

EXPLORING A REAL JURASSIC PARK
FROM THE DAWN OF THE AGE OF DINOSAURS
IN THE CONNECTICUT VALLEY



A Field Trip Sponsored by

THE GEOLOGICAL SOCIETY OF CONNECTICUT

GUIDEBOOK No. 9

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**EXPLORING A REAL JURASSIC PARK
FROM THE DAWN OF THE AGE OF DINOSAURS
IN THE CONNECTICUT VALLEY**

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A FIELD TRIP IN CELEBRATION OF THE 50th ANNIVERSARY (PRG)

2016 marked half a century since the dinosaur tracks were discovered at what is now Dinosaur State Park, in Rocky Hill, Connecticut. In order to commemorate this milestone fiftieth anniversary, the Geological Society of Connecticut held its annual meeting at the Park and invited world-famous dinosaur paleontologist Robert Bakker to give the keynote address. Dr. Bakker chose to discuss the regional paleontology of Connecticut and Massachusetts in his lecture, which he entitled “The Real Jurassic Park in the Connecticut Valley.” Given both the historical and scientific importance of fossils in this region to our understanding of life in the Early Mesozoic, as well as the location of the talk, Dr. Bakker’s topic was very appropriate. The lecture was highly attended, which is a testament to both Dr. Bakker’s fame and to the continued interest shared by professional geologists and the general public for paleontology. Indeed, paleontology is a great way for both these groups to come together and to talk science.

On this trip, we will have an opportunity to see first-hand some of the fossils that Bakker discussed. We will visit two field localities as well as three museums. As you read this guide you will see institutional abbreviations used to refer to specimens in the museum collections. ACM ICH is used for specimens in the Amherst College Ichthyology Collection, and SSM is used for specimens at the Springfield Science Museum.

The leaders of this field trip are a combination of geologists and vertebrate paleontologists who have a wide range of interests in the fossils found in Connecticut and Massachusetts. Each of them brings their unique areas of expertise and interest to this trip in order to provide an experience that will be, in my opinion, very unique. All of them are engaged in active research in the region covered by the trip and each will present highlights of their research for us to consider.

The topics covered on this field trip are wide-ranging and therefore there will be something of interest to almost anyone. For example, for those interested in dinosaur evolution, we will examine evidence for feathered dinosaurs as recorded in trace fossils. Surprisingly, one of the possibly feathered dinosaurs was an early ornithischian, the group from which birds did not evolve. Thus, this specimen provides evidence to support the hypothesis that feathers are a primitive feature for all dinosaurs. For those who are interested in paleoecology, we will explore the evidence that Early Jurassic dinosaur communities in this region were based on fish as a primary food source, rather than terrestrial herbivores. For those interested in dinosaur behavior and social dynamics, we will examine the trackways of large bipedal dinosaurs at two tracksites to evaluate whether or not the animals that made the tracks were gregarious. We will present multiple lines of evidence that the animals were carnivores and that they were probably non-social animals. For those interested in sedimentology and dinosaur locomotion, we will examine tracks made in deep, soupy sedimentary substrates that have been difficult to interpret. For those interested in technology, we will end our day at Dinosaur State Park, where we will learn about new techniques being used to remap the site and to provide a new generation of interpretive exhibits to museum goers. In addition to these wide-ranging topics, we will look at some unique fossils, such as the only body imprint of a sun spider-like animal in the world, which was found in Massachusetts.

Again, the intent of this field trip is to provide a unique experience examining the fossils of the Connecticut Valley, the deposits of which formed in the Late Triassic and Early Jurassic. Hence, we have titled the trip and its accompanying guide book “Exploring a real Jurassic Park from the dawn of the age of Dinosaurs in the Connecticut Valley.” We, the leaders of the field trip, look forward to sharing our knowledge and insights with you, and hope that you will share yours with us!

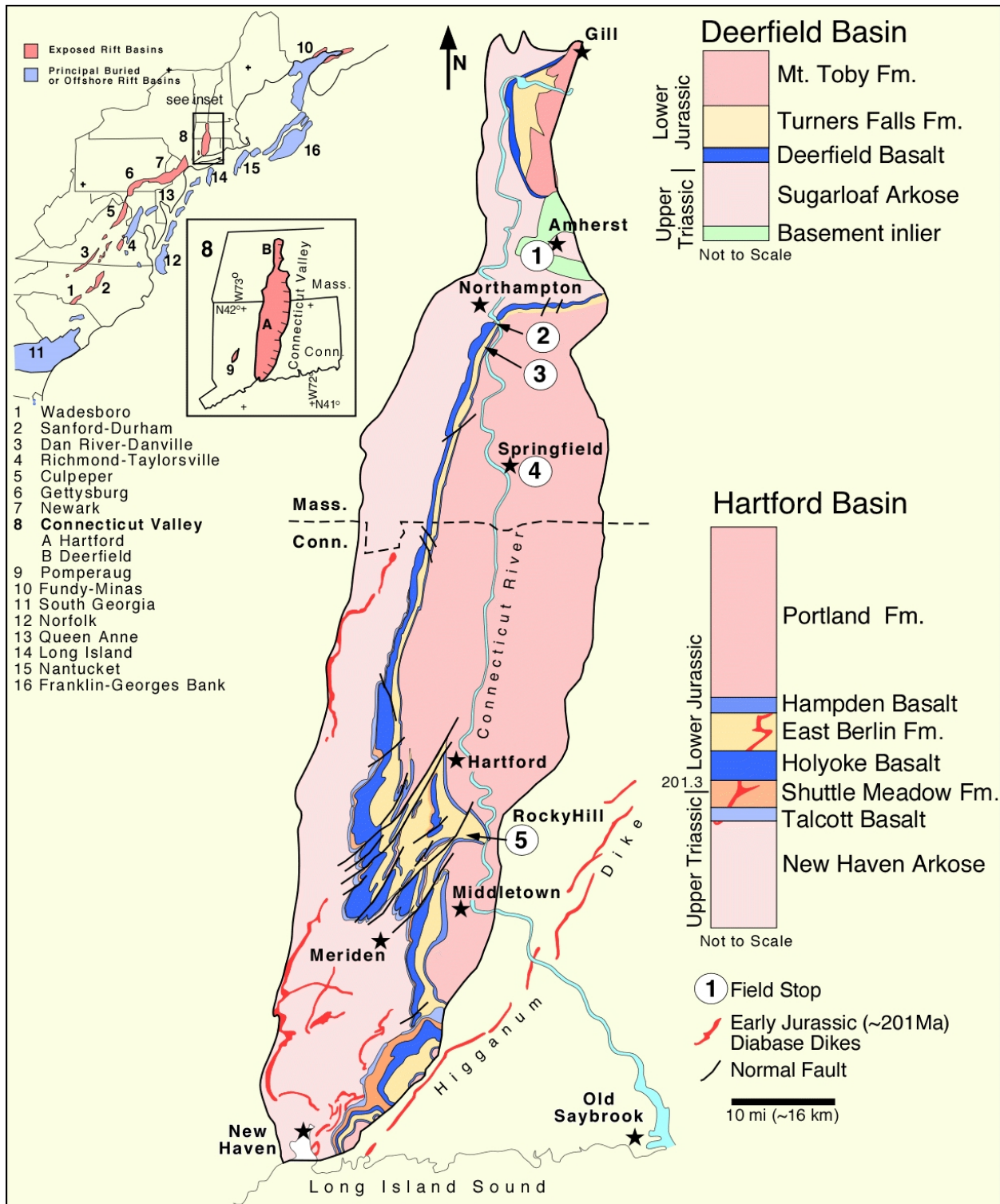


Figure 1. Simplified geologic map of the Hartford and Deerfield basins, with field stops.

INTRODUCTION (PML)

They are fraught with strange meanings, these footprints of the Connecticut.

– Hugh Miller, *Testimony of the Rocks*, 1857

More than 180 years after Hitchcock's first scientific descriptions of Connecticut Valley tracks in 1836, the fascinating trace fossils from the region remain an active field of research for paleontologists, sedimentologists, stratigraphers, historians of early American science, and other scholars. On this trip, we will view some of the finest known examples of Early Jurassic dinosaur tracks and other trace fossils from the Hartford and Deerfield basins.

Although the tracks themselves have changed very little in the two centuries since their discovery, theories about their origin and paleontological importance have changed considerably. Once viewed as imprints of ancient birds that were wiped out by the biblical flood, by the mid- to late-1800s the tracks became attributed to the presence of dinosaurs, organisms then modeled as sluggish, cold-blooded reptiles. By the mid-20th century, the Connecticut Valley theropod tracks, with their obvious bipedalism suggestive of high metabolism, played an important role in overturning earlier hypotheses of dinosaur physiology by supporting the modern hypothesis that at least some track-makers were the highly active, likely endothermic, relatives of modern birds (e.g. Galton, 1970).

The abundance of footprints and trackways in the Connecticut Valley, and the corresponding paucity of skeletal remains in the region, has led to lively debates about the anatomy, physiology, and behavior of the trackmakers, including swimming ability (Coombs, 1980 v. Lockley and Gillette, 1987), gregarious "flocking" behaviors (Ostrom, 1972 v. Getty et al., 2012), foot anatomy (Weems, 2003 v. Lucas et al., 2006), taxonomic diversity (Lull, 1953 v. Olsen and Rainforth, 2003), biostratigraphy (Hitchcock, 1858 v. Lucas and Tanner, 2007), etc.

This field trip is focused on the Connecticut Valley in Massachusetts, with one stop in central Connecticut. We will visit notable dinosaur track localities in the Northampton region, view the famous Hitchcock track collection at the Beneski Museum of Amherst College, learn about recent finds from the Gaulin site at the Springfield Science Museum, and end our day on familiar ground at Dinosaur State Park in Rocky Hill, Connecticut (Fig. 1).

ECOLOGICAL AND GEOLOGICAL CONTEXT (PML)

Goodbye to the Triassic (PML)

Spanning the Late Triassic (Norian-Rhaetian) and the Early Jurassic (Hettangian-Sinemurian), the sedimentary rocks and fossils of the Hartford basin record a critical period in Earth history. The early-Late Triassic (Carnian 237-228 Ma) was a time of great biotic change with the older forms of reptiles reaching something of an evolutionary apex, following their recovery from the largest biological crisis in the geological record – the catastrophic end-Permian extinction (see, for example, Fraser, 2006; Sues and Fraser, 2013). By the Late Carnian (228 Ma), a high degree of diversity and specialization was seen among the older reptilian lineages, including a diversity of crurotarsians (crocodilomorphs and their many relatives), the herbivorous dicynodonts, the archosaurs, and mammal-like reptiles (Fraser, 2006; Sues and Fraser, 2013). Strata and biota of this time have not been identified in the Connecticut Valley, however, they are represented elsewhere in eastern North America. There seems to have been somewhat of a decline in diversity from the Carnian into the Norian, but ecological diversity was still very high and these deposits comprise the bulk of the strata preserved in Eastern North America, although less so in the Connecticut Valley. For example, unique and highly specialized reptiles such as the arboreal glider *Icarosaurus* glided through the conifer forests, and the long-necked *Tanytrachelos* and the "deep-tailed

swimmer" *Hypuronector*, both diminutive aquatic predators, hunted in the waters of ancient lakes (Fraser, 2006; Fraser et al., 2007; Sues and Fraser, 2013; Fig. 2).

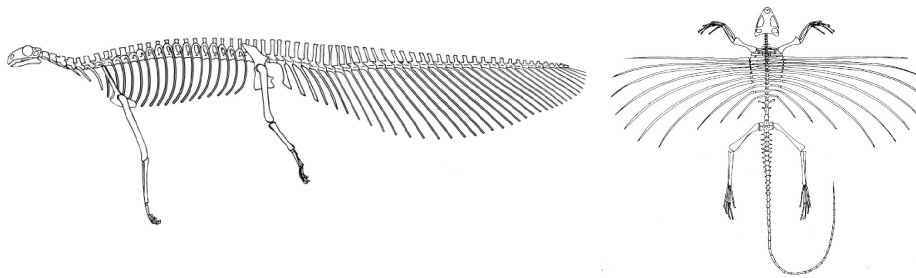


Figure 2. Specialized Late Triassic reptiles. Left: *Hypuronector*, 15 cm long. Modified from Colbert and Olsen, 2001. Right: *Icarosaurus*, 30 cm long, modified from Colbert, 1970.

By the mid- to late-Triassic, terrestrial and marine biomes hosted a diverse array of reptiles, including mammal-like reptiles, and amphibians. Add to this remarkable tetrapod radiation the arrival of the three major groups early dinosaurs, the theropods, the sauropodomorphs, and possibly the ornithischians (Sues et al., 2011; Nesbitt et al., 2013; Brusatte et al., 2010), and increased diversity and radiation among land plants such as conifers, and the Late Triassic certainly ranks as one of the most seminal geologic periods. The interval leading up to the Early Jurassic – the focus of this field excursion – was not, however, without incident. The astonishing biotic diversity achieved by the non-dinosaurian fauna in the early-Late Triassic (Carnian, 237-228 Ma), experienced a dramatic reversal of fortunes during the Late Triassic (Tanner et al., 2004; Huynh and Poulsen, 2005; Fraser, 2006; Whiteside, et al., 2007; Lucas et al., 2010; Sues et al., 2011; Fig. 3).

The first blow to the Late Triassic ecosystems came with the Carnian-Norian (228 Ma) turnover, with the disappearance of many tetrapods, including the large predatory rousuchians and heavy-skulled, herbivorous dicynodonts, among others (Benton, 2010). This event saw the disappearance of such highly specialized terrestrial and aquatic reptiles as *Hypuronector*, *Icarosaurus*, and *Tanytrachelos* (Fraser, 2006). In the marine realm, ammonite diversity was significantly reduced (Hallam, 1981). Further reductions in Late Triassic diversity occurred in the mid-Norian, about 214 Ma, perhaps related to the bolide that created the 100-km wide Manicouagan crater in Canada (Onoue et al., 2014).

The decline of the older forms of terrestrial and aquatic reptiles in the Late Triassic, such as the rousuchians, crocodylomorphs, aetosaurs, dicynodonts, phytosaurs, tanystrophids, icarosaurs, and others, allowed the dinosaurs to occupy vacant niches in the ecosystems. Originating in the Carnian, dinosaurs increased in diversity through the Late Triassic, but they did not become the dominant megafauna until the Early Jurassic. In a very real sense, the Late Triassic set the stage for the reign of the dinosaurs from the Early Jurassic to the terminal Cretaceous. This span of time, lasting 135 million years, is the longest period dominated by a major group of tetrapods. (Considering that living dinosaurs – the birds – outnumber mammals by a factor of two, it is reasonable to argue that the age of dinosaur dominance is not over!)

The Norian-Rhaetian (209 Ma) transition is noted for reductions in ammonoid, conodont, bivalve, and radiolarian diversity in the marine realm (Whiteside and Ward, 2011; Wotzlaw et al., 2014; Onoue et al., 2016), and an increase in dinosaur abundance and diversity on land (Olsen et al., 2002; Sues et al., 2011). The three major dinosaur lineages, the theropods, sauropodomorphs, and ornithischians originated before the Carnian, possibly the Ladinian or earlier (Sues et al., 2011; Nesbitt et al., 2013; Brusatte et al., 2010).

Rhaetian biotic patterns have been debated, with even the stage definition and duration challenged (Hallam, 1981; Tozer, 1990; Muttoni et al., 2010; Wotzlav et al., 2014; Lucas, 2016). What is clear is that the later part of the Triassic was a period of instability for both terrestrial and marine ecosystems, and a critical time of transition leading up to the catastrophic end-Triassic extinction (Hallam, 1981; Olsen et al., 2002; Sues et al., 2011; Whiteside and Ward, 2011; Wotzlav et al., 2014; Lucas, 2016). The final knockout punch to the already reeling Late Triassic marine and terrestrial ecosystems arrived with one of the largest known terrestrial eruptions of basalt – the Central Atlantic Magmatic Province (CAMP) at the 201 mya Triassic-Jurassic boundary [1] (Whiteside, et al., 2007). In 2013, the base of the Hettangian stage (earliest Jurassic) was established at Kuhjoch, Austria, in the Karwendel Mountains of the Northern Calcareous Alps, based on the first occurrence of the ammonite *Psiloceras spelae tirolicum* (Hillebrandt, A.v., et. al., 2013). The consensus radiometric date for the Tr-J boundary is 201.3 Ma, which, in the Hartford basin, places it in the Shuttle Meadow Formation, several hundred meters above the earlier pick at or near the base of the Talcott Basalt, around 201.5 Ma (*ibid*, 2013). This revision implies that the lower part of the Shuttle Meadow Formation should have a depauperate assemblage of terrestrial vertebrates compared to younger Hettangian-Sinemurian strata, for example the Portland Formation. Whether or not the CAMP event is the proximate cause of the end-Triassic extinction, it no doubt was a major disruptor of global ecosystems during the terminal Triassic (Olsen, 1999; Whiteside, et al., 2007; Fraser, 2006).

Welcome to the Jurassic Park (PML)

The Early Jurassic was a time of great rebuilding for global ecosystems, assembled from spare parts that survived the series of biotic collapses during the Late Triassic and the major end-Triassic extinction. Early Jurassic ecosystems were populated with organisms adapted for survival into the coming period of relative stability. Apparently, dinosaurian physiology was well suited for survival in this rebuilding world. With many of the older forms gone, the dinosaurs enjoyed an "ecological release" into depopulated niches (Olsen et al., 2003). Dinosaur diversity increased above the Tr-J boundary and they almost certainly increased in total population.

In the Connecticut Valley, this Early Jurassic recovery is recorded in fluvial and lacustrine rocks long noted for their abundant dinosaur footprints. Although bones are scarce in the Connecticut Valley, except for those of fossil fishes, the fossils together, ranging from tiny insects to large apex terrestrial predators, provide clues to the composition, structure, and distribution of Early Jurassic ecosystems at sub-tropical latitudes in north-central Pangaea from 201 Ma to at least 190 Ma.

On this trip, we will explore the tracks and trails left by the survivors of one of the largest mass extinctions in the geologic record. The causes and consequences of this extinction are the subject of vigorous study and debate. The geologic time scale and the definition of the Triassic and Jurassic stages are based on the marine record. Therefore, of prime interest to the researchers are high-resolution correlations between the terrestrial and marine record.

1 In 2013, the base of the Hettangian stage (earliest Jurassic) was established at Kuhjoch, Austria, in the Northern Calcareous Alps, based on the first occurrence of the ammonite *Psiloceras spelae tirolicum* (Hillebrandt, A.v., et. al., 2013). The consensus radiometric date for the Tr-J boundary is 201.3 Ma, which, in the Hartford basin, places it in the Shuttle Meadow Formation, several hundred meters above the earlier pick at or near the base of the Talcott Basalt, around 201.6 Ma (*ibid*, 2013). This revision implies that the lower part of the Shuttle Meadow Formation should have a depauperate assemblage of terrestrial vertebrates compared to younger Hettangian-Sinemurian strata such as the Portland Formation.

Recent progress has been made in correlating Late Triassic and Early Jurassic continental and marine strata using paleomagnetic reversal stratigraphy (Kent et al, 2017). Determining where the strata of the Hartford basin fit in relation to the standard marine ammonite stages and other continental sequences will help clarify the influence of regional and global events on biostratigraphic patterns, especially the end-Triassic extinction and the rise of the dinosaurs during the Early Jurassic.

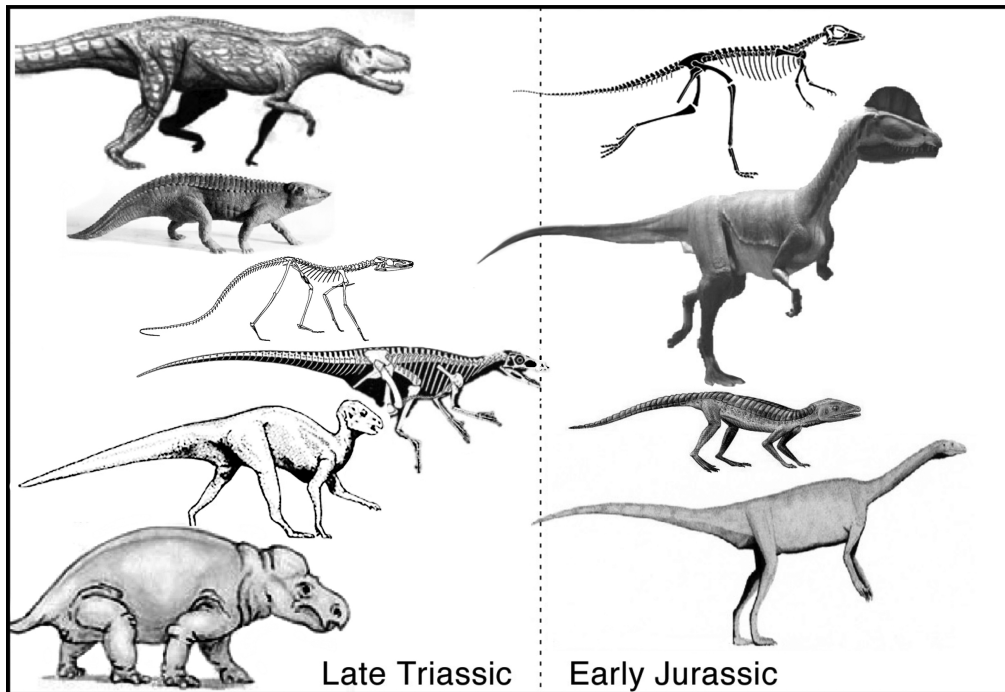


Figure 3. Diagram of tetrapod change across the T-J boundary. Late Triassic fauna from top: rausuchian, aetosaur, crocodylomorph, theropod, ornithischian, and dicynodont. Early Jurassic fauna include, from top: *Anchisaurus*, a prosauropod; *Dilophosaurus*, a theropod; protosuchian crocodylliform; generic prosauropod. Extant species from these times are not shown. Not to scale.

The Connecticut Valley: The Hartford and Deerfield Basins (PML)

The Hartford Basin (Fig. 1), comprising the southern two-thirds of the Connecticut Valley Lowland, is part an extensive series of early Mesozoic age rifts formed during the breakup of Pangea. Ranging in age from Late Triassic (Norian) through Early Jurassic (Sinemurian, and possibly younger), rocks of the Hartford Basin are organized as formations within the Newark Supergroup (e.g. Olsen, 1988; Kent and Olsen, 2008). The small northern extension of the Hartford Basin is called the Deerfield Basin (Fig. 1).

The geology of the Connecticut Valley has been extensively described in numerous publications, for example, Hubert, 1978, LeTourneau and McDonald, 1985, Lorenz, 1988, Horne et al., 1993, LeTourneau and Olsen, 2003, Olsen et al., 2003, Kent and Olsen, 2008, LeTourneau and Thomas, 2010, LeTourneau et al, 2015, and LeTourneau and Pagini, 2017.

In summary, the Hartford and Deerfield basins are elongate half-grabens with master border faults on their eastern sides (Fig. 4). Strata in the basins generally dip about 15 degrees to the east, but large amplitude folds create a system of broad anticlines and synclines within the otherwise basic structural configuration (Fig. 1).

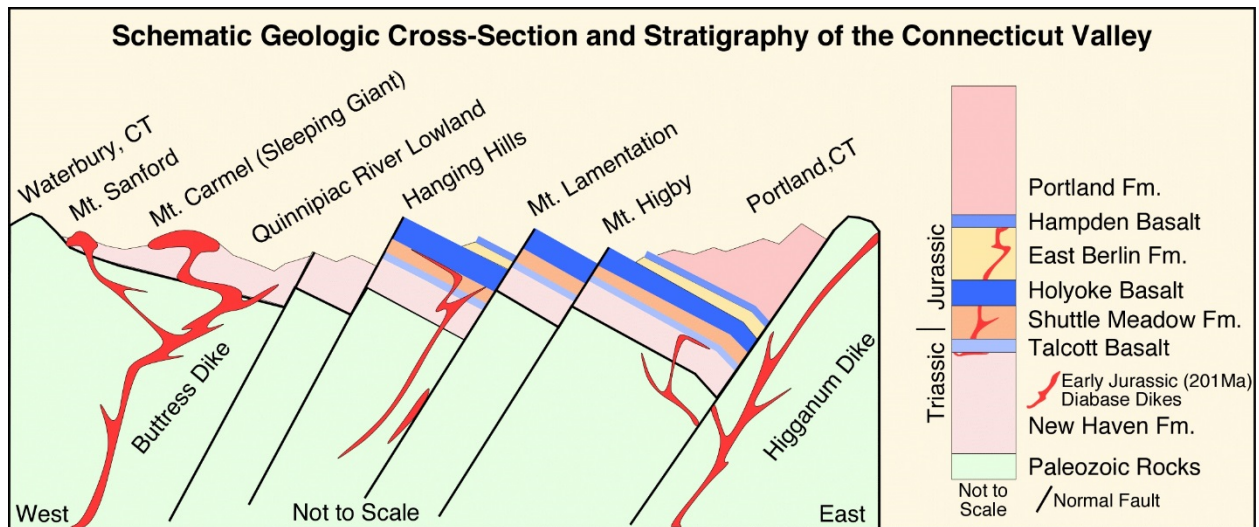


Figure 4. Schematic cross section of the central Connecticut Valley. Not to scale.

The Connecticut Valley is one of a large suite of similar Triassic-Jurassic age rift basins found along the eastern margin of North America, in Greenland, the British Isles, the Iberian Peninsula, and Morocco. Formed during the early stages of the breakup of Pangea, the rifts date from about 230 Ma to 180 Ma, plausibly comprising the largest known rift system on the planet. The depositional environments in the Connecticut Valley include braided and meandering rivers, alluvial fans, playas and salt flats, and perennial lakes. In vertical sequence, the depositional environments are organized into facies associations formed under the cyclic alternation of humid and arid climatic conditions (Fig. 5).

Asymmetrical subsidence localized the deepest portions of the basin adjacent to the fault-bounded eastern margin. The border fault consists of several segments that coalesced as subsidence continued. Relay ramps formed between fault segments in Durham, Glastonbury, and Manchester, Connecticut. There, large alluvial wedges prograded into rift lakes from southeast to northwest to form broad littoral shoals, such as those at Dinosaur State Park.

Lacustrine black shale units invariably thicken toward the eastern basin margin where they intercalate with coarse littoral and alluvial fan deposits (LeTourneau, 1985). Footwall uplift resulted in short, steep drainages feeding small basin-margin alluvial fans. The presence of a few larger alluvial fan complexes may be a result of the capture of established antecedent drainages, or their location at breached footwall drainages near overlapping segments of basin-margin normal faults. This paleogeographic model for the Hartford Basin is supported by studies of modern rifts in Death Valley and East Africa, and structural models based on modern and ancient rifts, which suggest that extensional terranes share a similar tectonic framework.

Syn depositional tectonics and periodic climate variability exerted primary control on sedimentation. Alternating “wet” and “dry” paleoclimate conditions resulted from periodic changes in the shape of Earth’s orbit, axial precession, and amount of axial tilt (Olsen, 1986). Termed “Milankovitch cycles”, orbital variations overprinted the tectonic framework creating a predictable pattern of alternating arid and humid facies (e.g. Olsen, 1986; Olsen et al., 2005; Kent and Olsen, 2008).

basic phalangeal formula correct (Bakker, 2015). Lull (1915, 1953) followed Hitchcock (1862) and argued that the pads were mesarthral in position (pads centered between the joints) in Connecticut Valley tracks, even though the former noted that pads are generally arthral in lizards. Heilmann (1926), Peabody (1948), and Baird (1957), supported the idea that most Triassic-Jurassic tracks had arthral pads, and Padian and Olsen (1984) showed that the pads of the Komodo Dragon are arthral. Olsen and Baird (1986), Olsen et al. (1998), Olsen and Rainforth (2003), and Rainforth (2003) followed the arthral pad position. However, recent workers (Smith and Farlow, 2003; Milan, 2006; Hone et al., 2009) note that ratites do not show consistent relationships between pads and phalangeal articulations. Further, relationships between pads and phalangeal articulations have been noted to vary between taxa, individuals of a species, and between digits of a single foot.

Functional and cladistics considerations, however, do allow some useful generalizations for reconstructing osteology from tracks. Observations on the hand and foot of *Homo sapiens* are relevant. As noted by many, the pads of our hands are strongly mesarthral, the mechanical advantage of which is clear. In flexion, there must be room for the fingers to close, pads in an arthral position make that difficult. Conversely, our knuckles have pads, and in knuckle-walking apes they are very well-developed, the functional significance of the pads being protection of the joints. Our manual proximal phalanges on digits II-V have two pads with a crease at the metacarpal-phalangeal joint, while digit I has but one on the proximal phalanx. Our feet, however, have large pads on the plantar surface below our metatarsal phalangeal joints (as well as a sesmoid bone), which are subject to extreme hyperextension, and the distal joints of digits II-V have an underlying pad that also contains the ungual, but a crease under the penultimate phalanx.

A simple hypothesis relating pad position to function is that pads have an arthral position in joints subjected to load-bearing in hyperextension and mesarthral in joints subject to flexion, with a similar rule applying to the dorsal surface. Where phalanges are short or the digits are subject to little flexion, they can be expected to be underlain by coalesced pads (Fig. 6). This model for arthral pads is primitive for the Dinosauria and is supported by the cladistics analysis and preserved soft tissue in the Cretaceous theropod *Concavenator* (Cuesta et al., 2015).

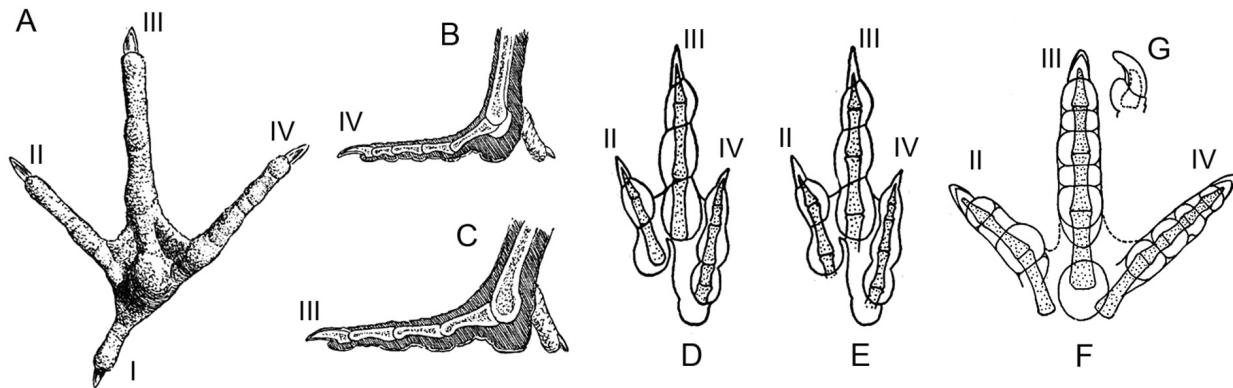


Figure 6. Pad vs. articulations (joint) positions in Galliformes (chickens, turkeys, etc.) and interpretations of their relationships in *Grallator*, all arranged to be appear as a right foot. A: Sole of chicken (*Gallus gallus*) left foot – swellings are the pads and underlie the joints (arthral position). B: Longitudinal section of a chicken digit IV – note arthral position of pads under phalangeal joints. C: longitudinal section of a chicken digit III– note pads under joints. D: Right *Grallator cursorius* footprint (Lull, 1904) from the Connecticut Valley, with joints reconstructed in mesarthral (between the joints) position. E: Same, with joints reconstructed in arthral position. F, right turkey (*Meleagris gallopavo*) foot showing arthral pad position. A-C from Heilmann (1926), flipped; D-G from Peabody (1948) with D and E flipped.

Primitively, within amniotes, the length of non-ungual bones distal to the carpals and tarsals tend to decrease distally, a feature we inherited. This primitive condition is also retained by crocodylians, the Komodo monitor, and early dinosaurs, in both hand and foot. However, many later Jurassic and Cretaceous dinosaurs deviate from this pattern, especially in the manus, seem most strikingly with the apomorphies in the manus of the Paraves. Significant deviations from the primitive condition in the pes in ratites in which distal, non-ungual phalanges of digit IV tend to be short and subequal. Unsurprisingly, the shortened phalanges of digit IV in ratites tends to be underlain by a single pad, while the pads on the hyper-extending digit III are strikingly arthral. As mobility decreases, this hypothesis suggests a large pad should encompass more bones. Conversely, *Gallus* (chicken) retains a mostly primitive condition (apart from the avian fused metatarsus and rotated first toe, or hallux).

Thus, the primitive condition in dinosaurs is to have a pedal phalangeal formula of 2, 3, 4, 5 for digits I, II, III, and IV. As in *Gallus* the primitive pedal plantar pads are hypothesized to be arthral and they are 1, 2, 3, 4 in number, one less than the number of phalanges. The condition seen in ratites, is a highly-modified condition that is not necessarily relevant for early Mesozoic dinosaurs, which likely retained the primitive arthral arrangement. This is supported by the strong consistency seen in Connecticut Valley track conventionally grouped in *Grallator-Anchisauripus-Eubrontes* plexus.

The currently recognized tetrapod footprint ichnogenera in the Valley are *Grallator*, *Anchisauripus*, and *Eubrontes*, *Otozoum*, *Anomoepus*, *Batrachopus*, *Rhynchosauroides*, and *Ameghinichnus* (Fig. 7), despite the huge number of names created from 1836 to 1865 by Edward Hitchcock and his son Charles. To this list of eight ichnogenera that we will use here, can be added a tetrapod burrow *Cynodonipus* (see Stop 1). Brontozoids, a term revived by Rainforth (2004, 2005) encompasses the currently familiar ichnogenera of *Grallator*, *Anchisauripus*, and *Eubrontes*, which were conceptually grouped in *Brontozoum* by Hitchcock (1847). These three facultatively tridactyl ichnogenera are characterized by having a low divarication angle, a short hallux that only rarely impressed; and a hand that never left a palms-down, or pronated, imprint. This in contrast to other major Connecticut Valley ichnotaxa. For example, *Otozoum* and *Batrachopus* both have a large digit I. *Anomoepus* has a long digit I, wide divarication, and pronate hand imprint. *Rhynchosauroides* is quadrupedal and digit IV is the longest on both the five-toed hand and foot. *Ameghinichnus* has 5 digits and is quadrupedal, but has toes that are almost equal in length and hands and feet almost equal in size.

