# TEXAS GIANTS: Dinosaurs of the Heritage Museum of the Texas Hill Country

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### The Heritage Museum of the Texas Hill Country

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Acrocanthosaurus, a large carnivorous dinosaur and a likely maker of some of the dinosaur footprints at the Heritage Museum of the Texas Hill Country. Painting copyright 2003 Michael W. Skrepnick.

## **Texas Giants: Dinosaurs of the Heritage Museum of the Texas Hill Country**

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#### Introduction

This report describes a remarkable dinosaur tracksite preserved on the grounds of the Heritage Museum of the Texas Hill Country (HMTHC), situated along Farm to Market Road 2673 between the communities of Sattler and Startzville in Comal County. The goals of this publication are twofold. On the one hand, we want to provide sufficient information about the tracksite and its dinosaur trackways to be useful to paleontologists, geologists, and other professional scientists. At the same time, however, we want to explain our findings in language that is attuned to lay readers, so that they can appreciate the significance of the HMTHC tracksite as a time capsule that preserves moments in the lives of creatures that lived long before ourselves.

This study is the culmination of literally decades of research by many persons, some of whom are authors of the report. Many other people, particularly students and museum volunteers, assisted us with the logistics of our work (some of them providing splendid meals for the field workers!). Rena Bonem, Mike Hawthorne, Mike O'Brien, David Riskind, Peggy Maceo, David and Margaret Akers, Glen Kuban, Ronnie Hastings, and Billy Baker helped us in a timely manner with our field work on dinosaur tracksites across much of Texas. Financial support for field activities came from Indiana-Purdue University Fort Wayne, the Vertebrate Paleontology Laboratory of the University of Texas, and the National Science Foundation.

Unless otherwise indicated, all artwork for this report was created by the authors. However, several other individuals or institutions provided us with photographs or drawings; these are duly noted in figure captions. We particularly thank Michael Skrepnick for letting us reproduce some of his life restorations of dinosaurs, some of them created specifically for this publication.

Our research builds on the work of many other scientists. We dedicate this report to the memory of four recently deceased individuals whose research was particularly influential: David L. Amsbury, John H. Ostrom, Bob F. Perkins, and William A. S. Sarjeant. Our science and our lives are made poorer by their absence.

#### **Box 1: Museum Catalog Numbers**

Several pieces of artwork used in this publication illustrate fossils that are curated in the collections of natural history museums. Some readers may find it helpful to know the details of where these specimens are housed. Consequently the catalog numbers of the specimens are provided in the figure captions. The museums represented by the acronyms employed in catalog numbers are as follows: AC: Amherst College; BMNH: Natural History Museum, London; CU-MWC: University of Colorado-Museum of Western Colorado; FMNH: Field Museum of Natural History; IRSNB: Royal Institute of Natural Sciences, Belgium; MNA: Museum of Northern Arizona; MOR: Museum of the Rockies; NCSM; North Carolina State Museum of Natural Sciences; NMC: National Museums of Canada; OMNH and OU: Sam Noble Oklahoma Museum of Natural History; SM: Strecker Museum (now Mayborn Museum), Baylor University; SMU: Southern Methodist University; TMM: Texas Memorial Museum; TMP: Tyrrell Museum of Palaeontology; UA: University of Arkansas Museum; UMNH: Utah Museum of Natural History; USNM: National Museum of Natural History, Smithsonian Institution; YPM: Yale

#### **Discovery and Study of the Tracksite**

In the public imagination, dinosaurs are perhaps the most remarkable creatures that ever lived. The average person on the street might be forgiven for thinking that to find the fossil remains of such exotic animals, one must travel to equally exotic parts of the world-a belief undoubtedly reinforced by movies and television shows about dinosaurs-and it is certainly true that many dinosaurs are discovered in faraway places.

But this isn't always true. Sometimes spectacular dinosaur discoveries are made, quite literally, in one's own back yard.

This is exactly what happened to the late Ken Thayer, a retired postal worker, in June of 1982. Mr. Thayer lived on a property along Texas Farm-to-Market Road 2673 (Fig. 1), a few miles west of Sattler in Comal County (GPS coordinates are 29° 50.278' N, 98° 13.279' W). The state highway department had removed material from the side of the hill for use as road fill. Some young people playing on the newly exposed surface discovered numerous three-toed impressions in the rock surface. Mr. Thayer could step directly from his home onto a flat rock surface that had been trod by dinosaurs more than 100 million years ago.

Soon after the discovery, the new dinosaur tracksite was visited by numerous geologists and paleontologists. Richard H. Sams published a brief notice of the site in the Bulletin of the South Texas Geological Society, with preliminary observations about trackway orientation.

**Figure 1.** Location of the Heritage Museum of the Texas Hill Country and Mountain Creek tracksites. A) United States Geological Survey (USGS) digital elevation model of the part of Comal County, Texas (location indicated in the inset; state map reproduced from USGS 7.5 minute Sattler quadrangle map) containing the Heritage Museum tracksite (marked by black asterisk). White areas indicate higher elevations, and black areas low elevations. The road immediately to the north of the tracksite is FM 2673. B) USGS Digital Orthographic Quarter Quadrangle, obtained from the Texas Natural Resources Information System website. Heritage Museum tracksite indicated by white asterisk. The Mountain Creek tracksite is immediately adjacent to the east and southeast, visible as a light colored area curving around the same hill as the Heritage Museum site. C) Aerial view showing the property line of the Heritage Museum. The tracksite is the light-colored, slightly curved area immediately to the right of the photograph center. Individual dinosaur trackways in this surface are indicated by black dots.







Miles





TMM mapping party missed a faint print in this trackway between their O10 and O11. Step lengths in the L trackway are highly variable; the distance between L1 and orienting the site's dinosaur footprints, but does have a few limitations. It does not include several footprints later discovered at both the east and west ends of the site. made after O1. "Trail 1" is the single crawl mark, and "Trails" 2 and 3 comprise the double crawl mark. The TMM map is of inestimable importance for locating and and number labels identify individual footprints and the trails in which they occur. Prints in trackways are numbered to reflect their sequence; thus O2 is the footprint The JOF trackway (not shown on this map) was either not seen or disregarded by the map-makers. There is an error in the numbering of footprints in the O trail; the Figure 2. Map of most of the HMTHC track surface, redrafted from the original made by personnel of the Texas Memorial Museum (TMM) in July 1982. Letter 2, for example, is so much greater than between L2 and L3 as to suggest that a footprint between L1 and L2 as numbered was either not preserved or missed.

Wann Langston, Jr., Kyle Davies, Frances Zimmer, and Scott Kelly of the Texas Memorial Museum (University of Texas at Austin) made a map of the trackways then exposed in July 1982 (Fig. 2). Additional footprints had been uncovered by the time James Farlow of Indiana-Purdue University Fort Wayne (IPFW) spent a day at the site nearly a year later. Farlow worked under the assumption that this single visit might be the only opportunity he would have to study these trackways (which nearly turned out to be the case). With but a single day to work, Farlow spent no time trying to identify the trackways as labeled by Langston's crew. Instead, he made provisional trackway designations of his own as he measured and photographed prints and trails, working from east to west across the site (Table 1: tables are at the back of this book).

Farlow was not able to return to the tracksite until March 2000, by which time it had been acquired by the Heritage Museum of the Texas Hill Country (HMTHC). Farlow returned in May 2001 and in later years with geology students from IPFW. Working alongside volunteers from the museum and the Paleontological Association of South Texas, Farlow's students cleaned the prints, made new measurements of the trackways, correlated Farlow's 1983 trail designations with those on the UT-Austin map, traced outlines of individual footprints onto plastic sheets for later measurements in the lab, and took casts of several of the better-preserved footprints. Directed by a local surveyor, Richard Solis, some of Farlow's students mapped trackways that had not been seen by the UT-Austin group. Work was done at both the HMTHC site and on an adjoining property to the east, the Mountain Creek site. At the same time, Brenda Kirkland and Wann Langston, Jr., made detailed observations on the rock sequence in which the HMTHC tracksite occurs. Subsequent observations on the HMTHC rocks were made by William Ward and Susan Hovorka.

One particularly noteworthy effort involved photographing the HMTHC tracksite from an elevated platform (Fig. 3). We attempted to shoot the rock surface from as nearly directly overhead as possible, overlapping each exposure. These photographs were later used to create a photomosaic of much of the tracksite.

Describing what we know about the HMTHC footprints and the dinosaurs that made them gives us an opportunity to explain how geologists and paleontologists reconstruct events of the far distant past. We are, in many ways, like forensic investigators at a crime scene. We cannot observe what happened, but we can try to reconstruct past events from the clues that are left behind. Sometimes the clues are not clear enough to tell us everything we would like to know, but we do what we can with what information we have.

Figure 3. Jim Whitcraft photographing the track surface in 2002.



#### **Geologic Setting of the Tracksite**

Like many dinosaur tracksites across central Texas, the HMTHC tracksite is an exposure of the Glen Rose Formation. This formation is part of a larger packet of sedimentary layers known as the Trinity Group, which in turn is part of the Comanche Series of rocks (Fig. 4). The Comanche Series was formed during the early part of the Cretaceous Period, a little over 100 million years ago.

The Glen Rose Formation is composed largely of limestone (carbonate) that was deposited on the bottom of a warm, shallow sea (an early version of the Gulf of Mexico) that gradually spread across Texas from the south (Figs. 4, 5). A line of reefs constructed largely by **rudists**, a group of odd (at least to us) **bivalves** ("clams" if you will) rimmed the edge of the continental shelf, and small, patchy occurrences of these rudists occurred inside this outer rim (one such patch is preserved on the grounds of the HMTHC, stratigraphically beneath the tracklayer). Sometimes, behind the reefs, the shallow waters of the shelf teemed with a diversity of marine plants and animals: algae, invertebrates, fishes, and marine reptiles. At other times, depending on water depth, salinity, and temperature, the shelf environment became hostile to all but the hardiest of marine organisms.

The HMTHC tracksite is positioned in the upper portion of the Glen Rose Formation, one of many dinosaur tracksites in Texas situated at this level (Fig. 6). The track-bearing horizon actually consists of at least three distinct layers. In all of these the dominant mineral is calcite, a form of calcium carbonate (CaCO<sub>3</sub>). The texture of the limestone provides important clues to the exact environment in which the dinosaur prints were made. Much of the rock consists of tiny clumps of micrite (a short term to designate microcrystalline limestone that formed from limey mud). The fine-grained texture of the limestone indicates that water action at the time of deposition was not very rough, or the fine particles of limey mud would have been washed away by currents. The water could not have been very deep at the time the dinosaurs left their tracks (or else these land animals would have been bobbing at its surface like reptilian corks); very likely the track surface was above water level.

Figure 4. Diagrammatic cross-section of Lower Cretaceous Comanche Series rocks from north (southeastern Oklahoma) to south across Texas (modified from Scott and others, 1992). Comanchean rocks were deposited as sediments during the Early part of the Cretaceous Period. Distinctive packets of sedimentary layers in a particular area that can be distinguished from other such packets above and/or below them are recognized as formations (abbreviated Fm), such as the Glen Rose Formation (in which the HMTHC dinosaur tracksite occurs). The total thickness of Lower Cretaceous strata in a particular area is conveyed by the illustrated thickness of the relevant stratigraphic column; thus the Valley Mills Composite section is much thinner than its counterpart from Waller County. Measured thicknesses are indicated in meters, and in some cases also in feet. Thicknesses of surface exposures (SE Oklahoma to Austin area) are measured from the bottom of the outcrop. Thicknesses of subsurface sections (the three sections at the right of the diagram) are measured in distance below the surface. Distances between rock sections are indicated across the top of the diagram in miles and kilometers; note that the vertical thicknesses of rock sections are exaggerated 1400 times in comparison with the horizontal distances between them. Numerical ages (in millions of years; Ma) are also shown. Sandstones are identified by a stipple pattern, shaly limestones by horizontal lines with small vertical bars, limestones by a blocky pattern, and dolomites by a backslash pattern. The greatest total thickness of sedimentary rocks is in the south, adjacent to or in the ancient Gulf of Mexico. Here marine sediments were able to accumulate almost continuously, their ever-increasing thickness causing the earth's crust to sag slightly under their weight-making it possible for still more sediments to pile up. To the north, on or close to dry land, sands of the Antlers, Twin Mountains, and Paluxy Formations were deposited. Over the course of the Early Cretaceous the waters of the Gulf gradually spread northward, displacing dryland environments and allowing marine limestones to be deposited instead of sandstones. However, the process was not uninterrupted. Thus in the Fort Worth area the marine Glen Rose Formation spread over the terrestrial Twin Mountains Formation, only to have terrestrial conditions re-established during deposition of the Paluxy Formation. However, this triumph of dryland sediment deposition was only temporary, and marine sediments of the Walnut Formation were then deposited over the Paluxy. Eventually the waters of the Gulf would link up with marine waters spreading southward from the Arctic Ocean to split the North American continent in two.







Figure 5. Reconstructing landscapes during the Early Cretaceous. A) Paleogeographic reconstruction of North America about the time that the Glen Rose Formation was deposited. Interpretations are based on the geographic distribution of sedimentary and other kinds of rocks, as well as structural features of those rocks. Dark brown represents mountains and other highlands, tan = low-lying land areas, light blue = shallow marine conditions flooding the continental margin, and dark blue = open ocean. The ancestral Gulf of Mexico was beginning its encroachment on the continent; it would eventually link up with the marine tongue spreading from Canada to split North America into eastern and western segments. The Heritage Museum tracksite would have been along the margin of the dry land region associated with the Llano Uplift. Paleogeographic reconstruction by Keith Minor. B-E) Modern shallow marine environments that help us visualize the Early Cretaceous landscape in the vicinity of the Heritage Museum. B) View of the Florida Keys from the air, looking eastward toward the Atlantic Ocean. The white line running across the tree-covered islands is U.S. Highway 1. Beyond the highway, toward the top of the photograph, is a nearly linear white stretch of shallow water marking the crest of offshore reefs. In the foreground (below the highway in the picture) is a tidal delta composed of coral-algal sand, pelleted grains, and lime mud. Brown areas are submerged seagrass flats, cut by tidal channels floored with white carbonate sand. Small black patches near the lower right-hand corner of the photograph are small keys surrounded by white sediments on which occur mounds made by brine shrimp. This seascape reproduces on a much smaller scale habitats analogous to those that existed on the landward side of the reefs of coastal Texas during the Early Cretaceous. C) Bowen Tidal Flat near Townsville, northeast coast of Queensland, Australia, at low tide. Note the tidal channels crossing the flat. This photograph shows how large tidal mudflats can be; the Early Cretaceous carbonate mudflat along the ancient Texas coast was probably even larger. D) Dried algal mats on the margin of a mangrove-lined central lagoon, Florida Keys. Susan Hovorka provides the scale. The substrate here was dry enough for a person to walk on without sinking into the mud, but the waterline on Hovorka's jeans shows that deeper water areas were very close by. E) Mangrove tree, Andros Island, Bahamas. Modern mangrove trees did not exist during the time of Glen Rose deposition, but some Early Cretaceous gymnosperm trees are thought to have had a similar lifestyle.

Also present in the limestone in some abundance are **peloids**, which are small, roounded particles composed of micrite without any recognizable internal features. Some peloids probably originated as fecal pellets of small marine invertebrates.

Rocks at the HMTHC site are not exclusively limestone, however. Interbedded and somewhat mixed with limestone (albeit not in the tracklayers themselves) are beds of clay. In contrast to the lime sediments, which were generated in the marine environment by chemical and especially biological activity, the clay sediments were derived from weathering and erosion of rocks on the land (which would have been somewhere to the north of the HMTHC site, and probably not far away).

Such **terrigenous** clays can be carried long distances from the land into marine environments. They are light enough to be carried by the wind, as happens today, when dust particles are blown from the Sahara Desert far across the Atlantic Ocean before they are finally dropped. Clay sediments are even more readily transported by water-from the mouth of the Mississippi River far out into the Gulf of Mexico, for example. Clays may travel in turbid layers of fresh water floating on top of heavier salt water, as dense plumes of muddy water, or as waves move sediment along the bottom of the sea. In the specific case of muddy beds in the Glen Rose Formation at the HMTHC, the presence of clay beds probably indicates temporary fluctuations in sea level, such that the normal marine processes of carbonate deposition were interrupted, allowing terrigenous clays to be carried away from the shore to blanket previously deposited limy beds.



**Figure 6.** Stratigraphic section of rocks at the HMTHC tracksite. A) Aerial photograph (compare with Fig. 1) showing where the composite section (part B, left) was measured. Thicknesses of rock layers are measured in feet, with zero corresponding to the bottom of the section, located along FM 2673. Stratigraphically higher beds are encountered at progressively higher elevations up to the top of the section. B) Most of the exposed rocks in the vicinity of the HMTHC represent the Glen Rose Formation, but a portion of the overlying Walnut Formation occurs at the top of the stratigraphic section. The left-hand column shows the composite section. The right-hand column expands the portion of the composite section that crops out on the grounds of the museum (light green), with the track horizon indicated in dark green. Features of particular beds, including characteristic fossils, are indicated at the right of the section.

Numerous fossils can be seen in the rocks at the HMTHC site. In the track-bearing layer these include **foraminiferans**, **ostracodes**, and **dasycladacean algae**. Foraminiferans are protozoans (single-celled "animals") that manufacture a tiny (often the size of a sand grain), hard skeleton, or **test**, to house the cell. In some foraminiferans the test is made from sediment particles that the protozoan finds on the sea floor and glues together. Among this group of forams is *Orbitolina*, which manufactured vaguely frisbee-shaped tests and is one of the most common fossils in the Glen Rose Formation, and which is found in beds above the track layer at HMTHC.

The abundant forams in the track layer, however, are **miliolids**, a group of forams that make their shell not by cementing particles that they collect, but rather by secreting their limey skeleton. Miliolids are beautiful fossils; seen under a microscope, their tests have a shiny, milky appearance like fine china, and the shapes of these tests can be quite extravagant.

Ostracodes are tiny crustaceans (distant relatives of crabs and shrimp) that secrete two calcareous shells. When these animals die, their shells accumulate on the sea floor like any other sediment particle.

Dasyclads are a kind of seaweed. The plant secretes lime around itself, and eventually this material winds up on the sea bottom. Because dasyclads are plants that need sunlight for photosynthesis, their presence in the track layer tells us that the water above this layer could not have been very deep, because water absorbs sunlight very quickly with increasing depth. Of course, this is something we already knew from the presence of the dinosaur tracks-the reptiles couldn't have been making footprints if the water was hundreds of feet deep!

The dasyclads, miliolids, and ostracodes may be telling us more than that, though. All of these groups of organisms are often very abundant in waters that do not show the salinity normally seen in seawater, but rather are either more brackish, or saltier, than usual, or that fluctuate between brackish and excessively salty conditions.

Dasyclads, miliolids, and ostracodes may tolerate a salinity that departs from that of normal seawater, but few other kinds of marine organisms do, and this may explain another feature of the tracklayer: It contains very few burrows of marine animals. Under favorable conditions, the sediment of the sea floor is riddled with vertical and horizontal grooves, squiggles, and tunnels made by animals as they plow across or through the sediment on their business-sometimes constructing hiding places from predators, and sometimes actually eating the sediment to digest its organic matter. Trace fossils of this kind are often preserved in sedimentary rocks. The scarcity of such burrows and trails in the HMTHC tracklayer suggests that conditions may not have been suitable for a diverse assemblage of bottom-living animals, and abnormal salinity would be a prime candidate in making the habitat less than ideal.

