# Respiratory physiology of the dinosaurs

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## Summary

Dinosaurs were among the most distinctive and successful of all land vertebrates. Attempts at reconstructing their biology have become commonplace. However, given the absence of closely comparable living models, deciphering their physiology necessarily remains speculative and determination of their metabolic status has been particularly problematical. Nevertheless, many paleontologists have advocated the notion that they were probably "warm-blooded" (endothermic), thus providing a model supposedly essential to the interpretation of these animals as having led particularly active, interesting lives. Those suppositions notwithstanding, the apparent absence of respiratory turbinates in dinosaurs, as well as likely ectothermic patterns of thermoregulation in very early birds, argues strongly that these animals were unlikely to have achieved the metabolic status of modern terrestrial endotherms. These data are not necessarily inconsistent with current models of active lifestyles of dinosaurs. *BioEssays* **20**:852–859, 1998. © 1998 John Wiley & Sons, Inc.

## Introduction

There is far more to dinosaurs than just their impressive appearance in museum displays and fearsome demeanor in popular movies. In many respects, they were probably the most successful of all land vertebrates. Their 150+ million year cosmopolitan reign over the terrestrial environment (from the Late Triassic to Late Cretaceous) far exceeds the duration and magnitude of dominance by any other group of tetrapods, including the mammals and their ancestors. Dinosaurian diversity was spectacular, and their variety encompassed some of the most specialized herbivores and carnivores ever to have existed. Little wonder that so much energy has been devoted to understanding the biology of these long extinct reptiles.

No other aspect of dinosaur biology has sparked more interest or controversy than have attempts to decipher their metabolic status. The currently popular notion that dinosaurs may, like living mammals and birds, have been endothermic (or "warm-blooded") provides a model that reinforces interpre-

tation of these animals as having led particularly active, interesting lives. The more traditional alternative, that dinosaurs were ectotherms (or "cold-blooded"), is conventionally, albeit mistakenly, associated with unintelligent brutes leading sluggish, sedentary lives.

Obviously, however we might prefer to imagine dinosaurs in life, accurate reconstruction of vertebrate evolutionary history necessitates that only reasoned, objective evaluation of appropriate data be considered. Unfortunately, this has often not been the case. Rather, as Professor James Farlow has pointed out, "the strongest impression gained from reading the literature of the dinosaur [metabolic] physiology controversy is that some of the participants have behaved more like politicians or attorneys than scientists, passionately coming to dogmatic conclusions via arguments based on questionable assumptions and/or data subject to other interpretations." [1] Fortunately, innovative analytical techniques have recently provided exciting new insight into the subject. In the following sections, we provide an overview of current perspectives on dinosaur respiratory physiology.

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## Metabolism in tetrapods, living and extinct

Endothermy, or warm-bloodedness, is one of the major evolutionary developments of vertebrates and among the most significant features that distinguish existing birds and mammals from reptiles, amphibians, and fish. Endothermy,

which has clearly evolved independently in birds and mammals,[2] provides these organisms with distinct physiological and ecological benefits and may be largely responsible for the present success of birds and mammals in aquatic and terrestrial environments. Elevated rates of lung ventilation, oxygen consumption, and internal heat production (via aerobic metabolism), which are the hallmarks of endothermy, enable birds and mammals to maintain thermal stability over a wide range of ambient temperatures. As a result, these animals are able to thrive in environments with cold or highly variable thermal conditions and in many nocturnal habitats generally unavailable to ectothermic vertebrates. Furthermore, the increased aerobic (oxygen-consuming) capacities of endotherms allow them to sustain activity levels well beyond the capacity of ectotherms. With some noteworthy exceptions, ectotherms, such as reptiles, typically rely on nonsustainable, anaerobic metabolism for all activities beyond relatively slow movements. Although capable of often spectacular bursts of intense exercise, ectotherms generally fatigue rapidly as a result of lactic acid accumulation. Alternatively, endotherms are able to sustain even relatively high levels of activity for extended periods of time. This enables these animals to forage widely and to migrate over extensive distances. The capacity of bats and birds to sustain long-distance, powered flight is far beyond the capabilities of modern ectothermic vertebrates.[3]

Given the significance of metabolic status to the lifestyles of extant vertebrates, it is hardly surprising that identification and elaboration of physiological parameters associated with vertebrate ecto- and endothermy have received so much attention in the last four decades.[4] However, by itself, the physiology of extant taxa usually provides little, if any, historical perspective into the metabolic status of long extinct taxa.

Until very recently, endothermy has been virtually impossible to demonstrate clearly in extinct forms. Endothermy is almost exclusively an attribute of the "soft anatomy," which leaves a poor, or usually nonexistent, fossil record. Physiologically, endothermy is achieved through prodigious rates of cellular oxygen consumption: in the laboratory, mammalian basal, or resting, metabolic rates are typically about six to ten times greater than those of reptiles of the same body mass and temperature; avian resting rates are often greater still—up to 15 times reptilian rates. In the field, metabolic rates of mammals and birds often exceed those of ectotherms of equivalent size by about 20 times.[5] To support such high oxygen consumption levels, endotherms possess profound structural and functional modifications to facilitate oxygen uptake, transport, and delivery. Both mammals and birds have greatly expanded rates of lung ventilation, fully separated pulmonary and systemic circulatory systems, and expanded cardiac output. They also have greatly increased blood volume and blood oxygen-carrying capacities, as well as increased tissue aerobic enzymatic activities.[6] Unfortunately, these key features of endothermic physiology are unlikely to have ever been preserved in fossils—mammalian, avian, or otherwise.

