocodilians and theropods. *Terrestisuchus* (upper left, upper center) *Alligator* (upper right), and theropods, *Herrerasaurus* (lower right, lower center), and *Unenlagia* (lower right). Note the marked similarity between the crocodilian and theropod pubes. Modified from Ruben *et al.* 1997b, Crush 1984, Colbert and Mook 1951, Novas 1993, and Bonaparte 1984.

maintaining the volume of the body cavity, may aid the reduced rectus abdominus in its supportive role.

Birds, like lizards, rely on costally powered lung ventilation. The ribcage of all extant birds is composed of a series of ossified pairs of vertebral and sternal ribs. Intercostal joints between vertebral and sternal ribs consist of synovial, condyloid articulations that allow fore-aft movement of the ribs during lung ventilation. Consequently, during inhalation, avian ribs rotate so that the posterior end of the sternum is depressed, thus generating negative pressure in the visceral cavity and filling the air sacs (Schmidt-Neilsen 1971; Fedde 1987; Brackenbury 1987). Additionally, the articulations of the sternal ribs (especially in terrestrial and arboreal birds) are not evenly distributed along the lateral aspect of the sternum; rather, they articulate in close proximity to one another on the anterior portion of the sternum. These factors, combined with the serial increment in the length of successive pairs of ribs, serve to maximize the ventral excursion of the sternum. The highly derived avian lung-air sac system, which permeates the entire visceral cavity, precludes the distinct transverse separation of avian body cavity that is typical of diaphragm-breathing tetrapods and is dependant on the aforementioned skeletal features (Duncker 1972, 1974, 1989).

In arboreally roosting birds the pelvis, and especially the pubis, has been modified to take on an accessory ventilatory role during such periods (Figure 8) (Baumel *et al.* 1990). The pubis serves as the major attachment site for extensive suprapubic and infrapubic muscles that serve to rotate the pelvis and tail downward

thereby ventilating the posterior air sacs, which are located largely beneath the pelvis (Baumel *et al.* 1990).

This system, requires that the pubis be nearly horizontal and, more importantly, to extend well beyond the posterior extremity of the ilium and ischium. In ratites—a group of birds with a long terrestrial history—the pubis is reduced in length, does not extend beyond the ischium and ilium, and hence can not function in ventilation of posterior air sacs. Additionally, avian costal ventilation is probably relatively ineffective during arboreal roosting when the weight of the body is often rested against the sternum, thus inhibiting the normal thoracic ventilatory movements. Therefore, it is likely that the suprapubic musculature is functionally linked to arboreality.

#### Extinct taxa

Given their relationship to living sauropsids, extinct sauropsids (*e.g.*, early crocodilians, dinosaurs, pterosaurs, *Archaeopteryx*, and enantiornithine birds) probably possessed septate lungs. However, they were unlikely to have possessed avian-style, flow-through lungs. The ribcage-pectoral girdle complex of these forms lacks indications of any thoracic musculoskeletal capacity for inhalatory filling of abdominal air sacs. Contrary to Paul (1988), we find that these taxa lacked avian-like intercostal rib joints and expansive sternae (Weishampel *et al.* 1990), structures without which unidirectional airflow cannot be maintained in the

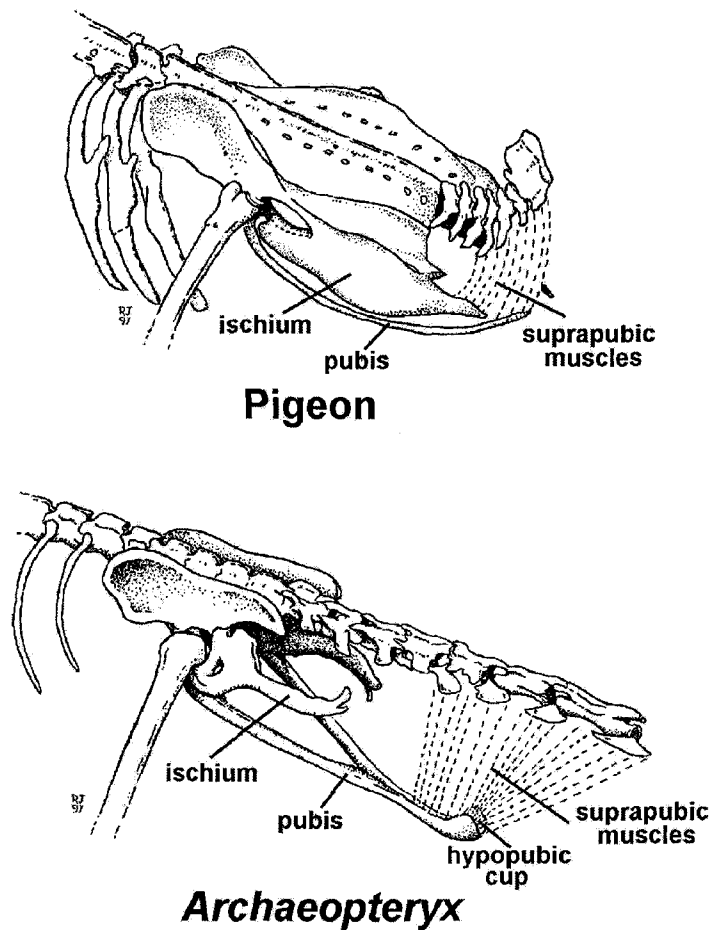


Figure 8. Pelvic and tail skeleton and suprapubic musculature of modern arboreally roosting birds (*e.g.*, pigeon) and *Archaeopteryx*. In both extant and extinct arboreal birds, marked projection of the distal pubis posterior to the ilium and ischium is associated with suprapubic musculature rotation of the pelvis and tail. Such movements facilitate ventilation of the nonvascularized air sacs during arboreal roosting. This condition of the pubis is broadly inconsistent with the morphology of the theropod pelvis and with hepatic-piston diaphragmatic breathing. Anterior is to the left of the figures. From Ruben *et al.* 1997b.

modern bird lung. These thoracic modifications first appear in Cretaceous ornithiurine birds (Hou *et al.* 1996; Martin *et al.* 1998).

Pneumatization of the axial skeleton in pterosaurs, dinosaurs, and *Archaeopteryx* has been regarded as positive evidence of the presence of an extensive avian-style lung-air sac system in these taxa (Britt *et al.* 1998; Ostrom 1991; Wellnofer 1991). This notion is based largely on close affinities between theropods and birds and the assumption that pneumatization of vertebrae necessarily reflects the presence of extensive birdlike, nonvascularized air sacs throughout the visceral cavity. However, skeletal pneumatization plays no role in lung ventilation, nor is it necessarily indicative of any particular lung morphology. Rather, it is the unique avian thoracic morphology that is requisite for proper ventilation of the highly specialized avian flow-through lung (Fedde 1987). As in modern birds, the vertebrae of dinosaurs and pterosaurs and the forelimbs of pterosaurs were probably pneumatized by retroperitoneal diverticulae from the anterior portion of the lung. Currently there is no evidence that any non-avian archosaur had abdominal air sacs, much less an avian-style lung.

### *Theropods*

Some have argued that theropods were able to use sternal movements to ventilate avian-style flow through lungs (Paul 1988). However, the largest described theropod sternum (*Velociraptor mongoliensis* [GI 100/25, Barsbold 1983]), when compared to trunk length, is only about half the size of than the

smallest modern avian sternum—that of the kiwi (*e.g.*, USNM 289857). In addition, unlike most birds, those few theropod taxa in which sterna are fossilized show an even distribution of a few costal articulations along the sternum.

The Early Cretaceous compsognathid *Sinosauropteryx* (Chen *et al.* 1998; personal observation) retains, along with ocular and integumentary tissues, preserved traces of much of the contents of the visceral cavity. The cavity exhibits complete thoracic-abdominal separation, delimited by a transversely oriented subdivision coincident with the anterior surface of the liver (Figure 9).

Additionally, theropods possessed reduced lumbar ribs, well-developed gastralia, and a strikingly (early) crocodilian-like, elongate pubis and pubic apron (Figure 7). These are consistent with the hypothesis that theropod dinosaurs, like modern crocodiles (and, especially, early crocodilians), probably possessed a bellows-like septate lung, and that the lung was ventilated, at least in part, by a hepatic piston-diaphragm powered by diaphragmatic muscles that extended between the pubic bones and liver. Significantly, fossilized preservation of abdominal contents whose general topography is consistent with diaphragm breathing is not unique to *Sinosauropteryx*. Similar transverse segregation of the viscera is seen in an undoubted diaphragm breather, *Pholidocercus*, a mammal from the Eocene Messel formation of Germany (von Koenigswald *et al.* 1988) (Figure 9).

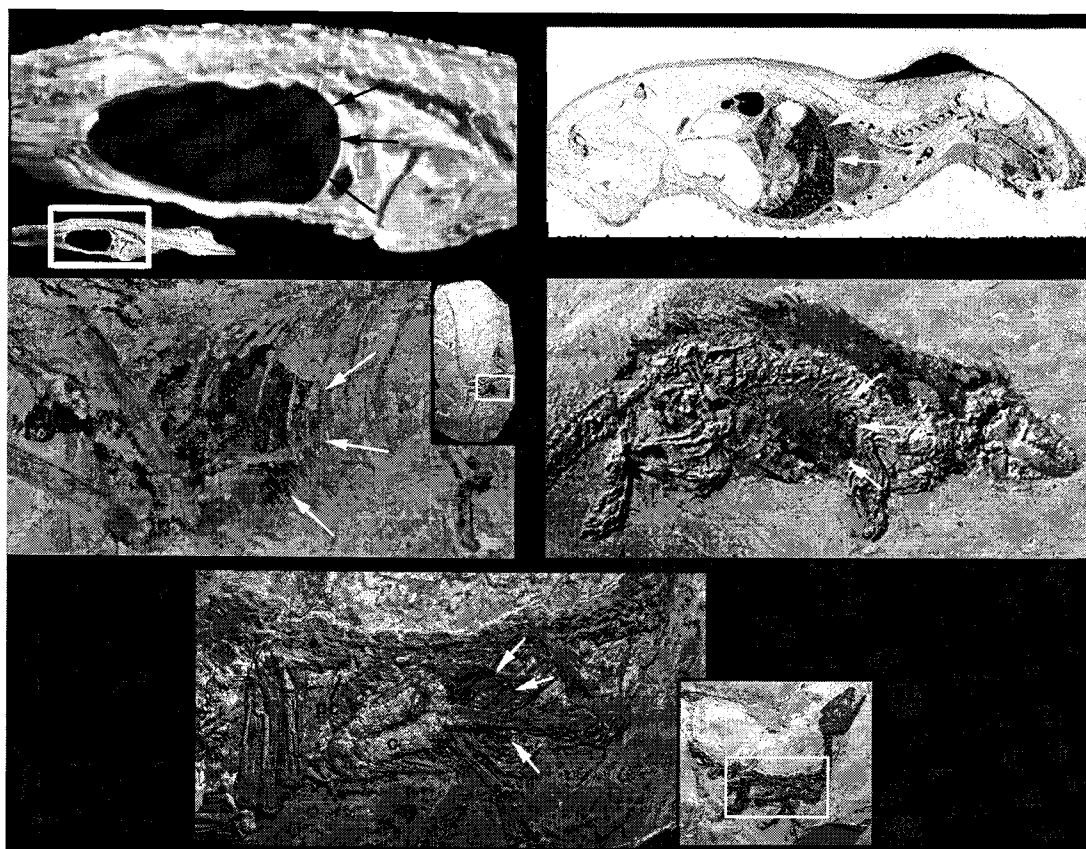


Figure 9. Similar body cavity partitioning in the American alligator (*Alligator*) (upper left), the compsognathid theropod dinosaur (*Sinosauropteryx*) (middle left), the maniraptoran theropod dinosaur (*Scipionyx*) under ultraviolet illumination (bottom), the rat (*Rattus*) (upper right), and the Eocene mammal *Pholidocercus* (modified from von Koenigswald *et al.* 1988) (lower right). Arrows delineate the complete vertical subdivision of the pleuro-pericardial and abdominal cavities. Insets show entire animal for perspective.