And where might we expect such conditions to occur? Not in offshore waters, where the great volume of water would prevent excessive dilution of sea water by rain, or excessive saltiness due to evaporation. Rather, we would expect abnormal salinity close to shore, where the water is very shallow, and where the bottom might actually be above water level at times. Further evidence for this interpretation comes from the presence of mud cracks preserved in parts of the tracklayer. Mud cracks form when water dries up, and the mud surface splits and curls up at the edges of those breaks. The texture of the rock in the tracklayer further suggests that at least some of the mud cracks developed in an algal mat that covered the sediment surface. Once again, the notion that the water was very shallow, or the bottom even high and somewhat dry, is also supported by the presence of the dinosaur footprints.

However, the water depth increased after the interval during which the footprints were made. Rock samples collected from the bluff at the south edge of the tracksite have a greater diversity of fossils than in the tracklayer: foraminiferans, four different kinds of dasyclads, a thin-shelled kind of bivalve, oysters, **echinoderms**, and even a piece of bone (possibly from a sea turtle). The water depth still would not have been great-perhaps between half a meter and 2 meters--but it was deep enough to maintain normal salinity. This is indicated by the presence of echinoderms (sea urchins, starfishes, and their relatives), which do not tolerate water salinity much different than that of normal seawater.

Putting all of this information together, during the geologic interval when the rocks of the HMTHC were formed, this patch of real estate was situated at the inner margin of a very wide and shallow continental shelf sea at a time when the ancestral Gulf of Mexico was beginning a long, slow, herky-jerky encroachment onto the land. In this very shallow water environment, wave action was normally gentle rather than turbulent. Most of the time the site was underwater, but at least once it was exposed, giving several dinosaurs the chance to walk across its surface.

#### **General Description of the Tracksites**

*The Heritage Museum Tracksite*. The longest dimension of the HMTHC tracksite is oriented east to west, with a low bluff bounding its southern margin (Figs. 2, 7-10). Because the rock layer containing the prints disappears beneath the overlying rocks of the bluff, there are undoubtedly many more dinosaur footprints beyond the limits of the present exposure. In addition, what is probably the same layer is again exposed at the Mountain Creek site immediately to the southeast of the museum, where some very nice dinosaur prints occur.

Three conspicuous, nearly linear features cross the site in a northwest-southeast manner, nearly perpendicular to the main trend of the dinosaur trackways (Figs. 2, 11). The three linear features are nearly parallel. These traces are probably crawl marks of some kind of animal, and may have been made by animals crawling toward or away from the water.

But what kind of animal? We will return to this question later.

**Figure 7.** A) First of a series of photographs showing much of the HMTHC tracksite as it looked in 1983, photographed from the bluff at the south side of the site, looking to the north. This first shot shows the extreme end of the HMTHC tracksite. Note the spot from which TMM 43002-1, the "stacked" footprint, was cut. Identifications of footprints are given in terms of either their Farlow 1983 assignments, later identification numbers, or in some cases both. B) Just to the left of the area shown in A; note footprints in common (e.g. 01F3, 01H1). Some footprints (01J1, 01J2, 01J3, 0103) are exposed in a rock layer immediately beneath the one containing most of the footprints; the edge of the overlying main layer is adjacent to footprints 01E1 and 01E2). The footprints in the underlying rock layer are very likely transmitted prints. C) Continuing to the left from B. After the dense accumulation of footprints at the east end of the site, we are now in an area with few well-preserved prints. However, there are numerous shallow, vague impressions here (and across much of the entire site, for that matter) that could well be poorly preserved footprints.





Figure 8. A) Continuing to the left from Fig. 7C, this view emphasizes the "barren" region of the site, where there are few well preserved footprints. However, the first of the long trackways, the B trail, can now be seen at the left (west) edge of the exposure. B) Continuing to the left from A. Much of the B trail and parts of the C trail are now in view, and we first see the single crawl mark. Interestingly, print B4, perhaps C20, and a possible footprint just below B5, seem to step on the single crawl mark. The "threeway" overlap of trails C, JOF 12, and a third trackway (Figs. 15A, 16A) can be seen near the north edge of the track surface. C) Continuing to the left from B. Much of the single crawl mark can now be seen, along with more of the C trail, and part of the E trail.





**Fig. 9.** A, B) Continuing to the left from Fig. 8C. The double crawl mark now comes into view, along with much of trails E and F. Note how trail C markedly changes direction along its length-the only trackway at the site to do so.

Fig. 10. Photomosaic of the tracksite created from elevated shots (Fig. 3) taken in 2002. Plastic crosses littering the site were temporary features used to create landmarks for splicing individual photographs together. Although we attempted to shoot photographs from as nearly directly overhead as possible, some distortion around the edges of images occurred. Resulting significant mismatches in the photomosaic are labeled as such on details taken from the overall image. A) Photomosaic of most of the tracksite. The site runs roughly east to west, with a low bluff along its southern margin. Two concrete slabs provide useful landmarks (also shown in Fig. 2); the smaller of these is to the east of the larger. Rectangles delimit regions shown in greater detail in parts B-E of this figure (following pages). B) Detail 1, the eastern portion of the site, with some of the more prominent footprints labeled (cf. Figs. 7, 12-note deterioration of some footprints due to weathering over the interval of time separating Farlow's 1983 photographs and the 2002 image shown here). Tracks in this part of the site were not mapped by Langston's party in 1982. C) Detail 2, showing the more easterly portion of the site mapped by Langston's group (Figs. 2, 8-11, 14-18). D) Detail 3, showing footprints in the area between the large and small concrete slabs (Fig. 2), most of which were of poor quality by 2002. E) Detail 4, showing prints at the western edge of the area mapped by Langston (Fig. 2) as well as tracks subsequently found even further to the west (Figs. 20-22). The track surface curves to the northwest beyond the western limit of this photograph. In 1983 Farlow observed a few footprints in this area, most of which were of poor quality by 2002.

Like the dinosaur footprints, the long linear features are examples of **trace fossils**, which are indications of the activities of ancient living organisms recorded as traces in rocks or other hard objects. Trace fossils include such things as damage to bones or shells of animals caused by teeth or other death-dealing implements of meat-eating animals, fecal droppings (yes, such things really do fossilize!), marks made by plant roots in ancient soils, burrows and crawl marks in sediments, and of course footprints. Trace fossils contrast with **body fossils**, which, as the name would suggest, are shells, bones, wood, or other physical remains of a dead organism that become fossilized.

A **footprint** is an impression in sediment made by a single foot, and a **trackway** or **trail** is a series of footprints made one after the other by the same animal. Of course, English is such a versatile language that some of these terms also have other meanings; for example, a "trail" can also be a path cut through the woods. Similarly, the word **track** is sometimes used to describe a single footprint, and other times as another word for "trackway", and "trackway" is itself sometimes used to describe an extensive surface covered by footprints, what we here call a **tracksite**. This fuzziness in usage is perhaps unfortunate, but the meaning here should be clear from the context of our discussion.

Dinosaur trackways cross the site from one end to the other (Figs. 2, 10, 12-22). A nice feature about many of the trackways is that they are quite long, with numerous footprints made by the same animal (Table 2). Most of the dinosaur trackways are on the same bedding surface, but there is a patch near the eastern end of the site where this layer has eroded away to reveal an underlying rock layer, and several footprints are present in this lower layer (Fig. 7B). This underlayer is also exposed at the western end of the site, where trackway 01M is preserved on both the main layer, and where this rock layer has been removed, on the underlayer (Fig. 21).









Although it might seem odd to find the same dinosaur trail on different rock layers, this is actually a common occurrence at footprint sites. Rock layers often originate as thin, stacked layers (beds) of sediment. Big dinosaurs were heavy animals, and when such a dinosaur walked across a surface composed of several thin sediment layers, one on top of the other, the dinosaur's foot made a print not only in the surface across which it actually walked, but also indented some of the underlying sediment layers. Such undertracks are called **transmitted** or **ghost tracks** by paleontologists.

Experiments on track formation carried out by British paleontologist Phillip Manning, building on earlier work by sedimentary geologist J. R. L. Allen, have shown how the mechanics of sediment deformation change the size and shape of a transmitted footprint. With increasing depth over the first several sediment layers, the footprint becomes shallower and less clearly defined, but also bigger. The increase in size with greater sediment depth occurs because the weight of the animal pressing down on the substrate creates a "force bulb" of pressure that initially radiates outward as well as downward from the trackmaker's foot into the pile of sediments. At some level below the surface, however, the deformation becomes less, and below this point the transmitted prints decrease in size until they peter out altogether.

Paleontologists from the Texas Memorial Museum collected a series of stacked footprints from near the eastern end of the site (Fig. 23). The same print could be seen on the main tracklayer and on two layers beneath it, over a total rock thickness of 10.7 cm (about 4 inches). Going from the top layer deeper into the stack, the footprint becomes shallower and broader and less clearly defined. In the lowest layer (Fig. 23H) the print is little more than a faint, basin-shaped depression. Because the deepest print in this series is larger than the surface print, the force bulb was still expanding at this level.

Even the best-preserved HMTHC footprints are of indifferent quality compared with those from some other dinosaur tracksites. Consider, for example, the famous Paluxy River dinosaur footprints at Dinosaur Valley State Park near Glen Rose, Texas (Fig. 24). These prints also occur in the Glen Rose Formation, but at a lower stratigraphic level than the HMTHC tracks, and so are older than those from Comal County. The Paluxy River footprints are often deeper, with well-defined edges that nicely show the shape of the track. Considerably older dinosaur footprints from both the eastern and western United States can be even better preserved than that, revealing sharply defined claw marks, impressions made by toe pads, and sometimes even indications of individual scales on the undersides of the dinosaur's toes.

The quality of preservation of the HMTHC footprints varies from one trackway to another, and even among footprints within the same trail. Most of the footprints in the E trail (Fig. 17) are little more than oblong depressions, while the G trail (Fig. 20) comprises very nice footprints with clearly defined toemarks. Despite the poor quality of many of the prints in the C and E trails, individual footprints within those trackways are in some cases better preserved (Figs. 15, 17).

Along with the footprints that were identified as such, there are many faint depressions of the track surface that were too obscure for us to confidently recognize as dinosaur tracks, but which we nonetheless suspect could well be especially poorly preserved prints (Figs. 7-9). Given the reduction in clarity of footprints that are preserved as transmitted prints, it is tempting to think that many of the poorly preserved footprints, as well as the vague depressions, are just such transmitted prints that were made by dinosaurs that actually walked on a sediment layer above the one in which their tracks now occur.



**Fig. 11.** The crawl marks. A) Photograph taken by Texas Memorial Museum personnel during mapping of the tracksite in 1982; Wann Langston is seen in the left foreground. The picture was taken from the bluff to the south of the site, facing north. Footprints in dinosaur trails E, F, I, and K are indicated. Narrow straight lines crossing diagonally from top to bottom are joint cracks in the Glen Rose rock; they are unrelated to the crawl marks or the dinosaur trackways. B) Another view from the bluff, taken in 1983, again looking north, showing long portions of both the single and double crawl marks. Although not labeled, trackway E is the prominent dinosaur trail cutting diagonally across the center of the photograph. C) Elevated shot of the single crawl mark taken in 2002, looking to the northwest. In this view, the more prominent, tread-like or ladder-like part of the crawl mark is on the left. A meter stick can be seen to the left of the crawl mark near the top of the picture. E) Cast of a portion of the double crawl mark (TMM 43002-6), made in 1982 while the surface was freshly exposed and unweathered. The more prominent part of the crawl mark is on the right. The scale is marked off in centimeters and inches. F) Close-up of the more prominent half of the double crawl mark, showing ladder-like cross bars.

However, another feature of the "stacked" print (Fig. 23) makes us uneasy about jumping to that conclusion. The upper surface of the main footprint (Fig. 23D) was partly filled by a thin plug (a natural cast; Fig. 23A-C). According to accounts of the people who discovered the tracksite, similar plugs covered some of the other prints at the time of discovery, but popped loose in response to later weathering. The existence of such plugs indicates that the tracks filled by them are probably not transmitted prints. Had the footprints been transmitted prints, they should have been filled not by a thin, concave-up plug of sedimentary rock, but rather by a thick convex projection firmly attached to the undersurface of the overlying rock layer, as in the ghost prints of the "stacked" print (Fig. 23). Instead, these footprints were likely made in the surface across which the dinosaurs walked, as depressions in that surface. The footprints then were exposed to the elements long enough for sediment plugs to partially fill them.

Although we cannot rule out the possibility that some of the HMTHC footprints are actually transmitted prints, we think it more likely that most or all of them are "real" footprints, pressed into the surface across which their makers actually walked. If this is true, then variability in footprint quality within and among trackways is more likely due to differences in the consistency of the muddy substrate at different parts of the site, and/or at different times.

*The Mountain Creek Tracksite*. Immediately east of the HMTHC property line, the same tracklayer, or one very close in stratigraphic position to it, continues in an easterly and southeasterly direction around the side of the hill (Figs. 25-28). The Mountain Creek site actually consists of two exposures of track surface separated by a short stretch covered by loose sediment and vegetation.

Most of the Mountain Creek footprints are less well preserved than those of the HMTHC site, but some of them are quite good (Figs. 29, 30). An especially interesting feature of one of the trails is the possible, but questionable, occurrence of forefoot (manus) impressions in association with the usual three-toed hindfoot tracks (Fig. 30M). As we shall see, if these really are manus impressions, this has a bearing on the identification of their maker.

As with the track surface of the HMTHC site, the Mountain Creek tracksite is dotted with numerous vague depressions that cannot confidently be identified as individual footprints, or linked up with other depressions in trackway sequence. These may nonetheless be poorly preserved footprints made at different times, under different sediment conditions, than the footprints we have identified as such.



**Figure 12.** Footprints at the eastern part of the HMTHC tracksite; compare with Figs. 7, 8. See tables 2-6 for footprint and trackway measurements. Each trackway or isolated footprint was assigned its own label; thus 1983 6 was the sixth trackway recognized by Farlow in 1983. Footprints are numbered according to their position in a trail; print 1983 6-2 was the second footprint seen in trackway 1983 6. A) Isolated footprint 1983 1, near the extreme eastern edge of the site as exposed in 1983. In this and other photographs of individual footprints and trackways of the HMTHC site, a meter stick provides the scale, but not all of the meter stick is shown in every picture. However, one can usually make out major tick marks in the meter stick, which are 10 centimeters (about 4 inches) apart. B) Trackway 1983 3. C) Parts of trackways 01A (1983 6) and 01C (1983 5); the lovely young woman is Mrs. Karen Farlow. D) Footprint 01C3 (1983 5-1); print made by right foot. E) Footprint 01A7 (1983 6-3; a right). F) Trackway 01E (1983 7). G) Footprint 01E1 (1983 7-1; left). H) Cast (negative replica) of footprint 01E1. In this and other casts, topography is reversed from that of the actual print. I) Footprint 01E3 (1983 7-3); left. J) Trackway 01F (1983 8). K) Footprint 01F3 (1983 8-1; left). L) Trackway 1983 9. M and N) Footprints 1983 9-1 and 1983 9-2; which of these is left and right is uncertain. O) Isolated (?) footprint 1983 10.



**Figure 13.** Casts (negative copies) of footprints from the eastern part of the HMTHC site. A) Footprint 01A7 (1983 6-3; see Fig. 7A, 12C, E for the actual footprint). B) Footprint 01B1; right. C) Amalgam of footprints 01A6 (1983 6-2; a left, and faintly seen on the left of the amalgam) and 01C3 (1983 5-1 (a right, and seen on the right of the amalgam). See Fig. 12C for the actual footprints. D) Footprint 0102; left-right symmetry uncertain. See Fig. 7A for the actual footprint



**Figure 14.** Trackway B. A, B) Two segments of the trackway as seen in 1983; the animal was moving away from the viewer (reader). C) Elevated shot of part of the trail as seen in 2002; the animal was moving toward the viewer. D) Footprint B2 (1983 11-1; right). E) Footprint B3 (1983 11-2; left). F) Footprint B4 (1983 11-3; right). G) Footprint B5 (1983 11-4; left). H) Footprint B7 (1983 11-6; left). I) Footprint B8 (1983 11-7; right).





**Figure 15.** Trackways C and JOF 12. A) Elevated shot of the two trails as seen in 2002; animal C was moving toward the viewer, and animal JOF 12 away from the viewer. The "three-way overlap" amalgam (Figs. 8B, 16A) is near the bottom of the photograph. B, C) Two portions of the C trail, as seen in 1983. The animal was moving away from the viewer. Note slight pressure ridges surrounding some of the C trail prints, made as sediment squeezed up around the margins of the dinosaur's foot.

C22

C21



**Figure 16.** Trackway JOF 12 and isolated print 1983 17; see Fig. 15A for an elevated view of the JOF trail. A) The "three-way overlap" amalgam (see also Fig. 15A). In this view, the "heel" of footprint C26 comprises the pointed region at the lower right hand portion of the amalgam. Part of print JOF 12-1 is headed in the opposite direction at the top of the amalgam, with only one toe clearly seen. Isolated footprint 1983 14 (possibly part of Langston's A trail) comprises the left part of the amalgam, and is the most clearly seen of the three prints. B) Footprint JOF 12-2; left. C, D) Footprint JOF 12-3 (right); C shows the print in the ground, and D is a cast. E) Isolated footprint 1983 17; symmetry uncertain.



**Figure 17.** Trail E and associated trackways. A) Elevated shot of E trail as seen in 2002; the animal was moving toward the viewer. B-D) Portions of the E trail as seen in 1983. D) Footprint E14 (1983 16-11; right).



**Figure 18.** Trail F and associated trackways. A) Elevated shot of this region of the site as seen in 2002; dinosaurs F, I, and O moving away from the viewer. B) Portion of F trail as seen in 1983; the animal was moving away from the viewer. Note that the dinosaur stepped on part of the double crawl mark at F19. C) Footprint F23 (1983 18-6; right).







**Figure 19.** Trails H, I, K, and O. A) Elevated shot of portions of all three trails as seen in 2002. All three dinosaurs were moving away from the viewer. B, C) Ground views of parts of trails I and K as seen in 1983; both animals moving away from the viewer. D) Cast of O15; right. E) Cast of I 23; right.



**Figure 20.** Trackway G. A) Ground view of most of the trail as seen in 1983; the animal was moving away from the viewer. B) Elevated view of the severely degraded trail as seen in 2002; the animal was moving toward the viewer. C. Footprint G2 (1983 26-2; right), possibly the best-preserved footprint at the site at the time the photograph was taken. The landowner at the time had painted the footprint.










**Figure 22.** Trail 01K (1983 28), a sequence of four footprints characterized by a long step length. A) Elevated shot of the trackway as seen in 2002; the dinosaur was moving away from the viewer. B, C) Two shots of the trackway as seen in 1983, again with the animal moving away from the viewer. D) Footprint 01K1 (1983 28-1; right). E) Footprint 01K2 (1983 28-2; left). The footprint-bearing rock surface curves to the north beyond the section shown in these photographs (seen in the upper left of part A of this figure). A few indifferently preserved footprints occur here.

