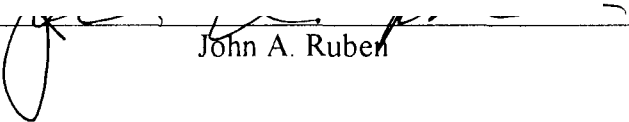AN ABSTRACT OF THE THESIS OF

Nicholas R. Geist for the degree of Doctor of Philosophy in Zoology presented on June 2,

1999. Title: Reconstructing the Paleobiology of the Dinosaurs.

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Abstract approved: _____

John A. Ruben

Dinosaurs represent one of the most successful evolutionary radiations of

terrestrial vertebrates, with a myriad of forms that dominated the terrestrial environment

for over 180 million years. Despite the fact that dinosaurs are the focus of extensive

popular and scholarly investigation, relatively little is actually known of their biology.

The most reliable interpretations of the paleobiology of the dinosaurs, as well as other

extinct taxa, depend on a synthetic approach that employs the uniformitarian principles of

comparative and functional morphology, physiology, and embryology. This thesis is an

attempt to apply such a multifaceted, interdisciplinary strategy to a broad range of

biological questions about the dinosaurs, including aspects of behavior, phylogeny, and

metabolic status. Specifically, the phylogenetic interpretations and biological

reconstructions of dinosaurs in this study are based largely upon detailed examination of

extant forms, in particular, their two closest relatives, crocodilians and birds.

Chapter Two addresses suggestions that some dinosaurs may have exhibited

reproductive behavior similar to extant altricial birds, with highly dependant offspring.

Comparisons of skeletal evidence from a variety of living archosaurian dinosaur relatives

is shown to be consistent with a more crocodilian-like, precocial pattern of reproductive

behavior. Chapter Three presents the two major contrasting perspectives on the phylogenetic relationships of various extinct archosaurs and birds, as well as a critical evaluation of the viable scenarios for the origin of avian flight. Current dogma notwithstanding, the supposed linear relationship between birds and theropod dinosaurs is demonstrated to be unlikely. The fourth chapter is an experimental approach elucidating the water and heat savings mediated by nasal respiratory turbinates in a range of avian species. These structures are shown to have a significant functional role tightly correlated to the elevated metabolic rates characteristic of living endothermic vertebrates.

Collectively, this thesis uses a broad, multidisciplinary approach that draws from our knowledge of a range of biological parameters of extant vertebrates to provide a more complete, reasonable, and relevant perspective on the paleobiology of the dinosaurs.

Reconstructing the Paleobiology of the Dinosaurs

by

Nicholas R. Geist

A THESIS

Submitted to

Oregon State University

In partial fulfillment of
the requirements for the
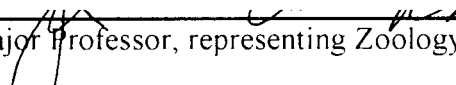degree of

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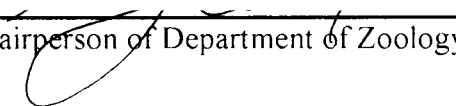Completed June 2, 1999

Commencement June 2000

Doctor of Philosophy thesis of Nicholas R. Geist presented on June 2, 1999
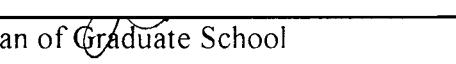
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Contribution of Authors

Terry Jones was involved in data collection, analysis, and writing of Chapter Two, Juvenile Skeletal Structure and the Reproductive Habits of Dinosaurs. Dr. Alan Feduccia was involved in the organization and critical review of Chapter Three, Gravity-Defying Behaviors: Identifying Models for Protoaves.

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CHAPTER 1:

GENERAL INTRODUCTION

In terms of morphologic diversity and longevity, dinosaurs were probably the most successful radiation of terrestrial vertebrates. A myriad of forms, from bipedal, chicken-sized, predatory theropods to elephantine, herbivorous sauropod behemoths that were the largest of all terrestrial animals, dominated the terrestrial environment for well over 150 million years--a timespan nearly three times the 60-65 million-year duration of The Age of Mammals. Despite their evolutionary importance, relatively little dinosaur biology is well understood. Over the last two decades, there has been a renaissance of popular and scholarly interest concerning the behavior, evolutionary relationships, and metabolic status of dinosaurs. However, relatively few studies have explored these parameters utilizing the multifaceted analysis frequently required to understand the biology of long-extinct taxa. In the following body of work, I address some of these questions about dinosaur biology by applying principles of physiology and embryology as well as the more traditional disciplines of comparative and functional morphology.

More specifically, this work has been guided by one overarching principle: it is not possible to determine the biology of long-extinct taxa solely on the basis of the inevitably incomplete evidence supplied by the fossil record. Therefore, the most reliable interpretation of dinosaur paleobiology is necessarily based upon knowledge

of the fossil record supplemented by a thorough understanding of the biology of their two closest extant relatives, crocodilians and birds. However, determination of which of these two groups is always the most appropriate model for understanding dinosaurs is far from clear. The problem centers on one obvious set of difficulties: neither extant taxon is likely to be the ideal model for dinosaurs. Both crocodiles and birds exhibit a number of anatomical, behavioral, and physiological specializations unlikely to have been present in dinosaurs (e. g., crocodilians are relatively sedentary, semi-aquatic, quadripedal ectotherms; birds are highly active, feathered, flying, bipedal endotherms). In many cases, the only solution has been to examine attributes of both groups with a view towards a more comprehensive perspective of what range of features may have been present in dinosaurs.

In Chapter 1, I address specific aspects of dinosaurian reproductive behavior and development. It has been suggested that the reproductive behaviors and developmental patterns of some ornithischian dinosaurs resembled those of altricial birds (e. g., songbirds), with relatively immobile, immature hatchlings confined to the nest and requiring extensive parental care (including feeding) to survive (Horner and Weishampel 1988; Horner 1996). However, direct evidence for this type of bird-like reproductive behavior is absent. These earlier assertions of a songbird-like reproductive pattern in juvenile dinosaurs were based on the supposed degree of ossification of fossilized long bone articular elements (epiphyses) and the extent of calcified cartilage that forms the growth plate in all juvenile archosaurian long bones. In this chapter, I reevaluate the accuracy of these claims based on the morphology of

long bone epiphyses in a variety of extant archosaurians, including juvenile

crocodilians (all are precocial) and a variety of precocial and altricial birds.

Additionally, I propose a more rigorous set of criteria for determining developmental

status in juvenile archosaurians based upon ossification of pelvic elements.

Chapter 2 is concerned with the evolutionary relationships of dinosaurs and the

origin of avian flight. Several current phylogenetic scenarios assert that birds are the

direct descendants of a particular group of theropod dinosaurs, and that flight therefore

must have developed in a terrestrial context within these cursorial bipeds (Gautier

1984; Padian 1985; Ji *et al* 1999). However, in the more traditional (and perhaps,

more rational) model for the origin of birds and avian flight, the protoavian ancestor is

thought to have been derived from within an assemblage of small arboreal early

Mesozoic archosaurs (Heilmann 1927; Bock 1961). According to this scenario, tree-

dwelling protoavian ancestors developed flight through a series of selectively

advantageous intermediate stages, progressing from leaping to parachuting to gliding,

eventually culminating in fully powered, flapping flight. This model benefits from

numerous living and extinct arboreal vertebrates that engage in analogous non-

powered aerial activities using height as a plentiful source of gravitational energy.

Close reexamination of known fossil forms, as well as new discoveries from the Early

Mesozoic adaptive radiation of arboreal archosaurs, are likely to provide valuable

insights into the origin of birds.

Several other compelling lines of evidence further challenge the current

dinosaur-to-bird phylogenetic scenarios. The theropods postulated as the closest bird

relatives appear in the stratigraphic record at least 70 million years after the first known bird, the Late Jurassic *Archaeopteryx*. Additionally, recent information about respiratory physiology and embryological development is contradictory to a theropodan origin of birds (Ruben *et al* 1999; Burke and Feduccia 1998). In Chapter 2, I summarize these data along with new information that challenges current conventional wisdom for a theropodan ancestry of birds.

The acquisition of endothermy, or "warm-bloodedness," was one of the notable evolutionary events in the history of vertebrates, and is among the most significant physiological features that distinguishes birds and mammals from other vertebrates. The elevated activity levels and thermal independence that endothermy confers to these organisms probably plays a major role in their success in a variety of cold or fluctuating thermal environments unavailable to ectothermic vertebrates. Additionally, endothermic vertebrates are capable of prolonged bouts of aerobic activity far beyond the limited abilities of extant ectotherms.

Clearly, a more complete understanding of the metabolic status of dinosaurs (i. e., endo- vs. ectothermic) can provide valuable insights into many aspects of their biology. A number of previous hypotheses suggesting endothermy in dinosaurs have been based on a variety of loose correlations (i. e., bone histology, supposed endotherm-like growth rates, fossil bone isotope composition, etc.) that are unsupported by empirical data (Reid 1998; Ruben *et al* 1998; Kolodny *et al* 1996). Endothermy is, however, largely a product of soft tissues that are rarely preserved as

fossils (i. e., the visceral organs and brain and central nervous system), and is therefore usually impossible to examine in extinct organisms.

Along with the benefits of endothermy are certain physiological costs: endotherms experience oxygen consumption and lung ventilation rates approximately an order of magnitude higher than ectotherms of equivalent mass. Elevation of lung ventilation rate in endotherms is a potential avenue for dangerously accelerated levels of respiratory evaporative water loss (REWL). The realization that nasal respiratory turbinates, convoluted, epithelially-lined structures in the nasal passages of virtually all birds and mammals, have a direct functional link to the high lung ventilation rates typical of endothermic vertebrates provides a reliable means of determining the metabolic status of extinct vertebrates, including dinosaurs. Significantly, no known dinosaur possessed respiratory turbinates (Ruben *et al* 1997).

Chapter 3 focuses specifically on the role that nasal respiratory turbinates play in the maintenance of endothermy in extant birds, demonstrating the tight functional link between nasal respiratory turbinates and decreased rates of REWL in a variety of birds. Previous reports (Hillenius 1992, 1994) have shown a tight functional correlation between mammalian endothermy and the presence of nasal respiratory turbinates. Ruben *et al* (1997) operated under the assumption that avian respiratory turbinates exhibit a similar physiological functional linkage to endothermy as those of mammals, but direct data supporting this notion was limited. This information on the fundamental physiological significance of nasal respiratory turbinates in birds, because of their close evolutionary relationship to dinosaurs, is crucial to our

understanding of dinosaurian energetics. Specifically, the knowledge that all known theropod dinosaurs lacked respiratory turbinates (Ruben *et al* 1997) is telling us that these animals had probably not attained routine metabolic rates approaching those of birds: that is, theropods were, by definition, likely to have been ectotherms.

CHAPTER 2

JUVENILE SKELETAL STRUCTURE AND THE REPRODUCTIVE HABITS OF
DINOSAURS

by

Nicholas R. Geist and Terry D. Jones

Abstract

Skeletal ontogeny in extant archosaurians (crocodilians and birds) indicates that perinatal pelvic girdle morphology is associated with overall developmental maturity (for example, altriciality versus precociality). Comparison of the skeletal anatomy of perinatal extant archosaurians and perinatal dinosaurs suggests that known dinosaur hatchlings were precocial. These data are consistent with overall similarity in nesting behavior of dinosaurs and modern crocodilians.

Fossils of juvenile dinosaurs can provide key information regarding dinosaur life history and physiology. To evaluate whether hatchling dinosaurs were altricial (nestbound) or precocial (mobile and relatively independent), we examined skeletal structure in a variety of extant, perinatal precocial birds (emu [*Dromaius*], malleefowl [*Leipoa*], ostrich [*Struthio*], brush turkey [*Talegalla*]), perinatal altricial birds (macaw [*Ara*], cockatoo [*Cacatua*], eagle [*Haliaeetus*], starling [*Sturnus*]), and perinatal crocodilians (*Alligator, Caiman*) (all crocodilians are precocial at birth), and compared characteristics with skeletal features of perinatal dinosaurs (J. R. Horner and D. B. Weishampel, 1988).

This comparison reveals that the extent of ossification of the pelves at hatching may be a reliable indicator of the altricial or precocial nature of archosaurian neonates. Specifically, the pelves of late-fetal crocodilians and precocial birds are more ossified than are those of altricial birds (Fig. 1; Table 1) (J. M. Starck, 1989). This observation is consistent with the structure of the major locomotor muscles of the hind limb, many of which originate from the pelvic girdle in both crocodilians and birds. Juveniles that are active cursors immediately upon hatching require a rigid, stable site of origin for limb musculature. In contrast, pelves of perinatal altricial birds are poorly ossified. However, even altricial juveniles become active within the nest in a matter of days following hatching and postnatal ossification of the pelvic girdle is relatively rapid. Nearly complete ossification may take place within the first week. Consequently, if a fossilized embryo with well-ossified pelvic elements can be reliably identified, this criterion for distinguishing altricial from precocial neonates may be applied with some

Figure 1. Ossification of the pelves in representative hatchling birds: (a) altricial, or nestbound, (starling [*Sturnus*]); (b) precocial, or mobile (malleefowl [*Leipoa*] [Yale Peabody Museum, 1171]). The pelvis of *Leipoa* is completely ossified (the dashed line outlines the ossified posterior region of the ilium); the corresponding region of the ilium of *Sturnus* is cartilaginous. Pelves of perinatal altricial birds are significantly less ossified than those of perinatal crocodilians and precocial birds at equivalent developmental stages (preparations are from cleared and stained specimens).
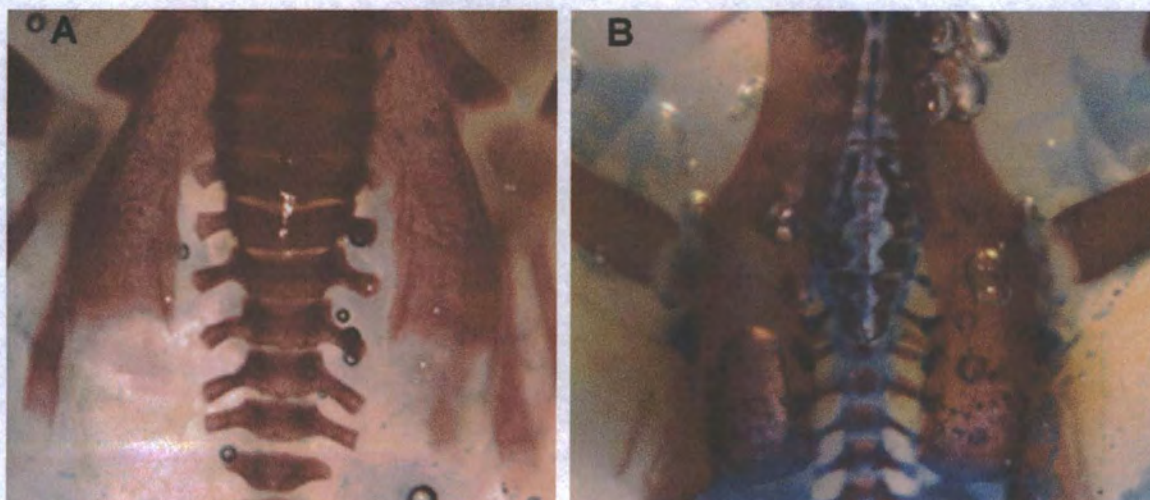
Figure 1

Table 1: Hatchling condition (altricial or precocial) and pelvic development in a variety of birds and crocodilians. ● = pelvis poorly ossified; ◉ = pelvis well ossified. All known dinosaur perinates had well-ossified pelves. * Data from Starck (2).

