The Metabolic Status of Some Late Cretaceous Dinosaurs

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Analysis of the nasal region in fossils of three theropod dinosaurs (*Nanotyrannus, Ornithomimus,* and *Dromaeosaurus*) and one ornithischian dinosaur (*Hypacrosaurus*) showed that their metabolic rates were significantly lower than metabolic rates in modern birds and mammals. In extant endotherms and ectotherms, the cross-sectional area of the nasal passage scales approximately with increasing body mass M at $M^{0.72}$. However, the cross-sectional area of nasal passages in endotherms is approximately four times that of ectotherms. The dinosaurs studied here have narrow nasal passages that are consistent with low lung ventilation rates and the absence of respiratory turbinates.

Knowledge of dinosaur metabolic physiology can help improve understanding of their feeding and reproductive habits, as well as their routine modes of existence. Similarly, because birds are probably descendants (*1*) or near relatives of dinosaurs

(*2*), insight into dinosaur metabolism is likely to yield valuable clues to the evolution of endothermy in birds. However, anatomical structures that are causally linked with ecto- or endothermic metabolism in living tetrapods and thus could be particularly helpful in interpreting the metabolic status of extinct taxa are usually composed of soft tissues that are unlikely to fossilize (such as four-chambered hearts, complex lungs, and so on). Consequently, deciphering the metabolic status of dinosaurs has traditionally been limited to divining attributes putatively correlated with, but not necessarily causally linked with, maintenance of either low or high metabolic rates [such as fossil bone oxygen isotopic composition, growth rates, and bone histology (*3*)] Certainly their sheer mass probably enabled many dinosaurs to be bulk homeotherms (*4*), but paleontological evidence for dinosaur metabolic rates has been equivocal at best (*3, 5*).

The presence or absence of nasal respiratory turbinates in fossilized tetrapods may be used to infer the metabolic status of long-extinct groups (*6*). Here we present evidence that respiratory turbinates and other nasal passage modifications associated with endothermic rates of lung ventilation were absent in a variety of theropod dinosaurs and in at least one group of ornithopod ("duckbill") dinosaurs.

Respiratory turbinates (respiratory conchae) are epithelially lined, scroll-like, ossified or cartilaginous structures located in the anterior nasal passages of more than 99% of all extant birds and mammals (Fig. 1 and Fig. 2, B and C); their presence increases the surface area of the nasal passage. During inhalation and exhalation, respiratory turbinates act as intermittent countercurrent heat exchangers. By this process, they function to reduce the otherwise dramatically accelerated rates of respiratory evaporative heat and water loss that would accompany the high lung ventilation rates typical of endothermic taxa (*7–9*). Embryological studies indicate that the overall anatomical similarity of respiratory turbinates in birds and mammals is a product of convergent evolution; that is, these structures are likely to have evolved independently in mammalian and avian lineages (*10*). In contrast, respiratory turbinates are universally absent in extant ectothermic tetrapods. Field metabolic and lung ventilation rates in ectotherms are only about 5% of those of similarly sized endotherms (*11*) and are less likely to be associated with accelerated rates of respiratory loss of water and heat.

Together these observations suggest that the transition to high metabolic and lung ventilation rates in both protobirds and protomammals was probably accompanied by the independent, concurrent evolution of respiratory turbinates. Similarly, expansion of the nasal cavity to accommodate the presence of respiratory turbinates might also be expected to have occurred during the evolution of endothermy. Accordingly, the presence of respiratory turbinates and enlarged nasal passages in fossil taxa can serve as causally linked indicators of elevated lung ventilation rates and, by extension, of high routine metabolic rate. In extinct forms, the absence of respiratory turbinates and of nasal passage modifications associated with them is a likely indicator that metabolic and lung ventilation rates were sufficiently low that evaporative respiratory loss of heat and water was not a problem (*6, 8*). Evidence for the existence of incipient respiratory turbinates has previously been described in therocephalian therapsids, which are Late Paleozoic taxa not far removed from the ancestry of mammals (*6*).