**Preservation of the footprints**. After the HMTHC and Mountain Creek prints were made, they sat exposed at the mud surface for some unknown interval of time. Hours? Days? Weeks? They may have baked for some time under the hot sun, with the sediment in which they were impressed becoming harder, and possibly even cemented into a hard surface. Eventually the track surface was buried by later sediments, which were also converted to sedimentary rock. Long after the sea withdrew from the region, erosion of the landscape uncovered the Glen Rose Formation, setting the stage for discovery of the tracksite.

## **Box 2: Naming Dinosaurs and Their Tracks**

To facilitate communication about the diversity of living things, biologists have long assigned scientific names to recognized species of plants and animals. Our own species is named *Homo sapiens*, which means the "wise human being"- a designation that suggests that the namer of our species was perhaps excessively optimistic about the human condition. By convention, a scientific name has two components, the more inclusive (and thus literally) generic name, which is the first of the two names, and the second, more exact, specific name. Both names are written in italics, and the first letter of the generic name is capitalized.

There can be more than one species in a genus. In our own genus *Homo*, for example, paleoanthropologists recognize some extinct primates that were very similar to us, but not similar enough to be regarded as members of our own species. These include *Homo habilis*, *Homo erectus*, maybe *Homo neanderthalensis* (if the Neanderthal people were in fact a different species than our own, an interpretation that is controversial), and the mysterious *Homo floresiensis*, tiny people whose remains were recently found in southeast Asia.

The same system is used to name dinosaur species. Anybody who has heard anything at all about dinosaurs is aware of *Tyrannosaurus rex*, but laypersons are often surprised to learn that all dinosaur species had two parts to their scientific names, such as *Allosaurus fragilis*, *Triceratops horridus*, and *Stegosaurus stenops*. In many contexts it isn't necessary to report the full scientific name of a dinosaur. For example, unless one is explicitly concerned with differences among the various species of the big ornithopod *Iguanodon*, it is enough just to use the generic name in discussing such animals.

The first dinosaur footprints to receive scientific scrutiny were discovered in rocks of the Connecticut Valley in the early 1800s. These tridactyl (three-toed) prints came to the attention of the Reverend Edward Hitchcock of Amherst College, a pioneering American geologist. Hitchcock published a series of articles and books about the Connecticut Valley footprints that remain valuable scientific documents to this day.

In Hitchcock's time scientists had not yet discovered enough complete dinosaur skeletons to have an idea of what the reptiles were like, and so Hitchcock had no way of knowing that his tridactyl footprints had been made by bipedal dinosaurs. Instead he identified their makers as a group of extinct flightless birds-about as accurate an identification as was possible at the time, and remarkably prophetic, given that we now think birds are derived from small carnivorous dinosaurs.

Hitchcock went on to create names for the Connecticut Valley footprints, such as *Grallator*, *Anchisauripus*, *Eubrontes*, and *Anomoepus*. Thus the practice arose of naming distinctive footprint shapes. Hitchcock's system of Connecticut Valley footprint names was further developed in the first half of the 20th Century by Richard Swann Lull of Yale University. Naming dinosaur trace fossils is now a well-established procedure in paleontology. Both ichnogenera (major kinds of footprint shapes) and ichnospecies (distinctive varieties of ichnogenera) are recognized.

One must keep in mind that the names apply to the footprints, and not to the creatures that made them. There is consequently a parallel set of scientific names for trace fossils that is independent of the names of the animals themselves. *Eubrontes*, for example, is an ichnogenus, not a genus. We don't know what genus of theropod dinosaur was responsible for making prints of this ichnogenus, and the *Eubrontes*-makers may have been different genera of dinosaurs in different places where this ichnogenus occurs as a trace fossil.

Tridactyl dinosaur footprints from the Glen Rose Formation of Texas were first found in 1908. The first scientific description of such footprints was published in 1917 by Ellis W. Shuler of Southern Methodist University. Shuler named these fossils *Eubrontes (?) titanopelopatidus*. Shuler apparently considered his new footprints similar enough in shape to some of the much older Connecticut Valley footprints to warrant assigning them to the same ichnogenus, but was not confident enough in this conclusion to do so without question. The ichnospecies name *titanopelopatidus* was interpreted by Shuler to mean "the lime mud strider", which is certainly an apt description, but is rather a tongue-twister.

In 1935 Shuler described a second Glen Rose Formation tridactyl dinosaur trackway, which he named *Eubrontes (?) glenrosensis*. A splendid footprint of the trackway was removed from the bed of the Paluxy River and mounted in the bandstand in the Glen Rose town square, where it remains to this day. Mike O'Brien of the Texas Department of Parks and Wildlife has made casts of this specimen (Fig. 40L), because the footprint itself, being exposed to the elements, will eventually weather away.

In 1974 Wann Langston argued that Shuler's first species, *Eubrontes (?) titanopelopatidus*, was not scientifically valid on the grounds that a type specimen had not been secured for any museum collection. Langston further suggested that the maker of this invalid ichnospecies might have been the big *Iguanodon* known on the basis of skeletal material from Texas sites. Were any further footprints of this animal to be found in the Glen Rose Formation, Langston suggested that they might best be referred to an Early Cretaceous ichnogenus found in British Columbia, *Gypsichnites*. Langston also concluded that Shuler's second species, *Eubrontes (?) glenrosensis*, was less like Hitchcock's Eubrontes than like a second British Columbian ichnogenus, *Irenesauripus*.

Shuler's illustrations of *Eubrontes (?) titanopelopatidus* are rather inadequate, but to James Farlow's eye they are not different enough from *Eubrontes (?) glenrosensis* to warrant distinguishing between them. What ichnogenus is most appropriate for these footprints-a name which would likely apply to at least some of the Heritage Museum footprints--is also uncertain. Are they most like *Eubrontes, Irenesauripus, Megalosauropus*, or some other ichnogenus of theropod footprints? And are they enough like those named footprints to justify assigning them the same name, or are they different enough to warrant having their own name? This question is presently being investigated.

Figure 23. Texas Memorial Museum 43002-1, a "stacked" series of different expressions of the same footprint in successive rock layers. This specimen was removed from the eastern edge of the HMTHC tracksite in 1982 (Fig. 7A). The scale bars are marked in centimeters and inches. A-C) Different views of a sediment plug (a natural cast) that partly filled the main (surface) footprint. Part A of this figure shows the plug in oblique view lying as found in the footprint, B shows the plug from directly overhead, and C shows the underside of the plug. The plug is about 45.5 centimeters (cm) long, 35 cm wide, 1 cm thick, and 2.5 cm deep on its upper, concave side. D) The main (actual) footprint; length = 51 cm, width = 35 cm, and greatest depth = 4.3 cm. The rock layer containing this surface print (Bed 1) is about 2 cm thick at its edge, away from the footprint. Because the rock layer's thickness is less than the greatest depth of the footprint, this means that the deepest part of the print was pushed below the lower level of the surrounding sediment layer of Bed 1 by the dinosaur's weight to create the bulge seen in: E) Underside of the rock layer (Bed 1) containing the main footprint, showing a convex projection of the footprint below the rest of the underside of the rock layer. F) Concave counterpart of the version of the footprint shown in E, an impression in the surface of the rock layer (Bed 2) immediately beneath the rock layer containing the main footprint. This version of the footprint is the first transmitted print beneath the main footprint. The three toes of the footprint can still be seen, but are not as clear as in the main footprint. On this surface the footprint is about 51 cm long, 39 cm wide, and 3.9 cm deep. The rock layer (Bed 2) containing this first transmitted print is 2.5-3 centimeters thick. G) Underside of the rock layer (Bed 2) containing the first transmitted print, showing a convex projection of the first transmitted print. H) Upper surface of the rock layer (Bed 3) beneath the layer containing the first transmitted print, showing the concave counterpart (the second transmitted print) of the version of the print seen in G. Toe marks can no longer be seen. The track is 56.5 cm long, 40 cm wide, and 3.4 cm deep, so it is bigger but shallower than the first transmitted footprint and the main footprint.



**Figure 24.** Theropod footprints from the dolomitic bedrock in the bed of the Paluxy River, Dinosaur Valley State Park, Somervell County, Texas. The mud that became the tracklayer was thicker and perhaps softer than that at the Heritage Museum tracksite at the time the dinosaurs crossed it, so the Paluxy River footprints are commonly deeper and better preserved than those at the HMTHC site. However, the ancient mud was rather sticky, so when the dinosaurs lifted their feet off the ground, the mud around the footprint edges often collapsed inward to partially roof toe marks, as in the left toe of the footprint shown in part C, and several of the footprints in A, in which the surface expression of toe marks becomes little more than slashes in the rock. Consequently the surface expressions of footprints do not always faithfully replicate the shapes of the trackmakers' feet. A) Several footprints at a site near the confluence of Denio Branch with the Paluxy River; the prints were under water at the time this shot was taken. B, C) Probable sequence of two footprints at the Main Tracksite in the park. C) Overhead view of the second footprint (a left) in the probable trackway. Note the unusual groove extending behind the right (innermost) of the three main toes, probably made by the first toe of the foot (which normally did not touch the ground). This toe impression was probably made as the foot slid forward and downward into the mud. A meter stick provides the scale in B, and a scale marked in both centimeters and inches does so in C.

## What Kind of Dinosaurs Made the Footprints?

Paleontologists recognize three major lineages of dinosaurs: theropods, sauropodomorphs, and ornithischians. Theropods were the meat-eating dinosaurs and their close relatives. Sauropodomorphs were huge, long-necked plant eaters. Ornithischians were a diverse lot of plant eaters that came in all sizes and shapes.

To identify, as closely as possible, the dinosaurs responsible for the HMTHC footprints, we have to consider features of the various groups of dinosaurs that might be expressed in footprints. Before doing that, however, we need to consider some features of dinosaur trackways and footprints in general, and the HMTHC and Mountain Creek tracks in particular.

The **pace** of a trackway is the distance from one footprint to the next print made by the opposite foot (Fig. 31). A **stride** is the distance from one footprint to the next print made by the same foot. Two successive paces and an associated stride define the **pace angulation**. This angle expresses how zig-zagged or linear the trackway is. If an animal places one foot nearly in front of the other as it walks, its trackway will be narrow, and come close to falling on a straight line. When that happens, the pace angulation will be close to 180°. If, instead, the animal is more of a waddler than a strider, its trackway will be broader, with prints made by the left foot some distance away from those made by the right foot, and the pace angulation will be much lower.

Another aspect of the way an animal walks is how it positions its feet with respect to the overall direction in which the animal is traveling. This **footprint rotation** is another trackway feature that can be expressed as an angle. Imagine a line running from the back to the front of the footprint, and extending beyond the footprint in both directions. Eventually this line will cross another line that traces the path of animal as it moves forward, and we can measure the angle made by the two lines. If the front of the footprint points away from the line of the animal's path, we give this rotation a positive value. If the front of the footprint points toward the line of the animal's path, we assign the footprint rotation a negative value (we can also describe such a trackmaker as being "pigeon-toed").

Some dinosaurs walked on all fours, a style of movement designated as **quadrupedal**. Strictly **bipedal** dinosaurs walked only on their hind legs (Fig. 32). Some dinosaurs didn't restrict themselves to only one of these styles of movement, and seem to have switched between quadrupedal and bipedal movement as circumstances warranted.



In reasonably well preserved footprints, one can see impressions made by the individual toes. The fingers of an animal's hand or forefoot, and the toes of its hindfoot, are collectively termed **digits**. By convention, digits are numbered from the thumb or big toe outward, using Roman numerals.

We are now ready to apply all this to interpreting the makers of the HMTHC and Mountain Creek footprints. All of the good footprints at the site have three toe marks, so we can describe them as **tridactyl**. With one possible exception, the trackways show no signs of having prints made by both a forefoot and a hindfoot. Unless one wants to imagine the animals doing handstands to walk across the site, it is pretty clear that most or all our dinosaurs were bipedal.

Right away this eliminates sauropodomorphs as potential makers of the HMTHC and Mountain Creek tracks. Although some of the earliest sauropodomorphs of the Triassic and early Jurassic Periods may have been, at least some of the time, bipedal, by the Cretaceous Period sauropodomorphs were represented only by the sauropods proper, and all of these dinosaurs were quadrupedal. Now, sauropod trackways are known from several Texas sites in the Glen Rose Formation, including several sites in Texas. In fact, what may be the best preserved sauropod trackways in the world come from Dinosaur Valley State Park. Apart from having been made by quadrupeds, sauropod footprints also differ from the HMTHC prints in having very different shapes; sauropod hindfoot prints, for example, are not tridactyl, but look like a blend of the footprints of an elephant and a tortoise. Sauropod hindfoot prints are also usually much bigger than the HMTHC footprints.

That leaves us with ornithischians and theropods as possible HMTHC and Mountain Creek trackmakers. We can eliminate some groups of ornithischians as trackmakers on the grounds that they were quadrupedal or did not live during the Cretaceous Period, but that still leaves one very diverse group of ornithischians as candidates: the **ornithopods**. These plant-eating dinosaurs came in many different sizes, but some of them were easily big enough to have made the HMTHC footprints. Even better, many big ornithopods had three toes on their hindfeet (Fig. 33), digits II (the innermost toe, digit I, having been lost), III (the middle toe), and IV (the outer toe). On the basis of their skeletal anatomy there is some question as to whether large ornithopods are likely to have walked very often on their hind legs only, or whether they preferred to walk quadrupedally. Skeletal evidence notwithstanding, there are tridactyl footprints from sites around the world that paleontologists have attributed to large, bipedally walking ornithopods, and so we need to consider them as possible HMTHC trackmakers.

Theropods habitually walked on their hindlegs. The theropods big enough to have made the HMTHC footprints had four toes, but one of these (the one corresponding to our own big toe) was a tiny thing way up on the side of the foot (Fig. 34)-so high that it would not have touched the ground unless the dinosaur sank extremely deep in mud (Fig. 24C), or walked in a very unusual fashion. So big theropods are also candidates as HMTHC trackmakers. As in ornithopods, the three toes on which theropods walked are digits II-IV, digit I being small and insignificant, or lost altogether.

**Figure 25**. First of a series of photographs showing the Mountain Creek site as it appeared in 2002. Trackways and isolated footprints were assigned the letter prefix S, followed by a letter code, beginning with trails closest to the HMTHC site and then moving eastward and southeastward away from it. The Mountain Creek site consists of two exposures of track-marked bedrock separated by a covered interval. A) Overview of the western portion of the site (adjacent to the HMTHC property), looking in a southeasterly direction. Trackway SB is to the left of the person in the foreground. B) Western edge of the site, showing isolated footprint SA, looking roughly northeastward. C) Continuing to the east of B, with another view of trail SB and isolated print SC. In addition, note numerous vague circular or elliptical depressions (e.g. Landmark 1), which very likely are poorly preserved dinosaur footprints.





**Figure 26**. Continuing southeastward along the western portion of the Mountain Creek tracksite. Parts A-C show overlapping portions of this surface. Note numerous labeled footprints, as well as many more vague impressions that likely constitute poorly preserved prints.



**Figure 27**. Further along the western portion of the Mountain Creek tracksite, note overlap between this set of photographs and Figure 26 at print SH1. The western portion of the Mountain Creek tracksite ends to the right of trackway SJ seen in C.



**Figure 28**. Footprints in the southeastern portion of the Mountain Creek tracksite. View roughly to the northeast. The southeastern part of the site begins just to the left of isolated print SM, and ends a short distance to the right of the SR trackway.

**Figure 29.** Footprints and trackways from the western portion of the Mountain Creek site; compare with Figs. 25-27. Measurements provided in Tables 2-6. A) Isolated footprint SA. In this and other photographs from this site, the scale is given by a card marked off in both centimeters and inches. Circular black or white objects seen in many of these photographs are poker chips, which we used to keep track of footprints while working at the site (but forgot to remove prior to photography!). B) SB trail. C) Footprint SB-2; left. D) Footprint SB-3; right. E) Isolated print SC. F) SD Trail. G) Footprint SD-1; symmetry uncertain. H) SE trail. I) Isolated footprint SF. J) Isolated footprint SG. K) SH trail. L) Footprint SH-2; right. M) Footprint SH-3; left. N) Final three footprints in SI trail. O) Footprint SI-5; right. P) Last four footprints in SJ trail. Q) Footprint SJ-2; right? R) Footprint SJ-3; left?





**Figure 30**. Footprints and trackways from the southeastern portion of the Mountain Creek Site; compare with Fig. 28. A) Isolated footprint SM. B) SN trail. C) Footprint SN-1; left? D) Footprint SN-2; right? E) Well-preserved footprint first seen in 2000, from which a cast was made; a right. F) Three footprints in SO trail and neighboring footprints. G) Footprint SO-2 (left), touching the heel of isolated footprint SP. H) Footprint SO-3; right. I) Footprint SO-4; left. J) Footprint SO-5; right. K) SQ trail. L) SQ-1; right. M) SR trail. Note possible (but very questionable) forefoot (manus) impressions associated with both footprints in this trackway. N) Footprint SR-2; left?

At this point we should look at a distinctive feature of the way that both ornithopods and theropods carried themselves on their feet. At the core of the hind leg of land-living vertebrates is a set of bones running from the hip to the foot. The thigh bone (the one connected to the hip bone in the old spiritual) is the **femur** (Fig. 32A). The femur joins at the knee with the **tibia** (with a smaller bone, the **fibula**, on the outside of the tibia). Beyond the tibia and fibula are the bones of the ankle, and beyond the ankle the bones of the foot, the **metatarsals**. The individual toes (digits) are composed of a series of individual toe bones, or **phalanges**, attached at the ends of the metatarsals. The claw-bearing bones, the **unguals**, are the last of the phalanges.

Humans and bears walk flat-footed, with the metatarsals and their enveloping soft tissues touching the ground (or forming the instep in humans). Many animals, however, walk with the metatarsals off the ground, so that only their digits actually touch the ground; we describe such animals, appropriately enough, as **digitigrade**. Cats, dogs, and deer are familiar examples of digitigrade animals, as are birds. In fact, people sometimes say that the knees of chickens and other birds point backwards, not realizing that what they think is the knee is actually the ankle, and what they think is the lower leg is the foot.

Theropods and ornithopods were both digitigrade animals (Figure 32), and so the back of a footprint made by one of these dinosaurs-what we might call in a purely descriptive sense the "heel"-was actually made by the back of the toe region, where the digits linked up with the metatarsals. Like colossal poultry, bipedal dinosaurs usually carried their metatarsals well off the ground. This means that if you want to compare your own size with that of one of the HMTHC trackmakers, you should compare the length of the dinosaur's footprint with the length of a print that you would make if you walked tiptoe!

To get some idea of the size of the HMTHC and Mountain Creek dinosaurs, measurements of the average lengths of footprints (Table 2) for each individual trackway range from about 340-610 millimeters (about 13-24 inches; 1 inch = 25.4 mm). Whether ornithopods, theropods, or both, these were pretty big animals.

But back to the main question: How can we choose between theropods and ornithopods as possible makers of the HMTHC footprints? Or might individuals of both groups of dinosaur have been responsible for different trackways?

