

The Evolution of Endothermy in Terrestrial Vertebrates: Who? When? Why?

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ABSTRACT

Avian and mammalian endothermy results from elevated rates of resting, or routine, metabolism and enables these animals to maintain high and stable body temperatures in the face of variable ambient temperatures. Endothermy is also associated with enhanced stamina and elevated capacity for aerobic metabolism during periods of prolonged activity. These attributes of birds and mammals have greatly contributed to their widespread distribution and ecological success. Unfortunately, since few anatomical/physiological attributes linked to endothermy are preserved in fossils, the origin of endothermy among the ancestors of mammals and birds has long remained obscure. Two recent approaches provide new insight into the metabolic physiology of extinct forms. One addresses chronic (resting) metabolic rates and emphasizes the presence of nasal respiratory turbinates in virtually all extant endotherms. These structures are associated with recovery of respiratory heat and moisture in animals with high resting metabolic rates. The fossil record of nonmammalian synapsids suggests that at least two Late Permian lineages possessed incipient respiratory turbinates. In contrast, these structures appear to have been absent in dinosaurs and nonornithurine birds. Instead, nasal morphology suggests that in the avian lineage, respiratory turbinates first appeared in Cretaceous ornithurines. The other approach addresses the capacity for maximal aerobic activity and examines lung structure and ventilatory mechanisms. There is no positive evidence to support the reconstruction of a derived, avian-like parabronchial lung/air sac system in dinosaurs or

nonornithurine birds. Dinosaur lungs were likely heterogenous, multicameral septate lungs with conventional, tidal ventilation, although evidence from some theropods suggests that at least this group may have had a hepatic piston mechanism of supplementary lung ventilation. This suggests that dinosaurs and nonornithurine birds generally lacked the capacity for high, avian-like levels of sustained activity, although the aerobic capacity of theropods may have exceeded that of extant ectotherms. The avian parabronchial lung/air sac system appears to be an attribute limited to ornithurine birds.

Introduction

Endothermy in birds and mammals is a major physiological specialization that has profoundly affected the biology of these animals. It is a defining feature of extant mammals and birds and distinguishes them from reptiles and other vertebrates. Endothermy provides distinct physiological and ecological benefits, and thus it may well be largely responsible for the present success of birds and mammals in a wide range of aerial, aquatic, and terrestrial environments (Ruben 1995; McNab 2002). Elevated rates of lung ventilation, oxygen consumption, and internal heat production (through aerobic metabolism), all hallmarks of endothermy, permit the maintenance of thermal homeostasis over a wide range of ambient temperatures. This enables endotherms to thrive in habitats with cold or highly variable thermal conditions and in nocturnal niches generally unavailable to ectothermic vertebrates (McNab 2002). But endothermy provides other important benefits as well. The expanded aerobic capacity associated with endothermy allows these animals to sustain levels of activity that are well beyond the capacity of ectotherms (Bennett 1991; Ruben 1995). With some noteworthy exceptions, ectotherms, such as reptiles, are generally limited to nonsustainable, anaerobic metabolism for all activities beyond relatively slow movements. Although capable of spectacular bursts of intense exercise, ectotherms generally fatigue rapidly as a result of fuel store depletion and lactic acid accumulation (Bennett 1991; Ruben 1991). In contrast, the elevated rates of aerobiosis of endotherms enable these animals to sustain even relatively high levels of activity for extended periods of time: mammals and birds are able to maintain extensive territories or home ranges, to forage widely, and to migrate over large distances (Ruben 1995). The physiological capacity of bats and birds to sustain long-distance powered

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flight is far beyond the aerobic capabilities of modern ectotherms (Bennett 1991; Ruben 1991, 1995).

Given the significance of endothermic status to the lifestyle and ecological success of extant mammals and birds, it is not surprising that the evolutionary origins of this attribute have received considerable attention (e.g., Bennett 1991; Ruben 1995; Else et al. 2004). Endothermy is the cumulative result of a cascade of physiological adjustments and morphological modifications, and it is clearly a derived attribute that evolved from an ectothermic ancestral state. However, although these modifications almost certainly took place independently in the avian and mammalian lineages, it has remained largely unclear when each of these lineages attained endothermic status. In addition, there has been considerable speculation about the metabolic status of specific groups of extinct amniotes, such as the dinosaurs and pterosaurs (e.g., de Ricqlès 1974; Bakker 1980; Barrick et al. 1997; Horner et al. 2001). These taxa have attracted attention not just because of their close phylogenetic affinity to birds, but also because they were highly successful vertebrates in their own right and dominated the terrestrial and aerial ecosystems of the Mesozoic Era.

In this article, we critically examine evidence for when, and in which groups of tetrapods endothermy first appeared. We also evaluate data bearing on possible selective factors that may have driven early phases in the evolution of mammalian and avian metabolism.

Selective Factors in the Evolution of Endothermy

Endothermy in mammals and birds is defined by elevated rates of resting (or routine) aerobic metabolism, which are usually about five to 15 times greater than that in ectotherms of similar mass and body temperature (e.g., Bennett 1991; Bennett et al. 2000). Routine metabolism is, of course, the primary source of heat that terrestrial endotherms utilize to maintain stable body temperatures. Additionally, although activity physiology is not a component of endothermy *sensu stricto*, most birds and mammals have aerobic capacities and stamina that far exceed those in most ectotherms. For example, avian and mammalian field metabolic rates generally exceed reptilian rates by 20- to 30-fold (e.g., Nagy 1987). Hypotheses explaining the transition to endothermy from ectothermic ancestors have traditionally focused on direct selection for either (i) increased thermoregulatory capacity via elevated resting metabolic rate or (ii) selection for increased stamina and elevated levels of sustainable activity. In the latter scenario (the "aerobic capacity" model), resting metabolic rate is thought to have increased as a fortuitous by-product of continuous selection for elevated aerobic capacity.

Support for the aerobic capacity model for the origin of endothermy is provided by empirical evidence for a link (as yet unexplained) between resting and maximal rates of aerobic metabolism in a number of extant vertebrates (e.g., Dutenhofer

and Swanson 1996; Boily 2002). In contrast, even substantially elevated resting metabolic rates provided little thermoregulatory benefit to lizards (Bennett et al. 2000). Additionally, as discussed below, incipient elevation of resting metabolic rates seems to have first appeared in lion- to bear-sized predators (pristerognathid thercephalian synapsids; 250 million years ago) that lived in tropical or near-tropical climates. These taxa were likely to have been inertial homeotherms even without the benefit of endothermy. There would seem to be little selective advantage in elevation of resting metabolic rate for thermoregulatory purposes in such animals.

Certain attributes of plasma membrane physiology in tetrapods might provide further insight into the origin of endothermy. Consider, for example, the nature of mammalian and avian plasma membranes and maintenance of their sodium/potassium ion gradients. These gradients, which are generated by $\text{Na}^+\text{-K}^+\text{-ATPase}$ pumps (the so-called sodium pumps), are required to support a variety of functions, including the active cellular uptake of organic molecules (e.g., amino acids and sugars) for cellular nutrition and protein synthesis (Clausen et al. 1991) and action potential generation. The plasma membranes of lab rat and pigeon (*Columba*) kidney and liver cells, when compared to those of lizards, seem particularly leaky to Na^+ and K^+ ions (Hulbert and Else 1990). In order to maintain normal solute concentration gradients at the plasma membrane (i.e., relatively high $[\text{K}^+]$ at the inner surface and relatively high $[\text{Na}^+]$ at the outer surface), these leaky plasma membranes apparently require generation of significantly increased levels of metabolic energy (Else and Hulbert 1987). Elevated leakiness in mammalian and avian plasma membranes is apparently correlated with elevation (50%–60%) of tissue protein and phospholipid concentrations. In addition, mammalian liver and kidney tissues also exhibit a qualitative alteration in plasma membrane phospholipid composition compared to those of reptiles. Plasma membranes from each of these organs in mammals have a 35% greater concentration of polyunsaturated fatty acids (greater unsaturation index) but significantly reduced total unsaturated fatty acids. Furthermore, certain long-chain polyunsaturated fatty acids, specifically arachidonic and docosahexanoic acids, 20- and 22-carbon phospholipids, respectively, are relatively more abundant. Finally, in mammals, linoleic acid (18-carbon), another polyunsaturated long-chain fatty acid, occurs with less frequency than in reptiles (Else and Hulbert 1987; Else et al. 2004).

These changes in protein and phospholipid composition may well be causally linked to increased membrane leakiness and, ultimately, to the increased metabolic cost of plasma membrane ion-gradient maintenance in the cells of endotherms. Elsewhere, the evolution of these leaky, supposedly "inefficient" plasma membranes in endotherms is hypothesized to have been a necessary link for increased thermogenesis rather than to have fulfilled expanded demands for plasma membrane work per se (Hulbert and Else 1990). A similar thermogenesis-dedicated

explanation has been offered for enhanced heat production associated with increased rates of futile proton (H^+) cycling at the apparently leaky inner mitochondrial membranes of birds and mammals (Brand et al. 1991). However, as with mass-specific metabolism, mass-specific rates of mitochondrial proton leakage seem to decrease with increasing body size in mammals. Accordingly, variation in thermogenic proton leakiness has been proposed to account for mass-related differences in mammalian resting metabolic rates, that is, the “mouse-elephant” metabolism curve (Porter and Brand 1993). However, this explanation fails to account for virtually identical mass-related changes in metabolic rates of almost all ectotherms (Hemmingsen 1960), taxa in which it is hardly likely that any aspect of cellular metabolism is dedicated expressly to heat production.

If the ultimate function of increased plasma- and/or mitochondrial-membrane leakiness were simply to facilitate endogenous heat production in endotherms, then a greater proportion of total cellular metabolism should be associated with these processes in mammals and birds than in reptiles. Vertebrate tissues clearly specialized for thermogenesis dedicate unusually high fractions of total cellular metabolism to membrane-ion gradient maintenance, for example, mammalian brown adipose tissue (Himms-Hagen 1990) and billfish brain heater organs (Block 1991). Nevertheless, *in vitro* incubation of liver and kidney slices demonstrates that ectotherms and endotherms devote similar fractions of total tissue oxygen consumption (25%–35%) to maintenance of plasma- and mitochondrial-ion homeostasis (Hulbert and Else 1990; Brand et al. 1991). Consequently, there is no compelling reason to assume that either the mitochondrial or plasma leaky membrane fractions of general resting metabolism have more to do with a necessity for heat production in endotherms than they do in ectotherms. Certainly, there is a large increment in absolute rates of metabolism devoted to maintenance of leaky membranes in endotherms. However, metabolic rates devoted to all cellular functions in endotherms have increased by about the same magnitude: the maintenance of leaky membranes does not constitute a “special category.”

We suggest that these factors are consistent with selection for increased aerobic capacity (i.e., the aerobic capacity model), which would have required ever-increasing rates of aerobic ATP production to support progressively enhanced levels of sustainable activity. However, they are broadly inconsistent with thermoregulatory models for the origin of endothermy. In the latter case, selection for greater heat production capacity *per se* would likely have resulted in dedication of a greater fraction of resting metabolism to “futile” heat-producing, rather than ATP-producing, processes in avian and mammalian plasma membranes. Clearly, this is not the case.

Endothermy in the Fossil Record: Limitations and New Insights

Traditionally, it was virtually impossible to clearly demonstrate endothermy in fossil taxa because it is almost exclusively an attribute of the “soft anatomy,” which leaves a poor, and usually nonexistent, fossil record. Certainly, the high rates of cellular oxygen consumption that are the foundation of endothermy are supported by a large aggregate of structural and functional modifications, from enzymatic to cellular to tissue level, that enhance all aspects of the uptake, transport, and assimilation of oxygen. Both mammals and birds have highly specialized lungs with expanded pulmonary capacities and ventilation rates (Duncker 1978; Perry 1992), fully separated pulmonary and systemic circulatory systems, and expanded cardiac output (Bennett 1991). They also have greatly increased blood volume and blood oxygen-carrying capacities (Bennett 1991), as well as higher mitochondrial density and enzymatic activities (e.g., Else and Hulbert 1985; Ruben 1991, 1995; Else et al. 2004).

Unfortunately, these key features of endothermic physiology are unlikely to have been preserved in fossils. Previous hypotheses concerning possible endothermy in extinct vertebrates have therefore typically relied primarily on supposed correlations of metabolic rate with a variety of weakly supported criteria, such as predator-prey ratios, relative brain size, fossilized trackways, and correlations with avian or mammalian posture (e.g., Bakker 1980). Close scrutiny has revealed that virtually all of these correlations are, at best, equivocal (for reviews, see Bennett and Ruben 1986; Farlow et al. 1995).

More recently, a number of reconstructions have centered on an assumed relationship between growth rate and bone microstructure (e.g., Reid 1984; Horner et al. 2001; Padian et al. 2001; Padian and Horner 2002). In particular, the distribution of two histological types of compact bone—lamellarzonal and fibrolamellar, which differ in their fibril organization and degree of vascularization—is often thought to be indicative of bone depositional rates and, indirectly, with overall growth rates and metabolic status. Lamellarzonal bone is the primary bone of extant amphibians and most reptiles. It is poorly vascularized, contains relatively few primary osteons, and often has a layered appearance, within which incremental growth lines are often visible. This bone type forms comparatively slowly and has been associated with low growth rates and ectothermy. In contrast, fibrolamellar bone is well vascularized, with abundant primary osteons, and has a fibrous, woven appearance. It is often deposited during the initial rapid growth period of extant juvenile mammals and birds and has therefore been associated with high growth rates and endothermy. The widespread presence of fibrolamellar bone among dinosaurs has, for example, been interpreted as indicative of endothermic, or at least “intermediate,” metabolic status for these animals (Reid 1984; Horner et al. 2001; Padian et al. 2001; Padian and Horner 2002).

However, it is increasingly clear that there is no simple relationship between bone microstructure, bone growth rates, and metabolic rates (Starck and Chinsamy 2002; Chinsamy and Hillenius 2004). First, in many dinosaurs, both histological types of bone may be found in the same bone at different stages of growth (Reid 1984). Also, in numerous dinosaur genera (e.g., Reid 1997; Erickson and Tumanova 2000), as well as in several nonmammalian synapsids (e.g., Botha and Chinsamy 2000), regions of fibrolamellar bone alternate with annuli of lamellar bone or stop-growth lines, indicating at a minimum the presence of episodic or cyclic fluctuations of bone depositional rates. Second, extant reptiles are able to form fibrolamellar bone, which indicates that a high basal metabolic rate is not a prerequisite for such bone microstructure (Reid 1984, 1997). Conversely, small endotherms, such as shrews, small birds, bats, and rodents, often form simple, avascular, lamellated bone that resembles the type found in lizards and amphibians (de Ricqlès 1974; Reid 1984), despite having high metabolic rates. Moreover, although fibrolamellar bone is often formed during the early stages of growth, when relative growth rates are highest in virtually all tetrapods, paradoxically, this is also the stage when avian hatchlings, particularly those of altricial birds, are poikilothermic ectotherms (e.g., Visser and Ricklefs 1993; Dietz and Drent 1997). In fact, there is not even a clear relationship between metabolic status and growth rate: growth rates of extant alligators are about four times those of marsupials and approximate the growth rates of many placental mammals (Ruben 1995). Perhaps the purported high growth rates of some dinosaurs are correlated with elevated metabolic rates, as Wedel (2003) and others have suggested, but there is neither compelling empirical evidence to corroborate that assertion nor a known mechanism by which growth rates and basal metabolic rates are obligatorily linked. It is also possible, for example, that the reported growth rates of, for example, sauropod dinosaurs (e.g., Erickson et al. 2001; Padian et al. 2001; but see Chinsamy and Hillenius 2004) reflect an unusually high allocation of the overall energy budget to growth, made possible by their comparatively low maintenance costs resulting from low metabolic rates. Nor is there a clear correlation between growth rate and histological type: a recent study by Starck and Chinsamy (2002) documents that a single type of bone tissue can result from a wide range of bone depositional rates. These studies emphasize that the relationships between metabolic strategy, bone depositional rates, and bone microstructure are complex and that extrapolating physiological parameters from bone microstructure or deduced growth rates is highly problematic.

