

Generating Heat: New Twists in the Evolution of Endothermy

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The crocodile rests in the water, only its narial openings and eyes protruding from the water's surface. It is watching and waiting for a meal on feet (or with fins, scales, or feathers) to move by, when it will snap up its victim in its jaws, crush it, and munch it down in one piece.

We all know that crocodiles and other extant reptiles are ectotherms, warming their bodies by basking in the sun, then cooling off in the water. But a new hypothesis suggests that modern crocodilians are descended from warm-blooded (endothermic) animals and secondarily reevolved ectothermy. A group led by Roger Seymour of the University of Adelaide, Australia, postulates that the crocodile is descended from endotherms, animals that produce heat internally. John Ruben, of Oregon State University, and Willem Hillenius, of the College of Charleston, South Carolina, posited a vehement critique of this paper, and Seymour ardently defended it—all in the November/December 2004 issue of *Physiological and Biochemical Zoology*. But this begs the question: do crocodilians represent an example of parallel evolution of endothermy, with a somewhat unusual twist, or have they and their ancestors always been ectothermic?

The evolution of endothermy is a fairly intensively studied niche topic. Evolutionary biologists agree that full or partial endothermy must have arisen separately in a number of species, among which are some sharks, tunas, reptiles, and, either together or separately, birds and mammals. Even some insects are endothermic. Because the animals in which endothermy originally evolved are long since extinct, the papers on evolution of endothermy are speculative. Many are based on observation of living animals or experimentation: metabolic studies, exercise physiology, cold-stress responses, and anatomical evidence. Some studies compare extant animals to fossils. And others even discuss the role of behavior in the evolution of endothermy. But it is unlikely that the true origins of endothermy will ever be found, as the fossil record provides only food for speculation, not proof.

Fascination with reptiles

Other cutting-edge hypotheses are based on crocodilian biology, and some of the earlier research on temperature tolerance—in an attempt to explain the mass extinction of dinosaurs in the Cretaceous—was done in the 1940s on American alligators. Edwin H. Colbert, curator of fossil reptiles, amphibians, and

fishes at the American Museum of Natural History in New York; Raymond B. Cowles, a zoologist at the University of California, Los Angeles; and Charles M. Bogert, curator of amphibians and reptiles at the American Museum of Natural History, subjected American alligators, *Alligator mississippiensis*, from hatchling size up to nearly two meters in length, to heat—tying them to stakes or frames on a lawn in the sun or immersing them in hot water—and to cold water. They found that the animals were more cold tolerant than heat tolerant. Although their experiments—which would never be allowed by an animal care oversight committee today—did not support the hypothesis that excessive heat at the end of the Cretaceous could have extirpated the dinosaurs, they also didn't show why crocodilians should have been the last reptilian member of the archosaurs to survive.

However, in the 1950s, Cowles went on to study metabolism in other reptiles, devising fur coats for the savannah monitor lizard, *Varanus exanthematicus*, forming a layer of insulation. But putting fur on them didn't make them endotherms, as they still needed heat from their environments. In a more recent review of the field, published in *Evolution* in October 2000, Albert Bennett and James Hicks, of

the University of California, Irvine, and Alistair Cullum, of Creighton University in Omaha, Nebraska, pointed out that Cowles's experiment showed that development of a layer of insulation in reptiles would have limited the development of behavioral thermoregulation (basking in the sun, jumping into water, and so on). Nevertheless, several authors note that insulation would need to be a prerequisite or corequisite of evolving endothermy. Cowles's lizards, apparently, were ectothermic.

The fascination with reptiles for studying the evolution of endothermy continued. In the early 1960s, Herndon G. Dowling, who was curator of the Bronx Zoo's Reptile House, studied shivering in the female Burmese python (*Python molurus bivittatus*) that laid her eggs on exhibit at the same time every year. He recalls, "We had both Asian (*P. molurus*) and African (*Python sebae*) [pythons] lay eggs at the same time and were looking for the reason for the temperature of the former remaining steady, whereas that of the African varied with the temperature of the enclosure. The obvious muscle contractions of *P. molurus* [as she coiled around her clutch of eggs] showed the way, and we got an NSF grant to set up labs and provide instruments to record the various effects." Dowling stuck thermistors from a brand-new telethermometer into the snake's coils and noted that she was raising her body temperature above that of her surroundings.

