Paleontologists long considered dinosaurs to have had the reptilian metabolism popularly referred to as cold-blooded. But in 1970, paleontologist John Ostrom of Yale University suggested that dinosaur metabolisms may have been more mammal- or bird-like than reptilian. There soon followed an article in *Scientific American* by paleontologist Robert Bakker titled “Dinosaur Renaissance” in which was presented evidence and analysis to support warm-bloodedness in all dinosaurs. Bakker thereby initiated debate, still ongoing, about the nature of dinosaur metabolism. In this chapter, we review the evidence supporting mammal- or bird-like dinosaur metabolism and evaluate the debate over this complex and fascinating subject.

**Some Terms and Concepts**

Before studying dinosaur metabolism, we need to become conversant with some basic terminology and concepts. Metabolism is best defined as the chemical processes that provide energy to and repair the cells of an organism. In popular terms, vertebrate metabolisms either are cold-blooded (fishes, amphibians, and reptiles) or warm-blooded (mammals and birds). The nearly equivalent technical terms are ectothermic (for cold-blooded) and endothermic (for warm-blooded or its exaggerated synonym, hot-blooded), based on the Greek roots *ecto* (outside), *endo* (inside), and *thermos* (temperature).

Ectotherms (figure 13.1) receive most, or all, of their body heat from an external source, usually directly from the sun. In contrast, endotherms generate most, or all, of their body heat internally. Endotherms characteristically have high rates of heat production. Ectotherms, however, typically have a slower metabolism. Vertebrates that maintain a nearly constant body temperature (usually \(\pm 2^\circ\) centigrade) are called homeotherms, whereas those in which body temperature varies daily, seasonally, or throughout their life cycles are heterotherms (from Greek *homeos*, similar, and *hetero*, different).

Today, different metabolisms are found in different kinds of vertebrates. The very diverse and dominant land vertebrates, mammals and birds, are...
endotherms, whereas the less diverse reptiles and amphibians are ectotherms. The current success of endotherms relative to ectotherms has incorrectly fueled the notion that ectothermy is an inferior type of metabolism (box 13.1). Also, the great difference in metabolism between living endotherms and ectotherms suggests a marked dichotomy in vertebrate metabolism, endotherm on one side, ectotherm on the other. But endothermy and ectothermy describe only the broad ends of a spectrum of vertebrate metabolisms (see figure 13.1). Some ectotherms, such as tuna, maintain high body temperatures, whereas some endotherms, such as tenrec shrews, are hard pressed to maintain a high constant body temperature. There is great variety in existing vertebrate metabolism, and there is no reason why such variety should not have been present during the past, even in the age of dinosaurs.
The Information

Metabolism is determined by chemical reactions in the enzymes, blood, and internal organs. None of these structures in dinosaurs are known to have fossilized, so it might seem there is very little direct information about dinosaur metabolism. Indeed, wouldn’t we need a time machine and a thermometer in order to determine the body temperatures and metabolisms of dinosaurs!

Fortunately, fossils preserve quite a variety of information on dinosaur metabolism, although much of it is indirect. This information can be organized into several categories and most of it, as we shall see, has been interpreted in different ways.

Posture and Gait

Living ectotherms have sprawling postures and gaits, whereas living endotherms, with a few exceptions, have upright postures and gaits (figure 13.2). The exceptions are mostly aquatic mammals, such as seals and walruses, that have sprawling limbs admirably adapted to propelling them through the water. Living vertebrates show a nearly perfect correlation between posture and metabolism. This correlation may indicate that extinct animals with an upright posture, the dinosaurs, were endotherms.

Two criticisms can be leveled at this conclusion. First, no cause-and-effect relationship has been established between posture and metabolism. Maybe ectotherms can have an upright posture, some (the dinosaurs?) did in the past, and it is only a coincidence that all living ectotherms happen to be sprawlers.

A second criticism is that not all dinosaurs may have had an upright posture. Stegosaurs, ankylosaurs, and ceratopsians have been reconstructed with upright hind limbs and sprawling or semi-sprawling forelimb postures. What does this indicate about their metabolisms? Does it mean (facetiously) their posterior halves were endothermic and anterior halves ectothermic? It probably indicates that factors other than metabolism, such as the heavy skulls and armor of stegosaurs, ankylosaurs, and ceratopsians, which forced a slow and powerful sprawling forelimb posture, also determined a dinosaur’s posture.

