Warm-Blooded Dinosaurs: Evidence Pro and Con

Dinosaurs may be gone but they are not forgotten. In fact, the beasts, which have been extinct for nearly 70 million years, are currently the center of a lively controversy among paleontologists. The controversy concerns whether the dinosaurs as a group were warm-blooded the way birds and mammals are or whether they were cold-blooded like modern reptiles.

The proponents of warm-blooded dinosaurs seem to have captured the popular imagination. Both a book* and a television program† intended for general audiences have treated the hypothesis favorably. The idea, after all, is revolutionary; it contradicts the traditional view that dinosaurs, which have always been classified as reptiles on the basis of their skeletal anatomy, were, like other reptiles, cold-blooded creatures whose body temperatures fluctuated with those of the environment. Moreover, the idea is appealing because it could help explain how dinosaurs, which were the dominant land animals for some 140 million years, were so successful for so long.

Many—if not most—paleontologists, however, have remained skeptical about the possibility that dinosaurs were warm-blooded. The skeptics, whose views have not been widely broadcast among the public, are concluding that the hypothesis may be revolutionary and appealing but it is nonetheless wrong. As the situation now stands, proponents of warm-blooded dinosaurs have developed several lines of evidence in support of their position while the critics maintain that all the lines are flawed with regard to either the data or their interpretation.

A central issue in the discussion concerns the level of activity displayed by dinosaurs. Reptiles generally have the reputation of being slow and sluggish creatures not capable of much sustained activity. This inactivity is often attributed to their being cold-blooded (ectothermic) animals. When ectotherms are cool, their metabolic rates are low and the animals do not produce enough energy to permit vigorous action. Only by taking advantage of environmental heat sources—basking in the sun, for example—can reptiles and other ectotherms warm their bodies and raise their metabolic rates to levels that permit a high degree of activity. (Metabolic rates double or triple with every 10°C increase in body temperature.)

Thus, ectotherms are at a disadvantage compared with endothermic animals. The metabolic rates of endotherms are high enough to produce the heat required to maintain a constant warm body temperature and thus to support a continuous high level of activity. In other words, endotherms are independent of their environment and always ready to go, whereas ectotherms are at the mercy of the environment when it comes to producing enough energy to hunt for food or escape their predators.

Working independently, Robert Bakker of Johns Hopkins University and John Ostrom of Yale University concluded that dinosaurs did not fit the picture of the slow, sluggish reptile. They based this conclusion on their studies of the anatomy of dinosaur bone fossils. They showed, for example, that the animals were relatively long-limbed. Moreover, they walked with an erect posture, like that of birds and mammals, in which the limbs are held in a near vertical position beneath the shoulder and hip sockets.

Long limbs and an erect posture permit a great deal more agility and speed than does a sprawling gait, which is characteristic of animals whose limbs project out to the side. The investigators hypothesized that the fully erect postures reflected high continuous levels of activity that in present-day vertebrates are correlated with endothermy. (All modern endotherms have erect postures, whereas all modern ectotherms are sprawlers.) Bakker wrote in the journal *Discovery* in 1968 that the animals were "fast, agile, energetic creatures that lived at a high physiological level reached elsewhere only by the later, advanced mammals" (Fig. 1). With Peter Dalton of the University of Bridgeport, he has suggested that dinosaurs as a group were different enough from ordinary reptiles to deserve removal from the class Reptilia and incorporation into a new class, the Dinosauria.

To Bakker, the remarkable success of the dinosaurs seems puzzling if they were cold-blooded. He points out that, even though mammals existed for most of the 140 million years of dinosaur dominance, mammals remained small and insignificant until dinosaurs were extinct. The mammals were endothermic, yet dinosaurs were competitively superior to them. And Bakker thinks that their superiority would be hard to explain unless dinosaurs, too, were endotherms.

Of course, not everyone agrees that high activity necessarily means that the dinosaurs were endothermic. Philip Regal of the University of Minnesota points out that the common picture of the sluggish reptile is misleading. They can, for example, move very rapidly if startled. In addition, he has shown that some lizards are as active as rodents under given conditions, although the reptiles' endurance is not as good as that of mammals. Regal suggests that the duration of reptilian activity is limited not by their ectothermy but rather by their hearts and circulatory systems, which do not pump blood as effectively as the cardiovascular systems of birds and mammals. As a result, the tissues of reptiles become deficient in oxygen during activity and the animals must rest until this oxygen debt is paid off.

