Lesson 4: Moving Around

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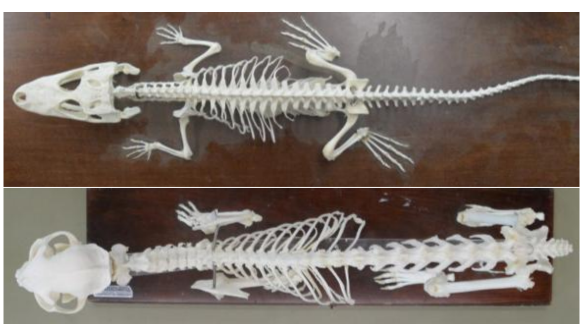
Learning objective for lesson 4: Students will learn about general modes and styles of locomotion in major dinosaur groups

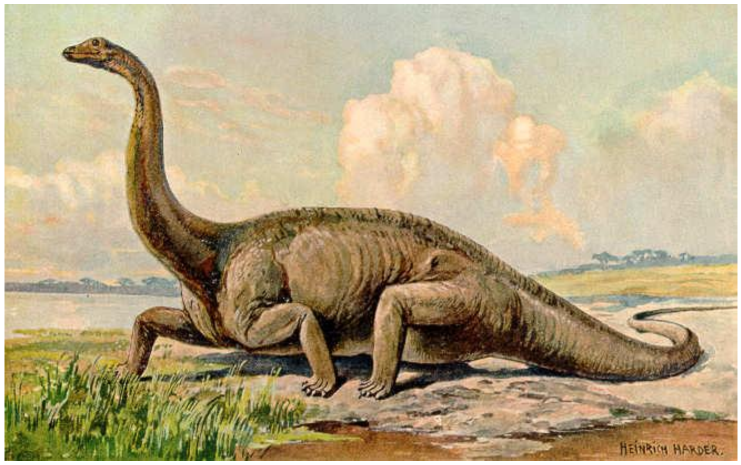
Learning objective 4.1: Classify stance in dinosaurs by comparing to modern animals

Lizards, turtles, crocodiles, and salamanders all have what is termed a **sprawling** stance. In a sprawling stance, an animal's humerus and femur project horizontally, with elbows and knees strongly bent. Mammals and birds have what is termed an **erect** stance. In an erect stance, an animal's humerus and femur project vertically, such that all the limbs point straight down from their girdles.



The skeletons of an alligator (*Alligator mississippiensis*) and a domestic cat (*Felis catus*) in dorsal (top-down) views, showing the difference between a sprawling and an erect stance. Photographs by J. Edwards.

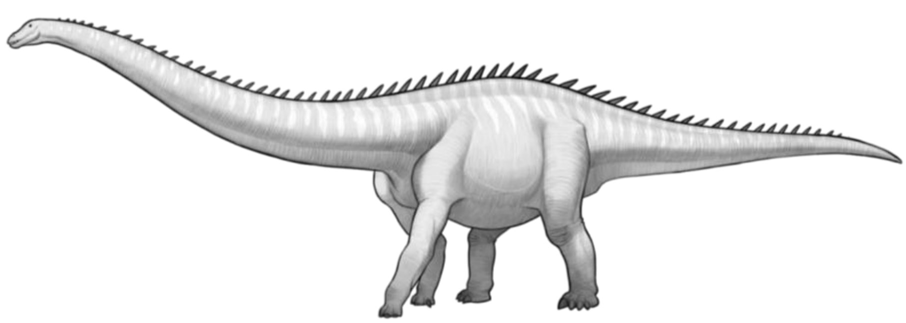
The skeletons of an alligator (*Alligator mississippiensis*) and a domestic cat (*Felis catus*) in anterior (front) views, showing the difference between a sprawling and an erect stance. Photographs by J. Edwards.



A sprawling *Diplodocus*, by Heinrich Harder (1916).