In another approach, the oxygen isotope ($^{16}\text{O}/^{18}\text{O}$) composition of fossilized bone phosphate has been used to assess the thermal physiology of fossil taxa (e.g., Barrick and Showers 1995; Barrick et al. 1997). Preserved isotope ratios purportedly reflect in vivo body temperature, and the apparent lack of variation between samples from the body core and the extremities

in a variety of dinosaurs was presumed to signal the presence of homeothermy and high metabolic rates in these taxa. However, in addition to uncertainties of the stability of bone oxygen isotopes during the fossilization process (e.g., Kolodny et al. 1996), several erroneous assumptions render these conclusions doubtful. For example, this approach assumes that bone deposition rates are equally continuous for the different bones compared. However, varying distributions of rest lines (i.e., annuli or stop-growth lines; see above) reported among different bones of many dinosaurs (e.g., Reid 1997) indicate that this assumption is often not supported. Furthermore, Barrick and Showers (1995) and Barrick et al. (1997) incorrectly apply a definition of homeothermy, which delimits only the temperature fluctuations of the body core, to the thermal variation between the body core and the extremities. In fact, there are abundant data demonstrating that many birds and mammals often maintain a considerable thermal gradient between body core and extremities, and the temperatures of their extremities are routinely closer to ambient temperatures (Randall et al. 2002). Moreover, these authors assume that homeothermy can only be accounted for through endothermic physiology; as discussed above, this assumption has repeatedly been falsified. Finally, the conclusions reached by Barrick and Showers (1995) are not statistically supported by their own data (Ruxton 2000). Fossilized bone oxygen isotope ratios likely reveal little, if any, definitive information about the metabolic physiology of extinct taxa.

Fisher et al. (2000) describe evidence of a fossilized four-chambered heart with a fully partitioned ventricle in an ornithischian dinosaur, *Thescelosaurus*. These authors suggest that the absence of a foramen of Panizza between the ventricles, as well as the presence of a single aortic arch, argues for a high, perhaps endotherm-like metabolic rate in this dinosaur. Unfortunately, several anatomical errors and questionable assumptions errors cast serious doubts on this interpretation. Contrary to Fisher et al. (2000), the ventricles of extant crocodilians are, like those of birds, fully separated: the foramen of Panizza is located at the base of the aortic arches, not between the ventricles (e.g., Axelsson and Franklin 1997). A fully partitioned heart is thus present in both crocodilians and birds, and its presence among dinosaurs not only was likely but also affords little inference concerning metabolic rates. The presence of a single aortic trunk (rather than the paired aortic trunks of extant reptilians) might have been more diagnostic, but this cannot be substantiated from this specimen. Since neither the pulmonary arteries nor the carotids are preserved (Fisher et al. 2000), it is clear that the cardiovascular complex of this specimen is incomplete. Significantly, the left side of this specimen (where the "missing" aortic arch would most likely have been) is absent from the fossil. Finally, it remains unclear whether the specimen is a fossilized heart or merely an ironstone concretion (Rowe et al. 2001). This specimen appears to provide

little, if any, reliable insight into the metabolic physiology of dinosaurs.

Several authors have proposed an endothermic status for theriodont synapsids on the basis of maxillofacial pits and foramina on the snouts of these animals (e.g., Brink 1956). Supposedly, these pits and foramina indicate the presence of sensory vibrissae and, by extension, a complete insulatory coat of fur over the rest of the body. However, such maxillofacial foramina, which are associated with the infraorbital vasculature and innervation, occur widely among amniotes, including many forms that lack vibrissae (e.g., Romer 1956). A concentration of such foramina typically occurs around the jaw margin because this region serves important tactile functions during feeding, even in scaled forms such as turtles, lizards, or crocodilians. In number, shape, and distribution, the maxillofacial foramina of the lizard *Tupinambis* are almost identical to those of the cynodont *Thrinaxodon* (Estes 1961). Clearly, the presence of maxillofacial foramina does not necessarily indicate the presence of vibrissae. Furthermore, it is far from clear that sensory hairs on the snout indicate an insulating pelage. Although it is often axiomatically stated that vibrissae are modified hairs, the evolutionary origins and primitive functions of hair are, in fact, far from clear. Maderson (2003) points out that insulation could not have been the primitive function for evolving protohairs, because the insulative properties only emerge with the presence of a fur coat, in which hairs must surpass a certain minimal size and density. The evolution of integumentary appendages is not very clear, but it is unlikely that a fully developed coat of fur evolved all at once. Possible intermediate morphologies, such as short, stubby protohairs or longer but isolated protohairs, would contribute little to insulation but could have had mechanosensory or protective roles (Ruben and Jones 2000; Maderson 2003). In that case, sensory vibrissae, which are fully functional even as single hairs, may have evolved long before insulatory fur. The oldest fossilized fur is from Late Paleocene multituberculates (Meng and Wyss 1997) and possibly from Early Cretaceous eutherians (Ji et al. 2002). Hillenius (2000) infers that a complete insulatory fur coat may have been present as early as Late Triassic mammals. However, these inferences may have more significance for the advent of metabolically based thermoregulation than for the initial rise of aerobic metabolism that preceded it.

In a similar line of argument, putative filiform or featherlike integumentary structures have recently been described in a variety of small theropod specimens from Early Cretaceous deposits in China. Although there is considerable uncertainty about the chemical nature and anatomical identity of these structures in some cases (e.g., Lingham-Soliar 2003), and although other specimens are probably birds rather than theropod dinosaurs (Jones et al. 2000a; Maryanska et al. 2002), these structures have been interpreted by some as evidence that theropod dinosaurs possessed an insulative covering suggestive of endothermic homeothermy. However, the presence of even

a fully developed set of feathers in nonavian theropods or in the Mesozoic avian ancestors of extant birds does not necessarily signal the presence of endothermy or even an approach to it. Although feathers have an insulatory role in many extant birds, their presence does not preclude ectotherm-like behavioral thermoregulation. Like modern reptiles, some living birds utilize behavioral thermoregulation to absorb ambient heat through their skin, despite the presence of feathers. During nocturnal periods of low ambient temperatures, body temperature in the roadrunner (*Geococcyx californicus*) declines by approximately 4°C. After sunrise, the roadrunner raises its feathers, exposes poorly feathered parts of its body (apteria) to solar radiation, and warms ectothermally to normal body temperature (Ohmart and Lasiewski 1971). Similar use of incident solar radiation has also been documented from a number of other fully feathered birds (Lustick et al. 1970). Likewise, feathered ectothermic theropods, which are thought to have lived in a warm, sunny climate, would have had little difficulty with behavioral thermoregulation. Indeed, even a fully feathered *Archaeopteryx*, whether endothermic or ectothermic, could easily have achieved homeothermy (Ruben 1991). Finally, since feather antecedents appear to have been present initially in small, arboreal archosaurs from the Middle Triassic Period (ca. 220 million years ago; e.g., Jones et al. 2000b), interpreting the function of feathers or feather-like structures in dinosaurs is highly problematic.

Perhaps more to the point, virtually all of these arguments are based predominantly on apparent similarities to the mammalian or avian condition, without a clear functional correlation to endothermic processes per se. Feathers, for example, do not produce heat, nor do they contribute to the uptake, transport, or delivery of oxygen. While they serve a wide range of functions in extant birds, it remains very much unclear which of these, if any, is the most primitive (Maderson and Alibardi 2000). Among tetrapods, endothermy is a derived condition, and questions of when this status was acquired in any evolutionary lineage can only be answered with positive evidence of osteological, or at least preserved, features that are clearly functionally linked to the derived physiological processes and attributes that underlie endothermy. Recently, two lines of evidence have shed new light on the antiquity of endothermy. These include the presence of respiratory turbinates, which are indicative of elevated routine metabolic rates (a key attribute of endothermy), and evidence of lung structure and ventilation, which reflect the maximal aerobic capacity of the taxa involved.

Evidence for Elevated Routine Metabolic Rates: Respiratory Turbinates

Function of Respiratory Turbinates in Extant Amniotes

Nasal turbinates, or conchae, are convoluted bony or cartilaginous projections from the walls of the nasal cavity. These structures are found in most modern amniotes and range in com-

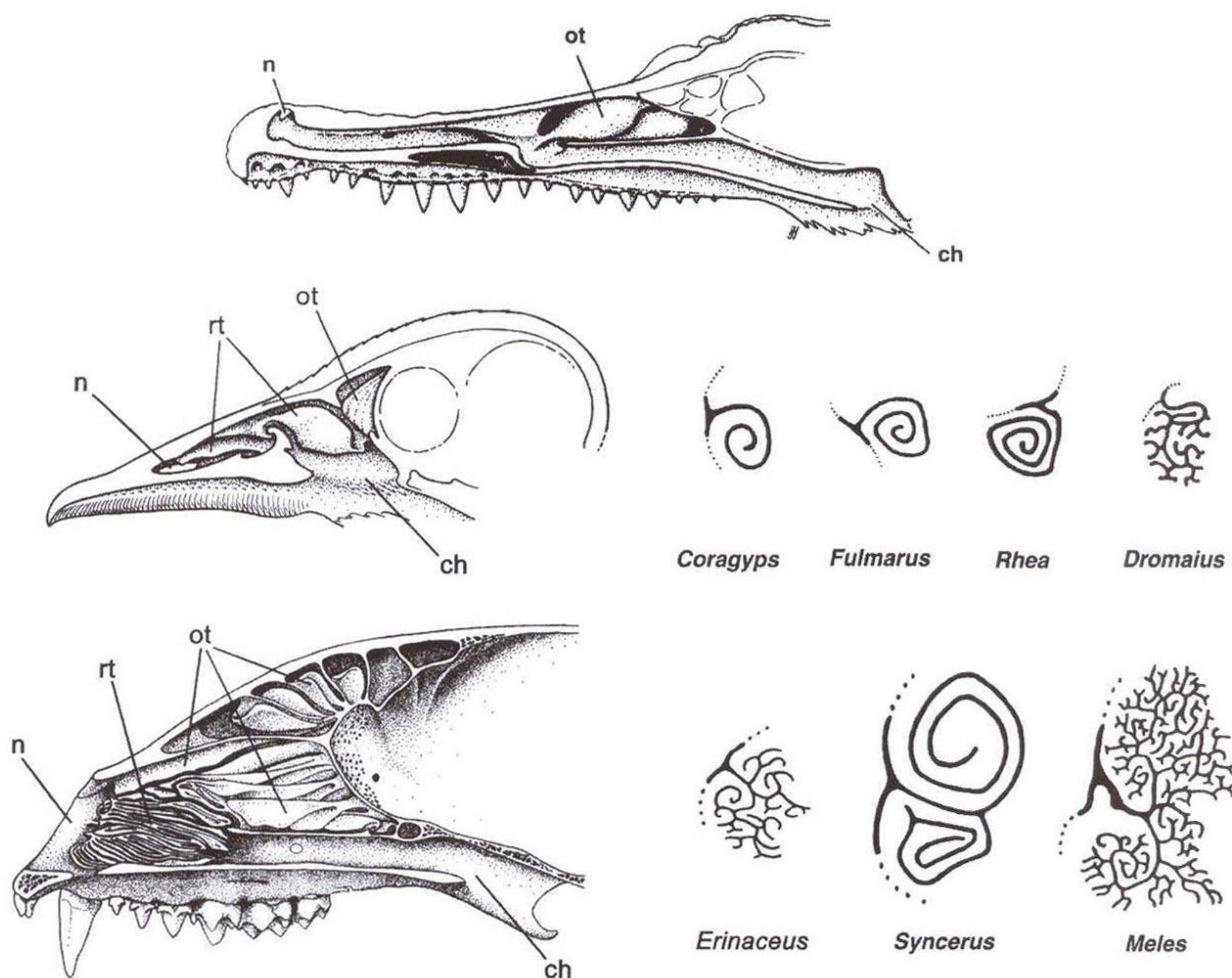


Figure 1. Nasal passages of extant amniotes. Reptiles, such as crocodilians (*top*), have up to three simple nasal conchae, all of which are exclusively covered with olfactory epithelium. In contrast, birds (*center left*) and mammals (*bottom left*) typically possess complex respiratory turbinates in addition. Also shown are cross sections of the respiratory turbinates of representative birds (*center right*) and mammals (*bottom right*). Abbreviations: *n* = external nostril; *rt* = respiratory turbinate; *ot* = olfactory turbinate; *ch* = internal nostril. Modified from Hillenius (1994).

plexity from comparatively simple curls in reptiles to elaborately scrolled or branched structures in birds and mammals (Fig. 1). The turbinates are covered with moist epithelium and principally serve to increase the surface area available to these membranes.

There are two distinct types of turbinates, olfactory and respiratory, which differ in the type of epithelium they bear and in their location within the nasal cavity (Hillenius 1994). Olfactory turbinates are nearly ubiquitous among amniotes. These are lined with sensory (olfactory) epithelium and are generally situated outside the main path of respiratory air. Olfactory turbinates function specifically to enhance the sense of smell and are unrelated to metabolic physiology. In contrast, respiratory turbinates are found only among birds and mammals; they are completely absent in all modern reptiles. In both mammals and birds, the respiratory turbinates project directly into

the main nasal air stream, are covered exclusively with non-sensory "respiratory" epithelium, and have a distinct functional association with endothermy (Hillenius 1992, 1994; Geist 2000).

