Selective Factors Associated with the Origin of Fur and Feathers[1]

JOHN A. RUBEN[2] AND TERRY D. JONES

Zoology Department, Oregon State University, Corvallis, Oregon 97331-2917

SYNOPSIS.   Conventional wisdom notwithstanding, fur and feathers are unlikely to have arisen in direct association with elevated metabolic rates in early mammals, birds, or their ancestors. A complete insulative fur coat probably appeared first in the earliest mammals long after mammalian ancestors (therapsids) had attained mammalian, or near-mammalian, metabolic rates. The evolution of feathers was unlinked to the evolution of modern avian metabolic rates since early, fully flighted birds (*i.e., Archaeopteryx*) retained an ectothermic metabolic status. Recent claims of "feathered dinosaurs" should be regarded with caution.

INTRODUCTION

No other anatomical features differentiate mammals and birds from each other so readily as do fur and feathers. Yet, as different as birds and mammals are from each another, the two are also distinguished from all other vertebrates by their common possession of one overarching physiological attribute, true endothermic homeothermy while at rest, or "warm-bloodedness" (Ruben, 1995). Their unique metabolic status has occasionally even led to erroneous, cladistically based assertions that birds and mammals share a close evolutionary relationship (Gardiner, 1982). Not surprisingly, the origins of fur and feathers have frequently been evaluated in the context of endothermy and the metabolic status of early mammals, birds, and their ancestors.

Conventionally, the development of fur or feathers, accelerated metabolic rates, and maintenance of relatively high and stable body temperatures are thought to have been tightly linked. In mammalian ancestors, selection for enhanced thermoregulatory capacity is often assumed to have resulted in the simultaneous evolution of elevated metabolic rates and insulatory fur or hair (Broili, 1941; Brink, 1956). Similarly, since endothermic thermoregulation is often assumed to be inextricably linked with capacity for powered flight, feathers in avian ancestors are assumed by many to have developed in response to selection for both insulation and flight (*e.g.*, Bock, 1985).

In fact, neither of these scenarios for the evolution of avian and mammalian endothermy are fully consistent with available evidence. Recent discoveries, both fossil and physiological, indicate that enhanced capacity for thermoregulation is likely to have had little to do with elevation of metabolic rates in either mammalian or avian ancestors. Similarly, feathers and powered flight in birds probably developed long before endothermy. In the following pages, we discuss likely scenarios for the origin of fur and feathers in light of this new evidence.

ENDOTHERMY IN LIVING AND EXTINCT TETRAPODS

Endothermic homeothermy, 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, provides 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 sta-

bility over a wide range of ambient temperatures (Scholander *et al.*, 1950). As a result, these animals are able to thrive in environments with cold or highly variable thermal conditions, and in some nocturnal habitats unavailable to ectothermic vertebrates (Crompton *et al.*, 1978). Furthermore, the increased aerobic (oxygen-consuming) capacities of endotherms allow them to sustain activity levels well beyond the capacity of ectotherms (Bennett and Ruben, 1979). With some noteworthy exceptions, ectotherms, such as reptiles, typically rely on non-sustainable 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.

Until 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 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 6–10 times greater than those of reptiles of the same body mass and temperature; avian resting rates are often greater still—up to 15 times the reptilian rates. In the field, metabolic rates of mammals and birds often exceed those of equivalent-size ectotherms by about 20 times (Nagy, 1987). 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 (Ruben, 1995). These key features of endothermic physiology are unlikely to have ever been preserved in fossils—mammalian, avian, or otherwise.

Consequently, previous conjecture concerning the possible presence of endothermy in a variety of extinct vertebrates has relied primarily on hypothesized correlations of metabolic rate with a variety of weakly supported, circumstantial arguments, including, but not limited to, predator–prey ratios and correlation's with avian or mammalian posture (Bakker, 1980). Close scrutiny has revealed that these correlations are, at best, equivocal (Ruben, 1995).

Recently, scenarios for possible endothermy in extinct taxa have 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 "fibro-lamellar" bone of many birds, mammals, and dinosaurs, most of the bony matrix is deposited by abundant primary osteons that produce a fibrous, woven appearance. Fibro-lamellar bone is well vascularized (Reid, 1997).

Lamellar-zonal bone has been associated with ectothermy and fibro-lamellar with endothermy. Fibro-lamellar 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 fibro-lamellar 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 (Chinsamy and Dodson, 1995; Reid, 1997).

Much of this scenario is inconsistent with a variety of paleontological and biological data. For example, fibro-lamellar bone is known to be present in the skeleton of extant, rapidly growing turtles, crocodilians, and lizards (Reid, 1997). Moreover, long bones in numerous dinosaurian genera have regions of both fibro-lamellar and lamellar-zonal histology (Chinsamy and Dodson, 1995; Reid, 1997).

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 (g/day) for all amniotes scaled positively (slope $\sim$ 0.7) with increasing adult body mass, but reptile y-intercept elevations (‘‘a’’ values) were reportedly only about 10% those of endotherms (Case, 1978). 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 have used 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 g/day, rather than the more accurate 42 g/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 (Ruben, 1995). In this context, it is especially significant that alligator growth rates are virtually indistinguishable from estimated growth rates for the bipedal theropod dinosaur *Troodon* (Ruben, 1995). Additionally, Chinsamy and Dodson evaluated growth rate in three genera of dino-

saurs and found no broad pattern of elevated growth rates (Chinsamy and Dodson, 1995).