Dinosaurs in the usual sense (excluding birds, which most paleontologists think evolved from a group of small theropods) are--inconveniently--extinct, making it impossible to trail one with an eye for distinctive features of its spoor. Even worse, for most dinosaurs we have no idea what the underside of the sole of the foot of the living animal looked like. Exceptions to that statement include the famous dinosaur "mummies", in which a carcass became desiccated in the hot sun, its skin shrunk to a leathery shroud that left an impression in sediments that eventually buried the corpse and then turned to stone. There are also some dinosaur footprints that are so excellently preserved that they even show impressions of scales on the underside of the trackmaker's foot, but we cannot always be certain that we know exactly what kind of dinosaur made these prints. It therefore remains true that most dinosaurs are known only from their skeletons.



**Figure 31.** Terminology for describing dinosaur step lengths. A pace is the distance between two successive footprints made by the opposite feet (left to right, or right to left). A stride is the distance between two footprints made by the same foot (left to left, or right to right). Pace 1 in this photograph is from right footprint 1 to left footprint 1, and pace 2 is from left footprint 1 to right footprint 2 (don't be misled by the meter stick place ahead of the left footprint for scale; pace 2 goes obliquely to the right of the meter stick, and the lines representing paces and stride are narrower than the meter stick). The stride here is from the first right print to the second right print. The angle formed by two successive paces (pace 1 and 2 here), the pace angulation, is close to 180 degrees in trackways of bipedal dinosaurs like this one.

Figure 32. Bipedal and potentially bipedal dinosaurs; A-D theropods, and E-F ornithopods. A) TMP 95.110.1, a beautifully preserved, articulated skeleton of the ornithomimosaur Ornithomimus edmontonensis from the Late Cretaceous of Alberta. Arrows indicate leg and foot bones; some of the toe bones (phalanges) are missing from this specimen. B) An equally beautiful tyrannosaurid specimen, TMP 91.36.500, Gorgosaurus libratus, from the Late Cretaceous of Alberta. C, D) The dromaeosaurid Deinonychus antirrhopus; both photographs copyright Yale Peabody Museum of Natural History. C) Mounted skeleton. D) Left foot, composed mainly of YPM 5205; photograph by Walter Joyce. E) SMU 73181, left foot of an Early Cretaceous "hypsilophodontid" dinosaur from Texas. F) Skeletons of Tenontosaurus tilletti from Montana, mounted at the Sam Noble Oklahoma Museum of Natural History, University of Oklahoma. These fossils were collected by personnel from the University of Oklahoma (including Wann Langston) in 1942. The large individual (OU 10132) is a fairly complete specimen (the skull on the mount is a reconstruction assembled from casts of actual bones; the tail was missing in this specimen, and so fabricated for the mount). Langston began mounting this skeleton just before going into the U.S. Navy during World War II. The skeleton was found in association with the remains of at least four juveniles, none of which was complete. The large skeleton is mostly real bone, but the small skeletons are composites composed of casts of bones of more than one individual. Note that the large individual is mounted as though walking quadrupedally, while the younger individuals are mounted as bipeds.





Figure 33. Foot skeletons of medium-sized and large ornithopod dinosaurs. A) OMNH 58340 (left foot), *Tenontosaurus tilletti*, an Early Cretaceous form from North America B) WPL Campto B (right foot), *Camptosaurus dispar*, a Late Jurassic iguanodontoid from the western U.S. C) IRSNB 1534 (right foot), *Iguanodon bernissartensis*, an Early Cretaceous iguanodontid from Europe. D-F) Late Cretaceous hadrosaurids from western North America. D) MOR 794 (right foot), a species of *Brachylophosaurus*. E) DMNH 1493 (left foot), *Edmontosaurus annectens*. F) MOR 471 (right foot), unidentified lambeosaurine hadrosaurid.

Consequently if we say that we think a footprint was made by (for example) a *Tyrannosaurus*, what we are really saying is that the footprint is the right size and shape to match what we think the foot of a *Tyrannosaurus* would have looked like if we mentally reconstruct soft tissues surrounding the dinosaur's foot skeleton, and that the footprint is in rocks from the right geological time and place, based on what we know about the distribution of *Tyrannosaurus* skeletons.

So to try to identify the dinosaurs that made HMTHC prints, we must first see if there are any features in the foot skeletons of theropods and ornithopods that would cause us to prefer one or the other of them as trackmakers (Figs. 33, 34). One obvious difference is that the ungual of large theropod toes comes to a rather sharp point, while the final ungual of large ornithopod toes is blunt and broad. In life the ungual phalanx would have been capped by a horny claw or nail. We might therefore expect footprints made by large theropods to have sharp claw marks, and those made by large ornithopods to have blunt toe tips. In wellpreserved dinosaur footprints claw marks can often be seen, but this is not an infallible indicator. For one thing, the claws of large animals often become blunt through abrasion against the ground. In addition, the circumstances of formation and fossilization of a footprint may prevent clear claw marks from being preserved. So while the presence of sharp claw marks is reason for thinking that a big tridactyl dinosaur footprint was made by a theropod, the absence of such claw marks doesn't necessarily mean that it was made by a big ornithopod.

One possibility for distinguishing between theropod and ornithopod footprints is the relative stoutness of the toe marks. If we compare the width across toe bones with the lengths of those toe bones, and with the overall lengths of the toes, it is immediately apparent that big ornithopods have rather short, stout toes, while big theropods have longer, skinnier toes (Figs. 33, 34). This is dramatically clear if we plot a graph of the width of the second phalanx of the middle toe (digit III) against the overall length of that toe (the summed lengths of all the phalanges in the toe; Fig. 35). For smaller dinosaurs (with smaller feet), there is some overlap of data points for the two groups of dinosaurs. Above a certain size (digit III length about 200 mm [8 inches]), however, ornithopod toes become much broader for a given toe length.

We have to be careful in comparing footprint proportions with those of foot skeletons. We would obviously expect the widths of the flesh-covered toes of a living animal (the things that would make the toe marks in footprints) to be somewhat greater than the widths of the toe bones of the same animal. Furthermore, the length of the skeleton of a toe will not be the same as the length of the toe mark in a footprint. All we can measure on most dinosaur footprints is a toe mark's free length, which is how far the toe mark sticks out past the spot where that toe meets adjoining toes (Fig. 36). The free length will likely be less than the skeletal length of the same toe for two reasons. First of all, in theropods, at least, the base of the first phalanx of digits II and III may not usually have touched the ground. Second, depending on how far out along a toe the webbing of skin and other tissues between the toes extended, this would shorten the length of the toe mark as compared with the length of the toe's skeleton. On the other hand, in life the horny nail or claw covering the last phalanx of a toe would have added to the length of the toe mark in a footprint.

Free lengths and other measurements of HMTHC and Mountain Creek footprints were made from tracings of footprint outlines drawn in the field with indelible markers on sheets of clear plastic (Figs. 37, 38). Such measurements obviously are not infallible indicators of footprint shape, because they can only be as reliable as the tracings on which they are based. Footprints are three-dimensional surfaces, and tracings are two-dimensional abstractions of those complex surfaces. Deciding what the edge of the footprint really is can be tricky. The footprint shape may look different with changes in lighting, and different observers may not see the footprint outline exactly the same way.







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Figure 34. Foot skeletons of medium-sized and large theropod dinosaurs. Note the relatively long and narrow toes of these feet. A) NCSM 14345 (right foot), the Early Cretaceous North American allosauroid Acrocanthosaurus atokensis (see Figure 47 for the entire skeleton of this dinosaur). Bipedal dinosaurs usually walked with most of the lengths of their main foot bones (metatarsals) well off the ground; only the toes and the lowest parts of the metatarsals touched the ground. The individual toes (digits) are identified with Roman numerals from the inside of the foot outward. Digit I (equivalent to the big toe of humans) is the innermost toe of theropods, but usually was carried high off the ground. It can be seen peeking out to the right of the metatarsals in this view. The main walking toes of theropods were digits II (innermost), III (middle), and IV (outermost). Digit V (equivalent to the human little toe) had either been lost or greatly reduced to a splint-like remnant in most Cretaceous theropods. The individual bones (phalanges; singular phalanx or phalange) of the toes are numbered with Arabic numerals from the base of the toe outward. Conveniently, if one disregards the clawbearing phalanges (unguals), the number of phalanges in a digit corresponds to which digit it is; thus there are two non-ungual phalanges in digit II, three in III, and four in IV. In this specimen, the terminal half of phalanx II-3, all of phalanges III-3 and III-4, the terminal half of IV-4, and all of IV-5, are missing, and were replaced here with fabrications modeled after other large theropod foot skeletons. B) UMNH VP C481 (right foot), a species of the Late Jurassic allosauroid Allosaurus. The claw of digit III and parts of other phalanges are missing, and fabricated. Digit I lies beside the rest of the foot. C) UA 74 (right foot), a medium-sized, Early Cretaceous theropod dinosaur from Arkansas (possibly an ornithomimosaur). Position of the fragmentary unguals is speculative. D) FMNH PR 2211 (right foot), a half-grown, Late Cretaceous Canadian tyrannosaurid, Gorgosaurus libratus. E) MOR 657 (left foot), a species of the Late Cretaceous, western North American tyrannosaurid Gorgosaurus or Albertosaurus. The scale is 6 inches long. F) MOR 590 (left foot), a species of the Late Cretaceous, western North American tyrannosaurid Daspletosaurus; scale bar 6 inches. G) FMNH PR 2081 (right foot), the huge Late Cretaceous, western North American tyrannosaurid Tyrannosaurus rex. Phalanges IV4 and IV5 of this specimen are fabricated. The large calipers are marked off in centimeters.

Even if we can be certain that the footprint outline accurately conveys the print's shape, we must always keep in mind that the footprint is not simply a replica of the foot that made it. It is, instead, a record of the footprint's interaction with a soft substrate. Consequently the shape of the footprint may reflect sediment conditions at the time it was made as much or more than the shape of the trackmaker's foot. In addition, what the trackmaker was doing while making footprints can result in a considerable variety of possible print patterns all made by the same foot.

All caveats duly noted, we can now look at Figure 39, which plots the maximum width of digit III (the middle toe) against the free length of that toe. The data in this and in the comparisons to follow constitute mean (average) values for a trackway, if measurements could be made on more than one print in that trackway, but also include values for single footprints where only one print in the trail could be measured.

In addition to showing data for the HMTHC footprints, Figure 39 plots data for tridactyl dinosaur footprints from many other sites, both in Texas and other parts of the world, and from the entire Mesozoic Era, that have been interpreted as having been made by either theropods or ornithopods (Figs. 40-41). There is no guarantee that those identifications are correct, but we can at least compare the HMTHC prints with what are thought to be ornithopod and theropod footprints.

Unsurprisingly, given the difference between big ornithopods and big theropods seen in foot skeletons (Figs. 33-35), footprints attributed to large ornithopods tend to have fatter toe marks than prints thought to have been made by big theropods (there is, in contrast, little or no difference between prints attributed to small theropods and small bipedal ornithischians). Although some of the HMTHC prints (those made by animals G, O, 01I, 01J, and SC) fall among the points for theropods, most of them plot much higher, indicating quite stout toe marks-more what one would expect for big ornithopods, although one very large footprint attributed to a theropod from a site outside Texas (Fig. 400) likewise has a rather broad digit III.



Figure 36. Measurements of footprint shape. In a print made by the left foot like the one illustrated here, the impression made by the inner toe (digit II) will be on the right side of the footprint, and that of digit IV (the outer toe) on the left side. The inner side (the one closest to an imaginary plane running through the midline of the trackmaker's body) of a footprint, or any part of a footprint, is described as being medial, and the outer side is termed lateral. Important landmarks used in measuring footprints include the tips of the three toe marks (A: Toetip II; B: Toetip III; C: Toetip IV), the hypexes, or deepest indentations in the regions between adjacent toes (F, H), and the "heel" (J: the most posterior part of the footprint). Measurements made using these landmarks include: the distance from toetip II to toetip III (A-B), from toetip III to toetip IV (B-C), and overall toetip width (II-IV) across the footprint (A-C); the lateral hypex length of digit II (A-H), medial (B-H) and lateral (B-F) hypex lengths of digit III, and medial hypex length of digit IV (C-F); the width across the hypexes between digits II-III and III-IV (F-H); the distance from the heel to hypexes II-III (J-H) and III-IV (J-F); the distance from the heel to toetip II (J-A), toetip III (J-B), and toetip IV (J-C). Another set of useful measurements, related to several of those already described, expresses the degree to which digit III (the middle toe) projects forward beyond the rest of the footprint. Line segment **D-I** indicates the length of the footprint parallel to the midline of digit III. At point E this line segment is crossed by a line segment connecting the tips of digits II and IV, dividing line segment D-I into what can be called the "backfoot" (E-I) and the digit III projection or toetip extension (D-E). The line segment connecting the two hypexes (F-H) divides line segment D-I into the footprint "palm" (G-I) and the Digit III free length (D-G). Line segment A-C connecting the tips of digits II and IV is itself divided into two segments by the digit III midline at point E; A-E is the distance from the tip of digit II to the midline, and C-E is the distance from the tip of digit IV to the midline. Finally, the interdigital angle (IDA II-IV) between the inner and outer toes is formed by the intersection of lines drawn through the long axes of the two toe impressions.



**Figure 35**. Plot of the width at the distal end (the end away from the base of the toe) of phalanx III-2 (see Fig. 34A) against the overall length of digit III (the summed lengths of all the phalanges [including the ungual] in this toe) in various kinds of theropods (black symbols) and ornithopods and other ornithischians (open symbols). The width of phalanx III-2 provides a minimum estimate of the toe's width about midway along its length. Note the clear tendency for theropods to have relatively narrower toes than ornithischians of comparable toe length, particularly among larger forms.





**Figure 37**. Outlines of footprints from the HMTHC site. All footprints drawn to the same scale (about 153 mm-roughly 6 inches), with the scale shown beneath the print in the upper left hand corner. Clear outlines are for left footprints, and light grey fillings are for rights. Print labels identify the trackway in which a print occurs, and which print in that trackway it was.



**Figure 38**. Outlines of footprints from the Mountain Creek site. All footprints drawn to the same scale (about 153 mm-roughly 6 inches), with the scale shown beneath the print in the upper left hand corner. Clear outlines are for left footprints, light grey for rights, and dark grey for prints whose left-right symmetry is uncertain.



O C (1983 13)	🔀 01C (1983 5)	SG
△ B (1983 11)	+ 01D	X SH
∇ F (1983 18)	X 01E (1983 7)	♣ SI
▷ G (1983 26)	\varTheta 01F (1983 8)	⊕ SJ
ЧH	<b>O</b> 01I	M SN
$\triangle$ I	• 01J	X SO
ΠJ	▲ 01K (1983 28)	⊙ SQ
¢κ	▼ 01L	∆ SR
<b>0</b>	2000 (Cast) trail	∀ SS
[] Q	◀ SA	⊳ st
🕂 JOF12	sc 🕈	+ Ornithischian
🖂 01A (1983 6)	SD	Theropod
— 01B (1983 4)	♦ SF	Texas Theropod

Footprints attributed to large ornithopods also frequently have relatively shorter toes compared to length of the rest of the footprint (the "palm" of the footprint-Fig. 36) than do prints attributed to large theropods (Figs. 40, 41). We can examine this tendency by dividing the free length of digit III by the palm length (the higher the ratio, the longer the toe region is compared with the palm), and then plotting this against overall length of the footprint (Figure 42). There is a clear trend for bigger footprints, whether theropod or ornithischian, to have a relatively short digit III free length. For any given footprint length, however, prints attributed to theropods have relatively longer III free lengths than do prints attributed to ornithischians.

Some HMTHC dinosaurs (such as animals G, O, 01I, and 01J) have relatively long toes in this comparison, and plot nicely among prints attributed to theropods, but others (such as dinosaurs F, I, J, and K) have relatively short toes and are more like presumed ornithischian footprints. What is especially nice is that many of the tracks that have relatively long as opposed to short toes in the comparison of digit III free length with footprint palm length also have long and skinny instead of short and stout toes in the comparison of digit III free length with digit III maximum width.

At first glance, our look at toe mark lengths and widths leads us to think that the HMTHC trackmakers included both theropods and ornithopods, and perhaps more of the latter. However, there are complications that suggest that we shouldn't jump to that conclusion.

Some of the trackways contain prints that are quite variable in toe thickness. Prints made by animal J, for example (Fig. 37), include both some of the stoutest toe marks as well as toe marks whose thickness is more like that seen in footprints thought to have been made by theropods. This suggests that the relative fatness of toe marks could be due as much or more to sediment conditions at the time they were made as to the actual shapes of the toes. In addition, filling of the prints by sediment layers after they were formed can obliterate footprint shape, if those filling layers do not cleanly separate from the actual prints when uncovered. All of these complications could apply to the HMTHC footprints, and so the shapes of the prints may in many cases be misleading. That being the case, we should explore other features of footprints and trackways that might serve to discriminate between ornithopod and theropod trackmakers.

**Figure 39**. Graph of the maximum width of the impression of the middle toe (digit III) against the free length of the middle toe in HMTHC footprints. The symbols in the graph are keyed to individual HMTHC trackways. In addition, data for dinosaur footprints from other sites around North America are plotted. Asterisks are for footprints attributed to ornithopods and other ornithischians. Vertical lines are for footprints attributed to theropods; thick vertical bars are for presumed theropod footprints from Lower (Early) Cretaceous sites in Texas (Glen Rose Formation [excluding the HMTHC and Mountain Creek sites] and the Fort Terrett Formation). Non-Texas localities include sites from the Upper (Late) Triassic to Lower (Early) Jurassic of the eastern (Newark Supergroup [specimens include footprints assigned to the ichnogenera *Anomoepus*, *Grallator*, *Anchisauripus*, and *Eubrontes*]) and western (Moenave and Navajo Formations) U.S., Middle to Upper Jurassic of the western U.S. (Entrada [*Megalosauropus*] and Summerville Formations), LowerCretaceous of Western North America (Dakota [*Caririchnium*] and Gething [*Ornithomimipus*, *Amblydactylus*] Formations), and the Upper Cretaceous of the western U.S. (Raton Formation [*Tyrannosauripus*). Some of these footprints are illustrated in Figs. 40 and 41.