"Here was a cold-blooded animal that generally does not care for its young, that was protectively incubating its eggs," says Peter Brazaitis, who was a keeper at the zoo at the time. Dowling's subsequent paper, coauthored with Victor Hutchison, now professor emeritus at the University of Oklahoma, and then-graduate student Allen Vinegar, is often cited to prove that some pythons indeed have the ability to raise their body temperatures through internal physiological mechanisms. Dowling, who is retired from New York University, remarks, "This heat production is probably related to the fact that *P. molurus* ranges farther north (approaching the Temperate [Zone]) than any other Asian



In the 1960s, Herndon Dowling noted that the Burmese python, Python molurus bivittatus, at the Bronx Zoo shivered as she remained wrapped around her clutch of newly laid eggs. Use of the thermistor showed that the shivering was thermogenic and maintained the clutch at an appropriate temperature for development. Photograph: © Wildlife Conservation Society.



By measuring an American alligator's oxygen consumption on a treadmill, Colleen Farmer and colleagues found that alligators' basal metabolic rate was low, while their maximal oxygen consumption during exercise was moderately high. Photograph: Andrew Gillman, University of Utah.

python, and probably it was adapted to retain the brooding temperature" on cool nights. He points out that years later, other researchers found that the Australian python, *Morelia spilota*, which ranges to southern Australia, also was "reported to 'shiver' to raise [its] body temperature during brooding."

Running reptiles on treadmills

Reptile metabolic studies continue to attract those who seek to understand the reasons for endothermy. Colleen Farmer, of the University of Utah in Salt Lake City, has studied exercise physiology in reptiles—running them on a treadmill—to determine rates of oxygen consumption with respect to their basal metabolic rate (BMR). BMR is the amount of metabolism necessary to sustain the internal organ function of an organism absent any activity. Farmer notes that in ectotherms the standard ratio of the maximal to the resting metabolic rate, which is called the aerobic scope, should range between 5 and 10. That means that an active animal should be increasing its oxygen consumption between 5 and 10 times that measured at rest, as hypothesized by Bennett and Ruben in a paper published in *Science* in 1979. They stated that endotherms would have higher aerobic scopes than ectotherms.

Bennett and Ruben, along with Hicks, continued their work by again looking at metabolic rates in resting savannah lizards and found that even when they were fed excessively, increasing their visceral metabolic rates, the animals became neither endothermic nor homeothermic (maintaining a constant body temperature). Bennett and Ruben referred to the aerobic scope as the absolute increment of the maximal rate of oxygen transport above the resting rate of oxygen transport. This, they said, should be higher in endotherms. Farmer notes that Bennett and Ruben's hypothesis on the aerobic scope of endotherms versus ectotherms is called the aerobic capacity model. It posits that high BMR evolved as a response to selection for aerobically supported locomotor performance. "When I was making these measurements," says Farmer, "I was getting aerobic scopes that



Development of parental behavior, as is illustrated by this American alligator (Alligator mississippiensis), may have been important in the evolution of endothermy. This mother alligator was digging up her nest to release the young (top) and had picked up one of her hatchlings in her jaws (bottom). She then carried the hatchling to the water, where she released it. Recent papers hypothesize that crocodylians' ancestors were endothermic and these animals have re-evolved ectothermy. Photographs: © Myrna Watanabe.

were far too variable for this hypothesis to be correct.... You can find vertebrates that have very high VO_{2max} [values] that are not endotherms, so there's got to be a better explanation." VO_{2max} is the maximal oxygen uptake capacity of the lungs. Farmer adds, "I knew that pythons had thermogenesis when they were taking

care of their eggs, and I knew that temperature was important to their development, and I knew that hormones were important to metabolic rate—my data didn't fit the other well-established paradigm." Farmer points out that the American alligator has an aerobic scope that is greater than 40 when activity is mea-

sured on a treadmill. But if measured on a flume, which would measure swimming activity, Farmer suspects the aerobic scope of an alligator would be much higher than 40, although this may not be the case. She adds that alligators have "a very low BMR, while having a moderate maximal rate of O_2 consumption when exercising on a treadmill." Their aerobic scopes are too high for them to be ectotherms, but they aren't endotherms, either.