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*) (Barrick and Showers, 1994). 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 (Ruben, 1995). Additionally, fossil bone oxygen isotope ratios may be strongly influenced by ground water temperatures (Kolodny *et al.*, 1996). Consequently, fossilized bone oxygen isotope ratios in dinosaurs are likely to reveal little, if any, definitive information about dinosaur metabolic physiology.

In contrast to previously adduced lines evidence, only the respiratory turbinates have a strong functional association with endothermy (Fig. 1) (Hillenius, 1994; Ruben, 1995). In both mammals and birds, endothermy is tightly linked to high levels of oxygen consumption and concomitant elevated rates of lung ventilation. Respiratory turbinates, which occur in greater than 99% of all extant birds and mammals, facilitate an intermittent countercurrent exchange of respiratory heat and water between respired air and the moist, epithelial linings of the turbinates (Schmidt-Nielsen *et al.*, 1970). In doing so, they significantly reduce respiratory water and heat loss that would otherwise be associated the high rates of lung ventilation associated with mammalian and avian endothermy. Additionally, it has long been suggested that the ubiquitous occurrence of vascular shunts between respiratory turbinates and the brain indicates that these turbinates may be utilized as brain ‘‘coolers’’ in birds and mammals (Baker, 1982; Bernstein *et al.*, 1984). Facilitated brain cooling would be especially critical during periods of elevated ambient temper-
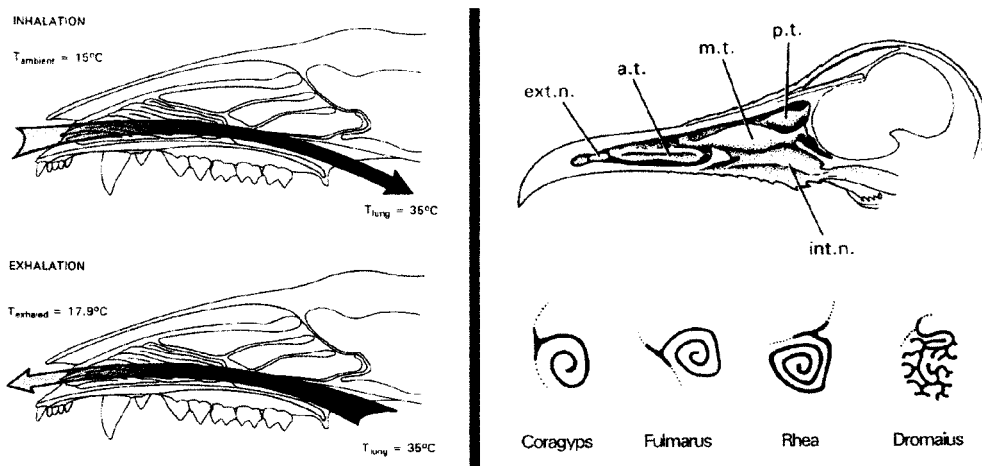
FIG. 1. Left: The water recovery mechanism of respiratory turbinates in mammals. During inhalation, ambient air passes over the respiratory turbinates (olfactory turbinates are situated above the arrows) and is warmed to body temperature. Inhaled air is saturated with water vapor, and the turbinates 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 nasal turbinates. As a consequence, exhaled air becomes supersaturated with water vapor and excess moisture condenses on the turbinates. Right: The nasal turbinates of birds in sagittal and cross sections; anterior and middle turbinates serve a respiratory function. In both mammals and birds, the olfactory turbinates (posterior turbinates in birds) are located out of the main stream of respiratory airflow and are functionally and anatomically distinct from respiratory turbinates. Abbreviations: a.t., anterior turbinates; ext.n., external nares; int.n., internal nares; m.t., middle turbinates; p.t., posterior turbinates.

atures or during extended activity when rates of internal heat production would be highest.

METABOLISM AND INSULATION IN EARLY MAMMALS AND THEIR ANCESTORS

Extant mammals, including prototherians (egg-laying mammals) and therians (marsupial and placental mammals), probably last shared a common ancestor about 160 mya (Rowe, 1992). At any particular mass, most extant mammals (including monotremes and marsupials) maintain generally similar temperature-corrected metabolic rates, and are alike in a wide range of other endothermy-related physiological processes and anatomical structures (*e.g.*, hair, enucleated red blood cells, lung structure, blood oxygen carrying capacity, diaphragm, sweat glands, etc.) (Ruben, 1995). Consequently, it is most parsimonious to conclude the common Mesozoic ancestor of mammals had achieved a similar, endothermic grade of respiratory physiology.

Interpretation of more ancient mammalian or pre-mammalian physiological status rests with linkage of fossilized morphology to metabolic rate. Mammalia probably evolved from cynodont therapsids, or "mammal-like" reptiles, by sometime late in the Triassic (~200 mya) (Rowe, 1992) and it has long been suggested that at least near-endothermy had been achieved in late therapsids (Brink, 1956).

In fossil mammals and mammal-like reptiles, the presence of nasal turbinates is most readily revealed via bony ridges by which these structures attach to the walls of the nasal cavity. Attachment-ridges for olfactory turbinates are located posterodorsally, away from the main flow of respiratory air, whereas those of the respiratory turbinates are situated in the anterolateral rostrum, directly in the path of respired air. Ridges for olfactory turbinates are found throughout the mammal-like reptiles, including earlier, ancestral forms such as pelycosaurs. However, rudimentary anterolateral rostral ridges for support of respiratory turbinates first appear in some large, late Paleozoic therocephalian therapsids, *e.g., Glanosuchus,* a wolf-like pristerognathid.