Despite these criticisms, the correlation between posture and metabolism in living vertebrates is striking. A subset of this correlation, that all living bipeds are endotherms, also suggests that bipedal dinosaurs were endotherms. But to believe that these correlations indicate endothermic dinosaurs, we must agree that posture is controlled by metabolism, a conclusion still open to some debate.

Figure 13.2
Upright posture characterizes living endotherms, whereas living ectotherms have a sprawling posture.
Speed, Levels of Activity, and Agility

High levels of activity characterize living endotherms, whereas today’s ectotherms generally are slower, more sluggish, and less agile. The qualifier “generally” needs to be used here because some living ectotherms, for example sea turtles, are capable of great speed and agility, if only for short periods of time. Nevertheless, evidence for speed, sustained activity, and agility in dinosaurs would be more consistent with them having had an endothermic rather than an ectothermic metabolism.

Speed, sustained activity, and agility in dinosaurs is evident in their skeletal structures, brain size, and brain complexity, and in the speeds estimated from dinosaur trackways. As we saw in Chapters 4 through 9, the skeletons of some dinosaurs, especially small theropods and ornithopods, in many ways resemble those of fast-running birds and mammals. Key features of this resemblance include elongate, slender limbs and limb joints indicating an ability to flex acutely at the elbow, wrist, knee, and ankle joints. Hollow bones, large claws, limb proportions indicative of habitual bipedality, and long, rigid tails for precision balance during running contribute to the impression of speed and agility in some dinosaurs (Figure 13.3). Some theropod and ornithopod dinosaurs thus seem to have been every bit as quick and agile as living birds and mammals, suggesting that these dinosaurs may have been endotherms.

Some paleontologists assert that the larger dinosaurs, such as ceratopsians, galloped like living endothermic rhinoceroses. But this argument is inconsistent with the limb structures and trackways of the large, quadrupedal plant-eating dinosaurs, which indicate they were slow, powerful walkers. The skeletal evidence for speed, high levels of activity, and agility in dinosaurs, and the inference of endothermy from this evidence, is confined to theropods and ornithopods.

**Figure 13.3**
The theropod Deinonychus well displays many skeletal features suggestive of speed, sustained high activity, and agility.
Relative brain size and complexity provides a second line of evidence of speed, high activity levels, and agility in some dinosaurs. These characteristics of living endotherms require great motor and sensory control by larger and more complex brains than in living ectotherms. If we compare the relative brain sizes of dinosaurs to that of a living ectothermic lizard (figure 13.4), theropods and most ornithopods appear to have been relatively "brainy." But sauropod, ankylosaur, stegosaur, and ceratopsian brain sizes fall well below the line set by the lizard.

Brain complexity in dinosaurs can only be inferred from endocasts of empty fossil skulls (see box 8.2). These empty skulls act as molds that reproduce the brain's overall configuration, and the location and number of the associated blood vessels and nerves. Dinosaur brain casts, however, reveal typically reptilian levels of brain complexity (figure 13.5). These casts do not preserve special structures, such as extremely large cerebral hemispheres, that might be linked to speed, high activity levels, and agility.

A third line of evidence for dinosaur speed, activity, and agility comes from their trackways. In Chapter 11 we saw that dinosaur speeds can be estimated from trackways. Most dinosaur trackways indicate slow walking, which is the normal speed of all living vertebrates, ectotherms, and endotherms alike. But, a few trackways document small theropods running as fast as a living antelope.

**Figure 13.5**
The brain of *Tyrannosaurus rex* is typically reptilian in its level of complexity.
So the evidence for speed, high activity levels, and agility among dinosaurs seems to support endothermy only in small theropods and ornithopods. But some paleontologists point out, as we did at the beginning of this discussion, that some living ectotherms can be very fast, active, and agile. It might be that speedy, active, and agile theropods and ornithopods were ectotherms.