An erect stance has a number of advantages over a sprawling stance. One advantage is that an erect stance positions the limb bones directly under the body. This allows the limb bones to passively support the body's weight without muscles having to strain. Holding a "push-up position" forces our forelimbs into a sprawling stance, and it is hard, because supporting our weight with bent arms requires our muscles to do a lot of work. Not surprisingly, most animals that have a sprawling posture do not use their limbs to support their weight very often. The life of a lizard is mostly spent resting on its belly. Lizards are relatively inactive (compared to mammals and birds) and rise to walk and run infrequently. So, a sprawling posture suits lizards just fine. Active animals like mammals and birds need a more efficient stance. Most lizards are also not very large, so they have little weight to support. Naturally, the weight supporting benefit of an erect posture is more helpful to larger animals that have more weight that needs supporting. Another advantage of erect posture is that it allows all the limb bones to contribute to the length of a stride. This improves speed, because, if every step you take is longer, you can potentially cover ground more quickly.

All modern tetrapods share an ancestor that had a sprawling stance. Birds and mammals evolved their erect stances independently of each other. Did dinosaurs sprawl like crocodiles and lizards, or stand erect like mammals and birds? Erect and sprawling postures are easy to identify based on limb joints and the articulation angles of limb girdles. The evidence is clear. Dinosaurs stood erect.

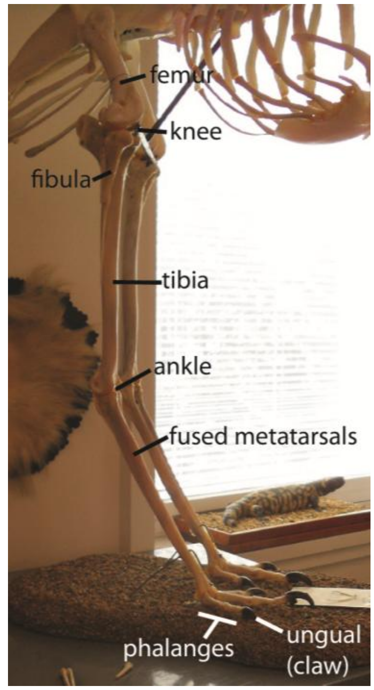


Today, we know that *Diplodocus* and other dinosaurs had an erect stance. Illustration by J. Ang

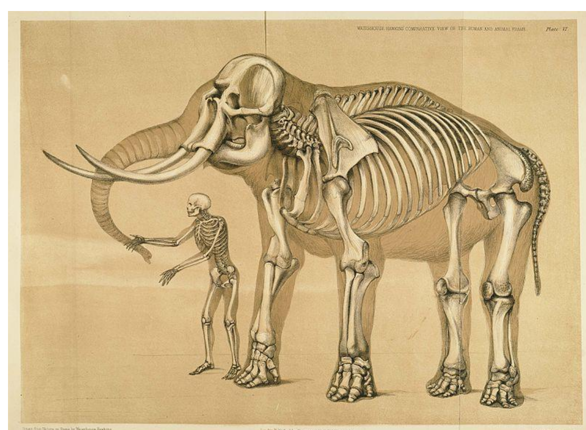
Learning objective 4.2: Evaluate locomotion styles in dinosaurs by comparing with extant animals.

An erect posture is advantageous for fast locomotion and for supporting body weight. Among animals with an erect posture, there are those that have evolved to maximize these advantages. **Cursorial** limbs are limbs specially adapted for fast locomotion. To further increase stride length, cursorial limbs are elongated. In particular, cursorial limbs tend to have very long lower leg bones (the bones below the elbows and knees). Cursorial animals also often stand on their toes (**digitigrade** posture), or stand only on toenails that have been modified into hoofs (**unguligrade** posture). Cheetahs and ostriches are modern examples of animals with cursorial limbs and digitigrade posture. Horses and antelope are modern examples of animals with cursorial limbs and unguligrade posture. Humans are not cursorial, and we stand simultaneously on our toes, the flat of our feet, and our heels (**plantigrade** posture). In plantigrade animals, the phalanges and metatarsals make contact with the ground. Some dinosaurs show cursorial adaptations, in particular the ornithomimid theropods. Ornithomimids have a digitigrade stance and long metatarsals.