Endotherms make good parents

So why do alligators, which can produce real power if they need it for swimming, mating, aggression, defense, or feeding, need a very high aerobic scope? The answer, suggests Farmer, is parental care. If Seymour and his colleagues are right, crocodylians are an unusual case, and the parental care hypothesis, he notes, would be tenuous here.

But Farmer links her hypothesis to endotherms. "On average," she says, "there is a correlation between higher levels of activity and endothermy. I think the explanation lies in that endotherms provision their young." She notes that animals with a high VO_{2max} have much endurance, which is important for fighting for mates, social status, size of foraging range, and ability to forage. "The energy requisite for feeding young in birds and mammals is roughly two- to fivefold greater than for a nonreproductive individual of the same species." Farmer explains that endotherms can have a rapid rate of reproduction, and because they feed their offspring, the young can grow faster than young that receive no parental care and are on their own for feeding. "This idea of being at your optimal temperature 24 hours a day is going to speed up growth," says Farmer.

Pawel Koteja, of Jagiellonian University in Kraków, Poland, has in recent years also come to the conclusion that the origin of endothermy is related to parental care. He summarizes the two types of hypotheses on its evolution. "The first assumed that thermoregulatory advantages were sufficient to explain the evolution [of] high basal metabolic rates and endothermy in

birds and mammals,” he notes. “The second assumed that the evolution of high BMR was (at least initially) a side effect of a selection for other traits.” He adds, “My hypotheses that endothermy evolved as a side effect of intensive parental care associated with feeding the young [published in *Proceedings: Biological Sciences* in 2000] belong to the second group.” Koteja sees the parental care model as an “alternative to all the ‘thermoregulatory’ hypotheses as well as an alternative to the ‘aerobic capacity model.’” He notes, “The keystone of the ‘parental care’ models is that the cost of an increased metabolic rate of adults is rewarded by several advantages to embryos and/or juveniles.” Farmer, however, hypothesizes that parental care came first. “I’m saying there’s independent selection for metabolic rate—it’s about rapid rates of reproduction.” In Farmer’s view, the gist of endothermy can be distilled simply to a better chance of survival.

Searching for clues among other taxa

Although Koteja admits that the fossil record doesn’t preserve characters that would give an indication of “an association of social-family structures and endothermic physiology in ancestors of birds and mammals,” he believes that he and his colleagues can, at the very least, look for a heritable basis for metabolic traits. They are studying this in the bank vole, *Clethrionomys glareolus*, a small, wild European rodent that adapts well to laboratory conditions. In a paper that appeared in *Evolution* this past March, Koteja and colleagues reported “a positive additive genetic correlation between BMR and the aerobic capacity in a wild rodent species, which provides the strongest so far available evidence for plausibility of the aerobic capacity model.” Yet, he adds, “I am convinced that the mechanism alone would not be sufficient to result in the tenfold difference between the metabolic rates of reptiles and birds or mammals.” Extrapolating the results of this study, he notes that if selection were for high aerobic capacity, BMR would be increased. But, he says, he would expect



Barbara Block, of Stanford University, inserts a tag into a giant bluefin tuna to trace its movements. Tunas have evolved endothermic mechanisms to keep their muscles warm for their long-distance swimming and deep diving. Photograph courtesy of Barbara Block.

that the aerobic scope should also increase, which, indeed, did not occur in the evolution of birds and mammals, leading him back to parental care as a likely evolutionary path to increased BMR.