Consequently, previous hypotheses concerning possible endothermy in a variety of extinct vertebrates, especially dinosaurs, have relied primarily on supposed correlations of metabolic rate with a variety of weakly supported criteria [including, but not limited to, predator:prey ratios, fossilized trackways, correlations with avian or mammalian posture, etc.[7–9]]. Notwithstanding, close scrutiny has revealed that virtually all of these correlations are, at best, equivocal.[10,11]

Recently, conjecture regarding possible dinosaur endothermy has centered on the assumed relationship of bone histology to growth rates in ecto- and endotherms. Two histological types of compact bone have been recognized in extant vertebrates, differing qualitatively in their fibril organization and degree of vascularization. The primary bone of extant amphibians and most reptiles is termed "lamellar-zonal." Here, compact bone is deposited by relatively few primary osteons, principally by periosteal deposition. Histologically, lamellar-zonal bone has a layered appearance, within which incremental growth lines are occasionally recognized; it is also poorly vascularized. In the fibrolamellar bone of many birds, mammals, and dinosaurs, most of the bony matrix is deposited by abundant primary osteons that produce a fibrous, woven appearance. Fibrolamellar bone is well vascularized.[12]

Lamellar-zonal bone has been associated with ectothermy and fibrolamellar with endothermy. Fibrolamellar bone is often held to be correlated with high growth rate that requires rapid deposition of calcium salts. Such rapid growth is supposedly possible only in systems with high metabolic rates associated with endothermy. Thus, the primary correlation is, supposedly, between growth rate and bone structure. Accordingly, it has been widely accepted that growth rates of extant endotherms in the wild are about an order of magnitude greater than in ectotherms. Given the widespread occurrence of fibrolamellar bone in dinosaurs, their growth is often assumed to have been rapid, as in birds and mammals. According to this scenario, also like mammals and birds, they must have been endothermic, or nearly so.[12,13]

Much of this scenario is inconsistent with a variety of paleontological and biological data. For example, fibrolamellar bone is known to be present in the skeleton of extant, rapidly growing turtles, crocodilians, and lizards.[12] Moreover, long bones in numerous dinosaurian genera have regions of both fibrolamellar and lamellar-zonal histology.[12,13]

Bone histology notwithstanding, there is also reason to question the presumed magnitude of variation in growth rates between endotherms and reptiles, especially crocodilians,

the closest living relatives of birds and dinosaurs. In the most frequently cited comparative study, regressions for maximal sustained growth rates (gm/day) for all amniotes scaled positively (slope ≈0.7) with increasing adult body mass, but reptile y-intercept elevations ("a" values) were reportedly only about 10% those of endotherms.[14] However, criteria for calculating these regressions were not equivalent: endotherm "adult weight" approximated mass at sexual maturity, and mass at a similar stage in the ectotherm life cycle would seem appropriate to facilitate construction of regressions on an equal-footing basis. Nevertheless, American alligator (*Alligator mississippiensis*) adult weight was plotted at 160 kg, a value far in excess of the species' actual 30 kg mass at sexual maturity. In addition, growth rate for the alligator was listed at 28 gm/day, rather than the more accurate 42 gm/day. If the corrected daily growth increment, as well as the more appropriate 30 kg adult mass, is assumed for the American alligator, growth rate for this ectotherm is actually about fourfold that of marsupials and approximates growth rates in many placental mammals.[6] In this context, it is especially significant that alligator growth rates are virtually indistinguishable from estimated growth rates for the bipedal theropod dinosaur *Troodon*.[6] Additionally, Chinsamy and Dodson evaluated growth rate in three genera of dinosaurs and found no broad pattern of elevated growth rates.[13]

In another scenario, relative quantities of fossilized bone oxygen isotope ($O^{16}:O^{18}$) were purported to demonstrate relatively little in vivo variation between extremity and deep-body temperature in some large dinosaurs (e.g., *Nanotyrannus*).[15] This was assumed to signify that these large dinosaurs were endothermic since living endotherms, unlike ectotherms, were presumed to maintain relatively uniform extremity vs. core temperatures. Unfortunately, there are abundant data demonstrating that many birds and mammals often maintain extremity temperatures well below deep-body, or core, temperatures.[6] Additionally, fossil bone oxygen isotope ratios may be strongly influenced by ground water temperatures.[16] Consequently, fossilized bone oxygen isotope ratios in dinosaurs are likely to reveal little, if any, definitive information about dinosaur metabolic physiology.