The chronically elevated rates of lung ventilation of birds and mammals—a consequence of their elevated rates of metabolism even while resting, and thus a key attribute of endothermy—could result in potentially deleterious desiccation and heat loss rates, as large volumes of warm, humid air are expelled from the lungs. However, respiratory turbinates provide a compensatory mechanism by absorbing a substantial portion of the heat and moisture contained in respiratory air through a mechanism of intermittent countercurrent exchange (Fig. 2; cf. Jackson and Schmidt-Nielsen 1964; Hillenius 1992; Geist 2000). In the absence of such a recovery mechanism, respiratory heat and water loss rates associated with continu-

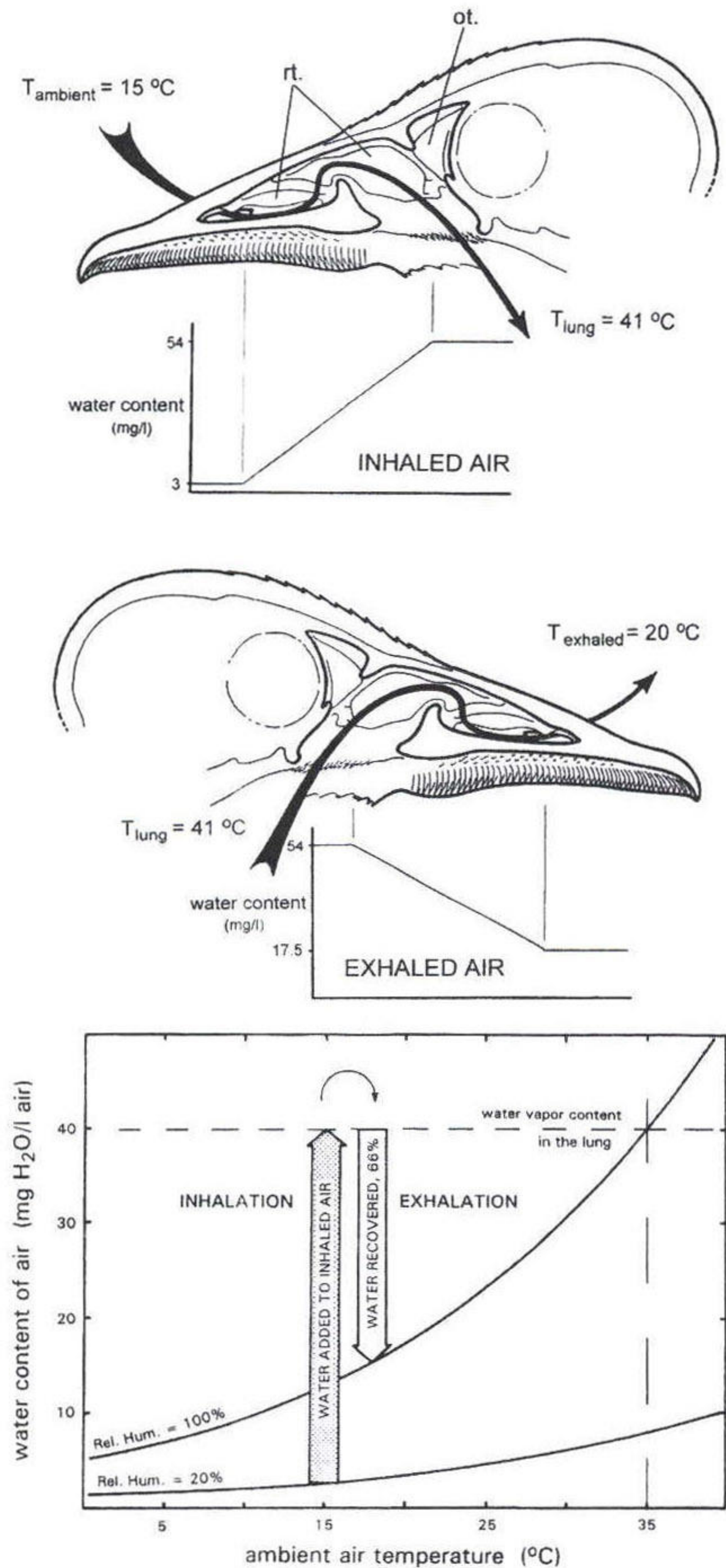


Figure 2. Mechanism of respiratory turbinate function in modern endotherms. During inhalation (*top*), ambient air passes over the respiratory turbinates and is warmed to body temperature. As a result, air is saturated with water vapor, and the turbinates are cooled by evaporative water loss. During exhalation (*center*), warm air from the lungs returns through the nasal passage and is cooled as it passes over the turbinate surfaces. Exhaled air temperature is thereby reduced, and water vapor condenses on the turbinate lamellae. This process results in a substantial reduction in the heat and moisture contained in exhaled air. The graph (*bottom*) depicts water vapor added to inhaled air (*shaded arrow*) and water condensate recovered from exhaled air (*open*

ously high rates of oxidative metabolism and lung ventilation would likely exceed tolerable levels, and endothermy itself might well be unsustainable (Fig. 3; Hillenius 1992; Ruben 1995; Geist 2000). Significantly, total surface area of the respiratory turbinates in both mammals and birds scales proportionately with mass-specific resting metabolic rates—both are proportional to body mass^{0.75} (Owerkowicz and Crompton 2001).

Respiratory turbinates are present in all extant nostril-breathing terrestrial mammals and birds; they are reduced or absent only in extremely rare cases, for example, in certain aquatic specialists such as whales, cormorants, and pelicans (cf. Hillenius 1994; Ruben et al. 1996). The widespread presence of respiratory turbinates among extant endotherms suggests that it is very difficult for such animals to circumvent the need for these structures through alternative sites or mechanisms for water recovery. It should also be pointed out that, energetically, respiratory turbinates are comparatively cheap to operate: the countercurrent exchange mechanism incurs no physiological energy expense (Collins et al. 1971). This contrasts sharply with potential alternative water recovery mechanisms, such as salt glands or enhanced kidney function, which require significant, and continuous, investments of cellular energy to function. On the other hand, maintenance of a countercurrent exchange mechanism in any portion of the respiratory tree other than the nasal cavity would be untenable: such exchange sites in the body cavity would necessarily preclude deep-body homeothermy, while the presence of such a system in the trachea would likely interfere with the stability of brain temperatures, because of the proximity to the brain-bound carotid arteries (e.g., Jones and Ruben 2001). The fact that deep nasopharyngeal temperature virtually equals core body temperature in extant mammals (e.g., Jackson and Schmidt-Nielsen 1964) and birds (Geist 2000) confirms that little or no heat exchange takes place in the trachea. Finally, the widespread distribution of respiratory turbinates among extant mammals and birds also indicates that these structures are likely a plesiomorphic attribute for these groups (although evolved independently in each clade; cf. Hillenius 1992, 1994; Geist 2000). The rare cases of reduction or absence of respiratory turbinates among these taxa (e.g., in cetaceans, pelecaniforms) all clearly represent secondary, highly specialized developments.

In contrast to the nearly ubiquitous presence of respiratory

arrow). Curves represent water vapor content of fully saturated air (relative humidity [RH] = 100%) and air at 20% saturation. In this example, inhaled air is modified from ambient air temperature and humidity (15 $^{\circ}\text{C}$, 20% RH) to lung air conditions (35 $^{\circ}\text{C}$, 100% RH). After cooling by the turbinates, exhaled air is still saturated but at only 18 $^{\circ}\text{C}$. Consequently, about 66% of the water vapor originally added to inhaled air is recovered. Abbreviations: *rt* = respiratory turbinate; *ot* = olfactory turbinate. Modified from Ruben et al. (1996); graph after Schmidt-Nielsen et al. (1970).

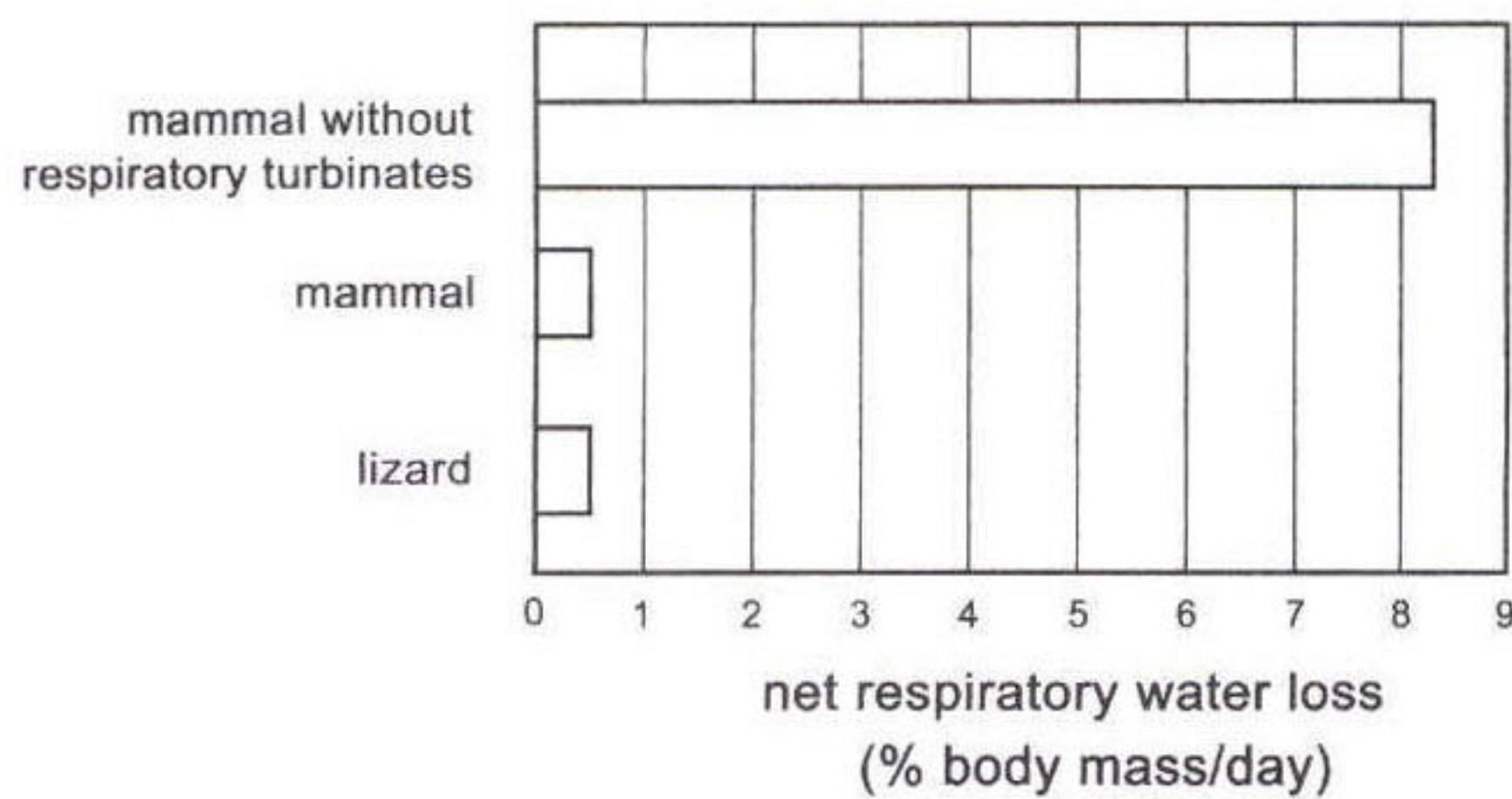


Figure 3. Daily net respiratory water loss rates (respiratory water loss – metabolic water production) for a free-living 1-kg reptile and 1-kg mammal and probable net respiratory water loss for a free-living mammal lacking the use of respiratory turbinates (i.e., with mammalian metabolic rates but with reptile-like nasal anatomy and net respiratory water loss rates per cubic centimeter of O_2 consumed). Without the water-conserving function of respiratory turbinates, daily water flux rates in mammals would be out of balance by about 30%. Calculations based on field metabolic and water flux rates for lizards and eutherian mammals (regressions provided by Nagy 1987 and Nagy and Peterson 1988), observed ventilation rates of lizards (regressions provided by Bennett 1973), and observed net rates of respiratory water loss in intact and experimentally altered mammals (Hillenius 1992). For thermoregulating lizards ($T_b = 37^\circ\text{C}$), net respiratory water loss (at $T_a = 15^\circ\text{C}$) approximates 1.8 mg H_2O per cubic centimeter of O_2 consumed (Hillenius 1992). Graph modified from Ruben et al. (1997).

turbinates in endotherms, these structures are entirely absent in all extant ectotherms (cf. Witmer 1995), nor are there other modifications of the nasal cavity designed specifically for the recovery of respiratory water vapor. Lung ventilation rates of these animals are sufficiently low that respiratory heat and water loss rates seldom create problems (Geist 2000; Randall et al. 2002). Note that nasal heat exchange and modest recovery of respiratory moisture do occur in thermoregulating reptiles (e.g., Murrish and Schmidt-Nielsen 1970). However, without complex respiratory turbinates, the “simple” nasal passages of ectotherms are effective only at low ventilation rates. For the chronically higher rates of metabolism and ventilation characteristic of mammalian and avian endothermy, specialized respiratory turbinate systems are necessary for complete heat and water exchange (Jackson and Schmidt-Nielsen 1964; Hillenius 1992, 1994; Geist 2000).

Finally, embryological and anatomical studies confirm that although the olfactory turbinates are a primitive attribute of amniotes, the respiratory turbinates are apomorphic structures in mammals and birds that arose independently in each lineage (Witmer 1995). The most parsimonious conclusion is that the respiratory turbinates evolved in concert with expanding chronic metabolic and lung ventilation rates and the origin of endothermy (Hillenius 1994). Consequently, the presence or absence of respiratory turbinates among fossil amniotes may be a good indicator of the minimal routine (i.e., resting) ven-

tilation rates and, by extension, metabolic rates of these taxa (Hillenius 1994; Ruben et al. 1996; Jones and Ruben 2001).

Respiratory Turbinates in Fossil Amniotes

Synapsids. Although turbinates are occasionally found preserved in fossils, their fragile nature usually precludes their preservation in fossils. Among fossil mammals and nonmammalian synapsids, the presence of nasal turbinates, as well as their function, is most readily revealed by the characteristic pattern of bony ridges, attachment scars left behind on the walls of the nasal cavity. Attachment ridges for olfactory turbinates are located posterodorsally, outside the main path of airflow, whereas those of the respiratory turbinates are located in the anterolateral rostrum, directly in the path of respired air. Ridges for olfactory turbinates are found throughout the synapsids, including ancestral forms such as pelycosaurs. However, ridges most likely associated with respiratory turbinates occur in only two lineages of advanced theriodonts, the therocephalians and cynodonts (Hillenius 1994), which suggests that the routine ventilation rates of these animals had risen sufficiently above ancestral levels to warrant the presence of a compensatory mechanism to limit respiratory water loss rates. The earliest appearance of these is in the Late Permian therocephalians, such as the bear-sized pristerognathid *Glanosuchus* (Fig. 4). However, pristerognathids retain the primary palatal condition of ancestral amniotes, where the anterior location of the internal nostrils limits the size of the nasal respiratory chamber. Consequently, their capacity to recover respiratory water vapor was probably limited as well, suggesting that the chronic ventilation rates of these early therocephalians likely had increased only relatively modestly beyond ancestral rates (Hillenius 1994). Significantly, in later therocephalians the nasal respiratory chamber became proportionately larger, and the internal nostrils migrated posteriorly (Fig. 5). This posterior migration preceded the development of the secondary palate in therocephalians (cf. Hillenius 1994), which most likely evolved for mechanical reasons relating to bite strength (Thomason and Russell 1986). As the respiratory portion of the nasal cavity became larger, more space became available for the conditioning of respiratory air and recovery of water vapor. This suggests that therocephalian ventilation rates were gradually expanding as well, which is consistent with the increasingly mammal-like composition of these groups (Kemp 1982, 1986). Attachment scars of respiratory turbinates also occur in several Triassic cynodonts, including the gomphodont *Massetognathus* (Fig. 4), indicating that cynodonts also possessed elevated resting lung ventilation rates and metabolic rates. The fact that the secondary palate of cynodonts, as well as other mammal-like features such as postural and masticatory modifications, evolved independently from that of therocephalians (Kemp 1982; Thomason and Russell 1986) suggests that the expansion of the metabolic rates of therocephalians and cynodonts oc-