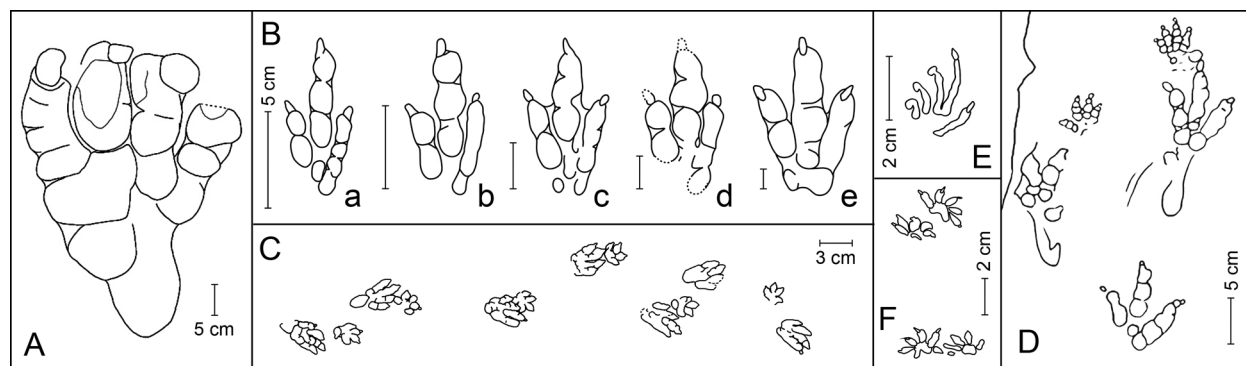


Figure 7. Footprint ichnogenera of the Connecticut Valley. A: Holotype of *Otozoum moodii* ACM ICH 4/1a (from Rainforth, 2003). B: Brontozoid tracks; a, Holotype of *Grallator parallelus* ACM ICH 4/1a; b, *Grallator parallelus* ACM ICH 23/2; c, Holotype of *Anchisauripus sillimani* ACM ICH 4/6; d, Holotype *Anchisauripus tuberosus* (partly reconstructed) ACM ICH 39/1; e, Holotype of *Eubrontes giganteus* ACM ICH 15/3 (a-c, e from Olsen et al., 1998); d, from Olsen et al., 2015; scale is 5 cm for all). C: *Batrachopus deweyii* ACM ICH 26/5 (from Olsen and Padian, 1986); D: Holotype of *Anomoepus intermedius* (= *A. scambus*) ACM ICH 48/1 (from Olsen and Rainforth, 2003); E: *Rhynchosauroides* sp., unnumbered Beneski Museum specimen collected by Shepard; F: *Ameghinichnus* sp. Dinosaur State Park specimen (original).

As has long been noted (Lull, 1953; Olsen, 1980; Olsen et al., 1992) *Grallator*, *Anchisauripus*, and *Eubrontes* ([2]) form a continuum with small tracks having a relatively longer digit III, and larger forms having a shorter digit III (Fig. 7). This suggests they should all be grouped into a single ichnogenus, because none are objectively diagnosable from the others, even in exceptionally preserved material with skin imprints. Regrettably, the name *Brontozoum* was regarded as invalid by Hay (1902) and suppressed by Baird (1957) in favor of *Eubrontes*. No one seems to want to call the generally diminutive *Grallator* a *Eubrontes* (which would be taxonomically and formally correct), and thus, Rainforth's term brontozoid is very useful.

Based on an arthral model of pad positions, brontozoid tracks (*Grallator*, *Anchisauripus*, and *Eubrontes*) were made by theropod dinosaurs, whereas *Otozoum* was produced by a basal sauropodomorph, informally and more familiarly called a "prosauropod" (see discussion at Stop 1). The *Anomoepus* trackmaker was a basal non-heterodontosaurid ornithischian, and *Batrachopus* was made by a protosuchian or sphenosuchian crocodylomorph (see discussion at Stop 1). *Rhynchosauroides* was made by lepidosauromorph (lizard, sphenodontian, or choristrodian), and *Ameghinichnus* was made by a mammalian synapsid (tritylodontid, trithelodontid, or mammaliaform such as a mammal). Discussion of these ichnotaxa and their trackmakers are found in Baird (1957), Rainforth (2003), Olsen (1988), Olsen et al. (1998), Olsen and Padian (1986), Olsen and Baird (1986), Olsen and Rainforth (2003).

There are probably only six valid ichnotaxa in the latest Triassic and Early Jurassic strata of the Connecticut Valley that are diagnosable by features resulting from the trackmakers' anatomy. This contrasts with the hugely inflated number names applied to the tracks in the Hitchcock collection in the Beneski Museum. Part of this situation is due to what was a typological approach to the tracks with no attempt to distinguish between differences in track form due to growth, individual variation or to extramorphological processes such as the interaction of the foot with the sediment as we shall see in the Beneski Museum at Stop 1. While the variations caused by extramorphological processes do not help us with identifying the trackmaker, they do tell us a lot about how the animals moved, again a major theme of Stop 1.

A major conclusion that can be drawn from the footprints is that at higher taxonomic levels the terrestrial communities were of low diversity, basically mostly small to large carnivorous theropod dinosaurs that appear to have been the most common forms, abundant small crocodile relatives (fully terrestrial forms); some herbivorous small ornithischian dinosaurs, and some medium sized to fairly large herbivorous prosauropod dinosaurs, and a few lizard- and mammal-like forms. This low diversity at high taxonomic levels might mask much higher species-level diversity that we have as yet no clear way to gauge. What is known is that these post end-Triassic extinction ichnological assemblages are much lower in diversity at high taxonomic levels than those that existed before the mass-extinction (Olsen et al., 2002). The apparent numerical dominance of carnivores that seems to be a violation of the basic trophic or Eltonian pyramid may be real. The base of the food chain may have been largely aquatic as we will discuss at Stop 2 and 5, the carnivorous dinosaurs may have primarily subsisted on fish and other carnivores that ate fish. Track assemblages from later Jurassic deposits have much more abundant herbivores suggesting the recovery to a more "normal" looking terrestrial community with more herbivores than carnivores.

2. Note that in the discussion that follows, the figure above, and at the field stops, specimens in the original Hitchcock collection of the Beneski Museum of Natural History will be referred to by the old AC numbers that appear as fractions, e.g., ACM ICH 15/3, the holotype of *Eubrontes giganteus*.

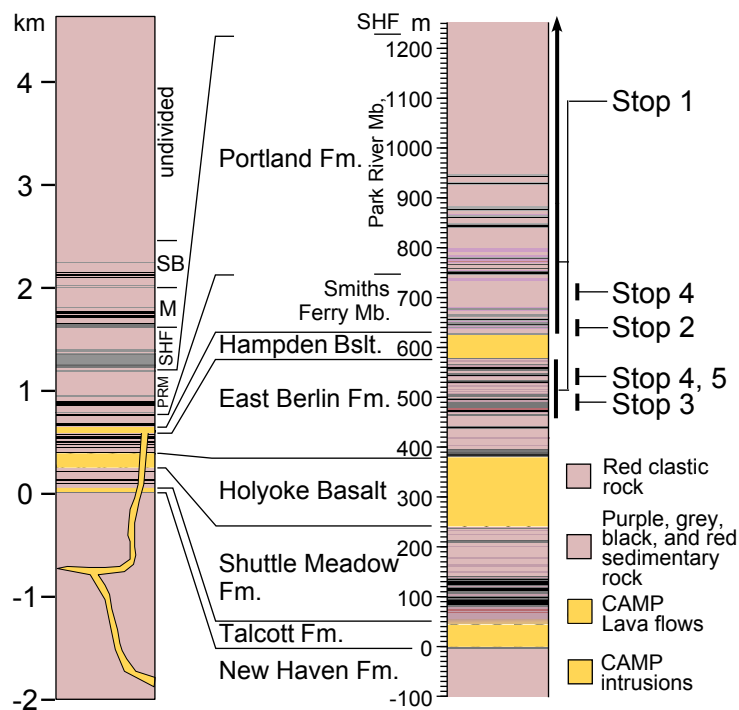
FIELD TRIP STOPS (PEO)

The field trip stops visit museum collections predominantly from localities or sedimentary strata of overwhelmingly Early Jurassic age from the Hartford and Deerfield basins (Fig. S1.1). While all of the outcrops (Stops 2, 3, 5) we will visit are within the Hartford Basin (Figs. 1, S1.1), many of the specimens in the Beneski Museum (Stop 1) are from similar age strata of the Deerfield Basin. The cyclical lacustrine strata, paced by Milankovitch climate cycles, of the latest Triassic-Early Jurassic strata of the Hartford Basin provide not only a guide to the changing climate of the basin, but also a metronome for telling time and a stratigraphic framework for precisely locating our field stops and specimens relative to each other (Fig. S1.1).

Stop 1: Beneski Museum of Natural History, Amherst College (PEO)

Edward Hitchcock originally housed his collection of trace fossils in a building called the Octagon and then moved it to Appleton Cabinet, built specifically for the collection, in 1855. In 1925, the collection was moved into storage in the basement Geology-Biology Building where it was nearly inaccessible, and then in the 1940s into the basement of the Pratt Museum, formerly the Pratt Gymnasium and now a dormitory. The ichnological collection was in the so-called “tombstone room” of the Pratt where the tracks were mounted on the walls and on, and in, handsome if difficult wood cabinets, all of which were unfortunately lit by hanging ceiling lights that made most of the tracks practically invisible without accessory illumination. In 2006, the collection was moved into its current location in the Beneski Museum, with excellent lighting and clever sliding panels allowing access to both sides of many slabs. It is the finest collection of dinosaur and other footprints in the World.

We will view the Hitchcock collection four phases: 1) a self-guided general tour of the museum, which will not be detailed here; 2) an examination of what were interpreted as footprints made by taxa



with thin toes, the *Leptodactyli* of Hitchcock, and are now known to record dinosaurs in motion; 3) an in-depth look at some of the most remarkable specimens in the collection that illuminate our knowledge of kinds of animals that produced the tracks, and 4) a look at trackways of aquatic insects and fish in the Hitchcock Collection.

Figure S1.1. Stratigraphy of the Hartford Basin (left) and detail of mostly the zone of extrusives (CAMP lavas) showing the main locations of the material in Museum collections (Stops 1, 4) and outcrops and exposures (Stops 2, 3, 5). Abbreviations are: M, Mittinegue Member; PRM, Park River Member; S, Smiths Ferry Member; SHF, South Hadley Falls Member; SB, Stony Brook Member.

Remarkable specimens in the Hitchcock Collection (PEO)

Most of the footprints in the Hitchcock collection are located in the “Dinosaur Hall” and the “Hitchcock Ichnology Collection” room. The latter is arranged as a series of galleries surrounded by walls, all of which have slabs on exhibit (Fig. S1.2). We will examine a number of key specimens that illustrate the ichnological record of the major groups of tetrapods present located at specific stations along a path that begins in Dinosaur Hall and weaves through the galleries of the Hitchcock Ichnology Collection.

Station 1: Eubrontes giganteus: Dinosaur Hall East (PEO). ACM ICH 15/3, preserved as a natural cast, is the holotype of *Eubrontes giganteus*. It is normally housed in the type room, but is out for our viewing. The taxonomic history of this specimen, summarized here, is given in Olsen et al. (1998). Hitchcock believed that this track was made by a bird. This specimen appeared in William Buckland's Bridgewater Treatise VI in 1836 and in Hitchcock's 1841, 1848, and 1858 works. It, along with the other tracks Hitchcock described, caused a sensation on both sides of the Atlantic and he was criticized due to the tracks' implications for biblical interpretation.

ACM ICH 15/3 was the first dinosaur footprint to be formally described and named (Fig. S1.3). In 1836 Edward Hitchcock named this specimen *Ornithichnites giganteus* and stated that he found this specimen in a quarry on the East side of Mount Tom along the Connecticut River after seeing flagstones from that quarry in Northampton bearing tracks. This locality is almost certainly Dinosaur Footprint Reservation in Holyoke (Stop 2) where we will see similar tracks. According to Hitchcock (1865), it was both the first specimen of the ichnospecies found and also the "original type of the ichnospecies." Thus, ACM ICH 15/3 must be the holotype (single specimen upon which a species is based) of *Ornithichnites giganteus* by original designation. Its status as holotype has been affirmed by Baird (1957) and Olsen et al. (1998).

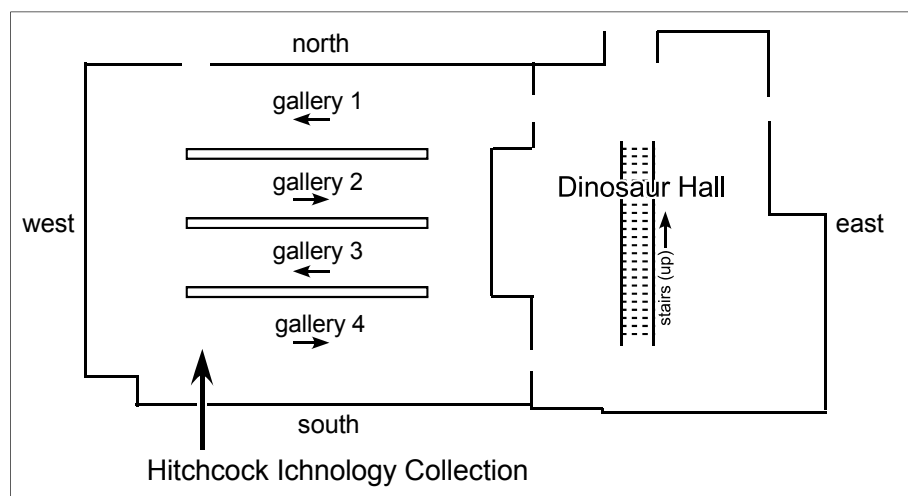


Figure S1.2: Map of the Dinosaur Hall and Hitchcock Ichnology Collection. Arrows below the gallery names show the direction of travel, beginning in the Dinosaur Hall and passing through the north door into the Ichnology Collection.

Although 15/3 was unambiguously established as the type of *Eubrontes giganteus* in 1836, C. H. Hitchcock replaced ACM ICH 15/3 with ACM ICH 45/8 as the type in Hitchcock's (1865) posthumously published "Supplement to the Ichnology of New England". This was based on the idea that 45/8 conformed more closely to his father's concept of the ichnospecies because the newer specimen has thicker toes. This was done despite the fact that the specimen was not collected until nearly 29 years after the ichnospecies was named (Hitchcock, 1865:23). This erroneous designation of ACM ICH 45/8 as the type specimen was perpetuated (e.g., Lull, 1953) until 1998 (Olsen et al., 1998). A nearly disastrous consequence of the misidentification of this historical gem occurred when the Boulder, Colorado headquarters of the Geological Society of America was built in 1972. The Pratt Museum sent ACM ICH 15/3 to the new headquarters on permanent loan and it was built into a wall. It returned to Amherst in 1997.

In 1836 Hitchcock established the name *Ornithichnites* (literally "stony bird tracks") as a name for fossilized bird footprints, rather than for the trackmaker. In 1841, Hitchcock changed the name to *Ornithoidichnites* to reflect the concept that they were bird-like tracks, and in 1845 he used *Eubrontes* for the *O. giganteus* trackmaker. Thus, *Ornithichnites giganteus* became *Eubrontes giganteus*. However, for unknown reasons, Hitchcock never again used the name *Eubrontes* in print, substituting instead the name *Brontozoum* in 1847. Hay (1902) recognized that *Eubrontes* had priority over *Brontozoum* and regarded *Ornithichnites* as an invalid name because it was never intended to be the name of an animal. This interpretation was followed by all subsequent workers (e.g., Lull, 1953). Current practice, however, dictates that trace fossil names be kept separate from biological ones (Sarjeant and Kennedy, 1973). *Ornithichnites* is a valid senior synonym of *Eubrontes*, but because it has not been used for 170 years, it would cause disruption to substitute the latter name for the well-known and popular *Eubrontes*.

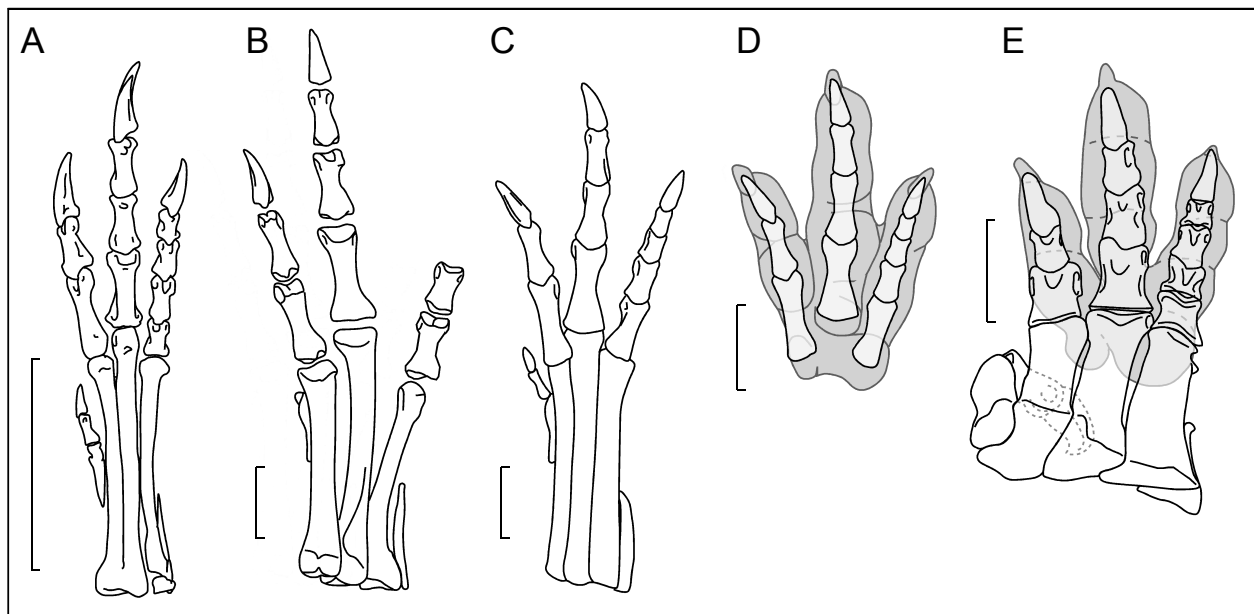


Figure S1.3. Osteological reconstruction and comparisons with osteological taxa of the holotype of *Eubrontes giganteus*, ACM ICH 15/3: A: right *Megapnosaurus* (*Syntarsus*) *rhodesiensis* foot (flipped from image of left foot, from Raath, 1969). B: *Dilophosaurus wetherelli*, right foot (flipped from original left in Wells, 1984). C: *Dilophosaurus wetherelli*, reconstructed right foot (flipped and corrected from photographs of UCMP V4214: <http://www.ucmp.berkeley.edu/dilophosaurus/closeup.html> as well as based on the complete right hind limb TMM 43646; <http://blogs.plos.org/paleocomm/2015/10/22/318/> as well as Wells, 1984). D: arthral-model reconstruction of *Eubrontes giganteus*, ACM ICH 15/3. E: right *Plateosaurus* foot placed in *Eubrontes giganteus* (flipped from Weems, 2003). Scale is 10 cm.

Although published details of the feet of Early Jurassic theropods are inadequate for detailed comparison with the tracks, the reconstructed foot skeleton of the *Eubrontes giganteus* trackmaker, assuming that the toe pads were directly below the toe bones (arthral pad model) is consistent with a theropod, and is indistinguishable from *Dilophosaurus wetherilli* (Fig. S1.3). That said, later Triassic and Early Jurassic theropod feet tend to be very conservative, with many apparent differences being indistinguishable from drawing inaccuracies and inconsistencies, parallax in photographs, and damage to specimens. Weem’s argument (2003) that *Eubrontes* (and *Gigantipus*) tracks were made by a “prosauropod” similar to *Plateosaurus* requires a nearly complete lack of correspondence between pad structure and osteology, which I regard as a very unparsimonious hypothesis (Fig. S1.3), given the apparent simple and excellent fit between the skeleton of *Dilophosaurus* and that reconstructed for *Eubrontes*.

The identity of the *Eubrontes* trackmaker has enormous implications. Considering that Olsen (1980) has shown a size dependent relationship between the brontozoid ichnotaxa *Eubrontes*, *Anchisauripus*, and *Grallator*, it would imply that all of these ichnotaxa were made by “prosauropods”. It therefore could imply there were no theropod footprints in the *Grallator-Anchisauripus-Eubrontes* plexus. Second, it would imply that “prosauropods” were the most common types of dinosaurs in Early Jurassic strata of Eastern North America (See stops 2 and 5). Finally, it would imply that *Otozoum* was not made by a “prosauropod”, which is also the most parsimonious hypothesis for the trackmaker of that ichnogenus (see below).

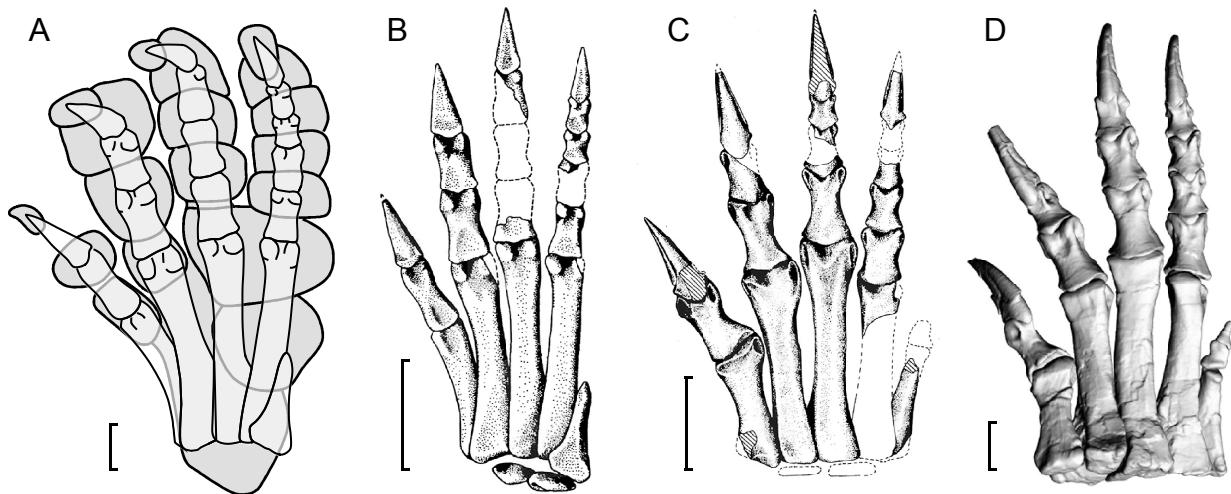


Figure S1.4. Comparison of the reconstructed left pedal skeleton, in bottom view, of *Otozoum moodii* with “prosauropod” feet that are flipped to make apparent digit order agree. A: Outline of *Otozoum* (from Rainforth, 2003) with superimposed reconstructed skeleton using the arthral model – note similarity to actual prosauropod skeletons (B-D). B: Flipped, plantar view of right *Anchisaurus polyzelus* foot (from Galton, 1976). C: Flipped dorsal view of right pes of larger *Anchisaurus polyzelus* (*Ammosaurus major*; from Galton, 1976). D: Flipped *Plateosaurus engelhardti* right foot (Late Triassic, Germany; from Mallison, 2010). Scale is 5 cm.

Station 2: Otozoum: Dinosaur Hall SE and gallery 1 north (PEO). *Otozoum moodii* (Figure S1.4) is one of the most impressive and enigmatic eastern North American footprints. Described and named by Edward Hitchcock in 1847, it is a large, nearly exclusively bipedal trace that is regionally rare, but locally fairly common in sandstone facies. It is known definitively only from post ETE strata, including the Portland Formation. Rainforth (2003) provided the most comprehensive treatment of *Otozoum*, including an analysis of possible trackmakers (Fig. 13, S1`4).

Rainforth's (2003) outline drawing (Fig. 13, S1.4) of the *Otozoum* foot allows the development of a hypothesis about the osteology of the trackmaker (Fig. S1.4). Assuming an arthral model to reconstruct the skeleton results in foot that is similar in proportion and formula to a primitive archosaur, except for the very reduced digit V. Such skeletal structure is seen in pseudosuchians, which is what led Olsen (1988) and Olsen et al. (1989) to interpret *Otozoum* as a "sphenosuchid crocodylomorph". However, this is wrong because crocodylomorph, feet have lost a phalanx in digit IV. Based on the number of pads, this specialized loss does not occur in *Otozoum*. The reconstructed foot is also very similar to that of basal grade non-sauropod sauropodomorphs, i.e., "prosauropods", such as *Plateosaurus* and *Anchisaurus*, the latter of which is known from the Portland Formation. Skeletal remains of "prosauropods" and definitive *Otozoum* are also known from the McCoy Brook Formation of the Fundy Basin (Sues and Olsen, 2015), and the Navajo Sandstone of the Glen Canyon Group (Lockley et al., 1999; Rainforth, 2003; Sertich and Loewen, 2010) in the Colorado Plateau region.

Referred *Otozoum* specimens, all from lower Portland Formation deposits at the Moody homestead, in South Hadley, MA, are on display in Dinosaur Hall. Examine the natural cast of single left foot imprint (ACM ICH 5/1) on the eastern side of the stairs (Fig. S1.2). It was figured by Hitchcock (1858, Plate 59). There is a lot of plaster on it but its form is representative. The track is distinguished from other large Connecticut Valley ichnotaxa by having four digits. Three point forward (digits IV, III, and II) and one (digit I) points sideways. Although not clear in this specimen, the number of pads decreases going from outer to inner toes. There is a large posterior pad that connects digits IV and III, and a rear pad that is interpreted as underlying digit V. Much better are the natural casts of a trackway in gallery 1, at station 2.

Pulled out from the cabinets in Dinosaur Hall will be the only *Otozoum* with hand imprints, ACM ICH 5/14, which is preserved as a natural cast. This slab was already broken when it was on exhibit in the Pratt Museum. The *Otozoum* are impressed on a surface trampled by small brontozoid tracks. Two *Otozoum* pedal tracks, both made by the right foot, are on the slab. There are two candidate hand imprints on either side of the anterior foot imprint. I initially interpreted these hand imprints as superimposed brontozoid (grallatorid) footprints (Olsen et al., 1992) because I thought that *Otozoum* was made by a prosauropod, and because I thought that hand traces were incompatible with then-current interpretations of sauropodomorphs (Farlow, 1992). I have since been swayed by Rainforth's (2003) arguments that the tracks are hand tracks because the left and right prints are mirror images that are symmetrical about the midline, and because there are no other brontozoid prints as large on the slab with *Otozoum* from this locality.

Several features are obvious in the hand traces. First, four digits are present (Rainforth, 2003), not five as suggested by Hitchcock (1858), Lull (1904), and others. Also, the medial-most digit is actually pedal digit II of the superposed right foot imprint. Second, there is no trace of large claws, or perhaps no claws at all. Third, the most posterior digit trace present is represented by an ovoid pad. Unfortunately, the hand traces are obscured by intersecting brontozoid tracks, as well as one of the *Otozoum* pedal tracks, and there is damage to the highest-relief natural casts by chiseling. Pads are obscure and only the general outline seems reliable.

In Figure S1.5 the outlines of the two hand imprints are superimposed, drawn, and averaged to provide anatomical information. What could be interpreted as small claw marks on the natural cast of the left manus are ignored, because such marks are not present on the opposite track. The result is not significantly different from the interpretation of Rainforth (2003), who interpreted the hand traces based on her composite (Fig. S1.5) as having the manus rotated outward, plantar surfaces pointing down and medially, with the digits directed approximately perpendicular to the trackway midline. Assuming a dinosaur made the track, she proposed that the manus print morphology was most consistent with a "prosauropod" hand, impressing digits II-V and holding the digit I off the ground. As she pointed out,

theropods are ruled out as making the hand imprints because they would make either tri- or didactyl imprints (see station 10). Further, I argue that Jurassic basal ornithischians are ruled out because they would have a pentadactyl hand imprint. The evidence again leaves only “prosauropods” as trackmakers.

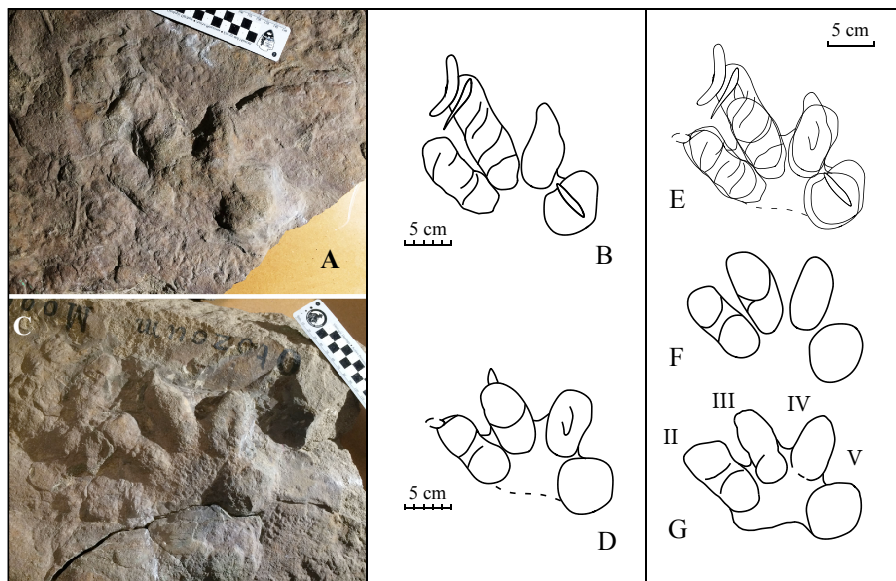


Figure S1.5. The *Otozoum moodii* hand, slab ACM ICH 5/14, and its composite form. A: Flipped natural cast of right hand, scale in cm. B: Outline drawing of A. C: Natural cast of left hand. D: Outline drawing of B. E: Superimposed outlines. F: Averaged outline. G: Composite from Rainforth (2003). Trackway midline towards bottom and lighting from lower right.

Reiss and Mallison (2014) argued that the Late Triassic prosauropod *Plateosaurus* had a hand that was incapable supporting the body in quadrupedal motion, and could serve only to stabilize the anterior body during feeding or drinking at ground level with laterally directed digits and medially facing palms. To the degree that Reiss and Mallison’s argument can be extended to other known “prosauropods” such as *Anchisaurus*, it agrees with Rainforth’s interpretation of *Otozoum*. The extreme pedal digitigrady in *Plateosaurus* (Mallison, 2010), however, is incompatible with *Otozoum*, because the *Plateosaurus* first digit would barely touch the ground, whereas in *Otozoum* digit I is almost completely impressed. This extreme digitigrady would bar “prosauropods” as an *Otozoum* trackmaker because non-sauropod sauropodomorphs have very similar feet. However, as noted before, the proportions of the pedal digits and the phalangeal formulae of non-sauropod sauropodomorphs is primitive at the level of Archosauria and such hypothesized digitigrady would require a much longer digit I than seen in any archosaur. Hence, whatever made *Otozoum* would have to have been an archosaur that walked with a much more plantigrade posture (as indicated by the occasional ankle imprint, Fig. S1.3). I conclude that the similarity in the proportions of the reconstructed pedal digits of and the phalangeal formulae of the foot, as well as the hand imprint, indicate that *Otozoum* was made by a “prosauropod” walking with a more plantigrade posture than *Plateosaurus*.

In summary, the primitive retention of a full complement of phalanges in pedal digit IV, the apparent raised and non-impressed digit I of the hand, the large size of the tracks, and proportional similarity to Early Jurassic sauropodomorphs such as *Anchisaurus*, makes the hypothesis that *Otozoum* was made by a “prosauropod” the most parsimonious hypothesis, given what we know of available Early Jurassic osteological taxa.

True undertracks on sandstone of *Otozoum* (ACM ICH 3/1) are on display here and on the second floor beneath the stairs. The layer comprising the slabs on display was below a few centimeters of mudstone that bore the true tracks of the slabs that crumbled away when the natural casts (ACM ICH 4/1

– Gallery 1N) were pried up. These are notable more for the length of the trackway they represent than for the details they preserve.

Proceed into gallery 1, heading west.

Station 3: *Otozoum*, Gallery 1 North (PEO). A series of *Otozoum* trackways, preserved as natural casts, are hung on the north wall of Gallery 1. ACM ICH 4/1a consists of four successive footprints, collected by Pliny Moody in 1847, and given to Hitchcock for his collection (Hitchcock 1865). The tracks are the holotype of *Otozoum moodii* Hitchcock 1847. They have been arranged with additional trackways, possibly of the same individual, but not demonstrably connected towards the west side of the north wall. The trackways are presumably the natural casts of ACM ICH 5/1, which we saw previously, although their exact relationship to ACM ICH 5/1 is unclear.

Station 4: *Sauropus (Chimera) barrattii*, Gallery 1 South (PEO). ACM ICH 20/4 is a sandstone slab with a thin red shale coat bearing a natural cast of a hand imprint that is the *Sauropus barrattii* holotype. The slab's history (see Olsen and Baird, 1986) is summarized below.

