PALEONTOLOGY

Were Dinos Cold-Blooded After All? The Nose Knows

John Ruben thinks he's found the Rosetta Stone that holds the key to the origins of warm-blooded land animals. "There's no real absolute answer," says the Oregon State University zoophysiologist; warm blood, after all, doesn't fossilize. But what he's found "is as good a Rosetta Stone as you can get." And it may solve puzzles that have perplexed scientists for decades: Which land animals first became warm-blooded, or endothermic, and why? And were the dinosaurs among them?

Ruben's Rosetta Stone is a tiny scroll of cartilage or bone in the nose called a respiratory turbinate. This scroll plays a vital role in controlling water and heat loss in endotherms, he says. If it isn't there, the animal almost certainly isn't endothermic. That's true today—and in fossils hundreds of millions of years old.

In a talk this week at the annual meeting of the Society of Vertebrate Paleontology in Pittsburgh and in a paper in press in the *Journal of Experimental Biology*, Ruben reports that he and colleague Willem Hillenius have used turbinates to trace endothermy back about 250 million years in the mammal lineage and 70 million years in birds. In both cases, they say, endothermy arose because it gave these animals greater stamina, not because they needed to regulate their body temperature, as many researchers have contended. And it did not arise—for any reason—in dinosaurs. This emerging picture of endothermy leaves dinosaurs out in the cold.

The work has received a warm reception from many researchers because these turbinates seem functionally linked to endothermy, unlike other traits that have been used in attempts to settle this question. Timothy Rowe of the University of Texas, Austin, says, "I think what he's got is the first major anatomical clue to endothermy. And it's based in modern experimental biology." David Weishampel, a paleontologist at Johns Hopkins University in Baltimore, calls it "extremely interesting and in the long run, extremely important. If he's correct that dinosaurs don't have turbinates ... the argument seems pretty compelling."

Skeptics, though, argue that turbinates may be less definitive than Ruben thinks or—conversely—that they are definitive and some dinosaurs had them. "It sounds interesting," says John Horner of Montana State University. "But the assumption needs to be rigorously tested. Dinosaurs are real brain teasers. They're not like anything living."

There's little debate about the issue's importance, however. "If I had to point to the two great adaptations made by vertebrates, one would be terrestriality. The other would be endothermy," says Albert Bennett, an evolutionary physiologist at the University of California, Irvine. Endotherms have a higher resting metabolic rate than that of ectotherms—and with that metabolic acceleration comes drastic changes in physiology and behavior. Muscle cells fill with mitochondria (cellular energy factories) as they become more aerobic, while enzymes associated with anaerobic metabolism decline. The circulatory system also changes. What an endothermic animal gains is stamina and the ability to maintain a constant warm body temperature. But there are costs as well: Energy requirements—food and oxygen intake—increase by about 20 to 30 times over those of reptiles, Bennett says. Which animals were the first to evolve this adaptation is no small question.

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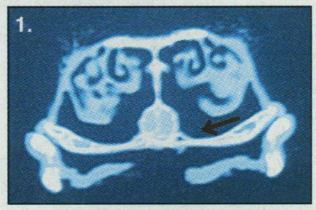

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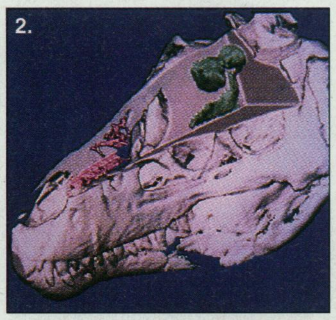

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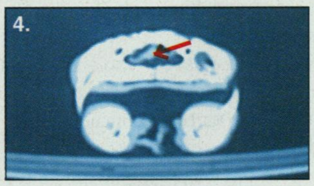


Follow the nose. Arrows indicate nasal passages. 1. A CT scan shows prominent respiratory turbinates in the passages of an ostrich. 2, 3. The 3D rendering of a *Nanotyrannus* skull, and a cross section of the jaw, shows a small passage that might be too tiny for turbinates. 4. Crocodiles have a similar condition.

A heated debate. It became a big question for dinosaur research in the 1970s. Paleontologist Robert Bakker, in papers and his book *The Dinosaur Heresies*, noted that dinosaurs showed signs of high activity levels—such as erect posture—that didn't really fit the classic portrait of ectothermic, reptilian behavior. Size was also a big issue: The huge animals needed to grow quickly—too quickly, researchers thought, for a creature with a reptilian metabolism. These notions spurred explorations of extinct physiology. People wanted to know, says paleontologist Peter Dodson of the University of Pennsylvania, Philadelphia, whether "dinosaurs lived life in the fast lane or in the slow lane."