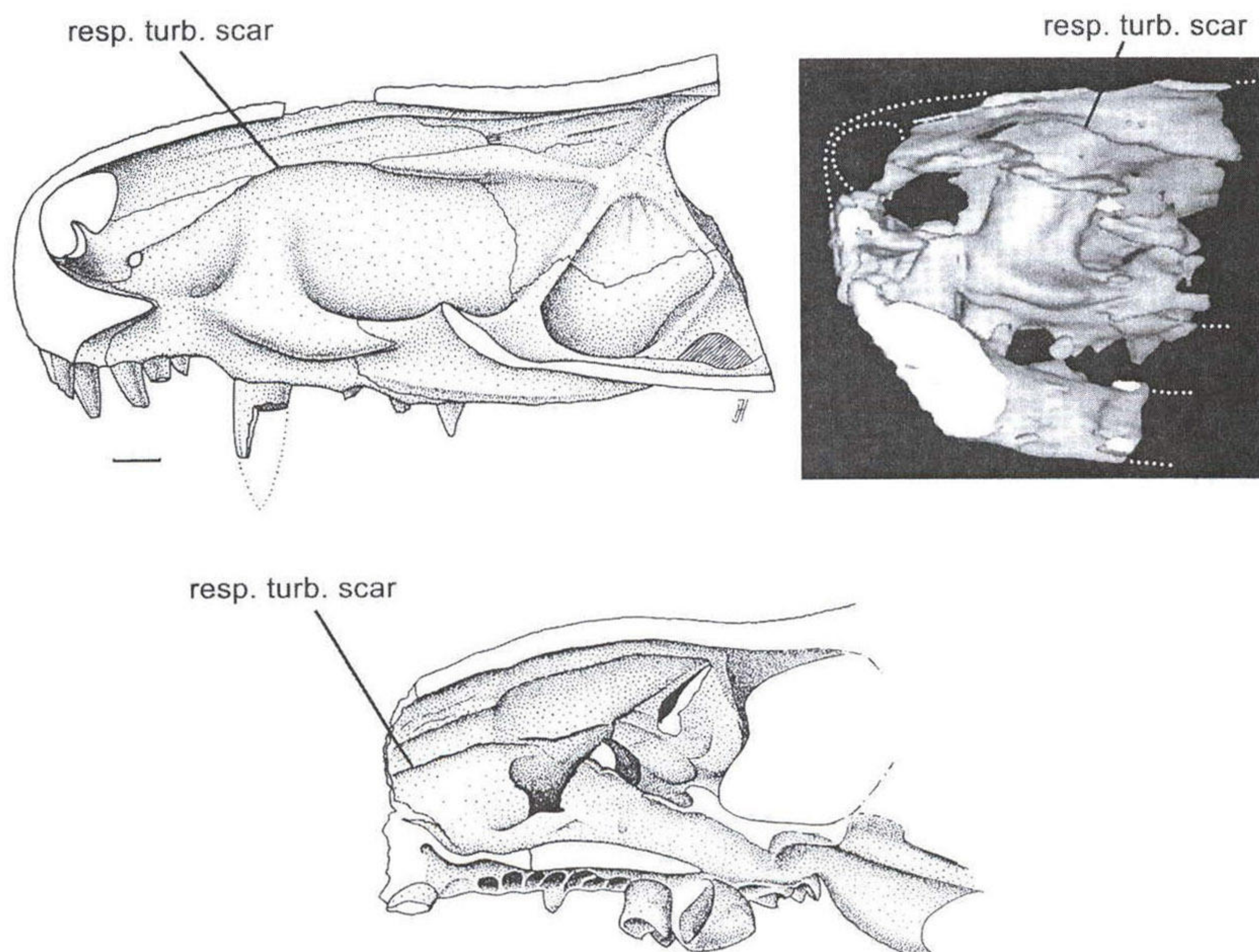


Figure 4. Respiratory turbinates in nonmammalian therapsids. Attachment scars for respiratory turbinates occur in Late Permian therocephalians, such as the pristerognathid *Glanosuchus* (top left) and an unnamed pristerognathid, SAM K226 (top right; three-dimensional reconstruction from CT scan). Respiratory turbinate scars are also found in Triassic cynodonts, such as *Massetognathus* (bottom). After Hillenius (1994).

curred largely independently in these two lineages (Hillenius 1994). Cynodonts gave rise to the earliest mammals toward the end of the Triassic Period (Hopson 1994). The nasal turbinal ridges of the earliest mammals are essentially identical to those of extant mammals (Hillenius 1994), suggesting that the evolution of “mammalian” routine respiration rates and endothermy was largely complete by this time.

Archosaurs. The study of the evolutionary history of the turbinates in birds and their relatives is somewhat more complicated. Although these structures sometimes ossify or calcify in extant birds, more typically they remain cartilaginous and lack bony points of contact in the nasal passage, making direct detection of their presence or absence in fossil material substantially more difficult. However, in extant endotherms the presence of respiratory turbinates is strongly correlated with a marked expansion of the cross-sectional area of the respiratory portion of the nasal cavity (Fig. 6; Ruben et al. 1996). This increased nasal diameter probably serves to compensate for the

considerable resistance to airflow posed by the complex turbinate system in endotherms, thereby keeping the energetic cost of ventilation to a minimum (e.g., see Staub 1991). Significantly, the relative diameter of the nasal passage in a series of non-mammalian synapsids approaches and, in the case of the cynodont *Thrinaxodon*, even attains avian/mammalian proportions (Fig. 6).

In contrast, computed tomography (CT) studies of several three-dimensionally preserved dinosaurs, including the theropods *Nanotyrannus* and *Ornithomimus* and the lambeosaurine hadrosaur *Hypacrosaurus*, indicate that the respiratory portion of the nasal cavity of all these taxa was restricted to a narrow, tubular passage: in all three cases the cross-sectional dimensions are identical to or smaller than those of extant ectotherms (Fig. 6; Ruben et al. 1996). No evidence of respiratory turbinates was found in these specimens, although remnants of olfactory turbinates were present in the posterior region of the nasal cavity of *Nanotyrannus* (Ruben et al. 1996; Jones and Ruben 2001). Moreover, the restricted dimensions of the respiratory

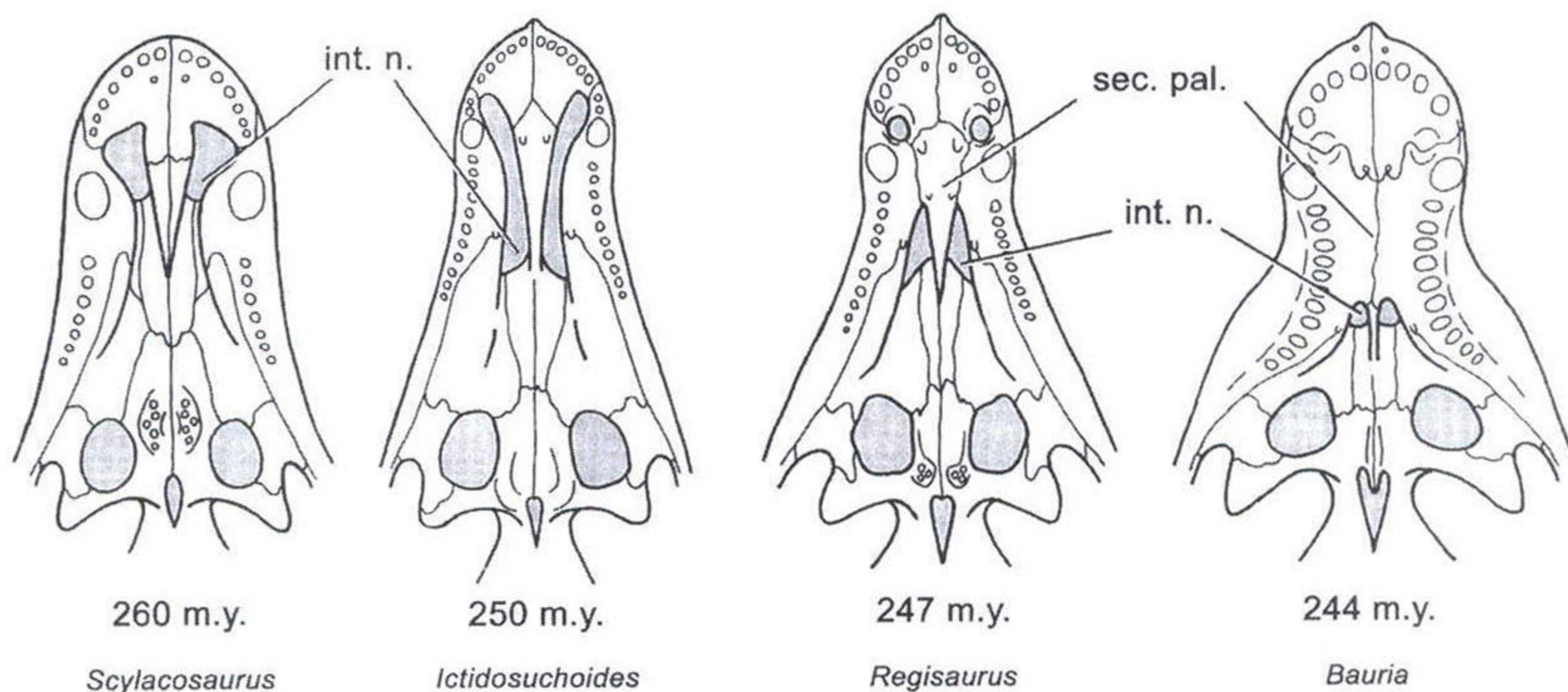


Figure 5. Evolution of the secondary palate in therocephalians. Schematic diagrams of the palatal configurations of representative therocephalians, scaled to a common size. The secondary palate itself probably evolved for mechanical reasons associated with jaw function (Thomason and Russell 1986) but was preceded by an expansion of the respiratory portion of the nasal cavity, as indicated by the posterior migration of the internal nostrils. This allowed more room for nasal conditioning of respiratory air and recovery of water vapor and suggests that routine ventilation rates and metabolic rates of therocephalians were progressively increasing. After Hillenius (1994).

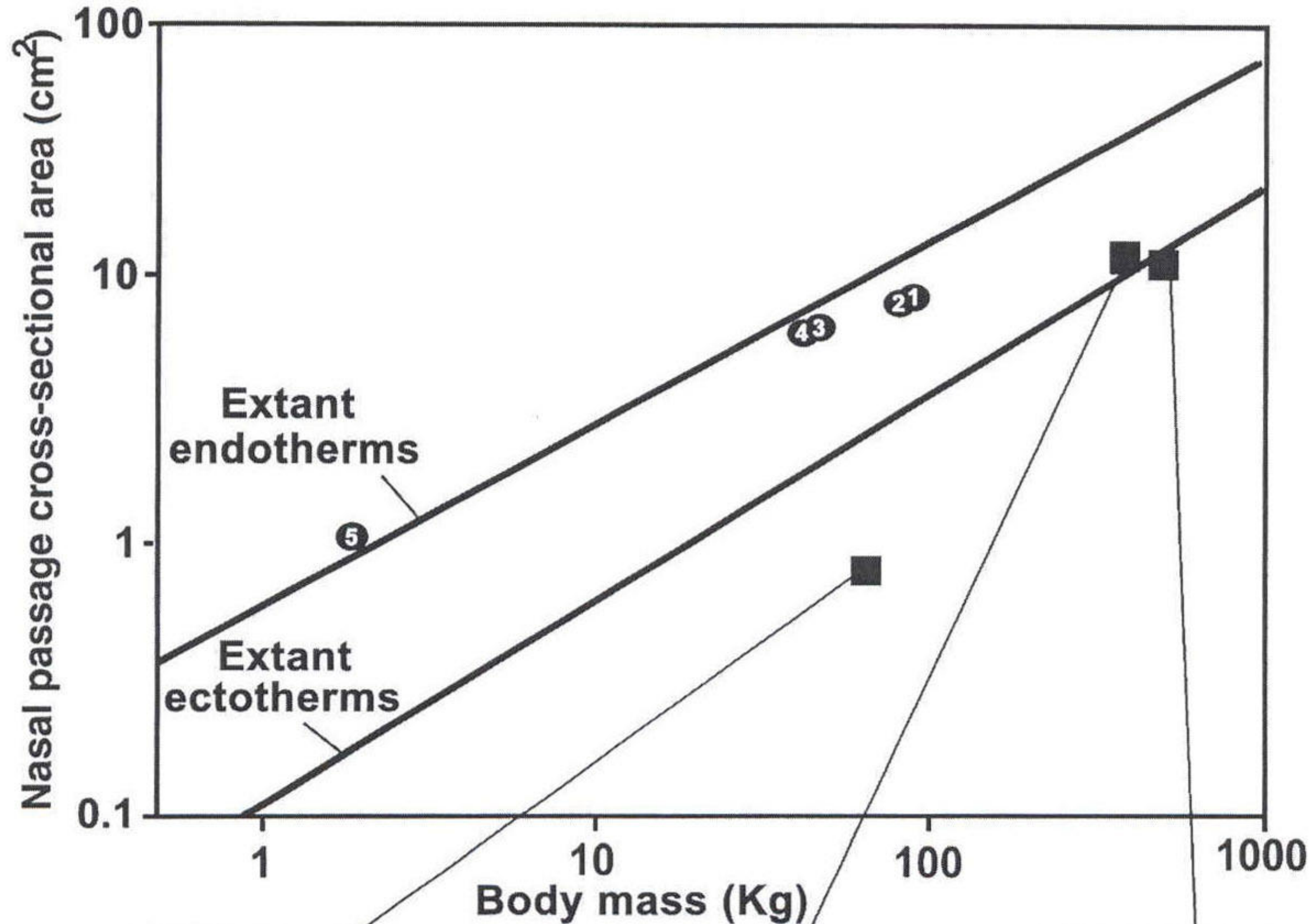
passages of all three taxa suggest that not only were such turbinates not preserved in the fossils, but they were also most likely absent in life.

In *Hypacrosaurus*, as in other lambeosaurines, the nasal passages continue dorsally into the supracranial crest, leading into a system of curved passageways and blind nasal diverticula. These are sometimes mentioned as possible sites for a turbinate-like respiratory heat exchange and moisture recovery system. However, the presence of notable sexual dimorphism in the crest morphology of lambeosaurines (Dodson 1975) makes it unlikely that these structures were linked to any particular mode of respiratory physiology, as it is unlikely that the metabolic status of males and females differed significantly. Others consider these cavities within the supracranial crest to relate more likely to olfactory functions or sound production (e.g., Weishampel 1997). The great diversity of form of the supracranial crest among different lambeosaurine species, as well as the total absence of a supracranial crest in the closely related subfamily of hadrosaurine hadrosaurids, further weakens the argument that these structures signify greatly divergent metabolic rates. The fact that endothermy is the aggregate result of so many morphological and physiological adjustments also poses a strong intrinsic constraint on these attributes (cf. Weibel 2000). For example, a highly modified lung cannot provide much metabolic benefit (i.e., is not selectively advantageous) unless the circulatory system and the cellular physiology are adjusted to process the additional oxygen. Such physiological and morphological constraints would tend to restrict the ability