BIRD	DEGREE OF PELVIC OSSIFICATION	HATCHLING CONDITION (11)
Budgerigar (*Melopsittacus*)*	◉	Atricial
Cockatoo (*Cacatua*)	◉	Altricial
Dove (*Columba*)*	◉	Altricial
Finch (*Lonchura*)*	◉	Altricial
Macaw (*Ara*)	◉	Altricial
Starling (*Sturnus*)	◉	Altricial
Eagle (*Haliaeetus*)	◉	Semi-altricial
Brush turkey (*Talegalla*)	●	Precocial
Buttonquail (*Turnix*)*	●	Precocial
Duck (*Cairina*)*	●	Precocial
Emu (*Dromaius*)	●	Precocial
Malleefowl (*Leipoa*)	●	Precocial
Ostrich (*Struthio*)	●	Precocial
Quail (*Coturnix*)*	●	Precocial
Alligator	●	Precocial
Caiman	●	Precocial

assurity. Significantly, the pelvic girdles of embryonic *Maiasaura* and *Orodromeus*

(J. R. Horner and D. B. Weishampel, 1988), as well all other known dinosaur

embryos, including *Hypacrosaurus* (Ornithischia) (J. R. Horner and P. J Currie, 1994),

Oviraptor (Theropoda) (M. A. Norell, personal communication), and *Therizinosaurus*

(Segnosauria) (P. Currie, personal communication) were apparently well ossified.

These observations indicate that precociality was possibly widespread in dinosaurs.

Previous hypotheses regarding altriciality in certain ornithischian dinosaurs

were based on longbone epiphyseal ossification (J. R. Horner and D. B. Weishampel,

1988; D. B. Weishampel and J. R. Horner, 1994). Longbone elongation in all extant

fetal archosaurians (birds and crocodilians) is centered in a massive cartilaginous cone

at each end of the shaft. The cartilaginous cone consists of a cap of articular cartilage

that overlies a distinct growth zone of proliferating chondrocytes (cartilage producing

cells). These chondrocytes, in turn, rest above a large, temporary mass of hyaline

cartilage.

In the perinates of all extant archosaurians, whether altricial or precocial, the

growth zone differentiates into distinct regions of proliferating and hypertrophying

chondrocytes. The chondrocytes themselves are superficial to a region of calcified

cartilage that is interspersed with spongy endochondral ossification (Fig. 2).

Longbone elongation proceeds as chondrocytes continuously produce new cartilage

that becomes calcified and is subsequently replaced by spongy endochondral bone. At

this developmental stage, and thereafter, the growth zone follows a curve roughly

parallel to the articular surface, which consists of a superficial cap of undifferentiated

Figure 2. Light micrograph of a longitudinal (sagittal) section of the distal femoral epiphysis in a two-week old emu (*Dromaius*). The pattern of longbone development illustrated here is typical of crocodilians as well as both precocial and altricial birds at equivalent developmental stages. **AC**, articular fibrocartilage; **EB**, endochondral bone; **HZ**, zone of hypertrophication and calcification; **PZ**, zone of proliferation; **UC**, undifferentiated cartilage. Magnification: 40x.
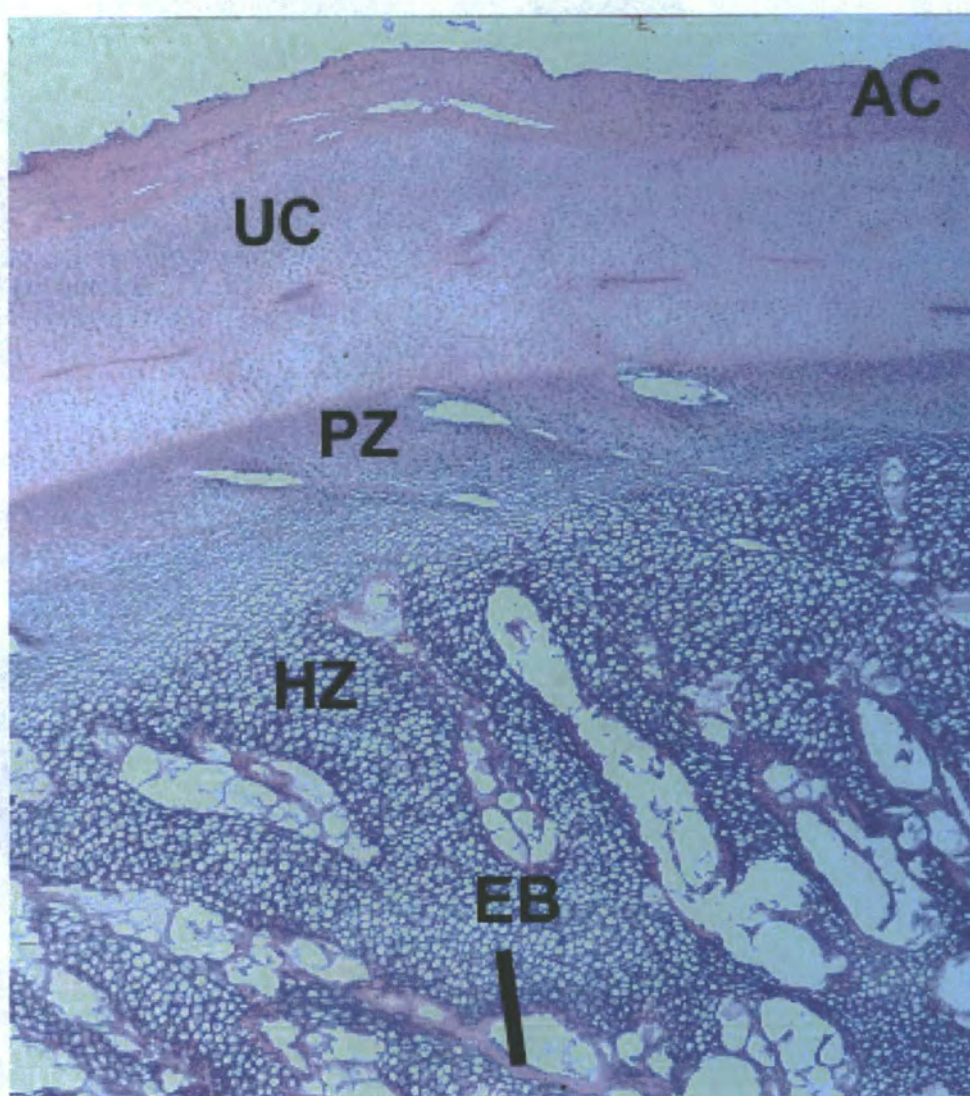
Figure 2

cartilage and fibrocartilage. Identical patterns of longbone development in other altricial and precocial birds (for example, Muscovy duck [*Cairina*], Rock dove [*Columba*], Japanese quail [*Coturnix*], Finch [*Lonchura*], Budgerigar [*Melopsittacus*], Barred buttonquail [*Turnix*]) have also been described elsewhere (J. M. Starck, 1989).

A series of skeletons from embryonic and hatchling ornithopod dinosaurs have recently been discovered. It has been suggested that apparently incompletely ossified femoral epiphyses in neonates of the hadrosaur *Maiasaura* (Archosauria: Ornithischia) indicates altriciality. The femoral epiphyses are composed of spongy endochondral bone overlain by a thin layer of calcified cartilage (J. R. Horner and D. B. Weishampel, 1988). There is no obvious indication of the articular fibrocartilaginous cap that is present on the longbones of all extant archosaurians. Consequently, the knee joint in nestling *Maiasaura* was assumed to have been functionally immature (D. B. Weishampel and J. R. Horner, 1994). However, the articular fibrocartilage cap is unlikely to fossilize (R. W. Haines, 1969). Moreover, the apparently incomplete epiphysis of *Maiasaura* does not differ significantly from the femoral epiphyses of extant juvenile crocodilians and precocial birds when the latter are prepared by bacterial maceration to remove the articular cartilage cap (Fig. 3). Thus, longbones of *Maiasaura* were likely to have originally possessed a typical archosaurian articular fibrocartilage cap. In life, this dinosaur's longbones were likely similar to those of all extant archosaurians, whether altricial or precocial. Moreover, the femoral growth plate of perinatal *Maiasaura* is similar to that of a two-week old chicken (*Gallus*), a thoroughly precocial taxon (C. Barreto et al, 1993).

Figure 3. Neonatal distal femoral epiphysis (frontal view) from: (a) the ornithischian dinosaur *Maiasaura* (Princeton University Museum, 23438), and from three precocial, extant archosaurians including (b) emu (*Dromaius*), (c) malleefowl (*Leipoa*) (Yale Peabody Museum, 1195), and (d) alligator (*Alligator*). The distal femoral epiphysis of *Maiasaura* closely resembles those of extant archosaurians insofar as all are composed (in part) of endochondral bone overlain by a thin layer of calcified cartilage. The femora of the extant specimens were prepared by bacterial maceration to remove the articular cartilaginous caps.
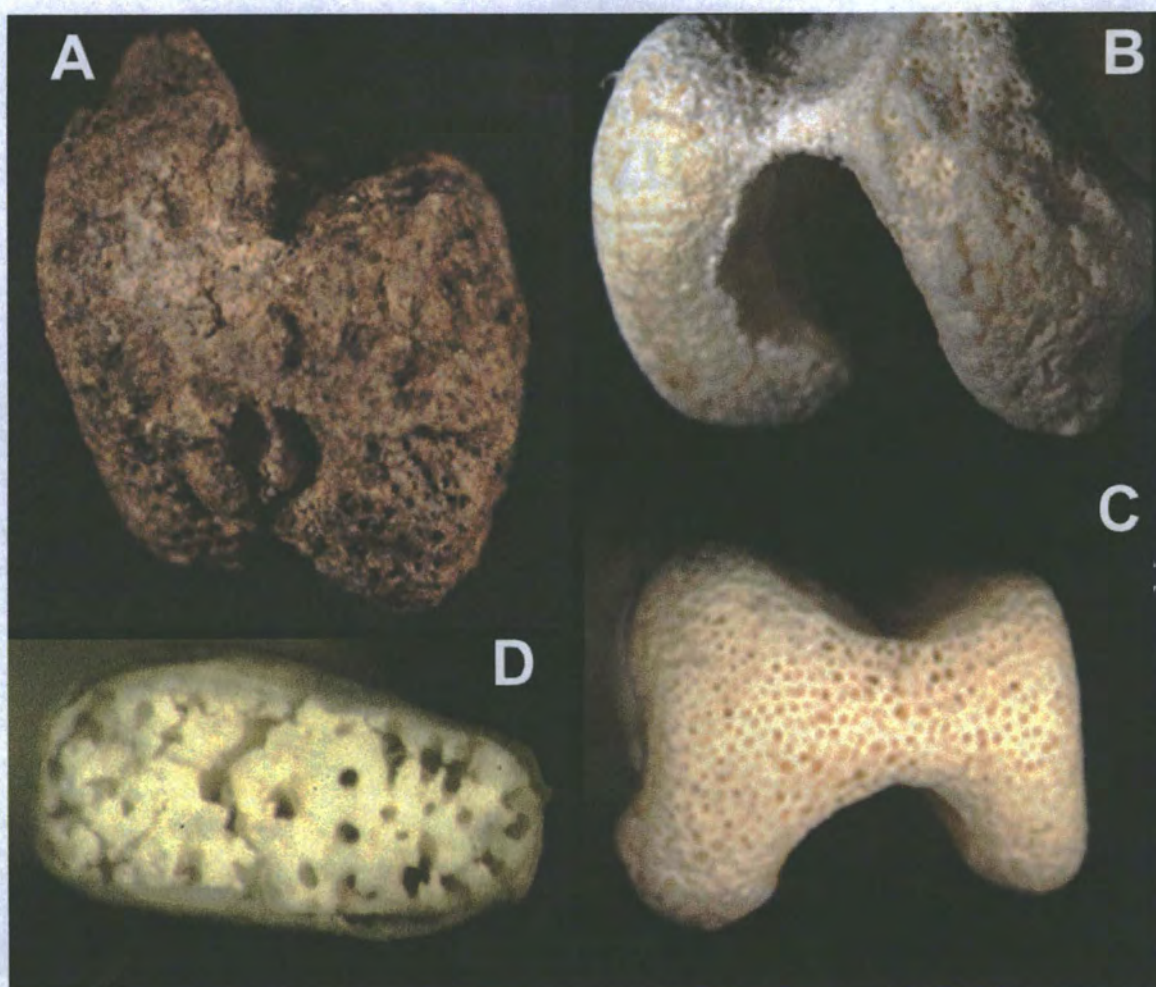
Figure 3

Embryonic femora of the hypsilophodont ornithopod *Orodromeus* (Archosauria: Ornithischia) were described as having "...well formed, smooth condyles which, although fully ossified in appearance, are formed entirely of calcified cartilage. Endochondral bone is not observed in the epiphyseal or metaphyseal regions (J. R. Horner and D. B. Weishampel, 1988)." This description is problematic insofar as in extant, perinatal archosaurians, whether altricial or precocial, articular condyles of the longbones are never composed of calcified cartilage. Calcified cartilage forms in the deepest layer of the growth zone, where it is a scaffold for the deposition of new endochondral bone. Without the association between calcified cartilage and endochondral bone, there is no capacity for longbone elongation. Consequently, we suggest that interpretation of perinatal longbone structure in *Orodromeus* deserves reexamination.