The nasal passage in extant archosaurs and mammals consists of an anterior vestibular region, typically adjacent to the nostrils. Immediately posterior to the vestibule

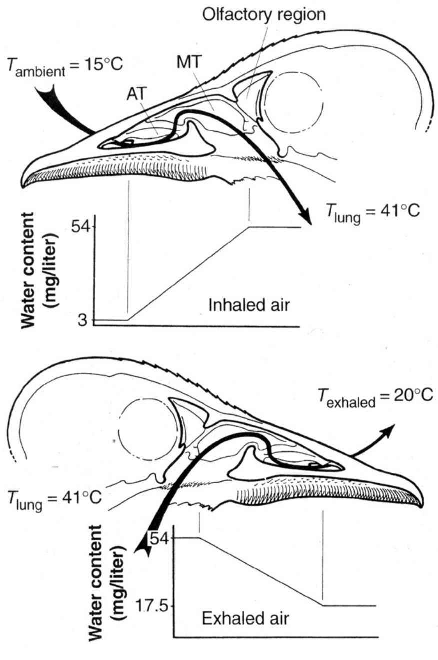

Fig. 1. The mechanism of respiratory turbinate function in modern endotherms. During inhalation (top), moist respiratory turbinate surfaces function to warm and humidify ambient air as it traverses the nasal passage. These same processes result in substantial cooling of respiratory turbinate surfaces. Upon exhalation (bottom), the process is reversed: Warm, moist exhaled air passes over the cooled surfaces of the respiratory turbinates. Exhaled air temperature is thereby reduced and water vapor condenses on respiratory turbinate surfaces. The result is a substantial reduction in the rate of respiratory loss of water and heat that would otherwise accompany high lung ventilation rates associated with endothermy (*7, 8*). Abbreviations: *T*, temperature; AT, anterior respiratory turbinate; MT, middle respiratory turbinate.

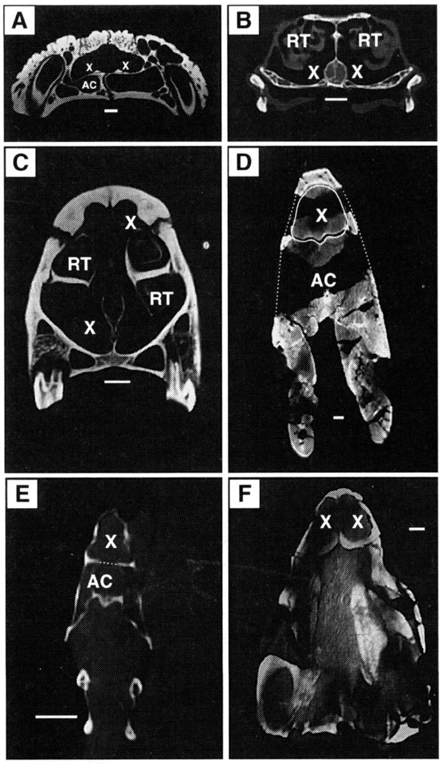

Fig. 2. Cross-sectional CAT scans of the nasal passage in (**A**) a crocodile (*Crocodylus*), (**B**) an ostrich (*Struthio*), (**C**) a bighorn sheep (*Ovus*), (**D**) the tyrannosaurid theropod dinosaur *Nanotyrannus*, (**E**) the ostrichlike theropod dinosaur *Ornithomimus*, and (**F**) the lambeosaurine duckbill dinosaur *Hypacrosaurus*. Respiratory turbinates in mammals and birds are housed in voluminous nasal passageways (see also Fig. 3). As in the alligator, the tubelike nasal passage (cavum nasi proprium) in these theropod dinosaurs appears to have been housed primarily within the maxillary and nasal bones. The main nasal passage in duckbill dinosaurs was probably an elongated nasal vestibulum, contained largely within the nasal bone (*17*). Some minimal postdepositional distortion of these fossils is evident. Nevertheless, the relatively narrow nasal passages in the dinosaurs indicate that, as suggested by their fossils, respiratory turbinates were probably absent in the living animals. Scale bar, 1 cm. Abbreviations: AC, accessory cavity; RT, respiratory turbinate; X, nasal passage proper.

