

Walking in Their Footsteps and What They Left Us: Dinosaur Tracks and Traces



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Dinosaur bones are body fossils—they were once part of the animal. Trace fossils, also called ichnofossils, are mostly sedimentary structures produced by animal behavior. They include, but are not limited to, footprints, burrows, and nests. Body fossils and trace fossils tell us different things. Body fossils tell something about how the animal looked in life and may enable us to estimate body size and mass. Trace fossils show what the animal actually did—for example, how it moved. They also can give us details about external features—shape of the pads on the feet, and even skin texture. By combining data from both sources, we can reconstruct a more complete picture of the lifestyles of prehistoric animals, such as dinosaurs, and work out how they did what they did.

Because trace fossils are produced by animal activity, they can also tell us things about the “tracemaker” that bones never could. Tracks, for instance, are preserved in place, so we know where the animal was when it was performing the activity. With bones, even when you find a complete skeleton, it could have been washed downstream for hundreds of miles. Aside from footprints, other dinosaur trace fossils that have been found include gastroliths and s. Gastroliths are stones found in the abdominal cavity of some dinosaurs. They probably helped them to digest plant food by acting like grinding teeth in the stomach. Some living birds, such as chickens and turkeys, swallow grit to use in a muscular bag called a crop, which performs a similar function. But perhaps the most unusual types of trace fossil are the s.

Coprolites

These trace fossils are ancient feces, which preserve information on diet and defecation patterns. Coprolites often contain direct evidence of diet, and can

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provide important information about feeding levels and paleoenvironments. The biggest problem with this type of fossil is linking a particular animal to a specific coprolite.¹

Researchers today use fecal remains to understand an animal's diet and dietary changes. Modern researchers have the capability to identify the animal that produced a particular fecal deposit. In the fossil record of dinosaurs, this task is very difficult to do, because we have no direct evidence of the diet of each species of dinosaur. Coprolites have been identified from various Mesozoic rock formations and have been attributed generally to herbivores or carnivores based on shape and content.² Although they are probably less common in the natural environment, carnivore feces are generally better preserved than those of herbivores, because they have higher calcium phosphate content, which results in a greater degree of mineralization.¹ Unfortunately, the morphology of coprolites can be highly variable, so shape rarely helps us identify the exact feces maker. However, we have been able to attribute some coprolites to specific animals, e.g., *Tyrannosaurus* and *Maiasaura*.

Dinosaur Tracks and Anatomy

The trace fossils that we are most concerned with in this chapter are dinosaur tracks. The word track can be used to mean either individual footprints, or a sequence of footprints. For this reason, we suggest that “tracks” not be used unless the meaning is absolutely clear. In this chapter, we will use the word “track” or “footprint” to mean a single impression of an animal's foot, whether a forefoot or a hindfoot, and we will use “trackway” to mean a sequence of such footprints made by a single animal at a certain time and place.

The study of tracks and trackways is more complex than it might first appear. We have to take into consideration several aspects of dinosaur anatomy and behavior: how they walked, how they placed their feet, how they stood, and the number of digits on each foot.

How They Walked

Dinosaurs may be bipedal, walking on their hind limbs only, like humans and birds; qua-

drupedal, walking on all fours, like cats or horses; or they can walk on two legs or all fours as their fancy takes them, like kangaroos or chimpanzees. This attribute is referred to as being facultatively bipedal.

How They Placed Their Feet

All tetrapod feet can be divided into two parts: the digits, toes or fingers, composed of bones called phalanges, and the rest of the foot, made up of bones called metacarpals or metatarsals. Dinosaurs walk on their toes, like cats and dogs, rather than flat-footed, like humans and bears. Thus, when we talk about a dinosaur footprint we are not talking about the impression left by the whole foot, but by parts of their toes and soft tissue structures such as fleshy “heel” pads. Sometimes dinosaurs left metatarsal (foot bone) impressions, usually when resting or walking under unusual circumstances.