Graviportal limbs are specially adapted for supporting extreme body weight. Graviportal limbs have bones that are robust and heavy. Graviportal limbs also tend to have large feet with large fleshy pads. These big feet and pads provide a solid support base and help to absorb impacts when walking. Graviportal limbs tend to be short and, when walking, their joints bend as little as possible. Elephants are modern examples of animals with graviportal limbs.



The emu (*Dromaius novaehollandiae*, a relative of the ostrich) has a digitigrade posture, where only the phalanges, and not the metatarsals, touch the ground. Photos of UAMZ specimen by J. Edwards, labelling by V. Arbour.

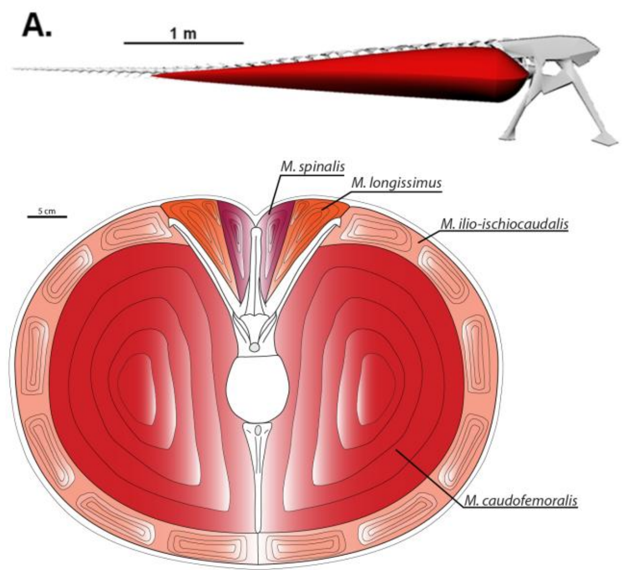


In this illustration by Benjamin Waterhouse Hawkins (1860), it is easy to compare the robust graviportal limbs of the Asian elephant (*Elephas maximus*) with the more slender bones of the human (*Homo sapiens*).

Animals that almost always walk and run on two legs, like birds and adult humans, are termed **obligate bipeds**. Animals that almost always walk and run on four legs, like turtles and horses, are termed **obligate quadrupeds**. Some animals like, basilisk lizards, walk on all four legs but rise on two legs to run. Such animals are termed **facultative bipeds**. Other examples of facultative bipeds include many primates, which may walk for short distances on their hind legs only, and kangaroos, which travel via bipedal hopping at high speeds, but walk on all fours at low speeds. It should be noted that the boundaries between these divisions are not always clear-cut: humans almost always walk bipedally, but we can certainly crawl on all four legs if we need to. Likewise, many quadrupedal animals can rear up onto their hind legs in order to reach food. For this reason, it is best to think of these words in terms of what the animal <u>usually</u> does.

The ancestor of all dinosaurs was an obligate biped. Most dinosaurs remained adapted to carry a majority of their weight on their hind legs and could probably at least stand on only two feet. Nevertheless, we classify sauropods, stegosaurs, and ankylosaurs as obligate quadrupeds, because, even if many of them could stand on two legs, it is unlikely that they frequently attempted to walk bipedally. Prosauropods are tricky: many were probably bipedal, but whether or not they were obligate or facultative bipeds is not always easy to determine. Some small ceratopsians were obligate and facultative bipeds, and larger ceratopsians were obligate quadrupeds. Pachycephalosaurs and theropods were obligate bipeds. Most small ornithopods were also obligate bipeds. Our understanding of the postures of large ornithopods, including hadrosaurs and iguanodonts, has changed over the years. Both of these groups have strong hind legs that are significantly longer than their front limbs. This indicated a bipedal stance; however, fossil footprints reveal a different story, and we'll come back to that later.