**Feeding Adaptations**

Living endotherms maintain a constant high body temperature and a fast metabolism by consuming and processing large amounts of food (energy). This means they eat more per body weight and process that food more quickly than ectotherms. Key to rapid processing are the teeth, jaws, and skulls of many endotherms, which allow the food to be broken down rapidly into small pieces, thereby increasing the food's surface area and releasing important nutrients so that the endothermic digestive system can rapidly assimilate them. If dinosaurs had tooth, jaw, and skull structures that indicate extensive processing of the food in the mouth, that might be evidence they had an endothermic metabolism.

When we look at the teeth, jaws, and skulls of dinosaurs, however, only among ornithopods do we find structures similar to the "food processors" of living endotherms. The powerful jaws and extensive dental batteries of ornithopods such as hadrosaurids are similar to the jaws and teeth of living endothermic horses or elephants that extensively grind the vegetation they consume (figure 13.6).

This might be taken to indicate that only the ornithopods possessed "food processors" suggestive of endothermy. But the teeth, jaws, and gastric mills of sauropods and some of the armored ornithischians don't indicate food processing inferior to that of living plant-eating birds. Theropod food processing doesn't look much different from the slicing of meat undertaken by living meat-eating mammals such as wild dogs and cats. We also need to remember that the large size of most dinosaurs would have forced them to process and consume large amounts of food, whether they were ectotherms or endotherms. Furthermore, the ornithopod grinding mechanism may simply reflect their dietary preference for tough, hard-to-process plant foods.

We simply cannot be certain what the food processors of dinosaurs indicate about their metabolism. The need to consume large amounts of food to support huge body masses, specialization on tough food items, or the need to feed a rapid, endothermic metabolism could explain the tooth, jaw, and skull structures of some dinosaurs, especially the ornithopods.

**Figure 13.6**

The dental batteries and powerful jaws of hadrosaurs resemble those of some living plant-eating mammals, such as the elephant.
Bone Microstructure

The external layer of bone of many living ectotherms contains few channels for blood vessels. In contrast, the compact bone of many living endotherms is full of large numbers of blood vessels (figure 13.7). This is thought to reflect the quick metabolism of endotherms, which requires rapid exchange of elements stored in bone such as calcium and phosphorus. It stands to reason that if dinosaur compact bone had many channels for blood vessels, then this would indicate endothermy.

Well-preserved dinosaur bone can be cut into thin wafers, and the microscopic structure of the bone can be determined. This has been done for all major groups of dinosaurs and reveals compact bone with numerous channels similar to that of many living endotherms (figure 13.8).

This might seem conclusive evidence for endothermy in all dinosaurs, but the correlation between metabolism and compact bone microstructure is not a perfect one in living vertebrates. Some large ectotherms (turtles and crocodiles) have compact bone with many channels, whereas some small living endotherms (certain mammals and birds) lack numerous blood channels in their compact bone. This suggests that bone microstructure may be more related to size than to metabolism, making the bone microstructure of dinosaurs inconclusive evidence of endothermy.

Another aspect of dinosaur bone microstructure is the recent identification of growth rings in the bone. These growth rings have been found in the bone of

**Figure 13.7**
The compact bone of living endotherms (above) has many channels for blood vessels, but that of ectotherms (below) has few channels.

Photos Courtesy The Natural History Museum (Neg. #104914N).
many kinds of dinosaurs, including some ornithopods, theropods, and ceratopsians. The rings are characteristic of the bone of living ectothermic reptiles. Periodic pauses in bone growth due to seasonal (or annual) temperature fluctuations cause the rings to form. Their presence in the bone of some dinosaurs may be compelling evidence of ectothermy. However, the bone of other dinosaurs, such as the ornithopod Dryosaurus, lacks growth rings and more resembles endothermic bone.

**Blood Pressure**

An endothermic metabolism requires high blood pressure and rapid blood circulation to move energy quickly through the body. Thus, living endotherms have consistently higher blood pressures than do ectotherms (figure 13.9). If we could estimate dinosaur blood pressures, this might indicate whether or not they were endotherms.

But how can we do this? It turns out quite easily if we recognize that a primary function of the vertebrate heart is to pump blood to the brain, which is usually elevated above the level of the heart. In other words, the vertical distance between the heart and the brain should be related, in some way, to the blood pressure, because sufficient pressure must be maintained to move blood to the brain, or the animal dies.