Data from extant specimens indicate that there are no qualitative differences in the development of longbone epiphyseal structure in archosaurians, whether altricial or precocial. It has also been suggested that the lack of well-formed processes for muscle attachment (for example, trochanteric processes) in neonatal *Maiasaura* may be indicative of its altricial nature (J. R. Horner and D. B. Weishampel, 1988). However, well-formed processes did not exist in any of our precocial or altricial neonates. These processes apparently form much later in response to muscle-induced mechanical stresses on the longbones.

It has also been hypothesized that contemporaneous preservation of juvenile and adult *Maiasaura* in, or near, presumed colonial nesting sites, somehow indicates

that neonates were altricial and that the young were completely dependent on adult care. However, this evidence is equivocal: parents and juvenile crocodilians as well as some precocial birds (for example, many shorebirds [Charadriiformes]) often remain in or near colonial nesting sites for some time after hatching (Lang, J. W., 1989; F. B. Gill, 1990). Similarly, the discovery of eggs in close association with an adult *Oviraptor* has been interpreted as evidence of bird-like parental behavior, including perhaps, endothermy, and incubation of eggs by adults (M. A. Norell et al, 1995). However, nest-attending and brooding behavior is widely distributed among extant crocodilians, lizards, snakes, and amphibians (W. E. Magnusson et al; G. K. Noble and E. R. Mason, 1933; S. A. Minton, 1987; W. E. Duellman and L. Trueb, 1986). For example, female *Crocodilus niloticus* often rest their lower throat or thorax directly on the nest for the duration of the 90-day incubation period (H. B. Cott, 1961). Speculation regarding parental incubation of eggs and endothermy based on the apparent brooding behavior of *Oviraptor* are, at best, tenuous.

Current evidence suggests that nesting behavior of dinosaurs was likely similar to that of modern crocodilians.

Acknowledgements

CHAPTER 3

GRAVITY-DEFYING BEHAVIORS: IDENTIFYING MODELS FOR PROTOAVES[1]

This manuscript is in press, American Zoologist

by

Nicholas R. Geist and Alan Feduccia

Synopsis

Most current phylogenetic analyses based upon cladistic criteria assert that

birds are the direct descendants of derived maniraptoran theropod dinosaurs, and that

the origin of avian flight necessarily developed within a terrestrial context (i. e., from

the "ground up"). This scenario for the evolution of powered flight is not supported

by most theoretical aerodynamic and energetic models or chronologically appropriate

fossil data. The more traditional model for the origin of flight derives birds from

among small arboreal early Mesozoic archosaurs. According to this scenario,

protoavian ancestors developed flight in the trees via a series of intermediate stages,

such as leaping, parachuting, gliding, and flapping. This model benefits from the

assemblage of living and extinct arboreal vertebrates that engage in analogous non-

powered aerial activities using elevation as a source of gravitational energy. Recent

reports of "feathered theropods" notwithstanding, the evolution of birds from any

known group of maniraptoran theropods remains equivocal.

Introduction

There are few viable scenarios for the origin of powered flight in the reptilian ancestors of birds. Protoavians initially took flight by leaping or falling from high places, such as trees or cliffs, or, alternately, they generated sufficient energy from running and leaping off the ground to become, and eventually remain, airborne. The latter scenario, commonly referred to as the cursorial (or "ground-up") theory for the origin of flight is not supported by living taxa that demonstrate an intermediate cursorial/aerial habit. The cursorial scenario for the origin of flight hinges largely on cladistic criteria that link protobirds to derived Late Cretaceous theropod dinosaurs (Ostrom, 1975; Gautier, 1984; Padian, 1985; Chiappe, 1995; Ji et al., 1998) without taking account of a variety of contradictory biophysical constraints (Tarsitano, 1985; Bock, 1965, 1985; Rayner, 1985a, 1985b, 1986, 1991; Ruben et al., 1997, 1999). Recent reports of "feathered theropods" notwithstanding, the origin of flying protoavians from any known coelurosaurian dinosaurs is unlikely.

Only the alternative evolutionary scenario for the genesis of avian flight, the arboreal (or "trees-down") theory, is consistent with the reservoir of potential energy provided by gravity available to tree-living animals. Additionally, this model has the advantage of being supported by numerous relevant extant vertebrate models for the intermediate stages of its evolution (Norberg, 1991; Feduccia, 1996). In this scenario, small archosaurian protobirds are hypothesized to have gone through a sequence of gravity-dependant aerial activities, such as jumping, parachuting, and gliding, which eventually culminated in powered flight. Also, unlike the ground-up theory, which

lacks chronologically and biophysically appropriate intermediate fossil forms, there exist numerous fossils of small, arboreal, reptilian gliders preserved from across the Permo-Triassic barrier (Carroll, 1978, 1988).

Physical Constraints on Protoflyers

Arboreal scenarios for the evolution of vertebrate flight originate with Darwin's hypothetical gliding model for the origin of flight in bats (1859). Marsh (1880) first promoted an arboreal hypothesis for avian flight. This theory, and subsequent elaborations, was bolstered by the publication of **The Origin of Birds** by Heilmann (1926).

Most compelling contemporary arguments for the initial stages in the origin of avian flight list two prerequisites, a.) small size, and b.) elevation. The macroevolutionary transition from a reptilian ancestor resulting in avian flight is most adequately explained if it can be demonstrated that there is a clear adaptive advantage at each intermediate (microevolutionary) stage (Bock, 1965, 1985). According to the modern scenario, the progressive elongation and elaboration of reptilian scales to feathers must necessarily have afforded fitness benefits to the organisms at each step. For a small tree dweller, the benefits are clear; any elaboration of the integument that increases surface area, especially along the limbs or flanks of the body, would tend to increase drag, slowing the rate of descent during a fall (Tarsitano, 1985). The development of a propatagium, a membrane extending between the shoulder and forearm that is essential to flight in extant birds (Brown and Cogley, 1996), would

have further increased lift and control in early parachuting protobirds. Lengthening

the scales further and flattening the limbs and bodies of small protoavians would have

allowed them to improve their parachuting capability while increasing aerodynamic

maneuverability, eventually resulting in more adept gliding performance. However,

the adaptive aerodynamic advantages provided by such minimal, incremental

increases in the length of the scales in very early protobirds would have been

unavailable to larger animals. The more massive an organism, the less effect a minor

enhancement of surface area will have on diminishing the rate or angle of a fall. This

is due to the relatively large Reynold's numbers (Re's) characteristic of larger

organisms moving through air (e. g., birds and bats have Re's in the range of 10^4 to

10^5; aircraft operate at Re's in the hundreds of millions). High Reynold's numbers,

typical of larger flying organisms, reflect the mass-related dominance of inertial forces

over the viscosity-induced drag of the aerial medium (Nachtigall, 1977; Norberg,

1990). Significantly, the largest living gliding mammals (e.g., colugos) weigh not

more than 1.75 kg (Nowak, 1991), and this may approximate the upper limit for

gliders.

Problems with a Cursorial Dinosaurian Origin of Flight

The first high profile theory for a terrestrial origin of avian flight was that of

Nopsca (1907, 1923). A number of other cursorial theories have since been offered in

recent decades (Ostrom, 1979; Padian, 1982; Caple, Balda, and Willis, 1983). Most of

these theories derive birds from theropod dinosaurs, with the latest phylogeny drawing

birds from "feathered, ground-living, bipedal dinosaurs" (Ji et al., 1998).

Cladistic assertions notwithstanding, the cursorial model is untenable on

mechanistic, energetic, and ecological grounds (Norberg, 1990; Rayner, 1985a, 1985b,

1988). The greatest constraint on a cursorial origin of flight is the inability of small

terrestrial organisms to run fast enough and jump high enough to glide in a way that

could have evolved into flapping, powered flight. For powered flight to be

energetically feasible, a terrestrial organism must have been able to run at a velocity at

least equal to that required to sustain a glide (Rayner, 1985b). A small (0.2 kg)

running animal must be able to sustain speeds of approximately 6 m/s (~22 km/hr) to

achieve gliding angles consistent with the initiation of flapping flight. Though a

number of small living reptiles and birds may reach this threshold speed during bouts

of anaerobic activity lasting only a few seconds; aerobically sustainable speeds are

much slower (Ruben, 1993; Bennett, 1982). For example, the top running speed of

Archaeopteryx has been estimated to have approximated around 2.5 m/s, or about 9

km/hr (Thulborn, 1985), and top speeds for small bipedal dinosaurs, estimated from

trackway evidence, were in the range of 3.3-4.4 m/s (12-16 km/hr) (Farlow and

Chapman, 1997). In any case, the transition from running

to gliding necessarily results in a decrease in velocity—a strategy counterproductive

for either prey capture or predator avoidance.

A variation on the cursorial theory, i.e., the terrestrial leaping, or "fluttering,"

theory for the origin of avian flight, argues that flapping, powered flight developed

directly from running and leaping in small, cursorial forms and, furthermore, that the transition from gliding to flapping flight is aerodynamically impossible (Caple et al., 1983, 1984; Balda et al., 1985). According to this scenario, feathers developed at the distal ends of the forelimbs of small terrestrial bipeds to enhance stability when leaping for insect prey, and subsequent additional selection for wing development resulted from increased stability during high speed running. Even if this hypothetical cursorial avian ancestor could run at a speed necessary to initiate flight, the immediate loss of power resulting from a leap would slow it down below the required threshold velocity. Therefore, the low forward speeds of a fluttering protobird during these initial aerial forays would have required a hovering-type of wingbeat, the most energetically and aerodynamically complex and demanding form of flight (Rayner, 1988).

The de novo origin of such a mechanically and behaviorally complicated form of flight in the immediate ancestors of birds, especially without having been preceded by a gliding stage, seems highly unlikely. Moreover, the transition from gliding intermediate to powered, flapping flight in hypothetical arboreal avian ancestors has been shown to be aerodynamically advantageous at each evolutionary step (Norberg, 1985, 1986; contra Balda et al., 1985). This model demonstrates that a net thrust force can be produced even in the slightest flapping motions of a gliding animal without loss of lift. Selection pressure was probably high for the increased control, stability, and maneuverability produced by such flapping motions in gliding protobirds (Norberg, 1991).

Surprisingly, current cladistic analyses fail to account for the basic physical constraints that rule out known theropods, all of which were terrestrial cursors, as avian ancestors. More specifically, the basic theropodan bauplan is inconsistent with the requirements for arboreality and flight. The mass of even the smallest known coelurosaurs, in the range of ~5 kg (i.e., compsognathids), is incompatible with the initial stages of flight in an arboreal avian ancestor (Tarsitano, 1985, 1991). Furthermore, the non-aerodynamic, stereotypically deep, laterally-compressed body shape of theropods, characterized by the relatively long, narrow, vertical to subvertical pubes, and the long, stiffened, counterbalancing tail typical of derived maniraptorans, is antithetical to arboreality. Additionally, the forelimbs of theropods are inevitably shorter than the hindlimbs--a condition opposite to that of volant birds (Feduccia, 1997). Nevertheless, the theropod theory for the ancestry of birds continues to have many supporters.

Advocates of a coelurosaurian ancestor of birds have argued that the recently described fossil Rahonavis ostromi from Madagascar represents a combination of derived avian and theropod characteristics that strongly supports a theropodan ancestry for birds (Forster et al., 1998). Rahonavis is said to possess an avian "elongate, feathered ulna" coupled with a typically theropodan vertical pubis that has a "well-developed hypopubic cup." However, close examination of Rahonavis refutes the presence of an Archaeopteryx-like hypopubic cup (Geist, 1999, unpublished observations). The hypopubic cup, a transversely flattened, spatulate elaboration of the distal pubis, was associated with specializations of the suprapubic musculature

Figure 4: Anterior view of the distal pubic "boot" of Rahonavis (left) and the maniraptoran theropod dinosaur Velociraptor (right). Both pubes are vertically to subvertically oriented and exhibit the stereotypical laterally compressed, theropodan morphology.
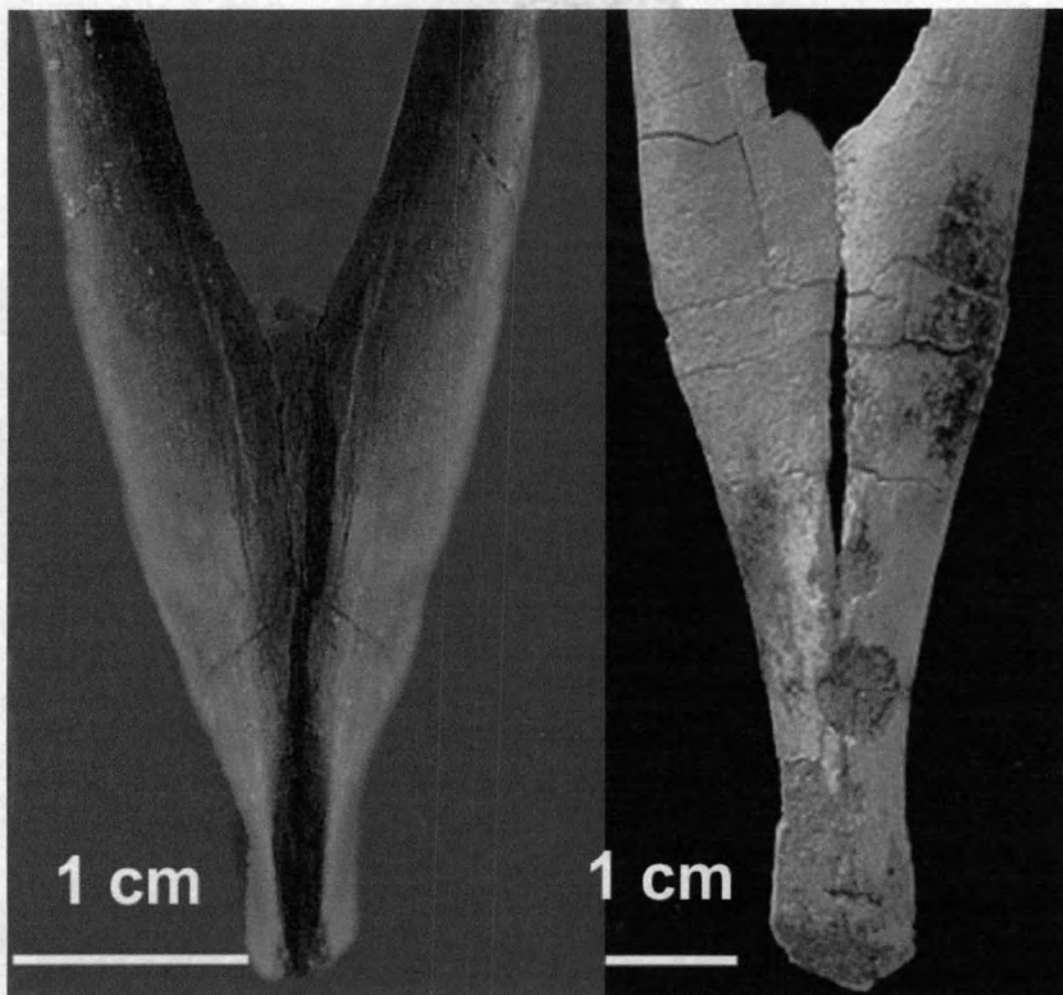
Figure 4