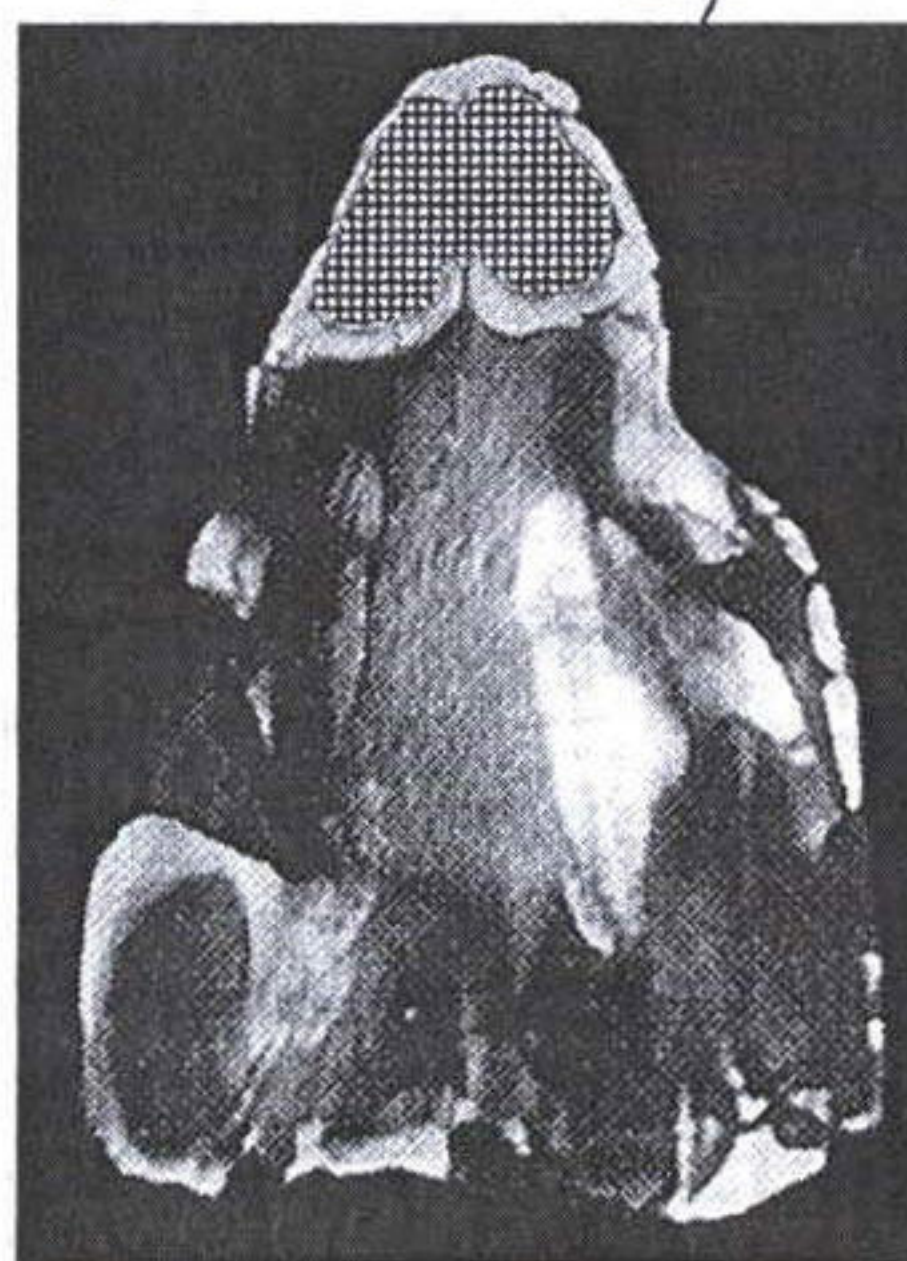
of closely related (i.e., comparatively recently diverged) taxa to have very different metabolic strategies.

Nasal passage cross-sectional area can be accurately quantified only from three-dimensionally preserved specimens, and this parameter therefore offers little direct insight into the metabolic status of many other archosaurs, especially early birds, whose fossils are often severely flattened or distorted. However, pneumatization of the skull, and especially the morphology of the paranasal sinuses, makes it possible to infer nasal passage dimensions in less well preserved specimens. In the theropods *Nanotyrannus* and *Ornithomimus*, the size of the respiratory nasal passage is severely constrained by the presence of large maxillary sinuses (cf. Fig. 6; Ruben et al. 1996). A similar system of sinuses is known from most other advanced theropods (tetanurans), in which the maxillary and/or promaxillary fenestrae—apertures in the rostral portion of the antorbital fossa—open into an expansive maxillary antrum and promaxillary sinus, respectively (Fig. 7; Witmer 1997). These sinuses are blind chambers that, although they communicate with the nasal cavity by means of small ostia, are not part of the respiratory passage: rather, their ceilings form much of the floor of the nasal passage. The presence of these sinuses indicates that, like that of *Nanotyrannus* and *Ornithomimus*, the volume of the respiratory passages of other tetanuran theropods was limited and that they likewise probably lacked respiratory turbinates.

The anatomy of the nasal cavity and antorbital sinuses of early birds is not markedly different from that of tetanuran theropods. Both maxillary and promaxillary fenestrae are



Ornithomimus

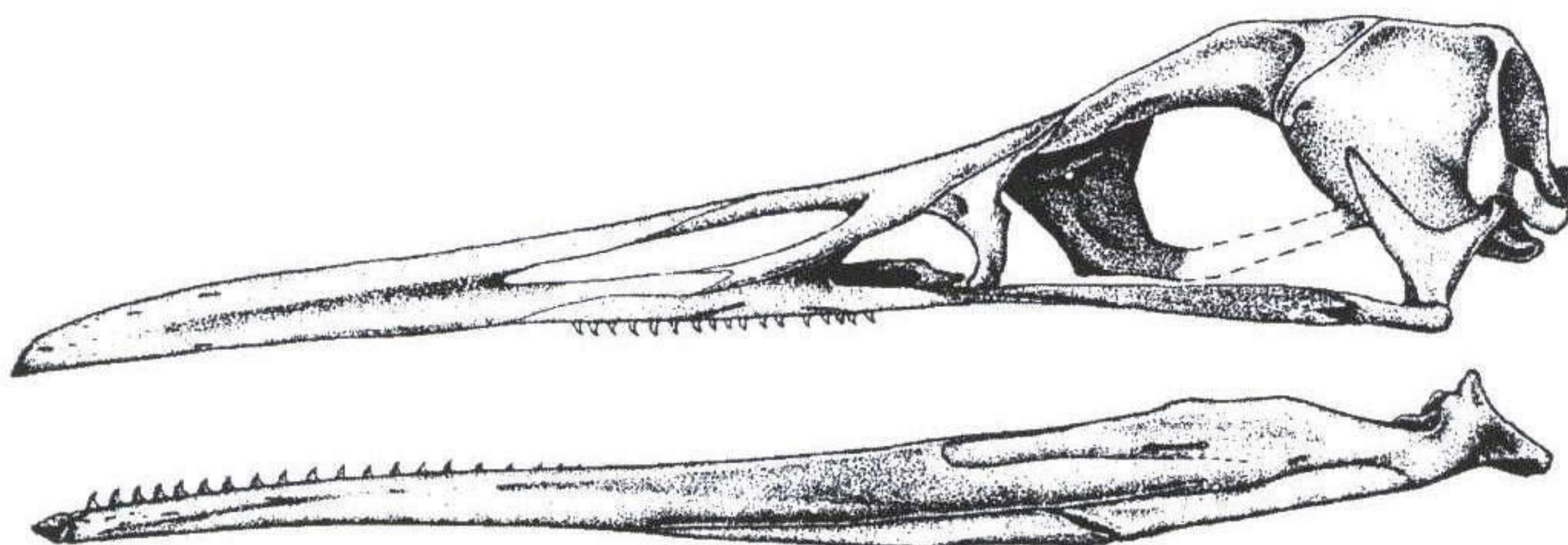
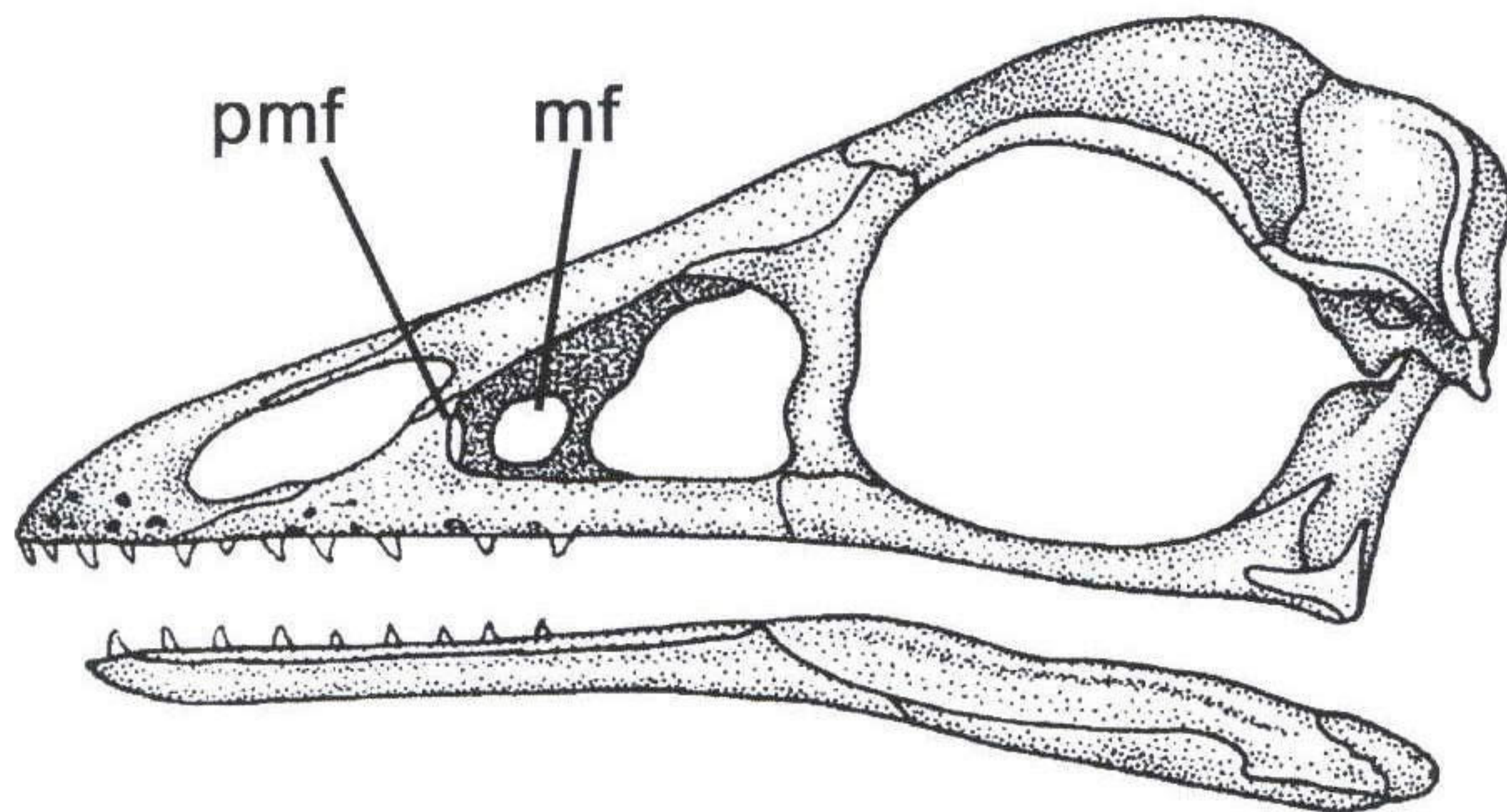
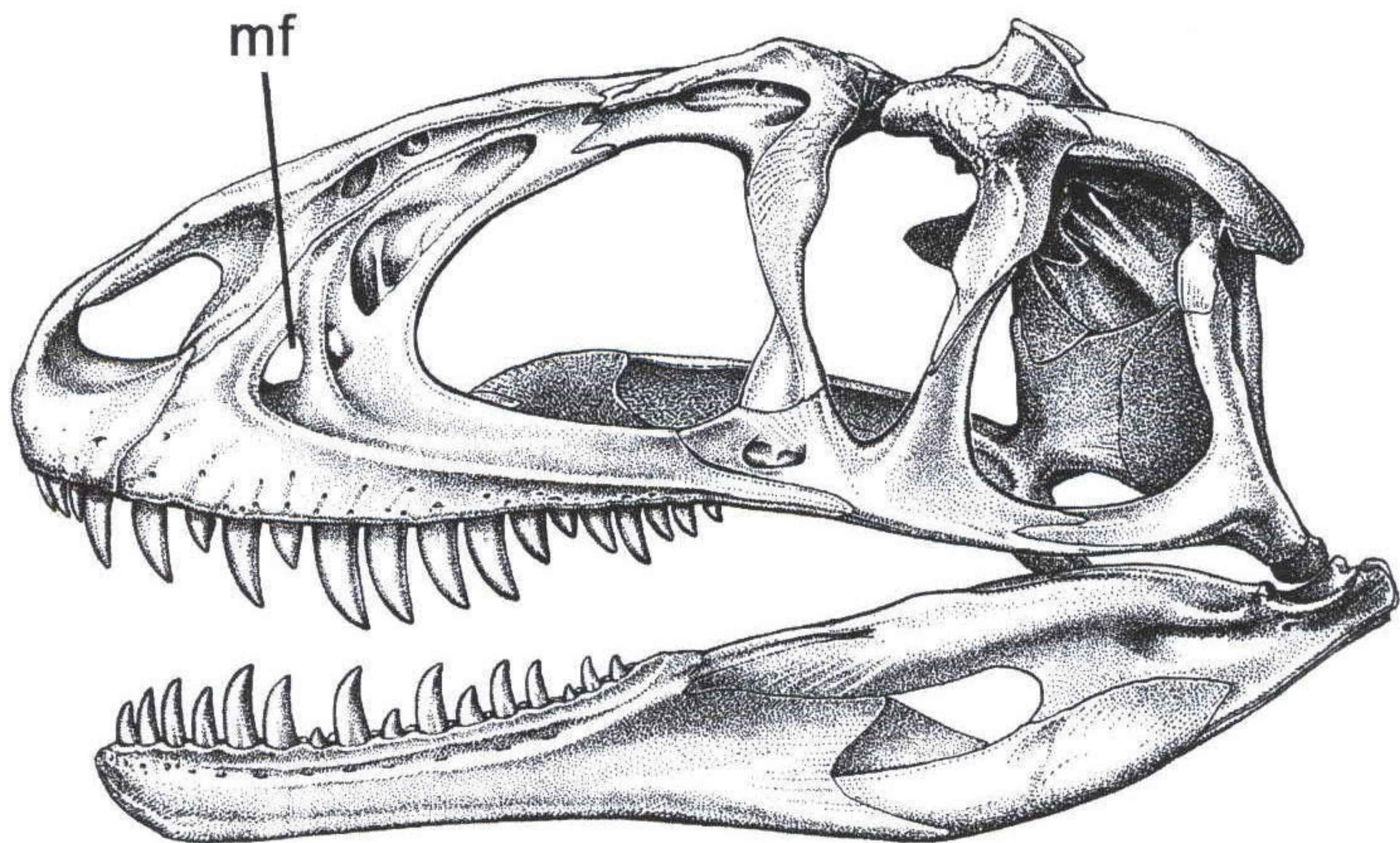


Hypacrosaurus



Nanotyrannus

Figure 6. Relationship of nasal passage cross-sectional area to body mass (M) in extant ectotherms (lizards and crocodilians; cross-sectional area = $0.11M^{0.76}$) and endotherms (mammals and birds; cross-sectional area = $0.57M^{0.68}$). Also plotted are three genera of Late Cretaceous dinosaurs—the hadrosaurid *Hypacrosaurus* and the theropods *Tyrannosaurus* (*Nanotyrannus*) and *Ornithomimus*—and five genera of Permo-Triassic therapsids: (1) a gorgonopsian, (2, 3) two primitive therocephalians, and the cynodonts (4) *Diademodon* and (5) *Thrinaxodon*. Values for dinosaurs and therapsids were not used in regression calculations. Modified from Ruben et al. (1996, 1997).



the antorbital cavity and nasal passage of the mid-Cretaceous ornithurine *Hesperornis* are remarkably modern and nearly indistinguishable from those of extant birds (Fig. 7; Witmer 1997). The arrangement of older ornithurines, such as the Early Cretaceous *Chaoyangia*, appears to be similar to that of *Hesperornis* (L. D. Martin, personal communication), but no reconstructions of their skulls have been published to date. The drastic reorganization of the nasal cavity of ornithurine birds appears to be at least partly associated with the expansion of the nasal passage to accommodate the respiratory turbinates (Witmer 1997) and thus may reflect a change in the metabolic status of these animals.