According to Regal, the ectothermy of reptiles may itself be due to the types of hearts that they have evolved. The hearts, which have advantages for some aspects of the reptilian life-style, cannot pump enough blood to support the sustained high metabolic rates characteristic of endotherms.

Regal concedes, however, that the dinosaurs probably had double-pump hearts similar to those of endotherms. Ostrom points out that the upright posture of dinosaurs means that they carried their heads above their hearts—sometimes high above their hearts, as in the case of Brachiosaurus with its 18-foot neck. Thus they needed high blood pressures to pump the blood to their brains; at the same time, blood had to be pumped to the lungs at low pressures to prevent their filling up with fluids forced through the walls of the small pulmonary blood vessels.

Mammals and birds achieve these goals simultaneously by means of a four-chambered heart that is essentially a double pump, one circulating blood to the lungs and the other circulating blood to the rest of the body. Because of their posture, dinosaurs needed a similar heart and, consequently, they probably had the circulatory equipment necessary for

**The Hot-Blooded Dinosaurs: A Revolution in Paleontology*. Adrian J. Desmond. The Dial Press/James Wade. New York. 1976. 238 pp. †A NOVA production, also entitled "The Hot-Blooded Dinosaurs."

0036-8075/78/0331-1424$00.75/0

an active life and endothermy. Endothermy is not an automatic consequence of possessing a four-chambered heart, however. Crocodiles have such hearts but are ectotherms.

Thus, whether dinosaurs were true endotherms relying on their own high metabolism to maintain warm bodies the way birds and mammals do is another question. Bakker definitely thinks they were. Ostrom, however, is more conservative. He maintains that some dinosaurs may have been true endotherms but that others may have simply been members of the broader class of homeotherms, that is, animals that can maintain a constant body temperature by any means, including those dependent on environmental heat sources.

The large size of dinosaurs may have been an adaptation to help them conserve environmental heat and thus maintain a warm body, according to several paleontologists. Although practically every piece of evidence concerning dinosaur temperature regulation is open to challenge at some point, no one questions that dinosaurs were large. Nicholas Hotton of the Smithsonian Institution calculates that 80 percent of living mammals are smaller than the smallest dinosaur, which weighed about 10 kilograms; more than half of the dinosaurs weighed more than 2 metric tons—a size attained by only about 2 percent of modern mammals.

The fact that there were no small dinosaurs suggests to many investigators that large body size was in some way critical to dinosaur survival. This hypothesis is not new. It was proposed by Edwin Colbert, now at the Museum of Northern Arizona, and his colleagues in 1946. More recent calculations performed by James Spotila and his colleagues at the New York State University College at Buffalo also suggest that large size may have played a role in maintaining a warm body temperature.

Based on a model they developed for heat conduction in reptiles, the investigators concluded that giant reptiles living in a warm climate, such as that prevailing when dinosaurs enjoyed their hegemony, could have maintained a constant warm body temperature even though they had a low, reptilian metabolic rate. Because of their large body size, the animals would have had a high heat storage capacity that would have dampened the changes in body temperature brought about by environmental temperature changes. Large reptiles with the high metabolic rates characteristic of endotherms might even have had a problem with overheating, according to the Spotila group. Nevertheless, Bakker points out that endothermy is an advantage even for large animals in warm climates. Mammals, some of very large size, have been the dominant land animals in the tropics for the past 65 million years.

A major link in Bakker's chain of evidence for endothermic dinosaurs are his calculations of the predator-prey ratios in several dinosaur fossil deposits. Endothermy while advantageous, is also very expensive because the high metabolic rates required to maintain it mean that the endothermic animal has to eat a lot. Thus it should take a substantially larger prey population to support an endothermic predator than an ectothermic predator of the same weight. Measurements of predator-prey ratios in modern animal communities show that endothermic predators require at least ten times the prey required by ectotherms. The ratios for the former are about 0.03 and for the latter they are about 0.3 to 0.5. Bakker's calculations of the ratios for the dinosaur communities gave values of about 0.03—in the range for endotherms—for all except the very earliest communities. He concluded that there was a sudden transition from ectothermy to endothermy during the evolution of dinosaurs.

One of the premises used by Bakker in interpreting his data has been questioned, however. Almost all measurements of metabolic rates have been performed with small—especially when compared with the sizes of dinosaurs—animals. But the energy requirements per unit weight (or the metabolic rates) of all animals are known to decrease as their weight increases. Only if the rate of the decrease is the same for endotherms and ectotherms will the predator-prey ratios for both groups of animals remain constant, with the value of the ratio for ectotherms staying about ten times greater than that for endotherms at all weights.