Recently, a juvenile maniraptoran theropod dinosaur with exquisitely preserved soft tissue was described. As well as having a remarkably preserved skeleton, *Scipionyx samniticus* retains fossilized skeletal muscles, trachea, large intestines, and liver *in situ* (Dal Sasso and Signore 1998a, b; Ruben *et al.* 1999). A section of the trachea is preserved in the posterior cervical region, immediately anterior to the scapulocoracoid complex (Dal Sasso and Signore 1998). Like the trachea of crocodilians, *Scipionyx*' trachea in this region is situated well ventral to the vertebral column. In contrast, the avian posterior cervical trachea, except in specialized, long-necked birds (*e.g.*, swans), is usually positioned dorsally and adjacent to the vertebral column, thereby facilitating entry of the trachea into the dorsally attached parabronchi (McLelland 1989).

In visible light, *Scipionyx*' liver appears as a small hematic halo restricted to the ventral margin of the ventral cavity (Dal Sasso and Signore 1998a, b). However, the liver is more accurately visualized under ultraviolet illumination, where it fluoresces as a suboval, indigo colored mass that extends from the vertebral column to the ventral body wall (Ruben *et al.* 1998). As in extant diaphragm breathers and *Sinosauropteryx*, *Scipionyx*' liver is situated ahead of the large intestine and fills the anteriormost portion of the abdominal cavity (Figure 9) (Ruben *et al.* 1998). Furthermore, as in crocodilians, mammals, and the theropod *Sinosauropteryx*, the anterior border of the liver in *Scipionyx* is transversely oriented and completely subdivides the visceral cavity into anterior pleuropericardial and posterior abdominal regions (Ruben *et al.* 1998). In the

theropods *Scipionyx* and *Sinosauroptryx*, and the mammal *Pholidocercus*, the pleuropericardial cavity appears empty because delicate lung tissues were not fossilized. Therefore, contra Claussens *et al.* (1998), these skeletal and soft tissue data are inconsistent with the possibility that theropods possessed avian-style lungs and abdominal air sacs and, therefore, with avian-style lung ventilation.

### *Early birds*

*Archaeopteryx* and enantiornithine birds also lacked the aforementioned thoracic skeletal modifications consistent with the ability to have ventilated an avian style lung. However, as in modern arboreal birds, we interpret the pubis in early birds to have been nearly horizontal and, more importantly, to have extended well posterior to the ilium and ischium (based on the arrangement of the best preserved examples of *Archaeopteryx*, *i.e.*, the Berlin and Solnhofen specimens, and known enantiornithine birds) (personal observation; Martin 1991; but see Ostrom 1976, 1985, 1986, 1991 for an alternative view). Importantly, *Archaeopteryx* and some early birds (*e.g.*, *Confuciusornis*) apparently possessed laterally expanded, dorsally concave hypopubic cups at the distal end of their pubes (Figure 8). The similarity of the pubic morphology of modern and early birds indicates that this hypopubic cup may have served as the site of origin for suprapubic musculature and is inconsistent with hepatic piston-diaphragmatic lung ventilation. Consequently, it is reasonable to conclude that when roosting in trees,

early birds probably also utilized suprapubic and infrapubic musculature to assist in ventilation of incipient nonvascularized posterior air sacs.

Unlike most early birds, *Archaeopteryx* has been interpreted as adapted for a terrestrial rather than an arboreal existence (Peters and G rgner 1992; Ostrom 1991). The severely opisthopubic pelvis and the presence of the hypopubic cup of *Archaeopteryx*, as in enantiornithines, signal that early birds, including *Archaeopteryx*, were probably adapted for a substantially arboreal existence. Hence, the pelvis of *Archaeopteryx* and other early birds may evince the likely long arboreal history of their ancestry.

### *Pterosaurs*

A birdlike lung is unlikely to have existed in pterosaurs. The proximal ends of the thoracic ribs in *Pteranodon* and other derived pterosaurs are completely fused to the notarial vertebrae (personal observation; Wellnofer 1991), thus precluding lateral expansion and contraction of the ribcage or ventral movements of the sternum (Figure 10). Clearly, the thoracic ribs could have had no active role in lung ventilation. Significantly, the prepubic bone of pterosaurs, which is superficially similar to the pubis of theropods and crocodilians, is well positioned for attachment of diaphragmatic muscles. Additionally, as in crocodilians and theropods, pterosaurs possessed well-developed gastralia and reduced lumbar ribs (personal observation; Wellnofer 1991). Therefore, it is likely that *Pteranodon*, and

perhaps other pterosaurs, ventilated their lungs with a hepatic piston driven diaphragm.

## ACTIVITY CAPACITY

As presented earlier, the absence of respiratory turbinates in dinosaurs, early birds, and pterosaurs indicates that they were likely to have maintained ectotherm-like resting, or routine, metabolic and lung ventilation rates. As in extant reptiles (*e.g.*, *Varanus*) costal breathing seems adequate to have supported active rates of oxygen consumption in such animals. Consequently, on the basis of the physiology of extant ectotherms, a specialized diaphragm to supplement ventilation in theropods seems superfluous. However, recent analysis suggests that expansion of lung ventilatory capacity might have allowed the reptile-like, multicameral, septate lungs of dinosaurs to have achieved rates of O<sub>2</sub>-CO<sub>2</sub> exchange that might have approached those of a few mammals with relatively low aerobic scopes (Hicks and Farmer 1998; Ruben *et al.* 1998). Perhaps the presence of diaphragm-assisted lung ventilation in theropods indicates that, although these dinosaurs maintained ectotherm-like routine metabolic rates, they were, nevertheless, uniquely capable of sustaining active oxygen consumption rates and activity levels beyond those of the most active living reptiles.

This hypothesized pattern of metabolic physiology in theropods may seem inconsistent with the presence of a hepatic piston diaphragm in extant crocodilians, none of which appears to have particularly enhanced capacity for oxygen

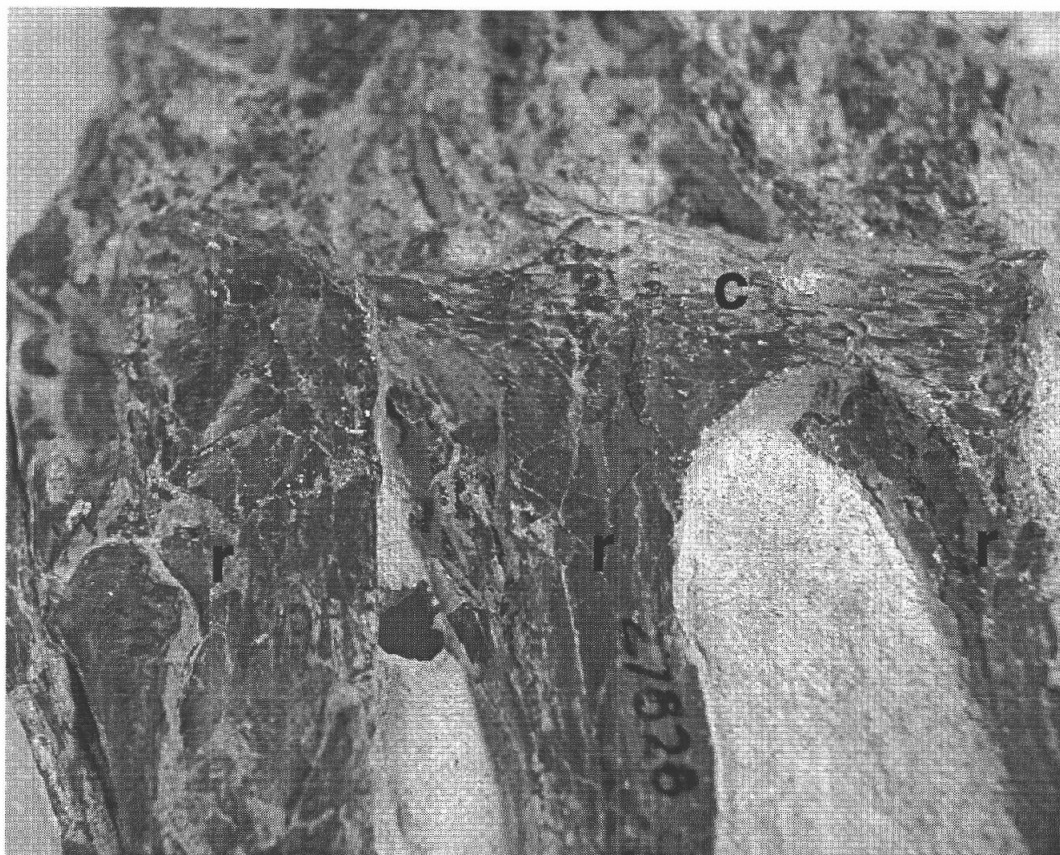


Figure 10. Ventral view of three notarial ribs of *Pteranodon* (KU 27828). Note complete fusion of their proximal ends to the vertebral column, thus preventing ribcage expansion and contraction. Abbreviations: c, centrum; r, rib.

consumption during exercise (Bennett *et al.* 1985). However, relatively low aerobic capacity in recent crocodilians, all of which are secondarily aquatic, might not represent the ancestral condition. Like theropods, early (Triassic) crocodilians (*e.g.*, *Protosuchus* and *Terrestrisuchus*) might also have had enhanced aerobic capacities because they appear to have been fully terrestrial, cursorial, and relatively active (Colbert and Mook 1951; Crush 1984).

Such a scenario may have afforded theropods, early crocodilians, and, perhaps, pterosaurs, the low maintenance cost of ectothermy combined with endurance similar to that in some modern endotherms. This strategy might have functioned optimally in the relatively mild, equable climatic regimes of most of the Mesozoic Era, where chronic maintenance of ectothermic homeothermy would have been possible (as in the modern *Varanus komodoensis* [MacNab and Auffenberg 1976; Spotila *et al.* 1991]).