Accordingly, initial phases in the evolution of ''mammalian'' oxygen consumption rates may have begun as early as the Late Permian (250 mya), some 40 to 50 million years prior to the origin of the Mammalia (Hillenius, 1994).

The presence of incipient respiratory turbinates in Permian therocephalians provides an early and essential roadmap for understanding the evolution of endothermy and hair in mammalian ancestors. Models linking the origin of hair with the initial stages in the evolution of endothermy in mammalian ancestors are largely falsified if the early incremental steps toward mammalian metabolic rate occurred in large, Late Permian therapsids. Many therocephalians appear to have been active, dog-, bear- or lion-size (20–100 kg) carnivores that inhabited regions with sub-tropical to tropical climates. There is no evidence that therocephalians possessed a hairy covering. Moreover, they were sufficiently large that, whether hairy or scaly, their thermal conductance was likely similar to that of large mammals. They were probably inertial homeotherms and were unlikely to have required a hairy or furry covering for thermoregulatory purposes (McNab, 1978). Accordingly, it is likely that initial stages in the evolution of mammalian metabolic rates were probably linked to selection for increased activity capacity (*i.e.*, the ''aerobic capacity'' model), rather than for enhanced thermoregulatory purposes (Bennett and Ruben, 1979; Ruben, 1995).

Lower-Middle Triassic cynodont therapsids (*e.g.*, the galesaurid *Thrinaxodon* and the traversodontid *Massetognathus*), as well as the earliest mammals (*e.g., Morganucodon*), appear to have possessed respiratory turbinate development similar to that of extant mammals. Consequently, lung ventilation rates and, by extension, metabolic rates of the earliest mammals, and at least some Triassic Period therapsids, are likely to have approached or been equal to those of extant mammals (Hillenius, 1994). A variety of these early Mesozoic therapsids are hypothesized to have possessed an insulative covering associated with true endothermic homeothermy (Brink, 1956). Evidence for therapsid fur centers on the presence of in-fraorbital pits and ridges in some lower Triassic cynodonts. These are hypothesized to have been associated with the presence of sensory vibrissae and, by extension, a hairy, insulative covering over much of the rest of the body. However, rostral foramina do not necessarily indicate the presence of vibrissae. Similar foramina are present in the skulls of living ectotherms whose scaly skins lack both vibrissae and hair (Estes, 1961, 1964); in the lizard *Tupinambis,* for example, rostral foramina are almost identical in shape, number and distribution to those of the cynodont *Thrinaxodon.* In any case, it is far from clear that sensory hairs on the snout indicate a pelage. The origin of hair is poorly understood, but if its initial function were sensory it is possible that vibrissae (and/or other sensory hairs) reflect the primitive condition and so might have appeared long before an insulative pelage had evolved (Maderson, 1972; Bennett and Ruben, 1986).

Surprisingly, very recent data suggest that a complete insulatory covering of hair or fur may not have existed until the appearance of the earliest mammals. Fossil evidence indicates that Harderian glands, structures associated with grooming and maintenance of insulatory pelage in extant mammals (Thiessen, 1992), occurred in the earliest mammals (*e.g., Morgancodon*) (Fig. 2) but were absent in therapsids (Hillenius, 2000). Unlike the mucoserous orbital glands of other tetrapods, the mammalian Harderian gland secretes primarily lipoidal products (Walls, 1942; Sakai, 1981, 1992; Olcese and Wesche, 1989). The function of the Harderian gland has been studied in rodents, where, during self-grooming episodes, Harderian gland lipids are spread across the fur, in a manner analogous to the preening behavior of birds (Thiessen, 1977, 1992). The Harderian gland secretions coat the fur and, like avian preening oils, provide a lipid barrier to cold and wetness and alter the reflectance quality of the pelage (Thiessen, 1977, 1992; Thiessen and Kittrell, 1980; Harlow, 1984).

Thus, although generalizations are necessarily speculative, the available evidence suggests that specialization in the septo-maxilla/nasolacrimal duct complex in early
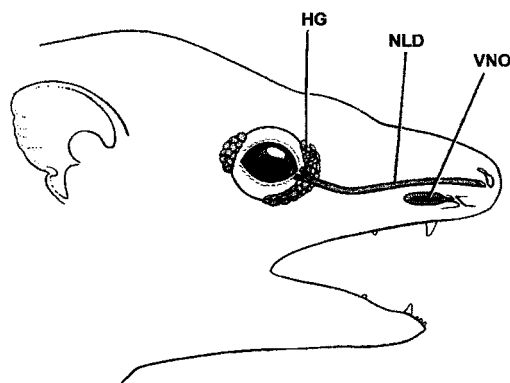
FIG. 2. The Harderian apparatus of mammals. The nasolacrimal outlet into the anterior rhinarium allows oily Harderian secretions to be transferred from the nostrils to the manus. Secretions are then rubbed into the fur to aid conditioning and maintenance of insulatory qualities of the pelage. The presence of this system in early mammals, but not their immediate ancestors (therapsids), provides the earliest fossil evidence for a fully developed pelage in the therapsid-mammal lineage. Abbreviations: HG, Harderian gland; NLD, naso-lacrimal duct; VNO, vomeronasal organ. Courtesy W. J. Hillenius.

mammals may have been correlated with the transformation of the Harderian gland to a lipid-secreting gland, and the release of its fluids onto the exterior of the snout and body. This might well have been correlated with the advent of fur as an insulative barrier.