In 1837, Edward Hitchcock gave the name *Sauroidichnites barrattii* to a hand imprint found on a paving stone that was likely excavated from the Portland Brownstone Quarries, in the lower Portland Formation (upper Park River Member) at Middletown, Connecticut. Olsen and Padian (1986) illustrated the specimen. On the same surface are one fairly clear small footprint and two small, poor tracks of possible brontozoids, as well as at least one *Batrachopus* trackway. There is no obvious relation between the relatively large hand on the slab and the relatively small brontozoid-like foot traces. In 1841, Hitchcock redescribed and refigured the hand, and in 1845 he renamed it *Sauropus barrattii*, applying the name to the animal. Hitchcock referred the specimen to *Anomoepus* in 1848, and renamed it *Chimaera barrattii* in 1858. His son, Charles H. Hitchcock, for good measure, renamed it *Chimaerichnus barrattii* in 1871 because *Chimaera* was preoccupied by a genus of rat fish. Hay 1902 concluded that *Sauropus* was the correct name of this ichnogenus and that name was used by Lull (1915, 1953), as it is here.

This hand imprint closely resembles one of *Anomoepus*, but was conflated with the brontozoid tracks on ACM ICH 1/1, as we shall see at Station 10. Unfortunately, the tracks on ACM ICH 20/4 lack sufficient context for meaningful interpretation, and hence they are largely of historical importance because they are among the first tracks that Hitchcock had to assign to quadrupeds. Additionally, restudy of the specimen reveals that Hitchcock's (1858) concept of *Sauropus barrattii* is an unnatural composite of two ichnotaxa resulting in perpetuated factual and nomenclatural misinterpretations for nearly 150 years (Olsen and Baird, 1986). Lull's (1904, 1915, 1953) *Sauropus* rendering has been often reprinted and used as the basis of additional inferences about trackmakers, posture, and behavior. It has also formed the basis of the ichnofamily Sauropodidae (Haubold, 1969). This convoluted situation requires rectification. First, only the Middletown slab (ACM ICH 20/4) can be the holotype of *S. barrattii*, because it was the only specimen figured in 1836 when the genus was named. In support of this, C. H. Hitchcock (1858, p. 55) stated, "This is the true type of the genus and species *Chimaera [Sauropus]*..." Considering that *Sauropus barrattii* does not belong with any of the brontozoid-like tracks on the slab, the type is an isolated hand. Further, because it is so worn as to be indeterminate, Olsen and Baird (1986) regarded the ichnogenus and ichnospecies as *nomina vana*, rendering them invalid.

All the other specimens attributed to *Sauropus* by Hitchcock (1858) prove to be either very sloppy and indeterminate tracks (13/2, 13/14), good specimens of *Anomoepus* (37/9), or crouching brontozoids (see below). Therefore, *Sauropus barrattii* as envisioned by Lull (1904, 1915, 1953), as well as the ichnofamily Sauropodidae (Haubold, 1969), have no basis.

Turn left and U-turn into Gallery 2 heading east.

Station 5: Dino pedal pathology Gallery 2 North (PEO). Opposite *Cynodontipus* is an unnumbered slab with a brontozoid trackway comprised of two right footprints and a left. The two left footprints are deep, but lack a digit II and have peculiar posterior pads, whereas the left print has three digits and normal pads. This is a case where digit II was lacking, probably due to pathology, on the trackmaker's right foot. A similar case is seen on ACM ICH 23/2 (Station 12).

Proceed east to wall.

Station 5: *Cynodontipus* is a burrow, Gallery 2 South (PEO). On gallery two's southern rack are two part and counterpart slabs of red sandstone with red mudstone partings (BMNH UC 1-3), as well as some small slabs normally stored in cabinets that are out for viewing. The traces on the slabs are among the most peculiar in the Hitchcock collection, and they are conceptually new to North America. The slabs exhibit several *Batrachopus deweyii* trackways and a single medium-sized brontozoid, but most remarkable are a series of delicate, crescentic scratch-like traces assigned to the ichnogenus *Cynodontipus* Ellenberger 1976.

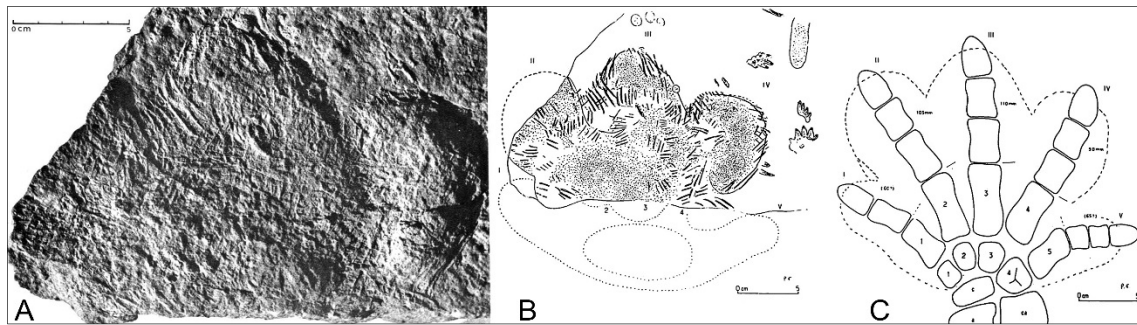


Figure S1.6. *Cynodontipus polythrix* from Ellenberger (1976). A: photograph of main slab from the Middle Triassic of Lodève, France. B: Interpretive drawing of A. C: Osteological reconstruction of right cynodont foot in the trace outline. Scale is 5 cm.

Cynodontipus polythrix, meaning “dog-tooth-foot with many-hairs” was named by Ellenberger in 1976 based on two slabs of Middle and Late Triassic age from France and Germany, respectively, that he interpreted as footprints of a hairy cynodont synapsid. These slabs have natural casts of multiple crescentic clusters of fiber or scrape-like impressions that Ellenberger reasoned were traces of hairy toes (Fig. S1.6). The French trace has been interpreted as a footprint and as evidence of hairy synapsids in the Middle and Late Triassic (e.g., Hunt et al., 1993; Lockley and Meyer, 2000; Kielan-Jaworowska et al., 2004; Silva et al., 2008).

However, analysis of more recently discovered material from the Late Triassic Fundy Basin of Nova Scotia, Canada (Fig. S1.7), Late Triassic of the Newark Basin, and Middle and Late Triassic of Morocco show that *Cynodontipus* is, rather than a footprint, a vertebrate burrow that terminates at a resistant subsurface bed interface, (Olsen et al., 2012; Sues and Olsen, 2015). Because the impenetrable interface was often a clay bed that was subaerially exposed prior to burial, there are often true footprints on the same surface intersected by *Cynodontipus*. The simplest hypothesis of the trace maker of *Cynodontipus* is that it was a produced by burrowing tetrapod. The only apomorphy visible in the traces are the scratch marks that appear to have been made by claws, and those are a plausible synapomorphy of the Amniota.

PEO first noticed two large part and counterpart slabs bearing *Cynodontipus* in the Hitchcock collection in the 1980s. However, there was no catalogue number on the slabs and no information in the Museum documents. At the time, PEO thought they might be feeding traces of the *Batrachopus* trackmaker, rather than a cynodont track, but no sensible geometric arrangement could be discerned. In 2004, however, a particularly informative specimen that revealed the true nature of *Cynodontipus* was

2004, however, a particularly informative specimen that revealed the true nature of *Cynodontipus* was found by Dr. Jessica Whiteside in the late Triassic Blomidon Formation (Sues and Olsen 2015) during a field trip led by PEO (Figure S1.7). The specimen could not be collected due to various factors, but slabs had multiple burrows resembling the systems reported by Voigt et al. (2011) from the Triassic of the Argana Basin in Morocco. The Blomidon Formation specimen also had clear *Cynodontipus*-type crescent-shaped scratch marks in positive hyporelief attached to the burrows, demonstrating their connection (Sues and Olsen, 2015).

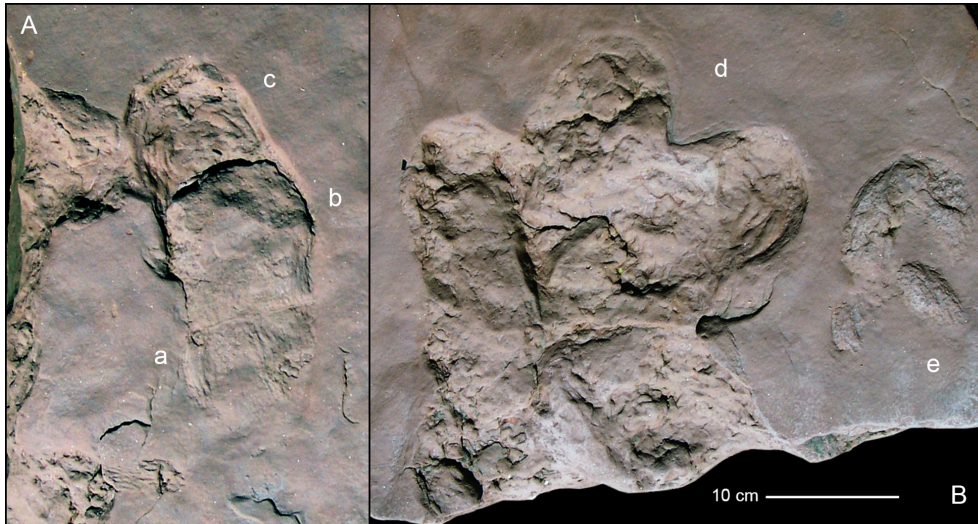


Figure S1.7. Slightly worn *Cynodontipus polythrix* burrow system from the Late Triassic Blomidon Formation of the Fundy Basin, Nova Scotia. A: Burrow fill: a, characteristic crescentic scratch marks of *Cynodontipus* where burrow intersected resistant bedding surface; b, 3-d burrow cast following bedding; c, upper surface of burrow visible where burrow fill has fallen out – note crescentic scratch marks on upper surface. B: same slab: d, lobed-appearing set of upper surfaces of burrows with crescentic scratches; e, two sets of *Cynodontipus* crescentic scratch marks. Scale for A and B is the same.

Also in the 1980s, PEO identified small slabs with clear *Cynodontipus*, *Rhynchosauroides* sp., and *Batrachopus deweyii*, some of which (BMNH UC 122, BMNH UC 116) were once attached to the larger slabs (BMNH UC 1-3). At the time, no locality data was found with the specimens. When the specimens were moved to the Beneski Museum, however, former Collections Manager Kate Wellspring found labels affixed to the back of a specimen (BMNH 60/26) that provided unambiguous locality and collector information. The label has a Hitchcock-like fractional number (60/26), although there are no specimens with numerators above 59 in Hitchcock's (1865) supplement, suggesting that the specimens were added close to or after his death. A handwritten paper label indicates that the specimen was discovered in 1864 by C.U. Shepard, an Amherst College mineralogist, and that it comes from a quarry on the east side of the Connecticut River in Turners Falls, Massachusetts. The other specimens probably came from the same locality based on similarity lithology and preservation style. Shepard's collection was purchased by the College in 1877 (Wilson and Fiske, 1888). In 1913, B.K. Emerson catalogued Shepard's footprint specimens (Rainforth, 2003), presumably adding Hitchcock-type numbers.

Based on the label, the *Cynodontipus* bed is in the early Hettangian (Blackburn et al., 2013) lower Turners Falls Formation of the Deerfield Basin, which correlates with the East Berlin Formation of the Hartford Basin and the Towaco Formation of the Newark Basin. The track assemblage is unique in the Connecticut Valley in having both *Cynodontipus* and *Rhynchosauroides*. PEO found *Cynodontipus* in the upper Park River Member of the Hartford Basin's Portland Formation in 2012, and *Rhynchosauroides* is known from some specimens in the correlative Towaco Formation (Olsen, 1988). That these specimens escaped mention is amazing, given that they likely were available to C. H. Hitchcock and Lull (1913, 1915, 1953).

Station 6: Noah's Raven Gallery 2 East (PEO). The tracks on ACM ICH 16/2 are the first footprints documented in eastern North America. Hitchcock (1836, p. 322) was aware of them, but he gave them only perfunctory mention (see section on Historical Context Appendix 1) until 1844 when he described his perspective on the dispute over who was first to understand the significance of the Connecticut Valley footmarks that developed between himself and James Deane. In this paper, he introduced the ACM ICH 16/2 specimen, apparently to diffuse the situation by documenting the discovery of tracks long before either he or Deane knew of them. Hitchcock states, "About the year 1802...Mr. Pliny Moody of South Hadley...then a boy, turned up with a plough upon his father's farm in that place, a stone, containing in relief five tracks of the *Ornithoidichnites fulicoides*...and it was put down as a door-step, because it contained tracks, and the neighbors used facetiously to remark to Mr. Moody, that he must have heavy poultry that could make such tracks on stone. After Mr. Moody (junior) had left home for school or college, Dr. Elihu Dwight of South Hadley purchased this stone, because it contained these tracks. It was retained by him nearly thirty years, when I purchased it for my cabinet, I think in 1839. Dr. Dwight used pleasantly to remark to his visitors, that these were probably the tracks of Noah's raven."

In 1858 and again in 1865, Hitchcock recounts that these were the first tracks to be found. He noted in 1858 added that they were then in his collection and assigned specimen number 16/2. In 1865, H. Hitchcock stated that ACM ICH 16/2 bears trackways that he called *Anomoepus minor* and *Ancyropus heteroclitus* (?). The nomenclatural history of ACM ICH 16/2 is very complicated, which is typical for Hitchcock's tracks. Olsen and Rainforth (2003) attempted to rectify this confusion and designated the specimen the lectotype of *Ornithoidichnites cuneatus* since it appears to be the only remaining specimen of three assigned to that species by Hitchcock 1841 (p. 488). However, the better of the two trackways on ACM ICH 16/2 is clearly *Anomoepus*.

Anomoepus is a bipedal, functionally tridactyl footprint less than 20 cm long that has a metatarsal-phalangeal pad of digit IV almost directly or directly in line with the axis of digit III in walking tracks (Olsen and Rainforth, 2003). This latter feature, visible in 16/2, is unique among early Mesozoic tracks. Further compared to brontozoids, Digit III is relatively short and the toes are widely splayed, which is also true of ACM ICH 16/2. Foot digit I (hallux) of *Anomoepus* is relatively long and often at least partially impressed, especially in sitting tracks. The latter is not evident, however, in ACM ICH 16/2. Of note, is that while the name *Ornithoidichnites cuneatus* has priority over *Anomoepus scambus*, *O. cuneatus* was never actually described and is therefore a *nomen nudum* (Olsen and Rainforth, 2003). Further, because name *Ornithoidichnites* had not been used since 1844, it should be considered a *nomen oblitum*. In any case, the type species of the latter is *O. (Eubrontes) giganteus*. Thus, the correct name for "Noah's Raven" is *A. scambus*.

Anomoepus are often found in a sitting posture with pentadactyl hand imprints, a fact that grieved Hitchcock since he wanted the bird-like tracks to be of bird origin. It is clear, however, that *Anomoepus* was made by an ornithischian similar to *Lesothosaurus* (see Station 13), below.

Turn right and U-Turn into Gallery 3, heading west.

Station 7: *Batrachopus deweyii* – crocodylomorph tracks, Gallery 3 North (PEO). ACM ICH 26/5 and 26/6, which are part and counterpart, exhibit fine examples of small quadruped tracks called *Batrachopus deweyii* (Fig. S1.8). The trackway on ACM ICH 26/5 and 26/6 is unusual in recording one foot imprint with digit I. As reconstructed using the arthral hypothesis (Olsen and Padian, 1986), the trackmaker's osteology is nearly identical to that of protosuchians and modern crocodylians. The pads number in *Batrachopus* suggests that digit IV had only four phalanges (instead of five), which is a

derived character for a clade including the Crocodyliomorpha. However, Olsen and Padian erred in showing a claw on hand digit IV in *Batrachopus* and *Alligator*. Modern crocodylians do not have claws on hand digits IV or V. Protosuchian crocodyliiform crocodyliomorphs are only one of three non-dinosaurian archosaur groups, including the sphenosuchian crocodyliomorphs and petersosaurs, to make it through the end-Triassic extinction. Protosuchian skeletal remains are the most common archosaurs found in eastern North America, and include *Stegomosuchus longipes* from the upper Portland Formation of the Hartford Basin, *Protosuchus micmac* from the McCoy Brook Formation of the Fundy Basin (Sues and Olsen, 2015), and undescribed material found by PEO in the Feltville Formation of the Newark Basin.

ACM ICH 26/5 and 26/6 earlier called *Sauroidichnites*, which is the type species of the ichnogenus, but the name *Batrachopus* was intended to replace this older name and was meant to name of the trackmaker. The type specimen of *Sauroidichnites deweyi*, ACM ICH 41/51, is from Turners Falls (Turners Falls Formation) and was figured by Hitchcock in 1843 (Pl. XI, fig. 9). It was thought lost by Olsen and Padian (1986) only to be rediscovered by PEO in 1995. Hitchcock states (1841), “Shown of the natural size on Pl. XI, f. 9, copied from the only specimen I have seen.”, and then, “...this is the first example in which I have any certain evidence that any of the numerous tracks upon the sandstone of the Connecticut valley were made by a quadruped...”. This specimen must be the holotype by original designation. Hitchcock later (1848) added a still better specimen to the list of assigned specimens (26/10: old No. 136) from Field's Orchard, Turner's Falls. That specimen is on the opposite wall of this gallery. Hitchcock (1858) listed ACM ICH 26/5 and 26/6 as *Batrachopus (Anisopus) deweyi*, and they were incorrectly listed Lull (1904, 1915, 1953) and accepted by Olsen and Padian (1986), as the type of the ichnospecies. Although Hitchcock (1858) did not record their locality, Olsen and Padian (1986) concluded that the matrix looks like East Berlin Formation from near Stop 3.

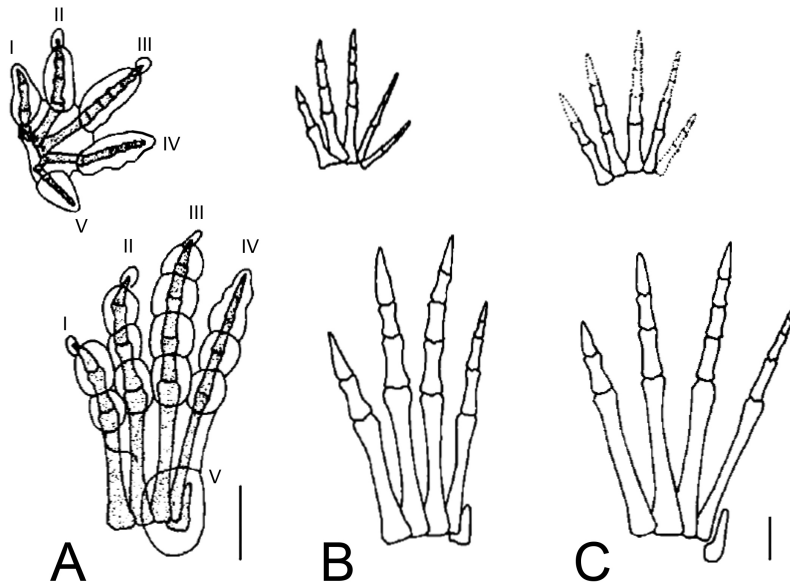


Figure S1.8: *Batrachopus deweyi* and comparison to crocodylians (slightly modified from Olsen and Padian, 1986). A: Composite of right hand-foot set of ACM ICH 26/5 with reconstructed skeleton. B: *Alligator* sp. hand and foot (from Romer, 1956). C: *Protosuchus richardsoni* hand and foot (from Colbert and Mook, 1951). Scale is 1 cm. All drawn as right hand-foot sets.

Station 8: Tales of feathers I - *Gigantipus caudatus* Gallery 3 North (PEO). ACM ICH 9/10 is a large trackway of Hitchcock's ichnospecies *Gigantipus caudatus*, discovered by Roswell Field at the Lily Pond on his farm. It is from the middle Turners Falls Formation. This slab illustrates two important features relevant to theropod postures and gaits and presence or absence of feathers or protofeathers (Fig. S1.9). Unlike *Eubrontes giganteus*, *Gigantipus caudatus* has a tail trace and normally has an imprint of digit I. As Weems (2003) argues, *Gigantipus caudatus* is best interpreted as a variant of *Eubrontes giganteus* that differs from typical examples because of differing behaviors that affected the degree to which the trackmakers were or were not walking fully on their toes. PEO would add also that the inclination of the body axis would also vary.

The tail drag is relevant to the identification of feathers in showing a series of small to large chevrons around a central groove, pointing in the direction of motion (Fig. S1.9). These are identical to the doubly ruffled grooves found in flysch (Craig and Walton, 1962) that are made as current-dragged tools crumple the surface of cohesive films like microbially-bound mud (Dzuynski and Walton, 1965). Such a tool mark appears feather-like although they are inorganic. Similar marks, present in ACM ICH 1/7 (station 11), have been interpreted as theropod feather imprints.

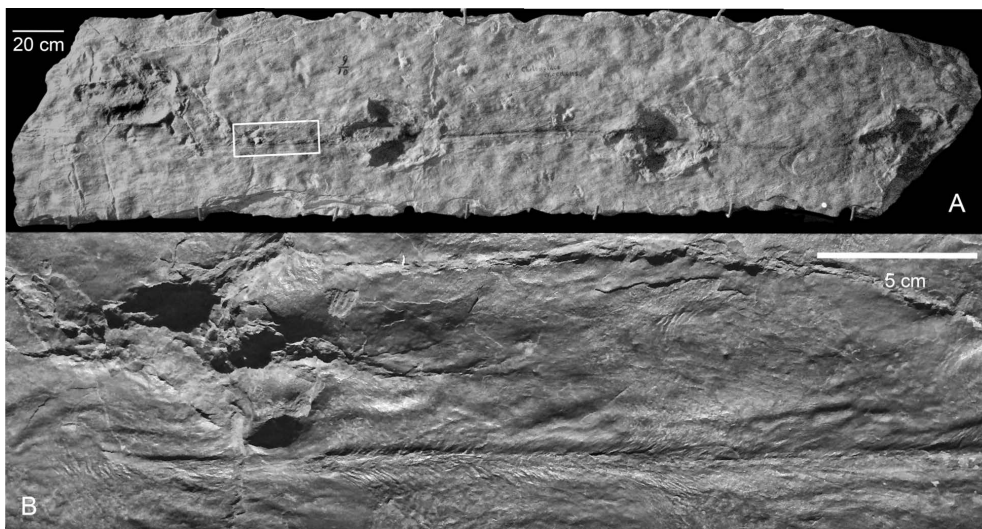


Figure S1.9: *Gigantipus caudatus* (ACM ICH 9/10). A: trackway overview. Note distinct hallux imprints and tail drag. B: Detail of white box in A showing tail trace with doubly ruffled grooves superficially resembling feathers.

Station 9: Tales of feathers II - Ænigmichnus multiformis Gallery 3 North (PEO).

Ænigmichnus multiformis (ACM ICH 51/15: counterpart on right [North] side of entrance to the Hitchcock collection) is a slab with many grooves and chevrons. These are tool marks caused by sticks or other objects dragged along the bottom by currents. The doubly ruffled grooves of various scales again require a cohesive microbially-bound film, which is relevant to Station 11.

Station 10: Sauropus redux: Theropod sitting trace – (PEO and MW) Gallery 3 South.

ACM ICH 1/1 is a large slab covered with various sized brontozoid trackways. It was excavated from Roswell Field's Orchard, in Gill, Massachusetts and procured at Dexter Marsh's auction in Greenfield in 1853. One trackway is of an animal in a sitting position (Fig. S1.10). This crouching trace, along with the similar ACM ICH 1/7, has produced much confusion. As with so many of the classic specimens, the taxonomy of this specimen is complicated and several very different ichnotaxa were conceptually conflated in the process (see Olsen and Rainforth, 2003). In 1843, Edward Hitchcock established *Ornithichnites lyellii* for an isolated, medium-sized track on ACM ICH 31/85, which came from the Turners Falls Sandstone of Turners Falls, Massachusetts. We would now call this track *Anchisauripus*. In succession, he renamed the track *Fulicopus lyellianus* (1845), *Aethyopus lyellianus* (1848), and *Amblonyx lyellianus* (1858). Hitchcock (1858) referred the trackways on ACM ICH 1/1 to *Amblonyx lyellianus* too. Both specimens were designated types of *Amblonyx lyellianus* by Hitchcock in 1865. The crouching trace on ACM ICH 1/1 was, however, referred to the ichnogenus *Anomoepus*, giving it and another specimen (ACM ICH 1/7) the new specific name *Anomoepus major* (see below Station 11).

Hitchcock interpreted this trackway as if it were the standard *Anomoepus* sitting pose because he thought he could see two parallel hand-foot sets and two "heel" imprints posterior to the footprints, and because of the presence of a more posterior and central "ischial" imprint. This was important because he

was clinging to near-correct idea that brontozoids were birds, but if this specimen had hands it must instead be a bird-like forms, such as *Anomoepus*. Figure S1.10 traces how this interpretation evolved. Hitchcock (1858, plate 8) provided a line drawing (Figure S1.10B) in which the left foot is drawn with dashes, except for two small circular depressions. Both hand imprints were drawn with solid lines and were based on Hitchcock's (1837) rendering of *Sauropus barrattii* (see Station 4). Only two irregular imprints are shown on his "Ambrotype sketch" (Hitchcock 1858, Plate 38; Figure S1.10A herein) where he drew the hand imprints, and only two small depressions are shown in the line drawing for the left foot. Lull (1904) traced the left half of Hitchcock's line drawing of ACM ICH 1/1, but turned the dashed lines into solid ones, labeling the illustration *Fulicopus lyellianus*. He reconstructed the trackmaker as similar to a sitting ornithopod and listed the type specimens of *F. lyellianus* as ACM ICH 1/1 and 31/85 (the latter only is the holotype). He correctly noted that the *Amblonyx lyellianus* left foot and the *Anomoepus major* left foot on ACM ICH 1/1 had the same deformity and, therefore, the same animal made them. Lull (1915) synonymized *Sauropus barrattii*, *Anomoepus major*, and *Amblonyx lyellianus*, the first having priority, and listed ACM ICH 1/1 and ACM ICH 1/7 as types. ACM ICH 31/85 was not mentioned. Lull (1953) retraced all of Hitchcock's (1858) *Anomoepus major* line drawings, again using solid lines, and repeated his previous opinion on the *Sauropus* synonymy and the supposed type specimens. He also provided a new trackmaker reconstruction (Figure S1.10).

ACM ICH 1/1 shows what are interpreted as a pair of hand imprints. This is a new interpretation that differs from that of Olsen and Baird (1986), in which PEO disparaged these marks as similar to other imprints on the surface. Additionally, what Hitchcock (1858) figured as the left "heel" of *A. major* is in fact a metatarsus imprint superimposed on a complete left foot of the same trackway (Fig. S1.10C, D, F-H). The two small imprints in front of the heel seem to be the only ones of the foot corresponding to that heel, as Hitchcock (1858) suggested. This is not unexpected in that birds, such as ratites, can often be seen sitting with metatarsi impressed but most or even all of one or both feet suspended above the ground (Fig. S1.10J). It is also possible for birds to rise from that position using only one foot and not impress the one that was suspended until the next step. The "ischial" imprint is faint and could conceivably be part of a foot imprint of a larger brontozoid on the same slab, but given its similarity to the genuine "ischial" imprint in (ACM ICH 1/7) it seems appropriate to retain it in its reconstruction (Fig. S1.10H, J).

Using the arthral hypothesis for joint reconstruction, the foot imprints of the sitting trackway on ACM ICH 1/1 fit the *Coelophysis* skeleton closely (Fig. S1.10H). They therefore confirm that these brontozoids are best interpreted as theropod tracks. The apparent hand imprints, however, pose a problem, as they did for Hitchcock. Gierlinski (1994) figured ACM ICH 1/1 (Fig. S1.10D) using my white water-soluble painted outline (unattributed) as a basis for his drawing of the tracks (Fig. S1.10E). He did not recognize the superimposed left metatarsal imprint and interpreted the apparent manus imprints as pointing forward, requiring hyperextension of the fingers and pronation of the hand, as Lull did (Fig. S1.10I). Lockley et al. (2003) also refigured ACM ICH 1/1, but left out the left foot imprint beneath the left metatarsal imprint, when supporting their symmetrical crouching interpretation. Regardless, the photographs without PEO's white lines show rather unambiguously that a left footprint occurs, although the crouch is also symmetric. Lockley et al. also appear to interpret the hand as pointing forward. As pointed out by Milner et al. (2009), however, for similar brontozoid tracks in the contemporaneous Moenave Formation of Utah, functional analyses of theropod forearms suggest that pronation of the hand was not possible (Carpenter et al., 2002; Senter et al., 2005). A much simpler interpretation is that the hand imprints were made by the dorsal surfaces of the subequal proximal phalanges of digits II and III (Fig. S1.10H). Reconstructed this way (but shown not flexed for simplicity), the hand imprints fit the *Coelophysis* skeleton perfectly. In a natural pose (Fig. S1.10J), the hand would be flexed with the palms pointing backward and medially, with only the knuckles of digits II and III resting on the ground. This pose matches both the preserved traces and the functional interpretations of a theropod hand. The result (Fig. S1.10J) is very close to the reconstruction by Milner et al. (2009). These are the most distinct theropod sitting traces known.

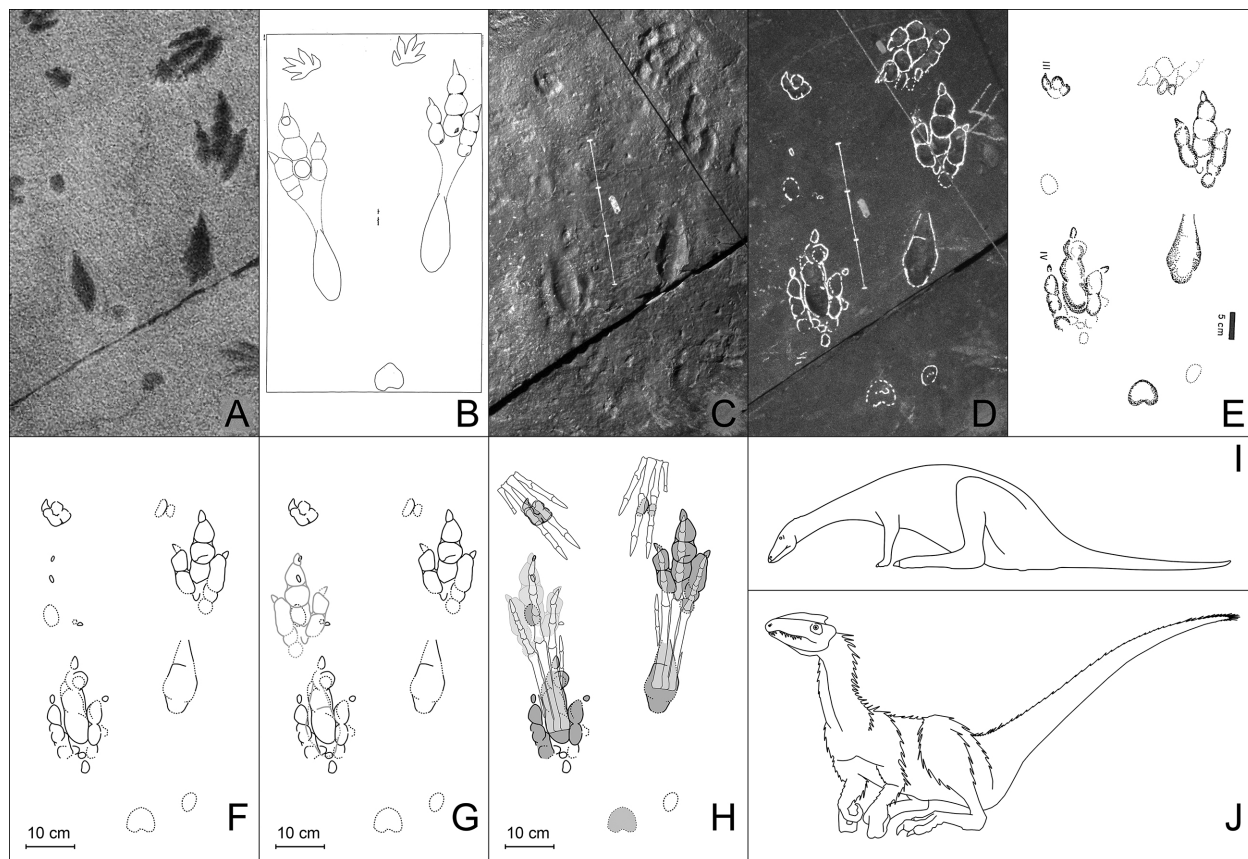


Figure S1.10. Sitting theropod trace ACM ICH 1/1. A: “Ambrotype sketch” of sitting trackway (Hitchcock, 1858). B: Drawing of same, with dotted lines for the left foot and solid lines for the conceptually derived hand (Hitchcock, 1858). C: photograph of the same area as in A and B. D: Photograph of same, with 1 tempura lines on track by PEO. E: Gierlinski’s (1994) drawing of D. F: Outline drawing of D by PEO. G: Same as F but with right foot (with metatarsal imprint) flipped and superimposed on left metatarsal imprint. H: Osteological reconstruction of hand and foot using the skeleton of *Coelophysis* from Colbert (1989) with modifications to the proximal metatarsal based on *Megapnosaurus* (*Syntarsus*) *rhodesiensis* (Raath, 1969) – note that hands would be flexed when resting with only the proximal phalanges of digits II and III in contact with the ground. I: Trackmaker imagined as a small ornithomimid (Lull, 1904), assuming a five-fingered hand. J: Trackmaker reconstructed as a theropod similar to *Megapnosaurus* (*Syntarsus*) *rhodesiensis*, with only the first two of knuckles of digits II and III on the ground.