How They Stood

Dinosaurs, like mammals and birds, have an erect stance. They hold their legs like vertical pillars under their bodies. When they move, their legs swing straight backwards and forwards. The opposite of this is a sprawling stance, such as in a lizard. Animals with a sprawling stance have to rotate their hips and shoulders.

Numbers of Digits

Dinosaurs may have three to five digits (fingers or toes) in each foot. As dinosaur trackers, we are only concerned with the number of digits that make contact with the ground in normal locomotion—their functional digits. Most theropods (meat-eating dinosaurs) have four digits on each hind foot, but all theropods are functionally tridactyl; that is, usually only three of their digits are recorded in their fossilized footprints. Many dinosaurs have a functionally tridactyl hindfoot. These groups include theropods, ornithomimids and stegosaurs. However, most quadrupedal dinosaurs have a pentadactyl (five digits) forefoot, although it is often difficult to discern the separate digits in front footprints, especially in hadrosaurs and sauropods (Fig. 1).



As shown in Fig. 1, different types of dinosaurs leave differently shaped footprints and have different trackway configurations (the order and position of footprints). As a general rule, theropods are bipedal with a three-toed footprint, and ornithomorphs are facultatively bipedal with a three-toed footprint. Sauropods, on the other hand, are quadrupedal with five toes front and back. These toes are generally hard to see in the trackway so sauropod tracks are identified more easily by their great size, the characteristic oval hind footprint, and the horse-shoe shaped front footprint. In contrast, ankylosaurs and stegosaurs have four-toed hind footprints and five-toed front footprints, but it is difficult to distinguish between the footprints of the two dinosaurs. The main difference is that ankylosaurs have a much longer outer toe (digit IV) than stegosaurs (Fig. 2).

Track Preservation and Classification

Tracks are made when an animal walks over the ground and exerts enough pressure to deform the surface. The amount of deformation is obviously related to the pressure per unit area that is transmitted through the animal's foot. This deformation, in turn, is related to weight, as large animals tend to exert more pressure per foot. However, other factors are also important, such as the relative size of the animal's foot, its weight distribution, and the moisture content and consistency of the sediment over which it walked. Tracks are best formed in wet and cohesive sediment, such as sand or mud. Tracks may be preserved as molds, the actual depression made by the animal's foot. They may also be preserved as casts, formed by the sediment that infilled the mold.

Most tracks are found in rocks that formed from sediments deposited beside the sea, on lakeshores, or near rivers. All of these areas would be intermittently wet and dry. The tracks formed when ani-