It is possible to estimate blood pressure based on the vertical distance between the heart and brain of a dinosaur (figure 13.10). Such an estimate is based
on the heart–brain distance/blood pressure relationship of living vertebrates and also requires certainty of the posture of the dinosaur. Blood pressure estimates suggest high, endothermic levels for most dinosaurs (Triceratops is a notable exception) and an incredibly high blood pressure (more than 400 millimeters of mercury!) for sauropods. It is questionable whether blood pressure as high as that estimated for sauropods could be maintained by any vertebrate circulatory system without an explosion. So, it seems likely that sauropods may have used arterial valves or muscular contractions in the neck, as do living giraffes, to help bring blood to the brain, and thus would have had a much lower blood pressure than estimated. Estimates of blood pressure, however, are consistent with endothermy in most dinosaurs, although critics point out that large heart–brain vertical distances in dinosaurs could be the determining factor here, not metabolism.

A second, speculative aspect of dinosaur blood pressure concerns the structure of the dinosaurian heart. Living endotherms have a fully divided four-chambered heart that separates aerated from nonaerated blood and thus acts as a double pump, producing high pressure for the aerated blood and lower pressure for nonaerated blood. This mechanism is especially significant because by lowering the pressure of the nonaerated blood, it prevents the rupture of tiny blood vessels characteristic of the lungs of endotherms. In contrast, ectothermic hearts have only two chambers that do not efficiently separate the aerated from the nonaerated blood. An exception is living crocodiles that have an imperfectly divided four-chambered heart (figure 13.11).
The closest living relatives of dinosaurs—birds and crocodiles—have four-chambered hearts. So some paleontologists think that dinosaurs had four-chambered hearts as well. Dinosaur hearts have not fossilized, so this remains speculation. But if dinosaurs did have four-chambered hearts, and if their high estimated blood pressure simply doesn’t reflect large heart-brain vertical distances, these lines of evidence suggest endothermy among most dinosaurs.

Geographic Distribution

Today, ectotherms cannot live in the extremely cold climates near the poles simply because there is not enough solar energy there with which to warm their bodies (figure 13.12). However, endothermic mammals and birds, such as polar bears and penguins, are capable of living in those colder regions of the globe not inhabited by ectotherms. So if the geographic distribution of dinosaur fossils indicates that they lived in cold climates, this might suggest endothermy in dinosaurs.

The current geographic distribution of dinosaur fossils encompasses Cretaceous localities as far north as Alaska, the Northwest Territories of Canada, and Svalbard (Spitzbergen), and as far south as Antarctica (figure 13.13). These are places where ectotherms do not live today. But the Cretaceous world was not as cold toward the poles as is today’s world, and because of continental drift, these Cretaceous dinosaur localities were not as poleward as they are today. Despite this, these locations would still have been far enough poleward during the Cretaceous to have experienced the polar “night”—winter months of virtually continuous darkness. This darkness would have prevented ectotherms from living in poleward regions, even if there were no polar ice caps and temperatures were warmer during the Cretaceous.

It also has been suggested that the poleward Cretaceous dinosaur fossils do not represent dinosaurs that lived in these regions year-round. Instead, they may represent dinosaurs that migrated over large areas and were only living poleward during the warmer, brighter portion of the year. So a hadrosaurid might have migrated the 3,000 kilometers from Alaska to Alberta in a given year, a trek of

![Figure 13.12](image-url)

Today, ectotherms do not live in cold poleward regions. If we plot the latitudes from which dinosaur fossils have been collected (far right), dinosaurs have a distribution that almost rivals that of living birds and mammals (far left).
60 days at a speed of 50 kilometers per day. To have migrated so far, a dinosaur would have had to be endothermic, or would it? Given the possibility of migration, it is difficult to be certain what dinosaur geographical distribution tells us about their metabolism.

**Bird Ancestry**

Dinosaurs arguably are the ancestors of birds (see Chapter 14). Living birds are endotherms (Figure 13.14), and there is no reason to doubt that all extinct birds, including Late Jurassic Archaeopteryx, the first bird, were endotherms. Indeed, the small size, skeletal structure, insulating feathers, and powered flight of Archaeopteryx strongly suggest an endothermic metabolism. The question thus arises, did endothermy in birds first evolve in Archaeopteryx, or did the theropod ancestors and close relatives of birds have an endothermic metabolism?