Station 11: Tales of feathers IV - Theropod sitting trace ACM ICH 1/7 (PEO)

southwest corner. ACM ICH 1/7 shows a sitting dinosaur track with the anterior part broken off exactly where one would expect hand imprints. The slab is from the Lily Pond Quarry (C. H. Hitchcock in Hitchcock, 1865) at Barton Cove, in the middle Turners Falls Formation of the Deefield Basin. As already mentioned, this slab was conflated conceptually with both *Sauropus* and *Anomoepus*. C. H. Hitchcock (in Hitchcock, 1865) listed ACM ICH 1/7 as a cotype of *Anomoepus major*, but this specimen was not described until 1865, although it was mentioned in 1858. We agree with Gierlinski (1994) that ACM ICH 1/7 is brontozoid. This conclusion is supported by osteometric comparisons of Olsen and Rainforth (2003) and like ACM ICH 1/1 is one of the rarest of tracks - that of a sitting of theropod. Both metatarsal imprints are present along with an apparent ischial imprint.

In 1996, Gierlinski (followed by Gierlinski, 1997, 1998; Kundrát, 2004), presciently interpreted marks associated with the right footprint as imprints of a feathered belly of a sitting theropod. That same year, the first non-avian dinosaur with feathers, *Sinosauropteryx prima* (Ji and Ji, 1996; Gibbons, 1996)

was reported. Although the simplest feather distribution hypothesis has them present in dinosaurs and their close relatives in the clade Avemetatarsalia (ornithodira), the marks that look like possible feathers on ACM ICH 1/7 are better interpreted as produced by the interaction of the right foot with cohesive, microbially-bound mud. Martin and Rainforth (2004) argued that the marks were produced as “pressure-release structures caused by movement of the tracemaker after it rested.” PEO has a different interpretation that derives from the fact that the most prominent of the features are clearly “directed” towards the claws of digits II and IV of the foot. In fact, they resemble the “doubly ruffled grooves” seen on the tail trace of *Gigantipus caudatus* (Station 8) and on the *Ænigmichnus multififormis* slab (Station 9). As such they are best interpreted as drag marks of the claws and foot as they glided into position on microbially-bound mud. While agreeing with Martin and Rainforth (2004) that these traces are due to the interaction of the foot with the substrate and are not feather imprints, the present interpretation has the marks made in the opposite direction, with the foot going forward, not backward. It is difficult to separate the anatomy of the trackmaker from the shapes caused by the interaction of the trackmaker with the sediment – this reflects Baird’s 1st axiom of paleoichnology, “A footprint is not a static record of morphology, but a dynamic record of an animal in contact with a particular substrate under particular environmental conditions” (Padian and Olsen, 1989).

Turn left and head east into Gallery 4.

Station 12: Dinosaur displaying and pathology Gallery 4 North (PEO). *Antipus bifidus* is a very peculiar trace on slab ACM ICH 23/2 (Fig. S1.11B). *Antipus bifidus* is not at all the same kind of trace as *Antipus fexiloquus*, which is clearly a few small impressions of actual feet with toes, based on Hitchcock’s (1858) figures. Hitchcock (1858) states, “The name is *Antipus binfidus*; the first part meaning that the feet point in opposite directions, the second part meaning that the feet have two branches.” He

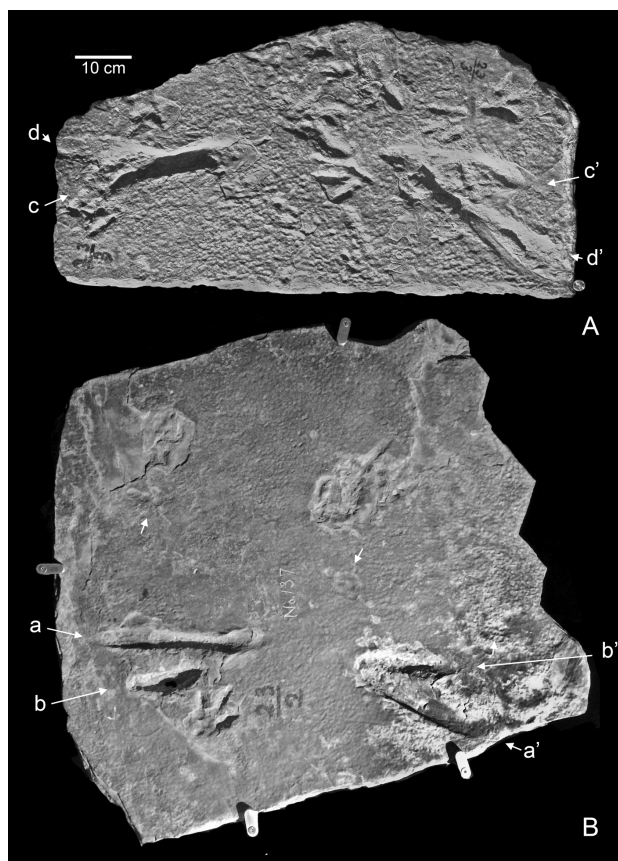


Figure S1.11. *Antipus bifidus*. A: ACM ICH 23/3. B: ACM ICH 23/2 (holotype). For explanation see text.

believed it was made by a giant lizard-like form with two giant toes on each foot that pointed outward. ACM ICH 23/2 is the holotype of the ichnospecies (C. H. Hitchcock in Hitchcock, 1865) and there is another somewhat similar specimen, ACM ICH 23/3, also from same source. Both slabs have associated *Anomoepus* and ACM ICH 23/3 has at least one sitting trace. ACM ICH 23/2 also has a trackway of brontozoid that is missing digit II on the right foot (small arrow on ACM ICH 23/2, Fig. S1.11) – another pathology similar to what is seen at Station 5, Gallery 2 North.

The symmetry of the traces seems to be rather different than Hitchcock thought. First, each groove appears to be a separate structure that shallows along its axis, away from its center (a, a'; b, b'; c, c'; d, d'": Fig. S1.11). Second, the longer traces on either side seem to be symmetrical to each other (a, a'; d, d'), as do the shorter traces (b, b'; c, c'). Additionally, longitudinal grooves occur in each trace. The simplest interpretation of these marks is that each symmetrical pair was produced by smoothly pushing the mud by symmetrically arranged limbs, each of which ascribed an arc in a plane nearly perpendicular to the ground and the mid-line. The only body parts that could move like this would be the forearms and hands of a bipedal tetrapod whose body was perpendicular to the long axis of the traces, with the hands closed (there are no clear digit marks). The trackway that bisects the grooves on 23/2 is an *Anomoepus*, but there is no obvious bisecting trackway on 23/3. The *Anomoepus* trackmaker was a small ornithischian and, based on hand reconstructions (Olsen and Rainforth, 2003), could have made the grooves. Viewed in this way, *Antipus binfidus* is best interpreted as a scratch display in which the forelimbs were used to mark the sediment. Careful analysis of the range of motion in the basal ornithischian arms is needed, however, to test the plausibility of this hypothesis.

Station 13: Tales of a feather V: *Anomoepus* Gallery 4 Southeast (PEO). In Hitchcock's (1865) Supplement to the Ichnology, he named and described *Anomoepus intermedius*, pointing out characters that relate to the problem of a bird origin for the tracks. It has bird-like hindlimbs and feet, but with a five-fingered hand and a long tail. *Anomoepus* combines very bird like hind limbs and feet with hands with five short fingers and a tail – a real problem if transformation of species, evolution, is not an option. Neither Darwin nor Huxley are mentioned in the 1865 volume, but it would be only three years later that T. H. Huxley would make explicit the evolutionary link between dinosaurs and birds in his analysis of *Compsognathus* and *Archaeopteryx* (Huxley, 1868) and in fact allude to the Connecticut Valley tracks, pointing out how so many are indistinguishable from birds.

Edward and C.H. Hitchcock (1865) stated that ACM ICH 48/1 (Fig. S1.12) has "...four trackways ...of *Anomoepus intermedius*, and four of *A. gracillimus*, probably the typical specimen of *A. intermedius*, showing impressions of all four feet and the tail." Lull (1904, 1915, 1953) and Olsen and Rainforth (2003) accept ACM ICH 48/1 as the holotype of the ichnospecies (the sitting trace), although the latter regard both *A. intermedius* and *A. gracillimus* as junior synonyms of *Anomoepus scambus*. Most of Hitchcock's 1858 comments about *Anomoepus* relate to this particular specimen, which is from the Turners Falls Formation at the "Ferry at Turner's Falls."

Hitchcock (1865) stated, "The tail of the *Anomoepus intermedius*, although rarely leaving an impression, did sometimes drag along and make a narrow continuous trail. This would indicate greater length, and perhaps tenuity. But how much of attenuation and elongation might be consistent with an ornithic type, we have no means of knowing. Professor Dana speaks of "a posterior elongation of the body as connected profoundly with inferiority of grade in the different types of animal life," and says that "it is the very one of all abnormal features to be looked for in the early birds." Upon the whole, the singular markings of the tail upon stone, with the exception perhaps of *A. intermedius*, do really suggest a curious coincidence between the caudal extremity of this genus, and that of the *Archaeopteryx*." Hitchcock (1858) makes special notice of the tail traces on ACM ICH 48/1 stating, "As confirmatory of these

conclusions, it ought to be added that this animal had a tail; for just before it sat down on all fours, we find a distinct tail-trace on the stone, and a less perfect one near the right extremity of the longest row, which would not have been noticed, had not the revelations made by the first, awakened careful scrutiny.” It is this “less perfect” tail trace that is revealing and unique, yet curious in that it was not figured in 1865.

In 1998, Emma Rainforth and PEO noticed that the “less perfect” tail trace on ACM ICH 48/1 had both distinct large scale or scute (*sensu* Lucas and Stettenheim, 1972) imprints proximally and what plausibly can be interpreted as “protofeather” imprints distally (Fig. S1.12). How peculiar that neither Hitchcock nor his son mentioned these detailed imprints on the tail trace, especially since they are so relevant to the questions consuming the former. Perhaps the shallowness of the traces prevented the Hitchcocks from seeing them, although they did notice that many of the footprints on the slab have the fine “pappilate” scale pattern on the pads.

Anomoepus was made by relatively small, gracile, facultatively bipedal ornithischian (Olsen and Rainforth, 2003). Both the foot and hand skeletal reconstructions are consistent with small ornithischians such as the “fabrosaurid” *Lesothosaurus*, although gracile thyreophorans such a *Scutellosaurus* cannot be ruled out (Olsen and Rainforth, 2003). In most ways, the trackmaker’s skeleton would be like that of *Dryosaurus*, in “Dinosaur Hall.”

In addition to the trackways on ACM ICH 48/1, including that of the sitting individual, what is visible on the trace is an irregular pattern of many sub-circular scales giving way posteriorly to a much more regular pattern of rectangular scales (Fig. S1.12). Further back, the scales are obscured and/or replaced by a faint and rhythmically constricted groove, away from which project fine striations. The striations are much finer and greater in number than the apparent swellings of the groove, and therefore the tail could not have made them as drag marks. The scale pattern is clearly a true imprint and the tail must have been lifted and not dragged, because the imprints are not smeared, at least for the part with the scales themselves. For the more posterior part, this is unclear. It is possible that the striations are imprints of filaments or fibers dragged along the mud, or that the groove is an impression of a narrow part of the tail dragged along the mud over the striations (although no chevron marks are evident). The filaments could arise from the ventral surface, perhaps along the feature that made the groove, or they could even be elongate filaments from the dorsal side of the tail. Nothing like them is seen on any other trace in the collection, however, and there is no resemblance to the ruffled chevrons seen in the tool marks.

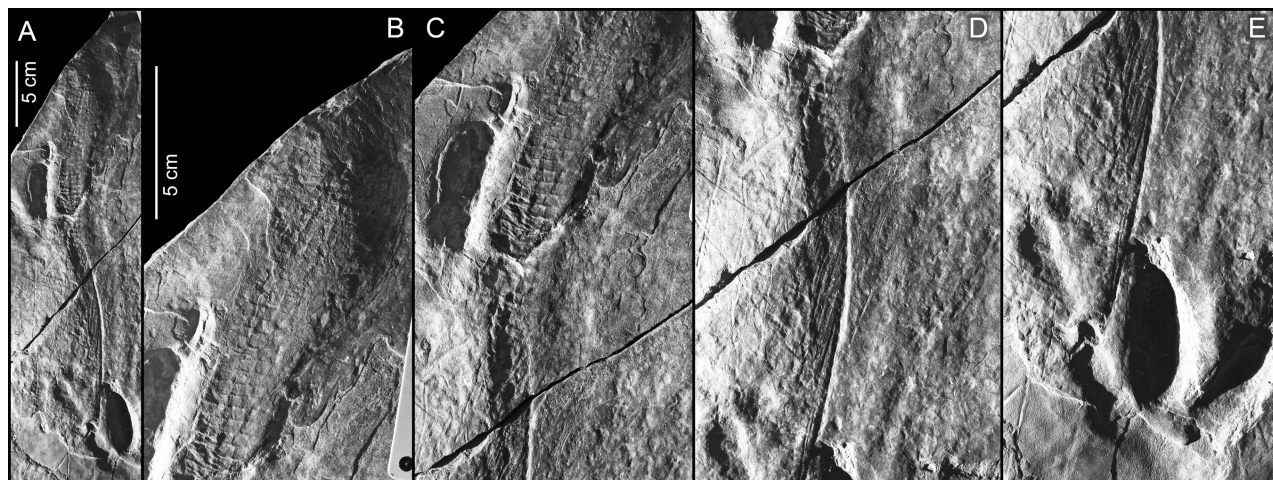


Figure S1.12. *Anomoepus scambus (intermedius)* with scale and ?proto-feathered tail imprint, slab ACM ICH 48/1. A: complete tail trace. B-E: progressively more posterior details.

It is striking that a combination of filaments (on the body) and rectangular scales on the tail is now known from the Late Jurassic ornithischians *Kulindadromeus zabaikalicus*, (Godefroit, et al., 2014), and perhaps *Daurosaurus olovus* and *Kulindapteryx ukureica* (Alifanov et al., 2014), all from the Kulinda locality in Siberia and perhaps all the same species. Another Jurassic ornithischian with filament-covered integument is *Tianyulong* from the Late Jurassic Daohugou assemblage of China (Zheng et al., 2009). The later filaments are preserved on the dorsal tail and some are also preserved on the rest of the body. The ventral side of the tail does not seem to preserve integument at all, although that is likely preservational. In addition, *Psittacosaurus* from the Early Cretaceous has bristle-like fibers on an otherwise scaled tail (Mayr et al., 2002), although no enlarged rectangular scales anywhere are present.

The *Kulindadromeus-Daurosaurus-Kulindapteryx* material, while having extraordinary preservation of integument, is rather dissociated and the topology of the scales is difficult to interpret. The reconstruction provided with the Godefroit article shows these rectangular scales only on the dorsal part of the tail, but the abstract and description note that there are, "...larger imbricated scales around the tail..." and that, "The tail of *Kulindadromeus* is covered by at least five longitudinal rows of slightly arched scales", respectively. Thus it would seem that the scales go around the tail as shown in another restoration by Andrey Atuchin used in the press release for the Godefroit, et al. (2014) article (<http://www.bristol.ac.uk/news/2014/july/fossils-found-in-siberia-suggest-all-dinosaurs-had-feathers.html>). Any reinterpretation of the scale arrangement will require first-hand examination and/or additional material.

The ACM ICH 48/1 *Anomoepus* is now the only example, other than *Kulindadromeus*, known in the Ornithischia to have rectangular scales on the tail. All other ornithischian scale patterns are either arranged as polygons, rosettes, rounded papillae, or tubercles (Czerkas, 1997; Mayr et al., 2002; Christiansen and Tschopp, 2010). What is very clear at this point is that there is a very large range of epidermal structures in the Ornithischia, and given the filaments present in *Kulindadromeus* and the related Kulinda forms, in *Tianyulong*, and the quill-like structures in *Psittacosaurus*, such filamentous integument along scales on parts of the body are most simply hypothesized to be primitive for the Ornithischia. This is consistent with a cladistic phylogenetic bracket approach, given the presence of a filamentous integument in pterosaurs (Sharov, 1971) and feathers, filamentous integument, and scales in saurischians (including birds). That a filamentous and insulating integument was a character at the base of the Ornithodira (Avimetatarsalia) should have been fairly obvious since the middle 1980s at least.

Sinking dinosaurs, penetrative tracks, and Hitchcock's Leptodactyli (SMG and PF)

Throughout the mid nineteenth century, Edward Hitchcock described and interpreted Early Jurassic footprints in a series of landmark publications (Hitchcock 1836, 1841, 1848, 1858). His classic reference material, significant for both scientific and historic reasons, now comprises the Hitchcock Ichnology Collection at the Beneski Museum of Natural History, Amherst College. From the outset (1836), Hitchcock recognized two major divisions within the tracks he was studying: the thick-toed Pachydactyli and the thin-toed Leptodactyli (Fig. S1.13). Pachydactylous animals were thought to have left tracks that "*show moulds or casts of toes wide in proportion to their length, with distinct claw and phalangeal impressions.*" By contrast, "*leptodactylous feet and tracks are narrow and rarely show phalanges or claws*" (Hitchcock, 1858, p. 30). Motivated by the dramatic variation in shape among Connecticut Valley vertebrate tracks (Fig. S1.13B), Hitchcock named almost a hundred ichnogenera and over twice as many ichnospecies (Rainforth, 2005).



Figure S1.13. Edward Hitchcock’s footprint menagerie. A: It began with seven species in 1836. B: By 1858 it had grown to dozens, many of which were thin-toed (leptodactylous) ichnotaxa.

Modern workers question the existence of so many different types of animals in one place at that time. An alternative explanation for high track disparity is for each species to have been capable of producing multiple ichnospecies; factors such as substrate consistency and limb motion are known to affect track form (Brand, 1979; Gatesy et al., 1999; Manning, 2004; Milàn, 2006; Milàn and Bromley, 2008; Diaz-Martinez et al., 2009; Jackson et al., 2010; Bennett and Morse, 2014; Razzolini et al., 2014). To illustrate this, Figure 1.14 (<https://youtu.be/MPoilhOrDVw>; <https://youtu.be/zwNYeQ9GSKQ>) shows sets of tracks made by an individual bird walking slowly across a range of substrates from dry (Fig. 1.14B) to progressively more wet (Fig. 1.14C-H; Gatesy and Falkingham, in press). A single foot can produce a variety of prints because track formation is not a simple molding process, but a dynamic interaction between animal and substrate (Baird, 1957; Padian and Olsen, 1984; Thulborn and Wade, 1989; Falkingham and Gatesy, 2014; Gatesy and Falkingham, in press). Such a “one-to-many” relationship between foot shape and track shape is essential to deciphering ichnodiversity in the Connecticut Valley and elsewhere.

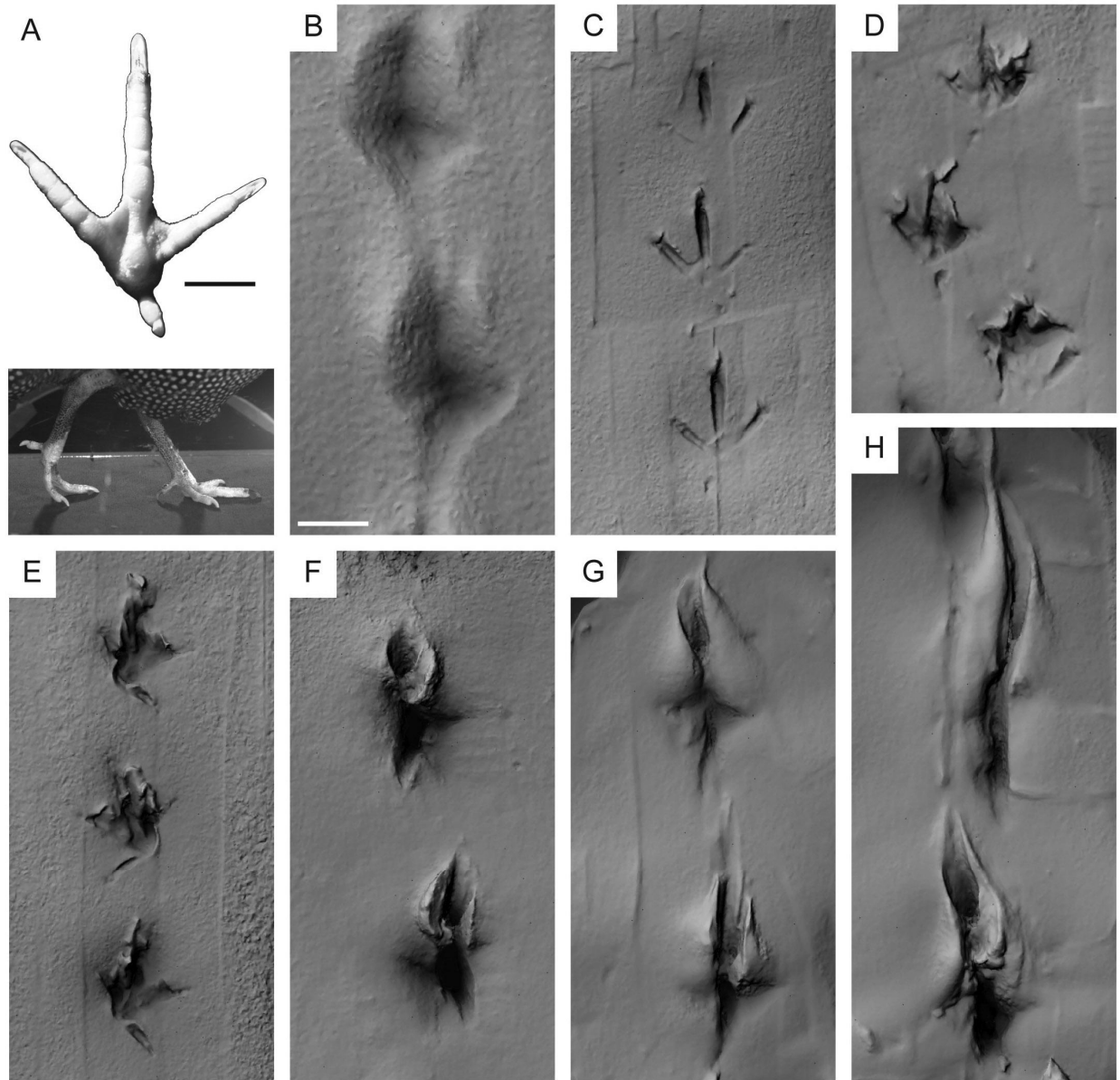


Figure S1.14. Track variants created by a single bird walking on substrates of different consistency. A: foot anatomy. B: Tracks made in dry, granular sediment. C: Tracks made in firm mud, closely resembling foot anatomy. D–H: Tracks made in wet muds that capture foot movement as the bird sinks well below the ground surface. Scale is 2 cm for foot and 5 cm for tracks. From Gatesy and Falkingham, in press.

Pachydactylous tracks (SMG and PF). Researchers are in general agreement that pachydactylous prints were typically made on relatively firm ground (Deane, 1844; Gatesy et al., 1999; Rainforth, 2005). Sediments receptive to thick-toed track formation were sufficiently deformable to retain an imprint, but firm enough to prevent the foot from sinking too deeply (Figs. 1.14C). Pachydactylous specimens exhibiting imprints of digital pads and claws are normally regarded as the most “foot-like.” As stated by Hitchcock, “*in truth a track in relief... scarcely differs from the foot petrified...*” (1858, p. 24). Given such presumed anatomical fidelity, pachydactylous tracks such as *Eubrontes*, *Anomoepus*, *Otozoum*, and *Batrachopus* have received more attention from modern ichnologists for taxonomy, faunal

analysis, biostratigraphy, and trackmaker identification (Baird, 1957; Olsen and Padian, 1986; Olsen et al., 1998; Olsen and Rainforth, 2003; Rainforth, 2003).

Even when interpreting pachydactylous tracks, care must be taken to recognize which surface a specimen represents. Paleoichnologists must also consider the depth dimension because in layered sediment, a single footfall can transmit force and deform deeper bedding planes as well (e.g., Hitchcock, 1858; Manning 2004; Boutakiout et al. 2006; Milan and Loope, 2007; Thulborn 2012). Splitting along any one of these distorted interlayer boundaries reveals an undertrack, the formation of which is demonstrated in a simple model representing one toe (Fig. 1.15A, B; <https://youtu.be/4vGLtGyx3-M>). Using a computer simulation (Falkingham and Gatesy, 2014), the flow of sediment around a horizontal cylinder descending vertically into a cohesive substrate can be visualized. In cross section, the toe can be seen to deform the air-sediment interface, forming a true track. Below the surface, a shallow white layer undergoes similar, although slightly less dramatic, modification. Splitting along the gray-white interface above this layer or the white-gray interface below would yield an undertrack. Note that the deeper white layer is barely altered; transmission of detailed foot contours is only possible over relatively short distances.

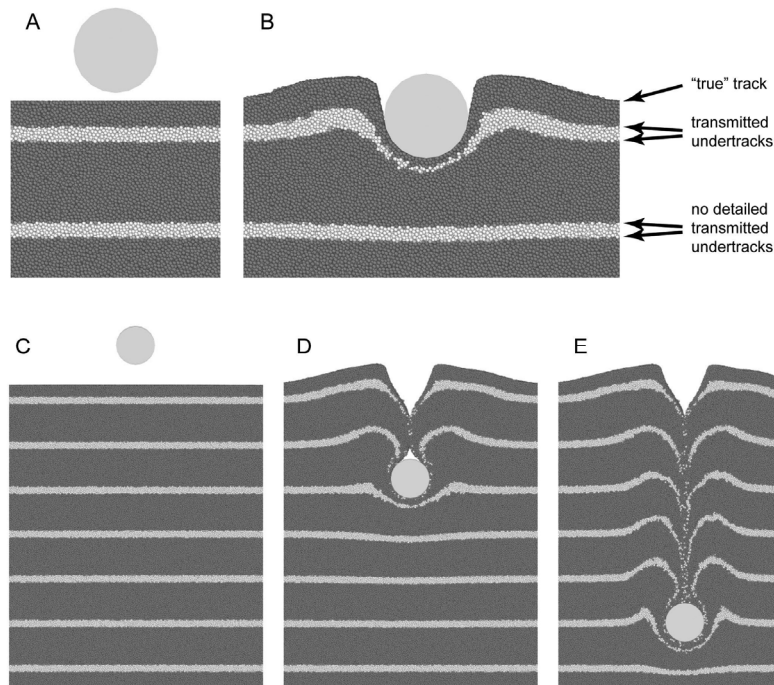


Figure S1.15. Computer simulation of idealized track formation. A toe is modeled as a cylinder and viewed in cross-section descending into a layered substrate. A–B: Pachydactylous tracks require firm ground and minimal sinking. A true track is created at the air-sediment interface with undertracks beneath. Detailed undertracks are only transmitted locally. C–E: Leptodactylous tracks entail deep penetration into soft substrates. A pattern of nested V-shaped structures, penetrative undertracks, are left in the toe’s wake.

Leptodactylous tracks (SMG and PF). Throughout his 29-year span of publications, Hitchcock maintained that most narrow-toed tracks were made by narrow-toed animals. Just as the feet of herons are more gracile than those of ostriches, he reasoned, so too did toe width vary in extinct species (Hitchcock, 1848). However as early as 1844, James Deane offered an alternative interpretation: “*If the foot was planted upon the stratum while yet too soft to retain its form, the impress was of necessity obliterated each toe being simply represented by a linear depression, that has sometimes been mistaken for the impress of a slender toe*” (Deane, 1861, p. 29). Rather than reflecting anatomical disparity, might thin-toed tracks have also been created by thick-toed feet (Marsh, 1848)? Recent workers, bolstered by experimental data (Gatesy et al., 1999; Milan, 2006), have followed Deane’s interpretation. Thin-toed tracks from the Connecticut Valley are now considered formational variants so “*dominated by substrate and kinematic factors*” (Rainforth, 2005, p. 290) as to preclude all but the most basic anatomical features.

We can again simulate a horizontal cylinder representing one toe, but this time penetrating deeply into a soft substrate (Fig. S1.15 C-E; <https://youtu.be/Dno1fGVeWko>). Unlike firmer ground, which yielded a true track conforming to the cylinder's contours and transmitted undertracks beneath (Fig. S1.15B), the upper layers of a soft substrate are unable to stop the toe from passing through. A series of nested V-shaped structures is left behind when viewed in cross-section (Gatesy et al., 1999; Gatesy, 2003; Olsen, 2002; Milan and Bromley, 2006). Sediment flowing around and over the cylinder converges from both sides to seal the space formed by the toe during its descent, creating the slit-like toe imprint (Ellis and Gatesy, 2013; Falkingham and Gatesy, 2014).

Given this unique mechanism of formation, leptodactylous undertracks differ somewhat from those in pachydactylous specimens. We refer to them as penetrative undertracks because the layers have been incised rather than distorted. Transmitted undertracks form *below* the descending toe, akin to a bow wave on a boat. If the toe sinks deeply enough, sediment can pass around and collapse, forming penetrative undertracks *above* the descending toe. At an intermediate toe depth (Fig. S1.15D), the third deepest white layer reveals transmitted undertracks. The shallowest white layer has already formed penetrative undertracks, while the second deepest layer has yet to seal shut.

Possible pitfalls of penetrative tracks (SMG and PF). Leptodactylous tracks can be confusing. Workers not aware of the penetrative formation mechanism might assume that the traditional, transmissive mechanism is responsible in all cases. Even those that are familiar with the possibility of deeply sinking feet might miss clues to the leptodactylous nature of their specimens. If surfaces from deep tracks are encountered in the field or collections and thought to be relatively shallow, errors are inevitable.

Removing most of the infilling matrix from penetrative undertracks reveals extremely thin slits “*appearing almost as if the mud had been impressed by the blade of a knife*” (Hitchcock, 1848, p. 140). Although such exposure faithfully follows natural laminar contours (Fig. S1.16A), a literal reading of surface topography as toe shape leads to a flawed reconstruction of pedal anatomy. The deeper a V-shaped surface is cleared, the narrower the toe responsible appears to have been (Fig. S1.16B). In an extreme example, Hitchcock (1841) went so far as to invoke “keel-shaped” toes in several leptodactylous taxa. Outside the Connecticut Valley, it's likely that workers using toe width as a diagnostic feature have incorrectly ascribed penetrative tracks to thin-toed, particularly avian, trackmakers.

Splitting penetrative tracks into slabs typically causes overlying material to remain in the deeply incised grooves (Fig. S1.17A). Thus, a surface that is sharply V-shaped in cross section can break into U-shaped profiles on part and counterpart. Most insidiously, broken laminae can blend with the steeper walls to give the appearance of a continuous surface—a “false bottom.” Such a style of exposure can be easily misconstrued as a shallow true track or transmitted undertrack rather than a deep, penetrative one. The two original specimens brought to Hitchcock's attention by Dr. James Deane in 1835 (Fig. S1.17B; ACM ICH 18/1 and 18/2) exemplify this illusion. Yet the presence of tracks on all four surfaces of these slabs confirms their true, penetrative nature.

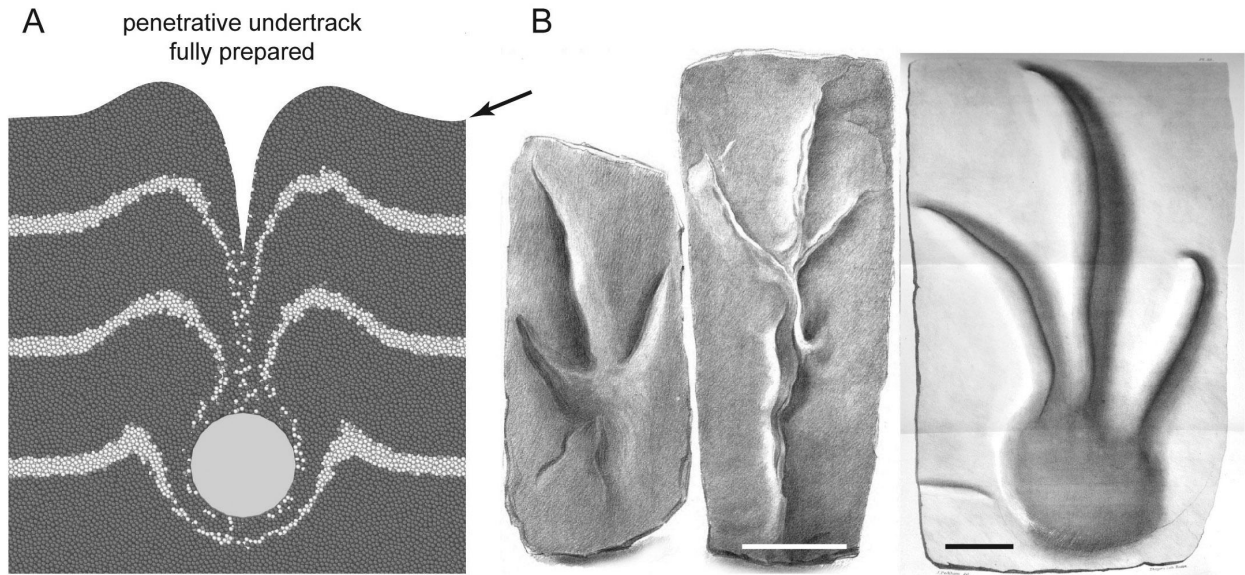


Figure S1.16. Full preparation of penetrative tracks and undertracks. A: A deep slit is exposed by removal of all overlying matrix. If interpreted literally as a mold of pedal anatomy, the toes would be reconstructed as being narrow and keel-shaped rather than their actual, larger diameter. B: Examples of leptodactylous specimens, including ACM ICH 34/11, 34/38, and 26/15, as illustrated by Hitchcock (1841). Scales are 5 cm.