Figure 5: Posterior view of the pubes of <u>Rahonavis</u> (left) and the London <u>Archaeopteryx</u> (right). The distal extremity of the pubes of <u>Archaeopteryx</u> and other early Mesozoic birds forms a broad, spatulate, hypopubic cup, a structure functionally linked to arboreality that is unknown in theropods. Abbreviations: hc, hypopubic cup; pb, pubic boot.
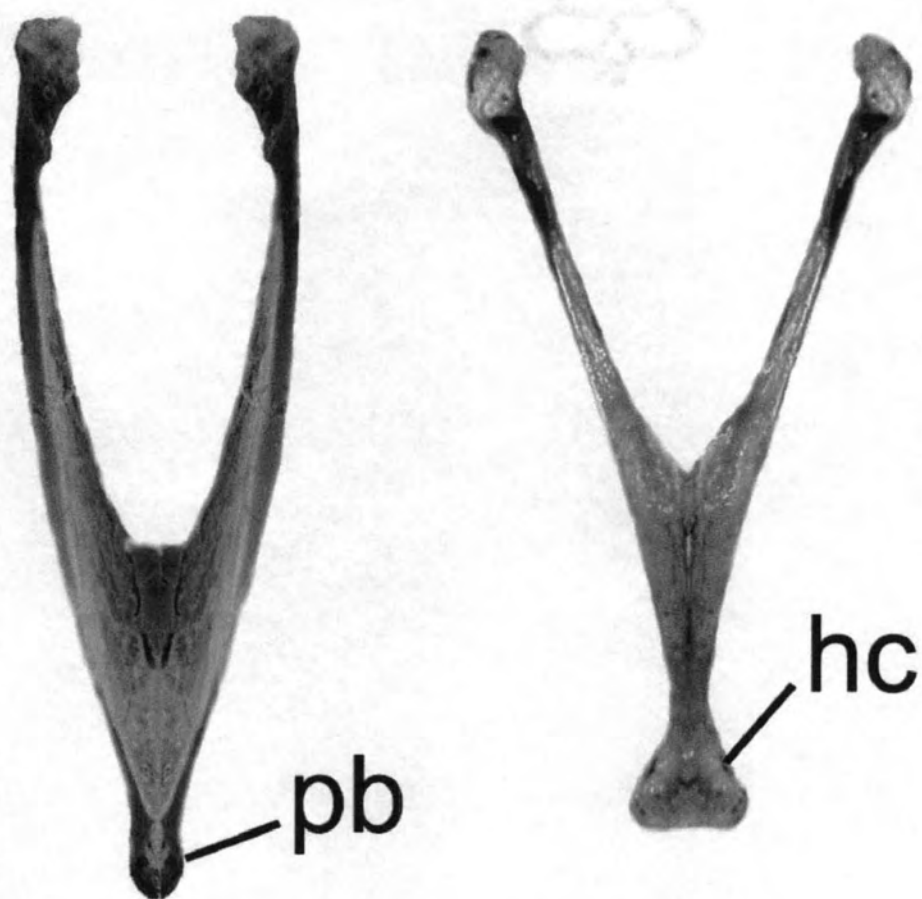
Figure 5

tightly linked to arboreality in early birds (Ruben et al., 1997). Rather, the pelvic

girdle of Rahonavis is typically theropodan, with a deep, laterally compressed, vertical

pubis, complete with distal boot (Fig. 4). The presence of the hypopubic cup in

Archaeopteryx and other early Mesozoic birds, rather than the typically coelurosaurian

laterally compressed pelves with sagittally elongated pubic boot, is likely to be a key

morphological feature distinguishing early birds from theropods (Fig. 5). The

distinctly non-avian structure of the pelvic girdle of Rahonavis lends credence to the

possibility that this fossil may represent a chimera composed of the hind quarters of a

small theropod and forelimbs of a bird, a possibility acknowledged by the authors

(Forster et al., 1998). Significantly, a wingless fossil of the similarly sized

enantiornithine bird Vorona was unearthed within the same quarry in close proximity

to Rahonavis (Forster et al., 1998; Gibbons, 1998) Recent descriptions of the

"protofeathered" theropod Sinosauropteryx prima (Chen, 1998), and a putative

feathered theropod (e. g., Caudipteryx)(Ji et al., 1998), claim to close the phylogenetic

gap between birds and dinosaurs even further; however, these assertions are based

upon equivocal evidence. The fibrous integumentary structures associated with the

fossils of the small compsognathid theropod Sinosauropteryx, which have been

described as having formed a downy external coat of "protofeathers," are virtually

indistinguishable from the elaborate bundles of dermal collagenous fibers frequently

seen along the dorsal midline of many living reptiles (Geist, unpublished

observations). The other supposed feathered theropod may just as reasonably be

interpreted as having been a secondarily flightless bird. A number of non-theropodan,

derived avian features of Caudipteryx, including a shortened, incipiently fused tail ("protopygostyle"), a ventrally oriented foramen magnum, vaned feather structure, along with questionable identifications of crucial characters of the skull (e. g., the nature of the quadrate-quadratojugal complex), make the theropodan classification of these fossils unlikely.

Phylogenetic scenarios for the origin of birds that are based solely upon cladistic criteria have resulted in interpretations that are in stark contrast to the various data from fossils and biophysical limitations. Significantly, a cladistic analysis of pterosaur relationships dictated that they were a sister group of dinosaurs (Padian, 1984) and, therefore, evolved "from small, active, bipedal terrestrial predecessors" (Padian, 1991). This phylogenetic interpretation constrained the biomechanical analysis of terrestrial locomotion in basal pterosaurs, resulting in the conclusion that the hindlimbs of the earliest forms were necessarily held in an upright, bipedal, parasagittal posture and digitigrade stance like that of theropods. As with cladistically-based phylogenies that derive birds from maniraptoran theropods, this interpretation necessitated a terrestrial, cursorial, origin of pterosaur flight. However, compelling fossil evidence for obligate quadripedal, plantigrade walking in basal pterosaurs has rendered these cladistically-based assertions of bipedality and "ground-up" flight untenable. Analysis of fossils of the rhamphorhynchoid pterosaur Sordes pilosus has revealed the presence of an extensive uropatagium, a flight membrane extending between the hindlimbs and tail (Unwin and Bakhurina, 1994). This finding implies that Sordes probably could not have walked with an erect, bidepal posture. In

addition, the recent discovery of a three-dimensionally preserved, articulated foot of

the basal pterosaur <u>Dimorphodon</u> confirms obligate quadripedality and plantigrade

stance as primitive features of the group (Clark <u>et al.</u>, 1998). These data are consistent

with putative pterosaur footprints showing impressions of the entire sole of the foot

(Lockley <u>et al.</u>, 1995; Bennett, 1997). This scenario illustrates the potential pitfalls of

any philosophical/functional approach based upon dogmatic adherence to a particular

phylogenetic interpretation that limits the use of available evidence in paleontological

reconstructions.

<div align="center">Living Models for the Protoaves</div>

In attempting to reconstruct a plausible scenario for the origin of avian flight,

one can look to the diverse array of living and fossil vertebrates that have used gravity

to engage in airborne activities. Though there are few true parachuters (descent angle

> 45 degrees) among extant vertebrates, there are numerous living gliders (descent

angle < 45 degrees) representing independent evolution of non-powered flight in five

vertebrate classes (Feduccia, 1997, Norberg, 1990).

Aerial amphibians include the "flying frogs" of the families Hylidae and

Rhacophoridae from Southeast Asia, Australasia, and Central and South America.

These animals use the webbing between their toes as flight surfaces, while sometimes

flattening their bodies to enhance aerodynamic effect. The Malaysian parachuting

frog <u>Rhacophorus</u> extends its limbs and webbed toes to slow its descent. Though it

lacks any significant measure of maneuverability, this talent is likely to be adaptive as

a predator avoidance device as well as protecting the frog from injury in accidental falls.

Parachuting reptiles include <u>Ptychozoon</u>, the "flying gecko," and the Bornean colubrid snake <u>Chrysopelea</u>. Perhaps the best reptilian flyers are found among the twenty or so species of the agamid lizard genus <u>Draco</u>, skilled gliders known from the Malay peninsula and western Pacific islands. The flight surface of these lizards is formed by a membrane stretched across 6 elongated ribs, an aerodynamic adaptation that allows <u>Draco</u> excellent maneuverability while gliding distances up to 60 meters.

Three mammalian orders, the marsupials, dermopterans, and rodents, have independently evolved arboreal gliding forms that use a skin flap stretched between the fore and hind limbs (Nowak, 1991). The marsupial gliders include three genera of flying petaurids of Australia (sometimes placed in the family Phalangeridae): <u>Petaurus</u>, <u>Petauroides</u>, and <u>Acrobates</u> (Nowak, 1991). The Southeast Asian order Dermoptera consists of a single family (Cynocephalidae), and genus (<u>Cynocephalus</u>), with 2 species. Known as colugos, or flying lemurs, these animals have a large gliding membrane attached to the neck and sides of the body. This membrane is better developed than in any other volant mammal, even forming a webbing between the fingers, toes, and tail. The membrane is so extensive that it renders them virtually helpless on the ground (Lekagul and McNeely, 1977).

Aerial adaptations are common in the Rodentia, with twelve genera of the broadly distributed family Sciuridae, and three genera of the African family Anomaluridae that glide. In addition, a number of arboreal primates from both the

Old and New World have developed parachuting abilities. Two lemurs of the genus Propithecus, commonly known as sifakas, not only have a small patagium, or "gliding membrane," analogous to that of birds, between the forearm and body, but also appear to use a thick, posteriorly-directed mat of fur on the forearms as a flight surface (Feduccia, 1993). These arboreal lemurs use their patagial and fur "wings" to slow descent and accomplish safe landings in branch-to-branch leaps that may span more than 10 m. Several New World primates also display semi-aerial adaptations. Among these are the highly arboreal sakis of genus Pitheca, known to leap and "glide" in a flying squirrel-like manner. Sakis can maneuver accurately while airborne to a target tree trunk, often adjusting their bodies so that they glide upwards at a steep angle just before contact (Moynihan, 1976).

One hypothesized selective advantage to parachuting or gliding animals is predator-avoidance (Bock, 1965, 1983, 1986), while another is the maximization of net energy gain during foraging from trees or cliffs (R. A. Norberg, 1983). Even the early, steep parachuting leaps of the first protobirds would have reduced the time and energy required for foraging, and an increased wing surface area would have slowed the descent while providing enhanced gliding performance and improving the likelihood of a safe landing (Norberg, 1991).

A Plethora of Fossil Gliding Reptiles

The fossil record indicates that a diverse radiation of small arboreal diapsid reptiles with gliding adaptations proliferated across the Permo-Triassic boundary.

Among them are early diapsids from the Upper Permian of the family

Coelurosauravidae, and Upper Triassic "dawn lizards" of the family Kuehneosauridae

(Carroll, 1978; Evans, 1982; Robinson, 1962; Colbert, 1970). In these reptilian

gliders, elongated ribs, or, as described in the recent reanalysis of Coelurosauravus, a

radially-oriented set of hollow, dermal, bony rods, probably supported a horizontal,

aerodynamic membrane analogous to that of the living glider Draco (Carrol, 1988;

Frey et al., 1997). Other unique adaptations for gliding are seen in several fossil

reptiles from the Late Triassic of Kirghizia (Sharov, 1970, 1971). The small (~20

mm), lizard-like Sharovipteryx (Podopteryx) mirabilis stretched a patagial membrane

between its relatively elongate hindlimbs and tail, as well as possibly having had a

smaller wing surface between forelimbs and its body (Gans et al., 1987). Sharov also

described the bizarre pseudosuchian reptile Longisquama from the same deposits.

Named for the row of tremendously elongated, feather-like scales on its back,

Longisquama could apparently fold these appendages down like the wings of a

butterfly to form a gliding surface (Haubold and Buffetaut, 1987). This diverse fossil

assemblage of small arboreal reptiles documents that a wide range of non-powered

gliding adaptations appeared prior to the evolution of vertebrate powered flight.