#### POTENTIAL PHYLOGENETIC PROBLEMS

Known theropods possessed pubes with a pubic boot rather than a hypopubic cup, well-developed gastralia, reduced posterior thoracic ribs, and, when present, diminutive sterna, which are consistent with hepatic piston lung ventilation but are inconsistent with ventilation of an avian style lung-air sac system. Nevertheless, some maniraptoran theropods (*e.g.*, *Velociraptor*) may have had a retroverted pubis (Norell and Makovicky 1997). However, in each of these cases, the pubis lacks a hypopubic cup (Figure 11) and does not extend appreciably

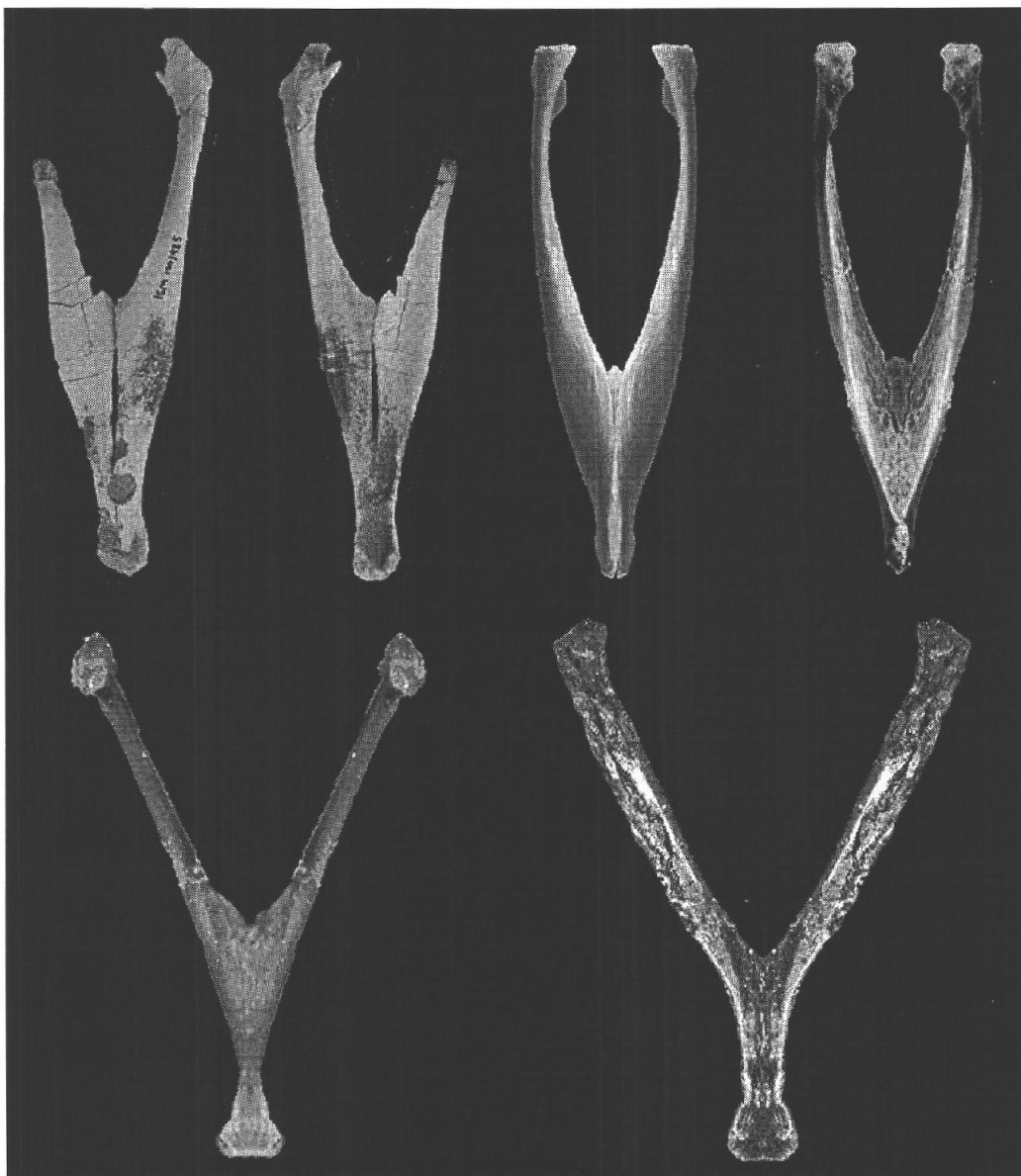


Figure 11. The pubes of theropods and birds. Anterior (upper left) and posterior (upper left center) views of the pubes of *Velociraptor* (GI 100/985), anterior (upper right center) and posterior (upper right) views of the pubes of *Rahonavis* (reconstructed from the right pubis), posterodorsal view of the pubes of *Archaeopteryx* (reconstructed from the right pubis of the London specimen) (lower left), and *Confuciusornis* (reconstructed from the right pubis of IVPP V 11552) (lower right). The pubes of theropods are especially similar to those of early crocodilians (Figure 7). Only the pubes of early birds (*e.g.*, *Archaeopteryx* and *Confuciusornis*) possess a dorsally convex, laterally expanded hypopubic cup at their distal ends.

beyond the posterior margins of the ischium and ilium—a morphology that is inconsistent with ventilation of avian style lungs. More likely, opisthopubis in theropods served to increase the power of the diaphragmatic muscles by increasing muscle length and absolute contractile distance (Hengst 1998). In fact, no known theropod shows evidence of reduced reliance on the hepatic piston diaphragm mechanism and/or transition toward features indicative of the presence of an avian-style lung and lung ventilation as one would expect if the commonly accepted mechanism and/or transition toward features indicative of the presence of an avian-style lung and lung ventilation as one would expect if the commonly accepted hypothesis of the relationship of dinosaurs and birds is correct.

Finally, the pubes of *Archaeopteryx* and enantiornithine birds are frequently represented as identical to those of theropod dinosaurs and indicative of a close relationship between the two groups (Padian and Chiappe 1998). Specifically, the pubes of both groups are conventionally represented as a distal, laterally compressed, sagittally extended boot (Ostrom 1976, 1986, 1991). However, as described above, early birds, including *Archaeopteryx* and *Confuciusornis*, clearly possessed a hypopubic cup at the distal end of the pubis (Figure 8 and Figure 11). Recently, the theropod *Rahonavis* was also reported as having possessed a well-developed hypopubic cup (Forster *et al.* 1999). However, examination of this specimen reveals that its pubes lacked a hypopubic cup and that its pubes are, overall, not significantly different than those of *Velociraptor* (Figure 11). The

pubes of theropods and early birds are apparently more broadly distinct from each other, both functionally and morphologically, than is generally assumed.

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### CHAPTER 3: CURSORIALITY IN BIPEDAL ARCHOSAURS

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## ABSTRACT

Relative total hindlimb length in cursorial birds is invariably more than one and a half times greater than in non-avian theropod and ornithomimid dinosaurs. Additionally, center of mass in cursorial birds is more anterior than in bipedal dinosaurs. These differences are tightly linked to contrasting cursorial modes and serve to morphometrically delineate variations in running styles in extant and extinct bipedal cursorial archosaurs. *Caudipteryx* has recently been described as a dinosaur and, therefore, would be expected to have utilized the dinosaurian mechanism of cursoriality. Surprisingly, hindlimb proportions and center of mass position in *Caudipteryx* are indistinguishable from those in cursorial birds and contrast sharply with those in all other bipedal dinosaurs. We suggest that *Caudipteryx* was likely to have utilized a running mechanism more similar to that of modern cursorial birds than to that of typical bipedal dinosaurs. These observations provide valuable clues about cursoriality in *Caudipteryx*, but may also have implications for interpreting the locomotory nature of its ancestors.

Cursorial mechanisms in mature bipedal archosaurs are of two distinct types. Bipedal dinosaurs were long-tailed cursors whose center of mass was located near the acetabulum (Alexander 1978, 1989; Galton 1970; Carrano 1998; Gatesy 1990; Gatesy and Beiwener 1991). Their hindlimbs (*i.e.*, femur, tibia, and metatarsus) were probably maintained in a generally vertical posture so that the animal's mass was balanced approximately over its feet (Galton 1970; Carrano 1998; Gatesy 1990) (Figure 12). During each stride the femur and distal limb segments probably swung broadly in the parasagittal plane (Carrano 1998; Gatesy 1990, 1991; Gatesy and Biewener 1991). Thus, bipedal dinosaurs can be characterized as having utilized a balanced, "first class lever" running style, with their long tails acting as a counterbalance to the head, neck, and trunk.

Alternately, ornithurine birds have lighter, foreshortened tails and their body mass is centered anteriorly, near the wings (Figure 12) (Alexander 1978, 1989; Gatesy 1990, 1991, 1999a, 1999b; Gatesy and Beiwener 1991; Pennycuik 1986; Norberg 1990; Roberts and Humphreys 1999; Manion 1984). Though necessary for stability during powered flight, this anterior center of mass is far from the pelvis. Therefore, any running bird adopting a dinosaur-like cursorial mechanism (*i.e.*, with the entire hindlimb swinging parasagittally) would be seriously out of balance and in chronic danger of falling. Nevertheless, in spite of their anterior center of mass, adept avian runners have evolved repeatedly from flighted ancestors (Feduccia 1999). In every case, locomotory specializations

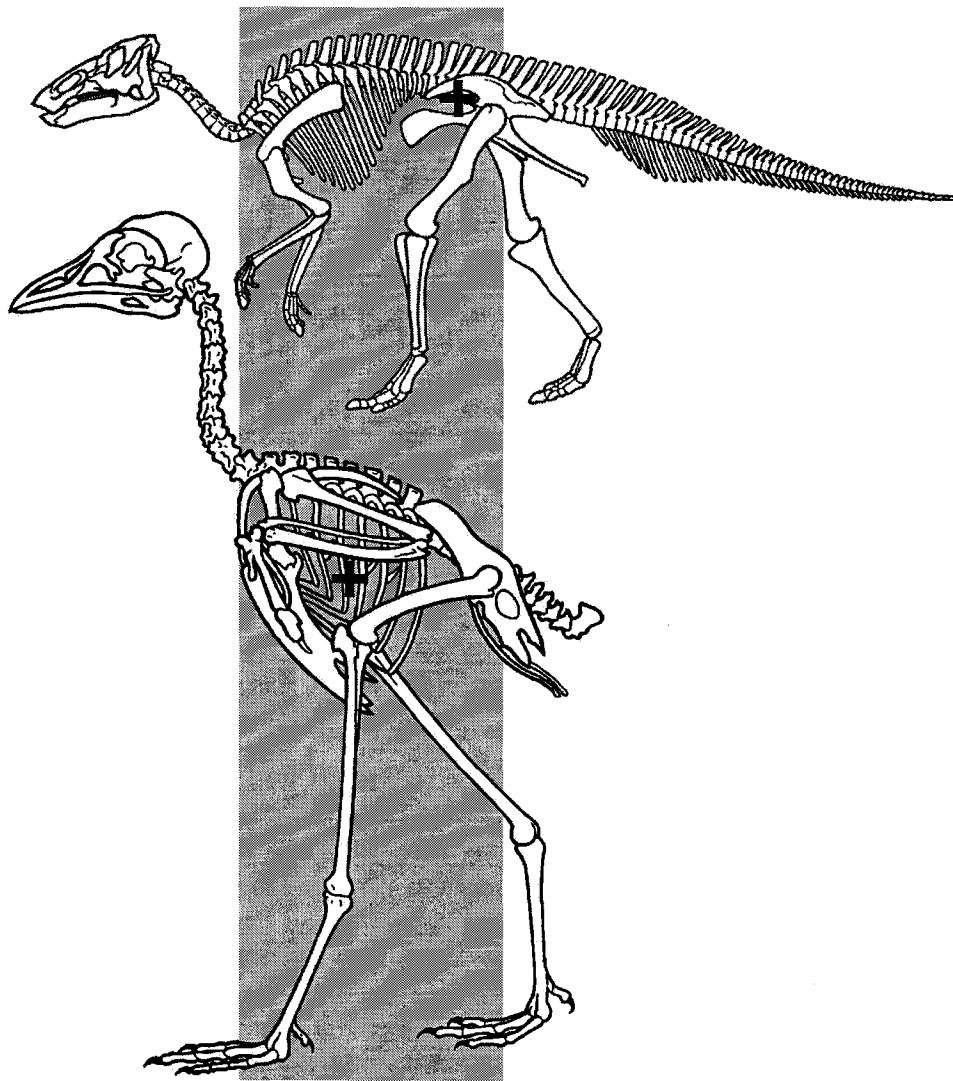


Figure 12. Hindlimb posture and center of mass (+) in bipedal dinosaurs (above) and cursorial birds (below) (Alexander 1978, 1989; Pennycuick 1986). Figures are scaled so that trunk lengths are approximately equivalent. Trunk and hindlimb proportions represent approximate means for the two groups.