We can go a little bit deeper into the anatomy of dinosaur locomotion by looking at the muscles of their closest living relatives – birds and crocodiles. In crocodiles and many birds, there is a large muscle called the **caudofemoralis**. The caudofemoralis pulls backwards on the hind leg and is important for powering birds and crocodiles when they walk and run. The caudofemoralis is anchored to the under surface of the ilium, to the caudal vertebrae, and to the chevrons. It attaches, via a tendon, to the femur.



The caudofemoralis muscle of the theropod *Carnotaurus*. The top image is a digital reconstruction of the tail from the side, and the bottom image shows a cross section through the tail with a vertebra in the centre. Figures 3 and 5 in Persons & Currie (2011) Dinosaur speed demon: the caudal musculature of *Carnotaurus sastrei* and implications for the evolution of South American abelisaurids. PLOS ONE e25763.

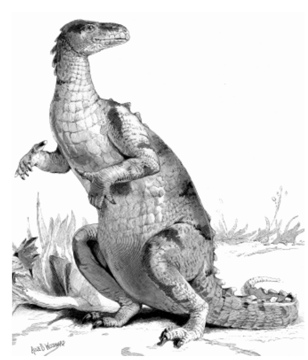
The femora of crocodiles and birds have a prominence of bone, called a **trochanter**, where the caudofemoralis muscle-ligament attaches. In addition to specially shaped ilia, caudal vertebrae, and chevrons, dinosaurs also have femora with these same trochanters. So, we can be sure dinosaurs also had a caudofemoralis.

Based on the size of the various anchor points, we can also say that some dinosaurs, like many theropods and hadrosaurs, had a large caudofemoralis relative to the other proportions of their bodies. This tells us that these dinosaurs were adapted for greater hindlimb power and were probably strong runners. We can even go a step further and compare the position of the muscle attachments. On most theropods, the trochanter is located high on the femur. A high muscle attachment would have allowed the caudofemoralis to repeatedly retract quickly – a useful adaptation for carnivorous animals that depend on their ability to swing their legs fast when sprinting after prey. On hadrosaurs, the trochanter is located further down on the femur (as it is in most herbivorous dinosaurs). This would have reduced the speed at which the caudofemoralis could have repeatedly retracted but would have granted the muscle better endurance, because each retraction would have pulled with greater leverage – endurance would have been important for an animal that needed to be constantly on the move and grazing from one patch of vegetation to the next.

Learning objective 4.3: Interpret ichnofossils for what type of locomotion is represented.

Ichnofossils are fossils that record traces of biologic activity. Fossil footprints, tooth marks, and burrows are all examples of ichnofossils. Fossil footprints provide the best direct evidence of how dinosaur moved. To become fossilized, a footprint must first be made in soft mud. The mud must then dry out and harden. Then, to protect the hardened footprint from erosion it must be buried but eventually re-exposed so that palaeontologists can identify it. Naturally, the odds of this sequence of events happening to any particular footprint are small. But consider how many footprints one dinosaur could have made throughout the entirety of its life and how many dinosaurs were alive during the more than 160 million years of dinosaur rule. In fact, dinosaur footprints are not uncommon fossils. Often, where one fossil footprint is found so are many others. Sometimes an entire series of dinosaur footprints are found. These fossil footprint assemblages are called **trackways**.

Studies of dinosaur trackways have helped to change our understanding of dinosaur posture and locomotion. For instance, it was once widely imagined that bipedal dinosaurs stood and walked in way not unlike the movie monster Godzilla – with their belly and torsos held vertically above their hips. This posture