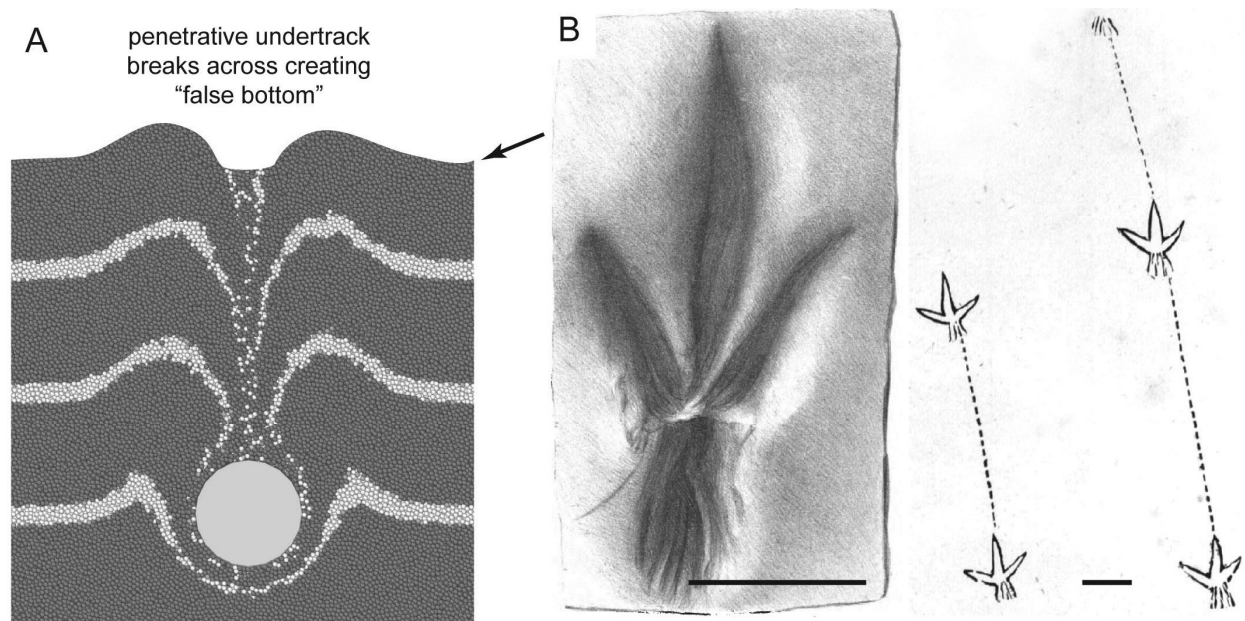


Figure S1.17. Fractures can break across laminae, rather than follow the steep walls in exposed penetrative undertracks. A: If the infilling matrix remains, a "false bottom" can be produced. B: Examples include ACM ICH 18/1 and 18/2, the "Great Folio" of Hitchcock (1836, 1841). Scales equal 5 cm for the single track and 10 cm for the trackways.

Because V-shaped deformations span laminae over a range of depths, the fracture pattern just described often repeats at more than one level (Fig. S1.18A). A single slab taken from the middle of a penetrative track volume therefore exposes penetrative undertracks on both sides. Tracks split into multiple slabs preserve the foot's passage through significant depths (Fig. S1.18B). Most dramatically, multi-slab specimens have been connected by wire or metal hinges to create "stony volumes" (Fig. S1.18C). The most famous example (Fig. S1.18D; ACM ICH 27/4) appears to show two shallow tracks transmitting undertracks over considerable depth, but is actually a pair of deceptively fractured penetrative tracks (Rainforth, 2005).

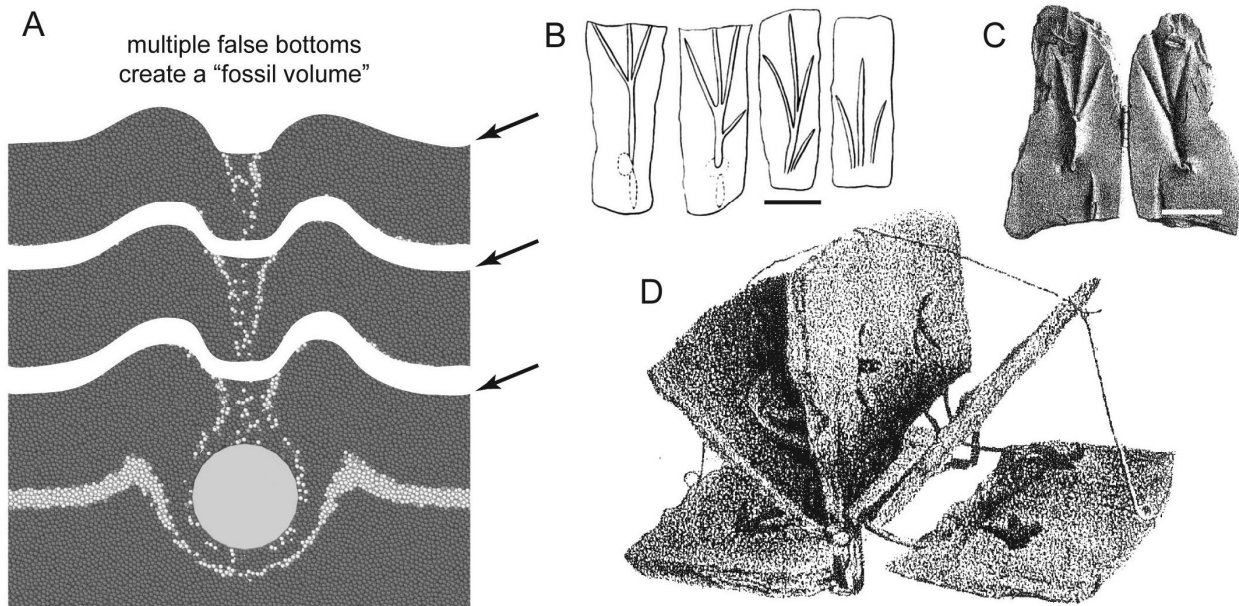


Figure S1.18. Formation of "fossil volumes." A: Splitting a deep track along bedding planes can produce multiple penetrative undertracks. B: ACM ICH 31/57, 31/58, 31/59, and 31/51 are four slabs of a single track as figured by Hitchcock (1848). C: ACM ICH 27/19 consists of two slabs connected by a metal hinge (Hitchcock, 1858). D: ACM ICH 27/4, Hitchcock's (1858) "fossil volume," is the best-known example of five leaves. Broken penetrative undertracks form false bottoms that appear to show transmission to great depths. Scales are 5 cm.

Finally, morphologically detailed tracks are sometimes found below penetrative undertracks (Fig. S1.19A). In a few specimens, the foot sank deeply yet remained stable enough to be withdrawn without destroying transmitted undertracks. For example, in ACM ICH 37/24, a pachydactylous track with digital pad and claw imprints lies below two surfaces bearing collapsed, leptodactylous tracks (Fig. S1.19B). Contrary to the popular conception that detail decreases with depth, such cases should make us pause about assuming that all pachydactylous tracks are shallow.

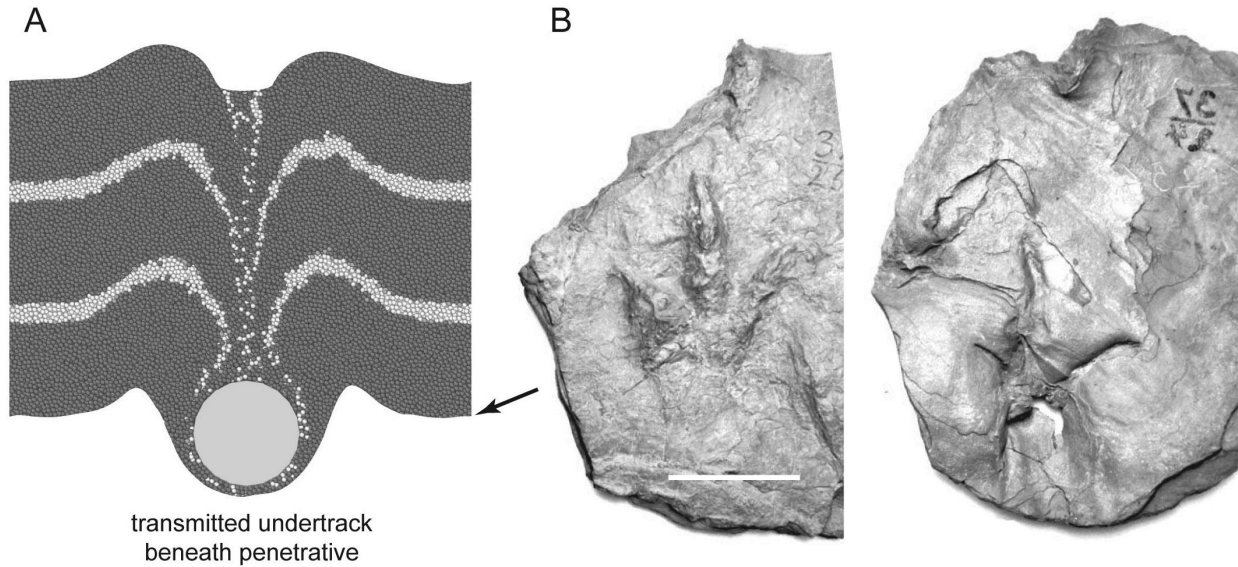


Figure S1.19. Deep tracks can preserve relatively detailed transmitted undertracks. A: Cross section showing this phenomenon. B: ACM ICH 37/24, an actual example in which the track on the left appears shallow, but lies below penetrative undertracks on the right. Scale is 5 cm.

Conclusions (SMG and PF). When animals walk on firm ground, the majority of foot movement occurs in air and is therefore not recorded. On softer substrates, each foot can sink deeply enough for the 3-D paths of its toes and long bones to be preserved in a sediment volume (Gatesy et al., 1999; Milàn et al, 2006; Huerta et al., 2012). For researchers interested in locomotion, deep tracks offer a fortuitous opportunity to sample the foot motion of extinct taxa, including dinosaurs (Fig. S1.20A). Paleontologists have used such trajectories to help inform and constrain reconstructions of pedal kinematics (Fig. S1.20B; Gatesy et al., 1999; Avanzini et al., 2012).

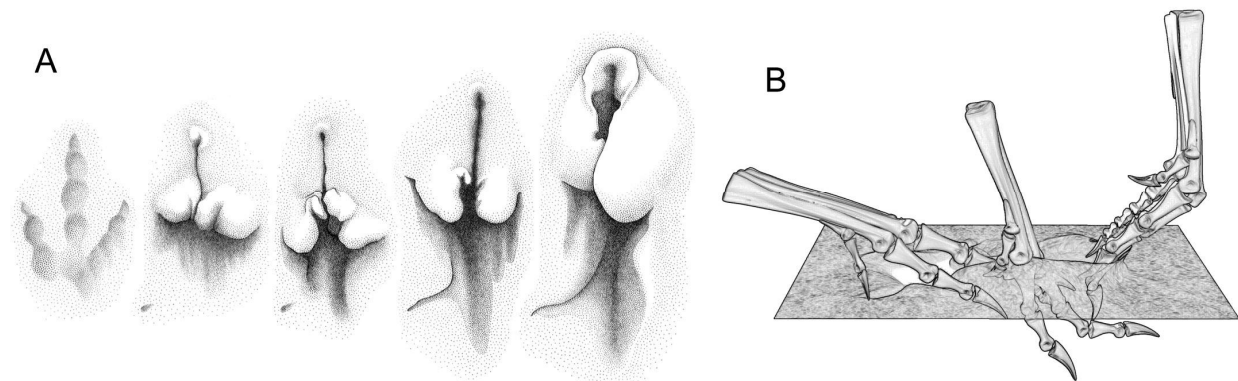


Figure S1.20. Tracks as a record of locomotion. A: Shallow to deep spectrum of Late Triassic tracks from Greenland (Gatesy et al., 1999). B: Softer substrates record more foot movement through the volume of sediment, thereby constraining reconstructions of locomotion (Gatesy, 2003).

Leptodactylous tracks are important to anyone studying fossil footprints. Thin-toed track formation is a major driver of morphological diversity (Rainforth, 2005; Gatesy et al., 1999; Milan and Bromley, 2008). By integrating this formation mechanism into a more complete picture of footprint creation, we hope to expand the overly restrictive, pachydactylous bias that pervades the field. We hope that using classic examples from the Connecticut Valley will help raise awareness about the potential for misinterpretation of tracks worldwide.

Trackways of aquatic insects in the Hitchcock Collection (PRG)

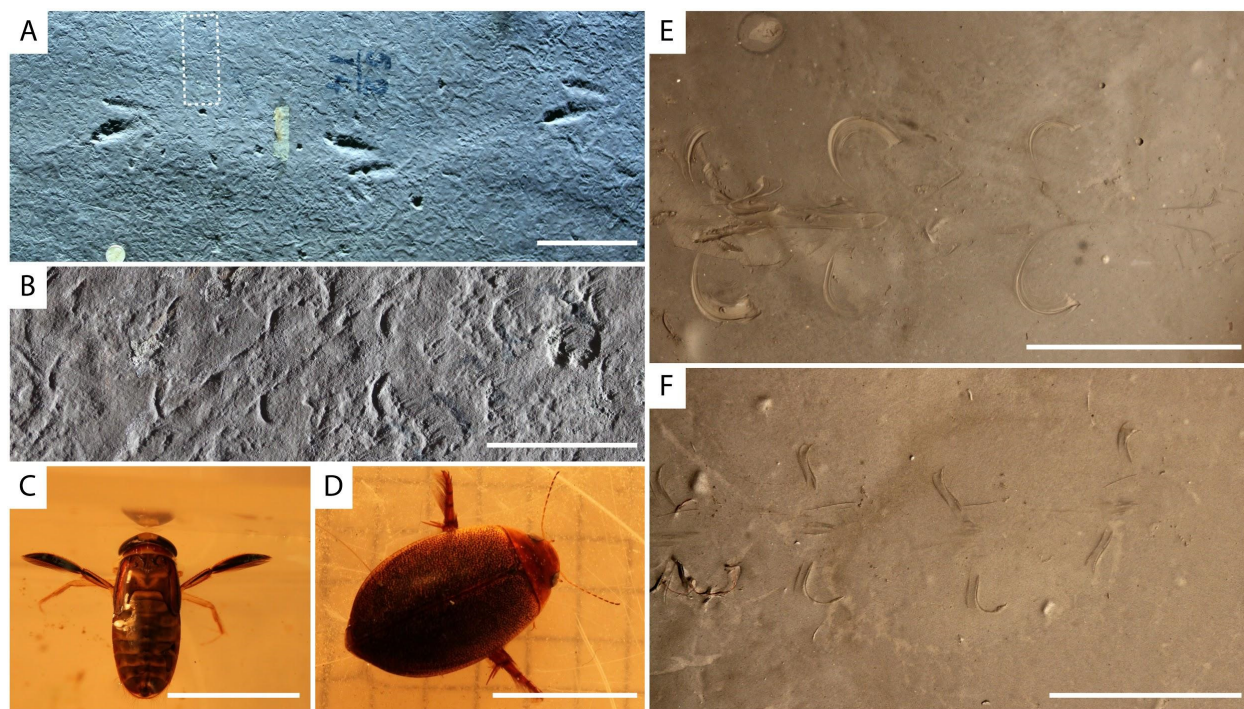


Figure S1.21. The ichnogenus *Lunulipes*, possible track makers, and modern analogs. A: Photograph of ACM ICH 52/14, a slab bearing seven *Lunulipes*, including the lectotype. B: Close-up of the boxed region in A showing a well-defined trackway. C: A water boatman (Family Corixidae) with its two swimming legs extended. D: A predaceous diving beetle (Family Dytiscidae) with its swimming legs extended. E: Trackway produced by a water boatman. F: Trackway produced by a predaceous diving beetle. Scales are 10 cm in A and 1 cm in all other panels.

Over the course of his career, Edward Hitchcock established 31 ichnogenera and 60 ichnospecies for invertebrate traces from the Hartford and Deerfield basins (Rainforth, 2005). Among these was the ichnogenus *Lunula*, which was erected for 11 trackways that were discovered in the Turners Falls Formation of the Deerfield Basin (Fig. S1.21A). The name *Lunula*, however, is preoccupied by a bryozoan and therefore Getty (in press) proposed *Lunulipes* as a replacement name for the ichnogenus. *Lunulipes* consists of two rows of crescent-shaped tracks that are oriented perpendicular to the direction of travel (Fig. S1.21B). Within each row the tracks are arranged singly, one in front of the other. Ten of the 11 trackways exhibit opposite symmetry, meaning that the tracks in either row occur directly opposite each other across the trackway midline. In the track room, we will examine ACM ICH 52/14, which has seven *Lunulipes* on it.

When Hitchcock (1865) erected *Lunulipes*, he proposed that it was made by a myriapod, such as a centipede or millipede. Later, Lull (1915, 1953) hypothesized that *Lunulipes* was a crustacean trackway, or that of an unknown arthropod. As researchers (e.g., Davis et al., 2007; Knecht et al., 2009; Eisman and Charney, 2010) have conducted experimental neoichnology with arthropods, however, it has become apparent that many myriapod and crustacean trackways bear little resemblance to the fossils. Rather, the morphology observed in *Lunulipes* suggests that the animal responsible for the trackways used only two legs during locomotion, and that they moved in unison. With this in mind, Loeb and Getty (2015) conducted experiments with water boatmen and predaceous diving beetles (Fig. S1.21C–D), which are

aquatic insects that beat a single pair of legs in unison as they swim. Both of these insect groups made *Lunulipes*-like traces in shallow water (Fig. S1.21E–F). Thus, experiments support the inference that *Lunulipes* was made by swimming insects that used one pair of legs. This hypothesis is also supported by the body fossil record of the groups to which the predaceous diving beetles and water boatmen belong, which overlaps with that of *Lunulipes* (Olsen et al., 1978; Grimaldi and Engel, 2005).

Considering that insect body fossils in the Hartford and Deerfield basins, apart from larvae, are rare and fragmentary (Huber et al., 2003), trace fossils like *Lunulipes* are invaluable in providing information about the region’s insects and their behavior.

Stop 2: Dinosaur Footprint Reservation (PEO)

In 1891, the Massachusetts legislature voted to establish the “Trustees of Reservations” (“Public” was deleted from the name in 1954 to avoid confusion with government-owned land) for the purpose of protecting lands and historic places for the public good (<http://www.thetrustees.org/about-us/history/>). Trustees of Reservations is the oldest regional land trust in the world. This (Stop 2) and Stop 3 (Little Tom) are held and managed by the Trustees. Secured in 1935, the 8-acre Dinosaur Footprint Reservation is one of the few places remaining that has tracks *in situ* much as they would have been seen by Hitchcock, in fact, this is almost certainly the site of the type specimen of *Eubrontes giganteus* (see below). Numerous tracks of *Eubrontes* are present, as well as other smaller brontozoids, *Anomoepus* and *Batrachopus* as well as plant remains and a host of sedimentary structures. Seeing the tracks, is very much a matter of the ambient light however, and sometimes they can seem nearly invisible.

Stratigraphy (PEO)

Strata at Dinosaur Footprint belongs to the Smiths Ferry Member of the Portland Formation (Kent and Olsen, 2008), which is the lowest division of the formation (Fig. S2.1). The back-slope hill to the immediate west of the site is comprised of Granby Tuff, Hampden Basalt, and intrusions of the Black Rock Diabase that in part were feeders to the tuff and flows. This site is shown on Hitchcock’s 1858 “Mt. Tom section” in Figure S2.1 along with the “Little Tom” (Stop 3) site. This part of the Portland Formation is cyclical, but as the individual cycles cause by climatic precession are 20 m thick, that cyclicity is not easily visible at this site. However, there is a dark mudstone at the western water’s edge overlain by gray then red siltstones and sandstones that comprise the projection of outcrop extending into the river. Based on astrochronology, of the orbitally paced (Milankovitch) lake-level cycles, U-Pb zircon dating of basalts in the Newark Basin, correlative to those in the Hartford (Blackburn et al., 2013), reveal the age of these strata is 200.9 Ma, which is about 660 ky after end-Triassic extinction.

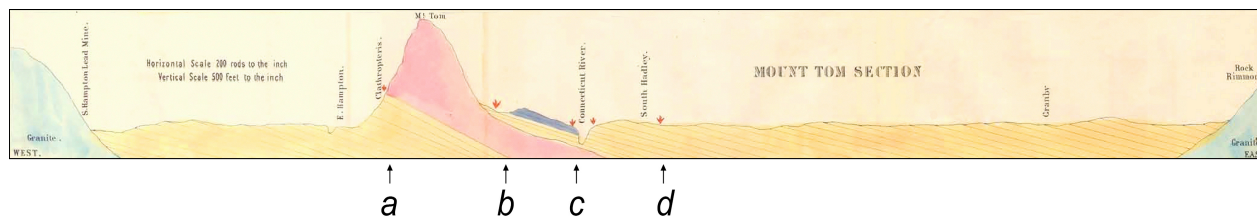


Figure S2.1. The “Mt. Tom Section” from Hitchcock (1858, Pl. III) extending approximately from 2 km west of Southampton to 3 km east of Ludlow, MA showing location of Stops 2 and 3. Metamorphic basement rocks are teal, Hartford Basin sedimentary rocks are yellow, Holyoke Basalt is pink, and Hampden Basalt, Granby Tuff, and sills of Black Rock Diabase are indigo. Bassett’s Quarry, in the Shuttle Meadow Formation, is at point *a*; Little Tom, in the East Berlin Formation, is at point *b*; Dinosaur Footprint Reservation, in the Smiths Ferry Member of the Portland Formation is at point *c*; and the Moody quarries, in the Park River Member of the Portland Formation are at point *d*.

Type specimen of Eubrontes giganteus (PEO)

The main evidence that this is the site at which the famous type specimen of *Eubrontes giganteus*, ACM ICH 15/3 (Fig. S1.3) was collected is in the 1836 paper in which he first describes it. Hitchcock (1836, p. 308) states, “These stones were obtained from a quarry in the southeast part of the same town [Northampton], on the east side of Mount Tom: and on resorting thither, I found numerous examples, some of them very fine, of several kinds of tracks. The strata at this spot, dip to the east, not more than 10°, and pass directly beneath Connecticut river, by which they are washed.”, and then referring to the ichnospecies (p. 317), “Occurring only at the quarry in Northampton, on the east side of Mount Tom, where it is abundant.”. The larger brontozoids at this site do, in fact bear a striking resemblance to ACM ICH 15/3, and as the holotype specimen is a natural cast and the track in the main area (up against the retaining wall for CT 5) are the moulds, it is quite plausible that its counterpart is still here *in situ*.

Parallel trackway orientations: evidence for gregariousness? (PRG)

Dinosaur Footprint Reservation is also well-known for being the locality from which dinosaurs were first inferred to be gregarious, or social, animals. The evidence to support this hypothesis was first presented by Hitchcock (1836), who noted that many of the *Eubrontes giganteus* trackways, which he thought had been made by giant birds, were parallel. Ostrom (1972) explored the gregariousness hypothesis further by surveying the site and generating the first complete map of the track surface. He identified a total of 134 footprints, which he ascribed to 33 animals, 28 of which left trackways and five of which left isolated footprints. Ostrom attributed 22 of the trackways and four of the isolated tracks to *Eubrontes giganteus*. He further noted that 19 (86%) of the *Eubrontes giganteus* trackways were headed to the west and that four of the five non-*Eubrontes* trackways were oriented in different directions relative to the *E. giganteus* trackways. Considering that he was unable to find evidence of a physical barrier, and that the trackway orientations were species specific, he concluded that the *Eubrontes giganteus* trackmakers must have been traveling as a group. Smith et al. (1996), showed that parallel trackways with the same preferred orientation as that reported by Ostrom occurred on beds 69 m above the main track bed, suggesting that long term trends affected animal behavior.

More recently, Getty et al. (2012) conducted another detailed mapping project (Fig. S2.2A) of Dinosaur Footprint Reservation and found 787 tracks. Further surveying brought the total number to 805, or six times more tracks than Ostrom reported. The additional tracks include those of small theropods, ornithischians, and basal crocodylomorphs (Fig. S2.2B–D). Only 28% of the trackways are those of herbivores (Fig. S2.2E). Two hundred twenty-two of the tracks, occurring in 39 trackways, along with 14 isolated tracks, were attributed to *Eubrontes giganteus*. Even with the much larger sample size, the *E. giganteus* still showed a statistically significant ($p < 0.01$ for Rayleigh’s R , Rao’s U , and chi-squared tests; $n = 53$), non-random and bimodal distribution, with 40 (75%) of the tracks and trackways oriented to the west, and the remainder oriented to the east (Fig. S2.2F). Getty et al. (2012), however, did not conclude that the preferred orientation necessarily indicated group behavior. They reported oscillation ripple marks on the main track surface, as well as above and below it, and noted that their crests were oriented in approximately the same direction as the trackways (Fig. S2.2G–H). Given that the crests of oscillation ripple marks form approximately parallel to shorelines, they suggested that the strongly bimodal distribution could have resulted from shoreline-parallel behavior. Further evidence to support the hypothesis can be found on beds 69 m above the main track layer, where sedimentary structures such as ripple marks and woody fragments (Fig. S2.2I) indicate that the shoreline had remained relatively stable and oriented northeast to southwest. The trackways on these upper beds also exhibit a statistically significant ($p < 0.05$ for Rayleigh’s R , Rao’s U , and chi-squared tests; $n = 49$), non-random orientation to the northeast and southwest, although there is more variability in trackway orientations (Fig. S2.2J). Nonetheless, Getty et al. (2012) did not reject outright the possibility of group behavior because groups of animals could follow shorelines and thus leave parallel trackways. We will come back to this topic when we visit Dinosaur State Park.

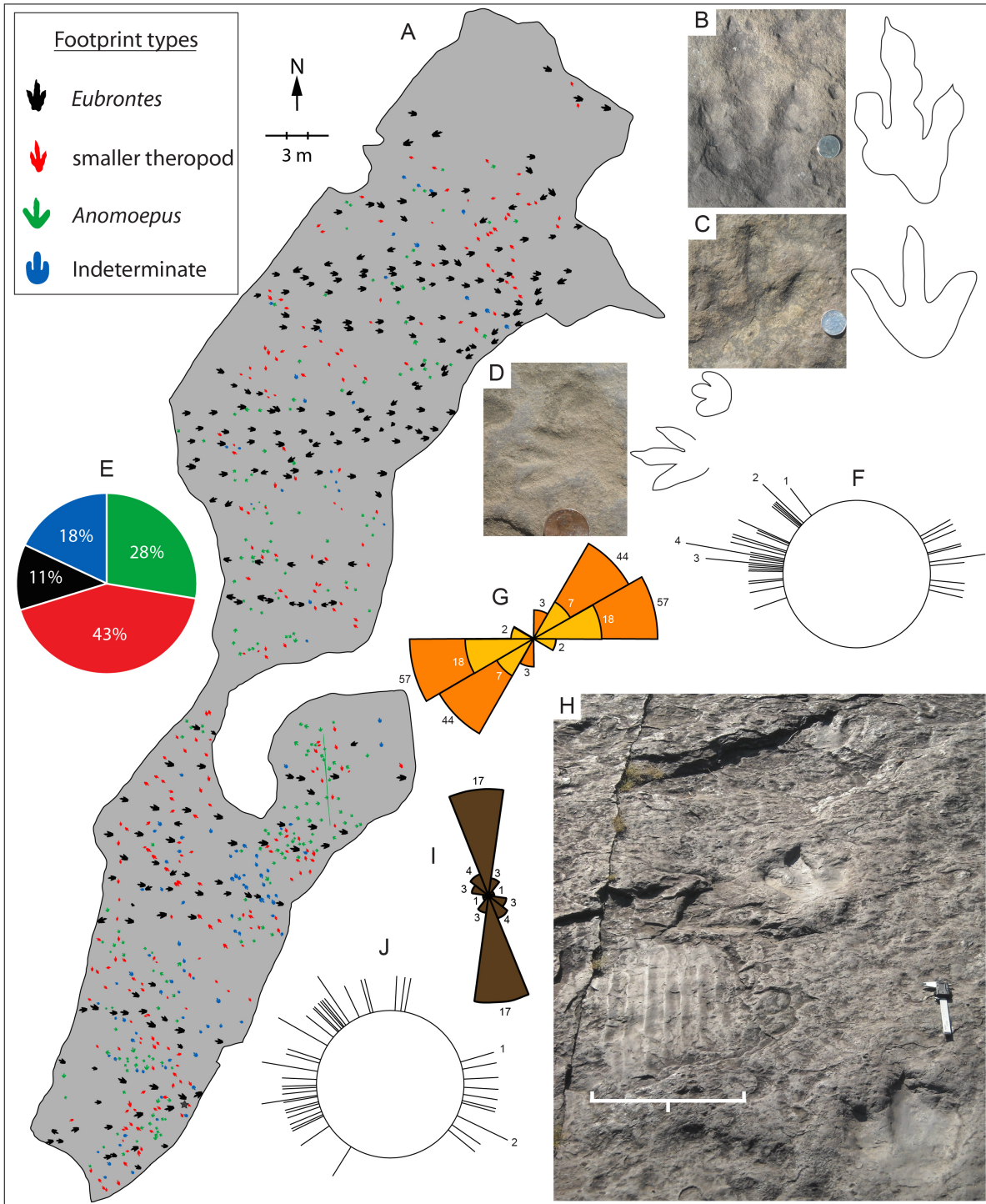


Figure S2.2. Tracks, structures, and orientations at Dinosaur Footprint Reservation. A: Map of the main surface, showing all 805 dinosaur tracks found. B: The theropod track *Anchisauripus* isp. C: The ornithischian track *Anomoepus scambus*. D: Basal crocodylomorph hand and foot tracks called *Batrachopus* isp. E: Proportions of the different trackway types. F: Rose diagram of *E. giganteus* orientations. G: Rose diagram of oscillation ripple crest orientations from above (light blue) and below (dark blue) the main track bed. H: Photograph of *E. giganteus* paralleling ripple mark crests (bracketed). I: Rose diagram of fossilized wood fragment orientations from 69 m above the main track bed. J: Rose diagram of *E. giganteus* on beds 69 m above the main track bed. Nickel for scale in B and C; penny for scale in D.

Theropod diet: what were they eating? (PRG)

Researchers (e.g., Olsen et al., 2003) have long known that the tracks of carnivores are more abundant than those of herbivores in Early Jurassic ichnofaunas. Furthermore, tracks of large herbivores, such as *Otozoum*, do not occur in association with those of large theropods (Rainforth, 2003). Such an inverted ecological food pyramid structure, with only a few small herbivores, can be seen at Dinosaur Footprint Reservation (Getty et al., 2012; Fig. S2.2E). Even adding the 18% of tracks that Getty et al. (2012) considered indeterminate to the number of herbivore tracks would still result in less than half of the tracks being made by herbivores. An even more pronounced disparity in number of herbivores relative to carnivores will be seen at Dinosaur State Park (Stop 5), where all of the tracks on the main beds are those of carnivores.

There are a number of possibilities as to why the tracks of carnivores might be found in higher proportions than those of herbivores, and these have been summarized by Wright (1997). For example, it is possible that our methods of discriminating the tracks of carnivores from those of herbivores might be flawed. It could also be that carnivores were more active than herbivores and therefore left more prints. After all, carnivores would need to actively hunt their prey. Assuming that the proportions of tracks ascribed to herbivores represents their actual abundance in the fauna, coupled with the small body size of the herbivores relative to the carnivores, has led some researchers (e.g., Olsen, 2010) to hypothesize that the carnivores primarily fed on fish.

Evidence to support this hypothesis comes from body and trace fossils. For example, Milner and Kirkland (2007) noted that *Dilophosaurus*, which is a possible trackmaker for *Eubrontes giganteus* (e.g., Lucas et al., 2006), has a variety of adaptations that would be beneficial to a fish-eating animal. They also noted that theropod teeth exhibiting fish-eating adaptations have been found in Early Jurassic rocks in Utah, and argued that that preferentially aligned swim tracks at the St. George Dinosaur Discovery Site resulted from fishing behavior.

Various lines of evidence from the Hartford Basin supports the hypothesis that the theropods were fish eaters. For example, a tooth reported by McDonald (1992) is morphologically similar to those from Utah that have been interpreted as bearing adaptations for piscivory. Additionally, the theropod tracks at Dinosaur Footprint Reservation exhibit two preferred orientations, which are correlated with the size of the trackmaker. As was already discussed, large theropod tracks assigned to *Eubrontes giganteus* are oriented parallel, or nearly so, to the paleoshoreline. By contrast, the tracks of smaller theropods are oriented perpendicular to the shore (Getty et al., 2012; Fig. S2.2A), suggesting that the animals were going into and out of the water, possibly in order to feed. Rare fish body fossils have been reported from the shallow water lake deposits through which the dinosaurs waded (Thorpe, 1936). Finally, as we will see when we visit the Springfield Science Museum, fish trails in shallow-water deposits provide direct evidence for fish living in (as opposed to washing in dead) the shallow water.

Stop 3: Little Tom Mountain Preserve (PEO)

The 73-acre Little Tom Mountain was secured by the Trustees of Reservations in 2002 from the former Mt. Tom Ski area. Mountain Park Road and the old Mount Tom Ski Road provide access the site, where exposures of Holyoke Basalt, East Berlin Formation, Black Rock Diabase crop out near the top of the hill to the north and east. A now-abandoned trap rock quarry in the Holyoke Basalt is at the north end of the preserve.

Stratigraphy (PEO)

The section at Little Tom Mountain was described by Olsen et al. (1989) and correlated with two other major sections in the Hartford Basin (Fig. S3.1). The middle and upper East Berlin Formation are exposed along the road, but are barely visible at times because of plant cover. The section at Little Tom was particularly challenging because of the considerable relief, intermittent outcrops, and intruding sills above the section along the road. The contact between the East Berlin Formation on the southeast side of the road is separated from the Holyoke Basalt on the northwest side by a significant fault that is down on the southeast. These sections are the only ones we will see on this trip that provide large-scale environmental context.