Yet most of the revelations, say Dodson, Weishampel, and others, have been rather murky. "The big problem is that the important traits related to endothermy don't fossilize," Bennett says. That means researchers have been left to squeeze metabolic information from fossil bones. Reese Barrick and William Showers of North Carolina State University, for example, have tried to tease clues from variations in the ratio of oxygen isotopes in bone. Such ratios are temperature-sensitive, Barrick and Showers have argued, and thus should be more variable in ectotherms than in endotherms. When they analyzed ratios in tyrannosaurus bones, Barrick and Showers found a consistency they ascribed to endothermy (*Science*, 8 July 1994, pp. 188 and 222).

But this work "has not been well received," says Anusuya Chinsamy-Turan of the South African Museum in Cape Town, because of questions about how fossilization could skew the isotope ratios. Alan Feduccia, an evolutionary biologist and specialist in avian evolution at the University of North Carolina, Chapel Hill, adds that consistent ratios indicate only that body temperature was steady, not how it was stabilized. Ectotherms with large enough bodies, like sea turtles, can have a fairly constant body temperature—and tyrannosaurs were bigger still. Although Barrick stands by the research, Weishampel says this and other efforts, such as comparisons of dinosaurian and modern reptilian bone growth rates, "have all become moribund. They are not tied closely to thermoregulatory styles."

Respiratory turbinates, Ruben argues, are very close. These coils of skin-covered cartilage or bone fill the front nasal passages of "over 99% of living mammals and birds," he says. [Exceptions tend to have specialized breathing apparatuses, such as elephants (trunks) and pelicans (sealed nostrils).] And they are completely absent in living reptiles.

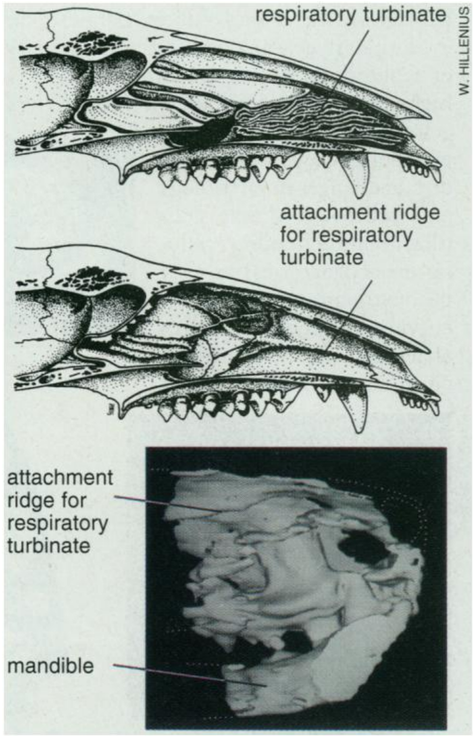
What explains this distribution, Ruben says, is endothermy. The same elevated metabolism that generates heat requires a lot of oxygen, so mammals and birds do a lot of breathing—their oxygen consumption rate at rest, in a lab, is about 20 times higher than that of similar-sized reptiles. And a lot of breathing tends to dry any animal out. Ken Nagy, a physiological ecologist at the University of California, Los Angeles (UCLA), who studies respiration, estimates that even a slow-breathing reptile loses 25% of its total daily water loss through its nose and mouth. Accelerate a reptile to a higher mammalian or avian breathing rate, Nagy says, and respiratory water loss would go up about 17 times. (Water intake would also increase, but endothermy is still a costly propoosition.)

Turbinates across time. Mammals and birds avoid this with turbinates. When an animal inhales, cool air passes over warm turbinate tissue, gaining heat and moisture—and cooling the turbinates, Ruben says. When the animal exhales, the newly cool turbinates recapture heat and moisture before it leaves the body. "So this is a character tightly linked to endothermy," says Hillenius, a former graduate student of Ruben's who is now at UCLA. "And not just linked but causally linked." That makes it a good marker of endothermy in the fossil record.

Except for one problem: Turbinates are delicate structures, and they often don't fossilize. But in mammals, say Ruben and Hillenius, they leave behind a distinctive ridge of bone in the nasal passage where the turbinate was attached; in birds, what remains are small bony buttresses. And by examining many specimens, Ruben and Hillenius found three other clues. One is location: A sense-related structure called the olfactory turbinate, also found in reptiles, can leave similar ridges, but the respiratory version is always attached much closer to the front of the passage. Second is size, because the nasal passage itself has to be large enough to accommodate the turbinates. Finally, small duct holes are present just above the ridge, to help the turbinates remain moist.