“What was the evolution of endothermy all about?” rhetorically asks Barbara A. Block, of the Hopkins Marine Station, Stanford University, Pacific Grove, California. “One hypothesis,” she continues, is “[aerobic] capacity or niche expansion. [These are] great hypotheses for birds and mammals. The animals you need to study to get the answers don’t exist anymore: they’re dinosaurs.” But she notes that in fish, researchers can study sister taxa of endothermic fish. “We can go to the sister taxa and ask, ‘What is the range of the animals, such as the bonito; how does it compare to endothermic taxa?’”

“In fish,” explains Block, “there are three endothermic groups: the tunas, the billfishes, and the lamnid sharks.” The sharks are not related to the other two fish groups and have separately evolved endothermic adaptations. Block notes that the people studying endothermy in fish are asking the same questions the people who study mam-

mals ask: Where does the heat come from? How is metabolic rate related to endothermy? What behavioral and ecological mechanisms led to this adaptation? Is evolution of heat conservation the following step, or did it evolve before high metabolic rate?

In a number of papers published last year (in *Physiological and Biochemical Zoology* and *Journal of Experimental Biology*), Kathryn Dickson, of California State University in Fullerton, and Jeffrey Graham, of the Scripps Institution of Oceanography in San Diego, describe the similarities between all three groups of fish, which show regional endothermy—heat organs that warm the brain, some that warm the eyes, others that warm the viscera, and methods to heat the slow-twitch locomotor muscles. These are all large, predatory, oceanic species that can migrate long distances and that also may dive deep down to layers of cold water, so they experience rapid temperature changes. Within the Scombridae, the family of mackerels, bonitos, and tuna, there is evidence of heat organs in almost all of the tunas, with some, such as the albacore and bluefin tunas, able to elevate the temperature in their muscles, eyes,

brains, and viscera. The butterfly mackerel, *Gasterochisma melampus*, has heater tissue in the cranium. The bonitos, on the other hand, are completely ectothermic.

Dickson and Graham agree with Block and her colleagues that endothermy arose separately in the sharks and scombrids—and perhaps separately among the various scombrids—when the ocean began to cool, at some point between 2 million and 40 million years ago. At that time, fish species died out, adapted to tolerate the colder water (as the bonitos did), or evolved endothermic mechanisms. Evolving endothermy would allow those species to exploit expanded thermal niches, including niches with coastal upwelling and in higher oceanic latitudes.

Mechanisms for generating heat

Tunas with endothermic adaptations can dive for food at greater depths and survive at higher latitudes than those fish that do not have these adaptations. Block and colleagues can test hypotheses about how these fish survive and differ from their ectothermic cousins because the Monterey Bay Aquarium has the fish species—endothermic bluefin and yellowfin tuna and ectothermic bonitos—and the equipment to carry out physiological and biochemical testing.

Not only must there be behavioral and ecological mechanisms that support endothermy, but there also need to be biochemical and physiological mechanisms. Among the adaptations in fish is the location of slow-oxidative myotomal muscle, which in endothermic fish is insulated under other tissue, rather than being just beneath the skin, as it is in ectotherms. This is the muscle that contracts during swimming. Conserving the heat thus produced is essential in maintaining a warm body temperature. Digestive functions also produce heat, and the presence of visceral countercurrent heat exchangers (part of the circulatory system), called *retia mirabile* (“wonderful nets”), allows this heat to be maintained in the body. Special organs may heat the brain or the eyes. For example, ocular muscles may heat the eyes in endothermic sharks,



Thermoregulatory and behavioral characteristics of the short-beaked echidna, Tachyglossus aculeatus, may be similar to those that developed in protoendotherms, ancestors of modern-day endotherms.
Photograph: Gordon Grigg.

and heater tissue derived from ocular muscles heats the cranium in both billfishes and butterfly mackerel. The advantages of warming the head may not be obvious. Says Block, “Warming your eyes helps you to have better retinal responses,” perhaps aiding in seeing predators. “Billfishes have gone to a lot of effort to heat the head.” Swordfish, she explains, dive to great depths to chase giant squid, so a warm head is advantageous to them.