Recently, filiform integumentary structures have been described in two specimens of the small Cretaceous compsognathid dinosaur *Sinosauropteryx*.[17] These have been interpreted by some as evidence that theropod dinosaurs possessed an insulative covering of "protofeathers," suggestive of endothermic homeothermy in dinosaurs. However, the exact composition and distribution of these structures remains unclear. They appear to be restricted primarily to the dorsal midline and may yet prove to be little more than an extensive subcutaneous series of collagen fibers. Additionally, in a number of other theropod dinosaurs in which
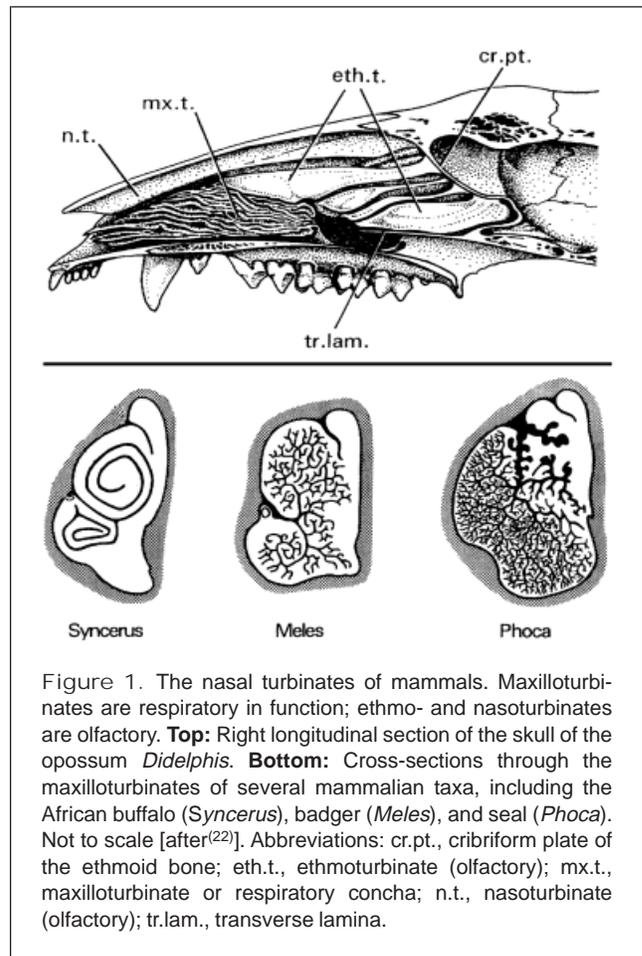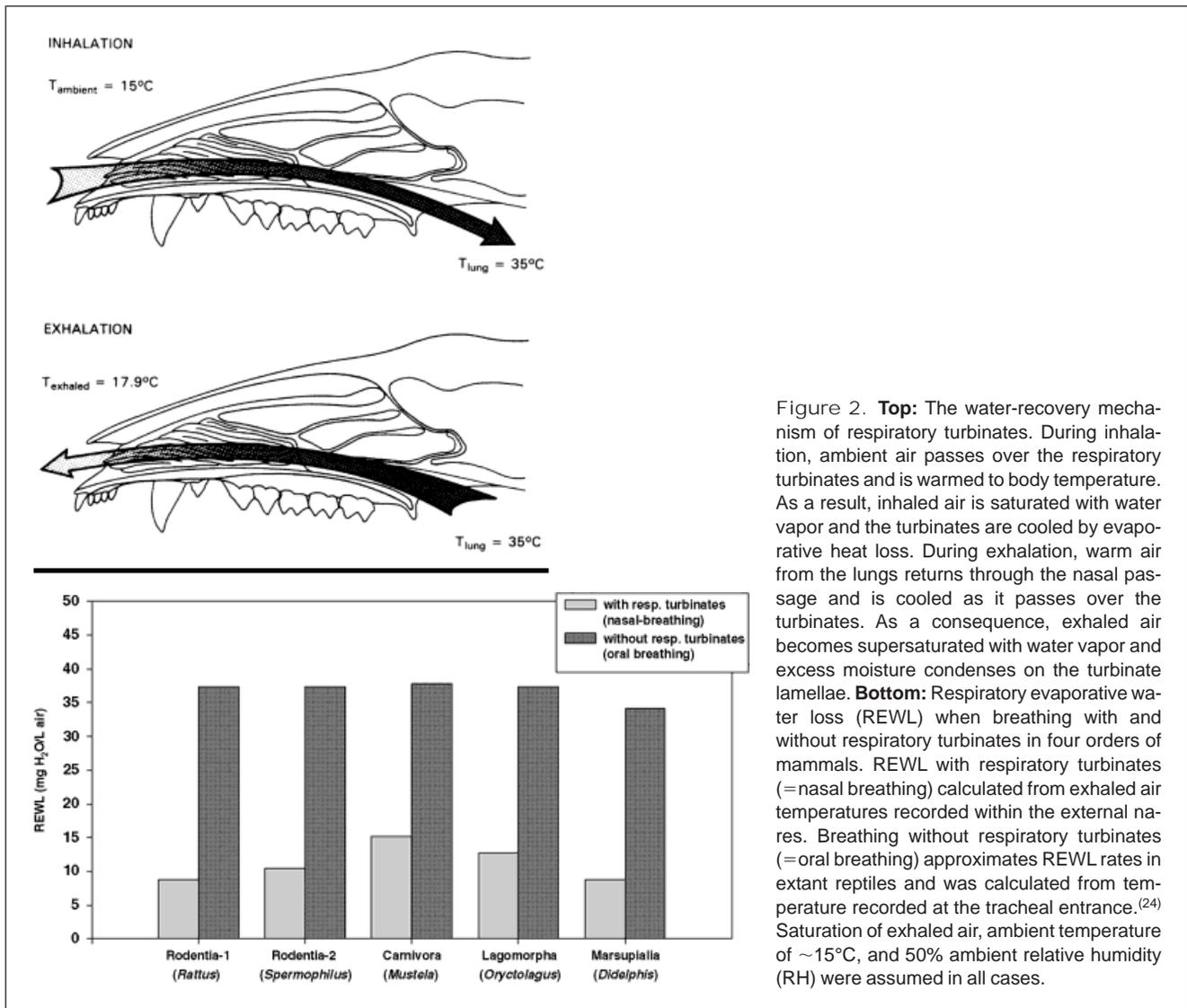