This question can't be answered definitively. As already discussed, many features of the small theropods are consistent with endothermy. That they gave rise to the birds, and are very bird-like in many ways, are also consistent with endothermy. Although the endothermy of birds may indicate endothermy in at least some theropods, it provides no clues to the metabolism of the other dinosaurs.

**Social Behavior**

Today, complex social behaviors are characteristic of many endotherms (Figure 13.15) and uncommon among ectotherms. The evidence reviewed in Chapter 12 suggests that some dinosaurs may have lived in groups and had some form of sociality based on visual display and parental care of young dinosaurs. On face value, this is consistent with endothermic dinosaurs. But some living reptiles form social groups to hunt and administer minimal care to their young, and not all living endotherms form social groups; some live solitary lives. Indeed, social behavior is not normally viewed as being caused by metabolism, but instead is related to other factors, such as the distribution of food resources in an animal's habitat.
Figure 13.15
Today, complex social behavior is characteristic of endotherms.

Figure 13.16
A 150-kilogram lion (endotherm) eats more food than a 150-kilogram crocodile (ectotherm) in a given period of time.
the inferred social behavior of some dinosaurs at best is consistent with, but not
strong evidence for, their endothermy.

**Predator-Prey Ratios**

Living endotherms need to consume more energy than do comparable-sized ectotherms. This means that a 150 kilogram lion eats more food, and more frequently, than a 150 kilogram crocodile. Therefore, in the wild, a lion must have more food items (prey) than a crocodile (figure 13.16). The predator-prey ratio, the body mass of predators to their potential prey, thus should differ for endothermic and ectothermic predators. Endothermic predator-prey ratios should be lower (less predator mass per prey) than the ratio for ectotherms. Extrapolating this to dinosaurs predicts that predatory dinosaurs should be rare relative to their potential prey dinosaurs if the predatory dinosaurs were endotherms, and more common if they were ectotherms.

A survey of dinosaur fossil collections reveals that predatory dinosaurs are relatively rare. For example, the greatest dinosaurian predator of all time, *Tyrannosaurus rex*, is known from only a few skeletons and a few other isolated bones. One of the most extensive dinosaur collections ever made, from the Upper Cretaceous badlands in Dinosaur Provincial Park, Alberta, Canada, contains only 3 to 5 percent predatory dinosaurs (figure 13.17). On face value, the scarcity of predatory dinosaurs suggests that they (and only they, because this tells us nothing about the metabolism of their prey) were endotherms.

There are, however, two insurmountable problems with using predator-prey ratios to infer dinosaur metabolism. First, it is not clear that the ratio of predators to prey today is simply determined by the food requirements of the predators. Other factors, such as food availability for the prey, are important as well. The second problem, and a very big one, is that we cannot be certain that collections of dinosaur fossils reflect the actual predator-prey ratios of dinosaurs. Taphonomic processes (see box 3.1) destroy many potential fossils, and may have biased the dinosaur-fossil record against predators or toward prey. If dinosaur predators and prey did not always inhabit the same environments, then fossil collections would not necessarily reflect their actual abundances. In light of these problems, studying predator-prey ratios of dinosaurs seems an unsatisfactory way to infer dinosaur-predator metabolism.

**Body Size**

Body size has already been mentioned as a factor in the evaluation of several of the lines of evidence for dinosaur metabolism. It is a very important factor in any consideration of vertebrate metabolism, because body size influences metabolism, and the metabolism of a vertebrate must be consistent with its body size.

To understand why this is so, we need to understand the relationship between the body size of an animal and its surface area. This relationship is best portrayed by two spheres, one large and one small (figure 13.18). The volume of a sphere is \(\frac{4}{3} \pi r^3\), where \(r\) is the radius of the sphere. The surface area of a sphere is \(2\pi r^2\), where \(r\) also is the radius. As a sphere becomes larger, its volume increases as the cube of its radius, whereas its surface area only increases as a square of its radius. The guaranteed result is that a larger sphere has a smaller surface area relative to its large volume, and a smaller sphere has much more surface area relative to volume.