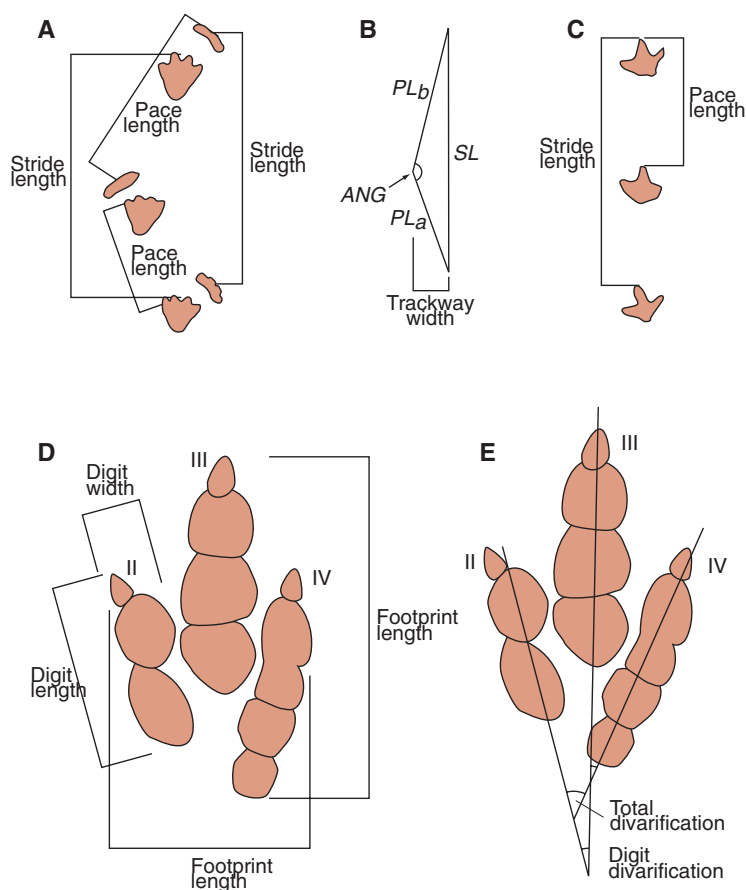


Fig. 1. Measurements of footprints and trackways. **A.** Pace length (PL) and stride length (SL) in a trackway of a bipedal dinosaur. Measurements can be taken from any point in the foot as long as the point used is specified and it can be easily identified on each footprint. For this reason the back of the heel or the tip of the middle toe are often used. **B.** The angles of the trackway angulation pattern; these are used as a measure of how in line the footprints are with one another. **C.** Pace and stride lengths in a quadrupedal trackway. Manus and pes trackways are treated separately. **D.** Measurements of footprint and digit lengths and widths. **E.** Measurement of divarification angles between the digits in a typical theropod track.

Fingers and toes are traditionally numbered from the inside to the outside and bones in the digits from the hand to the extremities. Thus, if you were to number the digits of your own hand the thumb would be digit I (roman numerals are always used for digits) and your little finger would be digit V. You have two bones in your thumb and three in all your other fingers. These bones are called phalanges (singular phalanx). Thus, the end bone in your thumb would be digit I, phalanx 2. A phalangeal formula is a shorthand for describing the number of bones and digits in a hand or foot and so the phalangeal formula for your hand would be 2,3,3,3,3 (assuming you have had no traumatic injuries or birth defects). Many dinosaurs have lost their inner and outer toe impressions. The pads in Fig. 1 show the phalangeal formula of theropods: 3, 4, 5.