**Figure 1.** The nasal turbinates of mammals. Maxilloturbinates are respiratory in function; ethmo- and nasoturbinates are olfactory. **Top:** Right longitudinal section of the skull of the opossum *Didelphis*. **Bottom:** Cross-sections through the maxilloturbinates of several mammalian taxa, including the African buffalo (S*yncerus*), badger (*Meles*), and seal (*Phoca*). Not to scale [after[22]]. Abbreviations: cr.pt., cribriform plate of the ethmoid bone; eth.t., ethmoturbinate (olfactory); mx.t., maxilloturbinate or respiratory concha; n.t., nasoturbinate (olfactory); tr.lam., transverse lamina.

impressions of skin are present, evidence of a featherlike covering is completely lacking.[18,19]

Perhaps more to the point, virtually all of the arguments used previously are based predominantly on apparent similarities to the mammalian or avian condition, without a clear functional correlation to endothermic processes per se. Until recently, no empirical studies were available that described an unambiguous and exclusive functional relationship to endothermy of a preservable morphological characteristic.

This situation changed with the realization that the respiratory turbinates (described below) that occur in >99% of extant mammals are essential to, and have a tight functional correlation with, maintenance of high lung ventilation rates and endothermy. Schmidt-Neilsen and others have shown that respiratory turbinates in desert-adapted animals help reduce respiratory water and heat loss,[20] but respiratory turbinates probably play a fundamental role in the physiology of almost all terrestrial mammals, regardless of environment.[21] It has also been discovered recently that respiratory turbinates and, presumably, elevated lung ventilation and

**Figure 2. Top:** The water-recovery mechanism of respiratory turbinates. During inhalation, ambient air passes over the respiratory turbinates and is warmed to body temperature. As a result, inhaled air is saturated with water vapor and the turbinates are cooled by evaporative heat loss. During exhalation, warm air from the lungs returns through the nasal passage and is cooled as it passes over the turbinates. As a consequence, exhaled air becomes supersaturated with water vapor and excess moisture condenses on the turbinate lamellae. **Bottom:** Respiratory evaporative water loss (REWL) when breathing with and without respiratory turbinates in four orders of mammals. REWL with respiratory turbinates (=nasal breathing) calculated from exhaled air temperatures recorded within the external nares. Breathing without respiratory turbinates (=oral breathing) approximates REWL rates in extant reptiles and was calculated from temperature recorded at the tracheal entrance.[24] Saturation of exhaled air, ambient temperature of ~15°C, and 50% ambient relative humidity (RH) were assumed in all cases.

metabolic rates also occurred in at least two groups of Permo-Triassic mammal-like (therapsid) reptiles.[22] Consequently, the respiratory turbinates represent the first direct morphological indicator of endothermy that can be observed in the fossil record.

Complex respiratory turbinates are also found in >99% of all extant birds. Although independently derived in avians[23], these structures are remarkably similar to their mammalian analogs, and a variety of data confirm that avian respiratory turbinates have a similar functional association with high lung ventilation rates and endothermy. Consequently, as in the therapsid-mammal lineage, the occurrence or absence of these structures provides a potential "road map" for revealing patterns of lung ventilation rate and metabolism in early birds and their close relatives, the dinosaurs.