Perhaps an insulative fur covering became a necessity only when taxa in the therapsid-mammal lineage became extremely small (*i.e.*, total length = 50 mm) and nocturnal (Crompton *et al.*, 1978). Both features occurred at the time of the origin of mammals (McNab, 1978). Thus, a hairy, insulative covering in mammals may have evolved in association with endothermic homeothermy, but long after mammal-like metabolic rates had evolved in therapsids.

METABOLISM AND INTEGUMENTARY STRUCTURES IN DINOSAURS AND EARLY BIRDS

Extant birds are accomplished endotherms and many (especially the songbirds) maintain the highest body temperatures and mass specific metabolic rates of any tetrapods. The fossil record indicates that modern bird orders were well defined by about 60 mya (Feduccia, 1996), therefore avian endothermy is likely to have been fully developed by about Late Cretaceous–Early Tertiary Periods.

As the birds are a monophyletic group, no extant endothermic sister taxon exists from which pre-Cenozoic inheritance of endothermy can be logically inferred (in contrast to the monotreme, marsupial and eutherian taxa of the mammals). The earliest known bird is the famous *Archaeopteryx lithographica,* a late Jurassic (145 mya), fully-flighted archaeornithine. It possessed (at least) complete wing and tail plumage and a striking superficial skeletal similarity to some carnivorous dinosaurs (Ostrom, 1976). However, its thermoregulatory status is still problematic. Previously described circumstantial evidence suggests that *Archaeopteryx* might well have been an ectotherm (Ruben, 1991; Chinsamy *et al.*, 1994) and aspects of the anatomy and reproduction of modern birds also suggest that flight preceded the appearance of endothermy in birds (Randolph, 1994). Nevertheless, *Archaeopteryx* is conventionally assumed to have been endothermic, in part because its well-developed flight plumage is thought to have provided a barrier to ambient radiation, sufficient to preclude effective ectothermic thermoregulation (Bock, 1985). However, the presence of even a fully developed set of flight, body, and contour feathers in Mesozoic avian ancestors of extant birds need not necessarily signal the presence of endothermy, or even an approach to it. Like modern reptiles, some living birds utilize behavioral thermoregulation to absorb ambient heat across feathered skin. During nocturnal periods of low ambient temperatures, body temperature in the roadrunner (*Geococcyx californianus*) declines by ~4°C. After sunrise, the roadrunner exposes poorly feathered parts of its body to solar radiation and warms ectothermically to normal body temperature. Additionally, a number of other fully-feathered extant birds can readily absorb and use incident radiant solar energy (*e.g.*, Hamilton and Heppner, 1966; Lustick *et al.*, 1970). An ectothermic *Archaeopteryx,* which is thought to have lived in a warm, sunny climate, might easily have had similar behav-

ioral thermoregulatory capacity. A fully feathered *Archaeopteryx,* whether ectothermic or endothermic, could easily have achieved homeothermy. Consequently, the appearance of well-developed plumage so early in avian history might well have been related to the evolution of powered flight, rather than with any particular thermoregulatory pattern (Martin, 1983; Ruben, 1991).

The apparent anatomical similarity between some Mesozoic archosaurs and *Archaeopteryx* is marked, and many workers accept a close phyletic relationship between the theropod dromaeosaurid dinosaurs (*e.g., Velociraptor, Deinonychus*) and primitive birds (Ostrom, 1990). Consequentially, the metabolic status of the theropod dinosaurs might provide valuable insight into the ecto- or endothermic nature of early birds

The presence or absence of endothermy in dinosaurs has been a topic of considerable discussion and sometimes acrimonious debate over the past twenty years. Certainly, many large dinosaurs were inertial homeotherms (Spotilla *et al.,* 1991), but, as discussed above, most lines of evidence (*e.g.,* predator–prey ratios, posture, bone histology, etc.) have produced little unambiguous support for endothermy in dinosaurs (Ruben, 1995).

Determination of the presence or absence of respiratory turbinates in theropods is likely to provide the most direct evidence for their metabolic status. However, several factors complicate the study of the evolutionary history of turbinates in birds (Fig. 1) and their relatives. Although, turbinates 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 (Ruben *et al.,* 1996). Increased nasal passage cross-sectional area in endotherms probably serves to accommodate both elevated lung ventilation rates as well as to

provide increased rostral volume to house the respiratory turbinates. Significantly, relative nasal passage diameter in a sequence of successively more recent, increasingly mammal-like therapsids, approaches and, in the very mammal-like *Thrinaxodon,* even attains mammalian/avian nasal passage cross-sectional proportions (Ruben *et al.,* 1998).