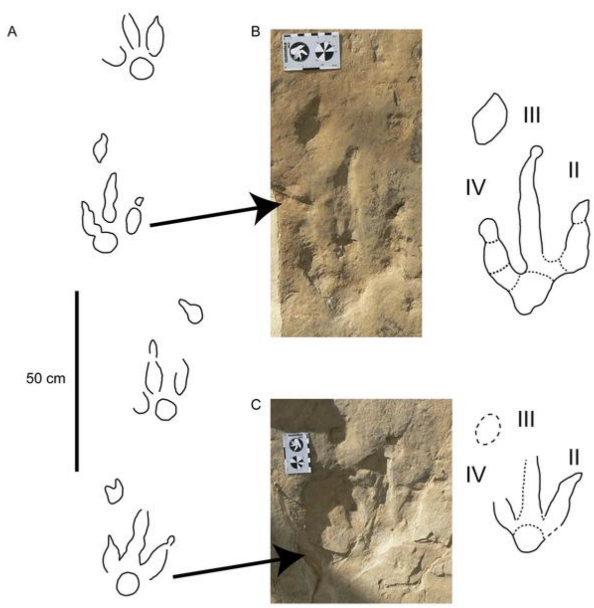


Was *Iguanodon* a biped? Early depictions (like this image by Alice Woodward, from 1895) often showed iguanodonts and hadrosaurs in kangaroo-like postures.

would have tilted dinosaur tails downward and caused a dinosaur's tail to drag behind it.

However, while fossil lizard and crocodile trackways often have tail drag marks, dinosaur tail drag marks are rare. We now know that most bipedal dinosaurs held their body in a more horizontal position and that both bipedal and quadrupedal dinosaurs held their tails off the ground.

Tracks of a modern iguana lizard, with tail-drag trail down the center. Photo by W. Scott Persons



The three-toed footprints in this trackway are from the hind feet of an ornithopod, and the smaller, oval or crescent-shaped prints are from the hands. Figure 5 from Castanera et al. 2013. Manus track preservation bias as a key factor for assessing trackmaker identity and quadrupedalism in basal ornithopods. PLOS ONE 8:e54177.

The trackways of hadrosaurs and iguanodonts have deep imprints left by their hind feet and show that these dinosaurs carried most of their weight on their hind legs. However, the trackways of hadrosaurs and iguanodonts also record shallow tracks made by their front feet. Hadrosaurs and iguanodonts were probably facultative bipeds that walked on all fours most of the time, but likely reared up on only their back legs to run.

Based on evidence from ichnofossils, *Iguanodon* was a facultative biped (ie. it usually walked quadrupedally), and would have carried its tail off the ground. Illustration by J. Ang.

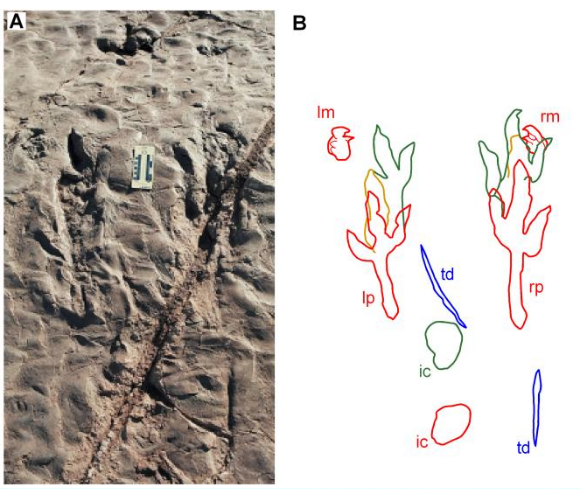
Trackways can also be used to determine how fast dinosaurs moved. When we run, we tend to take long steps, and so do most other animals. As noted previously, longer strides enhance speed. From trackways, we can measure the lengths of dinosaur strides and can usually estimate dinosaur leg lengths from the proportions of their footprints. From these two measurements, it is possible to estimate how fast a dinosaur was moving when its footprints were made. Unfortunately, because fossil footprints must be made in mud and because animals seldom run at full speed when stepping through sticky muck, trackways tell us about dinosaur walking speed and not usually about dinosaur running speeds.