But Hotton points out that data collected by other investigators suggests that the energy requirements for ectotherms decline somewhat more slowly than those for endotherms. His plots of the data indicate that ectotherms the size of dinosaurs would require as much food as comparably large endotherms. In other words, the predator-prey ratios for very large animals of both types would be the same; it would not be possible to determine whether dinosaurs were warm- or cold-blooded on the basis of predator-prey ratio measurements.

In reply to this criticism, Bakker says that he has shown that the predator-prey ratios for ectotherms do not decrease with increasing weight in the way suggested by Hotton. He determined the predator-prey ratios for a large number

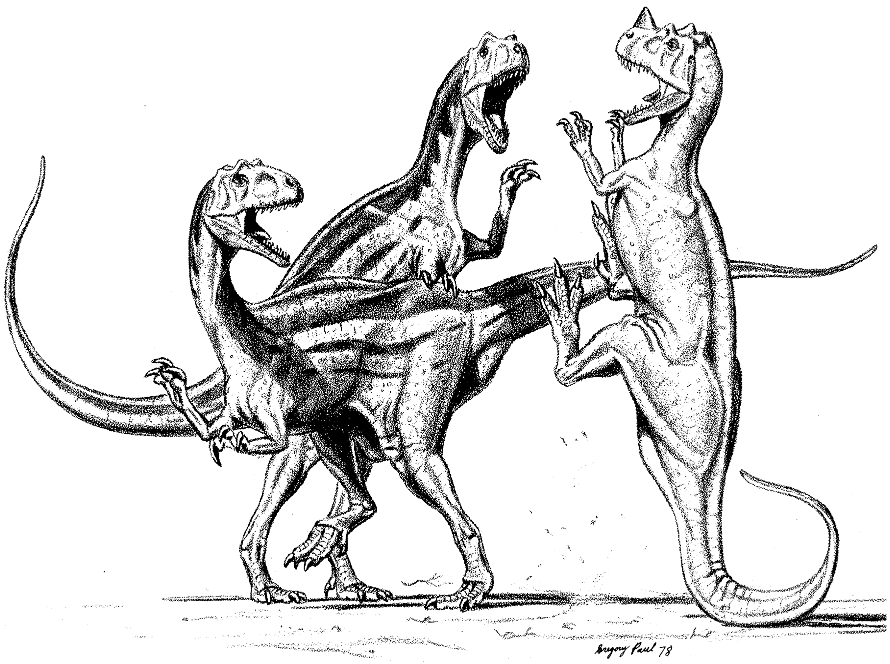

Fig. 1. Agile dinosaurs engaged in combat. The combatant on the right is a Ceratosaurus (average length about 15 feet and average weight about 2000 kilograms). The combination of an unusually powerful tail and large, sharp-clawed hindfeet suggests that Ceratosaurus fought kangaroo-style, balancing on its tail and punching out with its feet. On the left are a pair of allosaurs (averaging about 25 feet in length and 3000 kilograms in weight). Allosaurus was a fast predator with a well-developed jaw mechanism for slashing and bleeding to death its prey. (Illustration copyrighted by Gregory S. Paul, Falls Church, Virginia)

of fossil communities, including communities of endothermic mammals and of very primitive ectothermic reptiles, in addition to those of dinosaurs.

Although a few of the primitive reptiles called finbacks were as large as the smallest dinosaurs for which the ratios were determined, the dinosaur predator-prey ratios were always well within the range for endotherms, whereas the finback ratios were much higher and in the ectothermic range. Bakker says that for the finback predator-prey ratio to decrease to the values observed for very large dinosaurs, the metabolic rate of the finbacks would actually have to increase with increasing weight. Such a phenomenon has never been observed with living vertebrate animals.

Other investigators have questioned Bakker's calculation of the predator-prey ratio for at least one dinosaur community, that in the Oldman Formation of Dinosaur Provincial Park, Alberta, Canada. The arguments are too technical to reproduce but Pierre Béland and Dale Russell of the National Museum of Natural Sciences in Ottawa have calculated that Bakker's estimation of the prey value for the formation is about double what it should be and that his predator value is about half of what they find. Thus, the Ottawa investigators estimate that the predator-prey ratio for the Oldman Formation is about four times greater than that calculated by Bakker.

According to Russell and Béland, there was not enough food in the formation to support the population of predatory dinosaurs there, if they were endotherms. This suggestion agrees with a previous one made by James Farlow of Yale University.