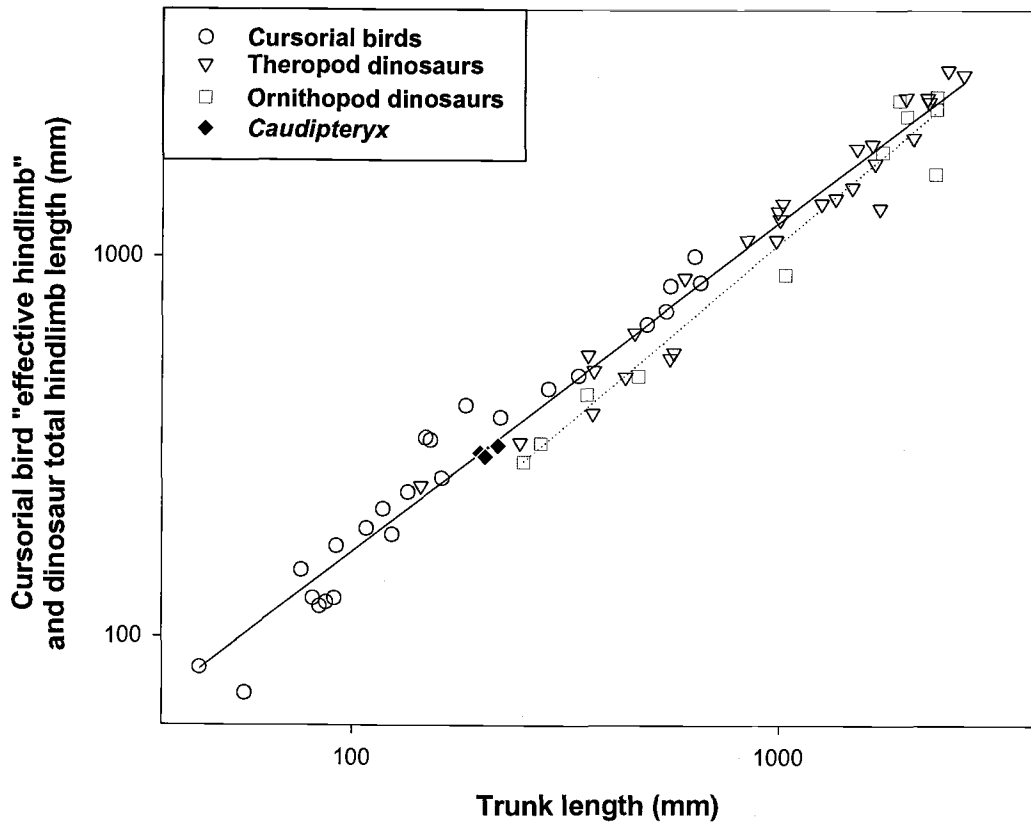


Figure 13. The relation of trunk length ( $T$ ) to total hindlimb length (femur + tibia + metatarsal III) in theropod (open triangles) and ornithopod (open squares) dinosaurs, and of trunk length to "effective hindlimb" length (tibiotarsus + tarsometatarsus) in cursorial birds (open circles). Diamonds represent the relation of trunk length to lower leg length (tibia + metatarsal III) in three specimens of *Caudipteryx*. Cursorial avian "effective hindlimb" and theropod total hindlimb length equals  $0.493T^{0.87}$ ; for ornithopod dinosaurs hindlimb length equals  $0.169T^{0.95}$  ( $R^2=0.971$ ,  $p<0.0000$ ). Extra sum of squares F-test determined that regressions for cursorial bird effective hindlimb length and theropod dinosaur total hindlimb length are indistinguishable ( $F_{(2,60)}=3.654$ ;  $p<0.05$ ). Solid black line represents regression for cursorial birds and theropod dinosaurs; dotted black line represents regression for ornithopod dinosaurs. Values for *Caudipteryx* specimens were not included in regression calculations. See Methods for details.

exhibited by avian cursors are remarkably similar to one another and are distinctly unlike those of dinosaurs.

During walking and running in highly cursorial birds, the femur is generally maintained subhorizontally with its distal end situated anteriorly, close to the animal's center of mass (Carrano 1998; Gatesy 1990, 1991, 1999a, 1999b; Gatesy and Beiwener 1991). In contrast to dinosaurs, the femur in cursorial birds contributes little to stride-length; rather, avian hindlimb movement and stride-length generation centers about the knee joint and results primarily from swinging of the lower leg (*i.e.*, tibiotarsus and tarsometatarsus) (Gatesy 1990, 1991, 1999a, 1999b; Gatesy and Beiwener 1991). In this regard, it is illustrative that the relative length of the stride generating hindlimb segments (tibiotarsus + tarsometatarsus), or "effective hindlimb" lengths, in mature cursorial birds, and total hindlimb lengths (femur + tibia + metatarsal III) in theropod dinosaurs, are identical (Figure 13).

These data indicate that, compared to the condition in bipedal dinosaurs, the lower leg, or "effective hindlimb" of cursorial birds is lengthened in apparent compensation for a lack of complete femoral participation in stride generation. Consequently, total hindlimb length in cursorial birds should be relatively greater for a given trunk length than in bipedal dinosaurs. If consistently true, these relationships could serve as a novel means to objectively delineate differences between contrasting cursorial mechanisms in bipedal archosaurs and they might also provide insight to unexpected locomotory mechanisms in extinct taxa.

We recorded data on hindlimb element (*i.e.*, femur, tibia [or tibiotarsus], metatarsal III [or tarsometatarsus]) and trunk lengths in mature, extant and extinct cursorial birds (from eight orders and 24 genera, including tinamou, cassowary, ostrich, galliforms, roadrunners, bustards, moa, and elephantbird) and a combined total of 40 genera of theropod and ornithomimid dinosaurs. Comparison of relative total hindlimb length in cursorial birds and bipedal dinosaurs demonstrates that for individuals of any given trunk length, total hindlimb length in cursorial birds is invariably more than one and a half times longer than in theropod and ornithomimid dinosaurs (Figure 14). We conclude that these sharply differing hindlimb proportions are tightly linked to contrasting locomotory mechanisms in dinosaurs and cursorial birds. Additionally, since cursorial mechanisms in the bipedal avian ancestor were likely to have resembled those in bipedal dinosaurs, we also conclude that the profound anatomical modifications that facilitate avian cursoriality are convergent responses to secondary resumption of cursoriality in distantly related taxa independently derived from their flighted ancestors (Feduccia 1999).

*Caudipteryx* has recently been described as a feathered dinosaur (Ji *et al.* 1998) and, therefore, would be expected to have utilized the dinosaurian mechanism of cursoriality. Surprisingly, relative total hindlimb proportions in *Caudipteryx* contrast sharply with those in all other bipedal dinosaurs but are indistinguishable from those in cursorial birds (Figure 14). Accordingly, based on

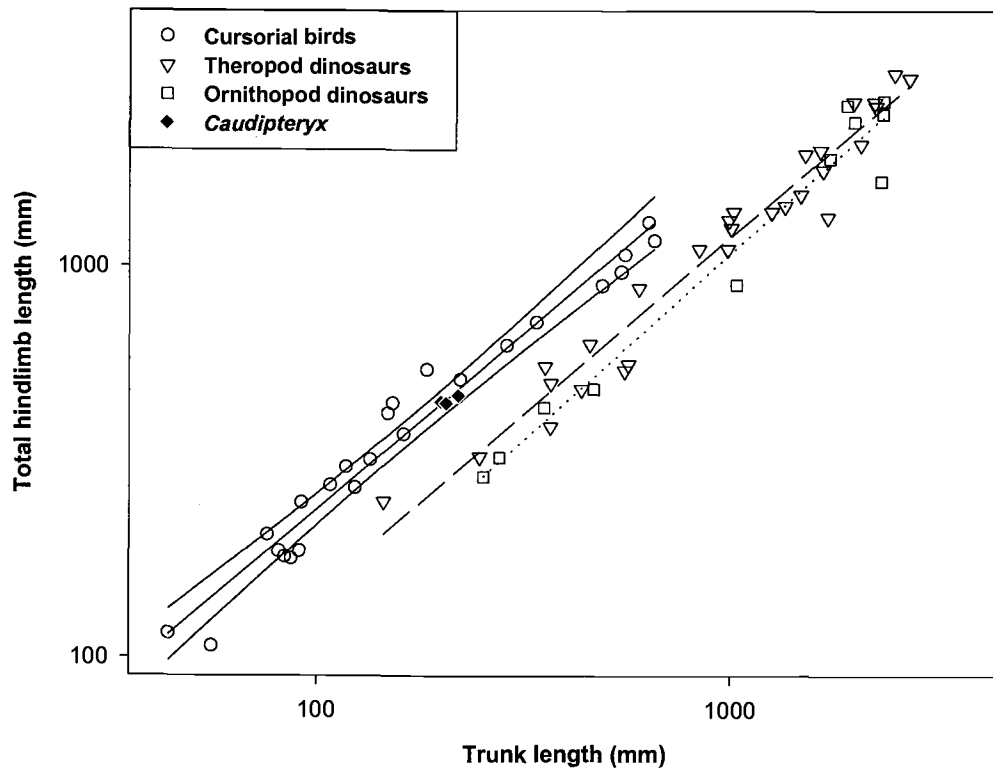


Figure 14. The relation of trunk length ( $T$ ) to total hindlimb length in bipedal archosaurs. For theropod dinosaurs (open triangles) hindlimb length equals  $0.356T^{0.91}$ ; for ornithopod dinosaurs (open squares) hindlimb length equals  $0.161T^{0.96}$ ; for cursorial birds (open circles) hindlimb length equals  $0.578T^{0.90}$  ( $R^2=0.979$ ,  $p<0.0000$ ). Diamonds represent the relation of trunk length to total leg length in three specimens of *Caudipteryx*. Solid black line represents linear regression for cursorial birds. Dashed black line represents the regression for theropod dinosaurs. Dotted black line represents the regression for ornithopod dinosaurs. Gray lines represent 99% confidence intervals for cursorial birds. Values for *Caudipteryx* specimens were not included in regression calculations. See Methods for details.

the tight linkage of hindlimb proportions to cursorial mechanisms in bipedal archosaurs, we suggest that *Caudipteryx* was likely to have utilized a running mechanism more similar to that of modern cursorial birds than to that of typical dinosaurs. With this in mind, it is particularly significant that lower leg (tibia + metatarsal) length in *Caudipteryx* is also indistinguishable from “effective hindlimb” length of cursorial birds and total hindlimb length in theropods (Figure 13).

The location of the center of mass in *Caudipteryx* seems to provide independent confirmation that it might have utilized locomotory mechanisms similar to those of cursorial birds. As described above, proportionately long hindlimbs and distinct locomotory mechanisms in cursorial birds are tightly linked to their anterior center of mass. Given that the relative hindlimb proportions of *Caudipteryx* are indistinguishable from those of cursorial birds, it was also likely to have had its center of mass situated anteriorly, rather than posteriorly, as in other dinosaurs. Significantly, an anterior, cursorial birdlike center of mass in *Caudipteryx* is demonstrated by application of Henderson’s mathematical-computational model for center of mass in tetrapods (Henderson 1999). This analysis indicates that center of mass in *Caudipteryx* was approximately 2.3 times further anterior to the acetabulum than in theropod dinosaurs (*e.g.*, *Deinonychus*) (Figure 15).