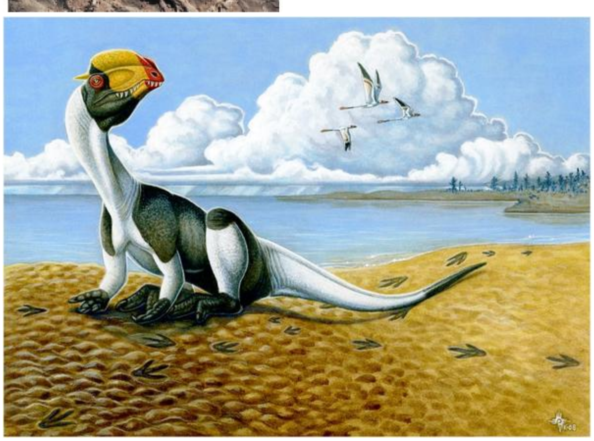
Finally, trackways can sometimes provide insights into other aspects of locomotion besides whether or not a dinosaur was quadrupedal or bipedal, or how fast it was moving. Some theropod trackways preserve long claw marks, and these are interpreted as 'swimming traces'. Other ichnofossils preserve the imprint of a dinosaur's body while it was sitting!

Learning objective 4.4: Evaluate the evidence for warm- or cold-bloodedness in dinosaurs.

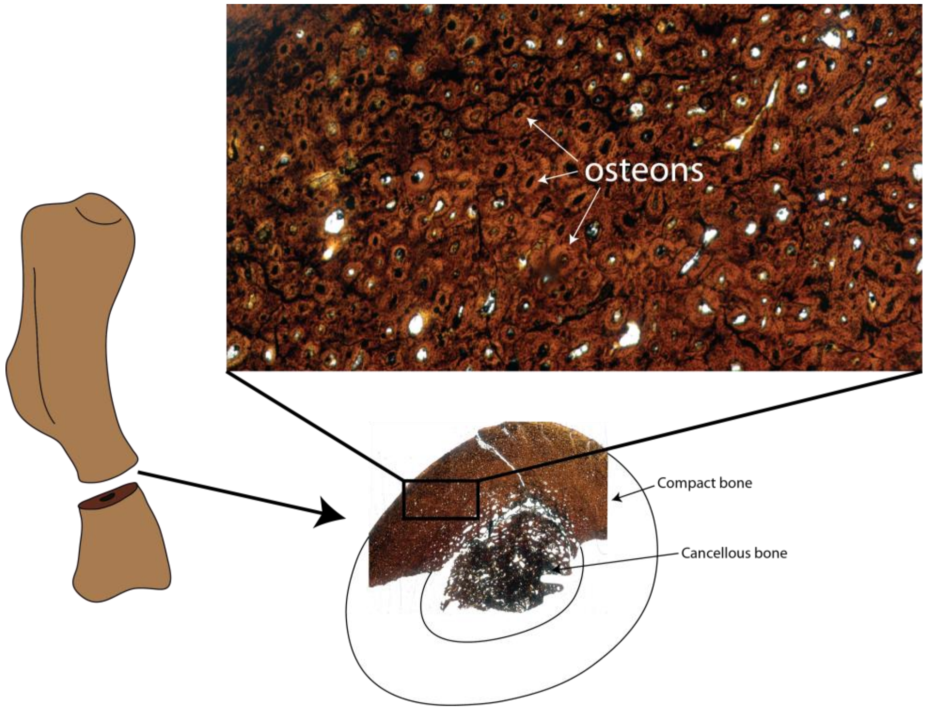
In many ways, the limb adaptations of dinosaurs are more similar to those of modern mammals and birds than they are to modern reptiles. Like birds and mammals, dinosaurs were likely "warm-blooded". The terms "**warm-blooded**" and "**cold-blooded**" are antiquated and can be misleading, as the blood of a "warm-blooded" animal is not necessarily any warmer than the blood of a "cold-blooded" animal. To avoid this confusion, we will use the term ectotherm to refer to "cold-blooded" animals and the term endotherm to refer to "warm-blooded" animals. **Ectotherms** are animals that adjust their internal body temperatures through behaviors that depend on temperature differences within their environment. For instance, to warm up lizards bask in the sun or on top of hot rocks, and to cool down lizards seek out shade or cool burrows. **Endotherms** are animals that regulate their own body temperatures through metabolic processes. To warm up, endotherms burn energy to generate internal heat, and, to cool down, they may sweat or pant.