Best exposed are two lake level cycles in the middle East Berlin Formation (*a* and *b* of Fig. S3.1), on the southeast side of the road. Both have black laminated mudstone sequences and the upper of the two is the Westfield Fish Bed. PEO first correlated this bed with the section that takes its name at Westfield CT along Miner Brook about 74 km south. Confidence in this correlation was based on its stratigraphic position with a thick red sequence above it, its specific microlaminated sedimentary fabric, and the presence of fish and conchostracan fossils. There is also a prominent ~2 cm turbidite that was speculated

to correlate with a widespread similar turbidite at several localities to the south (Olsen, 1988b). The correlation is important because it implies that the lakes were large (perhaps hundreds of kilometers long) and not local ponds or flood-plain lakes, and that the lake-level oscillations represented basin-wide, isochronous events. This was very important to the Milankovitch hypothesis (Olsen, 1986).

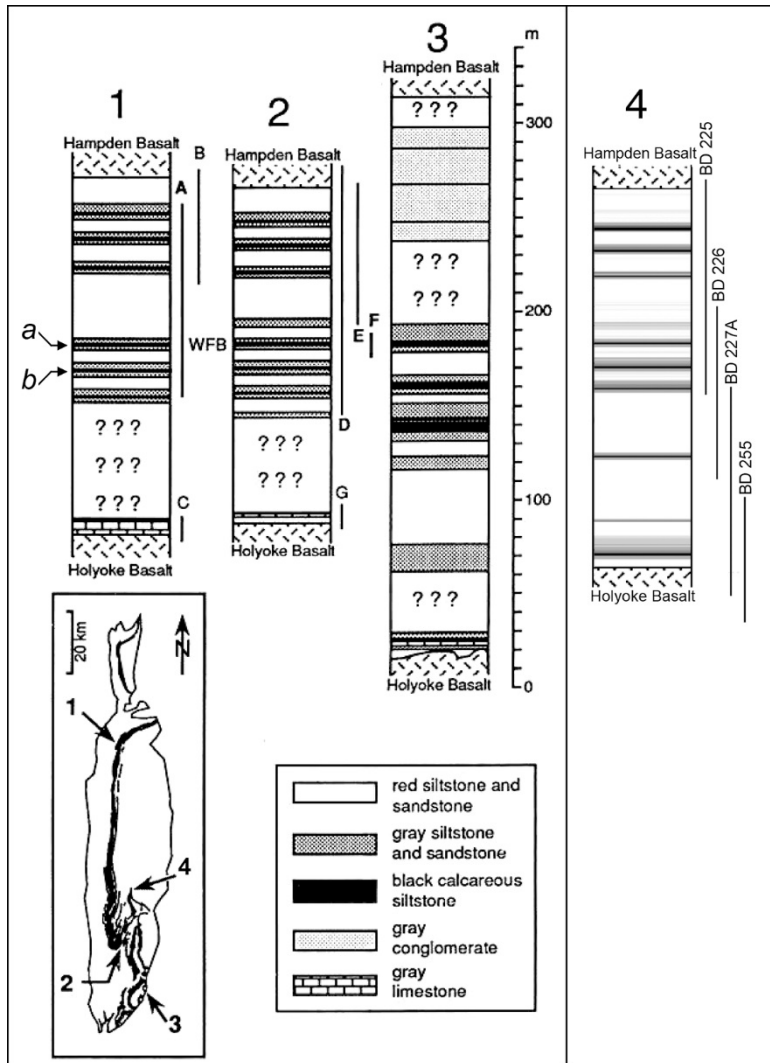


Figure S3.1. Correlation of the East Berlin Formation at three major areas of exposure. 1: Little Tom, Stop 3. 2: East Berlin-Westfield, central CT. 3: Gaillard syncline area, southern CT. 4: new composite at Hartford CT based on continuous cores for the Hartford MDC, South Hartford Conveyance and Storage Tunnel compiled by Steinen et al. (2015). Individual sections for 1-3 are indicated to the right of each column as follows: A, north west side Little Tom; B, 1-91 cut, Mountain Park, MA; C, railroad cut at Ashley Pond, Holyoke, MA; D, US 9, Ct 15, Ct 72 cuts, East Berlin, CT; E, 1-91, US 9 cuts, Cromwell, CT; F, Miner Brook outcrops, Westfield, CT; G, Spruce Brook outcrops, East Berlin, CT; details omitted for area 3.

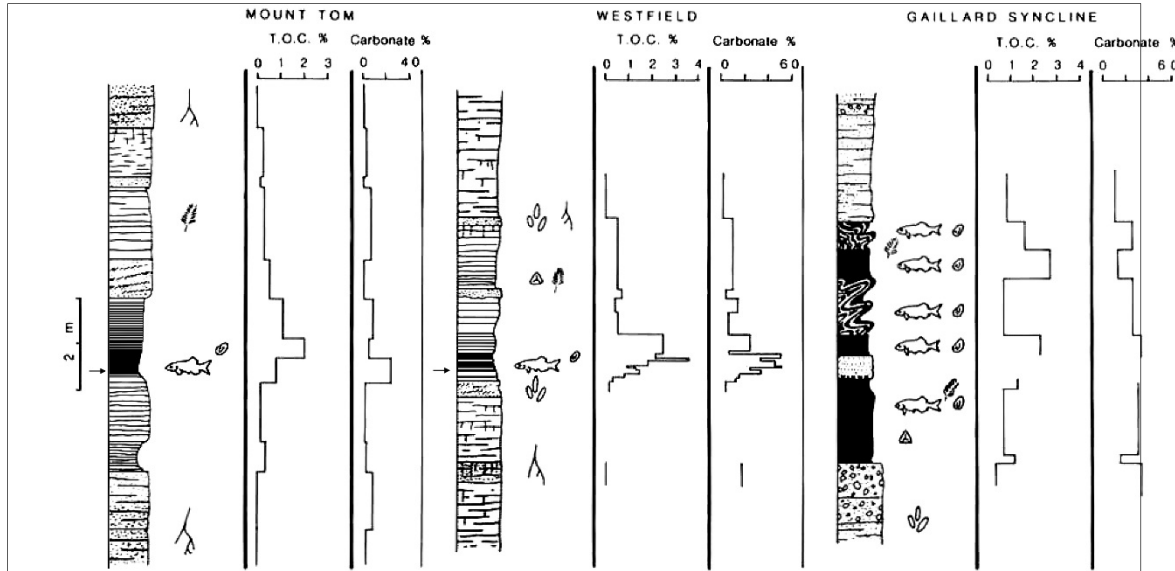


Figure S3.2. Details of correlative cycles at Stop 3 (Little Tom - Mt. Tom of this figure), Westfield, and the Gaillard Syncline (1A, 2F, 3 of Fig. S3.1). Arrows indicate position of Pompton Ash (Fig. S3.4). From Olsen et al. (1989).

Great lakes and lake cycles (PEO)

There is resistance to the idea that one can correlate meter-scale beds in continental sequences over long (> 100 km) distances in what is an area of poor outcrop. Such a correlation, however, was recently corroborated by the discovery of the Pompton Ash, first seen in the Newark Basin Army Corps of Engineers cores in the 1980s, found at the well-known East Berlin Formation exposures along CT-9 East Berlin, CT, and recognized as an ash in thin section by Tony Philpotts (Olsen, 2011; Olsen et al., 2016). Since then it has been found at all but one of the Hartford and Newark Basin localities at which the Westfield Fish Bed and its Newark Basin correlative (the Colfax Bed) were hypothesized to exist (Olsen et al., 2016). Not only does this ash unequivocally demonstrate that the cycles are correlatable basin-wide, but it also demonstrates, because the fish-bearing microlaminated bed in which it is interleaved is varved, that the lakes in the Newark and Hartford basin experienced the same climate signal at the seasonal level!

The sections, as presented in Figure S3.2, were pieced together from smaller sections and the composite has recently been corroborated by continuous core collected for a new diversionary tunnel (Steinen et al., 2015). It is clear now that lakes in the Newark and Hartford basins fluctuated to climate rhythms synchronously and that the lakes, when at high stand, were huge and may even have been connected by open water. In fact, what is known about cyclical sequence in the Culpeper Basin in



Virginia is consistent with correlation to the Newark and Hartford basins, if the lakes connected through the Gettysburg Basin, the composite mega-lakes would be in excess of 700 km long, considerably larger than any lake in the world other than the Caspian and Black seas.

Figure S3.3. Exposures of the cycles bearing the Westfield Fish Bed as it appeared in 1989. On right is PEO collecting fish (photo courtesy of N.G. McDonald).

Cycles of the middle East Berlin Formation (PEO)

The upper two of the middle triplet of lacustrine cycles are exposed along the road on the NW side of Little Tom (Fig. S3.1a, b, S3.2, S3.3). The upper cycle contains the Westfield Fish Bed (Fig. S3.1– S3.5). This bed has a calcareous, organic-rich, microlaminated interval (Fig. S3.4A), and contains the Pompton Ash (S3.4B, C), articulated fish (Fig. S3.4E), and *Bulblimnadia* sp. clam shrimp. This ash is weathered to a bright orange, probably from jarositic hydrous sulfates of potassium, sodium, or aluminum and iron, resulting from the degradation of pyrite that can be as much as 25 wt% of the ash (E. Stueeken, pers. comm., 2016). The pyrite is best explained as having formed in the pore space of the ash after deposition, rather than as part of the ash itself. The Westfield Fish Bed was deposited in a perennially chemical stratified, > 50 m deep lake (Olsen, 1990) with an anoxic hypolimnion that was at a minimum over 100 km long, and maybe over 700 km long.

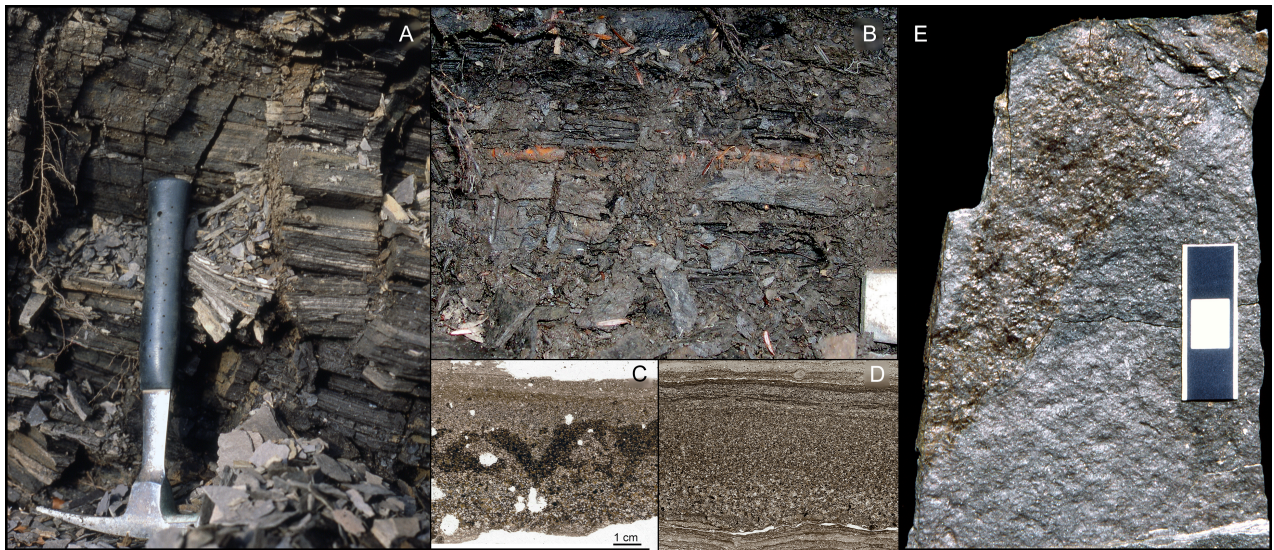


Figure S3.4. Facies, ash, and fish of the Westfield Fish Bed at Stop 3. A: Laminite of the fish bed, the facies that produces the fish and clam shrimp (hammer is ~28 cm). B: The orange-weathering Pompton Ash (hammer head is 2.5 cm deep). C: Thin section of Pompton Ash from Stop 3. D: Thin section of Pompton Ash from Parmalee Brook, Durham, CT. E: dephosphatized indeterminate fish (?*Semionotus*) from Stop 3 (scale is cm, courtesy of N.G. McDonald). (Both thin sections courtesy of A. Philpotts).

In order of abundance, the Westfield Fish Bed has produced *Semionotus* spp. (holostean gar relatives), *Redfieldius* spp. (paleonisciforms), *Diplurus* cf. *longicaudatus* (a coelacanth), and *Ptycholepis* (another paleonisciform). The Westfield Fish Bed produced one of the first recorded articulated fossil fish in North America, a *Redfieldius* from Westfield, CT, mentioned by Silliman in 1816 (Brignon, 2017). The *Semionotus* species from this bed have a very wide range of body forms and scale shapes, and comprised species schools similar to the cichlid fishes of the East African great lakes (McCune et al., 1984). Only *Semionotus*, and perhaps *Redfieldius*, have been found at this locality, however, and their preservation style makes them hard to identify. The fish here, and at other Westfield Fish Bed localities, are variably dephosphatized (Fig. S3.4E); that is, the phosphate in the bone has been mostly, or completely, dissolved early in diagenesis by microbially mediated post-burial processes (McDonald and LeTourneau, 1989; Leonard, 2013; LeTourneau et al., 2015). This can lead to complete disappearance of the fish, or just the faintest “ghost fish” might remain. This is almost certainly a more widespread phenomenon than realized (e.g., Meacham, 2016), and might be the norm rather than the exception.



The next cycle down section (b in Fig. S3.1) is exposed to the north, opposite the former ski area buildings. This cycle has yet to produce any fish, but they may have dephosphatized completely. This cycle is notable for having what look like stromatolites (Fig. S3.5). They are in the appropriate transgressive part of the lake cycle, but they also look like some types of penetrative footprints in cross section. PEO favors stromatolites. Which are they?

Figure S3.5. Are these stromatolites or penetrative footprints?

Dinosaur tracks from Little Tom Mountain (PEO)

We have already seen the *Batrachopus deweyii*, ACM ICH 26/5 and 26/6, that might be from this locality, possibly from near the sills high in the bluff. However, Hitchcock (1858) refers to what is probably this locality in naming a new species of a penetrative track, *Palamopus clarki* (Fig. S3.6). In regard to ACM ICH 12/1, Hitchcock (1858; p. 127) states that the locality, is, “Northampton (All of Mt. Tom east to the CT River was in Northampton in Hitchcock's time [Beers, 1873]), back side of Mount Tom, where it was discovered by Professor WILLIAM S. CLARK...” Footprints abound in these strata and are literally lying around.

Figure S3.6. *Palamopus clarki*, the tracks with more than 3 toes, from Hitchcock (1858, Pl 44, fig 2).



Volcanism, lava lakes, and mega-eruptions (PEO)

As seen at Little Tom and elsewhere, the East Berlin Formation is sandwiched between CAMP lava flows - the Holyoke Basalt below and the Hampden Basalt and its pyroclastic equivalent the Granby Tuff above. In addition, this is one of the few places that a CAMP dike system, the Bridgeport-Pelham dike (locally named the Black Rock Diabase) can be seen, especially along I-91, where it feeds the flow and pyroclastics as well as sending numerous sills and plutons into the East Berlin Formation (Foose, 1968; Philpotts and Martello, 1986).

The former Mt. Tom Quarry just to the north of the ski slope buildings has spectacular and important exposures of the Holyoke Basalt. Well-developed pegmatitic sheets are present low in quarry section, but still well above most of the thickness of the sheet. According to Philpotts et al. (1998) these formed from the expulsion of residual liquids from compaction of the underlying cooling crystal mush. As such, they are rich in incompatible elements, and it is from these kinds of pegmatitic sheets that datable zircons can be recovered (Blackburn et al., 2013), although that has yet to be done here.

The quarry also exposes numerous fissures that are filled with gray and drab sediments and basalt breccia spalled off the sides. Inasmuch as these fissures were connected to the surface and filled from above, they comprise the locally oldest East Berlin Formation. In many places, such as Ashley Pond to the south, the East Berlin Formation sediments in contact and overlying the Holyoke Basalt are gray and lacustrine. The sediment fill of these fissures was likely deposited in water infiltrating and saturating the basalt. The contact with the East Berlin Formation cannot be seen here, however, because of the down-to-the east fault separating exposures of the two formations between the quarry and the hill. Similar fissures in Basalt, albeit filled with red sediments, have produced bones in the Fundy Basin (Olsen et al., 1989). One needs to be alert for such things as bones, even in such an unusual setting.

The Pompton Ash is likely part of CAMP since it is andesitic to basaltic in composition (Olsen et al., 2016). It is likely the product of a Yellowstone-scale mega-eruption far away (like south Florida, a possible center of the CAMP plume) because it does not change thickness over a distance of 200 km. Despite the possibility that this ash is the result of a mega-eruption, it was but a puny part of the CAMP, one of the largest eruptive complexes on Earth.

Stop 4: Springfield Science Museum (PRG)

The Springfield Science Museum in Springfield, Massachusetts, was founded in 1899 in a room in City Hall. It is now a large, regional museum that attracts nearly a quarter of a million visitors a year, and is part of a larger entity called the Springfield Museums, which includes three other museums and a fourth, dedicated to Dr. Seuss, opening in June 2017. The science museum boasts eight halls, including one dedicated to dinosaurs and paleontology, as well as a planetarium and a live animal center. In addition to spilling over into the adjacent auditorium, the museum's Dinosaur Hall has been undergoing significant renovations in recent years. Among the new exhibits is one dedicated to dinosaur bones, including the left humerus (upper arm bone) of the Cretaceous sauropod *Alamosaurus sanjuanensis* collected by Frederic Loomis of Amherst College in 1924 in New Mexico (Dalman and Lucas, 2016). Additionally, the exhibit on local paleontology is being overhauled, with replicas of some of the dinosaur skeletons found in the Hartford Basin being added to augment the dinosaur tracks and other fossils already on display.

The trace fossil collection (PRG)

Although not as large or well-known as the ichnology collection of the Beneski Museum of Natural History, the Springfield Science Museum has a collection of 76 dinosaur track-bearing slabs from the Hartford and Deerfield basins, along with a few other slabs from different regions and geological time periods. Nine of the ten dinosaur track-bearing slabs described by Getty (2006) are on display throughout the museum, and the tenth will be returned to the exhibits soon. The ichnology collection has been amassed by generous donations from researchers and local people, as well as by active collection by museum staff and loans from other museums.

Among the highlights from the collection are trace fossils from the Gary Gaulin dinosaur tracksite, which is a small, privately owned locality in Holyoke, Massachusetts currently being studied (e.g., Dalman and Weems, 2013; Dalman and Lucas, 2015; Getty and Fox, 2015; Getty et al., 2016). The rocks at this site are derived from playa lake deposits of the East Berlin Formation, and some of the traces found there are exquisitely detailed and scientifically valuable. We will examine some of these specimens, and these are discussed in the following sections.

Exceptional specimens from the collections (PRG)

Diminutive dinosaur tracks. Dalman and Weems (2013) reported 16 trackways of small (track length 2.2–3.9 cm) ornithischian dinosaurs from two bedding planes 1.5 cm apart at the base of the 2.2 m section found at the Gary Gaulin site (Fig. S4.1A–B). They named the tracks *Anomoepus lacertoideus*, which is a new combination with the species name coming from Hitchcock's ichnotaxon *Corvipes lacertoideus*, which Olsen and Rainforth (2003), had considered a possible junior synonym of *Anomoepus scambus*. Dalman and Weems (2013) agreed with the ichnogeneric synonymy, but based on morphometric analyses of the tracks, chose to retain the ichnospecies name *lacertoideus* within *Anomoepus*.

These tracks are exceptional for a number of reasons. First, they were found in close association with each other, which goes against the conventional wisdom that small dinosaur tracks are relatively rare (Leonardi, 1981; Milan and Surlyk, 2015). The close proximity of these trackways could indicate trackmaker gregariousness. Second, they are in some cases extremely well defined, exhibiting pad and

claw details. (These first two points, coupled with the minute details seen in the invertebrate trace fossils described below, indicate unique environmental conditions led to the preservation of the traces.) Third, many of the trackways exhibit hand and heel imprints, along with tail drags, demonstrating that, like larger *Anomoepus* trackmakers, the animals were facultative quadrupeds that could switch from a bipedal to a quadrupedal gait.

Arthropod body imprint. In their paper on *Anomoepus* from the Gaulin tracksite, Dalman and Weems (2013) described a 3-cm long body imprint associated with the dinosaur tracks (Fig. S4.1C). This imprint has the serial segmentation, known as tagmatization, that is characteristic of arthropods, with identifiable anterior, central, and posterior regions. Two to three leg imprints project posteriorly and to the sides from the central region, and two imprints, presumably made by tail appendages, project backward from the posterior region. These authors suggested that a whip scorpion made the trace (Order Thelyphonida), a group of arthropods that, along with the spiders, belongs to the class Arachnida. They based their trackmaker assignment primarily on their interpretation of the anterior region, which they proposed was made by the enlarged pedipalps (second pair of appendages on the cephalothorax) that whip scorpions use to grapple with prey.

Dalman and Lucas (2015) reevaluated the arthropod body imprint and gave it a name, *Cheliceratichnus lockleyi*. They rejected the whip scorpion interpretation because this arthropod group has a single tail appendage and a larger central region than is seen in the body imprint. Rather than a whip scorpion, Dalman and Lucas suggested that the body imprint was made by an animal similar to a sun spider, an arachnid Order called Solifugae, which has a shorter central region than whip scorpions. They acknowledged, however, that the presence of two tail imprints is still a problem since sun spiders lack tail appendages. Thus, the maker of the trace is still unknown. One thing that can be said for certain, however, is that the animal that left the trace was alive when it imprinted the sediment because a trackway leads away from the body imprint.

Insect burrows. Thousands of burrows (Fig. S4.1D) attributable to the ichnospecies *Treptichnus bifurcus* have been identified at the Gaulin site (Getty et al., 2016), many on slabs also preserving *Anomoepus lacertioideus*. Based on modern analogs, the burrows are attributed to larval flies (e.g., Seilacher, 1955; Uchman, 2005; Muñiz Guinea et al., 2014), which thus adds to the depauperate insect fossil record in the Hartford Basin. Significantly, the burrows are preserved in three dimensions in thin mud laminae between fine-grained, cross-bedded sandstone layers. This mode of preservation allowed Getty et al. (2016) to test a previous hypothesis, proposed by Archer and Maples (1984), about how the burrow was constructed and to propose a new one that better fits the evidence provided by the fossils. *Treptichnus* and its modern analogues are usually considered feeding traces, although Getty (2016a) suggested that they are actually locomotion traces produced as larvae search for a pupation site.

Insect trackways. Patrick Getty and his colleague Robert Sproule each found a trackway (Fig. S4.1E), attributed to the ichnogenus *Bifurculapes*, at the Gary Gaulin tracksite in the summer of 2016. PRG donated one of the specimens to the Beneski Museum of Natural History (ACM ICH 300), and the other to the Springfield Science Museum (SSM 2016/11-4). These trackways represent only the second occurrence of the ichnogenus outside of its type locality in the Deerfield Basin, the first being in Early Jurassic deposits of Utah (Getty, 2016b). *Bifurculapes* is almost certainly the trackway of a winged (pterygote) insect due to the alternating left-right pattern of the track series, each of which has up to three tracks. Exactly what type of winged insect remains unknown, although some beetles make similar traces today (Eisman and Charney, 2010). After the discovery of the trackways, Getty (2016b) conducted a revision of the ichnospecies within *Bifurculapes* and concluded that only two, *B. laqueatus* and *B. scolopendroideus*, were distinct. The others were either junior synonyms of *B. laqueatus* or were too poorly defined to warrant separate ichnospecies designation.

Fish swimming traces. Patrick Getty and Robert Sproule also found sinuous trails (Fig. S4.1F) at the Gary Gaulin tracksite on two loose slabs, now identified as SSM 2016/11-1 and SSM 2016/11-3, in the summer of 2016. The trails were analyzed by PRG and then turned over the Springfield Science Museum for curation. A manuscript providing a thorough description and discussion of the traces is currently in review in *Northeastern Geoscience*. The trails consist of high-wavelength, high-amplitude grooves that are sometimes crosscut at irregular intervals by short groove segments with a smaller amplitude. They are attributed to the ichnogenus *Undichna*, which Anderson (1976) erected for Early Permian fish trails from South Africa. Those that consist of two intertwined grooves are assigned to *Undichna cf. brittanica*, whereas those consisting of only one groove are assigned to *Undichna unisulca*. The larger grooves are most likely to have been produced by the unpaired caudal or anal fins of a fish, which sweep out large arcs when the animal beats its tail, whereas the smaller grooves could have been produced by the pelvic fins. These trails are among the first fish traces found in the Hartford basin, and only the second occurrence reported in the Newark Supergroup (Benner and de Gilbert, 2009).

Four fish genera, including *Semionotus*, *Redfieldius*, *Ptycholepis*, and *Diplurus*, are recognized in the Hartford and Deerfield basins from body fossils (McDonald, 1992), but not all are likely to have produced the trails. Coelacanths such as *Diplurus* can be rejected because their trails, known from the Middle Triassic of Germany, are unlike *Undichna* (Simon et al., 2003). *Ptycholepis* is known from only three localities in the East Berlin Formation of Connecticut (McDonald, 1992), and its relatively rarity makes it less likely to have made the trails, although it cannot be ruled out. By contrast, both *Semionotus* and *Redfieldius* are common (Olsen et al., 1982; McDonald, 1992), and the trails could have been produced by either of them.

That these fish trails occur at a site containing theropod tracks provides convincing evidence that fish inhabited ephemeral pools through which dinosaurs waded on playa mudflats, and thus supports the hypothesis that Early Jurassic food chains were based on piscivory.

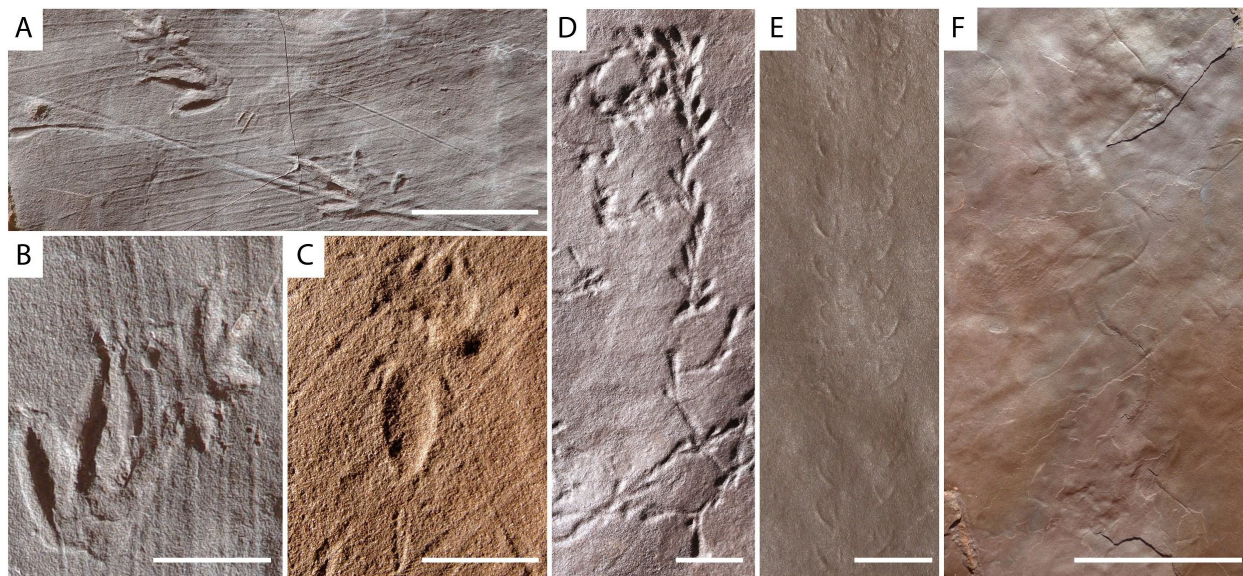
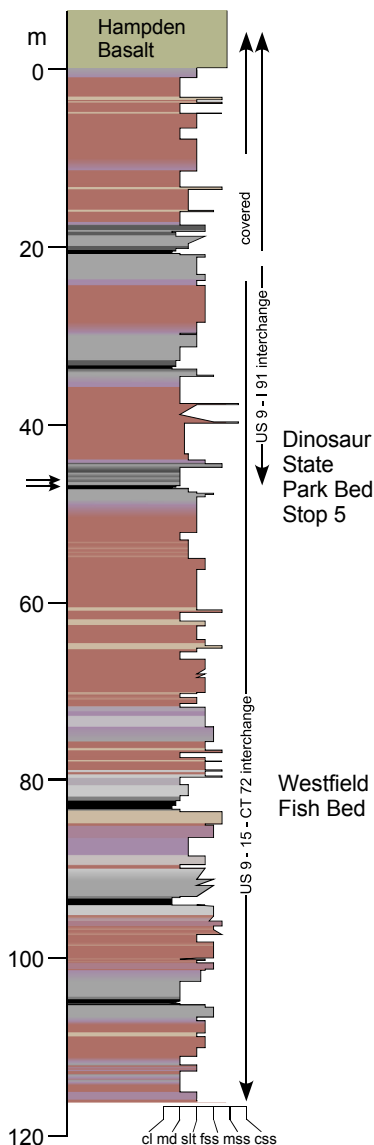


Figure S4.1. Trace fossils from the Gary Gaulin site that are now at the Springfield Science Museum. A: *Anomoeopus lacertoideus*, the trackway of a small ornithischian on SSM 2006/29-1. Note the tail drag. B: Close-up of the hand-foot set from A. C: *Cheliceratichnus lockleyi*, an arthropod body imprint preserved on SSM 2006/29-21. D: *Treptichnus bifurcus*, the burrow of a larval fly preserved on SSM 2013/4-7. E: *Bifurculapes laqueatus*, an insect trackway on SSM 2016/11-4. F: The fish trail *Undichna cf. brittanica* on SSM 2016/11-1. Scales are 5 cm in A and F; 2 cm in B and C; and 1 cm in D and E. Photographs in A–C are by Sebastian Dalman.

Stop 5: Dinosaur State Park (PEO)

The trackways at Dinosaur State Park (DSP) were uncovered in 1966 during excavations for a state building. Sidney S. Quarrier of the Connecticut Geological Survey, Joe Webb Peoples from Wesleyan, and John H. Ostrom of Yale, among others, recognized the site's importance and worked to have it preserved as an *in situ* display in a state park (see McDonald, 2010). Subsequently a large track-bearing surface was preserved beneath the DSP interpretive center (IC) where they are visible today, while the larger original discovery surface was buried for possible future exhibit. DSP is one of the most popular parks in Connecticut, attracting 50,000 visitors a year. *Eubrontes giganteus*, the most abundant track at the site, is now the state fossil.

Stratigraphy (PEO)

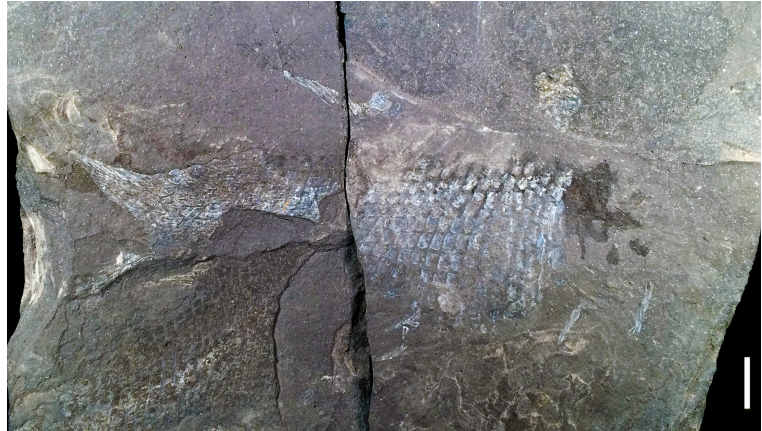


The largely gray strata of the footprint-bearing interval at DSP are located in the upper East Berlin Formation, as is clear from the proximity of the overlying Hampden Basalt. Byrnes (1972) described short cores taken at the site and these show that the footprint layers lie closely above a well-developed black shale, indicating that the tracks occur in the regressive phase of the orbitally paced lake laminated mudstone. However, the precise stratigraphic position of the main track-bearing horizon with the cyclical upper East Berlin sequence has been a bit of conundrum. Byrnes (1972) correlated the track-bearing unit with the uppermost Van Houten cycle that has black mudstone, placing it 17.4 m below the contact with the Hampden Basalt, a correlation followed by Olsen et al. (2003). However, close examination of these sections through Byrnes' descriptions of the cores shows that the thickness of red beds below the track level is too great to be accommodated by Byrnes' proposed correlation and fits better with the third black shale-bearing cycle from the top of the formation (Olsen et al., 2005; Fig. S5.1). Based on Drzewiecki et al. (2012) given a dip of 11° and a map distance of 220 m from the track bed to the mapped base of the Hampden Basalt, the track sequence should lie about 42 m below the basalt, which is consistent with this correlation.

The black shale underlying the track beds at the park was encountered in an excavation on West Street, just west of the park's service entrance. N.G. McDonald found clam shrimp similar to those found in the Westfield Fish Bed, as well as several dephosphatized *Semionotus* (Fig. S5.2), although this is certainly a different cycle.

Figure S5.1. Section exposed at the Rt 15-9 interchange at East Berlin, CT showing the correlative position of the DSP track level (upper arrow) and the fish (lower arrow) illustrated in Fig. S5.2, Colors approximate those of the rock.

Figure S5.2. Largely dephosphatized *Semionotus* from the laminated mudstone below the track beds at DSP found at excavation along West Street. N.G. McDonald collection.