**Respiratory turbinates in living endotherms**

Turbinate bones, or cartilages, are scroll- or baffle-like elements located in the nasal cavity of virtually all reptiles, birds, and mammals. In most mammals, these usually consist of two sets of mucous membrane-lined structures that protrude directly into either the main nasal airway or into blind "alleyways" immediately adjacent to the main respiratory airway (Fig. 1). Those situated directly within the main anterior nasal air passageway (i.e., the nasal passage proper), the maxilloturbinates or respiratory turbinates, are thin, complex structures lined with moist respiratory epithelia. Olfactory turbinates (=lateral sphenoids, naso- or ethmoturbinates) are located just out of the main path of respired air, usually dorsal and posterior to the respiratory turbinates. Olfactory turbinates are lined with olfactory (sensory) epithe-
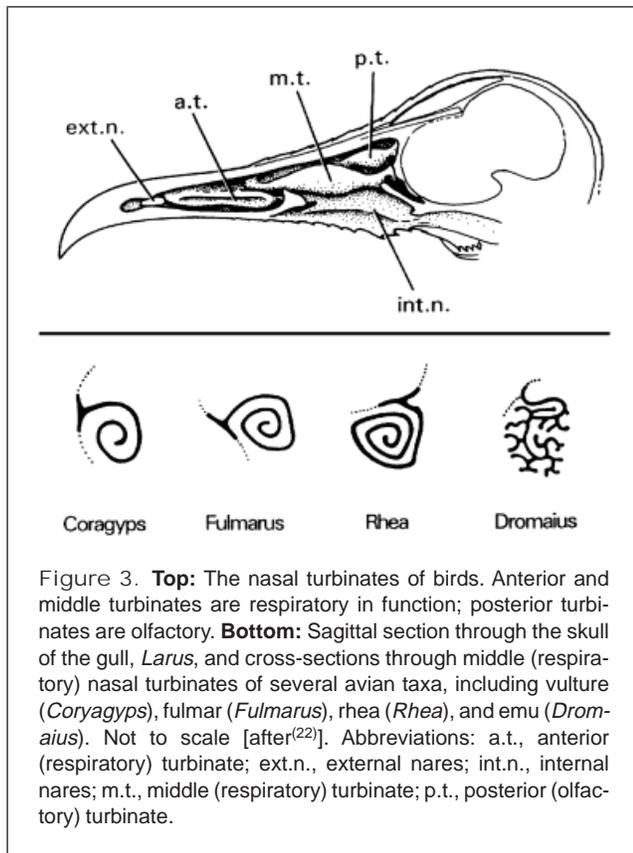
**Figure 3. Top:** The nasal turbinates of birds. Anterior and middle turbinates are respiratory in function; posterior turbinates are olfactory. **Bottom:** Sagittal section through the skull of the gull, *Larus*, and cross-sections through middle (respiratory) nasal turbinates of several avian taxa, including vulture (*Coryagyps*), fulmar (*Fulmarus*), rhea (*Rhea*), and emu (*Dromaius*). Not to scale [after[22]]. Abbreviations: a.t., anterior (respiratory) turbinate; ext.n., external nares; int.n., internal nares; m.t., middle (respiratory) turbinate; p.t., posterior (olfactory) turbinate.



**Figure 4.** The nasal turbinates of reptiles. All turbinates in these animals are exclusively olfactory in function. Right longitudinal section through the skull of *Alligator*. Not to scale [after[22]]. Abbreviations: a.c., anterior concha; ext.n., external nares; int.n., internal nares; m.c., middle concha; p.c., posterior concha.

lia and are the primary centers for the sense of smell.[22] They occur ubiquitously in all reptiles, birds, and mammals and have no particular association with the maintenance of endothermy.

Only the respiratory turbinates have a strong functional association with endothermy. In both mammals and birds (discussed below), endothermy is tightly linked to high levels of oxygen consumption and elevated rates of lung ventilation [e.g., avian and mammalian metabolic and lung ventilation rates in the field exceed reptilian rates by about 20 times[5]]. Respiratory turbinates create an intermittent countercurrent exchange of respiratory heat and water between respired air and the moist, epithelial linings of the turbinates (Fig. 2, top). Briefly, as cool external air is inhaled, it absorbs heat and moisture from the turbinate linings. This prevents desiccation of the lungs, but it also cools the respiratory epithelia and creates a thermal gradient along the turbinates. During exhalation, this process is reversed: warm air from the lungs, now fully saturated with water vapor, is cooled as it once again passes over the respiratory turbinates. The exhaled air becomes supersaturated as a result of this cooling, and "excess" water vapor condenses on the turbinate surfaces, where it can be reclaimed and recycled. Over time, a substantial amount of water and heat can thus be saved,
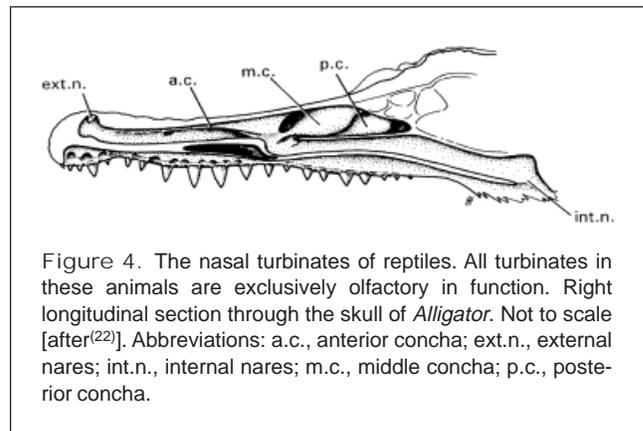
rather than lost to the environment (Fig. 2, bottom). In the absence of respiratory turbinates, continuously high rates of oxidative metabolism and endothermy might well be unsustainable insofar as respiratory water and heat loss rates would frequently exceed tolerable levels, even in species of nondesert environments[24]. Additionally, it has long been suggested that the ubiquitous occurrence of vascular shunts between respiratory turbinates and the brain indicates that these turbinates are also utilized as brain "coolers" in birds and mammals. This would be especially critical during periods of elevated ambient temperatures or during periods of extended activity typical of many birds and mammals, when rates of internal heat production would be highest.[25,26]