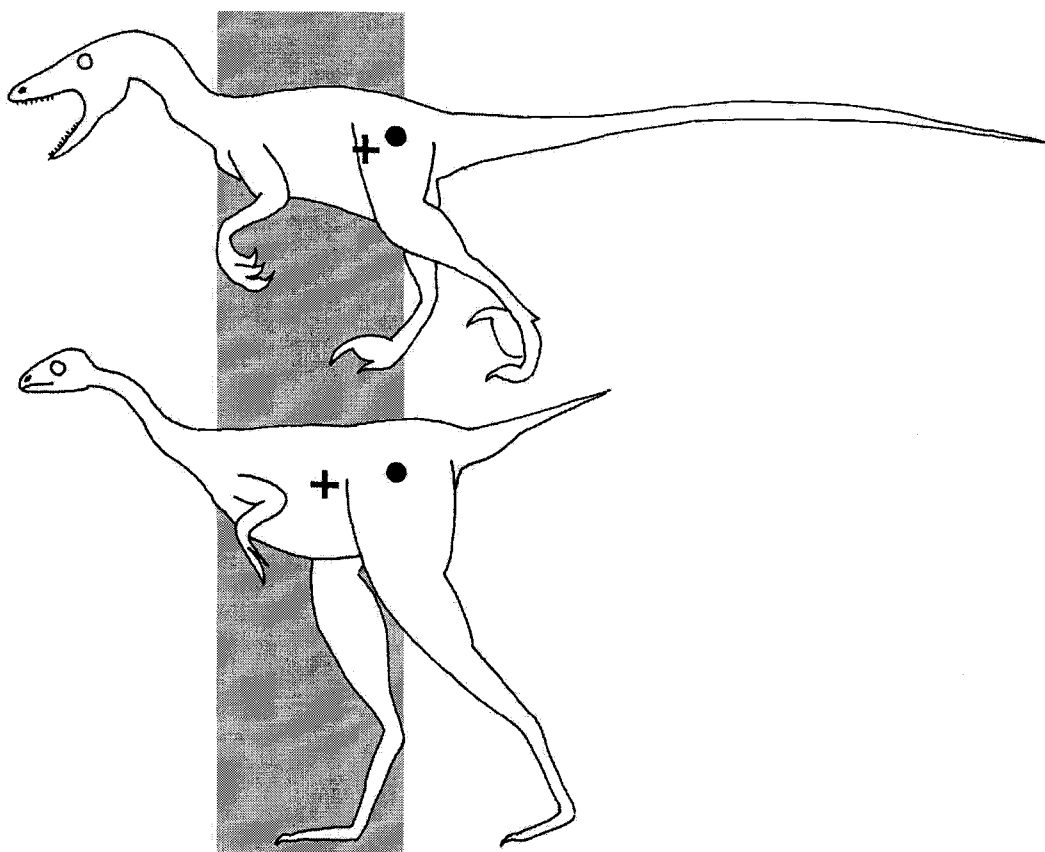


Figure 15. Estimated center of mass for *Deinonychus* (above) and *Caudipteryx* (below). Figures are scaled so that trunk lengths are equivalent. Relative to the acetabulum (•), center of mass (+) in *Caudipteryx* approximates center of mass in cursorial birds and is 2.3 times further anterior than in *Deinonychus*. *Deinonychus* modified from Paul (1985). *Caudipteryx* was reconstructed from NGMC 97-4-A and NGMC 97-9-A. See Methods and Henderson (1999) for details.

An anterior center of mass is also suggested by the brevity of *Caudipteryx*' tail, which is among the shortest, if not the shortest, of all bipedal dinosaurs. Additionally, as in cursorial birds, but unlike dinosaurs, the diminutive tail, as well as the complete absence of a femoral fourth trochanter, indicates that the caudofemoralis was not an important locomotory muscle. The likely absence of well-developed caudofemoralis musculature suggests that the short tail was likely to have been relatively narrow, with most of its musculature having been devoted to generating tail movement.

Of all bipedal dinosaurs, only *Caudipteryx* possessed cursorial birdlike limb proportions, center of mass, and, by extension, a cursorial birdlike running style. These observations might provide valuable clues about *Caudipteryx*' lifestyle, but they also may have implications for interpretation its taxonomic affinities. We suggest that the anatomical uniqueness of *Caudipteryx* must be consistent with one of the following alternatives: (1) *Caudipteryx* was simply an unusual theropod dinosaur whose cursorial ancestors abandoned dinosaurian locomotion and assumed the unique morphology and running style of cursorial birds; (2) *Caudipteryx* was a theropod dinosaur derived from flighted ancestors; (3) *Caudipteryx* was a post-*Archaeopteryx*, secondarily flightless bird and not a "feathered dinosaur." Alternative (1) is supported by current cladistic analyses that indicate that *Caudipteryx* is a coelurosauroid theropod (Ji *et al.* 1998; Sereno 1999). However, none of these analyses have considered *Caudipteryx*' extensive suite of cursorial birdlike locomotory characters and all other theropods were

typically dinosaurian in this regard (Figure 13, Figure 14, and Figure 15). In this context, it is important to reiterate that the same locomotory specializations present in *Caudipteryx* and cursorial members of eight avian orders are tightly linked to the latter taxa having been derived from flighted ancestors. Accordingly, it is difficult to construct a scenario in which the terrestrial theropod ancestors of *Caudipteryx* might have switched to a specialized, cursorial birdlike running style with an anterior center of mass, when they were already adept cursors with a posterior center of mass.

Alternative (2), *i.e.*, that some theropods were derived from currently unknown, flighted ancestors, has been suggested elsewhere (Paul 1985; Gee 1999). As noted above, *Caudipteryx*' locomotory adaptations are consistent with it having been derived from flighted ancestors. However, there is currently no strong evidence to support flighted ancestors for any other theropods. Nevertheless, this possibility cannot be dismissed. In light of problems associated with alternatives (1) and (2), perhaps alternative (3), *i.e.*, that *Caudipteryx* was a secondarily flightless, post-*Archaeopteryx*, cursorial bird, deserves closer scrutiny than it has received thus far. We find it a striking coincidence that the only truly feathered theropod was also the only known theropod likely to have utilized locomotory mechanisms identical with those of cursorial birds. We await further, more extensive taxonomic analyses for eventual resolution of this question.

## METHODS

### Hindlimb and trunk length data

Extant cursorial birds included “ratites”, bustards, roadrunners, and galliform birds. Extinct, presumably cursorial (or at least ground living) birds included moa and elephantbirds. Data were collected from avian and dinosaur specimens in museum collections or obtained from published data and/or scale reconstructions. Individuals were included only if the hindlimb skeleton were adequately known and the trunk was sufficiently known that the describers were able to confidently reconstruct the specimen.

The morphometric data collected from each individual included maximum femoral length, maximum tibia (or tibiotarsus) length (excluding the cnemial crest), maximum metatarsus (or tarsometatarsus) length, and trunk length (see Appendix). For this study, trunk length was defined as the distance from the first dorsal vertebrae and/or head of the first dorsal rib to the posterior rim of the acetabulum.

Juvenile birds have, for a given trunk length, longer hindlimbs than their adult counter parts (Manion 1984); the same has been hypothesized for tyrannosaurids (Russell 1970) and allosaurids (Foster and Chure 1999). Similarly, an undescribed juvenile velociraptorine theropod has a hindlimb-to-trunk length ratio = 2.0 (D. Burnham, pers. comm.), which is comparable to that seen in cursorial birds, but we exclude it from our analyses because of its obviously early stage of development. Additionally, *Sinornithoides youngi* was excluded from this

study. The specimen also exhibits a birdlike hindlimb/trunk length ratio, is very small, and possessed a cartilaginous sternum (Russell 1993). These observations indicate that this specimen, originally described as “nearing maturity,” may have been more immature than its describers supposed. To avoid confounding ontogenetic variables, the largest individual for each genus (for which we had data) was used in the analysis and data from known immature extant individuals were omitted as were extinct specimens whose maturity is in doubt.

The developmental maturity of *Caudipteryx* (NGMC 97-4-A and NGMC 97-9-A) is indicated by the well-ossified sternae, sternal ribs, wrist bones, and ankle bones (Ji *et al.* 1998). Similar ossification is present in two more recently discovered specimens cf. *Caudipteryx* (uncataloged IVPP specimen) and *Caudipteryx* sp. (IVPP V 12344), but the latter specimen also possesses ossified uncinate processes (Zhou, Z. and Wang, X., in press). Since these skeletal elements ossify late in development, there is little doubt that these individuals were mature.

#### Center of mass calculations

Lateral and dorsal profiles of *Deinonychus* were compiled from reconstructions in Henderson (1999). Lateral and dorsal profiles of *Caudipteryx* were reconstructed from NGMC 97-4-A and NGMC 97-9-A. The axial body profiles were mathematically combined to create a solid three-dimensional model from which body volume and the location of center of mass were calculated (see Henderson 1999 for details). The lung was conservatively assumed to have been

spherical with a volume equal to 10% of body volume and positioned at the anterior portion of the trunk. The density of the lung ( $0.4 \text{ kg/m}^3$ ) was estimated using the ratio of mass specific lung volume to mass specific lung parenchyma volume in a large Nile crocodile (Perry 1990).

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## CHAPTER 4: NONAVIAN FEATHERS IN A LATE TRIASSIC ARCHOSAUR

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## ABSTRACT

*Longisquama insignis* was an unusual archosaur from Late Triassic (Norian) lacustrine deposits in central Asia. *Longisquama* possessed a remarkable series of dorsal, paired, elongate integumentary structures, each of which, as in avian feathers, consisted of a calamus, rachis, barbs, and epidermal sheath. We interpret these structures in *Longisquama* as having been feathers, probably homologous with those in birds.

Avian feathers are individually molted, keratinized, epidermal structures that develop in a follicle. Each consists of a tubular base (calamus) that is continuous with an elongate, central shaft (rachis) that commonly bears distinct barbs. *Archaeopteryx*, the earliest known bird (145 my), possessed a complete plumage of flight feathers that differed little from those of many extant birds (Lucas and Stettenheim 1972; Feduccia 1999). Consequently, selective factors associated with the earliest stages of feather evolution, the morphology of the earliest feathers, as well as the taxonomic groups in which they first occurred, remain open to question.

We suggest that evidence for feathers that pre-date *Archaeopteryx* is represented by a series of integumentary appendages preserved in the archosaur *Longisquama insignis* (Archosauriformes: Longisquamidae). Fossils of the animal are known only from Late Triassic (Norian, ~220 my), lacustrine deposits at Madygan, Osh Province, Kyrgyzstan (Dobruskina 1980; Sharov 1970). The main slab/counterslab consists of the skull, vertebrae, ribs, furcula, forelimbs, and impressions of much of the accompanying integument (Figure 16). There are also five impressions of isolated integumentary elements from the same site (Sharov 1970)<sup>1</sup>.

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<sup>1</sup> All known specimens of *Longisquama insignis* are part of the collection of the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN). These include PIN 2584/4—holotype specimen, slab (+counterslab) of the anterior portion of the body (see Figure 16, Figure 17, and Figure 20); PIN 2584/5—partial individual feather (no calamus preserved) (see Figure 18); PIN 2584/6—mid-regions of two incomplete feathers; 2584/7—partial individual feather (no calamus preserved); PIN 2584/9—associated, distal portions of approximately six incomplete feathers (Figure 18). We directly examined these specimens at the University of Kansas, Lawrence, in April, 1999.