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is the nasal cavity proper (cavum nasi proprium); the boundary between the two is usually denoted by ostia through which various nasal gland ducts communicate with the nasal passage. The nasal cavity proper is broadly subdivided into a main respiratory passageway and a "blind" posterodorsal or posterolateral olfactory region. Posteriorly, the nasal passage is continuous with the nasopharyngeal duct. In addition, a variety of pneumatized cranial cavities (sinuses) communicate with portions of the nasal passage in many amniotes (*10*).

Cartilaginous or osseous conchae (or turbinates) lined with olfactory sensory epithelia are housed within the olfactory regions of the nasal passage. Additionally, in birds and mammals, sheets of osseous or cartilaginous, often coiled, respiratory turbinates (the middle turbinates of birds and the maxilloturbinates of mammals) project into the nasal cavity proper (Fig. 2, B and C). Respiratory turbinates are oriented with their long axis parallel to the main path of airflow and are lined with well-vascularized respiratory epithelia. Birds generally possess an additional, anterior set of respiratory turbinates located within the rostral vestibular region (*10*).

In crocodilians, the perimeter of the tubelike nasal passage is bounded laterally and ventrally by thin medial processes from the premaxillary and maxillary bones; the roof of the passage is formed largely by the nasal bone (Fig. 2A). The boundaries of the mammalian nasal passage are typically well-defined by the nasal, premaxillary, and maxillary bones (Fig. 2C). The nasal passage proper is poorly ossified in most birds (Fig. 2B).

Expansion of the nasal cavity is necessary to accommodate the presence of respiratory turbinates, as well as to facilitate increased lung ventilation rates in endotherms. Consequently, it is to be expected that most birds and mammals might possess nasal passageways with markedly larger cross-sectional areas than those of ectotherms of equivalent mass. Regressions for this variation in endotherm-ectotherm anatomy (Fig. 3) indicate that nasal passage cross-sectional area in birds and mammals is about four times that of a number of similarly sized modern reptiles.

Computed axial tomography (CAT) scans from the mid-snout regions of superbly preserved specimens of the Late Cretaceous theropod dinosaurs *Nanotyrannus* (Tyrannosauridae) and *Ornithomimus* (Ornithomimidae) reveals that their anterior nasal anatomy was like that of modern crocodilians. These dinosaurs had a narrow, tubelike nasal passage bounded laterally and ventrally by medial processes of the maxillary bone and dorsally by the nasal bone (Fig. 2, D and E, and Fig. 4). There is no trace of respiratory turbinates in the nasal

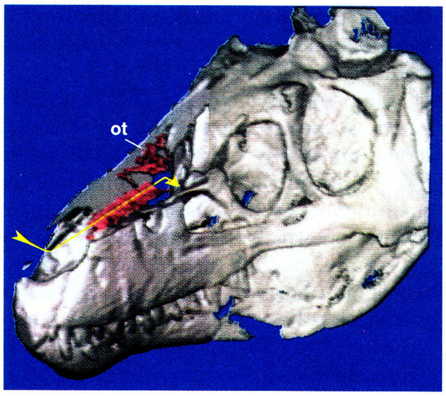

Fig. 4. The tubelike nasal passage of the tyrannosaurid dinosaur *Nanotyrannus*. The floor of the nasal passage was formed by medial processes of the maxillary bone, much as it is in modern crocodilians (Fig. 2, A and D). The yellow arrow marks the probable path of inhaled air through the nasal passage proper, moving ventrally into the nasopharyngeal region, posterior to the bony secondary palate (not shown in figure). Pink areas indicate the floor of the nasal passage. Abbreviation: ot, olfactory turbinate.