Complex turbinates comparable to those of mammals are also found in almost all birds[27] and share similar functions. The extent and complexity of the nasal cavity of birds vary widely with the shape of the bill, but in general, the avian nasal passage is elongate with three cartilaginous, or sometimes ossified, turbinates in succession (Fig. 3). The anterior turbinate is often relatively simple, but the others, particularly the middle turbinates, are often more highly developed into prominent scrolls with multiple turns. Sensory (olfactory) epithelium is restricted to the posterior turbinate. Like mammalian olfactory turbinates, this structure is situated outside the main respiratory air stream, often in a separate olfactory chamber. Embryological and anatomical studies indicate that only the posterior turbinate is homologous to those of reptiles; the anterior and middle turbinates have evolved independently in birds.[23]

The anterior and middle turbinates of birds, like the respiratory turbinates of mammals, are situated directly in the respiratory passage and are covered primarily with respiratory epithelium. These turbinates are well positioned to modify bulk respired air.

Previously published observations, as well as more extensive data recently generated in our lab, suggest that the turbinates of birds function as well as, or superior to, mammalian respiratory turbinates for the recovery of water vapor

**Figure 5.** The relation of nasal passage proper cross-sectional area to body mass in modern endotherms [birds (e.g., emu, ostrich, rhea, heron) and mammals (e.g., dog, opossum, raccoon, anteater, cape buffalo, human, horse)] and ectotherms (lizards and crocodilians), three genera of Late Cretaceous dinosaurs, and five genera of therapsids (values for dinosaurs and therapsids were not included in regression calculations). Dinosaurs masses (estimated from head and/or body skeletal length): ostrich dinosaur, *Ornithomimus* (Theropoda: Ornithomimidae), 70 kg (Campanian stage; Tyrrell Museum of Palaeontology specimen 95.110.1); "duckbill" dinosaur, *Hypacrosaurus* (Ornithischia: Hadrosauridae), 375 kg (Maastrichtian stage; American Museum of Natural History specimen 5461); tyrannosaurid dinosaur, *Nanotyrannus* (Theropoda: Tyrannosauridae), 500 kg (Maastrichtian stage; Cleveland Museum of Natural History specimen 7541) [modified from Ref. 28].
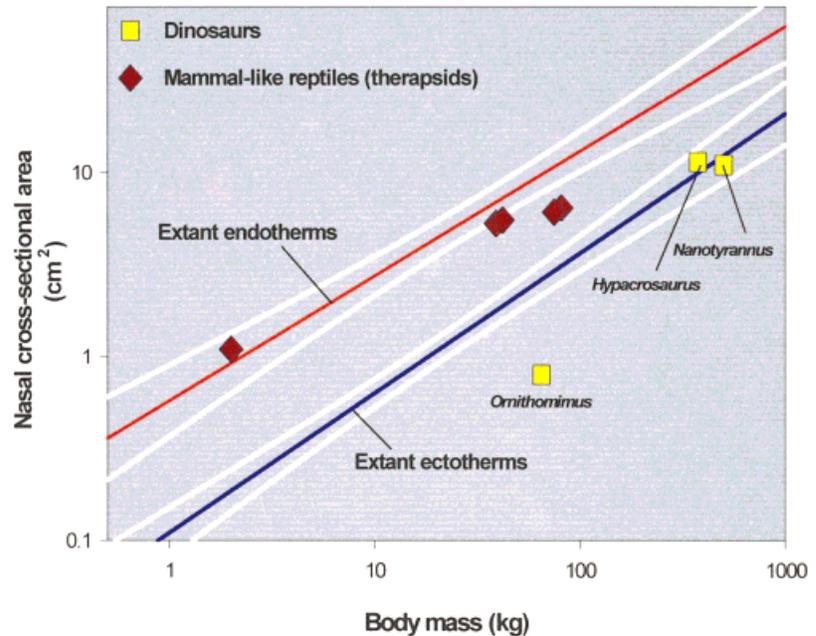
contained in exhaled air.[20] Consequently, in birds these structures probably represent an adaptation to high lung ventilation rates and endothermy, fully analogous to respiratory turbinates of mammals.