The appearance of an expanded, essentially “modern” avian nasal cavity in ornithurine birds represents the earliest relatively clear signal that chronic respiratory water loss had become a significant problem for the avian lineage. It implies that resting ventilation rates of ornithurines had reached a level significantly elevated beyond ancestral rates and were perhaps comparable to those of modern birds. It is possible that the resting ventilation rates of some or all nonavian dinosaurs and of the nonornithurine birds were modestly higher than typical reptilian rates but not yet so high as to warrant compensatory mechanisms to control respiratory water loss. However, at present there is no positive evidence to confirm that the resting ventilation rates of any theropod dinosaur or nonornithurine bird had expanded significantly beyond those of extant reptiles. It should be pointed out that these observations reveal little about the capacity for maximal ventilation rates and oxygen consumption during periods of activity.

Evidence for Elevated Active Metabolic Rates: Lung Structure and Ventilation

Lungs of Extant Amniotes

In addition to the ability to maintain thermal homeostasis through elevated resting metabolic rates, modern mammals and birds are also characterized by an expanded capacity for aerobically maintained activity. In both groups, this capacity is supported by highly modified lungs capable of sustaining high rates of respiratory gas exchange. Both lung morphology and ventilation mechanisms of endotherms are distinctly different from those of ectotherms, although mammals and birds follow two fundamentally different patterns.

Mammals have bronchio-alveolar lungs, which comprise a

hierarchical system of branching air passages, the respiratory tree, and millions of thin-walled, highly vascularized sacs (alveoli), where gas exchange takes place. The alveoli are distributed homogeneously throughout the lung and cumulatively provide a large respiratory surface area (Duncker 1978; Perry 1989). Ventilatory airflow is bidirectional, and each alveolus contributes actively in ventilation by functioning in a bellows-like manner. During inhalation, individual alveoli fill passively under negative intrapulmonary (alveolar) pressure generated by expansion of the rib cage and/or contraction of the diaphragm. Exhalation occurs largely as a result of increased intrapulmonary pressure caused by elastic recoil of the alveoli. These attributes, combined with a thin blood-gas barrier, provide alveolar lungs with a high anatomical diffusion factor (ADF, the mass-specific ratio of total vascularized pulmonary respiratory surface area to mean pulmonary blood-gas barrier thickness; Perry 1983, 1989; Duncker 1989) and enable such lungs to sustain high maximal rates of oxygen consumption during extended periods of intense activity.

In contrast, sauropsid amniotes have septate lungs, which differ both morphologically and ontogenetically from the bronchio-alveolar lungs of mammals. Whereas mammalian lungs develop by repeated subdivision of the embryonic lung buds (Wells 1954), in its generalized form the lung of modern nonavian sauropsids (“reptiles”) is broadly comparable to a single, oversized mammalian alveolus at the end of a single bronchus. Septa—vascularized ingrowths from the wall of the lung—finely partition the inner surface of the lung into a system of honeycomb-like cells that are the principal site of gas exchange (Perry 1983). These vascularized tissues, together with the air spaces they contain, constitute the “lung parenchyma.” However, sauropsids exhibit great variation in the pattern and distribution of the respiratory tissues within the lung. For example, septal height can vary, resulting in different parenchymal types (e.g., trabecular, edicular, and faveolar), and parenchymal distribution may vary from homogeneous to heterogeneous. Furthermore, the lungs of extant reptiles can have one or multiple chambers, and they vary in the degree of attachment to the wall of the thorax (Duncker 1978; Perry 1983). As in the mammalian lung, ventilatory airflow in reptiles is bidirectional. However, unlike alveoli, the respiratory units of the reptilian septate lung contribute little to air convection during ventilation. To prevent collapse, the septa are relatively stiff (Perry 1989, 1992), and especially in the deeper ediculae and faveoli,

Figure 7. Paranasal sinuses of a theropod dinosaur (*Sinraptor*; top), a basal bird (*Archaeopteryx*; center), and a mid-Cretaceous ornithurine bird (*Hesperornis*; bottom). Large paranasal sinuses are a prominent feature of the rostral skull of both theropods and basal birds. In particular, the maxillary (*mf*) and promaxillary (*pmf*) fenestrae indicate the presence of sinuses that severely constrain the size of the respiratory nasal passage, and they signal the likely absence of nasal respiratory turbinates. In contrast, the much smaller paranasal sinuses of ornithurine birds have been pushed caudally, and the maxillary and promaxillary fenestrae have been obliterated. The arrangement of *Hesperornis* is nearly indistinguishable from that of modern birds, and there can be little doubt of the presence of respiratory turbinates in this taxon. Modified from Currie and Zhao (1993; top), Martin and Zhou (1997; center), and Feduccia (1996; bottom).

respiratory gases move in and out primarily through diffusion (Duncker 1978, 1989). The result is a low overall ADF in reptiles (Perry 1983). To compensate, many reptiles maintain a large, usually ventral part of the lung as a less vascularized but more compliant region that assists in the ventilation of dorsal, less compliant but more vascular portions of the lung (Duncker 1978; Perry 1983). Although maximal oxygen consumption ($\dot{V}O_2$ max) in some varanid lizards is significantly higher than that in other reptiles, no extant reptile is capable of achieving maximal aerobic respiratory exchange rates greater than about 15%–20% of those of typical endotherms (Ruben et al. 1998; Hicks and Farmer 1999). Even in a best-case scenario, based on hypothetical improvements of the circulatory system and optimized pulmonary diffusion capacity, the reptilian septate lung might be capable of attaining about 50%–60% of these rates and might thus barely overlap with some of the less-active mammals (Ruben et al. 1998; Hicks and Farmer 1999).

Birds, like all sauropsids, also possess septate lungs, but they have circumvented the inherent constraints on respiratory gas exchange rates of the reptilian septate lung. The ancestral edicular/faveolar parenchyma has been modified into a system of narrow, tubular parabronchi, which give off numerous air capillaries (Perry 1983, 1992). Ventilatory airflow is unidirectional (in the neopulmo portion of the lung) or bidirectional (in the paleopulmo). Unlike reptiles, birds have a particularly high ADF (Perry 1983; Duncker 1989; Powell 2000). In addition, birds have modified the nonvascularized portions of the lung into a series of extensive, highly compliant air sacs that extend into the visceral cavity and aid in a specialized cross-current ventilation of the dorsal, vascularized parabronchi during both inhalation and exhalation (McLelland 1989; Perry 1992). As a result, avian lung ventilation and gas exchange rates are especially high (cf. Powell 2000).

The parabronchial lung of modern birds is securely attached to the vertebral column. In some birds—particularly those with notaria—distinct, inverted T-shaped hypopophyses serve as additional sites of attachment. Diverticula from the air sacs invade and pneumatize portions of the skeleton. However, pneumatization of the avian skeleton, with the exception of the long bones of the hindlimbs of a small subset of birds, is limited to the axial skeleton and forelimbs. It is not linked with respiratory function or specific lung morphology (Duncker 1989; McLelland 1989).

Extant amniotes utilize a variety of skeletomuscular mechanisms to ventilate their lungs. Lizards and snakes lack a complete transverse subdivision of the body cavity (with partial separation present in only some cases; cf. Duncker 1989) and rely primarily on lateral expansion and contraction of the rib cage; presumably, this resembles the primitive mode of pulmonary ventilation for tetrapods (cf. Carrier 1987). Some lizards, notably varanids, augment costal ventilation with contractions of the throat musculature during bouts of vigorous activity (e.g., Owerkowitz et al. 1999).

Costal action also contributes to lung ventilation in mammals and crocodilians. However, both crocodilians and mammals rely extensively on active, diaphragm-assisted lung ventilation, in which a transversely oriented septum, or diaphragm, completely divides the visceral cavity into pleuro-pericardial and abdominal compartments. In mammals, the diaphragm is itself extensively muscularized, and its contraction results in expansion of the pleural cavity and filling of the lungs (e.g., Ruben et al. 1987; Bramble and Jenkins 1993). In contrast, the crocodilian diaphragm is nonmuscular and consists of a sheet of connective tissue that closely adheres to the surface of the liver. Inspiratory movement is provided by bundles of longitudinal muscles that extend from the posterior and ventrolateral aspects of the liver to the pubis, the posterior gastralia, and the preacetabular process of the ischium. Contraction of these diaphragmatic muscles results in a piston-like, posterior displacement of the liver-diaphragm complex, which inflates the lungs (cf. Farmer and Carrier 2000a).

Birds, like lizards, lack a mammal- or crocodilian-like diaphragm and rely principally on costal lung ventilation. However, the rib cage and sternum of birds are highly modified to facilitate ventilation of the abdominal air sacs. Avian ribs possess a unique system of synovial intercostal and sternocostal joints that allow sagittal rotation of the sternum and shoulder girdle. Significantly, the distal end of each sternal rib is expanded transversely and forms a robust hinge joint with the thickened anterolateral border of the sternum (Fig. 8). Costal action results in a dorsoventral rocking motion of the posterior end of the sternum, which expands and contracts the air sacs (e.g., Schmidt-Nielsen 1971). These characteristics are present even in flightless birds (Schmidt-Nielsen 1971).

Lung Structure and Ventilation in Fossil Amniotes

Among extant tetrapods, the bronchio-alveolar lung type is unique to mammals, and the repeated subdivisions of the embryonic respiratory diverticulum that are its ontogenetic foundation (cf. Wells 1954) appear to be an apomorphic attribute of the synapsid lineage. Unfortunately, in the absence of surviving ancestral or intermediate lung morphologies or of preserved lung fossils, few positive data are available to illuminate the evolutionary history of the bronchio-alveolar lungs. The costal mechanism of lung ventilation in modern mammals appears to be largely unchanged from the ancestral amniote condition, and there are no clear attributes of rib morphology per se of fossil synapsids that might signal the acquisition of novel lung features. The appearance of a distinct lumbar region, with markedly abbreviated ribs or pleurapophyses, in advanced thercephalian (e.g., Kemp 1986) and many cynodont therapsids (e.g., Brink 1956; Kemp 1980) is sometimes mentioned as being correlated with the presence of a transverse diaphragm. Unfortunately, several problems detract from this interpretation. There are no clear osteological markers, such as muscle or