Bakker points out that even a fourfold correction in the ratio does not increase the predator-prey ratio for Oldman Formation enough to bring it into the ectothermic range. Moreover, he has determined the ratios for many additional dinosaur fossil deposits and consistently found low values in the endothermic range.

There are at least three lines of evidence, in addition to predator-prey ratios, to support the hypothesis that dinosaurs were warm-blooded. One of these lines is based on observations by Armand de Ricqlès of the University of Paris that the microscopic structure of dinosaur bones closely resembles that of the bones of many mammals. For example, dinosaur bones have a high density of Haversian canals, as do many mammalian bones. In contrast, the bones of most modern ectotherms have few of the canals.

Haversian canals carry blood vessels longitudinally through bone. Bone needs blood vessels because it is not an inert tissue but is metabolically active. Moreover, it is constantly undergoing remodeling as calcium and phosphate ions are removed and deposited in response to the body's needs.

One theory is that because endotherms have high metabolic rates, their bones would need more blood vessels and Haversian canals than the bones of ectotherms. de Ricqlès has suggested that the presence of a dense Haversian system and of certain other anatomical features in dinosaur bones indicates that the creatures were endotherms. In support of this idea, Bakker points out that the appearance of these bone patterns in dinosaurs coincided with the drop in predator-prey ratios he has observed.

Of course, not everyone agrees that well-developed Haversian systems are necessarily indicative of endothermy. Several investigators have indicated that the correlation between the canals and endothermy is not absolute. Investigators, including Donald Enlow, now at the West Virginia University School of Medicine, and S. O. Brown of the Texas A and M University have found that some present-day reptiles, certain turtles, for example, have many Haversian canals in at least some parts of their bones, and that a number of small mammals and birds have very poorly developed Haversian systems.

Dinosaur Distribution

Bakker also cites the geographical distribution of dinosaurs as evidence in support of their endothermy. Russell has found dinosaur fossils in areas that would have been near the Arctic Circle during the Cretaceous when the dinosaurs were living. Bakker's idea is that only true endotherms, which can supply their own body heat, could have functioned in cold northern climates where there is little sunshine, especially during the winter. Modern lizards, with the exception of a few small species that can hibernate in burrows in winter, are restricted to tropical and temperate climes.

Russell, however, says that the dinosaurs would not have had to be endotherms in order to live that far north. He points out that the climate during the Cretaceous was much warmer than it is now. Although the winters would have been dark then, he thinks that the dinosaurs found near the Arctic Circle would have been mobile enough to follow the sun south for the winter.

The final line of evidence supporting warm-blooded dinosaurs is the evolutionary link between dinosaurs and birds. Ostrom first noted the great similarity between the skeletons of Archaeopteryx, generally considered to be the first bird, and those of certain small carnivorous dinosaurs called theropods. He proposed that the theropods were the ancestors of the birds, which are indisputably endothermic.

Archaeopteryx resembled modern birds in that it, too, had feathers. Many investigators, including Ostrom, think that the main function of feathers is to insulate birds and protect these endotherms from excessive heat loss. Consequently, Ostrom thinks that the fact that Archaeopteryx had feathers is good evidence for the endothermy of the first bird and possibly of its close relatives, the theropods. Not surprisingly, there is a dissenting opinion, Regal's in this case, concerning the evolutionary role of feathers. He thinks that they might have functioned to prevent excessive heat uptake by ectotherms and not heat loss. Nevertheless, most paleontologists concede that if any dinosaurs were true endotherms, the best candidates are the theropod ancestors of Archaeopteryx.

Additional evidence supports this possibility. For example, measurements of brain volume of several types of dinosaurs that were performed by James Hopson of the University of Chicago, indicate that the brains of Archaeopteryx and its close dinosaur relatives were large compared to their body sizes. In contrast, he finds that the brains of other dinosaurs were small compared to the size of the animals and comparable in this regard to the brains of present-day reptiles. Hopson concludes that most dinosaurs, except the theropods, were less active than modern endotherms. He also hypothesizes that low activity suggests low metabolic rates because high rates, such as those characteristic of endotherms, should be reflected in high levels of activity, such as food-gathering. Hopson bases his conclusions on the assumption that high activity and complex behavior patterns require relatively large brains; he will, no doubt, be challenged on this point.

In fact, this whole controversy over temperature regulation in dinosaurs may never be resolved to everyone's satisfaction. Since dinosaurs cannot be rounded up and studied directly, both sides have to rely on their interpretations of the fossil record, which is incomplete, and on analogies with the physiology and anatomy of modern animals. All of the arguments—both pro and con—contain many opportunities for disagreement.

—JEAN L. MARX