The small Late Triassic thecodont Megalancosaurus preonensis of Northern

Italy (Calvaria, Muscio, and Wild, 1980) is an especially bird-like archosaurian reptile

that may provide valuable insight into the nature of protoavians (Feduccia and Wild,

1993). Megalancosaurus exhibits a suite of arboreal characteristics, including long

limbs with opposable digits, sharp, mobile claws, tarsi and pedes similar to those of

Figure 6: The strikingly bird-like head of Megalancosaurus. The posteroventral position of the foramen magnum is similar to that of birds and unlike the posterior orientation typical of theropods. Note the beak-like snout and the exceptionally large, bird-like orbits. As with the rest of the skeleton, the skull is extremely lightly built. The articulated left manus exhibits several scansorial adaptations, including semi-opposable, sharp-clawed digits and well-developed flexor tubercles.
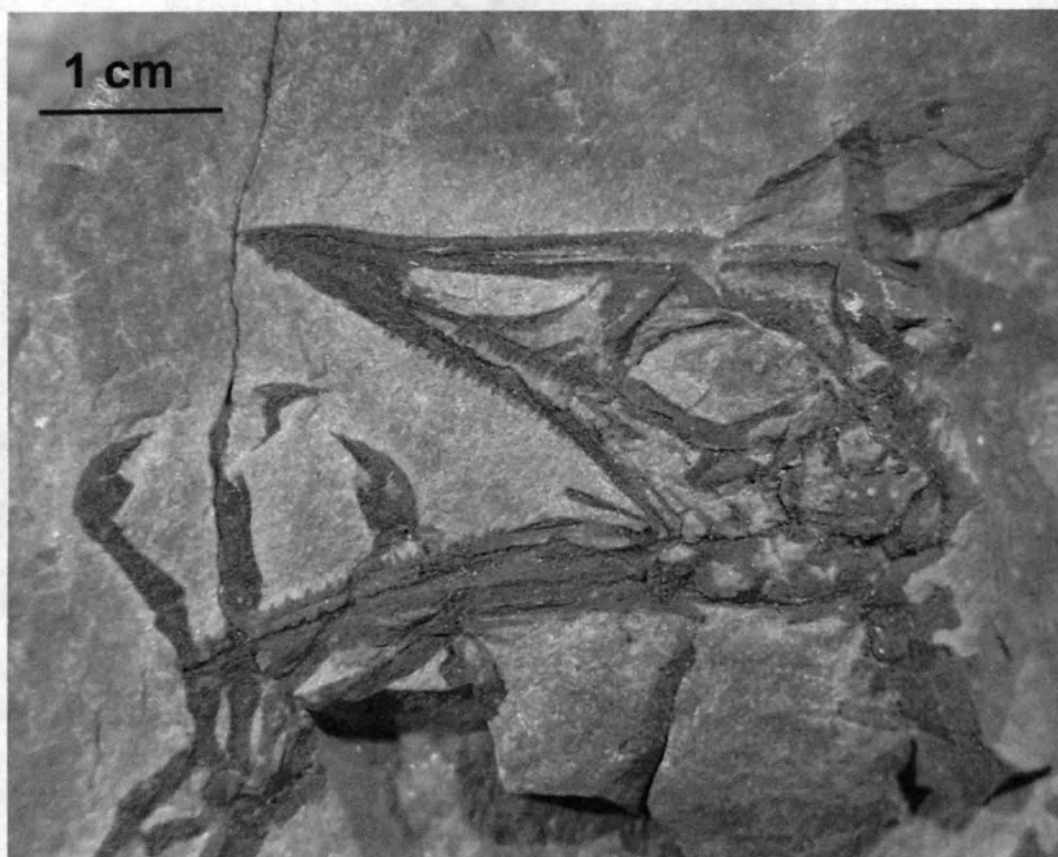
Figure 6

Figure 7: Gliding adaptations in the trunk and forelimb skeleton of Megalancosaurus. Left_lateral view of anterior trunk region. Note excavation of ribs and neural spines; virtually all elements of the axial skeleton of Megalancosaurus are lightened. The trunk is stiffened at the pectoral girdle by a notarium formed from fusion of the elongate neural spines of 4 dorsal vertebrae. Note the robust olecranon process of the ulna and shallow olecranon fossa of the humerus that limited extension of the elbow. Inability to fully extend the elbow, coupled with the presence of a tubercular process on the anterior aspect of the scapula analogous to the site of origin of the avian propatagium, indicates the probable presence of a propatagial membrane in Megalancosaurus. Abbreviations: not., notarium; ol. pr., olecranon process of the ulna.
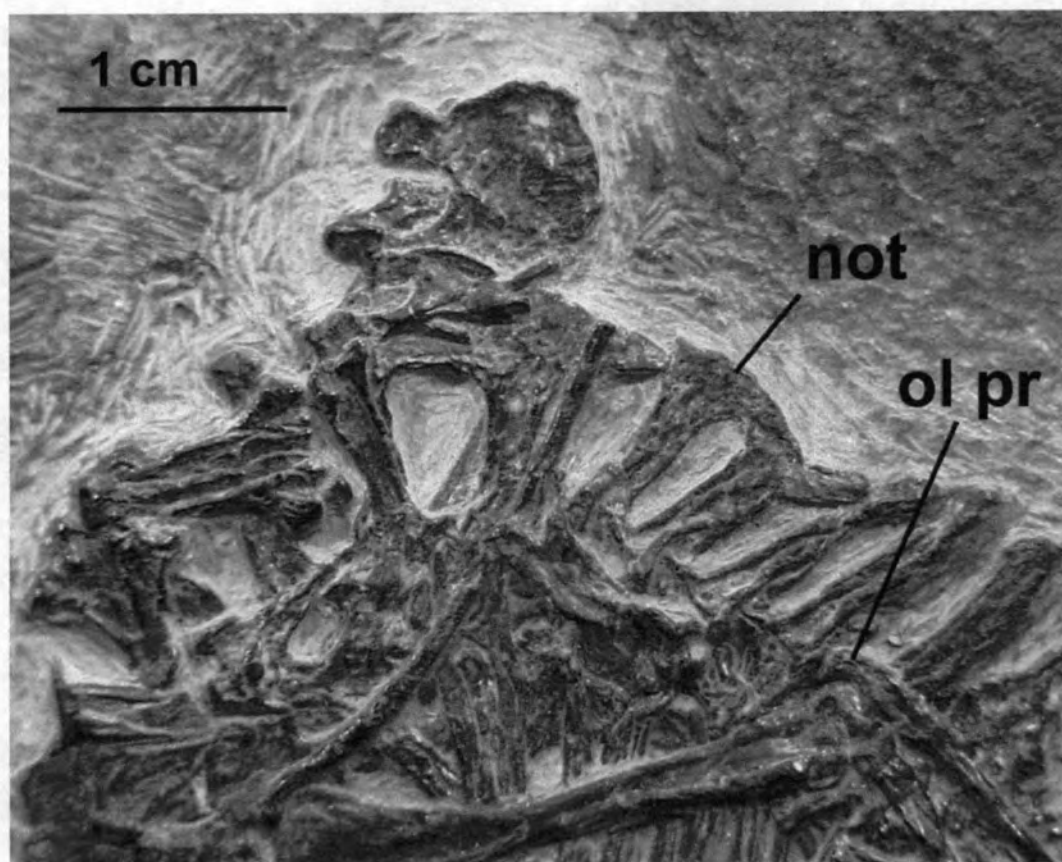
Figure 7

Figure 8: Comparison of the hind feet of Megalancosaurus (left), and the gliding marsupial Petaurus (right). Note the similarities between the first toes of both animals. In Petaurus, the highly modified first toe serves as a primary attachment site for extensive patagial gliding membranes (modified from Renesto, 1994).
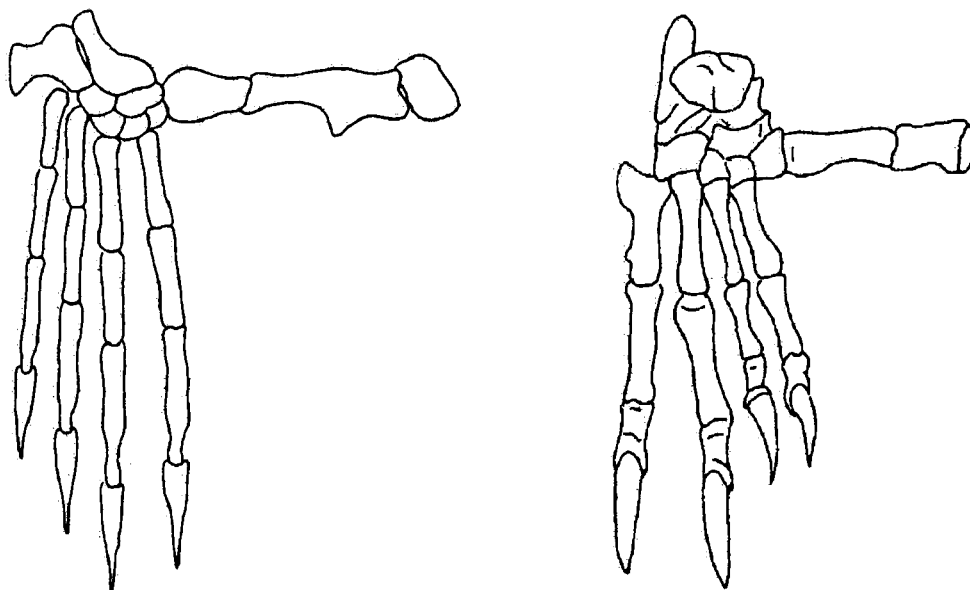
Figure 8

arboreal mammals, and a long, possibly prehensile tail (Renesto, 1994; contra Padian and Chiappe, 1997). The strap-like scapula is more bird-like than that of any other known archosaur. The anterior limbs, without manus, are, like those of Archaeopteryx and other volant birds, longer than the hindlimbs minus pedes--a condition never exhibited by theropods. The exceptionally light, bird-like head was positioned on a long mobile neck composed of six or seven elongate cervical vertebrae. The skull has a number of very bird-like features, including a posteroventrally positioned foramen magnum, relatively large orbits, and a tapered beak-like snout with small isodont teeth set in sockets (Fig. 6). Although Renesto (1994) states that "there is no evidence that Megalancosaurus was a glider," first-hand reexamination of the specimens indicates the likelihood that Megalancosaurus was a patagial glider (Geist, 1999, unpublished observations). These attributes include long anterior limbs with only partially extendable elbow, long and mobile rudder-like tail, notarium formed by 4 dorsal vertebrae, and a skeleton lightened by excavation of nearly every axial element (Fig. 7). Additionally, the first toe of Megalancosaurus exhibits "striking similarities with that of some phalangeriids (petaurids)" (Renesto, 1994). In these marsupial gliders, as in Megalancosaurus, the highly modified first toe is clawless and probably of little use in climbing. In Petaurus, this toe serves as a primary attachment site for the extensive patagial gliding membrane (Fig. 8). Though probably not the avian ancestor, Megalancosaurus represents a chronologically and biophysically plausible model for a gliding stage through which birds must have passed.

Conclusions

Current cladistic hypotheses derive birds from coelurosaurian dinosaurs. This proposed relationship is based primarily on the anatomical similarities between the urvogel Archaeopteryx and Late Cretaceous maniraptoran theropod dinosaurs (e. g., Velociraptor), forms that postdate Archaeopteryx by at least 50-60 million years. Such a relationship dictates that flight must have begun among terrestrial cursors, an idea that is

not supported by biophysical, ecological, or chronologically appropriate fossil data. Recent reports of fossils, which claim to further cement the bird-dinosaur relationship, must be regarded with skepticism. The partial fossil of Rahonavis ostromi has been described as a primitive bird that retains characteristics indicating a theropod ancestry, yet reevaluation of several key features of the pelvis support suggestions that this fossil may represent a chimera composed of the hind parts of a theropod with the forelimbs of a primitive bird found preserved in the same deposits nearby. The spectacular recent reports of "feathered theropods" from China are also dubious. First-hand examination of the fossils (Geist, 1999, unpublished observations) reveals that certain key characteristics claimed to bolster the dinosaurian nature of these forms are questionable, while other characters tend to support classification of these fossils as post-Archaeopteryx, secondarily flightless birds.

If the dinosaurian ancestry of birds is untenable, are there reasonable alternatives from the fossil record? The plethora of small gliding thecodonts that

proliferated during the Late Permian and throughout the Triassic were arboreal, as are the many living parachuting and gliding vertebrates that use the energy provided by gravity to take to the air. Some of these Mesozoic animals, such as the strikingly bird-like archosaur <u>Megalancosaurus</u>, though they are unlikely to have been the actual avian ancestor, may represent an evolutionary grade through which the ancestors of birds passed on the way to developing powered flight. Such forms provide us with a biophysically and ecologically relevant model for the early stages leading to the evolution of the flapping flight of birds.

Acknowledgements

CHAPTER 4: NASAL RESPIRATORY TURBINATE FUNCTION IN BIRDS

by

Nicholas R. Geist

This manuscript has been <u>invited</u> for submission to Physiological Biochemistry and Zoology

Abstract

Nasal respiratory turbinates are complex, epithelially-lined structures in the nasal passages of nearly all birds and mammals. During lung ventilation they act as intermittent counter current heat exchangers. Inspired ambient air is heated to body temperature and fully saturated with water vapor as it passes over the warm, moist nasal epithelium. As a consequence, the turbinate surfaces are cooled simultaneously. Upon expiration, exhaled air is cooled as it passes over the respiratory turbinates. Resulting water vapor condensation on respiratory turbinate surfaces then serves to "reclaim" respiratory heat and moisture that would otherwise be lost to the external environment.

Previous studies of the function of avian respiratory turbinates have focused primarily on their role in the water balance of relatively small taxa that inhabit desert environments. This study examined avian respiratory turbinate function during periods of routine activity in five orders of predominantly larger birds that inhabit more mesic, temperate climates. Net evaporative water and heat loss rates of birds using respiratory turbinates (nasopharyngeal breathing) were compared to those with turbinates experimentally bypassed (oropharyngeal breathing). Water and heat loss rates were calculated from lung tidal volumes and nasal and oropharyngeal exhaled air temperatures (T_{ex}). Ventilatory variables were determined using open-circuit respirometry and whole-body plethysmography. Resulting data indicate that respiratory turbinates are equally adaptive across a range of avian orders, regardless of

environment, by conserving significant fractions of the daily water and heat energy budget.

Additionally, nasal T_{ex} of birds were compared with those of similar mass ectotherms (lizards), all of which lack respiratory turbinates. The comparatively high nasal T_{ex} of reptiles in similar ambient conditions indicates that their relatively low metabolic rates and correspondingly reduced lung ventilation rates preclude the need for similar respiratory adaptations.

Introduction

Respiratory evaporative water and heat loss is a potential problem for many

amniote vertebrates. This situation is exacerbated in normothermic birds and

mammals due to their high routine pulmonary ventilation rates. Avian and

mammalian endothermy is characterized by levels of oxygen consumption in the field

that are approximately an order of magnitude beyond those of equivalently sized

ectotherms (Nagy, 1987). Lung ventilation rates of endotherms are similarly elevated

(Schmidt-Nielsen, 1984), creating a potential for greatly increased levels of respiratory

evaporative heat and water loss. Unique adaptations of the upper respiratory tract of

birds and mammals modify and condition respired air, minimizing what might

otherwise be unacceptably high rates of ventilation-related heat and water loss.

Alternately, the relatively low oxygen consumption, ventilation rates, and lung tidal

volumes typical of ectotherms probably obviates the necessity for similar adaptations

to reduce respiratory water and heat loss (Schmidt-Nielsen, 1984; Hillenius, 1992;

Ruben, 1995).