Although this may not strike you as intuitively correct, a quick calculation should convince you. Consider two spheres, one with a radius of 5 centimeters and the other with a 10 centimeter radius. Calculate the surface areas and volumes of both spheres, and then divide the surface area of each sphere by its volume. The result is that the surface area of the smaller sphere is 59 percent of its volume, whereas that of the larger sphere is only 30 percent of its volume. Smaller spheres have relatively larger surface areas than do larger spheres.
If we transfer this basic geometry to animals, we realize that small animals have much more surface area relative to their volume than do large animals. Much of metabolism is generating body heat, and the surface area of an animal determines how readily it can acquire heat from an external source, or how rapidly it loses its body heat. Small animals, such as mice and hamsters, have such large surface areas relative to their volume (or mass) that they lose heat very fast. As endotherms, they have an insulating coat of fur to help retard heat loss and use their very tachymetabolic metabolism to generate more heat to replace that being lost rapidly. They also shiver frequently to generate more body heat and hide in burrows or under vegetation to slow heat loss.

In contrast, an elephant has a much lower surface area-to-volume ratio than a mouse. Its problem, as an endotherm, lies in overheating because an elephant loses heat very slowly. For this reason, elephants have little in the way of insulating body hair and use their large ears as heat radiators by pumping blood into large vessels in the ears, thereby cooling it by increasing the blood’s surface area. Elephants also employ behavioral mechanisms to avoid overheating, such as bathing in rivers several times a day.

Ectotherms that receive most of their body heat from the sun also are affected by the surface area-to-volume relationship. Because of their relatively large surface areas, small lizards can heat and cool themselves rapidly. But because of its large size, a crocodile is slower to warm up and cool down.

Dinosaurs also must have been affected by the surface area-to-volume relationship, and this has to constrain our interpretation of dinosaur metabolism. Large dinosaurs, those that weighed about 1,000 kilograms or more, had very low surface areas relative to their volumes. This has inspired calculations that suggest very large dinosaurs, especially full grown sauropods, would have overheated if they had an endothermic metabolism. Indeed, these dinosaurs would have been inertial homeotherms ("gigantotherms," box 13.2), huge animals with a nearly constant body temperature due to their large size (which, via the surface area-to-volume relationship, produces thermal inertia) even though they might have had relatively slow, ectothermic metabolisms. Small dinosaurs, including baby and juvenile sauropods, based on their surface area-to-volume relationship, could have been either ectotherms or endotherms.

Dinosaur body size considered in light of the surface area-to-volume relationship makes endothermy in adult sauropods and some of the other larger dinosaurs (body weight well above 1,000 kilograms) seem improbable. It suggests that the largest dinosaurs were gigantotherms, but leaves open the question of the metabolism of small dinosaurs. Indeed, small juvenile dinosaurs may have had a metabolism different from their metabolism later in life at large adult sizes, so many dinosaurs could have been heterotherms.

**Other Information**

Very recently, two new kinds of information have been analyzed to determine dinosaur metabolism. This information focuses on bone chemistry and on bones characteristic of the nasal passages of endotherms.

The most common form (what chemists call an isotope) of the oxygen atom in nature has an atomic weight of 16 (abbreviated $^{16}$O), whereas the next most common form has an atomic weight of 18 ($^{18}$O). The bone of any vertebrate incorporates both forms of oxygen into its mineral matrix. The relative amount (ratio) of $^{16}$O to $^{18}$O in the bone depends on temperature. Some scientists have argued that in an endotherm the ratio of $^{18}$O and $^{16}$O should vary little between the limb bones and the bones in the core of the body (such as vertebrae) because the body temperature is nearly the same at both locations. They also argue that the temperatures of the extremities and body core are very different in an ectotherm, so the oxygen ratios should be very different at each location.
A consistency of oxygen ratios has been demonstrated in the extremities and core of the skeleton of *Tyrannosaurus rex*, suggestive of endothermy. However, there may be a problem with the basic argument underlying this conclusion. Various studies of living mammals and birds show that temperature varies considerably between their cores and extremities, at least as much as in living alligators. The reasoning behind using the oxygen ratios to determine metabolism thus may be flawed.