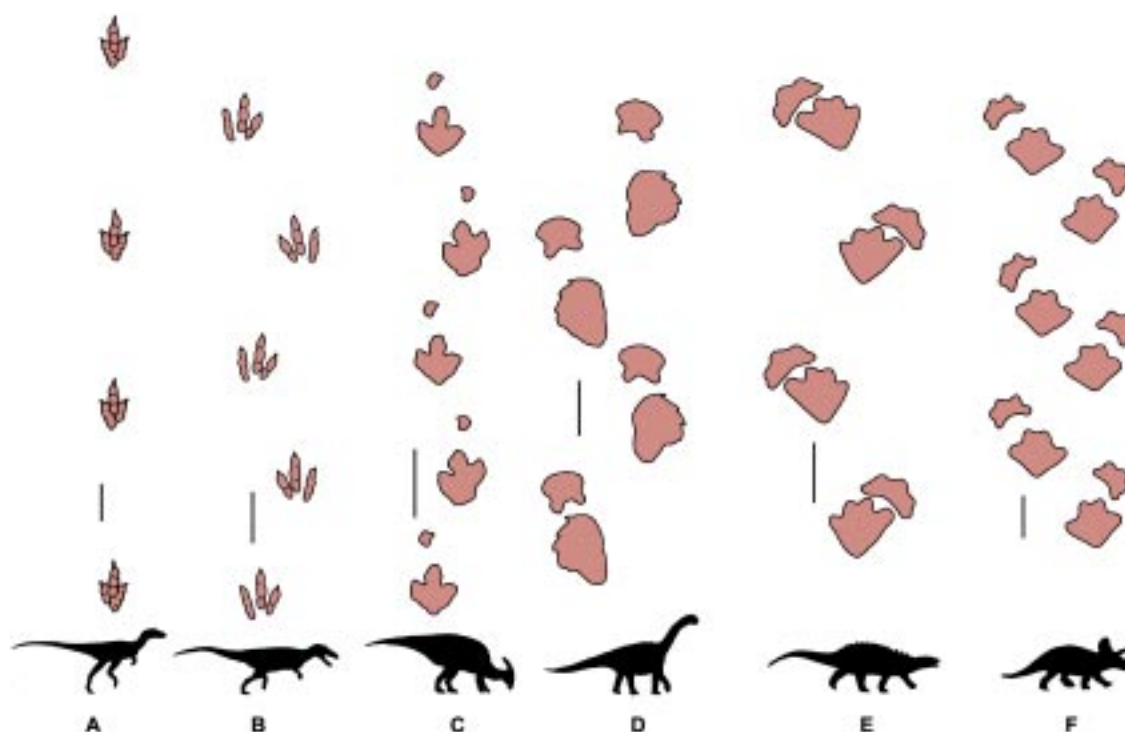


Fig. 2. Some common dinosaur trackways and their producers. **A.** *Grallator* trackway probably made by a small theropod such as . **B.** Large theropod trackway probably made by an allosaurid or megalosaurid. **C.** *Caririchnium*, large quadrupedal ornithomimid trackway probably made by an iguanodontid or hadrosaurid. **D.** *Brontopodus* trackway probably made by a brachiosaurid/camarasaurid sauropod. **E.** Large quadrupedal trackway probably made by a nodosaurid ankylosaur. **F.** trackway probably made by a horned dinosaur. (B and E redrawn after Wright, 1996; C, D and F redrawn after Lockley, 1989)

mals walk over damp sediment. The sediment then bakes dry in the sun. Some clay-rich sediments become very hard when this happens, actually forming an adobe-like surface. When the tide next comes in, or the wind blows fine sand or silt, or when the river floods, the footprints are covered with more sediment and thus preserved. Preservation is even more likely to occur in damp environments where algae often form mats that bind the sediment together so that it resists erosion.

On the whole, track fossilization is a rare event. Many more tracks are made than are ever preserved. Sometimes the tracks might not bake hard in the sun; or perhaps they did bake, but wind and rain eroded them away before they were covered. Tracks might also be trampled by animals to the point that they are unrecognizable.

Some studies have shown that there is a zone around a lake where tracks are most likely

to be preserved.³ This model of the preservation of tracks could be called the Goldilocks Preservation Model: too near the lake, and the ground is so trampled that no discrete tracks can be discerned; too far away, the sediment is too dry and footprints don't get covered over by more sediment often enough. The zone between these two extremes, however, would be "just right."

When we find a dinosaur trackway that we think was made by a particular species of dinosaur, we do not give it the same name as that dinosaur. We give it its own name that reflects an aspect of the track morphology (shape). We do this because we usually cannot be absolutely sure which species of dinosaur made the tracks. Tracks are named using a classification system parallel to the classification of animals. Tracks are ichnofossils (trace fossils), and as such are given ichnogenus and ichnospecies names, and are sometimes placed in ichnofamilies. Just as



dinosaur names may often be recognized by the suffix “-saurus,” trace fossil names can be recognized by suffixes such as “-ichnus,” “-podus,” or similar endings. The following common examples provide both the track names and their derivations:

Theropods

Eubrontes (true thunder),
Grallator (Grallae, i.e., heron/stork, -like)

Sauropods

Brontopodus (thunder foot)

Ornithopods

Caririchnium (track from Carir, Brazil)

s

(horned face [dinosaur] foot)

Ankylosaurs

Tetrapodosaurus (four-footed reptile)

It is not a good idea to name tracks to mean “tracks of a particular dinosaur,” because further research may reveal that the tracks were made by a different animal, thus causing the name to be misleading. Tracks cannot be renamed once the original name has been published. Tracks are classified on the basis of shape. The age and size of the tracks do not matter. For instance, two tracks that cannot be distinguished by shape will be given the same ichnogenus or ichnospecies name, even if one track is from the Cretaceous of China, and the other is a track from the Triassic of North America. It is highly unlikely that the same animal survived for so many millions of years. Thus, trace and body fossils do not correspond exactly.

Estimating Speeds from Trackways

In the past 20 or so years, tracks have been studied much more intensively than previously.