Within the specialized respiratory tract of birds, only the nasal cavities are

capable of significant modification of tidal air humidity and temperature during

periods of routine, or resting lung ventilation. The lungs and extensive system of

nonvascularized air sacs, located throughout the body cavity, are necessarily

maintained at, or close to, deep-body temperature, and therefore are unable to

participate as major sites of evaporative or condensative heat exchange during normal

respiration. The proximity of the trachea to the carotid arterial circulation along most

of its length precludes it as a primary site of heat exchange during respiration, as this would likely result in highly deleterious cyclical fluctuations of brain temperature (Baumel, 1993; Ruben *et al*, 1997). Additionally, even in long-necked birds (e. g., *Struthio*), the simple tubular geometry and high airflow velocities in the trachea suggest that considerable evaporative cooling between air stream and moist respiratory surfaces is unlikely (Schmidt-Nielsen *et al*, 1969). The buccal region and the oropharyngeal portion of the trachea participate substantially in heat exchange only during panting and gular flutter, specialized respiratory patterns closely associated with heat stress in birds (Weathers and Schoenbaechler, 1976; Dawson, 1981; Crawford and Schmidt-Nielsen, 1967; Lasiewski, 1972; Peltonen *et al*, 1988). It is only within the nasal cavities that morphological adaptations have evolved that are tightly linked to heat and water exchange during periods of routine breathing.

Extant amniote vertebrates possess one or more pairs of cartilaginous, epithelially covered projections within the nasal cavity known as conchae, or turbinates. In living reptiles these are relatively simple structures associated with olfaction, usually consisting of paired, dome-like cartilaginous projections from the lateral walls of the nasal cavity (Portman, 1961; Matthes, 1934; Hillenius, 1992). Alternately, birds and mammals nearly always possess additional elaborations of the nasal cavity, respiratory turbinates, that are absent in all ectotherms (Ruben, 1995; Hillenius, 1992, 1994; Witmer, 1995). Unlike the simple conchal structures of reptiles, avian respiratory turbinates are highly convoluted, often scrolled structures, lined with moist, mucociliated epithelium (Bang, 1961, 1971). Mammalian

respiratory turbinates, the maxilloturbinates (often referred to as inferior conchae in humans), are ossified, scrolled, lamellar extensions of the lateral walls of the maxillary bone (Hillenius, 1992). Avian respiratory turbinates are morphologically and functionally analogous, though likely not homologous, to the mammalian maxilloturbinates (Witmer, 1995). Respiratory turbinates of birds, also referred to as the anterior and middle conchae, are, like mammalian maxilloturbinates, situated directly in the path of respiratory air flow, greatly increasing the surface area of the nasal epithelial mucosa and simultaneously reducing the effective distance of respiratory air from the mucosal surfaces. Unlike the bony respiratory turbinates of mammals, avian turbinates are usually cartilaginous. These paired structures, as in mammals, extend from the lateral walls of the nasal cavity, where they function as intermittent counter-current heat exchangers (Schmidt-Nielsen *et al*, 1970). As inspired air passes through the nasal cavities and over the moist surfaces of the respiratory turbinates, heat and water are exchanged, warming and humidifying the air while simultaneously cooling the epithelium of the turbinates. The efficiency of this evaporative exchange is such that the temperature of the nasal surfaces may occasionally drop below the temperature of the ambient air (Jackson and Schmidt-Nielsen, 1964). Inspired air is fully saturated and approaches deep body temperature by the time it leaves the nasal cavity. During exhalation, air is cooled and becomes super-saturated as it passes over the turbinates, condensing and recycling excess moisture within the nasal cavities and minimizing evaporative heat loss. This mechanism allows birds and mammals to recover significant fractions of the water and

heat that would otherwise be lost to the environment (Schmidt-Nielsen, 1970; Hillenius, 1994).

Distinct olfactory conchae not associated with heat exchange are present in many birds. When present, these simple sensory structures are situated in a blind-ended, posterodorsal chamber of the nasal cavity, out of the main path of respired air (Bang, 1971). These conchae are probably homologous to structures associated with olfactory reception (e.g., naso- and ethmoturbinals of mammals) found in the nasal cavities of most other living tetrapods (Witmer, 1997).

Previous studies on the water economy of birds have focused primarily on respiratory turbinate function of taxa living in extreme environments (Schmidt-Nielsen *et al* 1970; Dawson and Bennett, 1972; Marder, 1972; Chappel *et al*, 1992; Withers, 1990; Tielman *et al*, 1999). However, since respiratory turbinates are present in virtually all Recent birds, independent of animal mass or the environment inhabited, their role in the water economy and heat balance of animals from less extreme environments calls for closer examination. In the present study, I have assessed turbinate function of birds from primarily temperate, mesic environments. All experiments were performed on resting birds at a moderate ambient temperature. Net respiratory evaporative water loss rates from birds breathing normally (i.e., nasopharyngeal breathing) were compared to water loss rates in individuals with turbinates experimentally bypassed (oropharyngeal breathing). Water loss rates were calculated from exhaled nasal and oral air temperatures recorded at the external nares and at the oropharynx near the exit to the trachea, respectively. Additionally, exhaled

air temperatures of the birds were contrasted with those of comparably sized lizards at similar body temperatures in identical ambient conditions.

Birds used in this study ranged from moderately sized to relatively large species representing five avian orders. All experiments were performed on resting animals at 15° C, an ambient temperature that approximates the daily mean in many temperate regions (Ruffner and Bair, 1984). A moderate relative humidity (50 ± 3%) was maintained during all exhaled air temperature recordings to approximate nasal turbinate function in relatively non-stressful, mesic environmental conditions.

Materials and Methods

Animals

Experimental animals included pigeons (Columbiiformes; Columbidae: *Columba livia*), Japanese quail (Galliformes, Phasianidae: *Coturnix coturnix*), Herring gulls (Charadriiformes, Laridae: *Larus argentatus*), American crows (Passeriformes, Corvidae: *Corvus brachyrhynchos*), and Canada geese (Anseriformes, Anatidae: *Branta canadensis*). Average masses of the birds were, quail, 117 ± 10.2 g; pigeons, 319 ± 45.2 g; gulls, 799 ± 45.1 g; crows, 357 ± 21.6 g; geese, 1857 ± 389.4 g. All animal masses are presented ± SEM. Gulls were captured on the Central Oregon coast. Pigeons and Japanese quail were obtained through local commercial sources. Crows and Canada geese were provided courtesy of local breeders, the Portland Audubon Society, and/or the Oregon State Department of Fish and Wildlife. A

minimum of five individuals of each species was used for the experiments. All animals were adults, as determined by size, information from their keepers, or, for the gulls, by plumage pattern. Birds were maintained in cages or pens with 12 hour light/12 hour dark photoperiod and fed and watered *ad libitum* at the facilities of the Oregon State Lab Animal Resources. All birds were fasted 8 to 12 hours prior to experimental protocols to ensure a post-absorptive metabolic state.

Reptiles used for expired air temperature experiments in this study were the Australian Bearded Dragon (Agamidae; *Pogona viticeps*). Mean lizards mass was 352 $\pm$ 21.7 g.

Determination of Metabolic and Respiratory Variables

Metabolic rate and lung ventilation parameters of resting birds were recorded simultaneously. Experiments were performed in custom-made cylindrical PVC respirometry chambers placed in a temperature and humidity controlled room maintained at 15°C ($\pm$ 0.3° C). Chamber volumes ranged from 7620 cm^3 to 59878 cm^3. The smaller chamber was used for all experiments on quail, pigeons, and crows. Gulls and geese were tested in the larger chamber. Uniform flow of dry air (corrected to STPD) from a pressurized source was maintained and continuously monitored with Cole-Parmer 150-mm, high-resolution, variable area flowmeters, calibrated frequently with a spirometer. In order to avoid stressing birds, flow rates were adequate to insure the concentration of oxygen in the chamber never fell below 20% during any

experimental period. Chamber temperature (T_a) was recorded every 5 minutes during the experiments with a thermocouple thermometer (Omega Instruments, model HH21) placed in the air outflow port. T_a was controlled and maintained at 15°C (± 0.4°C) during all experiments. Relative humidity of air in the chamber during the experiments was determined by placing an Extech model 5070C humidity meter/thermometer (calibrated for each run against a saturated salt solution=75%RH, accuracy ± 3%) in the outflow line (Hillenius, 1992).

Oxygen consumption was determined using open-circuit respirometry. A sample of the outflow air was passed through a column of drierite and ascarite before being drawn through an Applied Electrochemistry S-3A/1 oxygen sensor for determination of fractional oxygen content. The sensor was calibrated against a sample of dried outdoor air prior to each experiment. Readings from the oxygen sensor during the experiments were sampled at five-second intervals and recorded to disc through an analog-to-digital converter (Sable Systems CB405). Oxygen consumption (VO_2) was determined from fractional oxygen content of outflow air and flow rate according to equation 8 from Depocas and Hart (1956).

$$\dot{V}O_2 = \frac{f_r \bullet (F_{in} - F_{out})}{1 - F_{out}}$$

Flow rate (fr) is in liters/minute, F_{in} is the fractional oxygen content of incurrent air, and F_{out} is the fractional oxygen content of excurrent air.

Within the respirometer, unrestrained birds stood on a false bottom of wire mesh screen above approximately 2 cm. of vegetable oil to trap feces. All animals

were maintained in the darkened chambers for a minimum of 1 hr. prior to any data recording to ensure the establishment of equilibrium. Only data from resting animals, as determined by stable rates of oxygen consumption (*i. e.*, within 10% of the lowest recorded value) for continuous periods of at least 5 minutes, were used in the calculations (Bucher, 1981). Recordings of birds during activity, as indicated by sounds of excessive movement in the chamber and/or transient excessive fluctuations in oxygen consumption, were deemed unsuitable and excluded from the results.

Lung tidal volumes (V_T; min⁻1), ventilation frequency (f; min⁻1), and ventilation volumes (V_I; ml min⁻1), were calculated by using the metabolic chamber as a whole-body plethysmograph (Withers, 1977,1990; Bucher, 1981; Morgan *et al*, 1992; Maloney and Dawson, 1998). Pressure changes within the chamber due to the warming and wetting of tidal air during the breathing cycle were measured with a pressure transducer (Sable Systems PT100) connected to the chamber outflow port. All ventilation data were sampled at an interval of 0.1 s. for a total of 180 s, and recorded to disc via an analog-to-digital converter using commercial data acquisition and analysis software (Sable Systems, Datacan V). V_T (BTPS) was estimated from ventilation pressure deflections recorded in the respirometer using equation 6 from Malan (1973). Time lag between events in the chambers and the oxygen sensor was determined at each flow rate in order to coordinate ventilation traces with VO_2 recordings. Ventilation frequency (f) was measured directly from the traces. The plethysmograph was calibrated at the end of each run by calculating the mean pressure fluctuation determined from a minimum of ten injections of a known volume of air

into the chamber. The rate of the injections was controlled so that deflection kinetics were similar to those caused by lung ventilation (Maloney and Dawson, 1994). Chamber pressures were measured at the end of each experiment by opening a valve on the outflow line connected to a fluid-in-glass manometer. Flow rates into the respirometer were such that total chamber pressure was never more than 10 mm Hg, and generally less than 2 mm Hg, above ambient atmospheric pressure.

Expired Air Temperatures and Water Loss Rates

Expired air temperatures were recorded in a temperature and humidity-controlled room immediately upon completion of oxygen consumption and pressure measurements. T_a was maintained at $15.0^{\circ} C$ (± 0.4) and relative humidity at 50% ($\pm 3\%$). Birds were lightly restrained with an elastic and cotton tube placed around their bodies during temperature recordings. A hood was placed over their heads to calm the animals during these procedures when necessary. All birds except geese tolerated the restraints and hoods without any obvious signs of stress.

Expired air temperatures (T_{ex}) were measured with a 40-gauge copper-constantan probe and thermocouple thermometer (Omega Instruments, model TAC-386-TC). The tip of the probe was held 1 mm inside the external nares to record exhaled nasal air temperatures (Withers, 1990). Oral T_{ex} values were collected by inserting short lengths of tygon or rubber tubing into the mouths of the animals with one end positioned immediately posterior to the internal nares at the oropharynx,

thereby bypassing the upper respiratory tract and turbinates. Tubing diameter for each bird was adjusted so that it fit comfortably within the circumference of the buccal cavity. To record oral T_{ex}, the thermocouple was then inserted into the tube without touching its walls. During both nasal and oral respiratory cycles, the temperature recordings plateaued as equilibrium was reached between the thermocouple and expired air (Withers, 1990). T_{ex} was calculated from the average of at least 10 peak voltage readings after equilibrium had been established. Since exhaled air temperature varies with respiratory frequency, oral and nasal T_{ex} values were used in calculations only if ventilaton frequencies were within 10% of one another. The thermocouple was calibrated against a mercury-in-glass thermometer traceable to the U.S. Bureau of Standards. Water loss rates for nasal and oral breathing were calculated from saturation water vapor partial pressure values at respective exhaled air temperatures (Hillenius, 1992, 1994). Saturation water vapor partial pressure values were obtained from standard tables (CRC Handbook of Chemistry and Physics, 56th Ed.). Body temperatures (T_b) of the birds were recorded using a thermocouple inserted either deeply within the cloaca or deeply down the gullet of the animals immediately after expired air temperatures were recorded.

Lizards were maintained in terraria equipped with heat lamps prior to all recordings. T_b of the lizards was controlled at 36.5°C in order to: i.) approximate the preferred body temperature (T_{pref}) of 37°C (Bennett, 1973) and; ii.) to provide a similar T_a/T_b gradient to that of the birds for appropriate comparison of T_{ex}. Nasal T_{ex}

values for lizards were recorded as for birds. As with the birds, all measurements

were taken in a temperature and humidity controlled room (Ta=15° C, RH=50%).

Lizard T_b was recorded by insertion of a thermocouple deeply in the cloaca

immediately prior to and at the end of each T_{ex} recording.