Figure 40. Footprints attributed to theropod dinosaurs. Most of the specimens illustrated here are "casts" of footprints, which means that they are, to varying extent, replicas of the bottoms of the feet that made them. Some of these casts are natural, meaning that they were preserved from sediment that filled the original footprint. Others are artificial casts, meaning that they were made by filling the original footprint with plaster, latex rubber, or some other casting medium. Footprint casts reverse both the topography (depressions vs. elevations) and left-right symmetry from actual footprints, but they often show the shape of the footprint better than the print itself does. A) Cast of small theropod footprint from the Late Triassic of Virginia. The impression of the innermost of the three main toes (II) is on the left. B-C) Theropod footprints from the Early Jurassic of the Connecticut Valley of New England. B) Cast of YPM 3323, print assigned to the ichnogenus Anchisauripus; digit II impression on the left. C) Cast of YPM 2098, ichnogenus Eubrontes, digit II impression on left. D) MNA V3405 (duplicate of natural cast), Early Jurassic theropod footprint, digit II impression on right. E) Cast of CU-MWC 187.6, Middle Jurassic print from Utah assigned to ichnogenus Megalosauropus; digit II on left. F) CU-MWC 188.25 (duplicate of natural cast), Late Jurassic theropod footprint from Arizona; digit II on right. G-J) Early Cretaceous theropod footprints from Europe. G) BMNH R19979B, footprint from England; digit II at right? H) CU-MWC 199.6, print (natural cast) assigned to ichnogenus Buckeburgichnus; left-right symmetry uncertain. I-J) Lovely theropod trackway (ichnogenus Buckeburgichnus or Megalosauropus) from Los Cayos, Spain; J shows the first footprint in the sequence (a right; lens cap is for 35-mm camera). K) NMC 8513, footprint (duplicate of natural cast) from the Late Cretaceous of Alberta named Ornithomimipus, and possibly made by an ornithomimosaur; digit II at right. L-M) Early Cetaceous large theropod prints from Texas. L) Cast of Paluxy River footprint mounted in a bandstand in the town square, Glen Rose, Somervell County; digit II at right. M) Cast of TMM 43018-2, a print from Hamilton County; digit II at left. N) TMP 81.34.1, natural cast of large theropod (probably tyrannosaurid) footprint from the Late Cretaceous of Alberta; digit II probably at right. (Some paleontologists, however, have interpreted this as an ornithopod print.) O) CU-MWC 225.1, huge footprint (cast) from Late Cretaceous of New Mexico, assigned to ichnogenus Tyrannosauripus and very likely made by Tyrannosaurus. Digit II at left, and note likely (and unusual) impression of digit I below digit II impression, near bottom of photograph.

In addition to having relatively broader toe marks, footprints thought to have been made by ornithopods often differ from prints thought to have been made by theropods by being as broad or broader than they are long. This shape difference is partly related to the relatively greater stoutness of the individual toes in large ornithopods that we have already considered. However, it might also reflect a greater tendency for ornithopods to spread their toes out. We can examine this possibility two ways: first, by plotting the width across the tips of the two outer toes of the footprint against footprint length (Fig. 43), and second, by examining the interdigital angle formed by lines drawn through the impressions of the two outer toes (Figs. 36, 44).

There is indeed a tendency for prints attributed to ornithopods from other tracksites to be relatively wider than prints attributed to theropods, but the comparison does not provide really strong separation. That being the case, and because the HMTHC trackways are not represented by large numbers of measurable footprints for each trackway, we can't be very dogmatic in using this comparison to identify the trackmakers. Be that as it may, some of the HMTHC and Mountain Creek trackways (C, F, G, H, K, SI, SJ, and SQ) look relatively broad-footed, while others (01A, 01B, 01E, 01F, 01K, 01L, SA, SC, and SD) look more narrow-footed.

Footprints of large ornithopods are thought to have larger interdigital angles (averaging around 60°) than prints of big theropods (averaging around 53°). Most of the HMTHC trackways have interdigital angles closer to expectations for theropods, but some (C, F, H, 2000 cast trail, SF, SH, SN, SO, SQ) show more ornithopod-like values.

The shape analyses we have done so far rely on mean values for trackways, and because we know that some trackways show great variation in shape among the footprints in them, it is possible that our use of averaged values could give misleading results about true footprint shapes. We can check whether this is a problem by looking at only those footprint features that are least variable among the prints that occur within







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**Figure 41**. Footprints attributed to ornithischian dinosaurs. Except for the prints shown in A, D, and E, these are all natural or artificial casts. A) Duplicate of footprint in AC 52/10, assigned to ichnogenus *Anomoepus*; digit II at right. B) BMNH R1866A, large ornithopod footprint from Early Cretaceous of England; left-right symmetry uncertain. C-E) Late Early Cretaceous ornithopod footprints from Dinosaur Ridge, Colorado, assigned to ichnogenus *Caririchnium*. C) CU-MWC 200.8, duplicate of natural cast; left-right symmetry uncertain. D-E) Trackways at the site itself; note impressions of the hand (manus) associated with the trail of the larger animal in E. F) CU-MWC 209.21, large ornithopod print from the late Early Cretaceous Dakota Sandstone; left-right symmetry uncertain. G) TMP 77.17.6, natural cast of small (likely juvenile) ornithopod footprint from the Early Cretaceous of British Columbia assigned to ichnogenus *Amblydactylus*; digit II impression on left. H) TMP 87.76.6, hadrosaur print from the Late Cretaceous of Alberta; digit II probably at left.



O C (1983 13)	🔀 01C (1983 5)	SG
△ B (1983 11)	+ 01D	X SH
∇ F (1983 18)	X 01E (1983 7)	♣ SI
⊳ G (1983 26)	\varTheta 01F (1983 8)	ΦSJ
ЧH	<b>O</b> 01I	M SN
	• 01J	X SO
Πl	▲ 01K (1983 28)	⊙ SQ
¢к	▼ 01L	∆ SR
<b>-</b> 0	2000 (Cast) trail	∀ SS
[] Q	▲ SA	⊳ st
- ∲ JOF12	♦ SC	+ Ornithischian
🕅 01A (1983 6)	SD	Theropod
— 01B (1983 4)	♦ SF	Texas Theropod

**Figure 42**. Ratio of the free length of digit III/footprint palm length (an indication of how long the toes are compared with the rest of the footprint) in tridactyl dinosaur footprints of various sizes.



Γ	O C (1983 13)	♣ JOF12	▼	01L	X	SO
	△ B (1983 11)	🔀 01A (1983 6)		2000 (Cast) trail	$\odot$	SQ
	∇ F (1983 18)	— 01B (1983 4)	◄	SA	Δ	SR
	⊳ G (1983 26)	🔀 01C (1983 5)	۲	SC	$\nabla$	SS
	ЧH	+ 01D		SD	×	Ornithischian
	ΔI	X 01E (1983 7)	٠	SF	1	Theropod
	ΠJ	\varTheta 01F (1983 8)	×	SH	I	Texas Theropod
	¢к	● 01I	+	SI		
	<b>-</b> 0	• 01J	Φ	SJ		
	I Q	▲ 01K (1983 28)	M	SN		

Figure 43. Width across the toetips vs. footprint length in tridactyl dinosaur footprints.



O C (1983 13)	• 01J
△ B (1983 11)	▲ 01K (1983 28)
∇ F (1983 18)	▼ 01L
▷ G (1983 26)	2000 (Cast) trail
⊲н	◀ SA
$\Box$ I	
ΠJ	SD
♦ К	♦ SF
• 0	🗙 SH
🛛 Q	
	Φsj
🕅 01A (1983 6)	M SN
🔀 01C (1983 5)	X SO
+ 01D	⊙ SQ
X 01E (1983 7)	∆ SR
\varTheta 01F (1983 8)	∀ SS
<b>O</b> 01I	⊳ st

Figure 44. Interdigital angles of Heritage Museum and Mountain Creek trackways.



**Figure 45**. Cluster analysis of footprint shape parameters scaled to a common footprint length for Heritage Museum and Mountain Creek trackways. Where trail labels have the word "mean" following them, values used in the analysis represent averages for two or more footprints in the trail; otherwise values are for a single footprint in the trail. The cluster analysis groups trackways on the basis of overall similarity in their scaled shape parameters. Trackways joined by horizontal lines close to the left of the diagram have prints that are very similar in shape, and trails or groups of trails connected by horizontal lines farther to the right have prints that are less similar in shape. Apart from Mountain Creek print SF, which is very different from all the other prints, the analysis identifies two clusters of trackways. One of these includes trails I through Mountain Creek SI (unshaded in the diagram), including most of the trails whose footprints are similar in shape to tracks attributed to ornithopod dinosaurs. The other cluster (trails O through Mountain Creek SJ; shaded) includes trails with footprints that are more theropod-like.

the same trackway. If such parameters don't differ much within a trackway due to changes in substrate consistency or the animal's movements as it moved across the site, they are less likely to differ substantially from one trail to another for these reasons. They might therefore be the features most likely to record real features of the shape of the dinosaurs' feet, and possible differences in these features from one trackmaker to another.

Results of such a comparison are summarized in Table 3, which identifies the footprint shape features (Fig. 36) that are least variable within trackways, using two kinds of comparisons. One of these is the ratio of the largest value of a parameter among all the measured footprints in a trackway to the smallest value of that parameter among the footprints in the trackway. The second comparison employs a statistical value known as the coefficient of variation, which describes numerically how much the values of a parameter differ from the average value of that parameter, expressed as a percentage of the average value. Each of these two comparisons is done two different ways in Table 3.

For readers not wanting to wade through the lines of numbers in Table 3, here is the payoff: The footprint measurements that do not differ greatly among the footprints of the same trackway include the distances between toetips II and III, and between toetips III and IV, the distances from toetips II and IV to a line running down the midline of the footprint, the length of the footprint behind a line connecting toetips II and IV, and the distances from the "heel" of the footprint to the hypex between digits II and III.

We then scale these least variable footprint parameters to a common overall footprint length. This is like taking photographs of the prints, then either enlarging or reducing the images in size so that they would all have the same length from the "heel" to the tip of the middle toe, and after that determining how different the measurements of the selected shape parameters are from one trail to another.

The values of these "scaled" footprint parameters can be simultaneously compared using a statistical procedure known as cluster analysis (Fig. 45). This technique creates a tree-like branching diagram in which cases that are very similar are closely linked in the diagram (like the terminal twigs of a tree). These initial clusters then join with each other to form larger, more inclusive clusters (like a tree's branches), which then form still larger clusters until all of the data cases have been linked (as in a tree trunk). Members of a particular cluster are more like each other than they are like members of other clusters.

The analysis identifies two big clusters of trackways. Of those trackways with well-enough preserved footprints that the parameters of interest can be measured, the trails that are most ornithopod-like in the footprint shape comparisons made so far fall in one cluster, and the most theropod-like trails in the other cluster. This isn't terribly surprising, because the two different analyses are different ways of looking at some of the same shape features of the footprints. However, it is encouraging that this second, more rigorous analysis yields results generally consistent with the first, in which within-trackway variability in footprint shape wasn't considered.

Trackways attributed to theropods often differ from trackways attributed to ornithopods in features not just of individual footprint shape, but also in the arrangement and spacing of prints in the trail. These differences are expressed in the length of the dinosaur's step (pace or stride) in comparison with the length of its footprint, the pace angulation, and the footprint rotation with respect to the dinosaur's direction of travel. In general, trackways thought to have been made by large theropods are characterized by relatively long steps, higher pace angulations, and less negative rotation of the footprint than seen in trackways of large ornithopods. If we plot the average pace length against the average footprint length (measurements are summarized in Table 2) in each trackway (Fig. 46), dinosaur 01K stands out from all the other trackmakers in the length of its step, suggesting that it was moving more quickly than the other animals-just how quickly we'll consider later. If we look at the other dinosaurs, some (such as B, D, G, H, I, J, K, O, R, 01A, 01C, 01G, 01I, 01J, SO, and SQ) had paces on the long side (compared with the size of their footprints), while others (such as C, F, T, 01B, 01E, 01F, 01M, SB, SD, SH, and SJ) took shorter steps. Dinosaur E seems to have had an unusually short step for its size, but this may not be an entirely accurate perception; the footprints in this trackway are very poorly preserved, very likely with exaggerated lengths reflecting that poor preservation.

Pace angulation and footprint rotation are harder features to visualize using graphs, and so instead we will simply refer the reader to Tables 2 and 4. The average value of the pace angulation for a particular trackway ranges from  $134^{\circ}$  -  $180^{\circ}$ . Most of the trackways show negative average values of footprint rotation, indicating that most of the dinosaurs were slightly pigeon-toed (inward rotation); trackway averages range from  $-16^{\circ}$  -  $8^{\circ}$ .

We now have a number of features that we can compare among the HMTHC and Mountain Creek trackmakers, to see if they were more ornithopod-like or theropod-like. All of these comparisons are summarized in Table 5. On balance, footprint and trackway features (columns A-F of Table 5) of trails C, F, 01E, 01L, SD, SH, and SN are rather ornithopod-like, and trails G, O, 01A, 01I, 01J, and SC are theropod-like. There is a tendency for the ornithopod-like HMTHC trackways to have higher interdigital angles than the theropod-like HMTHC trackways, although there is a great deal of overlap in interdigital angle values between the two groups.

Trackway G (Fig. 20) is the most unambiguously theropod-like trail at the HMTHC and Mountain Creek sites. It has relatively long, slender toe marks, some of which narrow at their tips in a manner suggestive of claw impressions. Dinosaur G's prints show yet another indication that it was a theropod. The impression of the middle toe (digit III) shows a slight, "reversed-S" curvature, something very often seen in footprints attributed to large theropods.

Trackway SR (Figs. 28, 30M) may show a feature that, if real, would be particularly ornithopod-like. There were two recognizable footprints in this trail, and both of them had very faint, circular or elliptical marks near their front margins. The surface in which these footprints occur is very weathered. We would have dismissed the faint marks as meaningless irregularities in the rock surface (numerous other such marks occur in the vicinity of SR) except for the fact that they are positioned, relative to the SR footprints, in much the same way as forefoot (manus) impressions are in many trackways of large ornithopods (Fig. 41E). We do not claim that these marks really are manus prints, but only note the possibility.

Our footprint shape analyses suggest the possibility that the HMTHC and Mountain Creek trackmakers included both theropods and ornithopods. However, we emphasize the uncertainty in our tentative identifications. Although some of the trails appear to be distinctively theropod-like or ornithopod-like, many do not show a consistently theropod-like or ornithopod-like pattern. This casts doubt on whether the distinctions we have examined really do reflect differences in the kinds of animals that made the prints. Moreover, trackway 01E, which comes across as ornithopod-like on the basis of footprint outlines drawn in 2001 (Fig. 37), has prints that in 1983 looked rather theropod-like (Fig. 12G, I). We would be more comfortable in identifying the HMTHC trackmakers as representing two distinct kinds of animal if the prints fell into two distinct types, and there weren't so many trackways that seem to show a mixture of theropod-like and ornithopod-like features.



O C (1983 13)	♣ JOF12	010
△ B (1983 11)	🖾 01A (1983 6)	2000 (Cast) trail
0 D	— 01B (1983 4)	🛨 SB
⊖ E (1983 16)	🔀 01C (1983 5)	SD
∇ F (1983 18)	+ 01D	X SE
▷ G (1983 26)	X 01E (1983 7)	X SH
⊲н	\varTheta 01F (1983 8)	♣ SI
01	⊲ 01G	Φsj
ΠJ	¥ 01H	M SN
♦ К	011	X SO
<b>0</b>	• 01J	⊙ SQ
Q	▲ 01K (1983 28)	∆ SR
① R	▼ 01L	
⊗ т	01M	

Figure 46. Pace lengths of Heritage Museum and Mountain Creek trackways.

Consequently, we cannot exclude the possibility that there was but a single kind of dinosaur making the HMTHC footprints, and that the differences in print shape across trackways are simply "noise" due to variations in sediment conditions during the creation and preservation of the footprints. The biggest footprints at the site are only 1 1/2 times the size of the smallest. This size range could easily fall within the range expected for footprints made by a single species of animal. In modern alligators (reptiles distantly related to dinosaurs), for example, the ratio of maximum to minimum foot length in sexually mature individuals is at least 1.8.

If there was only one kind of trackmaker, it was probably a theropod rather than an ornithopod. It is easy to imagine ways in which sediment conditions could cause toe marks to be shorter and broader than the toes that made them. It is harder to picture sedimentary processes that would cause short and broad toes to leave longer and narrower impressions in sediment without deforming other features of the footprints.

**Possible Texas trackmakers.** From theoretical considerations of whether the HMTHC and Mountain Creek dinosaurs were theropods, ornithopods, or both, let us now turn to actual candidates for the trackmakers. Fossil bones have been found in the Glen Rose Formation and other rock units of comparable age at sites in northern Texas, Oklahoma, and Arkansas. Most of these bones were preserved in rocks that accumulated in more inland, terrestrial environments than the coastal situations in which dinosaur footprints are commonly preserved. Early Cretaceous Texas vertebrates were a diverse lot. They include sharklike and bony fishes, salamanders, frogs, lizards, crocodilians, small mammals, pterosaurs (flying reptiles), and dinosaurs.







**Figure 47**. *Acrocanthosaurus atokensis*, a large theropod dinosaur from the Early Cretaceous of Oklahoma, Texas, and probably other parts of North America. A) Skeletal reconstruction by Kenneth Carpenter; scale bar = 1 meter. B, C) Two views of NCSM 14345, mounted skeleton. The actual skull of the specimen is in the display case in front of the mount; the skull on the mount is a cast. Photographs by Vince Schneider.

At least three different kinds of theropod dinosaurs are known on the basis of skeletal material from these deposits (isolated teeth suggest an even greater diversity). One of these is *Deinonychus antirrhopus* (Fig. 32C, D, 48), a small theropod that starred in the Jurassic Park movies under the stage name of *Velociraptor*. *Deinonychus* and its relatives are thought to be closely related to birds, and fossils of such dinosaurs from China are preserved with feather impressions, so it is quite likely that in life *Deinonychus* sported some kind of feathery coat. An equally distinctive feature of these dinosaurs is a relatively huge claw

that was borne on digit II of the foot. The way the phalanges of digit II articulate indicates that this claw was usually carried well off the ground. Consequently we would expect footprints of *Deinonychus* to have two toe marks, not three-or if digit II did impress, it would leave a distinctively odd mark. None of the HMTHC or Mountain Creek footprints looks anything like this. Furthermore, they are much too big to have been made by *Deinonychus*, and so we can probably eliminate this theropod as one of our trackmakers.

In 1972, while searching for a lost cow, Mr. Joe Friday found fossilized bones weathering out of Early Cretaceous rocks of southwest Arkansas. These turned out to be the metatarsals and a few phalanges from a medium-sized theropod dinosaur (Fig. 34C). The specimen has been informally called "*Arkansaurus fridayi*." It was briefly mentioned in scientific publications soon after its discovery, but did not receive a detailed description until 2003, when American paleontologist Rebecca Hunt compared it with a variety of theropod dinosaur feet. Hunt concluded that "*Arkansaurus*" was a coelurosaur, but was unable to pin down its affinities more closely than that. The Arkansas theropod was comparable in size to an ornithomimosaur (dinosaurs roughly comparable in size to ostriches, but in some cases bigger), and some paleontologists have suggested that it belonged to that group. It is possible that some of the smaller Heritage Museum tracks were made by such an animal.

Many of the HMTHC footprints were probably made by bigger dinosaurs, and at least some of these were probably theropods. A good candidate for the large theropod trackmaker is *Acrocanthosaurus*, a big meat-eater whose skeletal remains are known from Early Cretaceous rocks in Oklahoma and Texas (Figs. 34A, 47). *Acrocanthosaurus* reached a total length of about 11 meters (36 feet), and in life weighed about 2000-3000 kilograms (2-3 tons; roughly as heavy as an adult female elephant). Many of the theropod-like footprints at HMTHC are the right size to have been made by this dinosaur, and *Acrocanthosaurus* is also thought to have made the large theropod prints known from the Paluxy River at Dinosaur Valley State Park. However, even though *Acrocanthosaurus* is a good possibility for the maker of at least some of the HMTHC footprints, there is no guarantee that this was the case. Large theropods were pretty conservative in foot shape, which means that the footprints of many of them probably looked quite a bit alike. It is possible that the HMTHC footprints were made by some presently unknown species of large theropod.