We have made enough measurements on skeletons that we can now get quite a bit of information about the trackmaker from the size of its foot. The basic measurement of a dinosaur footprint is its length. The length of a dinosaur’s foot (represented as FL) is related to the length of its leg up to the hip (represented as h). This ratio (FL/h) is different for different groups of dinosaurs, but as a general estimate, the hip height of a dinosaur can be estimated to be four times the footprint length. More accurate ratios for particular groups of dinosaurs have been worked out, as shown in Table 1.

Once you have a value for the hip height, and assuming you have a trackway with at least three footprints of the hind feet, you can start to estimate the speed of the trackmaker. The terms used in this explanation are illustrated in Fig. 1. Alexander made a series of observations on modern animals relating the length of their stride to the speed at which they were moving.^{4,5} The relationship between stride length and speed was constant for animals as diverse as horses, ostriches, hedgehogs, and people, so it is likely that a similar relationship would hold true for dinosaurs. The speed can be worked out as relative speed, which is stride length (SL) divided by hip height (h). This allows you to compare the relative speeds of two similar animals. We also have an equation to convert pace, stride length, and hip height into a numerical speed in meters per second. This equation may give slightly low speeds for running animals, so if the trackway was made by a running animal, the second equation works best (Table 2).

How do you know if a trackway was made by a walking or running dinosaur? The difference between walking and running is that running has a suspended phase where all the limbs

Table 1. Estimates of hip height (h) from footprint length (FL) (after Thulborn 1990)²⁸

Small theropods	$FL < 25 \text{ cm}$	$h = 4.5 \text{ FL}$
Large theropods	$FL > 25 \text{ cm}$	$h = 4.9 \text{ FL}$
Small ornithopods	$FL < 25 \text{ cm}$	$h = 4.8 \text{ FL}$
Large ornithopods	$FL > 25 \text{ cm}$	$h = 5.9 \text{ FL}$
Small bipedal dinosaurs in general	$FL < 25 \text{ cm}$	$h = 4.6 \text{ FL}$
Large bipedal dinosaurs in general	$FL > 25 \text{ cm}$	$h = 5.7 \text{ FL}$

**Table 2. Relative and absolute speed estimates** (after Alexander, 1989 and Thulborn, 1990)^{5, 28}

Walk	$SL/h < 2.0$
Trot	$SL/h = 2.0\text{—}2.9$
Run	$SL/h > 2.9$
Speed of walking dinosaurs (m/s)	$V = 0.25g^{0.5}SL^{1.67}h^{-1.17}$
Speed of running dinosaurs (m/s)	$V = [gh(SL/1.8h)^{2.56}]^{0.5}$

Relative speed is based on the ratio between stride length (SL) and hip height (h). Estimates of actual speeds are extrapolated from the speeds and stride lengths of modern animals determined by observation. V is the speed of the trackmaker and g is the acceleration due to gravity. All linear measurements are in meters and all temporal measurements in seconds.

are off the ground at the same time. As a quick approximation, if the stride length is more than eight times the footprint length, then the dinosaur was running. To be more accurate, work out the relative stride length, and if that is greater than 2.9, the dinosaur was running. If the relative stride is less than 2, the dinosaur was walking. If the stride length falls between these two values, then the dinosaur may well have been trotting. However, trotting is an unusual gait for any animal, because it is very energetically inefficient. Interestingly, juveniles seem to trot far more often than adults do.

Trackways also allow some assessment of the way the animals were walking (Fig. 3). Were their limbs directly under their body? If so, their tracks should fall in a single straight line. Were their limbs under their shoulders? If so, there should be two parallel lines of footprint in a single trackway. Trackways also show the position of the forelimbs relative to the hindlimbs—were they placed nearer or further away from the middle of the trackway? Such features can be characteristic of the trackways of certain animals. For instance, the trackways of small theropod dinosaurs often fall in a single straight line, whereas the trackways of large theropods and those of ornithomimids are in a slight zigzag pattern with the toes often pointing inwards. Sauropod dinosaur trackways commonly have forefoot impressions falling inside the hindfoot impressions, whereas those of ankylosaurs and stegosaurs tend to have forefeet falling slightly outside the hindfeet (Fig. 2). Such features can help to determine what kind

of dinosaur made the trackway in question. Contrary to popular belief, trackways rarely show tail drags, and this is one reason why we now think that dinosaurs hardly ever dragged their tails.