The recent application of computed axial tomography, or CT-scans, to paleontological specimens has greatly facilitated non-invasive study of details of the nasal region in fossilized specimens, especially those which have been ''incompletely'' prepared. In *Tyrannosaurus,* CT-scans clearly demonstrate that in life, this animal was unlikely to have possessed respiratory turbinates: they are absent from the fossil remains and, most importantly, nasal passage cross-sectional dimensions are virtually identical to those in extant ectotherms (Ruben *et al.,* 1996). Additionally, CT-scans of the nasal region of another theropod dinosaur, the ornithomimid *Ornithomimus,* as well as the ornithischian dinosaur *Hypacrosaurus,* also indicate the presence of narrow, ectotherm-like nasal cavities, unlikely to have been sufficiently voluminous to have housed respiratory turbinates. This condition is strikingly similar to the nasal region of many extant reptiles (*e.g., Crocodylus*) and is strong evidence for low lung ventilation rates and ectothermy, or near-ectothermy, in these dinosaurs (Ruben *et al.,* 1996).

Narrow nasal passages in theropods are associated with the ubiquitous presence of voluminous accessory rostral pneumatic sinuses and their distinctive external openings, the antorbital foramina (Witmer, 1997). In contrast, modern birds lack accessory antorbital sinuses because their broad nasal passages and respiratory turbinates virtually fill the nasal passage proper and leave little room for the presence of extensive paranasal sinuses. Significantly, *Archaeopteryx* possessed antorbital foramina and, by extension, extensive accessory sinuses identical to those of theropods (Fig. 3) (Witmer, 1997). Consequently, *Archaeopteryx,* like its relatives the theropod dinosaurs, was unlikely to have possessed respiratory turbinates or to have attained en-
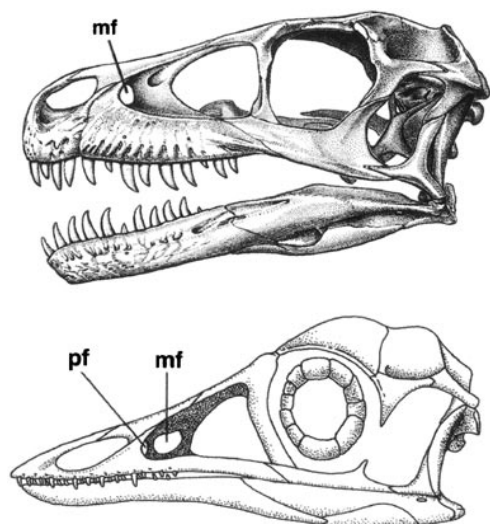
FIG. 3. The promaxillary and/or maxillary fenestrae in *Dromaeosaurus* (top) and *Archaeopteryx* (bottom) that open into paranasal sinuses, which are causally linked to narrow nasal passages and likely absence of nasal respiratory turbinates. Modified from Currie (1995) and Chatterjee (1997), respectively.
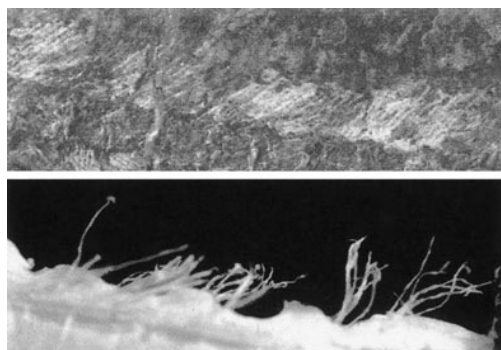

FIG. 4. Fibrous structures associated with the tails of the Cretaceous theropod dinosaur *Sinosauropteryx* (above) (Nanjing Institute of Geology and Paleontology #127586) and the extant lizard *Varanus* (below). In *Sinosauropteryx,* these have been referred to as "protofeathers" but may merely represent collagen fibers similar to those in this partially macerated specimen of *Varanus*. Image of *Sinosauropteryx* is a digitally produced negative.

dothermic metabolic status. In any case, Late Mesozoic climates were so mild and equable that even the earliest Jurassic birds were probably fully capable of relatively precise behavioral thermoregulation.

Feathers (*i.e.*, with well-defined rachis and barbs) are, therefore, most reasonably interpreted as having evolved primarily in association with flight, rather than for thermoregulatory purposes. As Feduccia (1996, p. 130) points out, "Feathers are the most complex appendages produced by the epidermis in any animal. . . their entire structure is oriented toward an aerodynamic end, and their structure, in both contour and flight feathers tends to degenerate in secondarily evolved flightless lineages. . . Indeed, that feathers would represent gross "overkill" for an insulating integumentary structure is perhaps the strongest argument against their having evolved in that initial context." It is likely that avian endothermy probably evolved long after the origin of avian flight and in association with selection for enhanced capacity for long-distance flight rather than for thermoregulatory purposes (see Ruben, 1991).

THE QUESTION OF THE "FEATHERED" THEROPOD DINOSAURS FROM CHINA

Three recently described fossil reptiles from the Early Cretaceous Era of northeastern China (Liaoning Province) are purported to represent feathered, or "protofeathered" theropod dinosaurs. These claims should be regarded with caution.

Sinosauropteryx, a compsognathid theropod, bears a continuous, midline frill of hair-like fibers that extend from the dorsal aspect of the neck to the back and tail (Ji *et al.*, 1998*a*). Initial claims that these fibers represent "protofeathers," each of which ". . . seems to be composed of a central rachis and branching barbs. . . ." (Currie, 1998, p. 241) have not been confirmed (Ji *et al.*, 1998*a*). Moreover, dissection of recent squamate material suggests that the hairlike frill might represent macerated collagen fibers (Fig. 4) (see also Unwin and Bakhurina, 1995, regarding collagen fibers in pterosaur fossils). These data apply equally well to interpretation of similar hair-like fibers, which occur on other theropod taxa from China.