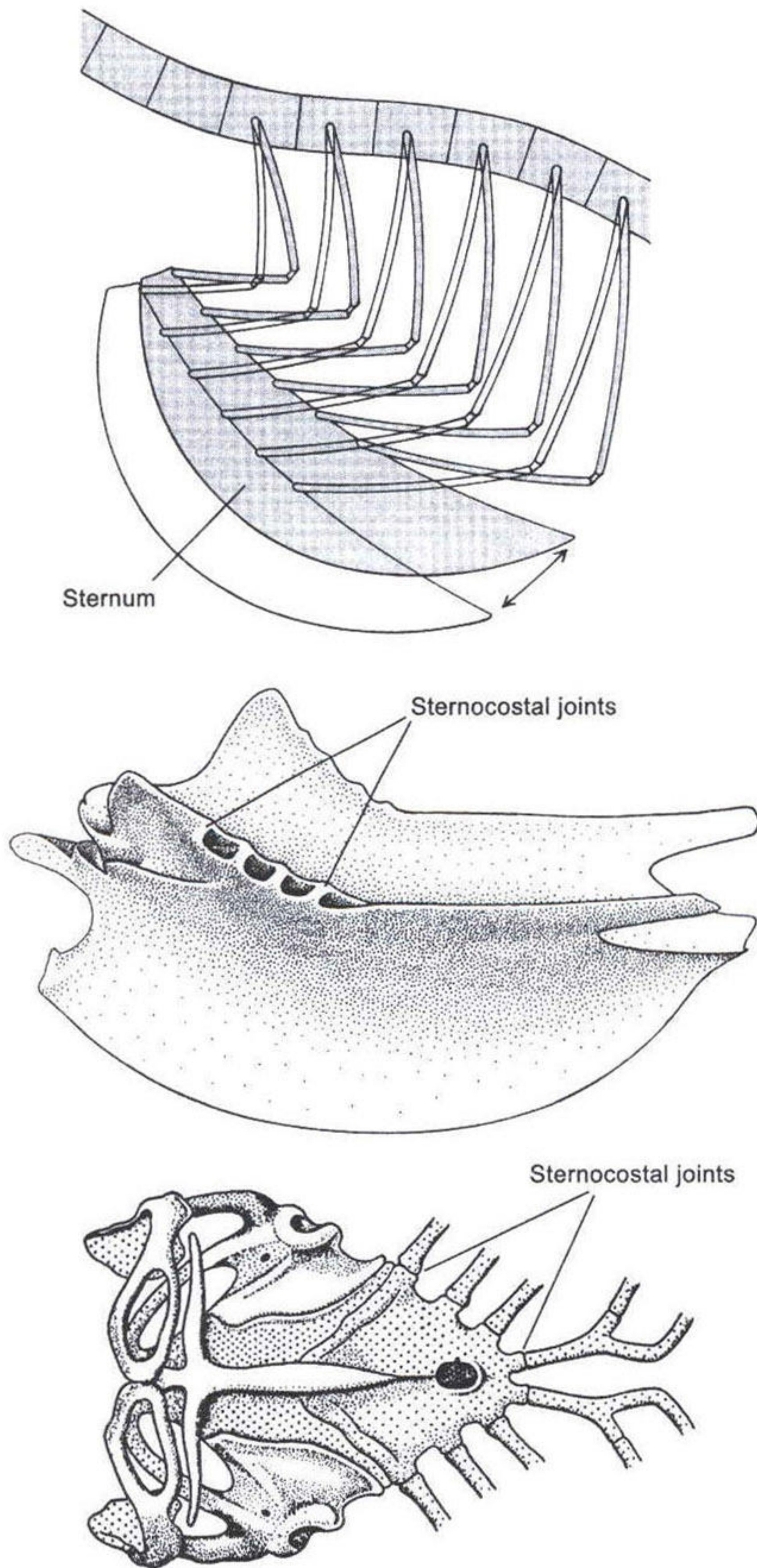
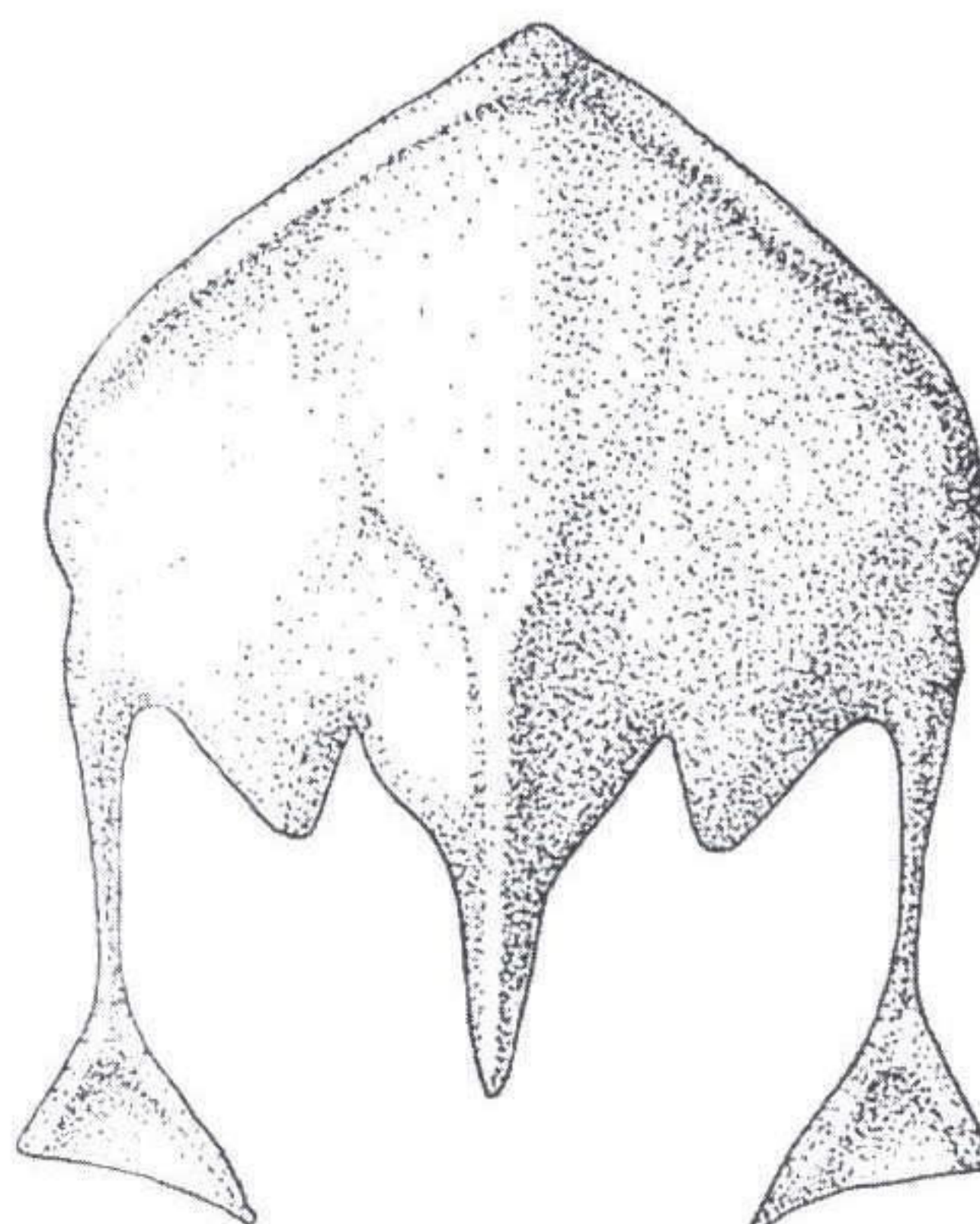
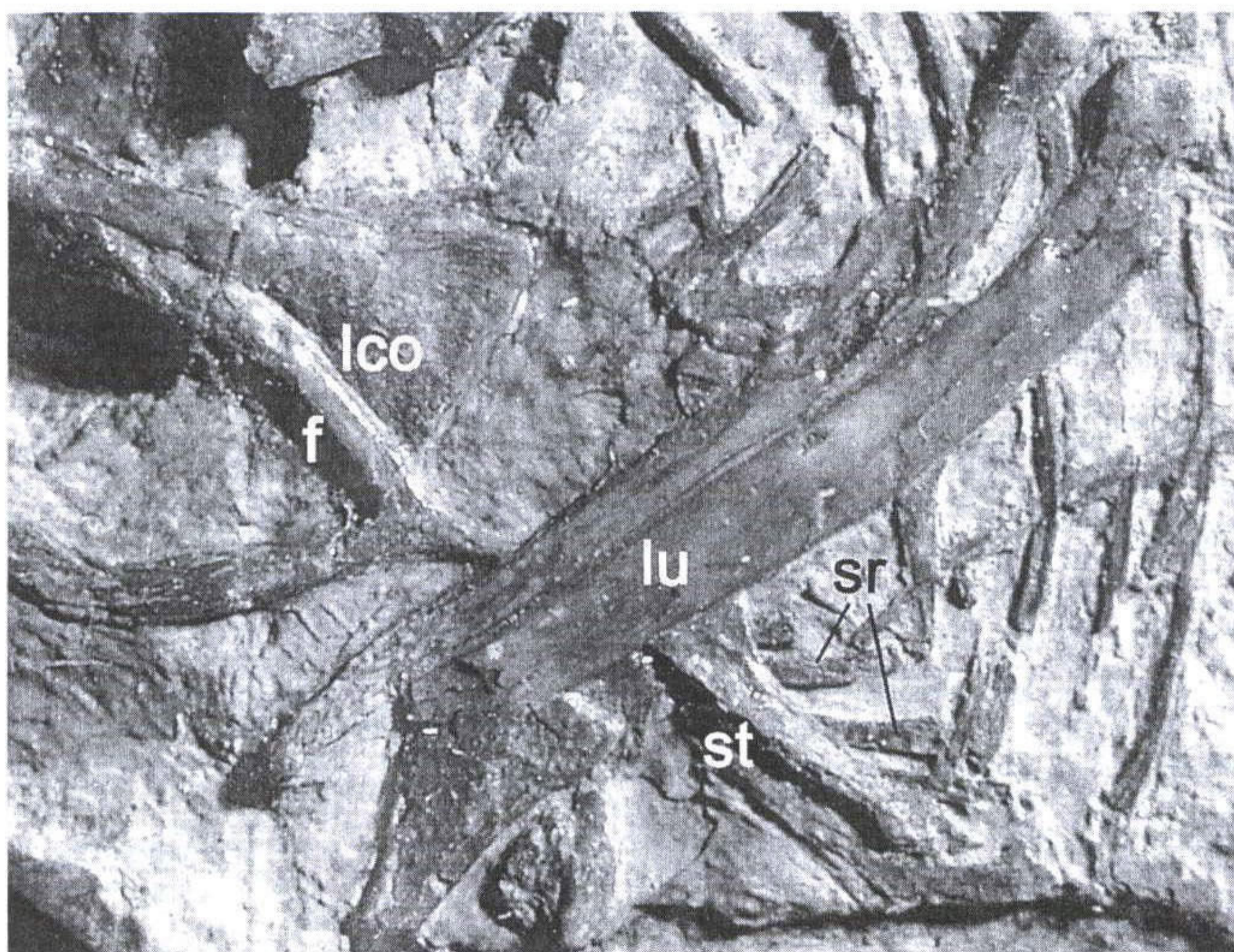
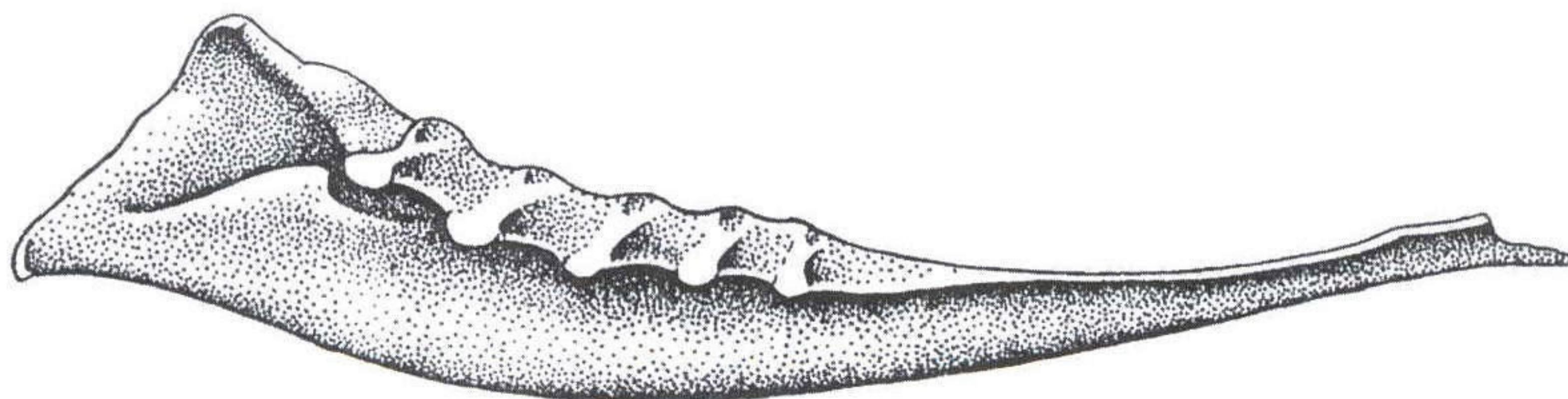


Figure 8. Lung ventilation in modern birds. Specialized intracostal and sternocostal joints facilitate dorsoventral rotation of the sternum, which expands and contracts the rib cage and ventilates the lungs and air sacs (*top*). This system is especially characterized by a series of transversely expanded sternocostal joints along the robust anterolateral margin of the sternum, illustrated here on the sternum of a heron, *Ardea* (*center*). In contrast, simple articulations between sternum and sternal ribs occur widely in amniotes (such as the lizard, *Lacerta*, shown here; *bottom*) and are not indicative of an avian-style lung ventilation. Modified from Schmidt-Nielsen (1971; *top*) and Romer (1956; *bottom*).

ligamental scars on the ribs or vertebrae themselves, that are unequivocally associated with the presence of a diaphragm, even in extant mammals. Rather, the argument rests on the contrast in shaft length between the thoracic and lumbar ribs, which indirectly suggests that the pleural and abdominal portions of the visceral cavity were distinct and perhaps fully partitioned entities. However, it is unclear whether there is a clear functional correlation between lumbar rib reduction and the presence of a diaphragm. Perhaps the reduction or absence of lumbar ribs permits visceral displacement resulting from diaphragmatic contraction (e.g., Brink 1956). Alternately, it also appears likely that lumbar rib morphology is correlated with postural and locomotory specializations of therapsids, such as the advent of dorsoventral flexion (e.g., Jenkins 1971). In that case, the presence of a diaphragm may still have been a prerequisite for lumbar rib reduction, as it mechanically isolates the pleural cavity from the abdominal cavity. Without a diaphragm, withdrawal of the ribs from the flanks might have negatively affected ventilation by allowing deformation of the flanks during inhalation and thereby reducing potential tidal volume. However, reduced or absent ribs are also known among reptiles, not only in crocodilians (which have a diaphragm and, in fact, separate pleural and abdominal pressures; cf. Farmer and Carrier 2000a), but also in some lizards (Hofstetter and Gasc 1969), which lack a diaphragm. Nevertheless, as the mammalian diaphragm especially affects metabolic rates during activity (Ruben et al. 1987) by permitting sophisticated integration of inertial movements of the abdominal viscera with the respiratory cycle during locomotion (Bramble and Jenkins 1993), it seems reasonable to infer the presence of a diaphragm in the cynodonts and therocephalians, in which such locomotory advances appear to have originated (Jenkins 1971). Moreover, the fact that both of these groups also exhibit evidence of respiratory turbinates, indicating elevated resting metabolic rates, represents a provocative parallel. Clearly, however, this does not constitute unequivocal proof of the presence of a diaphragm, and as yet there is no unambiguous signal in the synapsid fossil record for the origin of this structure and the elevated aerobic capacity it represents.

In contrast, the avian parabronchial lung/abdominal air sac system is characterized by a distinct set of osteological features that can be preserved in fossil forms. Specifically, the hinged ribs and specialized sternocostal joints that are associated with the unique sternally driven method of lung ventilation in modern birds represent an unambiguous correlate of this highly derived lung morphology. In this respect, the sternocostal joints of Late Cretaceous hesperornithiform birds, with transversely expanded distal ends of the sternal ribs and matching facets on the thickened lateral margin of the sternum, are essentially identical to those of modern birds (Fig. 9; Marsh 1880), and there is little doubt that the lung anatomy and ventilatory mechanics of hesperornithids are fully equivalent to those of modern birds. However, it is uncertain whether these features are



present in older or more primitive birds. The sternum of the Early Cretaceous ornithurine *Chaoyangia*, which closely resembles that of modern birds in several other respects (e.g., it is relatively elongate and fully keeled), is described as having a well-developed costal margin (Hou et al. 1996; Zhou and Hou 2002). Similarly, the sterna of the Early Cretaceous ornithurines *Yanornis* and *Yixianornis* are described as “hardly distinguishable from those of modern birds” (Zhou and Zhang 2001, p. 1260). However, detailed descriptions of the sternocostal joints of these taxa are not presently available.

By comparison, the sterna of enantiornithine and confuciusornithine birds appear to lack such well-developed sternocostal joints. Although several short, ossified sternal ribs are sometimes preserved in specimens of both taxa, the costal margin of the sternum of all of these forms appears to be relatively thin, and the sternal ribs lack the transversely expanded distal ends characteristic of those of modern birds (Fig. 9; e.g., Chiappe et al. 1999; Chiappe and Walker 2002; Sanz et al. 2002; Sereno et al. 2002; Zhou and Hou 2002). This is a critical distinction, because simple articulations between sternum and sternal ribs are not diagnostic for an avian-like lung ventilation mechanism: such articulations occur widely among amniotes, including mammals, crocodilians, and lepidosaurs (although not usually ossified; cf. Fig. 8). Although it is conceivable that ossification of simple sternal ribs in enantiornithines and confuciusornithines is related to a primitive version of the sternocostal lung ventilation mechanism of modern birds, there is no clear way to confirm this. It is, for example, equally possible that ossification of these sternal ribs helps to reinforce the sternal region in association with improved flight mechanics.

Finally, there is no evidence of hinged ribs, ossified sternal ribs, or specialized sternocostal joints in *Archaeopteryx* (Wellnhofer 1993; Elzanowski 2002). In these respects, the thorax of this basal avian most closely resembles that of generalized, ancestral amniotes. *Archaeopteryx* (Wellnhofer 1993; Elzanowski 2002), confuciusornithids (Chiappe et al. 1999; Zhou and Hou 2002), and at least some enantiornithines (e.g., *Eoenantiornis*, *Longipteryx*; cf. Chiappe and Walker 2002) also retain gastralia, dermal ossifications in the ventral abdominal region that are a primitive feature of amniotes and may reflect a relatively primitive mode of respiration.

Like basal birds, nonavian theropods and other dinosaurs also lack the morphological adaptations associated with the parabronchial lung/abdominal air sac system of modern birds. Avian-like jointed or hinged ribs are absent on all nonavian dinosaurs, and there is no indication of specialized sternocostal mechanisms like that of modern birds. Ossified sternal ribs are

documented for several dinosaurs, including oviraptorids (e.g., Clark et al. 1999), ornithomimids (e.g., *Pelecanimimus*; W. Hilleenius, personal observation), and dromaeosaurids (e.g., Norell and Makovicky 1999), but in each case these sternal ribs lack the distinct, transversely oriented distal expansions that form the sternocostal joints characteristic of the avian thorax. The sternal plates of dinosaurs, which are known from a variety of taxa, including oviraptorids (e.g., Clark et al. 1999), ornithomimids (Pérez-Moreno et al. 1994), and dromaeosaurids (e.g., Norell and Makovicky 1997), are generally short and in all cases lack the thickened lateral border and transversely oriented hinge joints for the sternal ribs that characterize modern avian sterna. The sternal plates of the immature dromaeosaur *Bambiraptor* are exceptionally long, but their lateral edges, including the region where the sternal ribs articulated, are described as thin (Burnham et al. 2000). Again, simple articulations between sternum and sternal ribs occur widely among amniotes and cannot be considered diagnostic for any particular lung morphology or ventilatory mechanism.

The presence of avian-like uncinate processes, posterodorsal projections on the thoracic ribs, in oviraptors (Clark et al. 1999), some dromaeosaurids (Norell and Makovicky 1999), confuciusornithids (Chiappe et al. 1999), and enantiornithine birds (e.g., Chiappe and Walker 2002) is sometimes mentioned in this context. However, avian uncinate processes appear to function primarily in strengthening the rib cage and stabilizing the shoulder girdle (e.g., King and King 1979); they have no particular role in sternocostal ventilation of the avian lungs. Uncinate processes are absent in screamers (Anseriformes: Anhimidae) and may be reduced in other birds (cf. Brooke and Birkhead 1991). Cartilaginous or ossified uncinate processes are also known from crocodilians and *Sphenodon* (e.g., Hofstetter and Gasc 1969) and even in several temnospondyl anamniotes, such as *Eryops* (Gregory 1951). Consequently, the presence of uncinate processes does not appear to be correlated with respiratory adaptations.