Superlatives— Biggest, Smallest, Fastest

What were the biggest dinosaur tracks ever found? Sauropods, without a doubt, made the biggest tracks. Tracks from the Jurassic of Gansu Province, China, are reportedly the biggest ever found, with a maximum dimension of 1.5 m. These have not yet been officially described, so it is not clear if this dimension includes the outer footprint rim, in which case the foot might only have been about 1 m long. Tracks from the Purbeck limestone group of the United Kingdom have been recorded with a maximum dimension of 1.3 m, although these have only been described in detail in a National Trust Report, not in a scientific journal. This dimension also includes the external rim, so the dinosaur's foot was probably nearer to 1 m long. Tracks from the Glen Rose site in Texas have been photographed with a toddler sitting in them, and maximum dimensions for them have been reported as 147 cm.⁶ Again, this is a maximum footprint dimension and the actual foot length in this case has been calculated as 1.1 m. Thus, most of the large sauropod tracks known so far indicate a foot length of slightly more than 1 m. In all of these cases, the trackmaker was probably 20–30 m (66–98 ft) long and weighed in excess of 20–30 tons.



The smallest dinosaur tracks ever found are considerably smaller than the feet of any known adult dinosaurs. Even the diminutive would have left tracks 40 mm long, but we now know of several tracks only 25–30 mm long. These have been found in Jurassic rocks from North America,⁷ and were probably made by juvenile dinosaurs.

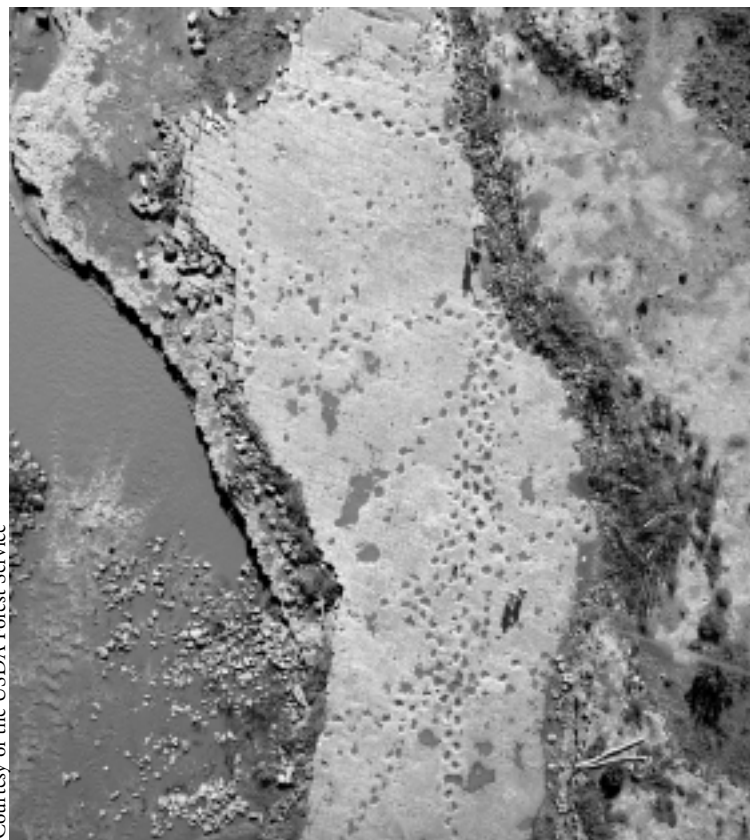
Several tracks made by running dinosaurs are also known. The fastest estimated speed calculated from such trackways is 40 kmph.⁸ Recently some tracks have been described from Jurassic age rocks in the United Kingdom.⁹ These tracks were made by a large meat-eating dinosaur, approximately 6 m in length, probably weighing 1–2 tons and moving at 30 kmph (20 mph). This speed is much faster than people previously thought possible for these dinosaurs, and shows that the idea of these animals lumbering around all the time is very far from the truth. Similarly, biomechanical analysis of *Tyrannosaurus rex* indicates that this dinosaur could not have moved much faster than 25–40 kmph (15–25 mph).¹⁰ *Tyrannosaurus* was much bigger and had longer legs, than the Jurassic trackmaker above, and larger animals tend to move relatively more slowly.