Two other genera, *Protarchaeopteryx* and *Caudipteryx,* clearly bear well-defined feathers, but the theropod status of either genus is dubious. *Protarchaeopteryx* is too poorly preserved for definitive
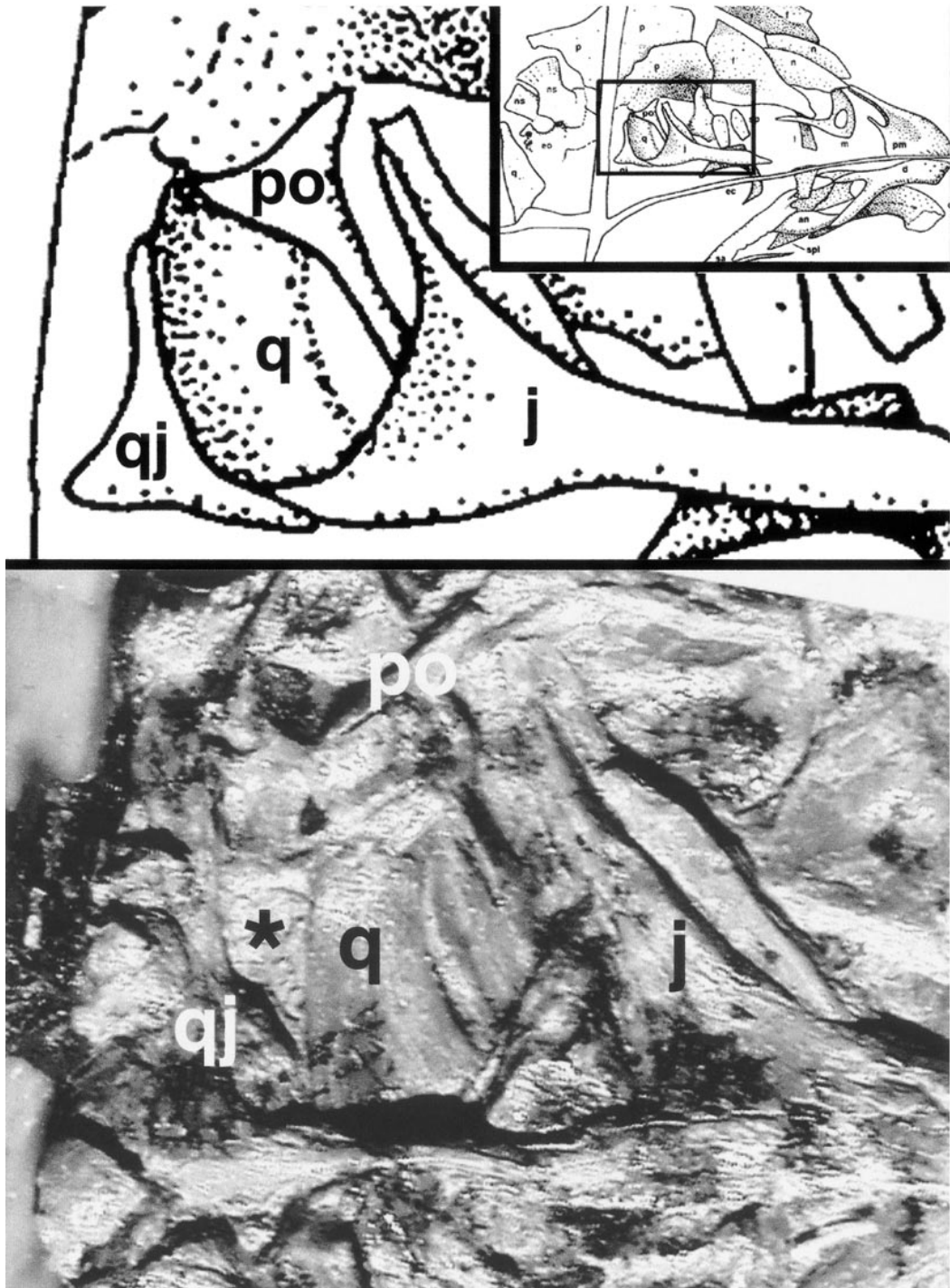
FIG. 5. The quadratojugal–quadrate complex in the Cretaceous flightless bird *Caudipteryx*. Above: as initially interpreted and illustrated; inset, skull of *Caudipteryx* (modified from Ji, Q. *et al.*, 1998*b*). Below: a photograph of the actual specimen (National Geological Museum of China, specimen number 97-9-A). Note the absence of contact between the quadrate and quadratojugal. Abbreviations: j, jugal; po, postorbital; q, quadrate; qj, quadratojugal; *, distinct gap separating quadrate and quadratojugal.

taxonomic analysis. However, its long forelimbs are not inconsistent with an avian status (Witmer, personal communication). *Caudipteryx* has short forelimbs and a feathered manus and is likely to have been a secondarily flightless bird. Claims for its theropodan classification center on three ''unambiguous'' morphological traits that supposedly indicate a preavian status. These include (1) a sutured, rather than ligamentous or loose, quadratojugal-quadrate contact, (2) quadratojugal contact with the squamosal, and (3) the presence of an obturator process of the ischium (Ji *et al.*, 1998*b*). However, in *Caudipteryx,* these attributes are either nonexistent or ambiguous. Previously published illustrations notwithstanding, there is no quadratojugal-quadrate contact and the quadratojugal is far too short to have contacted the squamosal (Fig. 5). Finally, an obturator process may or may not exist in *Caudipteryx,* but, in any case, a similar structure is also known to have occurred in some birds (*e.g., Concornis*) (Sanz *et al.*, 1995).