Similarly, the pneumatized vertebrae of sauropods, nonavian theropods, and *Archaeopteryx* have been cited as evidence of a birdlike parabronchial lung/air sac system (e.g., Bakker 1980; Perry and Reuter 1999; Christiansen and Bonde 2000; Wedel 2003). However, it is far from clear that postcranial skeletal pneumatization is inevitably associated with a parabronchial lung system. First, the functional significance of postcranial pneumaticity in modern birds is poorly understood, but it does not appear to be related to respiration or lung ventilation (see, e.g., McLelland 1989). Skeletal pneumatization certainly does not enhance lung ventilation in any way, because the air cavities

Figure 9. The sternum of the mid-Cretaceous ornithurine *Hesperornis* (top; lateral view) exhibits transversely expanded sternocostal joints and is indistinguishable from modern birds in this respect. In contrast, such specialized sternocostal joints are not known from enantiornithine birds, such as *Iberomesornis* (center) or *Cathayornis/Sinornis* (bottom; ventral view). Abbreviations: lco = left coracoid; f = furcula; st = sternum; sr = sternal ribs; lu = left ulna. Modified from Marsh (1880; top) and Zhou and Hou (2002; bottom).

are noncontractile and they cannot be evacuated within a bone. Instead, this phenomenon is most often considered to be associated with structural attributes, such as weight reduction and mechanical strength (e.g., Bühler 1992). Second, although ontogenetically the diverticula that invade the postcranial elements develop from the air sacs in modern birds (McLelland 1989), it is by no means certain that this process is necessarily tied to the parabronchial lung design. Pneumatizing tissues capable of inducing aggressive bone resorption are not unique to birds; they also occur in the cranial sinuses in crocodilians (Witmer 1995, 1997) and thus appear to be at least a plesiomorphic attribute of archosaurs (see also Gower 2001). Skeletal pneumatization per se is thus not inextricably linked to either air sacs or a particular lung morphology. Postcranial pneumatization is associated with air sacs in all modern birds, but this is perhaps coincidental: the existence of pneumatic cranial sinuses indicates that all that is minimally needed is a specialized portion of the respiratory tract from which diverticula can develop that invade adjacent bones. In this context, it is important to note that heterogenous lungs (i.e., those with distinct vascularized, parenchymal respiratory portions and nonvascularized, saclike portions) are not unique to birds but occur widely among sauropsids, including crocodilians (cf. Duncker 1978; Perry 1983). If postcranial pneumaticity, like cranial pneumaticity, requires nothing more than nonvascularized (i.e., "nonparenchymal") epithelia capable of inducing bone resorption, then conventional heterogenous septate lung designs could be adequate. Pneumatized vertebrae and ribs in nonavian dinosaurs and *Archaeopteryx* thus signify only the presence of such nonrespiratory, pneumatizing diverticula and possibly imply the presence of pulmonary heterogeneity. These structures do not preclude the possible presence of avian-like parabronchial lungs or some antecedent, "proto-parabronchial" version thereof, but they cannot be considered compelling evidence for the presence of such lungs. However, without the thoracic specializations associated with parabronchial lung ventilation, inferring the presence of a birdlike lung must be considered speculative.

Several authors have proposed that nonavian theropods and basal birds may have used their well-developed gastralia to ventilate an avian-like abdominal air sac system (e.g., Carrier and Farmer 2000). Although gastralia, dermal ossifications in the ventral abdominal wall that occur primitively throughout amniotes (Romer 1956; Carrier and Farmer 2000) but are absent in all extant birds, can hardly be considered a diagnostic correlate of a derived, avian-like lung/air sac system, it is also not clear that these ossifications necessarily preclude the presence of such a system, and this intriguing proposal deserves further investigation. Nonetheless, there are several problems with the proposed mechanism of cuirassal breathing, in which action of pelvic muscles is thought to depress the medial aspects of the gastralia, thereby generating negative intra-abdominal pressures that help fill the lungs during inhalation. In extant

crocodilians, as well as *Sphenodon*, the gastralia are not known to contribute to the generation of either negative or positive abdominal pressure during lung ventilation (e.g., Farmer and Carrier 2000b). Furthermore, in extant forms, the muscles postulated for cuirassal breathing in nonavian theropods (ischio-truncus and caudotruncus) insert not on the medial aspect of the gastralia but on the dorsolateral aspects instead (cf. Farmer and Carrier 2000b). There is, in other words, no extant example of the model proposed. Finally, in nonavian theropods the gastralia are limited to the ventral body wall, and an extensive, rather deep, open flank region exists between these structures and the posterior abdominal ribs. Negative abdominal pressures generated through the proposed cuirassal breathing mechanism would likely have resulted in paradoxical inward movement of this unreinforced lateral abdominal wall and caused unavoidable loss of ventilatory efficiency. At present, the cuirassal breathing model for ventilation in theropods and basal birds must be considered highly speculative at best.

An alternative model for lung ventilation in nonavian theropods invokes a crocodilian-style hepatic piston mechanism (Ruben et al. 1997, 1999). Fossilized remains of soft tissues of two theropod taxa, the compsognathid *Sinosauropteryx* and the maniraptoran *Scipionyx*, suggest that the abdominal cavity of both theropods was subdivided in distinct anterior (pleuro-pericardial) and posterior (peritoneal) cavities, separated by a transversely oriented septum. In both cases, pigmented stains representing the remains of liver and intestinal tissues are restricted to the posterior region and extend the full depth of the body cavity (Ruben et al. 1997, 1999). Lung tissues, themselves not preserved due to their delicate nature, were presumably restricted to the anterior region. Such a partitioning of the abdominal cavity closely resembles that of modern mammals or crocodilians but is incompatible with an extensive, birdlike abdominal air sac system. Extant birds lack a vertical subdivision of the body cavity, and the liver is located largely or entirely ventral to the lungs (Duncker 1978; Perry 1983; McLelland 1989).

In extant crocodilians, the vertically oriented liver and diaphragm function in conjunction with longitudinal diaphragmatic muscles to produce a piston-like mechanism for supplemental lung ventilation. The close resemblance of the liver and abdominal subdivision in *Scipionyx* and *Sinosauropteryx* to those of extant crocodilians suggests that a similar hepatic piston mechanism may also have been present in nonavian theropods. The diaphragmatic muscles of extant crocodilians originate from the pelvis and gastralia and insert on the lateral surface of the liver (Ruben et al. 1997; Carrier and Farmer 2000; Farmer and Carrier 2000a, 2000b). The triradiate pelvis of *Scipionyx*, *Sinosauropteryx*, and other nonavian theropods broadly resembles that of modern and especially basal crocodylomorphs (such as protosuchids and sphenosuchids) and could have readily served as attachment sites for crocodilian-like diaphragmatic musculature. Significantly, a small patch

of longitudinally oriented muscle fibers, which appears to be a remnant of the diaphragmaticus muscle, is preserved immediately anterior to the pubis in *Scipionyx* (Ruben et al. 1999). Hutchinson (2001) expressed reservations about this reconstruction, because pelvic muscles presumably occupied the anterior and posterior surfaces of the pubic apron. However, the diaphragmaticus of extant crocodilians does not originate from the pubic apron, but from the cranio-lateral edge of the distal end of the pubis, as well as more proximally on the pubis, the posterior gastralia, and the preacetabular portion of the ischium, and insert on the lateral surface of the liver (Ruben et al. 1997; Carrier and Farmer 2000; Farmer and Carrier 2000a, 2000b). Elsewhere, Hutchinson (2001) asserted that the lateral surface of the distal pubis and the pubic boot of theropods served mainly for abdominal muscles, including the rectus abdominus. Insofar as the crocodilian diaphragmaticus muscles are likely derivatives of the rectus abdominus (Carrier and Farmer 2000), there would appear to be no conflict between Hutchinson's (2001) reconstruction of theropod pelvic musculature and the presence of a diaphragmaticus muscular system in these animals. Other criticisms of the hepatic piston model for lung ventilation in nonavian theropods have been extensively reviewed elsewhere (Ruben et al. 2003; Chinsamy and Hillenius 2004) and need not be reiterated here.

Summary and Conclusions

Questions about when endothermic status was attained in any evolutionary lineage can be answered only with positive evidence of fossilizable attributes that are unequivocally and causally linked to this derived metabolic condition. Respiratory turbinates fulfill this criterion, as they reduce the cost in respiratory water and heat loss associated with elevated routine (resting) ventilation and metabolic rates in endotherms. Evidence for the absence or presence of respiratory turbinates suggests that endothermy was attained comparatively early in the synapsid lineage but relatively late in archosaurs. Attachment scars of respiratory turbinates in two lineages of Late Permian/Early Triassic synapsids, the therocephalians and the nonmammalian cynodonts, suggest that resting metabolic rates were gradually expanding in these taxa and that endotherm-like metabolic rates may have been attained some 30–40 million years before the appearance of the earliest “true” mammals.

In contrast, respiratory turbinates were apparently absent in dinosaurian archosaurs and early birds. Theropod dinosaurs, as well as archaeornithine and enantiornithine birds, retain a primitive configuration of the rostral skull, in which large paranasal sinuses restricted the volume and diameter of the respiratory nasal passage and in which there appears to have been little room for an extensive respiratory turbinal complex. However, the nasal cavities of Early to Late Cretaceous ornithurine birds were drastically altered: the paranasal sinuses were shifted caudally, and the respiratory portion of the nasal chamber ex-

panded. The design of the nasal cavity of Late Cretaceous ornithurines is nearly indistinguishable from that of extant birds, and it is likely that these birds had a fully functional complex of respiratory turbinates. This suggests that ornithurine birds had probably attained resting metabolic rates close to those of modern birds. However, this condition was unlikely to have been present in dinosaurs and early birds.

The apparently “late” evolution of endothermy in birds is also reflected in the postcranial skeleton, which indicates that the specialized ventilatory mechanisms associated with the parabronchial lung/air sac system of extant birds also first appeared in ornithurine birds. Hinged thoracic and sternal ribs, and especially the specialized, transversely expanded sterno-costal joints characteristic of the modern avian rib cage, are present in Late Cretaceous ornithurines but are not known from more primitive archosaurs. Enantiornithine and confuciusornithine birds, as well as some theropod dinosaurs, did possess ossified sternal ribs, but these apparently had only simple contacts with the sternum and, apart from being ossified, are not markedly different from those of typical nonavian amniotes. Moreover, many of these forms retain gastralia, a primitive attribute of amniotes that probably reflects a plesiomorphic state of lung ventilation and respiration. The presence of uncinata processes or pneumaticity is not considered indicative of an avian-like parabronchial lung.

Lung anatomy and ventilatory mechanisms are reflective of the maximal aerobic capacity of animals and their capacity to sustain high levels of activity. These observations therefore suggest that nonornithurine (i.e., enantiornithine, confuciusornithine, and archaeopterygine) birds, in addition to lacking evidence for elevated resting metabolic rates, also had not yet attained levels of maximal aerobic activity and endurance that are typical of modern birds. It is possible that they may have exceeded ancestral “reptilian” levels in these respects, but no unambiguous positive evidence to support that reconstruction has been identified. Other features of these taxa are consistent with this conclusion. For example, although *Archaeopteryx* and most confuciusornithines and enantiornithines were probably quite capable of powered flight (e.g., Rayner 1991; Sanz et al. 2002; Sereno et al. 2002), the sternum of these taxa typically lacks a well-developed keel (e.g., Wellnhofer 1993; Sanz et al. 1995, 2002; Chiappe et al. 1999; Zhou and Hou 2002). The sterna of confuciusornithines and enantiornithines are longer and more ossified than that of *Archaeopteryx* but have at best a low ventral ridge that is typically limited to the posterior portion of the sternum. In contrast, volant ornithurine birds, even Early Cretaceous forms such as *Liaoningornis* and *Chao-yangia*, have a well-developed keel that extends the entire length of the sternum (Zhou and Zhang 2001; Zhou and Hou 2002; the absence of a keel in hesperornithids, ratites, and several other ornithurines is related to flightlessness; cf. Feduccia 1996). In modern birds, the keel of the sternum is the site of attachment for both the pectoralis (downstroke) and sternocoracoi-

deus (recovery stroke) muscles. The presence of an essentially modern triosseal canal in enantiornithine birds indicates that the flight musculature of these birds had already achieved a modern avian configuration on the sternum (Sanz et al. 1995; Sereno et al. 2002). However, the poorly developed keel in these forms suggests that these flight muscles lacked the bulk seen in modern birds. This is consistent with an ectothermic reconstruction of the enantiornithine flight musculature, since ectothermic muscle is more powerful than endothermic musculature and less muscular volume is required to produce a given power output (Ruben 1991). One apparent exception is the Patagonian enantiornithine *Neuquenornis*, which has a prominent keel on the anterior part of the sternum (cf. Chiappe and Walker 2002). This may represent an independent development of aerobic flight musculature in this Late Cretaceous enantiornithine. Unfortunately, neither the rostral portions of the skull nor the costal margins of the sternum of the specimen are preserved to corroborate that possibility.

These observations are consistent with a scenario in which avian endothermy evolved well after the initial appearance of flight. In this scenario, the initial radiation of birds in the Early Cretaceous, which included especially the enantiornithine birds (cf. Chiappe and Dyke 2002), was comprised primarily of birds that did not yet have the full metabolic capacity and endurance for long-distance flight associated with modern birds. Endothermy apparently evolved in ornithurine birds, perhaps in response to selection for long-distance powered flight and stamina. In this light, it is perhaps significant that many Cretaceous ornithurines appear to have filled marine and shorebird-like niches, in which resources are often spread out thinly over long distances (Feduccia 1996, 2003). In contrast, enantiornithines and other basal birds typically were more terrestrial birds with perching capabilities (Chiappe and Dyke 2002) and lived in relatively more compact resource environments that did not require long-distance migration. In such an environment, ectothermally powered flight may still have been adequate.

Finally, no unambiguous evidence exists that clearly supports the inference of an endothermic metabolic status for dinosaurs. The apparent absence of respiratory turbinates among dinosaurs suggests that chronic respiratory water loss was not a significant physiological problem for these animals, which implies that resting ventilation rates were probably low compared with those of modern endotherms. It is conceivable that resting rates of some dinosaurs were elevated beyond those of typical extant ectotherms, yet not so high as to warrant a turbinate complex to control respiratory water loss. However, no evidence is currently available that indicates that dinosaurian resting ventilation rates had expanded notably above those of extant reptiles, and such reconstructions must be considered speculative. Dinosaurs also lack the skeletomuscular attributes associated with a derived, avian-like parabronchial lung/air sac system. It is theoretically possible that some dinosaurs had modified the primitive archosaurian lung into a "proto-

parabronchial" lung, but there is no evidence on which to base such a reconstruction, and this view must also be considered speculative. However, soft tissues preserved in two theropods, coupled with the widespread presence of a robust, rodlike pubis among theropods, suggest the possibility that these animals may have possessed a hepatic piston mechanism of supplementary lung ventilation. This suggests that the aerobic capacity of theropod dinosaurs may have been higher than typical of modern ectotherms. In fact, the pubis of some theropods is oriented vertically or exhibits marked posterior retroversion (e.g., *Herrerasaurus* and some dromaeosaurid theropods). This arrangement may have further enhanced lung ventilation, as an elongated diaphragmaticus muscle would have afforded additional posterior "travel" of the liver during hepatic piston ventilation. Theropod dinosaurs, therefore, may have had a unique combination of physiological attributes: low maintenance expenses combined with an expanded capacity for sustained activity.

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