Theropods consistently seem to have moved faster than the herbivorous dinosaurs, and bipedal dinosaurs were probably speedier than quadrupedal ones. Many plant-eating dinosaurs were very large indeed, and some were so large that may not even have had to fear the meat-eaters. The fastest herbivores were probably the ornithomids, but no trackway of a large running ornithomid has been found, and very few tracks of smaller running ornithomids are known. One exception is the Lark Quarry site in Australia.¹¹ Trackways of running quadrupedal dinosaurs have not yet been documented.

Limitations of Information

As useful and versatile as tracks and trackways are, there are still some things that cannot be calculated from them. For instance, weight cannot be determined directly from the depth of the tracks. This observation may seem counterintuitive; after all, the depth of a given track is surely related to the weight of the ani-

mal that produced it, or at least by the pressure exerted by each of its feet. These factors are related, and in fact we can sometimes tell which dinosaurs are “front heavy” and which “back heavy” by looking at the relative depths of their front and back foot impressions. However, the



Courtesy of the USDA Forest Service

Fig. 3. Photo of sauropod trackways from a blimp-mounted camera at the Picketwire Canyonlands Dinosaur Tracksite in the Purgatorie Valley in southeastern Colorado.

depth of the tracks is also related to the consistency of the ground, so a heavy animal might leave shallow footprints on a hard substrate, while a much lighter animal would leave deeper footprints in a softer substrate.

Beaches illustrate this complexity well. Beaches have several zones of sediment consistency, which continuously change with the tides. The zone furthest from the sea is made of sand that remains dry, except when it rains and perhaps during storms. If you walk in this sand, your footprints will be a few centimeters deep. Nearer the sea, the sand may have a crust, which you break through; here you may leave similar



footprints, but they will have a more jagged edge. Lighter animals would not break through such a crust, and would probably not leave any tracks at all. You may then encounter a zone of underpressured sand. This looks smooth and hard, but when you step on it, your foot sinks in as far as your ankle. Underpressured sand is common in the intertidal zone. The sea has retreated, but the sand has not yet settled. It is still precariously balanced in the same configuration as it was when the water was supporting the grains. As you step on it, the sand cannot support your weight and compacts to a more stable arrangement. Even nearer to the sea, the grains are still supported by water, and you will leave very shallow, but clear footprints. A simple experiment like this shows you the range of detail that may be seen in a footprint and also indicates the variety of factors we need to consider when interpreting fossil footprints.

Another common problem we face in interpreting trackways is the question of whether small tracks were made by juveniles or by adults of small species. Usually this question is not possible to answer. However, in two scenarios a juvenile trackmaker is the more likely interpretation. The first, and more convincing, is when the tracks are so small that no known adult dinosaur was small enough to have made them. The second instance is when both small and large tracks of the same morphology are preserved on the same surface, especially if the tracks seem to show gregarious behavior. It has been argued that this association of footprints would more likely represent juveniles and adults of the same species, than a coincidental assemblage of two or more species of adult dinosaurs in association.¹²

As mentioned earlier, most dinosaur trackways show normal walking behavior, but sometimes, we find a trackway that shows different kinds of behavior.

Limpers

Several trackways made by limping dinosaurs are known from different localities around the world. We can tell that the dinosaur was limping if one pace length is considerably and consistently shorter than the other.¹³

Squatters

Some dinosaur trace fossils were made by resting animals. They seem to have squatted down on all fours, leaving impressions of their hands, their feet and ankles, their noses, their pubic bones, and sometimes even the bottom of their tails. Impressions of this sort are known for at least two different species of small dinosaur.^{14,15}

Swimmers

Some dinosaur tracks have been interpreted as those of swimming dinosaurs.^{16, 17, 18} Some of these are probably either partial tracks or trace fossils made by other animals such as crocodiles,¹⁹ but the jury is still out on some of these traces. It seems likely that dinosaurs could have swum, most animals can; we just do not have any solid evidence of this activity.