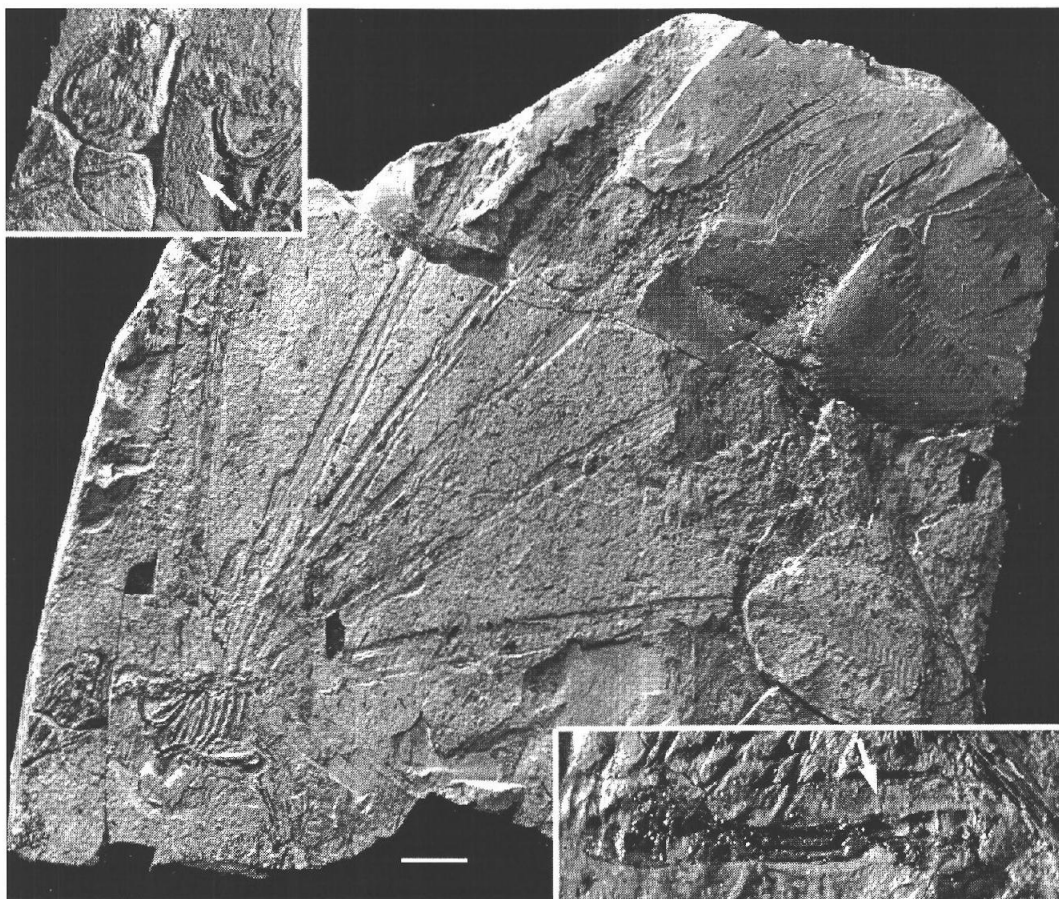


Figure 16. Holotype of *Longisquama insignis* from Late Triassic lacustrine deposits, Madygan (southern Fergana Valley), Osh Province, Kyrgyzstan (PIN 2584/4). Inset above: skull and neck; the arrow points to impressions of the elongate scale-like structures of the chin and neck. Inset below: the left humerus (digitally reversed from the counterslab [PIN 2584/4]); the elongate postaxial scales are indicated by the arrow. Scale bar equals 1 cm.

The anterior portion of *Longisquama*'s body was covered with imbricating scale-like structures; those on the chin and neck were particularly delicate and elongate (Figure 16, upper left inset). In addition, a series of shorter (~4 mm) scales (Sharov 1970) formed an apparent aerofoil-like surface along the postaxial margins of the forelimbs (Figure 16, lower right inset). Most remarkable, however, are the series of six to eight pairs of markedly elongate, bilateral, paraxial structures that occurred at segmental intervals along the animal's dorsum (Figure 16). These have previously been referred to as merely "long scales" (Sharov 1970) or "extremely modified horny scales" (Maderson 1972; Haubold and Buffetaut 1987), but we interpret them as non-avian feathers, albeit somewhat unusual in form.

As in birds, *Longisquama*'s non-avian feathers (henceforth, for the sake of brevity, referred to occasionally as "feathers") were discrete structures that consisted of a distinct shaft (quill) and vane (barbs). The shaft consisted of a calamus basally and a rachis distally. In bird feathers, the calamus is composed of a tubular outer wall surrounding an inner, thin-walled tube that is transversely partitioned by a series of cornified, cup-like, pulp caps (Lucas and Stettenheim 1972). As seen in three successive quills immediately adjacent to the dorsal vertebrae, the broad, tube-like calamus of *Longisquama* was approximately barrel-shaped and tapered proximally, a morphology consistent with its placement within, and origin from, a follicle (Figure 17). A series of four to six internal pulp cavities are preserved on the most anterior of the three preserved quills (Figure 16, Figure 17).

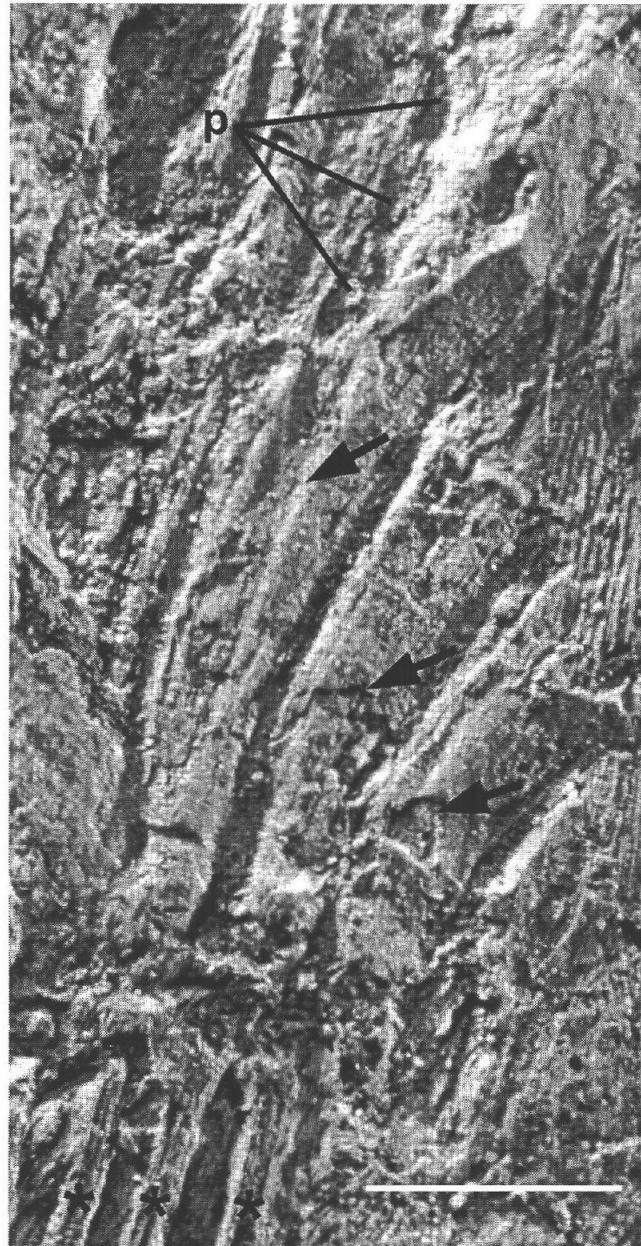


Figure 17. Calami at the bases of three successive quills that inserted on the left dorsum above the ribs (\*) of *Longisquama insignis* (PIN 2584/4). Note the proximal tapering as well as the distinct, hollow core (indicated by arrows) of each calamus. The presence of calami strongly infer that development of *Longisquama*'s non-avian feathers took place within a follicle. Apparent pulp cavities (p) are also preserved. Scale bar equals 5 mm.

In birds, the rachis is the long, often barb-bearing segment of the feather shaft. In *Longisquama*, the narrow rachis spanned about 90% of the feather's length and bore a series of barbs throughout its length (Figure 16, Figure 18, Figure 19, Figure 20). Portions of the rachis appear to have been hollow. However, as in birds, this may be a remnant of spongy, air-filled pith (Figure 18).

At their distal extremities, the feather vanes consisted of distinct, elongate barbs that branched regularly from the rachis (Figure 18, Figure 19, and Figure 20)<sup>2</sup>. Barbules were not present. Some of the individual barbs appear to have been branched and the distal ends of successive barbs formed a ribbonlike margin that was more delicate along the trailing edge of the feather (Figure 18). Branching and connections between successive barbs are unusual in avian feathers. However, developmental patterns resulting in branching of individual barbs and fusion of successive barb tips in avian feathers, via "branching" and/or "union" or fusion of organization centers within the ramogenic (or barb-forming) zone of developing avian feathers, are well documented (Lillie and Wang 1941). Additionally, examples of *Longisquama*-like barb structure in avian feathers are readily available. As in *Longisquama*, successive barbs in some avian feathers are separate proximally but are fused distally (for example, the head feathers of the

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<sup>2</sup> We interpret barbs to have been distinct from one another, rather than merely plications on a continuous surface, for two reasons. First, the texture and color of matrix comprising the barb surfaces are qualitatively different from that between the barbs: In a continuous surface, matrix quality would have been more homogenous. Second, some barbs appear to have been disturbed post-depositionally and are preserved in overlapped positions.

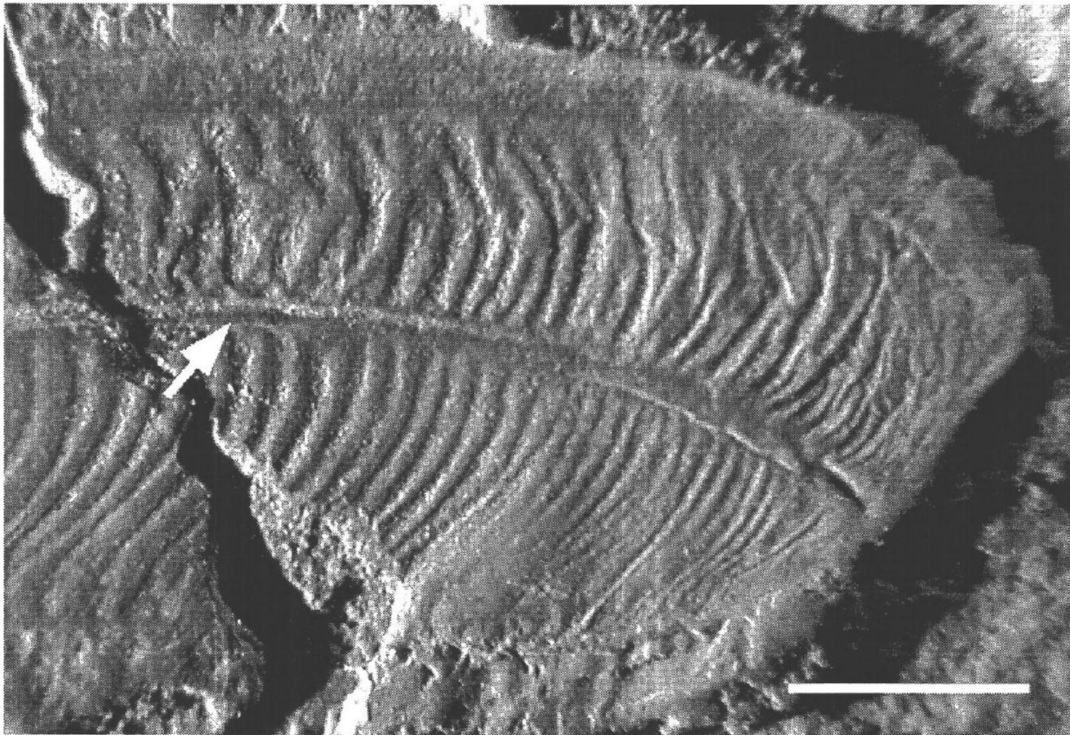


Figure 18. The distal portion of the feather vane of *Longisquama insignis* (PIN 2584/5). The arrow denotes where breakage reveals the hollow remnant of spongy, air-filled pith of the rachis. Note the distal fusion of the barbs at both the leading edge (above) and trailing edge (below) of the feather. Barbs are clearly distinct from one another except where they are fused distally and where they join the rachis. Post-mortem disturbance probably resulted in apparent overlapping of some barbs. Scale bar equals 25 mm.

curl-crested aracari, *Pteroglossus beauharnaesii*). Branching of individual barbs occurs, for example, in downy feathers of chickens (Lucas and Stettenheim 1972).