Three different kinds of ornithopod are known from the Early Cretaceous of Texas and adjoining states. The smallest of these is a presently unnamed basal euornithopod ("hypsilophodontid") known from multiple individuals from a possible nesting ground in Comanche County (Fig. 32E). This little animal is much too small to have made any of the HMTHC or Mountain Creek prints. Furthermore, it has an innermost toe (digit I) that is quite large compared with the three main toes-so large that it is hard to see how the three main toes could leave an impression without this big inner toe also registering.

The same is true of a rather bigger Early Cretaceous ornithopod, *Tenontosaurus*, which is represented by two species in Oklahoma and Texas, *Tenontosaurus tilletti* (Figs. 32F, 33A, and 48B) and *Tenontosaurus dossi*. Like the little Comanche County dinosaur, *Tenontosaurus* had a very large digit I on the hindfoot. Even though *Tenontosaurus* might have been big enough to make some of the smaller HMTHC tracks, that big digit 1 should have left an impression. Its body proportions suggest that *Tenontosaurus* was capable of moving on two or four legs, but probably moved on all fours only when walking slowly. Because most of the HMTHC and Mountain Creek trackmakers seem to have been in no hurry (see below), we would expect to have seen more indications of forefoot impressions if *Tenontosaurus* had been the trackmaker.


B

**Figure 48**. Life restorations of Early Cretaceous dinosaurs of North America (including Oklahoma and Texas). A) *Deinonychus*, a very bird-like, human-sized theropod. B) Up to no good: a pair of *Deinonychus* prepare to attack a group of the medium-sized ornithopod *Tenontosaurus*. Fossil sites in Montana provide compelling evidence that *Deinonychus* did prey upon *Tenontosaurus*. Paintings copyright 2003 Michael W. Skrepnick.

The biggest ornithopod in the Early Cretaceous Texas dinosaur fauna is also the most mysterious. In 1974 one of the authors of the present book, Wann Langston, reported fragmentary bones of a big ornithopod from several sites in Texas and Oklahoma. Eleven years later students from Sul Ross State University found vertebrae and other bones of a large ornithopod in the Bissett Formation of west Texas; later in 1985 the specimen was collected by the Vertebrate Paleontology Laboratory of the University of Texas. The vertebrae were (literally) dead ringers for their counterparts in *Iguanodon*, a very large Early Cretaceous ornithopod known from several species in Europe (Fig. 49), and a single species, *Iguanodon lakotaensis*, from South Dakota. Whether the bones from Texas represent a new species of *Iguanodon* has yet to be determined.

The two best-known European forms, *Iguanodon atherfieldensis* and *Iguanodon bernissartensis*, differ in size and presumed mode of locomotion. The first was the smaller and more lightly built of the two, and on the basis of its skeletal structure is thought to have been capable of both bipedal and quadrupedal movement. In contrast, the bulkier *Iguanodon bernissartensis* has proportionately longer forelimbs than its relative, and is thought to have been mainly quadrupedal.

Interestingly enough, three-toed footprints in Early Cretaceous rocks of Europe have often been attributed to *Iguanodon*. Some, but by no means all, of these were made by animals walking on all fours. Trackways of quadrupedal Early Cretaceous ornithopods are likewise known from North America (Fig. 41 E).

The bigger HMTHC and Mountain Creek dinosaurs would have been comparable in size to a large individual of *Iguanodon*, and if any of these prints were made by ornithopods, the Texas *Iguanodon* strikes us as the most likely candidate. However, as already noted, with one questionable exception there is no suggestion that the Comal County dinosaurs were walking on all fours. So if *Iguanodon* was one of our trackmakers, it was a species that was comfortable walking on its hind legs.

# How Fast Were the Dinosaurs Moving?

In 1976 the British zoologist R. McNeill Alexander published a technical paper in which he summarized the mathematical relationships among an animal's speed, the length of its stride, and the height of its hip above the ground according to the equation

speed =  $0.25g^{0.5}$  \* stride length<sup>1.67</sup> \* hip height<sup>-1.17</sup>

where speed is in meters/second and both stride length and hip height are in meters. Now this equation may look intimidating, but if we look at it carefully it is pretty easy to understand. We'll start with **g** in the equation, which is the gravitational acceleration of free fall, and has to be considered in order to compare the motions of animals of very different size. The gravitational acceleration takes the value 9.80665 meters/second<sup>2</sup>. In the first part of the equation, we raise g to the 0.5 power (something that is easy to do with many calculators), and then multiply this value by 0.25. When we do all this, we wind up with a value of 0.78289.

We next look at the stride length. You probably know from your own experience that when you run, you take longer steps than when you walk. So all other things being equal, the longer an animal's stride, the faster it is going. In the equation, this is expressed by raising the stride length to the 1.67 power-again, something that is very easy to do on most calculators.



**Figure 49**. The large, Early Cretaceous ornithopod dinosaur *Iguanodon*. A-C) Skeletons mounted at the Belgian Royal Institute of Natural Sciences, Brussels. A) Multiple skeletons of *Iguanodon bernissartensis*. B) IRSNB 1551, skeleton of *Iguanodon atherfieldensis*. C) IRSNB 1536, skeleton of *Iguanodon bernissartensis*. D) Skeletal reconstruction of *Iguanodon bernissartensis* in normal walking pose; drawing by David B. Norman. E) Life restoration of *Iguanodon bernissartensis*; drawing copyright 2001 Michael W. Skrepnick.

If an animal has very long legs, it can cover a great distance in a single step without having to move very quickly. For a given stride length, then, the longer the animal's leg length (which amounts to nearly the same thing as the hip height), the slower the creature's speed. This is indicated by raising the hip height to a negative power, -1.17.

To use Alexander's equation to estimate the speed of a dinosaur from its trackway, we must know the animal's stride length and its leg length (hip height). The stride length is easy-we simply measure that from the trackway.

Hip height is obviously a little trickier, because we don't have the living dinosaur in hand to measure. Hip height can be estimated indirectly from measurements made on the legs of fairly complete dinosaur skeletons. Alexander thought that multiplying footprint length by four provided a good estimate of hip height.

An Anglo-Australian paleontologist, Tony Thulborn, then made a detailed comparison of footprint lengths, foot lengths and overall leg lengths in many kinds of bipedal dinosaurs. He concluded that the length of a bipedal dinosaur's footprint would be roughly the same as the length of the dinosaur's metatarsus (the non-toe portion of the foot). Consequently the relationship between metatarsus length and hip height (which can be measured on a skeleton) should approximate the relationship between footprint length and hip height. For large theropods, hip height was therefore estimated as 8.60 \* footprint length<sup>0.85</sup>, and for large ornithopods as 5.06 \* footprint length<sup>1.07</sup>, where hip height and footprint length are both in centimeters. If the trackmaker cannot be identified with any confidence as being either large theropod or big ornithopod, Thulborn suggested taking the average of the estimates from the two equations, or alternatively, simply multiplying the length of the footprint by 5.7.

A Canadian paleontologist, Donald Henderson, subsequently tackled the problem of estimating hip height in a different way. He constructed three-dimensional computer models of movements of the hip and hindlimb skeletons of dinosaurs, using measurements made from actual skeletons, estimates of the likely range of motion possible at joints between the hip and the thigh, and at the knee and ankle, and the spacing of footprints in dinosaur trackways. Henderson's models suggested, ironically, that Alexander's original, simple estimate that hip height is about four times footprint length provides a better approximation than Thulborn's more complicated determinations.

Now all of this will only work if the footprint is normal in shape, and not shortened or lengthened by any unusual interactions between the dinosaur's foot and the ground. In some dinosaur footprints from the Paluxy River and other sites around the world, the trackmakers occasionally did something distinctly odd, and pressed the entire metatarsus against the ground instead of walking in the usual digitigrade fashion. Why the dinosaurs sometimes did this is unknown, whether it was an involuntary reaction to some feature of the mud or an interesting behavior on the part of the animals. Whatever the reason, the total lengths of such unusual footprints would estimate misleadingly long hip heights.

Odd footprints of that kind do not occur at the HMTHC site. However, the poor quality of many of the footprints, and the possibility that the circumstances under which the prints were made and preserved may have altered footprint lengths from what they would have been under ideal conditions, mean that we must be cautious in applying Alexander's equation to some of the HMTHC trails (e.g. trackway E).

Cautionary comments out of the way, we are ready to estimate the hip heights of the HMTHC dinosaurs, and then plug these numbers, along with the measured stride lengths, into the Alexander equation.

We will assume, following Alexander and Henderson, that hip heights of the trackmakers were four times the lengths of their footprints.

Trackmaker speed estimates are summarized in Table 5 (converted from meters/second to kilometers/hour, units which may be easier to relate to). All but one of the HMTHC dinosaurs seem to have been walking slowly, mostly at speeds of 5-10 kilometers/hour (about 2-6 miles per hour). Dinosaur E has an estimated speed of even less, about 3 kilometers/hour, but as previously noted, this creature's footprints are very poorly preserved, making estimates of hip height from them questionable, and therefore casting doubt on the trackmaker's speed estimate. In any case, none of these dinosaurs seems to have been in much of a hurry. Only animal 01K, with an estimated speed of 16-18 kilometers/hour (10-11 miles per hour), showed any hustle.

These are the kind of speed estimates that one usually gets when the Alexander equation is applied to dinosaur trackways. This isn't very surprising. Dinosaurs were probably no different than modern animals in not wanting to work any harder than necessary.

This doesn't mean that dinosaurs never moved quickly. Dinosaur tracksites from around the world show that some kinds of dinosaurs did indeed occasionally push the accelerator. One such site, in Kimble County, Texas, in rocks slightly younger than those at the HMTHC, has probable theropod trackways with estimated speeds of 34-44 kilometers/hour (21-27 miles per hour)-and this wouldn't necessarily have been their top speeds. By comparison, thoroughbred horses can reach speeds of 68 kilometers/hour (43 miles per hour). Highly trained human sprinters can go as fast as 36 kilometers/hour (22 miles per hour).

So if a time machine is ever invented, and it becomes possible to go back to the Cretaceous to see the HMTHC dinosaurs in the flesh, don't count on being able to outrun them if they really want to catch you!

### What Were the Dinosaurs Doing?

As far we can tell from the preserved trackway portions, most of the HMTHC dinosaurs moved in fairly straight lines as they crossed the site. The lone exception to this is animal C, which initially moved in a southeasterly direction, but then curved to the northeast (in the following discussion, it will be treated as moving in a northeasterly direction).

There is a striking pattern in the direction of travel of the HMTHC dinosaurs (Tables 6, 7; Fig. 50): more dinosaurs traveled in a northeasterly (NE) direction (the compass quadrant between 0° and 90°) than in all the other compass quadrants combined. The second most common bearing is to the southwest, but there are only a few more trackways whose azimuths (compass bearings) are in the southwest (SW) than in the southeast (SE) quadrant. The NE quadrant also has more trackways than the other three at the Mountain Creek site (Fig. 51), but it does not dominate the sample the way the NE quadrant does at the HMTHC site alone-arguably there is no real preferred orientation of the Mountain Creek trackways. If 2000 and later data for the HMTHC and Mountain Creek sites are combined (Table 7), the NE quadrant remains the strongest, with as many trails heading in that direction as in the other quadrants combined, and the SW quadrant has the second largest number of trails, but again by only slightly more than the SE quadrant.

"Mirror-image" arrangements of trackmaker bearings (with roughly the same number of trails heading in each of two compass directions about 180° apart) are quite common at dinosaur tracksites. They are usually interpreted as indicating that the animals preferred to head in one direction, or in the opposite direction, because of some linear geographic feature that influenced their movements. Given that, in order for



**Figure 50**. Directions of travel (azimuths) of the HMTHC dinosaurs. Zero degrees in these diagrams represents magnetic north, which is about 6-7 degrees east of geographic north; 90° is east, 180° is south, and 270° is west. The average bearing of each trackway is indicated as a line segment, the length of which corresponds to the number of footprints over which the average trackway bearing was measured; this is indicated by how many circles the line segment crosses. Thus the innermost circle represents azimuths based on a single footprint, the circle numbered 5 indicates a trail consisting of five footprints, and so on. A) 1983 data. B) 2000 and later data. Note the strong preference for movement in a northeasterly direction on the part of the dinosaurs.



**Figure 51**. Directions of travel (azimuths) of the Mountain Creek dinosaurs. In contrast to the HMTHC trackmakers, no strong preference for direction of travel is apparent.

footprints to be made and preserved, the dinosaurs had to have been walking in muddy areas, the most likely such feature to have affected the reptiles' motion would have been a shoreline. That is, the animals probably tended to move back and forth along the water's edge, rather than heading into or out of the water.

Such a scenario seems plausible for the HMTHC trackmakers, but doesn't account for the great preference of the northeasterly over the southwesterly direction of travel. If the dinosaurs had been moving one at a time along the shoreline, one might expect about half of them to have traveled in each of these directions. The fact that northeast was by far the preferred direction of travel suggests that something else

may also have influenced the dinosaurs' travel plans. Furthermore, the lack of strong preference for a northeasterly orientation on the part of the Mountain Creek trails, in contrast to those from HMTHC, suggests that the very strong northeasterly movement of the HMTHC dinosaurs may not have been constrained by any environmental features.

If the trackways were made over a fairly short interval of time, the possibility that the northeastheading dinosaurs were traveling as a group, which we can designate the hypothetical NE herd, must be considered. Evidence that at least some dinosaur species were social animals is known from both bone assemblages and tracksites. Catastrophic death assemblages, where dinosaurs of the same species were overwhelmed (sometimes in huge numbers) by some environmental calamity (drought, flood, or volcanic eruption) are known for several kinds of dinosaurs, both herbivores and carnivores. Tracksites are known where dinosaurs walking side-by-side seem to have simultaneously lurched to one side to avoid colliding with their neighbors. So there is ample precedent for considering the possibility that some of the HMTHC dinosaurs were part of a herd.

Indeed, some of the trails almost beg for this interpretation. Dinosaurs F, H, and I, and A, B, and D, constitute two groups in which the trackways remain parallel over many footprints, and the two groups of trackways are themselves parallel (Fig. 2).

If there were any footprint and trackway features in which members of this hypothetical NE herd could be shown to be more like each other, and less like the other HMTHC trackmakers, this would bolster our confidence that the herd was a real group of animals. In Table 5 we group the HMTHC trackways into three categories, based on the likelihood that they were part of a group. The first category includes animals that were likely not part of the group, because they were traveling in directions very different from the trend for the group. A second category consists of those most likely to have been part of such a group, partly because the trackways are fairly close together. Finally, a third category consists of those dinosaurs somewhat less likely to have been members of the hypothetical NE herd. One of the last of these is dinosaur C, who changed direction over the course of its trackway, but whose final direction of travel was northeast. The remaining animals in the third group had northeasterly directions of travel, but either had trails that cut across those of the most likely herd members, or (as in the case of trails examined in 2001) were not part of the main cluster of possible herd members.

If we restrict comparison to those dinosaurs most likely to have been members of a NE herd, and those least likely to have been members of the herd, the former tend to have trackways with higher pace angulations, and footprints with higher interdigital angles, than the latter. However, this difference between possible herd members and non-herd dinosaurs disappears if we include the somewhat less likely herd members in the comparison. "Herd" and "non-herd" members do not differ in footprint size, footprint rotation, or estimated trackmaker speed.

Of the four HMTHC trackways tentatively identified in Table 5 as being particularly ornithopod-like, two are also members of the possible herd. More interestingly, of the fifteen HMTHC trackways that in Figure 45 fall within the ornithopod-like cluster, ten are likely or possible members of the NE herd. In contrast, of the five HMTHC trackways in Table 5 tentatively identified as being particularly theropod-like, only one is a possible herd member; similarly, of the six HMTHC trackways that fall within the theropod-like cluster, only two are possible herd members.

If we look at the direction of travel of HMTHC and Mountain Creek trackmakers in terms of compass quadrant and membership in the ornithopod-like or theropod-like footprint shape cluster (Table 7), there are more ornithopod-like trackways in the NE quadrant than in all the others combined. There is no such possible pattern in the direction of travel of the most theropod-like trackways.

These possible associations of ornithopod-like trackways with the NE quadrant of travel and possible membership in the hypothetical NE herd, and of the most theropod-like trails with the non-herd category, support the hypothesis that a NE-traveling herd did in fact cross the HMTHC site. Unfortunately, as interesting as these associations are, they are not conclusive; none of them is, to use the jargon, statistically significant.

Our discussion of a possible NE herd has rather obviously assumed that the footprints of the possible herd members were all made at the same time. At present we have no way of knowing if this is so. It remains possible that the trackways assigned to the hypothetical herd were in fact made by animals walking by themselves at very different times.

However, if the trackways were made at different times, by solitary dinosaurs, we still have to explain why there is such a marked preference on the part of the trackmakers for walking in a northeasterly directionthe observation that led us to consider the possibility of a herd in the first place. Perhaps dinosaurs engaged in some kind of seasonal movements, just as many modern bird species-likely descendants of dinosaurs-do. If so, and if the HMTHC tracksite was made during such a seasonal wandering, there might have been a preferred travel direction on the part of dinosaurs traveling alone.

But this suggestion is at least as speculative as the herd hypothesis. Even though we cannot say with certainty that a herd existed, this strikes us as the best explanation for the strong northeasterly direction of travel of the HMTHC dinosaurs.

Herding or not, what were the dinosaurs doing out on a possibly featureless mudflat during low water? We can only offer what we hope is informed speculation. To begin with, if *Acrocanthosaurus* and/or *Iguanodon* were the trackmakers, we doubt that such mudflats were the only habitats they frequented, and we suspect that these weren't even their preferred habitats. Skeletal remains of both kinds of potential trackmaker are known from sedimentary rocks that formed in more inland situations.

If a herd, or solitary individuals of *Iguanodon*, were some of the HMTHC and Mountain Creek trackmakers, it is possible that food sources were nearby. A rather diverse plant assemblage has been found in the Glen Rose Formation, including conifers that may have had a lifestyle similar to that of modern mangrove shrubs. If ornithopods were able to eat what may have been somewhat salty fodder, they might have found reason at least occasionally to wander onto coastal marine mudflats.

Attractive bits of food that would have drawn big theropods like *Acrocanthosaurus* onto such mudflats are harder to imagine. The occasional stranded fish, large invertebrate, or marine reptile, perhaps? Or were such areas fairly open situations, where a foraging carnivore might be able to spot an herbivorous dinosaur a long way off?

It may be that the carbonate mudflats held no particular attraction for the dinosaurs. These big animals may have crossed the flats simply because they were there, and had to be crossed to get to more desirable locations.

### **The Texas Crawler**

As already noted, the three linear features that run across the HMTHC tracksite from northwest to southeast are important landmarks for describing the location of dinosaur trackways and other features of the site (Fig. 11). Each of these linear traces is about 20-25 centimeters (8-9 inches) wide, with innumerable small, slightly arcuate ridges cutting perpendicularly across the feature, like rungs on a ladder. Two of the linear traces closely parallel each other, maintaining a nearly constant distance (about 60 centimeters [2 feet]) between them despite minor jogs along their length (Fig. 11D). The third linear feature parallels the other two, but is about 4 meters (14 feet) beyond them in a northeasterly direction. The three linear features cut across the regional trend of joints in the rock.