Mammalian and avian respiratory turbinates have no analogs or homologs among any living reptiles or amphibians.[23] In living reptiles, one to three simple nasal turbinates are present, but these are exclusively olfactory in function (Fig. 4). Like the mammalian olfactory turbinates (nasal or ethmoturbinates), these are typically located in the posterodorsal olfactory portion of the nasal cavity. There are no structures in the reptilian nasal cavity (or the nasal cavity of any extant ectotherm) specifically designed for the recovery of respiratory water vapor, nor are they as likely to be needed. Reptilian lung ventilation rates are probably sufficiently low that pulmonary water loss rates seldom create significant problems, even for desert species.
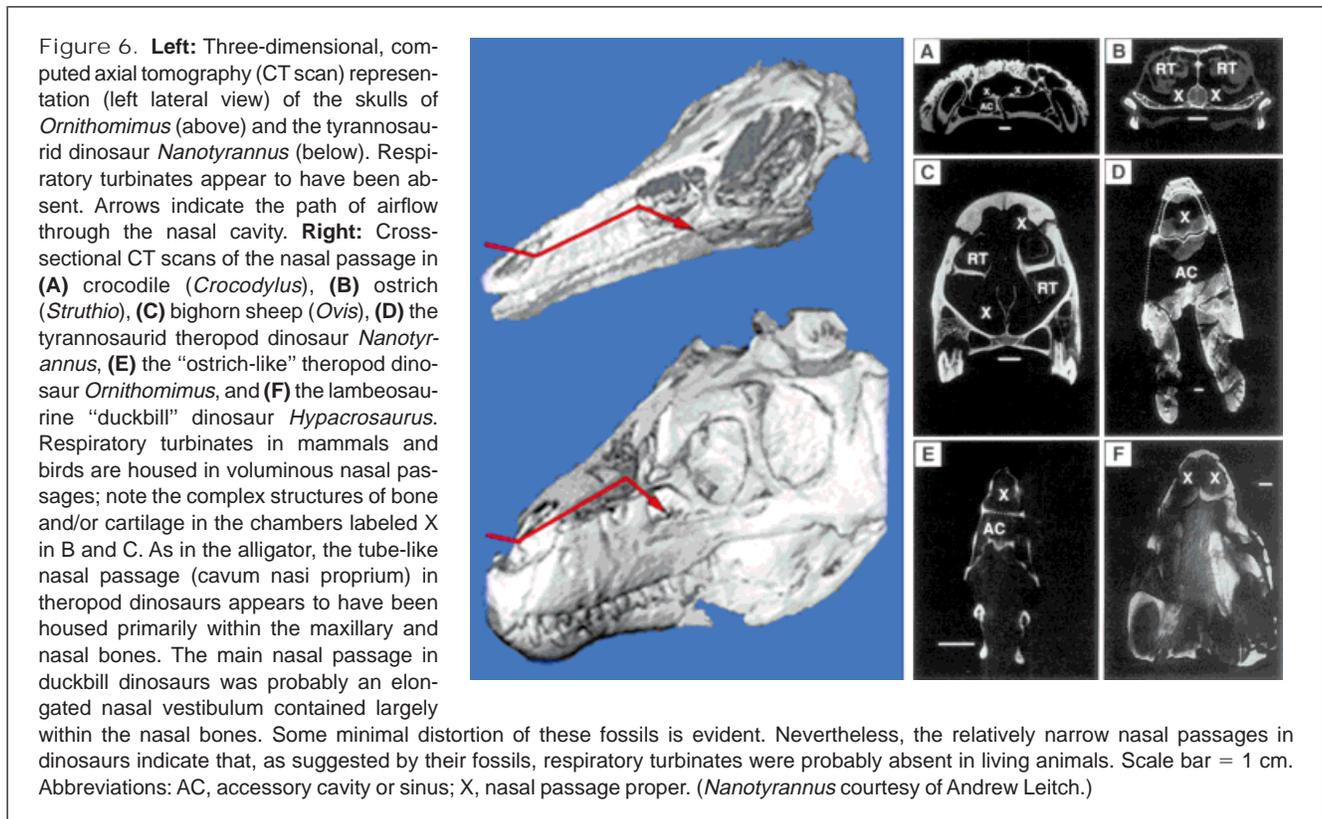
To summarize, physiological data imply that independent selection for endothermy in birds, mammals, and/or their ancestors was, by necessity, tightly associated with the convergent evolution of respiratory turbinates in these taxa. In the absence of these structures, unacceptably high rates of respiratory water and/or heat loss or central nervous system overheating would probably have posed chronic obstacles to maintenance of elevated rates of bulk lung ventilation or high sustained levels of activity consistent with endothermy.

Mere coincidence is unlikely to account for the striking anatomical and functional similarity of the independently derived avian and mammalian turbinate systems. This is because maintenance of the requisite alternating thermal countercurrent system at any portion of the respiratory tree other than the nasal cavity would be untenable. Intermittently cool and warm countercurrent exchange sites in the body cavity would necessarily preclude deep-body homeothermy; an efficient tracheal (or "wind-pipe") countercurrent system would inevitably result in chronic oscillation of brain temperature because of the proximity of the trachea with arterial blood bound for the brain (via the carotid circulation). Consequently, the confirmed absence of respiratory turbinates or similar structures is likely to be strongly indicative of ectothermic, or near-ectothermic, rates of lung ventilation and metabolism in any taxon, living or extinct.