SUMMARY

The evolution of endothermic metabolic rates and pelage and plumage in the earliest mammals and birds, respectively, followed radically different sequential chronologies. The presence of well developed respiratory turbinates in Middle Triassic Era cynodont therapsids signals that attainment of significantly elevated, possibly mammal-like, metabolic rates probably preceeded the origin of mammals by at least 10–15 million years. Nevertheless, the earliest fossilized evidence for the development of Harderian glands (in Late Triassic morganucodontids) suggests that the initial appearance of an insulatory pelage did not occur before the advent of the Mammalia. It is likely that the particularly diminuitive size and nocturnal habits of the earliest mammals would have provided intense selection for development of an insulative layer to assist in thermoregulation.

Conventional wisdom notwithstanding, the likely absence of respiratory turbinates in theropod dinosaurs and *Archaeopteryx* provides strong evidence that early birds were likely to have been ectotherms. Thus, the appearance of feathers and powered flight were likely to have preceeded the development of endothermy in the avian lineage. It is most parsimonious to assume that feathers evolved in response to selection for aerodynamic, rather than for thermoregulatory purposes.

REFERENCES

Baker, M. A. 1982. Brain cooling in endotherms in heat and exercise. Ann. Rev. Physiol. 44:85–96.

Bakker, R. T. 1980. Dinosaur heresy-dinosaur renaissance. *In* D. K. R. Thomas, and E. C. Olson (eds.), *A cold look at the warm blooded dinosaurs,* pp. 351–462. Westview Press, Boulder, Colorado.

Barrick, A. E. and W. J. Showers. 1994. Thermophysiology of *Tyrannosaurus rex*: Evidence from oxygen isotopes. Science 265:222–224.

Bennett, A. F. and J. A. Ruben. 1979. Endothermy and activity in vertebrates. Science 206:649–654.

Bennett, A. F. and J. A. Ruben. 1986. The metabolic and thermoregulatory status of therapsids. *In* N. Hotton, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), *The ecology and biology of mammal-like reptiles,* pp. 207–218. Smithsonian Institution Press, Washington, D.C.

Bernstein, M. H., H. L. Duran, and B. Pinshow. 1984. Extrapulmonary gas exchange enhances brain oxygen in pigeons. Science 226:564–566.

Bock, W. J. 1985. The arboreal theory for the origin of birds. *In* M. K. Hecht, J. H. Ostrom, G. Viohl and P. Wellenhofer (eds.), *The beginnings of birds,* pp. 199–207. Freunde des Jura-Museums, Eichstätt.

Brink, A. S. 1956. Speculations on some advanced mammalian characteristics in the higher mammal-like reptiles. Palaeontol. Afr. 4:77–96.

Broili, F. 1941. Haare bei Reptilien. Anat. Anz. 92:62–68.

Case, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Quart. Rev. Biol. 53:243–282.

Chatterjee, S. 1997. *The rise of birds: 225 million years of evolution.* The Johns Hopkins University Press: Baltimore.

Chinsamy, A. and P. Dodson. 1995. Inside a dinosaur bone. Am. Sci. 83:174–180.

Chinsamy, A., L. M. Chiappe, and P. Dodson. 1994. Growth rings in Mesozoic birds. Nature 368:196–197.

Crompton, A. W., C. R. Taylor, and J. A. Jagger, 1978. Evolution of homeothermy in mammals. Nature 272:333–336.

Currie, P. J. 1998. ''Feathered'' dinosaurs. *In* P. J. Currie and K. Padian (eds.), *The encyclopedia of dinosaurs,* p. 241. Academic Press, New York.

Currie, P. J. 1995. New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). J. Vert. Paleontol. 153: 576–591.

Estes, R. 1961. Cranial anatomy of the cynodont reptile *Thrinaxodon liorhinus*. Bull. Museum Comp. Zool., Harvard 125:163–180.

Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. Univ. Calif. Publ. Geol. Sci. 49:1–180.

Feduccia, A. 1993. Birdlike characters in the Triassic archosaur *Megalancosaurus*. Naturwissenschaften 80:564–566.

Feduccia, A. 1996. *The origin and evolution of birds.* Yale University Press, New Haven.

Gardiner, B. G. 1982. Tetrapod classification. Zool. J. Linn. Soc. 74:207–232.

Hamilton, W. J. and F. Heppner, 1966. Radiant and solar energy and the function of black homeotherm pigmentation: A hypothesis. Science 155: 196–197.

Harlow H. J. 1984. The influence of harderian gland removal and fur lipid removal on heat loss and water flux to and from the skin of muskrats (*Ondatra zibeticus*). Physiol. Zool. 57:349–356.

Hillenius, W. J. 1994. Turbinates in therapsids: Evidence for Late Permian origins of mammalian endothermy. Evolution 48:207–229.

Hillenius, W. J. 2000. Septomaxilla of nonmammalian synapsids; soft tissue correlates and a new functional interpretation. J. Morphol. 245:29–50.

Ji, C., Z. Dong, and S. Zhen. 1998a. An exceptionally well-preserved theropod dinosaur from the Yixian formation of China. Nature 391:147–152.