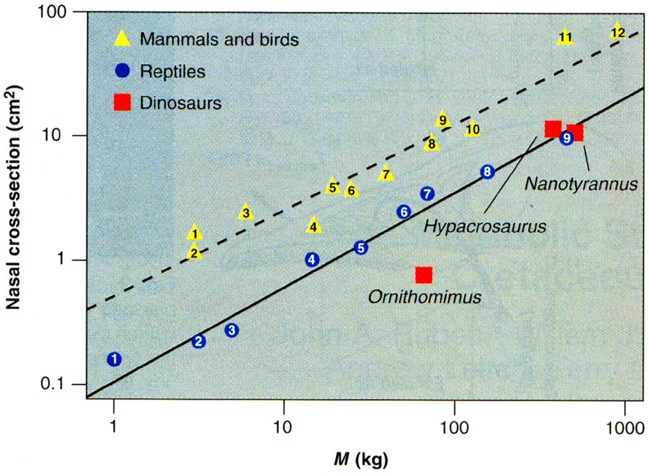

Fig. 3. The relation of nasal passage (cavum nasi proprium) cross-sectional area to body mass (*M*) in modern endotherms (mammals and birds), modern reptiles (lizards and crocodilians), and three genera of Late Cretaceous dinosaurs (*15*) (values for dinosaurs were not included in regression calculations). For mammals and birds, nasal cross section equals 0.57 $M^{0.68}$; SE = 0.358. For reptiles, nasal cross section equals 0.11 $M^{0.76}$; SE = 0.239. Numbers in yellow triangles indicate the following mammals and birds: 1, coatimundi (*Nasua*, 3 kg) and opossum (*Didelphis*, 3 kg); 2, great blue heron (*Ardea*, 3 kg); 3, raccoon (*Procyon*, 6 kg); 4, giant anteater (*Myrmecophaga*, 15 kg); 5, rhea (*Rhea*, 20 kg); 6, coyote (*Canis*, 25 kg); 7, emu (*Dromaius*, 40 kg); 8, human (75 kg); 9, black bear (*Ursus*, 85 kg); 10, ostrich (*Struthio*, 125 kg); 11, horse (*Equus*, 450 kg); and 12, African cape buffalo (*Syncerus*, 900 kg). Numbers in blue circles indicate the following reptiles: 1, false iguana (*Ctenosaura*, 1 kg); 2, monitor lizard (*Varanus*, 3 kg); 3, monitor lizards (*Varanus*, 4.8 kg and 5.0 kg); 4, crocodile (*Crocodylus*, 15 kg); 5, monitor lizard (*Varanus*, 28 kg); 6, alligator (*Alligator*, 70 kg); 7, crocodile (*Crocodylus*, 50 kg); 8, alligator (*Alligator*, 160 kg); and 9, crocodile (*Crocodylus*, 450 kg). Dinosaur masses, estimated from head or body skeletal length or both (*16*) are as follows: ostrich dinosaur *Ornithomimus* (Theropoda: Ornithomimidae), 65 kg (Campanian Stage; Tyrrell Museum of Palaeontology specimen 95.110.1); duckbill dinosaur *Hypacrosaurus* (Ornithischia: Hadrosauridae), 375 kg (Maastrichtian Stage; American Museum of Natural History specimen 5461); and tyrannosaurid dinosaur *Nanotyrannus* (Theropoda: Tyrannosauridae), 500 kg (Maastrichtian Stage; Cleveland Museum of Natural History specimen 7541).