Similar marks have been seen before. In 1962 French paleontologist Albert de Lapparent reported tridactyl dinosaur footprints from an Early Cretaceous site on the Arctic island of Spitzbergen (Fig. 52). De Lapparent thought that the prints had been made by *Iguanodon*, but other workers have attributed them to large theropods. What interests us now is not the dinosaur tracks, but rather several linear features with ladder-like crossbars that run across the track surface; de Lapparent noted these features, but was uncertain what they were. They look quite similar to the HMTHC linear traces in both size and shape, and their association with tridactyl dinosaur trackways is remarkably reminiscent of the situation in Comal County, Texas.

It is possible that such traces were made by some inanimate object that bounced or rolled across the mud surface, presumably moved by water, but it seems more likely that they are trace fossils made by marine animals of some kind that crawled through the mud. The HMTHC traces are nearly perpendicular to the preferred direction of travel of the dinosaurs. If the dinosaurs were in fact moving parallel to the shoreline, the tracemakers would have been moving either toward or away from the water. Some of the dinosaurs seem to have stepped on the crawl marks (Figs. 8B, 18B), indicating that the tracemakers moved across the site before these dinosaurs did.

The paired traces were obviously not made independently of each other, but had to have been made by an object with two sides separated by a fixed distance. One suggestion made by early observers at the site is that the marks were made by a sea turtle (Fig. 53). Fragmentary remains of sea turtles are known from the Glen Rose Formation, including a piece of bone found right at the HMTHC site. Sea turtles are reasonably common fossils from later Cretaceous rocks, including some forms that were quite big (Fig. 53F, G).

Female sea turtles make trails when they haul themselves onto beaches for nesting. The outer edges of the trace are dug by the big forelimbs (Fig. 53A-C); the turtle pushes down with her hands near the base of her first finger (the equivalent of our thumb). Inside these outer marks are impressions made by the smaller hindlimbs, and even the tail. Examination of modern sea turtles (Fig. 53D, E) suggests that the span across the base of the hand-and thus the outer width of a turtle trail-is roughly the same as the length of the turtle's shell, or a bit more than that. In a study of the ecology of loggerhead turtles (*Caretta caretta*), biologist David A. Nelson reported that, "When loggerheads crawl up on a beach, they leave an asymmetrical pattern of 90- to 100-cm-wide depressions in the sand" and that these turtles "attain a carapace length (straight line) up to 120 cm." Nelson's data on the width across loggerhead trails as compared with the size of the turtles match what we would expect from looking at the bodies of the turtles. Consequently if the HMTHC double crawl mark was made by a sea turtle, the animal would have had a shell at least 60 centimeters long-a big enough turtle, but nowhere near as big as some of the turtle monsters of the Late Cretaceous.

There are, however, difficulties with the sea turtle hypothesis. For one thing, why are there no marks



**Figure 52**. Photograph of a dinosaur tracksite on the Arctic island of Spitzbergen, taken by J. F. Hendricksen in 1960 and published by Albert de Lapparent in 1962. Tectonic deformation of the rocks after their formation has situated the track surface vertically. In addition to numerous tridactyl footprints in the surface, note the presence of crawl marks similar to those at the HMTHC site. Photograph used by permission of the Institut Géologique Albert de Lapparent, France.

made by the hindlimbs or the tail inside the double crawl mark? Furthermore, one side of the double crawl mark is much better developed than the other (Fig. 11E); one would think that a crawling sea turtle would have impressed the two sides of her trail equally. Extrapolating from that concern leads into the final objection to the turtle hypothesis: If these trails were made by sea turtles using their fore flippers, why is the single crawl mark (and the traces at the Spitzbergen site) unpaired? One might imagine preservational circumstances that could address all of these concerns, but the sea turtle hypothesis would be more attractive if we didn't have to engage in such special pleading.

There is also the question of what a sea turtle would have been doing, crawling out on a mudflat like that. This would hardly have been an ideal setting for nest building, and suitable beaches for egg-laying may have been far away. Perhaps the turtles-if such they were-found themselves trapped high and nearly dry during low tide, and were frantically scrambling to get into deep water before they succumbed to overheating or the gastronomic designs of a theropod?

In 1985 the late geologist Bob F. Perkins sketched, on the back of a cafe menu that he gave to Langston, an alternative hypothesis for the tracemaker (Fig. 54). Perkins proposed that the tracemaker was a huge snail, possibly *Nerinea incisa*. This was a snail with a very long (as much as about 40 cm, and conceivably longer), narrow, tightly-coiled shell. Perkins suggested that the more deeply impressed portion of the double crawl mark was made by the snail's "foot." The tip of the snail's shell lopped over to one side, and was lightly dragged in the mud to the side and behind the rest of the animal. The single crawl mark, Perkins suggested, was made by a similar snail that carried the shell tip off the ground.

Perkins' hypothesis accounts for both single and double versions of the crawl marks. Perhaps they were made by snails that were left behind by a retreating low tide, and were attempting to crawl back to deeper water.

We may never know for sure what kind of animal the Texas crawler was. Many kinds of trace fossils are very difficult to assign to their makers. Sedimentary features made by creatures crawling across the surface, or burrowing beneath it, often provide little detail about the anatomy of the structures that made those traces. As tricky as it can be to assign tridactyl dinosaur footprints to their makers, identifying the makers of trace fossils like the HMTHC crawl marks is even more difficult.















**Figure 53**. Modern and fossil sea turtles. A-E) Modern turtles. A-C) Female leatherback turtles (*Dermochelys coriacea*) returning to the sea after egg-laying; photographs by Frank V. Paladino. A, B) Trails made by turtles. C) Leatherbacks and large individuals of some other species drag themselves along using both fore flippers simultaneously. Smaller sea turtles use left and right fore flippers in an alternating fashion. D) FMNH 95997, hawksbill turtle (*Eretmochelys imbricata*), ventral view; white ruler about 15 centimeters (6 inches) long. E) FMNH 204848, green sea turtle (*Chelonia mydas*), ventral view. F, G) Fossil turtles. F) USNM V11651, *Protostega gigas*, Late Cretaceous, Kansas; dorsal view. The box held near the head of this mount is about 45 centimeters (18 inches) long. Much of this skeleton is reconstructed. G) SM P 7068 A-JJJ, large sea turtle skeleton from the Cretaceous Eagle Ford Formation, Gholson, Texas. Dorsal view, head directed downward The scale is 1 meter.

Figure 54. Sketches made by Bob F. Perkins in 1985 to illustrate his hypothesis that a huge snail (Nerinea incisa-not Nerinia, as in the sketch; the specific name roemeri has now been subsumed under the name incisa) was responsible for the Heritage Museum crawl marks. A) In this view the snail is crawling toward the viewer. The solid line beneath the snail represents the substrate. The snail's head and other soft parts are on the left, and the shell points to the right. B, C) The bulk of the snail's weight is in its head and muscular foot, which press down into the substrate, making the transverse, ladderlike parts of the trace. If the shell tip is off the ground, only this single crawl mark is made. However, if the shell tip touches the ground, it is dragged in the mud behind and to the side of the rest of the snail to leave the lightly impressed half of the double crawl mark.



#### **Conservation of the Tracksite**

The HMTHC footprints may be preserved in solid rock, but they are remarkably delicate features. They may not be exposed to the destructive floods that on occasion adversely affect dinosaur tracks in the bed of the Paluxy River, but they are unfortunately vulnerable to a more subtle, insidious attack. The rock surface containing the prints is constantly exposed to the elements, becoming quite hot in summer, and subject to freezing temperatures in winter. Such seasonal extremes gradually-and sometimes not so gradually-weather the limestone, breaking it apart and destroying its footprints. Some tracks that were sharp and clear when the site was first exposed are now hard to see (Fig. 55), and for many the maps, measurements, photographs and casts made during this study are the only records that remain. Now that the site has been acquired by the Heritage Museum, efforts are underway to preserve those footprints that remain. In fact, by purchasing this book you have helped raise the funds to make this possible.



**Figure 55**. Adverse effects of exposure to the elements on footprint quality. Footprint G2, arguably the finest print at the site when it was first discovered (Fig. 20), was considerably worse for the wear when this picture was taken in 2005. Additional cases of declining track quality can be seen by comparing footprints as they appear in the photomosaic (Fig. 10) with their appearance two decades earlier (Figs. 7-9, 11-12, 14-18, 22).

# Epilogue

The out-going tide was lower than usual, exposing more of the huge expanse of flat, muddy sea floor than in most of the month's low tides. Two large, clumsy marine animals had found themselves stranded on the exposed mudflat by receding water, and had laboriously tried to haul their way back to the open sea (Fig. 56). Their long, linear trails in the mud were ignored by a group of big, heavily built, herbivorous dinosaurs that marched across the exposed sea floor, walking on their hindlegs with their tails well off the ground, but their forelegs barely clearing it.

The huge plant-eaters, each of them weighing two or three tons, had stripped the last edible foliage from their most recent feeding grounds, and were now in search of new pastures. The unusually distant withdrawal of the sea had made it possible for the dinosaurs to take a short cut across a large bay, instead of having to take the longer dryland route around the bay's margin. A gentle breeze provided temporary relief from the humid air and the intense heat of the sun, and also carried the scent of fresh greenery from the other side of the bay. The plant-eaters eagerly plodded onward. In places the ground was firm, having baked long enough to dry out. In other spots soft mud splattered as the trackmakers trod upon it.

The wind changed direction, and the big herbivores were instantly nervous. They had detected a new odor, the acrid scent of a carnivorous dinosaur whose size rivaled their own. The meat-eaters seldom attacked fully grown plant-eaters, but their hunting behavior was unpredictable. The plant-eaters picked up the pace. Once they reached the trees lining the shore, they would be less exposed.

The earth has made its annual orbital trek around the sun more than one hundred million times since dinosaurs stepped across a marine mudflat that would one day be exposed on the grounds of the Heritage Museum of the Texas Hill Country. The mud is now rock, and the trackmakers-if any bodily remains of them still exist at all-are fossilized bones waiting to be discovered by a lucky paleontologist.

But their footprints remain, incontrovertible evidence that the dinosaurs once came this way. The details of their passage-how much like the little story told above-remain uncertain. But pass this way they did.

We look at the tracks they left, and wonder...



**Figure 56**. Once upon a time in the Cretaceous: paintings (copyright 2005 Michael W. Skrepnick) showing events that may have created the HMTHC dinosaur tracksite. A) A pair of large snails crawl across a mud flat toward the sea. B, C) A herd of *Iguanodon* pass through the area. D) A prowling *Acrocanthosaurus* attempts to locate its next meal.

### Sources of Information and Suggestions for Further Reading

The published literature on dinosaurs is enormous, and getting bigger all the time. The following list is a bit idiosyncratic. It emphasizes more recent works, and includes publications ranging from children's books to very technical books and journal articles (the last two marked with an asterisk). Most of the books in this list, however, are readily accessible to the lay reader, and either touch on topics discussed in the present work, or provide good recent accounts of some aspect of dinosaur paleontology. Emphasis in this bibliography is placed on publications dealing with Early Cretaceous vertebrates from Texas, and those concerned with dinosaur footprints. The journal articles cited are not intended to be comprehensive, but will quickly get the interested reader into the relevant technical literature. Most of the cited publications are in English, but some that are very useful are written in other languages-emphasizing the point that the study of dinosaurs and their tracks is an international enterprise.

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later years.		
1983 Farlow Data	1982 Langston Map	2000 and Later Farlow Data
Trackway 4		Trackway 01B
Trackway 5		Trackway 01C
Trackway 6		Trackway 01A
Trackway 7		Trackway 01E
Trackway 8		Trackway 01F
Trackway 11	Trackway B	Trackway B
Trackway 12*	not present	Trackway JOF12
Trackway 13*	Trackway C ("downtrail" portion)	Trackway C
Trackway 14 (singleton)*	Trackway A?	
Trackway 15	Trackway C ("uptrail" portion)	
Trackway 16	Trackway E	Trackway E
Trackway 17 (singleton)*	Trackway D?	
Trackway 18	Trackway F	Trackway F
Trackway 20	Trackway J?	Trackway J?
Trackway 21	Trackway I	Trackway I
Trackway 22	Trackway K?	Trackway K?
Trackway 23	Trackway H?	Trackway H?
Trackway 24	Trackway L?	Trackway L?
Trackway 26	Trackway G	Trackway G
Trackway 28		Trackway 01K

**Table 1**. Correlations of labels applied to the same dinosaur trackways in 1983, and 2000 and later years.

\*There is uncertainty about correlations of these trackways between Farlow's and Langston's 1982 data. Langston's map does not show a southward heading trail in the vicinity of trackways C and A, but Farlow recognized such a trail as number 12. The first footprint of JOF12 overlaps with prints of two other trails, which Farlow numbered 13 and 14 (the latter a single footprint). Farlow's trail 13 is plausibly the "downtrail" portion of Langston's trail C, and Farlow's trail 14 could be Langston's trail A, which was very faint. However, Langston's map shows trails A and C diverging from one another at this part of the site, which would make it difficult for both of them to be part of the three-way print overlap with Farlow's trail 12. Another possibility is that Farlow's trail 13 is actually Langston's trail A, but that leaves the downtrail portion of Langston's trail C unidentified in Farlow's tabulation.

**Table 2**. Summary measurements of trackways. A plus sign in the "number of footprints seen" column indicates that there may have been more prints than the reported number in the trail. For each measurement, the numbers reported are the mean (average) value, followed in parentheses by the range of values; where there is a single number in a cell, only one measurement of that parameter was made.

Trackway	Number of Prints Seen	Footprint Length (mm)	Pace (cm)	Stride (cm)	Pace Angulation (degrees)					
Heritage Mus	Heritage Museum Tracksite									
1983 trackway measurements (with 2000 and later data for the same trackways, where the identifications are reasonably certain):										
1983 1	1	510								
1983 3	2	490.0 (480-500)	140							
1983 4	2 (1983)	497.5 (475-520)	137							
(01B)	3 (2001)	523.3 (510-530)	117.5 (107-128)	243	180					
1983 5	1+(1983)	600								
(01C)	4 (2001)	520	165.8 (152-191)	318.5 (307-330)	164.5 (149-180)					
1983 6	4+ (1983)	360.0 (330-380)	118.1 (116-122)	231.1 (227-235)	158.0 (156-160)					
(01A)	9 (2001)	370.7 (340-390)	119.4 (109-130)	236.0 (225-251)	162.3 (160-165)					
1983 7	3+ (1983)	550.0 (53-59)	157.5 (157.5-157.5)	310	159					
(01E)	6 (2001)	552.0 (525-580)	142.6 (121-159)	281 (232-308)	159.3 (143-180)					
1983 8	2 (1983)	500.0 (500-500)	114							
(01F)	4 (2001)	452.5 (430-460)	124.7 (113-131)	244.5 (236-253)	152.0 (152-152)					
1983 9	2	370.0 (360-380)	132							
1983 10	1+	420								
1983 11	9 (1983)	507.8 (440-560)	165.4 (160-175)	328.4 (320-345)	166.4 (160-177)					
(B)	8 (2001)	502.5 (470-530)	162.1 (158-173)	322.7 (319-330)	175.2 (169-180)					
1983 12	5 (1983)	480.0 (470-500)	129.2 (114-135)	256.6 (239-267)	157.3 (147-164)					
(JOF12)	5 (2001)	445.0 (430-460)	131.0 (130-132)	260.5 (260-261)	170.0 (170-170)					
1983 13 ("downstroil"	10 (1983)	582.2 (560-600)	134.9 (127-142)	261.0 (254-272)	153.7 (145-164)					
portion of C)	9+ (2001)	558.1 (500-620)	138.7 (125-154)	258.6 (252-266)	138.0 (124-170)					
1983 14	1	420								
1983 15("uptrail" portion of C)	9 (1983)	490.0 (470-520)	150.7 (140-156)	295.0 (290-300)	158.0 (149-169)					
1983 16	16 (1983)	537.1 (500-560)	117.4 (97-137)	222.9 (164-260)	145.1 (114-180)					
(E)	11 (2001)		114.5 (99-131)	206.8 (171-238)	133.7 (101-161)					
1983 17	1	600								
1983 18	12 (1983)	505.6 (500-580)	138.9 (122-152)	271.2 (254-287)	163.4 (152-180)					
(F)	10 (2001)	488.1 (430-550)	135.0 (95-158)	265.4 (235-287)	167.3 (154-180)					

1983 19	2	460.0 (460-460)			
1983 20	3 (1983)	500.0 (500-500)	154.3 (154-155)	307	169
(J?)	3 (2001)	463.3 (460-470)	151.5 (151-152)	303	180
1983 21	6 (1983)	450.0 (430-480)	161.8 (157-168)	318.1 (315-323)	155.5 (151-160)
(I)	7 (2001)	484.3 (450-500)	160.2 (155-170)	317.0 (312-324)	167.4 (158-180)
1983 22	2 (1983)	505.0 (500-510)	159		
(K?)	7 (2001)	522.0 (500-545)	166.5 (145-183)	322.0 (312-328)	148.0 (136-160)
1983 23	6 (1983)	425.0 (380-450)	137.4 (127-142)	268.6 (264-277)	160.7 (147-180)
(H?)	5 (2001)	424.0 (410-440)	136.5 (132-141)	273.3 (270-277)	167.3 (156-180)
1983 24	4	495.0 (460-530)	129.9 (122-138)	243.9 (229-259)	141.0 (131-151)
1983 25	1	460			
1983 26	8 (1983)	548.7 (500-580)	172.0 (157-185)	331.5 (300-351)	152.5 (125-166)
(G)	6 (2001)	541.7 (500-580)	168.2 (152-180)	329.0 (310-351)	167.7 (155-180)
1983 27	2	465.0 (460-470)	173		
1983 28	4 (1983)	497.5 (440-550)	250.6 (246-259)	492.7 (490-495)	162.5 (157-168)
(01K)	4 (2001)	550.0 (540-560)	252.0 (249-257)	498.5 (497-500)	165.5 (161-170)
1983 29	1	500			
2000 and later	trackway mea	asurements:			
D	6	418.3 (340-480)	147.8 (137-155)	300.0 (281-330)	172.5 (163-180)
0	10	458.3 (440-475)	148.0 (137-153)	287.4 (248-300)	168.5 (160-180)
Q	5+	502.0 (460-550)	138.3 (133-147)	273.3 (269-282)	172 (166-180)
R	4	530.0 (470-590)	163.7 (162-166)	328.0 (326-330)	172.5 (165-180)
Т	4	460.0 (440-480)	133.7 (128-138)	262.5 (262-263)	154.5 (149-160)
01D	4	406.7 (380-430)	119.7 (118-122)	236.5 (234-239)	166.0 (162-170)
01G	3	450	152.5 (145-160)	290	144
01H	3	495.0 (470-520)	141.0 (130-152)	276	156
011	2	430.0 (415-445)	134		
01J	3	446.7 (420-460)	155.5 (154-157)	311	174
01L	3	540 (510-570)	154.0 (152-156)	298	151
01M	16	uncertain	147.3 (133-160)	280.1 (262-300)	152.2 (132-180)
010	3	510	152.0 (144-160)	295	152
Mountain Cree	ek Tracksite				
2000 Trackway	4	493.3 (480-500)	120.0 (109-140)	241.5 (240-243)	150.5 (146-155)
SA	1	380			
SB	3	446.7 (440-450)	125.0 (121-129)	245	157

SC	1	360			
SD	2	465.0 (450-480)	133		
SE	2	365.0 (360-370)	110		
SF	1	450			
SG	1	540			
SH	3	440.0 (430-460)	120.5 (118-123)	237.5	160
SI	6	339.0 (310-380)	101.7 (97-109)	201.6 (194-211)	170.3 (160-
SJ	5	415.0 (350-480)	113.1 (107-123.5)	229.0 (220-236)	180.0 (180-180)
SK	2	515.0 (500-530)			
SL	2	380.0 (380-380)			
SM	1	550			
SN	2	420.0 (410-430)	125		
SO	5	402.0 (380-420)	128.5 (120-133)	258.3 (252-263)	168.7 (166-170)
SP	1	510			
SQ	3	390.0 (370-400)	123.3 (122.5-124)	246	173
SR	2	532.5 (530-535)	147		
SS	1	460			
ST	1	360			

**Table 3**. Within-trackway variability of footprint size parameters. The ratio of maximum/ minimum (Mx/Mn) values was calculated for each parameter that could be measured on two or more footprints within a trackway. The coefficient of variability (100 \* standard deviation/ mean) was calculated for each parameter that could be measured on three or more footprints within a trackway. The mean values of the Mx/Mn ratio and V were then calculated across trackways, using Mx/Mn and V values for individual trackways as cases in the calculation. Parameters were then ranked in order of increasing variability (1 = least variable) according to: mean value of Mx/Mn ratio across trackways (R1), largest Mx/Mn ratio seen in a trackway (R2), mean value of V across trackways (R3), and maximum V seen in a trackway (R4); tied values were assigned the same rank. Overall footprint length (heel to toetip III) was not included in parameter rankings.