In addition, vanes at the distal extremities of *Longisquama*'s feathers were sufficiently delicate that details of their morphology can be resolved in spite of their being overlain by other feathers (Figure 19). Proceeding toward the body, barbs became increasingly massive and less delicate so that the extensive proximal vane consisted largely of a series of flattened, irregularly shaped barbs (Figure 16, Figure 20).

The extensive, proximal region of rachis and less-differentiated barbs created the unusual appearance of *Longisquama*'s feathers (Figure 16, Figure 20). In addition, the feather sheath was retained as an integral part of the mature feather where it formed a robust jacket enclosing the long proximal region<sup>3</sup>. This contrasts with the avian condition where the sheath cracks, flakes, and is otherwise eliminated by preening (Lucas and Stettenheim 1972).

The presence of a shaft, vane, and sheath are obvious attributes of avian feathers, but not of reptilian scales. Since the morphology of the calamus in *Longisquama* is consistent with each feather having been developed in an

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<sup>3</sup> The animal apparently was preserved in a quiet, lacustrine environment. Some skeletal elements were preserved, but most of the right-side feathers either floated away or rotated caudally. Feather preservation probably resulted from infill by fine-grain sediment. Proximally, a few of the left-side calami maintained themselves as hollow tubes that eventually fractured down their centers during compaction. The outer surface of the feather sheath was essentially featureless although underlying, compacted structures pressed outwardly against it. In the mid-feather region, the rachis and barbs are occasionally sharply defined where parts of the epidermal sheath broke away during collection of the specimen. Preservation of the rachis and individual barbs in this region is consistent with there having been enough empty space within the sheath that, when filled with fine-grained mud, the morphology of the structures within was faithfully recorded.

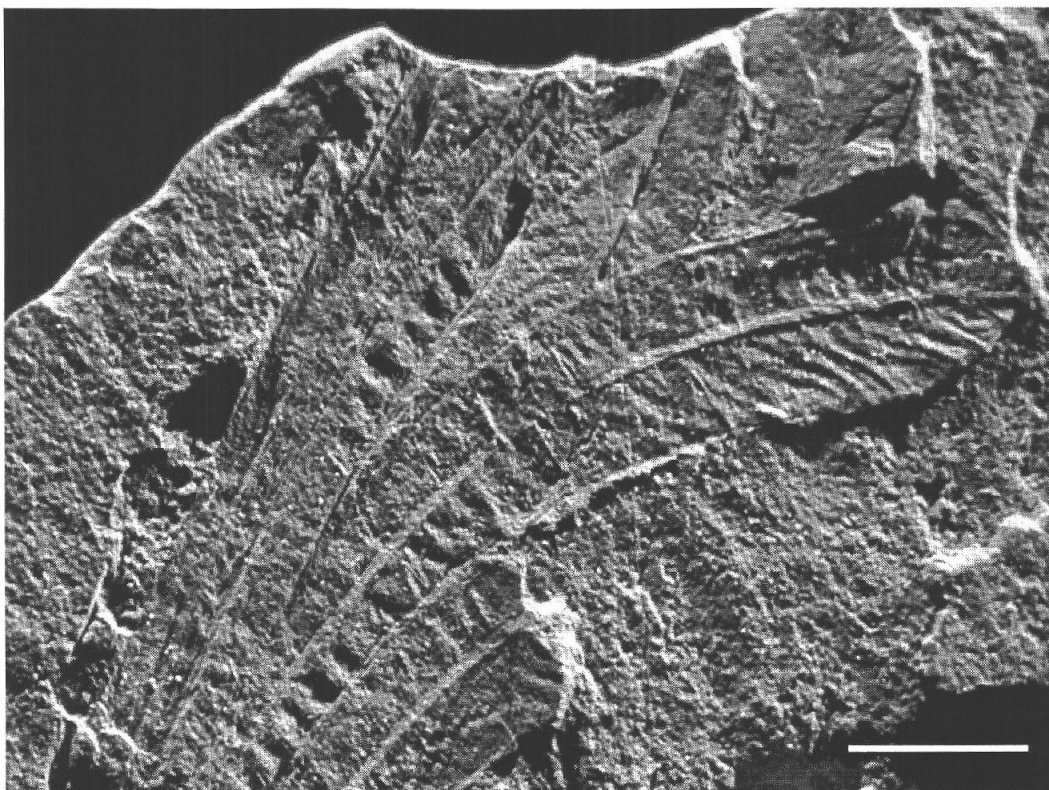


Figure 19. Distal ends of overlapped feathers of *Longisquama insignis* (PIN 2584/9). Vanes were sufficiently delicate that the structure of underlying feathers remains visible. Scale bar equals 50 mm.

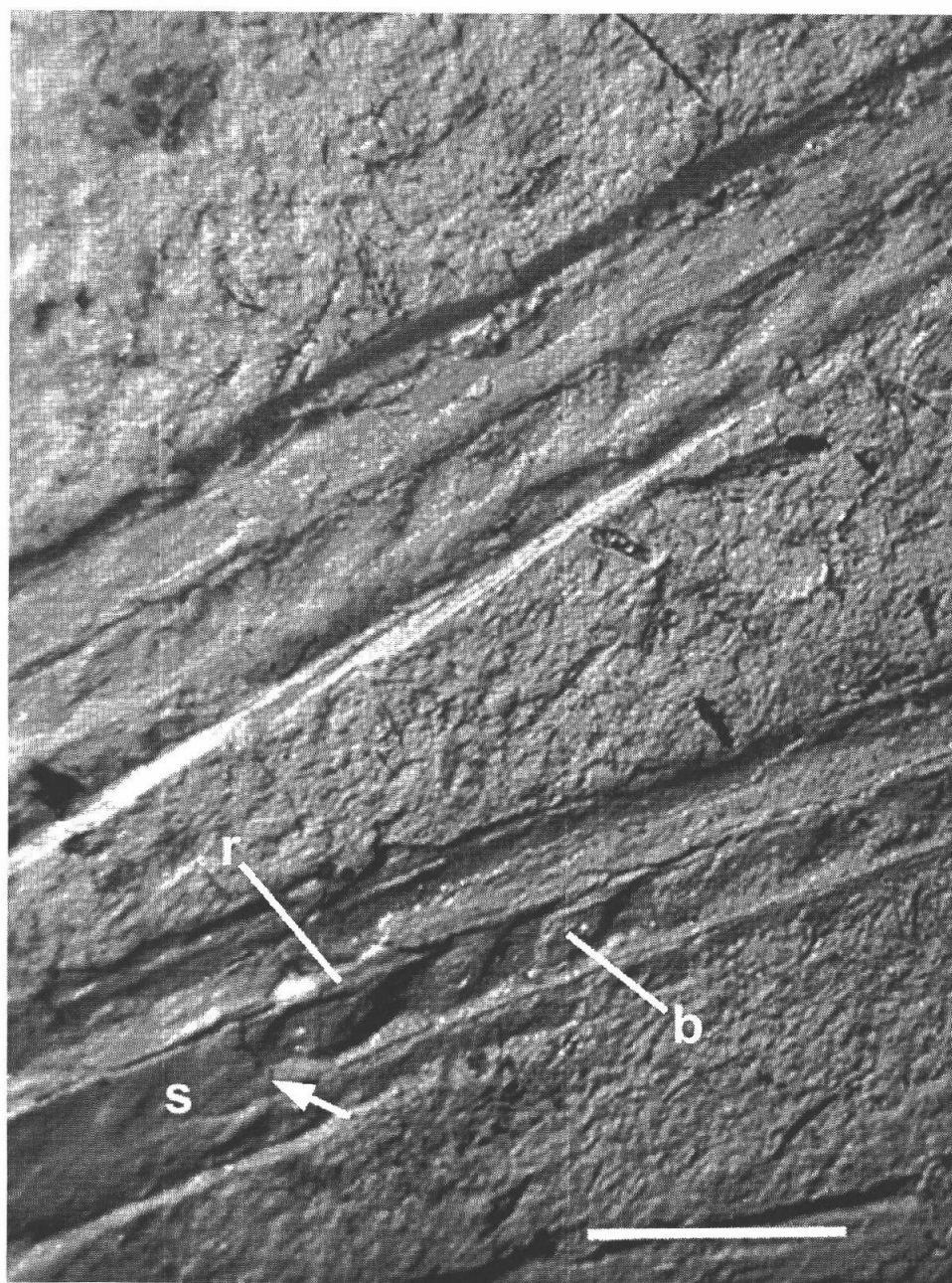


Figure 20. The sheath/rachis/barb complex of the proximal vane of *Longisquama insignis* (PIN 2584/4). The sheath (s) jacketed the stout barbs (b) and rachis (r). The arrow denotes where a portion of the sheath has broken away to reveal the underlying rachis and barbs. Scale bar equals 50 mm.

individual follicle, each was likely to have been formed, and possibly molted, individually. This varies sharply from keratogenesis on a reptilian scale. Because the latter lacks a follicular morphology, mature corneous materials form, and are usually shed, in large flakes or continuous sheets.

Given the absence of a thorough phylogenetic analysis, the taxonomic status of *Longisquama* is poorly understood. Consequently, the convergent or homologous nature of feathers in birds and *Longisquama* remains unclear. Nevertheless, we suggest that the shared, specialized characters (apomorphies) of feathers in these two taxa, including the calamus set in its presumed follicle, rachis, distinct barbs, and epidermal sheath, were unlikely to have evolved more than once. If *Longisquama*'s feathers are homologous with those in birds, they may provide insight into an evolutionary grade through which feathers passed almost 75 million years prior to *Archaeopteryx*, and, perhaps, before the origin of birds *sensu stricto*.

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## CHAPTER 5: SUMMARY

The three examples given here demonstrate that using the morphology and physiology of modern animals makes it possible to draw reasonable, testable, inferences regarding the biology, and especially the morphology and physiology, of extinct animals. The inferences drawn here, while giving us new insights into the physiology and general biology of extinct taxa, may be used as independent tests of current hypotheses about the relationships of birds and dinosaurs. If, as is commonly accepted, birds are living dinosaurs, one would expect to see transitions from typically dinosaurian to typically avian features in nearly all, if not all, respects. However, this is not the case.