Being an endotherm comes with a high cost. In order to maintain a constant optimal body temperature, endotherms must expend large sums of energy. Pound for pound, this means that endotherms most successfully consume a great deal more food than must ectotherms. Due in large part to this significant drawback, most organisms are ectotherms, not endotherms. However, endotherms do have a few significant advantages. First, endotherms





Left: This amazing ichnofossil, from the Lower Jurassic of Utah preserves the imprint of a sitting or crouching *Dilophosaurus*-like theropod dinosaur. Figures 4 and 7 in Milner et a. 2009. Bird-like anatomy, posture, and behavior revealed by an Early Jurassic theropod dinosaur resting trace. PLOS ONE 4:e4591.



When you cut apart a dinosaur bone and make a thin section, you can see the cells that form bone. Photographs of a hadrosaur thin section courtesy of Mike Burns, and all other elements of the illustration by Victoria Arbour.

can survive in cold climates, where finding a warm place to absorb heat is impossible. Second, endotherms are always ready for action. On a cold night or morning, before the external environment has had a chance to warm up, endotherms can function the same as they could in the middle of the afternoon, but ectotherms may be sluggish, making ectotherms easy predators to avoid or easy prey to catch. Third, although activities like sunbathing may not waste valuable energy they do waste valuable time. While ectotherms are forced to spend time basking in the sun or sheltering in the shade, endotherms can be out and about. Although they pay an energy cost, endotherms also do not need to take frequent stops and can maintain high activity levels.

The limbs of dinosaurs, which appear well adapted for the more active lifestyle of endotherms, are one of many arguments supporting the conclusion that dinosaurs were endotherms. Other evidence comes from the discovery that some dinosaurs had simple hair-like feathers. Endotherms benefit from insulating integument to help hold in the body heat that they burn energy to produce. When it comes to being large land-living carnivores and herbivores, endotherms tend to outcompete ectotherms (think about how few large modern reptiles there are compared to mammals). So, the overall pattern of dinosaur ecological success is most consistent with the pattern that would be expected for a group of endotherms.

The bones of dinosaurs also support the conclusion that they were endotherms. **Histology** is the technique of slicing samples of bones into very thin sections, such that the internal structure of the bone can be observed under magnification. Bone cells are called **osteons**. We know from studies of modern animals that endotherms grow their bones more quickly and have their osteons arranged in a different pattern than ectotherms. Dinosaur histology studies show that dinosaur bones grew fast and that dinosaur osteons were arranged like those of endotherms.

Although it seems clear that many small feathered dinosaurs were endotherms, there is still debate over whether all large dinosaurs were endotherms. It has been suggested that, instead of being endotherms, large dinosaurs were **gigantothermic**. As any shape increases in size, its surface area increases more slowly than its volume. This is called the **cube square law**. Larger animals, therefore, have relatively less surface area than do smaller animals. It is theorized that, even if big dinosaurs were ectothermic, their low ratio of surface area to volume would have prevented them from losing significant heat to the outside world, and, thus, they could have lived active endothermic-like lives without actually needing to produce body heat by burning energy. However, the theory of gigantothermic dinosaurs remains to be proven and lacks supporting evidence.

Supplementary Materials.

The Brain Scoop: Tetrapodal locomotion. [Video]

Canadian Museum of Nature: Ceratopsian Posture and Walk-cycle animation. [Video]

Dinosaur Tracking: *Tyrannosaurus* had extra junk in the trunk. [Blog post]

Not Exactly Rocket Science: Butch tail made *Carnotaurus* a champion dinosaur sprinter. [Blog post]

Pipestone Creek Dinosaur Initiative: Grande Cache Dinosaur Trackways. [Video]

The Ichnology of Jurassic Park is a detailed look at dinosaur footprints and other 'trace fossils' in everyone's favourite dinosaur theme park.

For a good explanation of the square-cube law and limits on animal sizes, check out "Could Godzilla exist?". [Video]

American Museum of Natural History: Were dinosaurs warm-blooded? [Video]

BBC Worldwide: Dinosaurs: Warm blooded vs cold-blooded. [Video]