Armed with this description, and some computerized tomography (CT) scans of fossil animals, Hillenius in 1994 traced respiratory turbinates back to the origin of mammals—about 160 million years ago—and beyond. He found them in six different cynodonts, mammalian ancestors that first appeared about 250 million years ago. He also saw them in a sister group that appeared a few million years earlier. But the tracks stopped just about there. In pelycosaurs, reptilian animals that sit at the base of the mammalian lineage about 300 million years ago, he detected nothing (*Evolution*, vol. 48, no. 2, 1994). Bennett, who has argued that a need for stamina, rather than for regulating body temperature in a variable climate, drove the evolution of endothermy, points out that mammal ancestors lived in tropical climates and would have had no need to generate heat. But for these predatory animals, the ability to chase over long distances could have been a big advantage.

Ruben then began to follow the avian lineage back in time. He made it as far back as the late Cretaceous, about 70 million years ago, to a bird called *Hesperornis*. The bird had large nasal passages and structures to support turbinates. A related bird, *Ichthyornis*, had a broad chest and big keeled sternum, with attachments for massive wing muscles. The muscle size, coupled with the location of the fossils—in the middle of an ancient sea, hundreds of miles from the shoreline—implied that the bird had the stamina and power needed for long flight. Says Feduccia, who believes endothermy in birds originated somewhat earlier: "That ain't no ectotherm."



Revealing ridge. *(Top)* A respiratory turbinate fills the nasal passage of an opossum. *(Middle)* A ridge reveals where it was attached. *(Bottom)* A CT scan of a therocephalian—an extinct mammal ancestor—shows a similar ridge.

But a class of more primitive birds, known as the sauriurine birds, showed none of the nasal architecture associated with endothermy. Its absence fits inferences about the lifestyle of the most famous sauriurine, *Archaeopteryx*, which lived about 160 million years ago. *Archaeopteryx* was apparently designed for short flights, says Ruben, not long runs: It had a skinny chest with no room for big muscles. Yale University's John Ostrom, who has examined all seven known *Archaeopteryx* specimens, pointedly reserves judgment on the bird's metabolic status, although he agrees that it was "an imperfectly designed flier."

And what about *Archaeopteryx*'s relatives, the dinosaurs? Ruben has examined CT scans of two specimens, *Nanotyrranus* (a smaller *T. rex*) and a birdlike dinosaur called an ornithomimid, and found nothing even close to a respiratory turbinate. "And the nasal passages are too small anyway," Ruben says. "Any turbinates would obstruct air flow." A direct physical examination of another dinosaur skull, from a *Dromaeosaurus* (a relative of the velociraptors, the compact hunters featured in *Jurassic Park*), yielded similar findings. From these representatives of three different groups, Ruben concludes, it would be very hard to argue that extinct dinosaurs were endothermic. Feduccia agrees: "This turbinate work is very convincing. Hot-blooded dinos are cooling down."

This does not mean dinos were slothful, Ruben adds quickly. Varanid lizards can cover several kilometers per day, he notes. Still, other scientists want to ensure his ideas meet the cool test of reality. Several worry that fossilization distorts fragile nasal structures, creating false impressions. Rowe notes that a true test for functional turbinates would be to measure their surface area—a small area wouldn't recover enough water—but even CT scans can't reveal that. And UCLA's Nagy thinks it's possible that endotherms could have lived without respiratory turbinates. The extra water required "is not insubstantial," Nagy says, particularly for animals living in a dry place. "But if you live in a wet place, you can just take extra time when drinking." Many dinosaurs, he points out, lived in wet places.

And Horner thinks that perhaps some dinosaurs had respiratory turbinates after all. He has a CT scan of the skull of a hadrosaur, a duck-billed dinosaur, with a turbinate attachment ridge. It meets all the criteria by which Ruben distinguishes respiratory turbinates from olfactory ones, he says. "If I thought it was olfactory," he says, "I wouldn't bring it up. Maybe different dinosaurs had different strategies."

That notion—that some dinosaur groups were ectothermic while some had a form of endothermy—gets a small chorus of approval. "It may have been, in the late Jurassic, that there was a mosaic" of adaptations, says Dodson. "I don't think it has to be one or the other," says Rowe. And Barrick says that his recent studies show a mixed bag of thermoregulatory styles among dinosaurs. More fossils may yield better answers. And that's the real value of Ruben's work, sums up Weishampel—his observation of turbinate function gives researchers something to look for: "Now it's a matter of the observations chasing the fossils."

–Joshua Fischman