At some sites no distinct dinosaur tracks can be seen, but the entire surface is very uneven. This surface may indicate that the whole area was trampled by dinosaurs, resulting in the overlap of so many footprints that no individual ones can be distinguished. This phenomenon has been termed *dinoturbation*.²⁰ In fact, it has recently been suggested, by analogy with modern large animal game trails and migration paths, that the compaction caused by dinosaurs may have had a huge influence on the landscape, even to the extent of dictating the course of some river channels.²¹

Some myths and misconceptions surround tracks and trackways. One recurring myth is that there are places in the world where footprints of humans have been found with dinosaurs. Absolutely no evidence supports this. All of the sites where this is alleged to have occurred have been shown to be a result of misinterpretation of poorly preserved tracks, a deliberate hoax, or both. The most famous of these sites is the Paluxy River tracksite in Texas. The so-called “man tracks” were huge, did not show any impressions of distinct toes, and bore only a slight resemblance to the shape of a human foot. The tracks were followed further along the riverbed where it became clear that they were actually the tracks of a large meat-eating dinosaur. The “man tracks” had been



formed when the deep, narrow toe impressions of these elongate tracks had slumped in, leaving only the broad, shallower metatarsal (foot) impressions.²² This interpretation was a case of mistaken identity, although some of the natural trackways found at this site had been embellished with artificially carved tracks in the shape of huge human feet.

Current and Future Research

Tracks have been used to increase our knowledge of the distribution of different groups of dinosaurs in space and time.^{14, 23} Many rock formations do not contain bones, but do preserve numerous tracks. These tracks are the only evidence recording the presence of dinosaurs at these localities. Tracks have also enabled us to challenge some earlier paleoenvironmental interpretations. For example, the dinosaur tracks discovered in a unit of Wyoming's Sundance Formation indicate that this unit was not always submerged under a shallow sea, as had been previously thought.¹²

One of the more recent and encouraging developments in ichnology is the use of tracks to increase the accuracy of dinosaur reconstructions. Tracks have been used to demonstrate that ceratopsians could not have had a fully sprawling forelimb stance,²⁴ and to show that the hands of iguanodontids and hadrosaurs were directed slightly off to the side rather than straightforward as shown previously.²⁵ Tracks also indicate gait patterns of dinosaurs and have shown how gait changes with size or speed.^{26, 9}

Computer animation programs are now available to test locomotion and trackmaking hypotheses, and have already been used with some success.²⁷ These programs can also be used to model unusual trackmaking situations—to

try to explain strange tracks or trackways. Computers have also been used for some time to make accurate topographic maps of footprints. The hope is that these footprint maps will allow more accurate and objective determinations of the differences between individual tracks and trackways. The extremely high accuracy of the Global Positioning System means that we can make maps of trackways accurate to within a few centimeters. New technology is used to document tracks in the field providing accurate information for the creation of 3-dimensional computer images in the laboratory.

The future of dinosaur tracking looks bright. New sites and different track types are being discovered all the time. The opening up of countries like China and Russia, and the expansion of exploration in polar regions, South America, and India means that the variety and quantity of tracks is likely to increase. Even in relatively well-studied areas of North America, new sites are constantly being discovered. One exciting example is the huge Red Gulch Dinosaur Tracksite in Wyoming.¹² These new track discoveries increase our knowledge of the diversity and distribution of dinosaurs and help us gain greater insights into their behavior.

Dinosaur footprints capture the imagination. It's wonderful to think that you can walk on the exact surface where a dinosaur walked one or two hundred million years ago. Tracks are very evocative. As you look along a trackway, you can almost see the animal wandering along ahead of you. Partly because tracks bring dinosaurs to life so convincingly, and partly because they can reveal aspects of behavior of these animals when they were alive, tracks and trackways complement information from body fossils and help us to construct a more complete picture of life in the Mesozoic.

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