Parameter	Treatment	Mean (Range)	Number of Trackways
Heal to Testin III	Mx/Mn	1.09 (1.00-1.31)	17
Heel to Toetip III	V	4.81 (1.07-8.88)	6
Testin II to Testin III	Mx/Mn	1.13 (1.00-1.30); R1 = 1, R2 = 2	14
	V	7.48 (4.12-11.05); R3 = 1, R4 = 3	6
Testin III to Testin IV	Mx/Mn	1.22 (1.03-1.49); R1 = 6, R2 = 7	15
	V	9.98 (5.77-14.22); R3 = 6, R4 = 5	5
Testin Width	Mx/Mn	1.13 (1.00-1.25); R1 = 1, R2 = 1	14
	V	7.83 (5.30-10.90); R3 = 3, R4 = 2	5
Toetip II to Footprint	Mx/Mn	1.19 (1.01-1.39); R1 = 4, R2 = 4	14
Midline	V	9.85 (7.15-16.82); R3 = 5, R4 = 8	6
Toetip IV to Footprint	Mx/Mn	1.17 (1.04-1.34); R1 = 3, R2 = 3	13
Midline	V	9.24 (4.79-12.14); R3 = 4, R4 = 4	5
Digit II Lateral Hypex	Mx/Mn	1.88 (1.00-5.02); R1 = 14, R2 = 14	14
Length	V	35.01 (2.12-73.96); R3 = 18, R4 = 18	6
Digit III Projection	Mx/Mn	1.63 (1.01-5.18); R1 = 12, R2 = 15	14
(Toetip Extension)	V	22.67 (10.57-63.53); R3 = 16, R4 = 16	5
"Dealtfeet" Length	Mx/Mn	1.16 (1.00-1.43); R1 = 2, R2= 5	14
Backioot Length	V	10.92 (5.77-14.31); R3 = 8, R4 = 6	5
Digit III Free Longth	Mx/Mn	1.30 (1.01-1.69); R1 = 11, R2 = 8	16
Digit III Free Length	V	15.21 (8.43-22.32); R3 = 14, R4 = 12	6

Eastarint Dalm Longth	Mx/Mn	1.30 (1.01-2.10); R1 = 11, R2 = 13	16
Footprint Pann Length	V	10.69 (2.99-15.07); R3 = 7, R4 = 7	6
Digit III Medial Hypex	Mx/Mn	1.29 (1.01-1.69); R1 = 10, R2 = 8	16
Length	V	13.05 (5.66-17.95); R3 = 11. R4 = 10	6
Digit III Lateral Hypex	Mx/Mn	1.28 (1.01-1.91); R1 = 9, R2 = 11	16
Length	V	16.30 (7.49-32.75); R3 = 15, R4 = 15	6
Digit IV Medial Hypex	Mx/Mn	1.77 (1.08-6.45); R1 = 13, R2 = 16	15
Length	V	32.80 (18.16-73.81); R3 = 17, R4 = 17	6
	V	1.20 (1.00-1.75); R1 = 5, R2 = 9	16
Heel to Hypex II-III	Mx/Mn	11.55 (6.98-17.09); R3 = 9, R4 = 9	6
	Mx/Mn	1.25 (1.04-1.77); R1 = 7, R2 = 10	16
Heel to Hypex III-IV	V	14.00 (3.55-22.89); R3 = 12, R4 = 14	6
Haal to Tastin H	Mx/Mn	1.19 (1.01-1.94); R1 = 4, R2 = 12	14
	V	7.58 (5.93-9.80); R3 = 2, R4 = 1	6
Heal to Testin W	Mx/Mn	1.16 (1.00-1.45); R1 = 2, R2 = 6	15
	V	12.27 (6.64-19.27); R3 = 10, R4 = 11	5
Width Across Hypexes	Mx/Mn	1.27 (1.01-1.49); R1 = 8, R2 = 7	16
II-III and III-IV	V	14.85 (4.93-22.67); R3 = 13, R4 = 13	6

- Least variable parameters (occur in lower half of all four rankings): Toetip II to Toetip III, Toetip III to Toetip IV, Toetip Width, Toetip II to Footprint Midline, Toetip IV to Footprint Midline, "Backfoot" Length
- Fairly low-variable parameters (occur in lower half of three out of four rankings): Heel to Hypex II-III, Heel to Toetip II

Most variable parameters (occur in upper half of all four rankings): Digit II Lateral Hypex Length, Digit III Projection, Digit III Lateral Hypex Length, Digit IV Medial Hypex Length **Table 4**. Measurements of footprint rotation (in degrees) with respect to the dinosaur's direction of travel (data only available for 2000 and later observations). Measurements were made by averaging the compass bearings of two successive footprints in a trackway, and then comparing the compass bearing of each footprint in the pair with that average; multiple measurements of this kind could be made for trackways with many footprints in them. Positive values mean that the footprint rotates outward, and negative values indicate that the footprint toes inward. Values are expressed as the mean (average) and range of values (if a range is not given, only one measurement could be made).

Trackway	Footprint Rotation
C (1983 13?)	-16.4 (-26 to -7)
B (1983 11)	-4.9 (-6 to -3)
А	8.0 (7 to 9)
D	5.0 (3 to 7)
E (1983 16)	1.6 (-9 to 9)
G (1983 26)	-1.6 (-6 to 1)
Н (1983 23?)	-6.5 (-8 to -4)
I (1983 21)	-7.8 (-12 to -5)
J (1983 20?)	-10.0 (-12 to -8)
K (1983 22?)	-5.7 (-10 to -1)
0	-0.4 (-12 to 14)
Q	-15.5 (-18 to -13)
R	4.7 (-5 to 10)
Т	-3.3 (-6 to -1)
JOF12	-3.0 (-6 to -1)
01A (1983 6)	1.8 (-1 to 4)
01B (1983 4)	-3.5 (-7 to 0)
01C (1983 5)	-7
01D	-2.0 (-2 to -2)
01E (1983 7)	-5.7 (-10 to -1)
01F (1983 8)	-3.0 (-4 to -2)
01G	4.0 (3 to 5)

01H	-7.5 (-8 to -7)
01I	-2
01J	-0.5 (-5 to 4)
01K	-8
01L	-9.5 (-12 to -7)
2000 Trackway	-2
SB	-2
SE	-5
SH	-4.0 (-10 to 2)
SI	-1.4 (-5 to 3)
SJ	-0.3 (-2 to 2)
SN	7
SO	-2.3 (-5 to 0)
SQ	-5.0 (-7 to -3)
SR	-6

**Table 5**. Summary comparison of features of HMTHC and Mountain Creek footprints and trackways. Columns A-F compare a series of measurements across the trackways; a minus sign means that average value for that feature is less than the grand average across all of the trackways, and a plus sign means that the trackway average is larger than the grand average across all trackways; "minus" entries further suggest that the feature could be ornithopod-like, and "plus" entries suggest that it could be theropod-like. Empty cells indicate that no data were available. A: Ratio of Footprint Length/Footprint Toetip Width; B: Ratio of Digit III Free Length/Maximum Width; C: Ratio of Digit III Free Length/"Palm" Length; D: Ratio of Pace Length/Print Length; E: Pace Angulation; F: Footprint Rotation. The ID column summarizes information in columns A-F by indicating whether the footprint and trackway features collectively suggest an ornithopod-like (O) or theropod-like (T) pattern; a question mark indicates a best guess in the face of conflicting information, and an empty cell means that there was so little information, or so much conflicting information, that we were unwilling even to guess about the nature of the trackmaker.

Interdigital angle values are averages for trackways (with the range of values for a trackway given in parentheses after the mean value; if a number is reported without a range, only one measurement was made for that trackway).

Bearing indicates the compass quadrant of the dinosaur's overall direction of travel. HMTHC animals (the Mountain Creek dinosaurs were not included in this particular analysis) whose bearings suggest the possibility that they were part of a hypothetical northeast-heading herd are assigned a value of 1 in the NE herd column; a question mark after the 1 means that the trackmaker is somewhat less likely to have been a herd member than trackmakers marked with a 1 without the question mark. Dinosaurs whose direction of travel make it very unlikely that they were part of such a herd are scored 0 in that column. Dinosaur 01M was not assigned to any of these categories; its footprints were so poorly preserved that its direction of travel was difficult to determine, although it was probably moving in a northeasterly direction.

The size column indicates whether the trackmaker had a mean footprint length greater than or equal to the average trackmaker footprint length across the trackways (scored +) or less than the average footprint length across trackways (scored -).

Trackway	A	В	C	D	E	F	ID	Mean Interdigital Angle II-IV (degrees)	Bearing	NE Herd	Size	Estimated Trackmaker Speed (kilometers/hour)
C (1983 13)	-	-	+	-	-	-	O?	61	NE*	1?	+	5.4
B (1983 11)	-	-	-	+	+	-		55.7 (38-90)	NE	1	+	8.8 (9.0)
D				+	+	+			NE	1	-	9.7
Е				-	-	+			SW	0	+	3.3 (3.9)
F (1983 18)	-	-	-	-	+	-	O?	57.0 (53-61)	NE	1	+	6.6 (6.6)
G (1983 26)	-	+	+	+	+	+	T?	42.0 (39-45)	SW	0	+	8.3 (8.3)
Н (1983 23?)	-	-	+	+	+	-		63.7 (51-73)	NE	1	-	8.1
I (1983 21)	-	-	-	+	+	-		47.6 (36-57)	NE	1	+	8.9
J (1983 20)	+	-	-	+	+	-		35.0 (21-44)	NE	1	-	8.7
K (1983 22)	-	-	+	+	-	-		41	NE	1?	+	8.6

Where only one trackmaker speed estimate is presented, it is based on data from 2000 or later. Where two estimates are given, the first is for data from 2000 or later, and the second (in parentheses) is from 1983 data.

0	+	+	+	+	+	+	Т	15	NE	1?	-	8.0
Q	-	+	-	-	+	-		47.5 (41-54)	NE	1	+	6.7
R				+	+	+			NE	1	+	8.5
Т				-	-	+			NW	0	-	6.9
JOF12	-	+	+	-	+	+		41.0 (40-42)	SW	0	-	7.1 (6.7)
01A (1983 6)	+	+	+	+	+	+	Т	47.3 (23-71)	SE	0	-	7.5 (7.8)
01B (1983 4)	+	-	-	-	+	+			NE	1?	+	5.2
01C (1983 5)	+	-	-	+	+	-		40	NE	1?	+	8.3
01D	-	+	+	-	+	+		42.5 (39-46)	SW	0	-	6.7
01E (1983 7)	+	-	-	-	-	-	O?	48.0 (32-62)	SE	0	+	6.3 (7.4)
01F (1983 8)	+	-	-	-	-	+		43	NE	1?	-	6.3
01G				+	-	+			NE	1?	-	8.4
01H				-	-	-			NE	1?	+	6.9
011	+	+	+	+		+	Т	37	SE	0	-	
01J	-	+	+	+	+	+	T?	25	SE	0	-	9.5
01K (1983 28)	+	-	-	+	+	-		39	NW	0	+	16.4 (18.1)
01L	+	-	-	-	-	-	O?	39	SW	0	+	7.1
01M				-	-				NE?	?	+	6.2
010				-	-				NE	1?	+	7.5
2000 Trackway	+	-	-	-	-	+		64	SW		+	5.5
SA	+	-	-					43	SW		-	
SB				-	-	+			NE		-	6.4
SC	+	+	+				T?	41	NE		-	
SD	+	-	-	-			O?	37	NE		-	
SE				+		-			NW		-	
SF	-	+	+			-		79	NE		-	
SG		-	-						SW		+	

SH	+	-	-	-	-		O?	64.5 (58-71)	NW	-	6.2
SI	-	+	-	+	+	+		55.5 (49-52)	SW	-	6.4
SJ	-	+	+	-	+	+		53.0 (53-53)	NW	-	6.2
SK									SE	+	
SL									SW	-	
SM									SE	+	
SN	-	-	-	-		+	O?	60.0 (58-62)	NE	-	
SO	-	-	-	+	+	+		68	SE	-	7.9
SP									SE	+	
SQ	-	-	+	+	+	-		74	NE	-	7.5
SR	-	-	+	-		-		53.5 (51-56)	NE	+	
SS	+	-	-					54	SW	-	
ST	-	-	-					53	SE	-	

\*Animal C changed its direction over the course of its trackway. Initially it headed SE, but its final bearing was NE.

**Table 6**. Overall direction of travel of dinosaurs (0 degrees = magnetic north). Where more than one number is reported for the direction of travel, the first number reported is based on 1983 measurements, made by sighting along the path of the entire recognized trackway, or the bearing of an isolated print. The second number (in parentheses) represents data from 2000 or later years, and represents either mean footprint bearing for a trackway, or the bearing of an isolated print. If only a single number is reported, it represents data either for 1983 (and so is associated with the 1983 number of the trackway), or 2000 and later years.

Trackway	Direction of travel (degrees)
Heritage Museum Tracksite	
1983 3	220
1983 4 (01B)	23 (38)
1983 5 (01C)	40 (49)
1983 6 (01A)	96 (119)
1983 7 (01E)	103 (121)
1983 8 (01F)	53 (43)
1983 9	56
1983 11 (B)	50 (52)
JOF 12	196 (190)
1983 13 ("downtrail" C?)	40 (42)
1983 15 ("uptrail" C?)	97
1983 16 (E)	237 (234)
1983 17 (D?)	74 (58)
1983 18 (F)	66 (70)
1983 20 (J?)	45 (48)
1983 21 (I)	55 (63)
1983 22 (K?)	48 (36)
1983 23 (H?)	60 (62)
1983 24	214
1983 25	55
1983 26 (G)	203 (207)
1983 27	65
1983 28 (01K)	320 (322)
1983 29	65
0	81
Q	74

Т	355
01D	204
01G	44
01H	55
011	130
01J	103
01L	252
01M	58
010	38
Mountain Creek Tracksite	
2000 Trackway	188
SA	218
SB	74
SC	72
SD	37
SE	317
SF	26
SG	255
SH	318
SI	190
SJ	303
SK	107
SL	225
SM	123
SN	64
SO	126
SP	112
SQ	45
SR	45
SS	221
ST	93

Table 7. Counts of the number of trackways heading in each of the four compass quadrants for the HMTHC and Mountain Creek Tracksites, and for the two sites combined						
		NE	SE	SW	NW	
HMTHC (2000 and Later Data)	All Trackways	18	4	5	2	
	"Ornithopod-Like"	10	1	3	1	
	"Theropod-Like"	2	3	1	0	
HMTHC (1983 data)		15	3	5	1	
Mountain Creek		7	5	6	3	
Combined HMTHC and Mountain Creek (2000 and Later Data)	All Trackways	25	9	11	5	
	"Ornithopod-Like"	13	2	6	2	
	"Theropod-Like"	3	3	1	1	

## Glossary

**Biped:** an animal that moves on its hind legs.

**Bivalves:** a group of molluscs characterized by two shells; includes clams, oysters, mussels, and their relatives.

Body fossils: the fossilized remains of ancient organisms.

**Digits:** an animal's fingers and toes.

**Foraminiferans:** a group of protozoans (single-celled organisms) that manufacture tiny skeletons (tests) to house themselves.

Footprint: a depression made in sediment by the foot of an animal.

**Footprint rotation:** the angle between the long axis of an animal's footprint and the animal's direction of travel.

Dasycladaceans: a group of seaweeds that secrete limey crusts around themselves.

Digitigrade: term describing animals that walk on their toes, with their metatarsals lifted off the ground.

Echinoderms: starfishes, sea lilies, sea cucumbers, sea urchins, and their relatives.

Femur: the large bone of the upper leg (thigh).

Fibula: the smaller of the two lower leg bones.

Metatarsals: the main bones of the foot, to which the toe bones attach.

Micrite: limestone composed of extremely tiny crystals.

Miliolids: a group of foraminiferans characterized by a smooth, porcelain-like test.

**Ornithischians:** a major group of plant-eating dinosaurs; includes ornithopods, stegosaurs, ankylosaurs, ceratopsians, and their relatives.

**Ornithopods:** a diverse group of ornithischian dinosaurs; includes tenontosaurs, iguanodonts, hadrosaurs, and their relatives.

Ostracodes: tiny shrimp-like crustaceans that secrete calcareous shells to cover their bodies.

Pace: the distance between two successive footprints made by the opposite feet.

Pace angulation: the angle between two successive paces.
Peloids: rounded lumps of fine-grained, limey mud that solidify to become components of limestones.

Phalanges: individual bones of the fingers and toes.

Rudists: an extinct group of bivalves that constructed reef-like build-ups of limestone.

Quadruped: an animal that moves on all four legs.

Sauropods: the biggest sauropodomorphs; quadrupedal, long-necked, plant-eating dinosaurs.

Sauropodomorphs: a group of very large, long-necked, generally quadrupedal, herbivorous dinosaurs.

Stride: the distance between two successive footprints made by the same foot.

Terrigenous: term used to describe sediments derived from erosion of continental rocks.

Test: a skeleton made by microscopic, one-celled organisms.

Theropods: meat-eating dinosaurs and their relatives.

Tibia: the larger of the two lower leg bones.

Trace fossils: sedimentary structures that preserve records of the presence and activities of ancient organisms.

Tracksite: an exposure of rock containing fossilized footprints.

Trackway: a series of footprints made one after another by the same animal.

Trail: another word for trackway.

**Transmitted (ghost) tracks:** impressions made in sediment layers below the one on which an animal actually walks as the animal's weight is transmitted downward through a series of stacked sediment layers.

Tridactyl: three-toed.

Unguals: phalanges beneath the claws or nails of fingers and toes.