Living mammals and birds have small bones in their nasal passages called *respiratory turbinates* (figure 13.19). These bones increase the surface area over which blood and moist tissues are exposed to the air. Respiratory turbinates thus play a vital role in the rapid breathing and high rate of oxygen
Living endotherms, such as the cat (A) have respiratory turbinates (B) that warm and moisten the air that is inhaled. Theropod dinosaurs (C) lack respiratory turbinates, so air flows directly into the mouth as in a living, ectothermic lizard (D).

Consumption characteristic of the endotherms. It is difficult to imagine an animal being endothermic without respiratory turbinates.

Most dinosaur skulls appear to lack respiratory turbinates, so air flowed directly from their nostrils into their mouths without first being warmed or moistened (figure 13.19). This provides strong evidence that dinosaurs were not endotherms like living birds or mammals. However, it does not mean that dinosaurs were as ectothermic as living lizards. The lack of nasal turbinates in dinosaurs thus suggests a metabolism between those of living ectotherms and endotherms.

**What Type of Metabolism(s) Did Dinosaurs Have?**

Having reviewed the many lines of information bearing on hypotheses of dinosaur metabolism, you should see how difficult it is to present a simple answer to the question about what type of metabolism(s) dinosaurs had. The following answers, however, are offered by different paleontologists.

1. All dinosaurs were ectotherms.
2. All dinosaurs were endotherms.
3. Dinosaurs were a diverse group of animals metabolically; some (at least some theropods and ornithopods) were endotherms and others were ectotherms.
4. Large dinosaurs, the sauropods and big ornithischians, were gigantothers as adults. Juveniles of these large dinosaurs, and the smaller dinosaurs, may have been either endotherms or ectotherms.
The evidence presented in this chapter suggests neither of the first two extreme views of dinosaur metabolism is correct. The third and fourth views, some combination of them or some variant, appear to best explain the evidence. There is, indeed, no simple answer to the question of what type of metabolism the dinosaurs had.

**Summary**

1. Warm-blooded vertebrate metabolisms are endothermic and tachymetabolic.
2. Cold-blooded vertebrate metabolisms are ectothermic and bradymetabolic.
3. Numerous lines of evidence have been brought to bear on the nature of dinosaur metabolism including: posture and gait, speed, activity levels and agility, feeding adaptations, bone microstructure, blood pressure, geographic distribution, bird ancestry, social behavior, predator-prey ratios, and body size.
4. Many of these lines of evidence are consistent with endothermy in at least some theropods and ornithopods, but most evidence does not support endothermy in the other dinosaurs.
5. Very large dinosaurs, such as the sauropods, were gigantotherms.
6. The evidence does not support extreme views of dinosaur metabolism, in other words, that all were ectothermic, or all were endothermic.
7. The evidence suggests a probable variety of metabolisms in dinosaurs, including endotherms and ectotherms, some of which were also heterotherms and gigantotherms.

**Key Terms**

- blood pressure
- bone microstructure
- brain complexity
- cold-blooded
- compact bone
- ectotherm
- endotherm
- “food processors”
- four-chambered heart
- gigantotherm
- heterotherm
- homeotherm
- hot-blooded
- metabolism
- polar “night”
- predator-prey ratio
- relative brain size
- respiratory turbinates
- surface area-to-volume relationship
- warm-blooded

**Review Questions**

1. Define the following seven terms: endotherm, ectotherm, tachymetabolic, bradymetabolic, heterotherm, and gigantotherm. Use each word in a paragraph describing dinosaur metabolism.
2. What are some common misconceptions about ectotherms and why are they wrong?
3. Which of the 11 lines of information presents the most convincing evidence for endothermic dinosaurs? Which presents the weakest?
4. Explain the surface area-to-volume relationship and its bearing on dinosaur metabolism.
5. What type(s) of metabolism(s) did dinosaurs have? Defend your answer.

**Further Reading**

- Bakker, R. T. 1975. Dinosaur renaissance. Scientific American, vol. 232, pp. 48–78. (The original article that argues all dinosaurs were endotherms.)

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