Respiratory Water and Heat Savings

Heat savings produced by nasopharyngeal breathing relative to oropharyngeal

breathing for quail, pigeons, gulls, and crows (at Ta=15°C, RH=50%) were estimated

from the calculated volume of H_2O reclaimed from exhaled air. The volume of H_2O

condensed during exhalation in the nasal passages and turbinates was estimated as the

difference of the volume of H_2O lost/min with turbinates experimentally bypassed,

and the volume of H_2O lost/min during nasopharyngeal breathing, assuming saturation

of exhaled air (Schmidt-Nielsen *et al*, 1970). REWL rates were determined assuming

saturation water vapor pressures at the respective exhaled air temperatures (CRC

Handbook of Chemistry and Physics, 1976). Daily respiratory heat savings were

calculated from 24 hour lung ventilation volumes (Table 2) and the latent heat of

evaporation (@584 cal/gm H_2O) assumed to have been recovered on the respiratory

turbinate surfaces during exhalation. Total daily caloric production was calculated

from 24 hour VO_2 using the caloric equivalent of 4.85 kcal/liter O_2 (Schmidt-Nielsen,

1990).

Data Analysis

Numerical values of all variables are presented ± SEM. VO_2 values (see table 3) for birds were accepted if they were within 10% of the lowest continual 5 minutes of VO_2 recorded for that animal during each individual run (Dawson and Maloney, 1994). Mean values of exhaled nasopharyngeal and oropharyngeal air temperatures recorded for each species were compared using paired t-tests. Results were considered significantly different if $P<0.05$.

Lung tidal volumes used to determine minute volume are given BTPS. Lung tidal volumes used for calculation of EO_2 are given STPD. Oxygen extraction efficiency (EO_2) was calculated as:

$$EO_2(\%) = \frac{\dot{V}O_2}{FE_{O_2}} * V_t * f * 100$$

Where FE_{O_2} is the fractional concentration of oxygen in chamber excurrent air, V_T = tidal volume, and f = frequency of respiration.

Results

Measured numerical mean values for animal masses, respiration frequencies, body temperatures, and exhaled narial and oropharyngeal air temperatures of four experimental avian species, and exhaled narial air and body temperatures of the agamid lizard *Pogona viticeps* are presented in Table 2. Exhaled air temperature data from resting birds was obtained from 4 of the 5 species used in this study. No reliable

Table 2. Measured values of physiological variables: mass, respiration frequency (F_{resp}), and body (T_b), exhaled narial (T_{exn}) and oropharyngeal (T_{exm}) temperatures of experimental animals. Exhaled air temperatures unavailable for *Branta*. Exhaled oropharyngeal temperatures unavailable for *Pogona*. (*Estimated respiration frequency for *Pogona* from Bennett, 1973). All measured values are given ± SEM.

Species name	Common name	Mass (g)	F_{resp}	T_B	T_{exn}	T_{exm}
Coturnix coturnix	Japanese quail	117±10.2	26.1±1.98	40.5±0.21	20.4±0.4	37.0 ±.03
Columba livia	Pigeon	319±45.2	21.9±1.44	40.7±0.13	21.4±0.5	38.2 ±.05
Larus argentatus	Herring gull	799±45.11	12.6±0.71	39.4±0.23	19.4±0.7	35.9 ±.03
Corvus brachyrhynchos	American crow	357±21.56	23.7±1.08	41.1±0.18	21.9±0.9	36.6 ±.04
Branta canadensis	Canada goose	1857±389.4	9.1±0.35	40.1±0.24	NA	NA
Pogona viticeps	Bearded Dragon	352±21.7	15.6*	36.5±0.43	31.3±0.67	NA

Table 3. Calculated respiratory and metabolic variables: oxygen consumption (VO_2), lung tidal volumes (V_T), oxygen extraction (EO_2), and daily water and heat savings achieved by nasopharyngeal breathing for experimental animals, where available. Reptilian VO_2 and EO_2 values from Bennett (1973).

Species name	Common name	VO_2 (cc/min)	V_T (ml)	EO_2 (%STP)	H_2O savings (mg/day)	Heat savings (cal/day)
Coturnix coturnix	Japanese quail	4.33 ±0.3	2.26 ±0.27	34.1±1.83	2666.4± 99.5	1546.7 ±57.7
Columba livia	Pigeon	7.91 ±0.96	5.24 ±0.16	35.2±2.09	5738.4± 555.8	3328. ±332.4
Larus argentatus	Herring gull	14.80 ±0.92	21.66 ±1.49	26.9±0.79	9600.4± 384.9	5568.8 ±223.3
Corvus brachyrhynchos	American crow	11.59 ±1.68	7.25 ±1.10	33.7±2.02	5087.3± 1029.9	2950.9 ±597.4
Branta canadensis	Canada goose	19.33 ±0.93	27.82 ±1.48	37.7±2.93	NA	NA
Pogona viticeps	Bearded dragon	0.86 ±0.054	2.14 ±0.13*	14.9*	NA	NA

Figure 9. Absolute rates of respiratory evaporative water loss (REWL) for four species of birds representing four orders, and a lizard (*Pogona*). Values calculated from exhaled air temperature, assuming saturation of respiratory air with water vapor. Black columns represent REWL rates of animals during routine nasopharyngeal breathing (using nasal respiratory turbinates). Hatched columns represent REWL rates with respiratory turbinates experimentally bypassed (oropharyngeal breathing). All experiments performed at $T_a=15°C$, RH=50%.
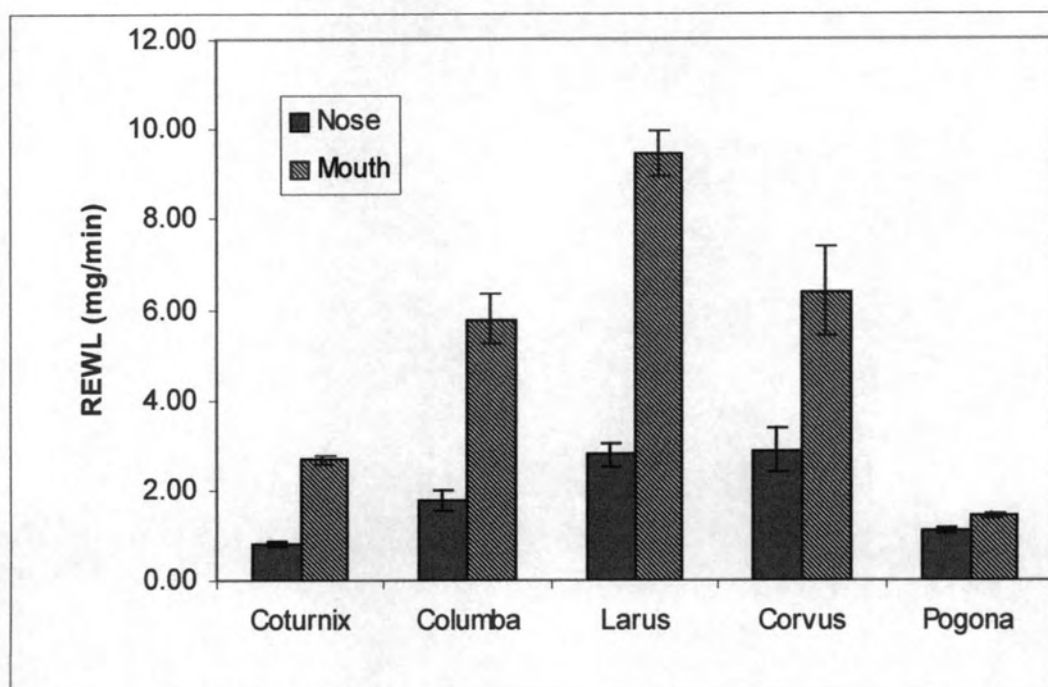
Figure 9

Figure 10. The percentage savings of daily caloric expenditure resulting from cooling of exhaled air and condensation of water in the nasal passages during nasopharyngeal breathing in four species of birds. Respiratory heat savings over a 24 hr. period were calculated from the difference in the volume of water present in saturated exhaled air at temperatures recorded at the oropharynx and the external nares, assuming the latent heat of evaporation=584 cal/gm H_2O. Water vapor saturation density values from standard tables (CRC Handbook of Chemistry and Physics, 1976).

Figure 10

Figure 11. Calculated rates of respiratory evaporative water loss (REWL) per cc O_2 consumed of four avian and one reptilian species. Data were obtained from exhaled air temperatures of resting animals, under control (nasopharyngeal breathing) and experimental (oropharyngeal breathing) conditions. $T_a = 15°C$.

Figure 11

exhaled air temperature data could be obtained for *Branta*, as the geese would not submit to handling, including hooding or placement of the thermocouple at the external nares, without exhibiting signs of extreme stre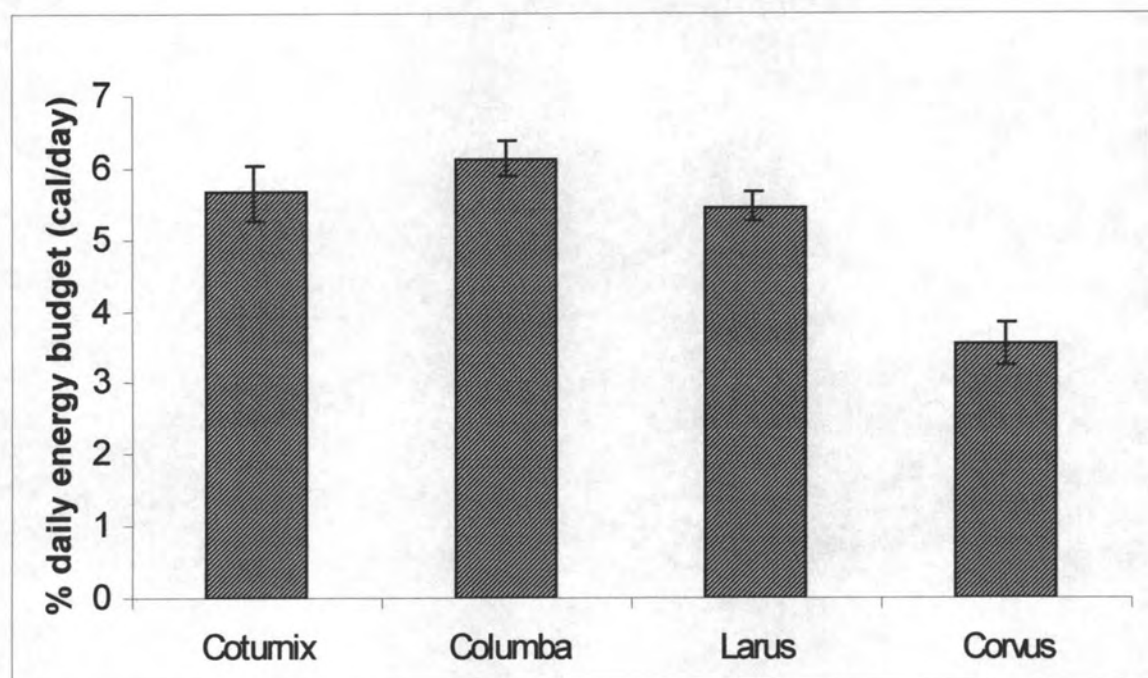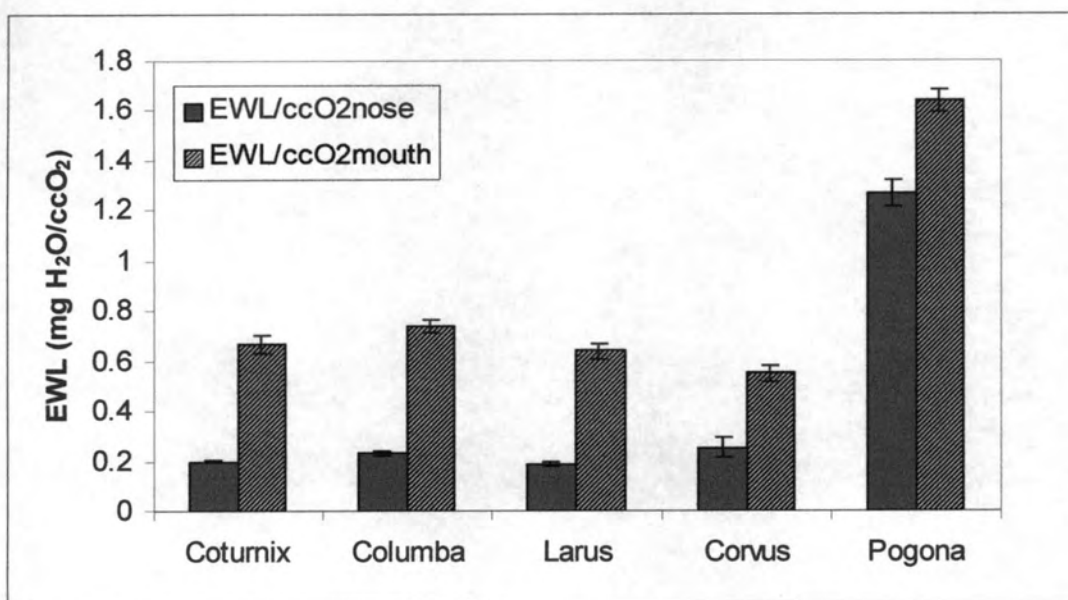ss (panting, elevated respiratory frequencies, flailing of the head, etc.). No exhaled oropharngeal air temperatures were obtained for lizards (*Pogona*). Oropharyngeal water loss data for the lizards were estimated by assuming that oropharyngeal exhaled air temperatures were approximately equal to body temperature. These data probably represent a slight overestimation of oropharyngeal water loss rates, as limited cooling of exhaled air undoubtedly took place in the trachea of lizards. Calculated values for oxygen consumption (VO_2), lung tidal volumes (V_T), oxygen extraction coefficients (EO_2), and daily water and caloric savings generated by condensation in the nasal passages and turbinate system are presented in table 3. Oxygen extraction coefficients for resting *Pogona* were assumed to be 14.9% (Bennett, 1973). Net daily water loss rates for bird species for both experimental (oropharyngeal), and control (nasopharyngeal), were calculated as the difference between water added to ambient air ($15°C$, 50% RH) during inhalation to reach saturation at T_b, minus water recovered at T_{ex} (Schmidt-Nielsen *et al*, 1970; Tielman *et al*, 1999). The estimated control (nasopharyngeal) and experimental (oropharyngeal) respiratory evaporative water loss rates of four bird species and one reptilian species are presented in figure 9. Caloric savings calculated from the volume of condensed water recovered in the nasal passages due to cooling of saturated exhaled air are expressed as a percentage of the animal's daily energy budget

in figure 10. Avian and reptilian water loss values per cc oxygen consumed are depicted in figure 11.