## Respiratory turbinates and the metabolic status of dinosaurs

Several factors complicate the study of the evolutionary history of turbinates in birds and, potentially, in their close relatives, the dinosaurs. Although they ossify or calcify in many extant taxa, these structures often remain cartilaginous and lack bony points of contact in the nasal passage proper of birds, thus greatly decreasing the chances for direct detection of their presence or absence in extinct taxa. Nevertheless, we have determined that the presence of respiratory turbinates in extant endotherms is inevitably associated with marked expansion of the proportionate cross-sectional area of the nasal cavity proper[28] (Fig. 5). Increased nasal passage cross-sectional area in endotherms probably serves both to accommodate elevated lung ventilation rates and to provide

**Figure 6.** **Left:** Three-dimensional, computed axial tomography (CT scan) representation (left lateral view) of the skulls of *Ornithomimus* (above) and the tyrannosaurid dinosaur *Nanotyrannus* (below). Respiratory turbinates appear to have been absent. Arrows indicate the path of airflow through the nasal cavity. **Right:** Cross-sectional CT scans of the nasal passage in **(A)** crocodile (*Crocodylus*), **(B)** ostrich (*Struthio*), **(C)** bighorn sheep (*Ovis*), **(D)** the tyrannosaurid theropod dinosaur *Nanotyrannus*, **(E)** the "ostrich-like" theropod dinosaur *Ornithomimus*, and **(F)** the lambeosaurine "duckbill" dinosaur *Hypacrosaurus*. Respiratory turbinates in mammals and birds are housed in voluminous nasal passages; note the complex structures of bone and/or cartilage in the chambers labeled X in B and C. As in the alligator, the tube-like nasal passage (cavum nasi proprium) in theropod dinosaurs appears to have been housed primarily within the maxillary and nasal bones. The main nasal passage in duckbill dinosaurs was probably an elongated nasal vestibulum contained largely within the nasal bones. Some minimal distortion of these fossils is evident. Nevertheless, the relatively narrow nasal passages in dinosaurs indicate that, as suggested by their fossils, respiratory turbinates were probably absent in living animals. Scale bar = 1 cm. Abbreviations: AC, accessory cavity or sinus; X, nasal passage proper. (*Nanotyrannus* courtesy of Andrew Leitch.)

increased rostral volume to house the respiratory turbinates. Significantly, relative nasal passage diameter in a sequence of therapsid reptiles (the immediate ancestors of mammals) approaches and, in the very mammal-like *Thrinaxodon*, even attains mammalian/avian nasal passage cross-sectional proportions (Fig. 5).

The recent application of computed axial tomography, or CT scans, to paleontological specimens has greatly facilitated noninvasive study of fine details of the nasal region in fossilized specimens, especially those which have been "incompletely" prepared. In the theropod *Nanotyrannus* (Fig. 6), CT scans clearly demonstrate that in life this animal was unlikely to have possessed respiratory turbinates: they are absent from the fossil, and, most importantly, nasal passage cross-sectional dimensions are virtually identical to those in extant ectotherms (Figs. 5, 6). Additionally, CT scans of the nasal region of another theropod dinosaur, the ornithomimid theropod *Ornithomimus*, as well as of the ornithischian dinosaur *Hypacrosaurus*, indicate the presence of narrow, ectotherm-like nasal cavities unlikely to have housed respiratory turbinates (Figs. 5, 6). This condition is strikingly similar to the nasal region of many extant reptiles (e.g., *Crocodylus*, Fig. 6).

The probable absence of respiratory turbinates in dinosaurs, and especially among the theropods, would seem to be confirmed by the occurrence of paired, accessory paranasal sinuses in these animals (AC in Fig. 6D,E)[29]. Such air-filled spaces leave little room for expansion of the nasal cavity and probably indicate that few, if any, dinosaurs possessed nasal passages sufficiently capacious to have housed respiratory turbinates. Together, these data represent strong evidence for low lung ventilation rates and ectothermy, or near-ectothermy, in dinosaurs.

**Conclusions**

Respiratory turbinates occur in virtually all birds and mammals and serve to alleviate a variety of potential problems that would otherwise be associated with endothermy. Their likely absence in dinosaurs provides the first causally linked fossil evidence that these animals were unlikely to have maintained metabolic rates equivalent to those of modern endotherms.

These observations are reinforced by evidence that the dinosaurs' close relatives, the earliest birds (e.g., *Archaeopteryx* and the enantiornithines) similarly had not attained endothermy.[24] Seasonal variation of bone deposition rates (e.g., lines of arrested growth) in the long bones of enantiornithine birds are indicative of variable body temperature, a thermoregulatory pattern generally inconsistent with endothermy.[30] Additionally, analysis of the physiology and anatomy

of extant birds suggests that avian flight may well have evolved prior to the evolution of avian endothermy.[31]

Finally, the metabolic status of the dinosaurs probably reveals less about their lifestyle than is generally supposed. Dinosaurs seem to have lacked basic anatomical attributes causally linked to endothermic modes of existence in modern taxa, but it would be erroneous to conclude that they were, therefore, necessarily similar in lifestyle to most modern, temperate-latitude reptiles (i.e., sluggish herbivores or "sit-and-wait" predators). Given the mild climates of the Mesozoic era, most dinosaurs were probably large enough to have been homeothermic (i.e., maintained a constant body temperature), regardless of their metabolic status[32], and the dynamic skeletal structure of many dinosaurs strongly suggests that they possessed bird- or mammal-like capacity for at least burst activity. Moreover, even if they were fully ectothermic, had dinosaurs possessed aerobic metabolic capacities and predatory habits equivalent to those of some large, modern, tropical-latitude lizards (e.g., *Varanus*), they may well have maintained large home ranges, actively pursued and killed large prey, and defended themselves fiercely when cornered.[33]

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