Tracks and trackmakers at DSP (JAH, JOF, and PMG)

Researchers at DSP have long held interest in observing and measuring dinosaur tracks, or *ichnofossils*, to test paleoenvironmental interpretations (McDonald and LeTourneau, 1988), infer whether trackmakers moved in isolation or as groups (Ostrom, 1972; Getty *et al.*, 2012), consider the means by which dinosaurs moved (Coombs, 1980), and identify possible trackmakers (Farlow and Galton, 2003). Although a variety of direct and derived measures of track morphology are possible, most involve physically or digitally measuring footprint/digit lengths, widths, orientations, and pace and stride lengths (Fig. S5.3; S5.4).

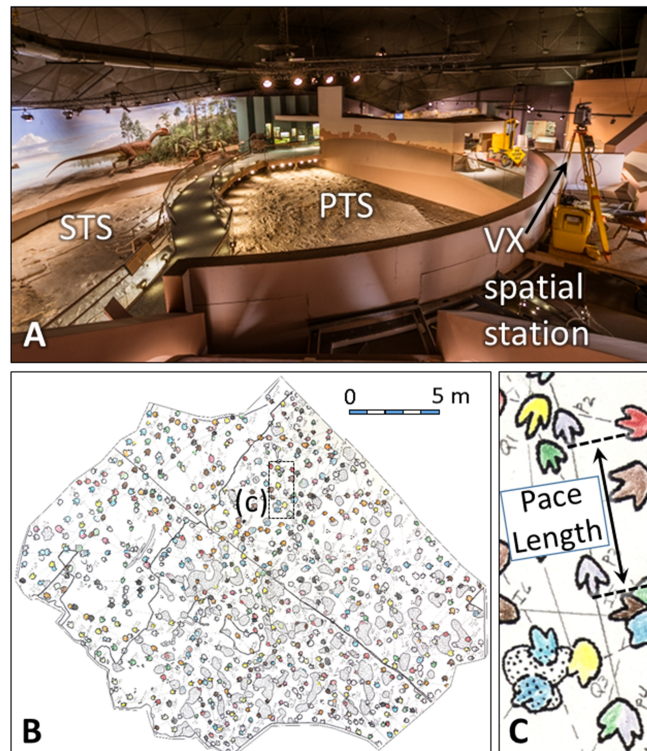


Fig. S5.3. Tracks and trackways in the Interpretive Center. A: View of tracksite including a primary and secondary track surface (PTS and STS) that was surveyed with a Trimble VX spatial station (arrow). B: Trace-map of the tracksite, constructed by Galton. C: Field-notes showing track names and illustrating path length as used by Farlow in a database of track morphometry measures.

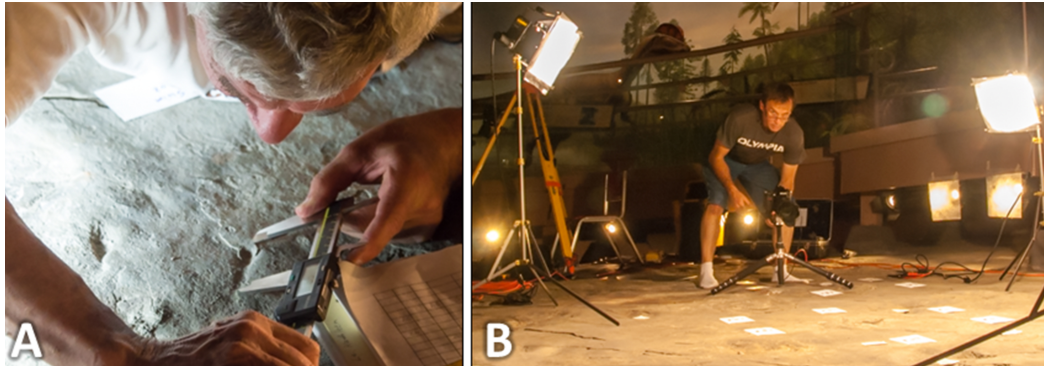


Fig. S5.4. Measuring track dimensions. A: Using traditional tools. B: By constructing photogrammetric models from high-quality digital images.

Footprints at DSP are typically tridactyl (three-toed), and most were clearly made by bipeds walking through soft sandy sediments (Fig. S5.5) in the littoral zone of a playa lake (LeTourneau et al., 2015). Additionally, unusual traces described by Coombs (1980) and discussed below, have been interpreted as traces from swimming dinosaurs (Fig. S5.5A, C).

The tracks cover a rather narrow size range for early Mesozoic tridactyl prints, roughly 30-45 cm in total length. This puts them in the size range of larger ichnospecies of the ichnogenus *Eubrontes* (as interpreted by Rainforth 2005). Although most of the DSP prints are not as beautifully preserved as the best specimens of Newark Supergroup tridactyl footprints in museum collections (Olsen et al., 1998; Rainforth, 2005), they are similar in morphology to large forms of *Eubrontes* (Fig. S5.6A). Most workers have interpreted the makers of large *Eubrontes* as theropods (cf. Olsen et al., 1998), although Weems (2003, 2006) proposed a hypothetical bipedal “prosauropod” dinosaur (herbivorous dinosaurs ancestral to or at least related to sauropods, now referred to as basal sauropodomorphs) with a greatly reduced digit I, as an alternative candidate. While possible, we consider Weems’ hypothesis unlikely, based on comparisons of measurements of the tracks with measurements of dinosaur foot skeletons (Fig. S5.6B). Known prosauropods have so long a digit I for the size of the foot that we would expect it to leave a mark in footprints. Furthermore, “prosauropods”, like ornithischian dinosaurs, have relatively stouter toes than theropods of comparable size. Granted that large *Eubrontes* have relatively fatter toes than do smaller

Eubrontes, we think that the relative width of the foot skeleton of large theropods (when one visualizes it surrounded with flesh) is a better match for big *Eubrontes* than the foot skeleton of a large “prosauropod”. Finally, it should be noted that the ichnotaxon *Otozoum* (Rainforth 2003) fits expectations for basal sauropodomorph footprints.

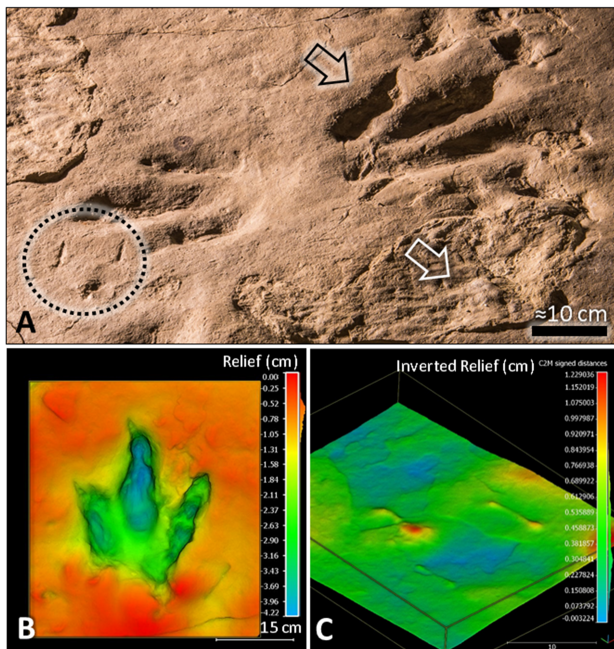


Fig. 5.5. DSP dinosaur tracks. A: Image of two common prints on the IC tracksite that include *Eubrontes* (black arrow) and unusual markings suggested by Coombs (1980) to be swimming traces (circle), and an imperfectly separated piece of overlying rock material covering the track surface (white arrow). B: Photogrammetric topographic data for this *Eubrontes* track. C: A topographically inverted “swim” track illustrating varying depths of indentation for “swim” tracks.

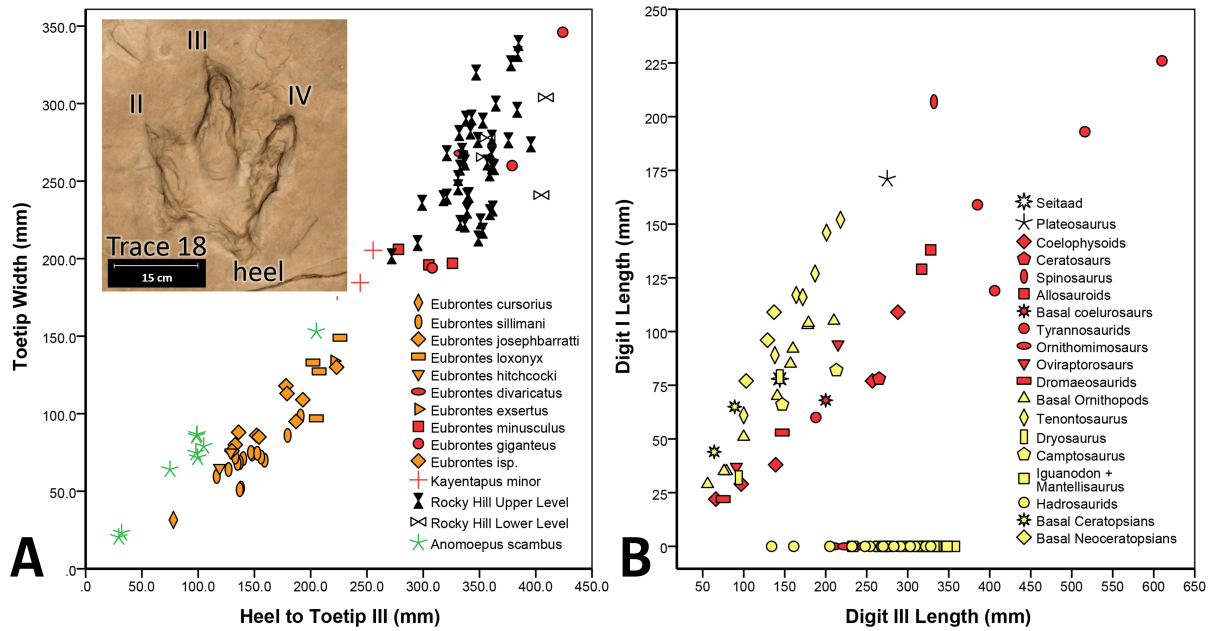
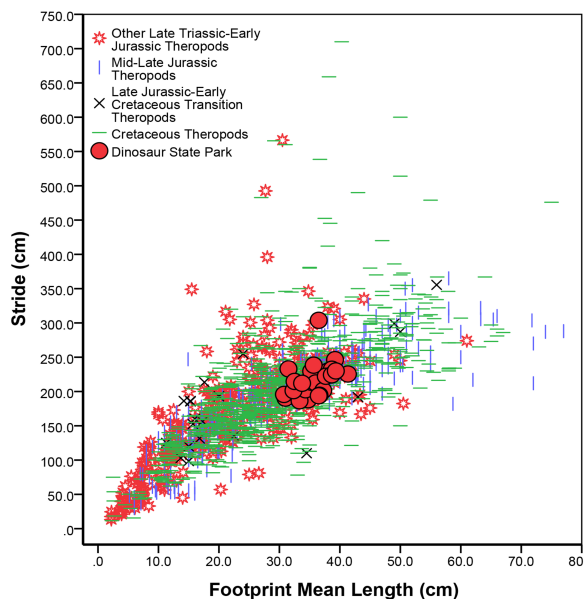


Fig. S5.6. Comparisons of DSP footprints to named Newark Supergroup ichnospecies, and foot skeleton proportions in bipedal/potentially bipedal dinosaurs A: Plot of width across toe tips relative to length. The Rocky Hill tracks clearly fall among large *Eubrontes* in this comparison. B: Digit I length relative to digit III length. Basal sauropodomorph (“prosauropod”) points in black, theropods in red, and ornithischians in yellow. Most data are for dinosaurs much later in time than the DSP trackmakers, but they nonetheless show trends probably applicable to interpreting the makers of early Mesozoic footprints. Some ornithischians and theropods have completely lost digit I (length = 0 in the plot). Prosauropods and most ornithischians generally have a relatively longer digit I than do most theropods.

If the DSP trackways were indeed made by theropods, the locomotor behavior recorded by most of them does not look unusual (Fig. S5.7). Their stride lengths seem consistent with their size, in comparison with other trackways attributed to theropods; none of the DSP trackways has so long a relative stride length as to suggest that its maker was moving unusually quickly. However, a trackway in the larger buried exposure shows an animal with the normal narrow track width preceding and following a section with an increased track width in which the animal presumably slowed down and possibly stopped. In the middle of this section there are imprints of the animal’s forefeet as palm prints that are opposite each other and medially directed (see Galton 2002; Farlow and Galton 2003; Galton and Farlow 2003).

As alluded to above, some DSP footprints, described by Coombs (1980), look odd (Fig. S5.5A, C). These prints consist of three parallel, linear claw (?) marks, the central mark of which projects farther



forward than the two peripheral marks. There can be a small mound of sediment at the back of the peripheral marks. Coombs made the correct interpretation that these odd footprints were made by tridactyl dinosaurs, and further proposed that the trackmakers were swimming in water deep enough that only their claws touched the bottom.

Figure S5.7. Mean stride length in a trackway as a function of mean footprint length (a proxy for trackmaker size) in trackways attributed to theropod dinosaurs. Bigger dinosaurs unsurprisingly took longer steps than smaller dinosaurs, but the relationship flattens out among bigger trackmakers. Scattered points above the “main sequence” presumably reflect running rather than walking animals. The DSP trackways fall among other trackways made by dinosaurs of the same size. Modified from Farlow *et al.* (2015).

Subsequently, trackways attributed to swimming tridactyl dinosaurs have been reported by other workers (e.g., Whyte and Romano, 2001; Milner et al., 2006; Ezquerro et al., 2007; Farlow et al., 2015; Xing et al., 2016). Like the DSP traces, these swimming traces (which Whyte and Romano named *Characichnos*) consist of parallel linear scratches, sometimes with sediment mounds behind them. Also like the DSP traces, swimming dinosaur prints sometimes show irregular step lengths, unlike those of typical walking bipedal dinosaurs.

On the other hand, there are some problems with interpreting the DSP tracks as *Characichnos*. For example, DSP tracks are arranged in nearly linear trackways, whereas *Characichnos* is typically less linear. Additionally, in *Characichnos* the traces made by one side of the body may be oriented at a different angle relative to the overall direction of travel than those on the other side, whereas in the DSP traces on both sides of the trackway are parallel to the direction of movement. Additionally, in *Characichnos* the mark of the central toe often extends about as far backward as the marks of the peripheral toes, unlike the DSP marks, in which the back edge of the central toe mark only goes back as far as the front edge of the peripheral marks. A final issue is timing. It would take a long time (possibly weeks) to raise the level of the lake, which is estimated at least 5000 km², by 1 to 2 m, which it would take to get the body of the theropods involved to float. These time intervals render it unlikely that normal and “swimming” tracks, both small and large, would be preserved on the same bedding plane.

Farlow and Galton (2003) noted that footprints made by a flightless bird in drying plaster showed some similarities to the DSP marks, suggesting that these atypical prints might have been made by dinosaurs walking on a firm substrate. Galton and Farlow (2003) subsequently noted that the small amount of extra desiccation involved, which probably occurred in a few hours or days at the most, would account for the “swimming” trackways involving different sized animals being preserved on the same bedding plane as the other “normal” trackways. They drew attention to just such a situation described by Thulborn and Wade (1989) in the Lower Cretaceous of Lark Quarry in Queensland, Australia. There the small theropod footprints on the firm substrate matched most of the characters shown by the “swimming” footprints at DSP.

The DSP tracks show enough similarities to *Characichnos* that Farlow thinks they might be swim traces, but Galton notes that detailed comparisons are needed of the traces at DSP with known swimming trackways and firm substrate trackways before a definitive answer is possible.

Trackway orientations: why aren't they parallel? (PRG)

Since its discovery in 1966, researchers who studied the site (e.g., Ostrom 1972; Farlow and Galton, 2003; Galton and Farlow, 2003) have noted that the *Eubrontes giganteus* trackways at DSP are randomly oriented. This lack of directionality is in stark contrast to what we saw at DFR (Stop 2), where the trackways are strongly bimodally distributed. If we took the orientations of the trackways at these two sites at face value, we would have evidence for gregariousness at one (Dinosaur Footprint Reservation) and an absence of evidence for it at another (Dinosaur State Park). Assuming that the *E. giganteus* at each of these sites were made by the same trackmaker, there are a couple of hypotheses about why the two track sites show such dissimilar trackway orientations. One is that the surface was exposed for an extended period of time during which several small herds of animals crossed the surface in different directions, thus obscuring any preferred orientations (Ostrom, 1972; Farlow and Galton, 2003; Galton and Farlow, 2003).

Another explanation is that the sedimentary environment in which the trackways were produced could have affected the direction the animals moved in. In arguing that the trackways at Dinosaur Footprint Reservation exhibited preferred orientations due to shoreline-paralleling behavior, Getty et al. (2012, 2017) favored this latter hypothesis. These authors point out that the main track bed at the DFR

site lacks evidence of subaerial exposure, whereas the beds at DSP were made in a playa lake that exhibited evidence of desiccation in the form of mud cracks. They contended that the permanent lake at DFR served as a physical barrier funneling the *E. giganteus* trackmakers to the northeast and southwest. By contrast, Getty et al. (2012, 2017) suggested that the evaporation of the playa lake at DSP permitted the dinosaurs to travel in different directions.

To further test hypotheses that *Eubrontes giganteus* parallelism was controlled by environmental constraints or by gregariousness, Getty et al. (2012) proposed that the orientations of trackways at different sites within the Hartford and Deerfield basins should be analyzed. If parallelism resulted from gregariousness, then other sites from playa lake paleoenvironments should exhibit parallel trackways, especially if there were few enough that the signal wasn't obscured. Significantly, the multiple trackways at two other sites from the playa lake facies of the East Berlin Formation, the Murray Quarry (Getty, 2005) and Powder Hill Dinosaur Park (Getty et al., 2015), lack strongly preferred orientations, and those parallel trackways that do occur exhibit differences in depth and morphology suggesting that the trackways were made at different times. Although preserving only a single *Eubrontes giganteus*, the Gaulin tracksite is as large as the Murray Quarry, which led Getty and Fox (2015) to argue that the track maker was either a lone animal, or at most part of a very dispersed group. Overall, the evidence from the tracksites within the Hartford Basin suggests that the primary control on trackway parallelism was in fact the physical environment, not gregariousness (Getty et al., 2017).

The recognition that the primary control on the trackway orientations at the Dinosaur Footprint Reservation site was environmental has implications for the type of animal that made the tracks. As is noted in other sections of this guide book, most researchers consider that the *Eubrontes giganteus* trackmaker was a theropod. Weems (1987, 1990, 2003), however, has consistently argued that the trackmaker was a basal sauropodomorph, or "prosauropod." Part of his argument is that it would not make sense for large carnivores to live in groups because individual animals would have, given the small size of the herbivores present, less food due to sharing in comparison to animals that lived alone. This becomes a moot point, however, given that the trackway parallelism resulted from animals following a shoreline.

Inverted ecological pyramid (PEO)

As seen at the Beneski Museum and at Dinosaur Footprint Reservation, the DSP assemblage is overwhelmingly dominated by carnivore tracks. The DSP level is at about 201.0 Ma, in the Early Hettangian of the Early Jurassic, or only half a million years after the end-Triassic-extinction. As noted in the introduction, and at Stop 2, this reflects a post-mass extinction community that was water-based, with theropods consuming fish and other carnivores.

Imaging, mapping, modeling and measuring the tracksite (JAH, JOF, and PMG)

The original tracksite, now buried to protect the tracks, was photographed in 1970 on a 3 m grid and a large photo mosaic was assembled (Galton, 2002; Farlow and Galton, 2003). A smaller tracksite uncovered in 1968 is viewable in the IC (Fig. S5.3A). The first map of the IC tracksite was prepared by Galton in 1981 by combining photographs of large hand-drawn traces of track outlines that were compared with a digitally "undistorted" oblique photograph of the tracksite taken in 1967-1968 (Galton and Farlow, 2003). This-map (Fig. S5.3B, C) has appeared in several publications (*e.g.* Galton 2002; Farlow and Galton, 2003; Galton and Farlow, 2003; LeTourneau et al., 2015), and we use it to reference individual tracks reported on herein. We also present new digital maps and models of the IC tracksite that were prepared using photogrammetric and laser survey data. Outcomes from these digital data sets serve the park's educational mission and are part of a continuing effort to understanding the site's paleontology.

Significant advances have occurred recently in the ability to map, measure, and model the three-dimensional character of many geological features (Bird *et al.*, 2010; Westoby *et al.*, 2012; Heritage and Hetherington, 2007). In particular, ground based LiDAR or Terrestrial Laser Scanning (TLS) and new Structure-from-Motion (SfM) digital photogrammetry techniques have vastly improved the resolution and precision of 3D mapping. Moreover, there has been a commensurate evolution in 3D “point cloud” software that has enabled advanced visualization and measurement not previously possible (Bates *et al.*, 2009; Lallensack *et al.*, 2016).

Paleontologists have effectively used TLS and SfM, particularly on dinosaurian trace fossils (Bates *et al.*, 2008; Matthews *et al.*, 2016; Falkingham *et al.*, 2016). This includes detailed mapping of historically significant tracksites (Falkingham *et al.*, 2014), experimental tests on tracks from modern organisms to compare with ancient tracks (Milàn and Falkingham, 2016), and efforts to use 3D modelling to develop “objective” measures of tracks that apply geometric rules to define non-arbitrary track outlines (Lallensack *et al.*, 2016; Falkingham, 2016). The latter is surprisingly difficult because of the complex interactions between the trackmaker’s foot anatomy, the biomechanics of movement, and the nature of interactions with and preservation by the sediments (Falkingham, 2016). At DSP Farlow and Galton (2003) have used conventional techniques to measure tracks (Fig. S5.4A). Other than meeting abstracts (*e.g.* Hyatt and Roseine, 2013; Hyatt *et al.*, 2016), this is the first account of TLS and SfM (Fig. S5.4B) derived measures from this important paleontological site.

In this section, we describe ongoing efforts to use both conventional (*i.e.* caliper, compass, tape measures) and new digital techniques to image, map, model and measure the IC tracksite. To this end, the specific objectives of this field guide contribution are to: (1) introduce the DSP tracks and trackmakers and associated morphometric measures, (2) describe our use of TLS, imaging, and SfM, (3) present associated educational products (maps, displays, models), and (4) summarize initial comparisons of conventional and digital measures of tracks, and describe ongoing efforts to analyze the 3D data sets from DSP.

Surveying, scanning, and imaging the tracksite (JAH, JOF, and PMG) Given the well-documented morphology of many of the DSP tracks (*cf.* Farlow and Galton, 2003), the IC tracksite provides an opportunity to compare detailed physical and digital morphometric measures. All georeferencing data for maps and models were measured directly, derived or related to survey data collected with a Trimble VX Spatial Station (Fig. 5.3A), a versatile robotic total station capable of georeferenced imaging, and slow-speed TLS. In the absence of available benchmarks within the IC, an arbitrary local coordinate system (in orthogonal meters) was established based on the first instrument position and aligning major axes to frame the tracksite. Following set up, ≈ 10 immobile reference points were surveyed for unique points on dioramas surrounding the tracksite to serve as resection points when setting up the VX at new locations. Additionally, eight replicate face-left and face-right measurements for 15 control targets dispersed around the tracksite indicate a relative precision for X-Y-Z measurements of $\approx 5 \text{ mm} \pm 3 \text{ mm}$, although the precision for measurements from a single station position are likely better than this. Also, in conjunction with imagery described below, ≈ 60 ground control points (GCP) were surveyed on the track surface using small colored stickers affixed to the track surface.

Twenty-nine TLS scans were performed with the VX to map the PTS and STS. Most scans were undertaken from a survey platform constructed above a false ceiling adjacent to the PTS (Fig. 5.3A), although it was necessary to conduct additional scans from ground level to fill in sites that were not visible from the platform. The final cleaned TLS point clouds (≈ 1.6 million points, mostly on the PTS) remain somewhat coarse for building detailed 3-dimensional models. However, VX data were essential for locating GCP in images described below.

Imaging the tracksite. Dim overhead lighting and bright spotlights (Fig. S5.4B) present challenges for imaging the IC tracksite. SfM techniques require sharply-focused, overlapping images that lack high contrast zones (like spotlight-produced shadows) and have minimal digital noise that arises in dim-lighting. To overcome these problems, we used three different methods for imaging. First, for TLS models (only), georeferenced images from the VX were used to locate GCPs. Second, we took near-vertical images in RAW format using a Nikon D600 full frame DSLR camera (35 mm prime lens) mounted on an ≈ 6.5 m tall monopod. To minimize motion-blur caused by sway of the monopod, images were captured with rapid shutter speeds (1/250s), compensated for with wide apertures (f/1.8) and high ISO (3200). The images were post-processed using Adobe Lightroom to filter ISO noise, adjust exposures to lighten shadows, dim spotlights, and warm white balance settings. These changes were synchronized for all images before exporting as high-resolution jpg and tif files. The monopod images worked well for constructing a photo-map for new museum displays, although derived SfM models have some data holes that limit 3D printing and detailed volume estimation. Accordingly, our third approach to imaging used the D600 with a zoom lens and focal lengths ranging from 50-65 mm mounted on a conventional tripod (Fig. S5.4B). High quality RAW images were captured with low ISO (100), narrow apertures (f/16), and long exposure times (0.5-1.5 seconds). Ground level images were collected from low-, mid-, and high-angle positions. Also, for these images, we draped filter cloth over the track-level spotlights, and used three or four portable tungsten studio lights with diffusers to fill shadows and provide even lighting (Fig. S5.4B). In total, we collected ≈ 580 images from 10 sites; all of which yielded excellent SfM models with confirmed sub-mm precision.

Image map construction. Monopod images and VX survey data were used to construct a rectified image map of the entire IC tracksite (Fig. S5.8). The map was assembled piecemeal before warping into registered survey space. Processed images were separated into spatially organized groups and aligned/blended in Photoshop. Blending masks were edited to remove extraneous features (e.g. the monopod, field assistants, etc.) to create multi-image blocks. All image blocks were flattened, combined (several times), re-aligned, and re-blended to create a single somewhat distorted image mosaic for the PTS and STS. Once assembled, each mosaic was calibrated (i.e. georeferenced) using GCPs. Where necessary, additional GCP calibration points were identified using georeferenced VX images. Each mosaic was then rectified in survey space, merged, and incorporated into educational products for the park as described below.

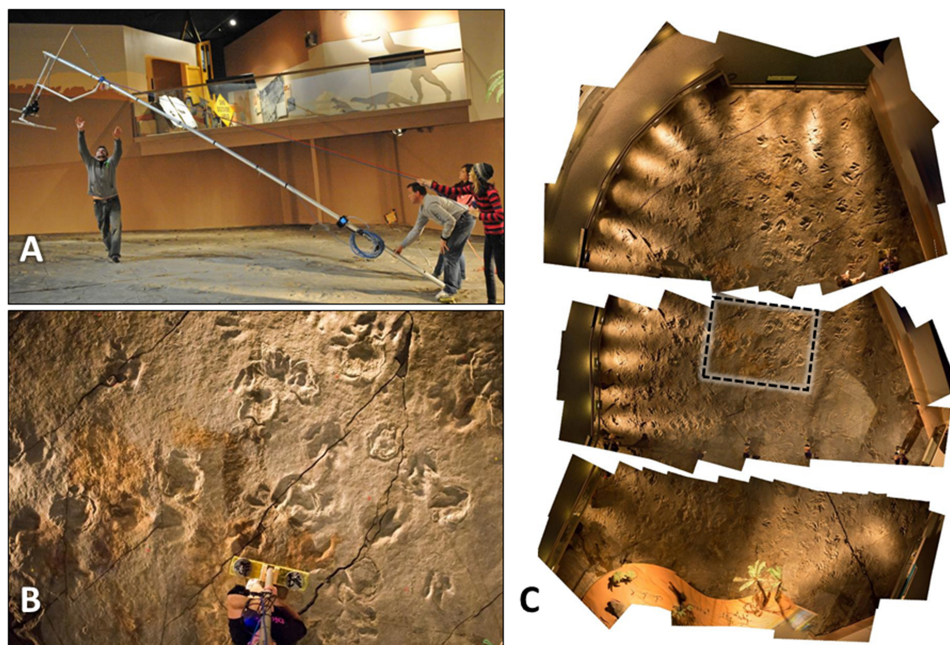


Figure S5.8. Image map construction. A: Raising a 6.5m monopod to take photos. B: Photograph of part of the track surface. Small yellow and red GPC dots were surveyed using the VX spatial station. C: Assembling images into mosaics in Photoshop so that a map of the entire IC tracksite could be made by creating a single image that was rectified using survey data.

SfM photogrammetry and point cloud workflow. Construction of all SfM data sets were performed with Agisoft Photoscan professional (AP), whereas subsequent manipulations were made with Cloud Compare, Surfer, and Blender software. A brief description of our workflow follows. See detailed accounts describing SfM imaging techniques in Falkingham (2012) and Matthews et al. (2016), as well as the quantitative and qualitative basis for SfM modelling in Snavely et al. (2008) and Fonstad et al. (2013).

AP is an increasingly popular SfM digital photogrammetry package that makes use of overlapping images to construct dense 3D point clouds that can be registered in survey space. Our AP workflow involves: adding and aligning overlapping images to create an initial cloud of tie-points, optimizing the quality of these tie points and generating a dense point cloud, cleaning the dense cloud and creating a triangulated mesh, filling holes, deleting unnecessary mesh elements, and texturing the model with RGB color data, and using GCP or scale bars in the imagery to transform models from pixel to scaled coordinates. Each step involves choices that influence the final model, although the quality and degree of overlap of initial images is important if models are to support detailed measurement.

AP also supports exporting models as point clouds, surface models, and orthorectified imagery in a wide variety of file formats for viewing (e.g. 3D-pdf, kmz, dem, geotif formats) and for analysis in other 3D and/or surface modeling packages. Our workflow involved importing AP point cloud models (in .ply format), transforming the model to a common origin, detrending the slope of the tracksite by creating a scaler (a measured matrix) of the distance from the track to a best-fit plane, constructing an orthorectified grid (typically with 1 mm point spacing), and exporting data for contour and/or additional visualizations or volume calculations. Similar to our AP workflow, these steps involve many decisions that influence the final model.

3D print workflow. Point-cloud derived models of tracks at DSP, whether developed photogrammetrically or scanned, are well suited to creating rapid prototypes (3D prints) of targeted tracks. To this end we generated stereolithography (.stl) 3D print files for several data sets. The general workflow begins in AP or Survey software by creating and cleaning a mesh for export as a surface file usually in .obj or .ply formats. These surface files have no thickness and will not print properly. Accordingly, in Blender (freeware) we create printable volumes by using a Boolean intersection operator to slice a solid volume with the surface model. 3D scale bars are added (Fig. S5.9) and the project is exported as an stl print file. There are many options for 3D printing. We use an additive Makerbot to create test prints, although higher quality prints are better obtained through commercial online 3D printing outlets (e.g. shapeways, ponoko, etc.).

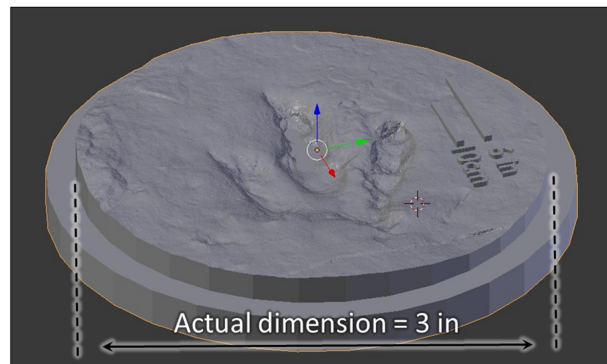


Figure S5.9. Blender model of a *Eubrontes* scaled to fit within a 3-inch PVC ring slid onto the model. This will aid school groups to cast the models using small amounts of modeling clay. Scale bars are included so that the size of the model can be compared with its real dimensions.

Comparing physical and digital tracks and developing objective measures (JAH, JOF, and PMG)

We have begun to compare digitally derived measures from SfM models (by Hyatt) with physical measurements of tracks at DSP (by Farlow). Initial comparisons focused on simple morphometrics that include footprint length, width, and pace length (Fig. S5.11). Although Farlow has many years of experience measuring tracks, Hyatt does not. Consequently, comparisons in Fig. S5.11 are influenced both by the measurement technique and expertise in selecting appropriate landmark positions (i.e. heel, II, III, IV). Overall, initial 2-sample pair-wise t-tests indicate no significant difference between physical/expert and digital/novice measures for footprint length ($p \approx 0.210$), but weakly significant differences for footprint width ($p \approx 0.051$) and pace ($p \approx 0.050$). Descriptive statistics for physical and digital measures (in Fig. S5.11) indicate that, on average, all three parameters differ by less than 15 mm (1.3 – 5.4% of the original measure). This indicates that digitally derived values provide reasonable approximations of physical measurements. It is likely, however, that much of the observed difference might be caused by the subjective nature of selecting track landmarks. Thus, we plan new comparisons that use landmarks identified on digital models by Farlow. These will compare physical and digital measures made by the same investigator on the same tracks, albeit at different times.