Discussion

Turbinate function

Nasal T_{ex} values of resting birds used in this study were significantly lower (P<0.05) than oral T_{ex} (Table 2). Nasopharyngeal breathing resulted in substantially lower rates of respiratory water and heat loss than oropharyngeal breathing in all birds that had the upper respiratory tract experimentally bypassed (Table 3). These data, coupled with previous reports of respiratory turbinate mediated reductions in REWL (Schmidt-Nielsen et a,l 1970; Brent et al, 1984; Withers and Williams, 1990; Maloney and Dawson, 1994) provide evidence for broad distribution within Aves of an effective counter-current heat exchange mechanism in the nasal cavities, at leastduring periods of rest or routine activity. Significantly, none of the avian species used in this study are highly specialized for life in extreme thermal or xeric environments. This suggests a range of crucial physiological functions of the avian upper respiratory tract and turbinate complex, including, but not limited to specific adaptations for life in deserts or extremely cold high latitude environments. In addition, it has been demonstrated that birds maintain their brain temperature below body temperature via specialized vasculature in the head, the ophthalmic rete (Pinshow et al, 1982; Crowe and Withers, 1979). Venous circulation associated with countercurrent heat exchange

in the nasal passages and respiratory turbinates is known to contribute to ophthalmic rete mediated cooling of the brain in a variety of resting birds (Bernstein *et al* 1978).

Water and Heat Savings

Average exhaled air temperatures measured at the oropharynx for the four avian species in this study averaged 3.5 °C lower than deep body temperature, compared to an average reduction of 19.6 °C for temperatures measured at the external nares, supporting the prediction that the trachea is not a major site of heat exchange during routine lung ventilation. Conversely, the relatively low exhaled air temperatures recorded at the external nares demonstrated that the nasal passages of the four avian species for which data were available participated significantly in respiratory heat exchange. In contrast, narial T_{ex} of lizards averaged only 5.2°C less than deep body temperature. This reduction is comparable to the average reduction of oropharyngeal T_{ex} relative to T_b from birds in this study.

Respiratory turbinate-linked cooling of expired air in the nasal passages resulted in a net reduction of REWL of 55% (crows), 69% (pigeons), 70% (quail), and 71% (gulls). Heat recovered in the nasal passages and associated respiratory turbinates during routine lung ventilation, even at a moderate ambient temperature (15°C) and humidity (50%), provided a daily caloric savings of 3.5% (crows), 6.1% (pigeons), 5.7% (quail), and 5.6% (gulls) of total daily caloric production over mouth breathing birds (figure 10). While nasal breathing conserves significant amounts of heat and water during routine behaviors in moderate ambient conditions, bypassing the

turbinate complex with specialized respiratory behaviors (i. e., mouth

breathing/panting and gular flutter) provides birds with an efficient means of dumping

excess metabolic heat during periods of heat stress.

Water Flux

It may be more meaningful to analyze REWL savings not only in absolute

terms, but also as a fraction of the total volume of water that the animal processes

through its body each day (water flux). Values for daily water flux in captive birds

scale allometrically, according to the equation:

log daily water flux (ml/day) = -0.059 + 0.694 log mass (g)

(Nagy and Petersen, 1988). Predicted water flux values (in g/day) for the species in

this study were, quail, 23.8; pigeons, 47.8; gulls, 90.4; crows, 51.6. The absolute

water savings at 15° C achieved by nasopharyngeal breathing over oropharyngeal

breathing for each species, calculated as the percentage of total water flux, resulted in

11.2%, 12.0%, 10.6%, and 9.9%, of total predicted daily water flux, respectively. This

portion of the animal's daily water balance is essentially "free" water, potentially

contributing to a direct reduction in energy expended by wild birds flying to or

searching for environmental sources of water. The 24-hour percentage saving

estimates given above are conservative values based on the lowest average ventilatory

volumes and VO_2 values recorded during each experimental run.

Turbinates as an Index of Metabolic Status

The independent evolution of endothermy (Kemp, 1988), and complex nasal respiratory turbinates in birds and mammals, coupled with the complete absence of similar structures in all ectothermic tetrapods, signals their fundamental correlation to, and apparent physiological importance for maintenance of endothermy, regardless of the environment inhabited. Notably, though specific aspects of the morphology of the avian nasal cavity and associated turbinates varies between higher avian taxa (Bang, 1971), respiratory turbinate structures often display little anatomical variation within closely related avian taxa, independent of the physical environment inhabited. For example, my own investigations of turbinate structure in a number of phasianid galliform birds indicates a stereotypical nasal morphology that is virtually indistinguishable between forms that inhabit tropical equatorial (Guinea fowl), desert (Chukar partridge), mesic-xeric (California quail), or high latitude arctic environments (ptarmigan). These observations are consistent with results of investigations of closely related species of songbirds from different habitats that demonstrate little or no physiological difference in respiratory turbinate-mediated heat and water savings (Schmidt-Nielsen, 1970). It is therefore reasonable to assume that the respiratory evaporative heat and water savings, as well as other physiologically important corollary functions (i.e., brain cooling) associated with respiratory turbinates are likely to have an adaptive physiological value over a broad range of environmental conditions. Even the relatively simple respiratory turbinates of pigeons used in the

present study produced a significant reduction of respiratory water and heat loss under the experimental conditions.

The few cases within Aves in which turbinates are greatly reduced are clearly secondary losses tightly associated with unique behavioral patterns. For example, many pelicaniform birds have either entirely occluded (e. g., pelicanids, sulids), or highly constricted nostrils (e. g., phaethonids and frigatids) as adults, and effectively bypass the upper respiratory tract (Bang, 1970), rendering the respiratory turbinates essentially useless as respiratory heat exchangers. This nasal morphology is correlated to the unique plunge-diving habits typical of this order. The presence of open nostrils in plunge divers would likely result in damage to the delicate respiratory turbinate complex. As a result, most pelicaniforms, including all adult sulids, phalacrocoracids, frigatids, and pelicanids, display only the most rudimentary development of respiratory turbinates in association with their highly restricted narial openings (MacDonald, 1960).

The complete absence of respiratory turbinates in all ectothermic vertebrates, and nearly ubiquitous presence in birds and mammals, further supports their intrinsic physiological importance in maintenance of high endothermic metabolic rates. Living ectothermic amniotes have relatively minimal capacities for sustained aerobic activity and correspondingly low lung ventilation rates preclude the necessity for analogous mechanisms of respiratory heat exchange (Hill and Wyse, 1976). The low metabolic and lung ventilation rates of extant reptiles typically result in low rates of respiratory

water loss relative to similarly sized avians, even when air is exhaled at body temperature (figure 9).

The widespread heat and water savings provided by respiratory turbinates in virtually all birds and mammals, regardless of habitat, signals their crucial physiological role in the maintenance of endothermic metabolism. The evolution of the respiratory turbinate complex in Aves was, nevertheless, likely a key preadaptation enabling birds to successfully invade and exploit extreme habitats, such as deserts and high latitude environments, unavailable to ectothermic tetrapods. These data strongly reinforce previous studies suggesting that the development of complex respiratory turbinates was tightly associated with the acquisition of homeothermic endothermy during avian evolution (Hillenius, 1992; Ruben *et al*, 1998).

SUMMARY AND CONCLUSIONS

Reconstructions of dinosaurs based on the functional morphology and comparative physiology of extant organisms can supplement our understanding of their biology. The appropriate choice of extant models for various aspects of dinosaurian biology is likely to provide fundamental insights into their behavioral patterns, phylogenetic relationships, and metabolic status. In addition, investigations based on uniformitarian principles of biological processes have the broader potential to elucidate a variety of other parameters associated with the more than 150 million-year cosmopolitan dominance of dinosaurs in terrestrial ecosystems.

Considerable recent speculation has focused on the social behavior of dinosaurs, especially aspects of their reproductive and developmental biology. It has been hypothesized that some Late Cretaceous ornithischian dinosaurs demonstrated altricial developmental and behavioral patterns much like those of living songbirds, with hatchlings physically unable to leave the nest and, therefore, requiring extensive feeding and protection from their parents. In Chapter 1, skeletal evidence from embryonic and juvenile dinosaurs is compared to a range of extant crocodilians and birds. The morphology of long bone epiphyses in these dinosaurs is consistent with developmental patterns seen in living precocial forms, and indicates that the reproductive and parental behavior of these dinosaurs was more likely to have resembled a precocial (mobile and relatively independent), rather than altricial, pattern. Additionally, I present new data for the skeletal ontogeny of pelvic elements

of embryonic and juvenile dinosaurs that is fully consistent with the developmental

pattern of ossification observed in extant crocodilians and precocial birds. Fossil

evidence for brooding in one species of theropod dinosaur has been posited as further

evidence for bird-like reproductive behavior (Norell et al, 1995). However, similar

nest-sitting and clutch guarding behavior is common in extant crocodilians (Cott

1961), as well as birds, and therefore likely represents an ancestral archosaurian

condition, rather than a derived behavior of dinosaurs and birds. Overall, it seems

probable that the reproductive behaviors of these ornithischians, while undoubtedly

uniquely dinosaurian in many ways, were, in general, more analogous to crocodilians

than birds.

Although there have been recent reports of "feathered theropods" (Ji and

Currie, 1999), classification of these organisms as dinosaurs remains questionable.

Current scenarios for evolution of birds from any known group of maniraptoran

theropods remain equivocal. Chapter 2 summarizes the inherent biophysical and

ecological problems with the origin of powered flight in any relatively massive,

terrestrial organism. Specifically, the large Reynolds's Numbers and terrestrial habits

of all known theropod dinosaurs proposed as bird ancestors indicate that were unlikely

to have been able to reach and maintain the minimum velocities thought necessary to

develop sufficient lift to initiate flapping flight. Rather, the organisms that best fit

accepted biomechanical and energetic models for the origins of powered flight in

vertebrates would have been small, tree or cliff dwelling gliders, similar to a number

of fossil and extant forms. Furthermore, the Late Jurassic appearance of the first bird,

Archaeopteryx, is inconsistent with the placement of highly derived, Late Cretaceous maniraptoran theropods as avian ancestors. The most chronologically appropriate archosaurs to serve as protobirds would therefore be Triassic to Middle Jurassic forms.

Significantly, an adaptive radiation of small, arboreal archosaurian forms proliferated during the Triassic Period. Many of these organisms displayed morphologies consistent with modern gliding vertebrates. Chapter 2 suggests one such organism, Megalancosaurus preonensis, as a potential model for the early stages in the origin of vertebrate flight. In particular, Megalancosaurus exhibits a number of specific morphological characteristics consistent with arboreality and gliding, two stages considered essential to the origin of avian powered flight (Bock, 1960; Norberg, 1990). Recently, however, Megalancosaurus and the small Triassic "avimorph" archosaur Cosesaurus aviceps have been erroneously described as aquatic forms and summarily dismissed as avian ancestors (Padian and Chiappe, 1998). In fact, Megalancosaurus displays a suite of distinctive characteristics more bird-like than any known theropod dinosaur (i. e., a lightly built head with expanded orbits and beak-like snout; ventrally positioned foramen magnum, narrow, straplike scapula, etc.), without any obvious aquatic adaptations. Additionally, a number of skeletal adaptations are consistent with the possible presence of a patagium, or gliding membrane. These adaptations include a forearm that was only partially extensible, consistent with the presence of a bird-like propatagium. Megalancosaurus also possessed a highly modified first digit on the pedes, strikingly similar to the modified first digit present on several mammalian gliders. This highly modified digit serves as a major point for

attachment of the extensive patagium in these extant forms. The presence of a notarium formed by the fusion dorsally of several elongate anterior thoracic neural spines stiffened the trunk, another character consistent with aerial activities. Though Megalancosaurus may not be the definitive avian ancestor, it, and other forms from the Late Triassic adaptive radiation of small tree dwelling archosaurians, provide compelling bioenergetic and chronologically appropriate alternative models for a likely stage through which avian ancestors passed.

Chapter 3 provides empirical data demonstrating the importance of the respiratory turbinate system of birds to their overall water and heat balance. Turbinate-mediated water and heat savings are shown to have a tight functional linkage to the elevated lung ventilation rates associated with endothermy in a variety of birds. Significantly, respiratory turbinates, independently evolved in birds and mammals (Witmer, 1997), are absent in all ectothermic vertebrates. Prior studies on the function of respiratory turbinates in a range of extant mammals have elucidated their fundamental importance to endothermic metabolic rates (Hillenius, 1992). Results of this study demonstrate that respiratory turbinates play a similarly significant role minimizing respiratory heat and water loss rates during periods of routine activity in a range of avian orders. Nose-breathing birds, on average, reduce respiratory evaporative water loss rates by approximately 70% when compared to birds in which the respiratory turbinates were experimentally bypassed. Additionally, water savings accrued via respiratory turbinates amount to about 6-8% of the bird's calculated daily energy budget, and 10% or more of their predicted daily water flux (Nagy and

Petersen 1988). These low levels of water (and heat) loss approximate those of equivalently sized reptiles, even though lung ventilation rates of endotherms are about an order of magnitude greater than similarly sized ectotherms. In addition, turbinates play a role in brain cooling in resting birds, acting as the center of convective heat transfer from cranial arterial-venous anastomoses during routine non-volant activity.

Elucidating the tight functional link between respiratory turbinates and maintenance of the elevated lung ventilation rates typical of endothermy in birds provides a key tool for determination of the metabolic status of extinct avian relatives, such as theropod dinosaurs. The presence of turbinates or traces of their presence in fossil forms is a likely indicator of elevated lung ventilation, and, by extension, metabolic rates. Significantly, the fact that no known dinosaur possessed respiratory turbinates indicates that they likely had low, ectothermic routine metabolic rates. Furthermore, applying physiological and morphological data to the fossil record indicates that the independent evolution of endothermy in birds and mammals was likely to have followed very different patterns. Fossil data from a sequence of Permian and Triassic therapsids shows a gradual, stepwise evolution of turbinate structures corresponding to a steady rise in metabolic rate (Hillenius, 1994). In contrast, fossil evidence from rostral anatomy, skeletal morphology, and bone histology indicates that the earliest birds lacked turbinates and were probably ectotherms, and that avian endothermy arose sometime in the Cretaceous radiation of ancestral shore/marine birds (Ruben 1996; Chinsamy and Dodson, 1995).

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Overall, this thesis is a synthetic treatment that attempts to provide a broad and novel perspective on the evolution and paleobiology of one of the most successful and least understood vertebrate groups, the dinosaurs. Prior suggestions of bird like reproductive behavior and avian type endothermy in some or all dinosaurs, and many current claims of a dinosaurian ancestry for birds are not supported by the results of this study.

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