Among the biochemical adaptations are increased amounts of myoglobin for carrying oxygen, and the ability to maintain a high heart rate because of increased activity and amounts of the SERCA2 enzyme, which is associated with higher calcium uptake and activity of ATPase in the heart.

From reptiles to...echidnas?

Gordon Grigg and colleagues at the University of Queensland in Brisbane, Australia, recently postulated that “the step from reptilian thermoregulation to endothermy is not as large as usually supposed because reptiles show nearly all the necessary elements.” In a paper published in *Physiological and Biochemical Zoology* in 2004, Grigg and colleagues indicate that the demarcation between reptilian ectothermy and endothermy in mammals and birds is not entirely clear. They note, for example, that homeothermy, in which an organism

maintains a constant body temperature, “may not be characteristic of even the majority of endotherms.” The serial steps leading to endothermy, each of which may be selected for evolutionarily, include lizardlike attributes such as basking and seeking shelter, internal insulation and a large body size (which maintains temperature by inertia), thermogenesis by muscular contraction (as in some pythons), increased leakiness of cell membranes (which creates heat), adaptation to a cooler climate (including possible winter hibernation), year-round activity in a warmer climate, ability to live in a cold climate (with obligate hibernation), and, finally, the ability to live in various climate types, as occurs with a typical endotherm.

Grigg and colleagues use the short-beaked echidna, an Australian terrestrial anteater, as an example of a mammal with characteristics that could be found in a protoendotherm, the animals that were ancestral to modern-day endotherms. Echidnas are monotremes, related to the platypus, and they are heterothermic. They fit Grigg’s last step for evolution to endotherms: They survive in various climates, from cold to hot. But their body temperatures over a day vary by as much as 2 to 5 degrees Celsius, and they show activity patterns related to the climate in which they live, indicating that they thermoregulate behaviorally to some extent. They can vary their peripheral blood flow to aid in heat loss, they undergo periods of short-term and long-term hypothermia (torpor and hibernation), and they can carry out their normal behaviors even at low body temperatures. Grigg and coauthors note that echidnas show homeothermic endothermy during incubation of their single egg.

Seymour and colleagues (including Grigg) take this line of thinking one step further. If animals can evolve endothermy, they hypothesize, then they can evolve back to ectothermy. “My hypothesis,” Seymour says, “stems from the clear correlation between endothermy, high metabolic rate, high arterial blood pressure, and the four-chambered heart that we see in living endotherms.” Having noted, however,

that crocodiles have a four-chambered heart but are ectotherms, he decided to study the structure of crocodile embryos to see if they can separate the arterial and venous blood supplies (which, during shunting, can mix within the heart in adult crocodilians), and create high systemic blood pressure. "It turned out that this was true," says Seymour, which he considers to be one of several important pieces of evidence that crocodilian ancestors were endothermic.

"It became apparent that the crocodilian lineage reverted to ectothermy sometime in the Mesozoic, and it may have been associated with the evolution of the semiaquatic crocodilian design that we see today," Seymour states. As Grigg points out, "Clearly, many earlier crocs were more active, terrestrial, and of a size and apparent behavior which

would be quite consistent with the evolution of endothermy *and* very different from the modern aquatic sit-and-wait predators." He adds, "There are no aquatic sit-and-wait endotherms that I can think of."

What's next?

Seymour suggests that both genetic and paleontological studies would yield more evidence for his hypothesis. "First, one could look for specific genes associated with endothermy.... Secondly, one could be aware that fossil basal archosaurs might show the kinds of features that paleontologists are calling insulation in theropod [feathered] dinosaurs." In other words, a search of the fossil record might show that the immediate ancestors of the early archosaurs may well have had features, such as insulating feathers, that

are found on feathered dinosaur specimens. This may be evidence that endothermy indeed could have evolved in early crocodilians that had insulation.

Koteja goes one step beyond that: "If one finds a paleontological record indicating a presence of parental care in the Mesozoic ancestors of crocodiles, the parental care model will get a substantial support." So finding evidence of feathers and parental care in crocodilian ancestors could be the key to understanding how and why endothermy evolved.

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