Ji, Q., P. J. Currie, M. A. Norrell, and S. Ji. 1998b. Two feathered dinosaurs from northeastern China. Nature 393:753–761.

Kolodny, Y., B. Lutz, M. Sander, W. A. Clemens, 1996. Dinosaur bones: Fossils or pseudomorphs? The pitfalls of physiology reconstruction from apatitic fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 126:161–167.

Lustick, S., S. Talbot, and E. Fox. 1970. Absorption of radiant energy in red-winged blackbirds (*Agelaius phoeniceus*). Condor 72:471–473.

Maderson, P. F. A. 1972. When? Why? And How?: Some speculations on the evolution of the vertebrate integument. Amer. Zool. 12:159–171.

Martin, L. D. 1983. The origin of birds and avian flight. Curr. Ornithol. 1:105–129.

McNab, B. K. 1978. The evolution of homeothermy in the phylogeny of mammals. Am. Nat., 112:1–12.

Nagy, K. A. 1987. Field metabolic rate and food requirements scaling in mammals and birds. Ecol. Monographs 57:111–128.

Olcese J., A. Wesche. 1989. The Harderian gland. Comp. Biochem. Physiol. 93A:655–665.

Ostrom, J. H. 1976. *Archaeopteryx* and the origin of birds. Biol. J. Linn. Soc. 8:91–182.

Ostrom, J. H. 1990. Dromaeosauridae. *In* D. B. Weishampel, P. Dodson, and H. Omolska (eds.), *The Dinosauria,* pp. 269–279. University of California Press, Berkeley.

Randolph, S. E. 1994. The relative timing of the origin of flight and endothermy: Evidence from the comparative biology of birds and mammals. Zool. J. Linn. Soc. 112:389–397.

Reid, R. E. H. 1997. Dinosaurian physiology: The case for "intermediate dinosaurs." *In* J. O. Farlow and M. K. Brett-Surman (eds.), *The complete dinosaur,* pp. 449–473. Indiana Univ. Press, Bloomington.

Rowe, T. 1992. Phylogenetic systematics and the early history of mammals. *In* F. S. Szalay and M. C. McKenna (eds.), *Mammalian Phylogeny,* pp. 129–145. Springer-Verlag, Berlin.

Ruben, J. A. 1991. Reptilian physiology and the flight capacity of *Archaeopteryx*. Evolution, 45:1–17.

Ruben, J. A. 1995. The evolution of endothermy: From physiology to fossils. Ann. Rev. Physiol. 57:69–95.

Ruben, J. A., W. J. Hillenius, N. R. Geist, A. Leitch, T. D. Jones, P. J. Currie, J. R. Horner, and G. Espe III. 1996. The metabolic status of some late Cretaceous dinosaurs. Science 273:1204–1207.

Ruben, J. A., T. D. Jones, and N. R. Geist. 1998. Respiratory physiology of the dinosaurs. BioEssays 20:852–859.

Sakai, T. 1981. The mammalian harderian gland: Morphology, biochemistry function and phylogeny. Arch. Histol. Jap. 44:299–333.

Sakai, T. 1992. Comparative anatomy of mammalian harderian glands. *In* S. M. Webb, R. A. Hoffman, M. L. Puig-Domingo, and R. J. Reiter (eds.) *Harderian glands: Porphyrin metabolism, behavioral and endocrine effects,* pp. 7–23. Springer-Verlag, Berlin.

Sanz, J. L., L. M. Chiappe, and A. D. Buscalioni. 1995. The osteology of *Concornis lacustris* (Aves: Enantiornithes) from the Lower Cretaceous of Spain and a re-examination of its phylogenetic relationships. Amer. Mus. Novit. 3133:1–23.

Schmidt-Neilsen, K. P., F. R. Hainsworth, and D. E. Murrish, 1970. Countercurrent heat exchange in the respiratory passages: Effect on water and heat balance. Respir. Physiol. 9:263–276.

Scholander, P. F., V. Walters, R. Hock, and L. Irving. 1950. Body insulation of some arctic and tropical mammals and birds. Biol. Bull. 99:225–236.

Spotilla, J. R., M. P. O'Connor, P. Dodson, and F. V. Paladino. 1991. Hot and cold running dinosaurs: Size, metabolism and migration. Mod. Geol. 16: 203–227.

Thiessen, D. D. 1977. Thermoenergetics and the evolution of pheromone communication. *In* J. M. Sprague and A. N. Epstein (eds.), *Progress in psychobiology and physiological psychology,* pp. 91–191. Academic Press, New York.

Thiessen, D. D. 1992. Function of the Harderian glands in the Mongolian gerbil (*Meriones unguiculatus*). *In* S. M. Webb, R. A. Hoffmann, M. L. Puig-Domingo, and R. J. Reiter (eds.), *Harderian glands,* pp. 127–140. Springer-Verlag, Berlin.

Thiessen, D. D., and E. M. W. Kittrell 1980. The Harderian gland and thermoregulation in the gerbil (*Meriones unguiculatus*). Physiol. Behav. 24:417–427.

Unwin, D. and N. N. Bakhurina. 1994. *Sordes pilosus* and the nature of the pterosaur flight apparatus. Nature 371:62–64.

Walls G. L. 1942. The vertebrate eye and its adaptive radiation. Bull Cranbrook Inst. Sci. 19:1–785.

Witmer, L. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. J. Vert. Paleontol. 17(Suppl. to 1):1–73.