First, as described in chapter two, birds utilize movements of the sternum or, when roosting, movements of the pelvis to ventilate their highly specialized lung-air sac system. In contrast, theropod dinosaurs, early crocodilians, and pterosaurs have the skeletal morphology indicative of the presence of a hepatic piston mechanism of lung ventilation and there is no indication that they possessed an avian style lung-air sac system. Additionally, theropods in which abdominal soft tissue is preserved demonstrate a transverse subdivision of the body that, in modern amniotes, is seen only in diaphragm breathers—crocodilians and mammals. Therefore, all known theropod dinosaurs likely utilized a hepatic piston lung ventilatory mechanism, and there is no reduced reliance on that mechanism in this

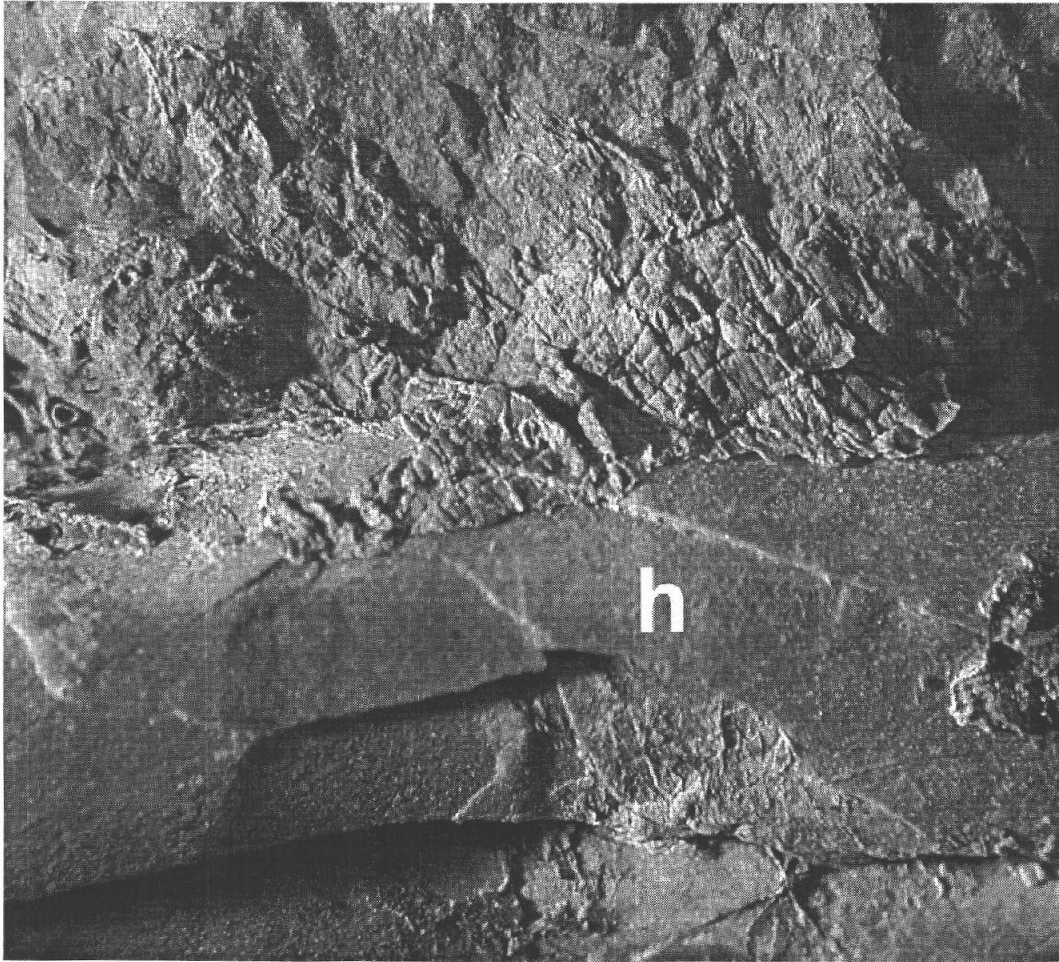


Figure 21. Mummified skin on the humerus (**h**) of the theropod dinosaur, *Pelecanimimus*. Similar skin is preserved on the forearm.

taxon. Moreover, although the pubes of birds and theropods have been presumed to have been similar, and supposedly show a dinosaurian-avian transition, those of theropod dinosaurs are fundamentally different in both form and function from those of birds.

Second, as demonstrated in chapter three, there is no transition from cursorial mechanism of dinosaurs, in which the center of gravity was located near the hip and the entire hindlimb generated stride length, to that of modern birds, in which the center of gravity is located more cranially and the femur is excluded from stride length generation. Significantly, morphometric data from the hindlimbs and estimated of the location of the center of gravity indicate that *Caudipteryx*, the only supposed dinosaur that was unquestionably feathered, is likely to have been a secondarily flightless bird rather than a feather dinosaur.

Finally, no known theropod dinosaurs had feathers. In the few specimens in which integumentary tissue has been preserved (*e.g.*, *Pelicanimimus* and *Sinosauropteryx*), this tissue lacks any feather structure (Figure 21). However, *Longisquama*, a non-dinosaurian archosaur, that probably co-existed with the earliest dinosaurs and predated *Archaeopteryx* by 75 million years, possessed feathers that are probably homologous with those of strongly suggests that feathers evolved before the origin of dinosaurs rather than within that taxa.

Although birds and dinosaurs share some morphological similarities, the data from these three investigations strongly suggest that, contrary to current phylogenetic hypotheses, it is unlikely that birds are descended from any known

dinosaurs. Therefore, I suggest that either the similarities between birds and dinosaurs are primitive characters that are also shared with their common ancestor or they were derived convergently.

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## **APPENDIX**

| Genus                  | Specimen       | Femur<br>length<br>(mm) | Tibia*<br>length<br>(mm) | MIII†<br>length<br>(mm) | Trunk<br>length<br>(mm) |
|------------------------|----------------|-------------------------|--------------------------|-------------------------|-------------------------|
| <i>Morococcyx</i>      | MCZ 2937       | 32                      | 48                       | 35                      | 44                      |
| <i>Coturnix</i>        | MCZ 3298       | 36                      | 44                       | 27                      | 56                      |
| <i>Geococcyx</i>       | MCZ 1495       | 56                      | 86                       | 64                      | 76                      |
| <i>Bonasa</i>          | KU 21279       | 61                      | 82                       | 44                      | 81                      |
| <i>Lagopus</i>         | KU 30585       | 61                      | 80                       | 40                      | 84                      |
| <i>Eudromia</i>        | KU 78091       | 56                      | 79                       | 44                      | 87                      |
| <i>Alectoris</i>       | MCZ 186        | 61                      | 80                       | 46                      | 91                      |
| <i>Hierophasis</i>     | MCZ 1625       | 76                      | 101                      | 72                      | 92                      |
| <i>Numida</i>          | MCZ 1648       | 83                      | 117                      | 76                      | 108                     |
| <i>Macrocephalus</i>   | MCZ 355        | 90                      | 127                      | 90                      | 118                     |
| <i>Phasianus</i>       | MCZ 1386       | 86                      | 112                      | 74                      | 124                     |
| <i>Chlamydotis</i>     | MCZ 194        | 80                      | 140                      | 101                     | 135                     |
| <i>Choriotis</i>       | KU 85182       | 87                      | 185                      | 150                     | 149                     |
| <i>Agrocharis</i>      | MCZ 2878       | 118                     | 189                      | 141                     | 153                     |
| <i>Gallus</i>          | OSU CVA        | 111                     | 151                      | 111                     | 163                     |
| <i>Meleagris</i>       | KU 88097       | 137                     | 232                      | 176                     | 185                     |
| <i>Pelecyornis</i>     | PU 15402       | 135                     | 216                      | 164                     | 223                     |
| <i>Anomalopteryx</i>   | BMNH A.3       | 178                     | 305                      | 146                     | 289                     |
| <i>Megalapteryx</i>    | MNZ 23700      | 231                     | 350                      | 139                     | 340                     |
| <i>Casuarius</i>       | KU 86290       | 230                     | 365                      | 300                     | 490                     |
| <i>Pachyornis</i>      |                | 250                     | 505                      | 215                     | 545                     |
| <i>Struthio</i>        | MCZ 828        | 234                     | 419                      | 420                     | 557                     |
| <i>Dinornis</i>        | Yorkshire      | 301                     | 655                      | 345                     | 635                     |
| <i>Aepyornis</i>       |                | 310                     | 565                      | 290                     | 655                     |
| <i>Sinosauropteryx</i> | NIGP 127587    | 86                      | 97                       | 67                      | 145                     |
| <i>Compsognathus</i>   | MNHN CHJ 79    | 110                     | 136                      | 81                      | 248                     |
| <i>Staurikosaurus</i>  | MCZ 1669       | 203                     | 245                      | 107                     | 358                     |
| <i>Eoraptor</i>        | PVSJ 512       | 152                     | 157                      | 81                      | 367                     |
| <i>Velociraptor</i>    | GI 100/25      | 200                     | 210                      | 95                      | 369                     |
| <i>Ornitholestes</i>   | AMNH 619       | 207                     | 162                      | 117                     | 437                     |
| <i>Ingenia</i>         | GI 100/30      | 228                     | 281                      | 125                     | 459                     |
| <i>Coelophysis</i>     | AMNH 7224      | 203                     | 221                      | 120                     | 556                     |
| <i>Syntarsus</i>       | QG 1           | 208                     | 223                      | 132                     | 567                     |
| <i>Deinonychus</i>     | MCZ 4371       | 336                     | 382                      | 164                     | 601                     |
| <i>Herrerasaurus</i>   | PVL 2566       | 473                     | 411                      | 223                     | 841                     |
| <i>Liliensternus</i>   | HMN R1291      | 440                     | 437                      | 231                     | 983                     |
| <i>Piatnitzkysauru</i> | PVL 4073       | 552                     | 492                      | 273                     | 990                     |
| <i>Eustreptospondy</i> | OUM J13558     | 520                     | 500                      | 235                     | 1002                    |
| <i>Struthiomimus</i>   | AMNH 5339      | 480                     | 535                      | 365                     | 1015                    |
| <i>Dilophosaurus</i>   | UCMP 37302     | 557                     | 525                      | 300                     | 1252                    |
| <i>Ceratosaurus</i>    | USNM 4735      | 620                     | 555                      | 254                     | 1351                    |
| <i>Elaphosaurus</i>    | HMN Gr.S 38-44 | 529                     | 608                      | 391                     | 1472                    |
| <i>Gallimimus</i>      | GI 100/11      | 665                     | 740                      | 530                     | 1511                    |
| <i>Allosaurus</i>      | UUVF 6000r     | 880                     | 730                      | 375                     | 1642                    |
| <i>Afrovenator</i>     | UC OBA 1       | 760                     | 687                      | 321                     | 1664                    |

|                         |                 |      |      |     |      |
|-------------------------|-----------------|------|------|-----|------|
| <i>Yangchuanosaurus</i> | CV 00215        | 550  | 494  | 297 | 1709 |
| <i>Albertosaurus</i>    | AMNH 5458       | 1025 | 990  | 625 | 1967 |
| <i>Sinraptor</i>        | IVPP 10600      | 876  | 776  | 410 | 2050 |
| <i>Gorgosaurus</i>      | NMC 2120        | 1040 | 1000 | 594 | 2206 |
| <i>Carnotaurus</i>      |                 | 1030 | 989  | 551 | 2225 |
| <i>Tyrannosaurus</i>    | CM 9380         | 1300 | 1140 | 684 | 2463 |
| <i>Daspletosaurus</i>   | AMNH 5438       | 1000 | 1271 | 763 | 2678 |
| <i>Lesothosaurus</i>    | Assemblage B17  | 104  | 129  | 57  | 253  |
| <i>Heterodontosaur</i>  | SAM-K1332       | 112  | 145  | 68  | 277  |
| <i>Yandusaurus</i>      | T 6001 (MK B-S) | 156  | 184  | 97  | 355  |
| <i>Hypsilophodon</i>    |                 | 150  | 254  | 84  | 468  |
| <i>Thescelosaurus</i>   | USNM 7757       | 412  | 328  | 157 | 1031 |
| <i>Ouranosaurus</i>     | GDF 300/381     | 811  | 785  | 295 | 1732 |
| <i>Anatotitan</i>       | AMNH 5730       | 1150 | 1020 | 420 | 1896 |
| " <i>Kritosaurus</i> "  |                 | 1045 | 943  | 363 | 1976 |
| <i>Iguanodon</i>        | IRSNB 1534      | 710  | 675  | 269 | 2297 |
| <i>Corythosaurus</i>    | AMNH 5240       | 1080 | 1000 | 380 | 2312 |
| <i>Edmontosaurus</i>    | ROM 5167        | 1240 | 1000 | 410 | 2318 |
| <i>Caudipteryx</i>      | IVPP (uncat)    | 146  | 193  | 113 | 200  |
| <i>Caudipteryx</i>      | NGMC 97-9-A     | 149  | 182  | 117 | 206  |
| <i>Caudipteryx</i>      | V 12344         | 149  | 196  | 124 | 220  |

\* tibiotarsus of birds

† tarsometatarsus of bird