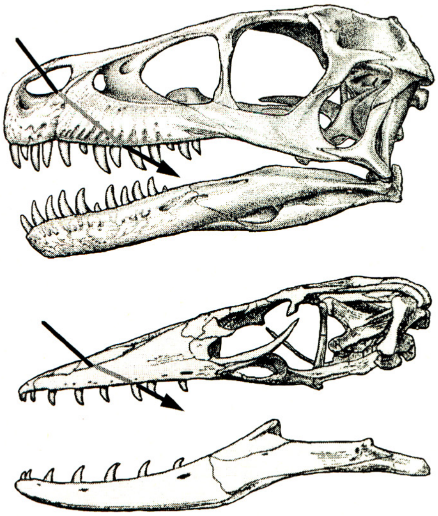

Fig. 5. Lateral views of the skulls of the of the maniraptoran theropod dinosaur *Dromaeosaurus* (Theropoda: Dromaeosauridae) (top) and the monitor lizard *Varanus* (Squamata: Varanidae) (bottom). The arrow shows the path of airflow through the nasal region into the oral cavity. In *Dromaeosaurus*, and probably in some other dromaeosaurid dinosaurs [such as *Deinonychus* (*13*)], the short direct path of airflow into the oral cavity was similar to that in *Varanus* (and many other extant lizards) and almost certainly precluded sufficient space to house respiratory turbinates {for *Dromaeosaurus* [figure modified from (*12*)], the presumed airflow route is based on the location of the nostrils and the anterior position of the vomer}. Dromaeosaurid dinosaurs are often assumed to be the sister group of birds (*18*).

passageways of these specimens. Additionally, because values for cross-sectional areas of the theropod nasal passages lie on or below the reptilian allometric regression (Fig. 3), respiratory turbinates were probably also absent in life. Similarly, CAT scans from a particularly well-preserved skull of the ornithischian dinosaur *Hypacrosaurus* (Ornithopoda: Hadrosauridae) also show no evidence of the presence of respiratory turbinates (Fig. 2F). Nasal cross sectional area in *Hypacrosaurus* is also coincident with the reptilian allometric regression (Fig. 3).

The proximity of the nostrils to the choanae (internal nares) in the maniraptoran theropod *Dromaeosaurus* (Dromaeosauridae) (*12*) and probably in *Deinonychus* (Dromaeosauridae) (*13*) as well is reminiscent of nasal cavity proportions in a variety of modern lizards (Varanidae, for example) (Fig. 5) (*14*). As in extant lizards, the abbreviated nasal passage associated with such a direct path of airflow into the oral cavity of these dinosaurs almost certainly precluded sufficient space in the nasal cavity to have accommodated respiratory turbinates.

Together the data indicate that a variety of Cretaceous theropod dinosaurs, and at least one genus of ornithischian dinosaurs, possessed crocodile- or lizardlike, relatively constricted nasal passages, devoid of sufficient cross-sectional area to have accommodated respiratory turbinates and endothermic lung ventilation rates. These observations do not necessarily either preclude or support the possibility that some or all of the taxa investigated here maintained routine metabolic rates somewhat greater than those of extant ectotherms.

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9. The rare exceptions in endotherms where respiratory turbinates are particularly poorly developed or absent are clearly related to secondary nasal or rostral specializations that preclude their presence. For example, turbinates and nostrils are absent in a number of diving birds of the order Pelecaniformes, including pelicans, gannets, and cormorants. Most of these birds are plunge divers and anterior open nostrils would be a potential liability in such cases [J. D. MacDonald, *Proc. Zool. Soc. London* **135**, 357 (1960)]. Similarly, respiratory turbinates are also absent or poorly developed in whales. However, in these exceptions, the presence of compensatory mechanisms serves to emphasize that endothermic lung ventilation rates necessitate some adaptation in order to counteract loss of respiratory water or heat {pelecaniformid birds maintain large nasal salt glands that probably allow them to drink sea water directly [P. C. Withers, *Comparative Animal Physiology* (Saunders College Press, Fort Worth, TX, 1992)]; at least some cetaceans possess a specialized nasal-cavity air compression mechanism for reduction of respiratory water and heat loss [W. H. Coulombe, S. H. Ridgeway, W. E. Elgin, *Science*, **149**, 86 (1965)]}.
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