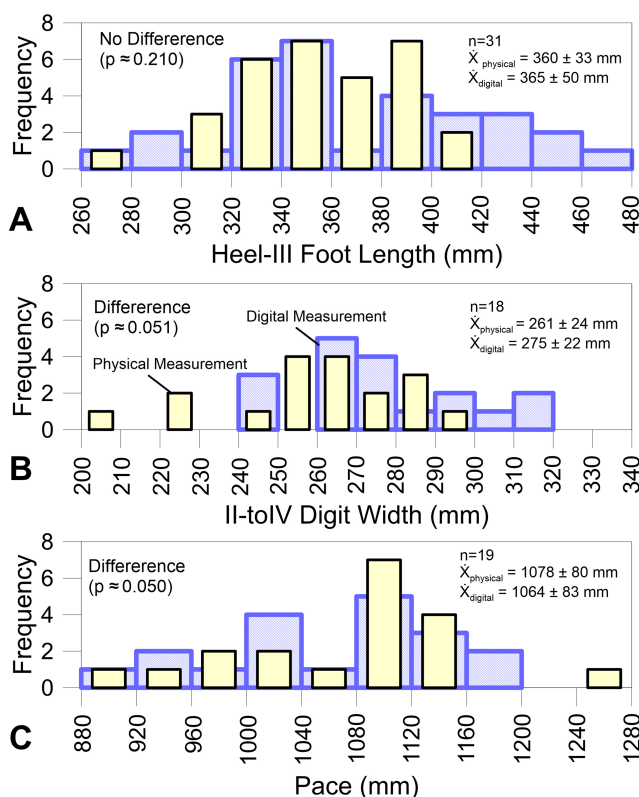
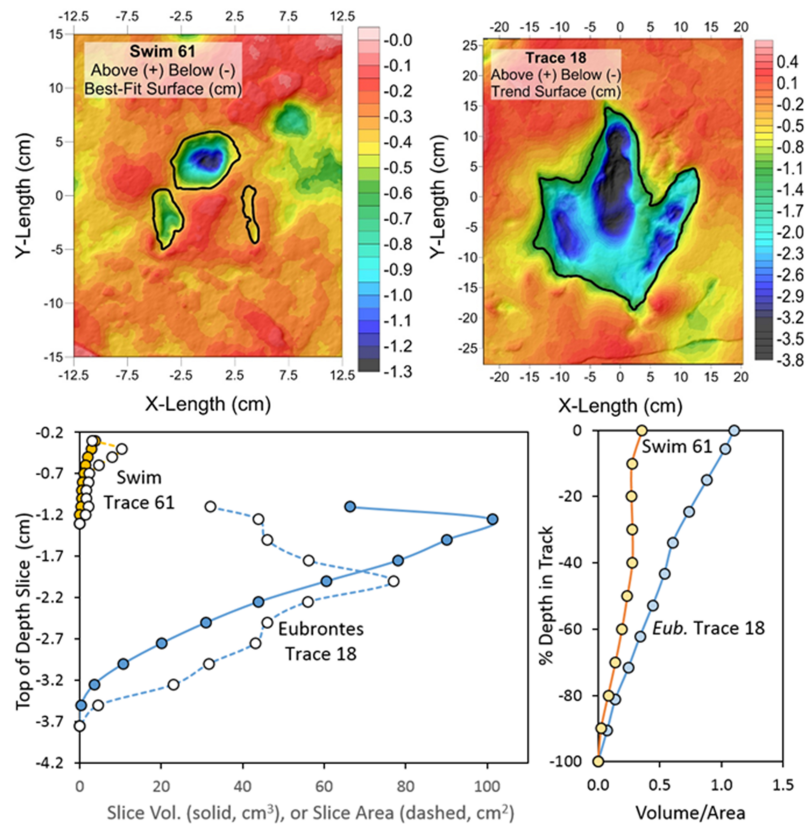


Figure S5.11. Comparisons of conventional physical (yellow boxes) and digital SfM (blue boxes) measurements for selected *Eubrontes*. A: Footprint length. B: Footprint width. C: Pace length. Mean and standard deviations for each group (upper right of each box), and results of pair-wise two-sample t-tests (upper left of each box) indicate no significant difference for measures of foot length, and weak differences for other measures.

Although 3D SfM data sets enable detailed measurement of tracks, most morphometric assessments rely on subjective interpretations of track outlines, which some have argued might be difficult to replicate. Indeed, Falkingham (2016) identifies 5 common approaches to identifying track outlines. He argues that new “objective” measures should be used to bracket morphometric measures related to track boundaries. These objective measures are developed by applying geometric rules to detailed 3D models of tracks. We are developing objective measures and associated morphometric data for tracks at DSP following the methodology of Lallensack *et al.*, 2016 (Fig. S5.12). This involves defining a non-arbitrary reference plane in X-Y space that is coincident with the original sediment

surface. The model is rotated into this plane, and distances are measured from the track to the reference plane to create color-coded visualizations for track depth normal to the reference plane. Track outlines (bold lines in Fig. S5.12A, B) are defined by contour lines and variations in slope within the track. Point cloud data are then orthorectified, rasterized, and extracted for contouring and length/area/volume analyses. Although we have just begun these procedures, it is clear that many morphometric measures might be derived from these objective 3D data sets. Such measures might be helpful in distinguishing trackmakers, perhaps even individuals, in a fashion similar to that depicted in Figs. S5.6 and S5.7. To illustrate, Fig. S5.12C, D presents depth-sliced measures (below the objective outline) of track area and volume for a *Eubrontes* and “swim” track from DSP. Not surprisingly, area and volume changes with depth differ substantially for these two tracks (Fig. S5.12C), even when the data are rescaled to consider volume-to-depth ratios for normalized track depth (Fig. S5.12D). The utility of these morphometric curves will be tested further as we continue to merge 3D data with the morphometric database prepared by Farlow.

Figure S5.12. Depth colored and SfM data plots identifying objective outlines of tracks.
 A: Possible swim track.
 B: *Eubrontes* track.
 C: Calculated volume (filled circles) and area (open circles) for the digital models.
 D: Ratios of volume/Area illustrate one of many 3-dimensionally derived morphometric measures that might be used to separate tracks and help to identify trackmakers.



Summary and Future Work (JAH, JOF, and PMG)

The IC tracksite at DSP has been measured and mapped using the 3D modeling techniques TLS and SfM. *Eubrontes* and theropod “swim” tracks are the most common tracks. Conventional morphometric measures and detailed observations by Farlow and Galton (2013) provide insight into the comparative size, direction of travel, and likely locomotor behavior of trackmakers at the site. New digital data sets described herein, although still being developed, have produced a scaled image map of the IC tracksite that has been spatially aligned with a previous trace-map by Galton (center part of Fig. S5.10) and is being used to augment a database of track measures developed by Farlow. We have also developed a poster and 3D prints to support educational activities at DSP, and are in the process of creating objective track measures to enhance the DSP track morphology database. In addition, future analysis of 3D morphometrics and spatial trends for specific tracks, analyzed within a GIS framework, might provide new insights as to the continuing debate and enigmatic origin of swim tracks at DSP.

ACKNOWLEDGMENTS

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S.M.G. and P.F. thank Kate Wellspring, Hayley Singleton, Tekla Harms, and Anna Martini of the Beneski Museum of Natural History for their gracious welcome to the Hitchcock Ichnology Collection. Robert Kambic and Beth Brainerd (Brown University) and Dan Goldman (Georgia Tech) provided valuable experimental assistance. Research was supported by the National Science Foundation and the Marie Curie International Outgoing Fellowship program.

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P.E.O. thanks Nicholas G. McDonald for helpful and vigorous discussions and especially for access to his fossil collections and information. This is a contribution to UNESCO-IUGS-IGCP Project 632.

ROAD LOG

Stop 1: Beneski Museum of Natural History, Amherst College (9:00AM)

42°22'22.69"N 72°30'43.98"W (Latitude and longitude are for parking lot)

Assemble at Hills Parking lot, off of College Street (Route 9) for entry into museum. Guidebooks will be distributed here. We will then exit the parking lot onto the sidewalk paralleling Route 9 west and walk 125 feet, and then turn left onto East Drive. Then we will walk 416 feet and turn right onto Barrett Hill Road. The entrance to the museum is approximately 270 feet west of the intersection, on Barrett Hill Road.

Mileage

- 0.0 Head west on College Street toward Dickinson St.
- 0.4 Continue onto MA-9 W Northampton Rd
- 6.5 Turn left to merge onto I-91 S toward Holyoke/Springfield
- 8.5 Take exit 18 for US-5 toward Northampton/Easthampton
- 8.8 Turn right onto US-5 S, Mt. Tom Rd
- 14.0 Turn left into Parking Lot

Stop 2: Dinosaur Footprint Reservation, Holyoke (10:55AM)

42°14'29.91"N 72°37'25.16"W

We will park in the U-shaped pull off on the north side of Rte. 5. Please note that collecting and hammering are not permitted here.

- 14.0 Head southwest on Northampton Street toward Mountain Park Rd.
- 14.6 Turn right onto Mt. Park Rd.
- 15.2 Turn right onto Mt. Tom Ski Rd.
- 15.8 Continue onto Mt. Park Rd.
- 15.9 Turn left into the parking lot next to the quarry

Stop 3: Little Tom Preserve, Holyoke (12:30PM)

42°15'09.32"N 72°37'51.54"W

We will have lunch at this spot.

- 15.9 Head south out of the parking lot
- 16.0 Turn left toward Mt. Park Rd.
- 16.2 Continue straight onto Mt. Park Rd.
- 16.6 Continue straight onto Mt. Tom Ski Rd.
- 16.9 Turn left onto Mt. Park Rd.
- 17.5 Turn right onto Northampton St.
- 19.0 Turn right onto Hampden St.
- 19.2 Take the I-91S ramp, on the left, toward Springfield
- 19.4 Merge onto I-91S
- 27.7 Take exit 8 for I-291/US 20E
- 28.3 Keep right to continue on exit 2, follow signs for Chestnut St.
- 28.4 Merge onto Chestnut St.
- 28.5 Turn right onto Liberty St.
- 28.6 Turn left onto Dwight St.
- 29.2 Turn left onto State St.
- 29.4 Turn left onto Elliot St.
- 29.5 Elliot St. turns left and becomes Edwards St.
- 29.6 Turn left into parking lot

Stop 4: Springfield Science Museum (2:20PM)

42°06'16.72"N 72°35'12.42"W (Latitude and longitude are for main parking lot)

There are two parking lots that we can use. One is adjacent to the building and the other is directly across Edwards Street. If both of these lots are full, additional parking can be found along Edwards Street.

- 29.1 Head southeast toward Edwards St.
- 29.2 Turn left onto Edwards St.
- 29.3 Turn right onto Chestnut St.
- 29.3 Turn left onto Harrison Ave.
- 29.5 Continue onto Boland Way
- 29.6 Continue onto Memorial Bridge
- 29.7 Turn west onto W Columbus Ave./Hall of Fame Ave.
- 30.1 Merge onto I-91 S via ramp on the left
- 30.3 Merge onto I-19 S
- 63.8 Take exit 23 for West St.
- 64.0 Turn left onto state highway 411/West St.
- 64.9 Turn right

Stop 5: Dinosaur State Park (4:30PM)

41°39'05.77"N 72°39'21.14"W (Latitude and longitude are for main parking lot)

This is our last stop. Parking is adjacent to the building.

APPENDIX 1: HISTORICAL CONTEXT (PML)

The First Tracks from the Connecticut Valley (PML)

I...know that geologists derive much satisfaction from contemplating these remains.

– Dr. James Deane, Greenfield, Massachusetts, 1835

The northern Connecticut Valley played an important role in the development of early American geology and paleontology. There, Amherst College professor Edward Hitchcock (1793-1864) scoured the local creeks and quarries, accumulating a collection of thousands of dinosaur tracks and other ichnological (trace fossil) material. His popular treatise, *The Ichnology of New England* (1858) was notable for its descriptions and lithographic plates illustrating the variety of tracks and other trace fossils from the Connecticut Valley. Although his *Ichnology* has been long surpassed by modern studies, it remains an important milestone in the history of American paleontology.

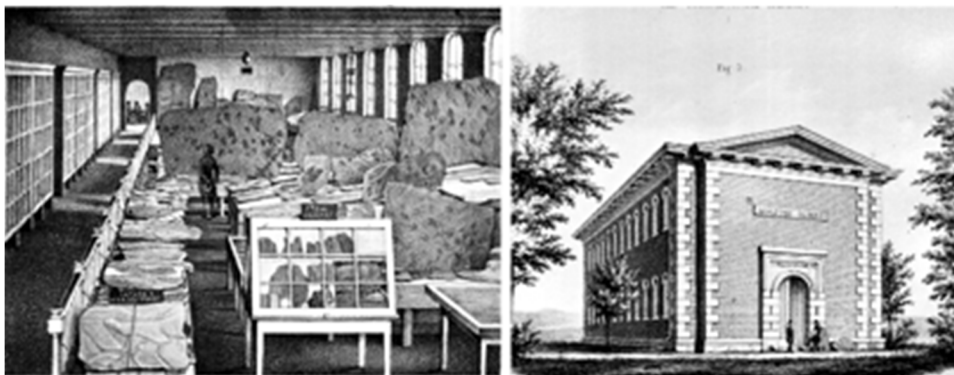


Figure A1.
Hitchcock's
Ichnological
Cabinet. Left: The
collection in 1858.
Right: The Appleton
Cabinet museum,
circa 1855.

Hitchcock's incomparable "Ichnological Cabinet" of thousands of specimens formed the foundation of the natural history collections at the college, occupying the entire lower floor of the 1855 "Appleton Cabinet," an early natural history museum (Hitchcock, 1858; Fig. A1). Today, over 160 years since it was first presented, Hitchcock's collection remains a popular exhibit at the new Beneski Museum of Natural History, built in 2006. One of the most popular exhibits in the Hitchcock Cabinet is the cleverly mounted "book" of rock layers, each "page" displaying dinosaur tracks.

According to Hitchcock (1844a), it is in the northern Connecticut Valley that young farmer Pliny Moody uncovered the first dinosaur footprints, then "bird tracks", while plowing a field in South Hadley in 1802 (Figs. A2–A3). Hitchcock recounts the provenance of the Moody tracks with an amusing anecdote: "...a stone, containing in relief five tracks of the *Ornithoidichnites fucoides*, (see Plate 48, fig. 55 of my *Final Report*)...was put down as a door-step...Because it contained tracks...the neighbors used facetiously to remark to Mr. Moody, that he must have heavy poultry that could make such tracks on stone." (Hitchcock, 1844a, p. 297).

Tracks were certainly noticed by quarry workers prior to the Moody find – track-bearing flagstones had been placed on the sidewalks of Northampton and Middletown as curiosities, possibly as early as the 1700s (Hitchcock, 1836). Nevertheless, the Moody-Dwight tracks remain the first finds that found their way into the scientific circles of early 19th century.



Figure A2. The Moody Farm track locality at South Hadley, Massachusetts. The slab shows a large prosauropod (*Otozoum*) trackway and smaller theropod (*Grallator*) tracks. Detail from Hitchcock, 1858.

These tracks (fig. 7 in Hitchcock, 1836, and Cat. 16/2 Hitchcock Collection, Beneski Museum) are likely the first evidence of dinosaurs, albeit trace fossils, found in North America, although they were not recognized as such at the time. This occurred some twenty years before Buckland's (1822) *Megalosaurus* was named in England, forty years before Richard Owen's (1842) definition of the *Dinosauria*, and fifty-six years before Foulke and Leidy's (1858) discovery and description of *Hadrosaurus* bones in Haddonfield, New Jersey.

Originally called bird tracks or "turkey prints," the three-toed imprints were popularized as the tracks of "Noah's Raven," by Dr. Elihu Dwight, who purchased the Moody slab around 1809 (Hitchcock, 1844a). The biblical moniker not only conformed to the theological view of Earth history prevailing prior to the emergence of modern scientific studies but was quite plausibly a clever attempt by Dwight at "branding" to increase the value of the specimen. The ploy, if indeed it was, had the intended effect – Edward Hitchcock of Amherst College purchased the specimen from Dwight around 1839 (Hitchcock, 1844a). Hitchcock's acquisition of the Moody tracks postdates his first paper (1836) on Connecticut Valley tracks.

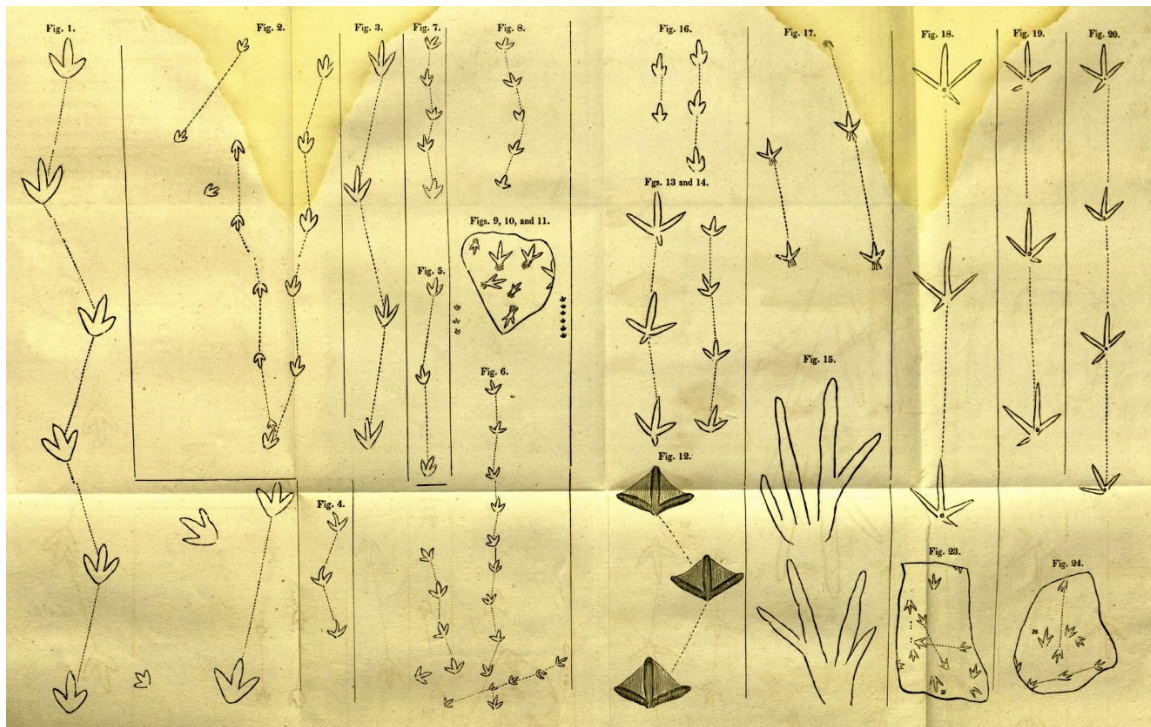


Figure A3. First illustrations of dinosaur tracks from the Connecticut Valley (Hitchcock, 1836). Pliny Moody's tracks are labeled fig. 7. Figs. 4 and 5, found in Northampton sidewalks, are from Mt. Tom. Fig. 17, from Montague, is possibly a Wilson-Deane trackway. Figs. 12–14 and 18–20 are sketches of recent bird tracks. Image: Biodiversity Heritage Library.

The second documented discovery of dinosaur tracks in the Connecticut Valley was made in 1834 by William Wilson and Dr. James Deane, both of Greenfield, Massachusetts. Wilson had been contracted to obtain flagstones from the quarry in nearby Montague, and when he went to inspect the product, "*he noticed very distinct tracks upon them, which he referred to 'the turkey tribe' "*" (Hitchcock, 1844a). Wilson then brought the tracks to the attention of his learned neighbor, Dr. Deane, who, in turn, wrote of their discovery in a letter to Professor Edward Hitchcock dated March 7, 1835 (Deane, 1844a; Hitchcock, 1844a). It is important to note that Hitchcock first learned of Connecticut Valley tracks from Deane in 1835. Once Hitchcock learned of their occurrence he began to vigorously search for tracks throughout the Amherst area, and at Gill and Montague near Turner's Falls. Within a few years, the tracks became a point of contention between Deane and Hitchcock, each claiming priority for their discovery (Deane, 1844a; Hitchcock, 1844a, 1844b).

The third find of tracks was brought to Hitchcock's attention by Col. John Wilson of Deerfield, who purchased quarry stones in Gill, MA from an area known as 'Horse Race' along the banks of the Connecticut River (Hitchcock, 1836, p. 308). Some of these tracks from the "Horse Race" are shown in Fig. A3, above (Hitchcock's figs. 3, 8, Plate 1).

Hitchcock (1836, p. 308-309) goes on to describe some of his own track finds in 1834–1836. Hitchcock states he found tracks in 1835, as follows: 1) In Northampton, on flagstones obtained from a quarry on the east side of Mount Tom (Hitchcock's figs. 1, 2, 4, 5 in Fig. A3, above); 2) in shale from the South Hadley canal; and, 3) in coarse sandstone from South Hadley near Mount Holyoke (Hitchcock, 1836, p. 309).

Acknowledging Moody, Dwight, and Wilson as the first to discover track impressions in the Connecticut Valley, Hitchcock notes that they regarded the specimens only as "objects of curiosity" (Hitchcock, 1844a). Hitchcock credits Deane as the first to recognize their scientific importance by bringing the Montague tracks to his attention, and making detailed plaster casts of the slab that he sent to both Hitchcock at Amherst and Silliman at Yale. The issue of who was the first to discover ancient tracks in the Connecticut Valley was much on Hitchcock's mind – he writes in detail about priority in 1844 (Hitchcock, 1844a, 1844b), and in his 1858 *Ichnology*. The same issues of priority surrounded the earliest discoveries of dinosaur bones in England in the early 1800s (Delair and Sarjeant, 1975). The fundamental problem, as Hitchcock lays it out is this: if a person finds a fossil, but does not know what it is beyond an object of curiosity, can that person lay claim to its discovery?

Stating that, "*The first account of the fossil footmarks on the new red sandstone of Connecticut river, was published by me in 1836,*" Hitchcock, continued to defend his claim, an argument that he called "*...a long and unpleasant digression.*" (Hitchcock, 1844a, p. 294, 301). Dr. Deane was obviously sorely vexed that Hitchcock claimed to be the discoverer of, what were then believed, ancient bird tracks (Deane, 1844a, 1844b; Hitchcock, 1844a, 1844b). Until their falling out over the claim of priority, Deane and Hitchcock were apparently on good terms. Deane also supplied Hitchcock with a number of additional specimens of tracks, plant fossils, and other trace fossils at least through 1841 (Deane, 1844a). After savaging each other in the pages of the *AJS*, both Deane (1844b, p. 401) and Hitchcock (1844b, p. 399) propose discussing the matter in private, as friends. The vigor with which each sought priority, and the intense interest in the tracks, at home and abroad, reveals the importance of the fossils to the development of modern geology and paleontology.

By the late 1830s and early 1840s, there was an explosion in the new field of ichnology. Finds of tracks were occurring in Europe and North America at what Hitchcock considered a dizzying pace, in light of his rapidly increasing collection.

Deane never placed his tracks in the appropriate biostratigraphic context, and until the end of his career, Hitchcock thought he had extended the stratigraphic range of birds into the New Red Sandstone (Jura-Trias in the Connecticut Valley). Although Hitchcock studied and illustrated dinosaur bones found in East Windsor, Ellington, and Springfield, he never made the leap of associating them with the tracks. It wasn't until Cope (1867) suggested that prosauropods were likely trackmakers that the tracks were attributed to dinosaurs.

The Connecticut Valley Trackmakers: Birds, Reptiles, or Bird-Like Reptiles? (PML)

...here are we introduced to birds of the Liassic ages that were scarce less gigantic than the roc of Sinbad the Sailor.

– Hugh Miller, *Testimony of the Rocks*, 1857

Hitchcock faulted Deane's description of the Montague tracks as those of birds, but with the dinosaur model yet to emerge, Hitchcock himself had no choice but to reluctantly assign the obviously bipedal tracks to extinct birds, specifically some long-legged variety of ancient ostrich or bustard (Hitchcock, 1858). Having identified two classes of tracks, those of "*Ornithoidichnites*, or tracks resembling those of birds; and *Saurioidichnites*, or tracks resembling those of Saurians," in his 1841 *Final Report on the Geology of Massachusetts*, Hitchcock hinted at the diversity of animals represented in the Early Mesozoic tracks.

It is noteworthy that Hitchcock's early work on the tracks (1836-1858) occurred when geology was in its infancy, and before Darwin (1859) published his *Origin of Species*. Concepts regarding the age and continuity of strata were debated in the early 1800s, and working concepts of stratigraphy and geologic time that we take for granted today were not firmly established.

Hitchcock understood that no fossil remains of birds were known from the New Red Sandstone (Permo-Triassic) in England or Europe: "...no trace of birds had hitherto been found deeper than the *Wealden* [Lower Cretaceous] formation" (Hitchcock, 1844a, p. 294). Hitchcock realized that pushing the origin of birds back into the Liassic presented great difficulties, especially in light of the lack of skeletal remains. Although, the ancient bird model would prevail throughout the remainder of Hitchcock's writings, the remarkable discovery of *Archeopteryx* in 1861 motivated him to further reflect on the origin of the tracks (Hitchcock, 1863). Finally, Hitchcock had a prehistoric bird, or a bird-like reptile of sufficiently ancient origins to shed light on the Connecticut Valley trackmakers.

In his 1863 paper, Hitchcock considered the implications of *Archaeopteryx* on his Connecticut Valley tracks: "*The recent discovery of a remarkable animal, called...Archaeopteryx...throws some light, I think, upon the thick-toed Lithichnozoa* [bird-like tracks of the Connecticut Valley], *while these [the tracks] reflect some light upon the feathered fossil*" (Hitchcock, 1863, p. 50). Indicating that scientists were divided on the classification of *Archeopteryx*, Hitchcock continued: "*For it had feathers, yet some of the ablest zoologists pronounced it a reptile. Others...believe it to have a predominance of ornithic characters, so...make it a bird.*" (Hitchcock, 1863, p. 51).

Comparing *Archeopteryx* to his tracks Hitchcock writes, "*Now between these characters [three forward-pointing toes, a long tail] and those of some of our [tracks], there are some remarkable analogies or resemblances as far as I can judge...*" (Hitchcock, 1863, p. 51). Although *Archeopteryx* solved some of Hitchcock's problems, namely bipedal gait and the presence of tail drags in some of the trackways, it raised other vexing puzzles – the first feathered reptile seemed too primitive for his trackmakers, especially his problematic *Anomoepus*, and the fact that birds do not have long bony tails.

He continued to strengthen his case for bipedalism in many of his trackmakers, noting of the front limbs of the trackmakers: "*...we have conclusive evidence that [fore-feet were] not used for walking,*

except perhaps occasionally, and imperfectly." In more than forty steps, Hitchcock's *Anomoepus* only displays two imprints of its front feet, and those in its resting pose, causing him to declare: "Indeed, we may safely assume that the principal object of the fore-feet was not locomotion...even in the gigantic *Otozoum*." (Hitchcock, 1863, p. 52). Unable to reconcile the characteristics of his tracks with the new find of *Archeopteryx*, Hitchcock then resorted to referring his tridactyl trackmakers to a separate division of birds that were more advanced in the Liassic than either *Archeopteryx* "...and perhaps the *Anomoepus*..." (Hitchcock, 1863, p. 55).

An addendum to Hitchcock's 1863 paper, written by the foremost mineralogist of the day, Yale's James D. Dana, states of *Archeopteryx* and Hitchcock's trackmakers: "Now by the recent discovery of the feathered fossil of *Solenhofen*, we have a corresponding inferior division of birds intermediate between birds and reptiles... The world will have finally to settle down to the belief that there were Reptilian Birds in ancient times..." (Dana, 1863a, p. 56-57). Surprisingly, in light of Dana's statement, he was apparently troubled by intermediate forms, like *Archeopteryx*, that suggested transformation (i.e. evolution) over time. In the same volume of the *AJS*, Dana concludes of his "Reptilian Birds": "We find in the facts no support for the Darwinian hypothesis with regard to the origin of the system of life" (Dana, 1863b, p. 321). Thus, by dismissing *Archeopteryx* as an evolutionary step, Dana shows his support for the special creation of extinct organisms. Nevertheless, by the end of the 19th century, Dana would become an ardent supporter of Darwin's theory of evolution (e.g. Dana, 1895).

While Hitchcock was documenting tracks and other trace fossils in the Connecticut Valley, some of the earliest evidence for Mesozoic dinosaurs was emerging from England. In the years 1818–1820, William Buckland retrieved bones from a large animal, subsequently named *Megalodon* in 1822 by James Parkinson (of Parkinson's disease fame) (Delair and Sargeant, 1975). *Iguanodon* bones were recovered by Buckland in the Wealden beds on the Isle of Wight in 1821. Gideon Mantell recovered and described partial skeletal remains of *Iguanodon* in 1822–1825; there is some evidence (in the form of an anonymous note) that Mantell may have found both *Megalosaurus* and *Iguanodon* bones before 1822 (Delair and Sargeant, 1975). Several years later, Mantell (1833, p. 268) reported the initial discovery of *Iguanodon* teeth by his wife.

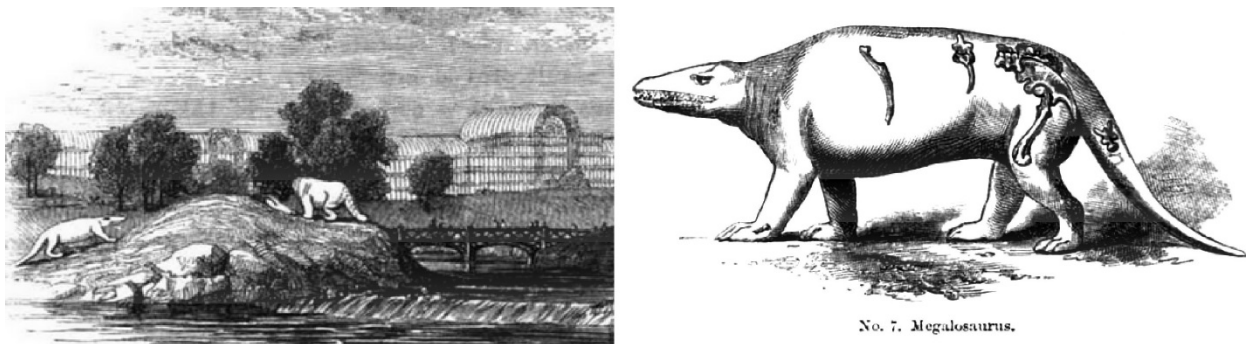


Figure A4. First reconstructions of dinosaurs. Left: Benjamin Waterhouse Hawkins' models of *Megalosaurus* (far left) and *Iguanodon* (center), portrayed as quadrupeds at the 1854 Crystal Palace exhibition. Detail from Owen, 1854. Right: Owen's (1854) reconstruction of Buckland's *Megalosaurus* as a quadruped. Note the few bones available to Owen at that time. Images: Biodiversity Heritage Library.

The unprecedented size of Buckland's and Mantell's reptile-like bones and teeth broke the existing reptile-bird-mammal models that the pre-eminent British anatomist, Richard Owen, had at his disposal. To accommodate unique characteristics of the fossils from the Wealden beds, especially their immense size, Owen (1841) was forced to erect an entirely new order, the *Dinosauria*, – a bold move, considering the scant remains recovered worldwide by that time.

Lacking any comparable bipedal dinosaur model, Owen reconstructed both Buckland's *Megalosaurus* and Mantell's *Iguanodon* as quadrupeds for London's Crystal Palace Exhibition of 1851 (Desmond, 1975). Responsibility for Hawkin's Crystal Palace reconstructions fell on Owen's shoulders (e.g. Desmond, 1975). Owen was an extremely accomplished anatomist, relying only on the evidence he had in hand (e.g. Owen, *Monograph*, 1853-1864).

In Owen's defense, it must be acknowledged that, early on, he had access to only partial remains (Fig. A4, right) of both *Megalosaurus* and *Iguanodon*. Of the partial *Megalosaurus* bones, Owen writes: "*The portions of skeleton originally discovered, and attributed by Dr. Buckland to his newly defined genus, Megalosaurus, consisted of a fragment of the lower jaw, a femur, a series of five vertebrae of the trunk, a few ribs, a coracoid bone, a clavicle, and some less certainly recognizable fragments*" (Owen, 1857, p. 2). Furthermore, Owen attributes the incorrect "horn of the *Iguanodon*" to Mantell's original (1827) description (Owen, 1855, p. 45). Placing the bone in its correct place as a "thumb", Owen notes that the idea of the dermal horn "...has been so long fixed and so generally received, that, although the objection above advanced may unsettle it, yet additional reasons may be expected before it will be finally abandoned" (Owen, 1855, p. 47). Owen also recognized that most of the weight of both *Megalosaurus* and *Iguanodon* must have been carried by their enormous hind limbs in an upright stance (limb posture) more akin to a mammalian model than that of sprawling lizards. Owen's dinosaurs did not sprawl like modern lizards: "These remarkable extinct Dinosaurs were of large, if not gigantic, size; with the trunk lifted, higher than in other reptiles, upon four unusually developed limbs" (Owen, 1857, p.1).

Important developments regarding bipedalism in dinosaurs were occurring simultaneously with the publication of Owen's *Monograph*, including Beckles 1854 discovery of bipedal *Iguanodon* tracks, and Leidy's 1858 discovery of *Hadrosaurus* from the U.S. He was aware of Beckles finds, but apparently, Leidy's work was too recent for Owen's initial dinosaur models. Owen did, however, recognize that *Megalosaurus* was capable of maintaining an active lifestyle, "*with the superior energy and activity which a carnivorous reptile ...might be expected to possess in contrast with the heavier and more bulky herbivorous Iguanodon.*" (Owen, 1857, p.19)

An ichnological breakthrough occurred with Beckles 1854 discovery of large tridactyl footprints and extensive trackways in the Wealden-age beds of southern England (Fig. A5). The tracks confirmed that: "*bipedal animals having tridactyle feet of enormous proportions lived during the Wealden epoch.*" (Beckles, 1854, p. 462). Moreover, his finds confirmed that bipedal trackmakers spanned the interval from the Triassic (Jurassic of the Connecticut Valley) through the Cretaceous of England. Because his finds were only comparable to Hitchcock's Connecticut Valley tracks, Beckles was forced to lean toward the bird, or bird-like reptile, models. It is, he stated, "*undetermined whether these gigantic creatures were birds, or reptiles with ornithic characters.*" (Beckles, 1854, p. 462). Beckles did, however, make a bold leap in associating the tracks with *Iguanodon* bones that were being found in southern England. Thus, it appears that Beckles was the first to associate dinosaur tracks with a particular animal, noting that he was cautious of overturning Hitchcock's ancient bird model.

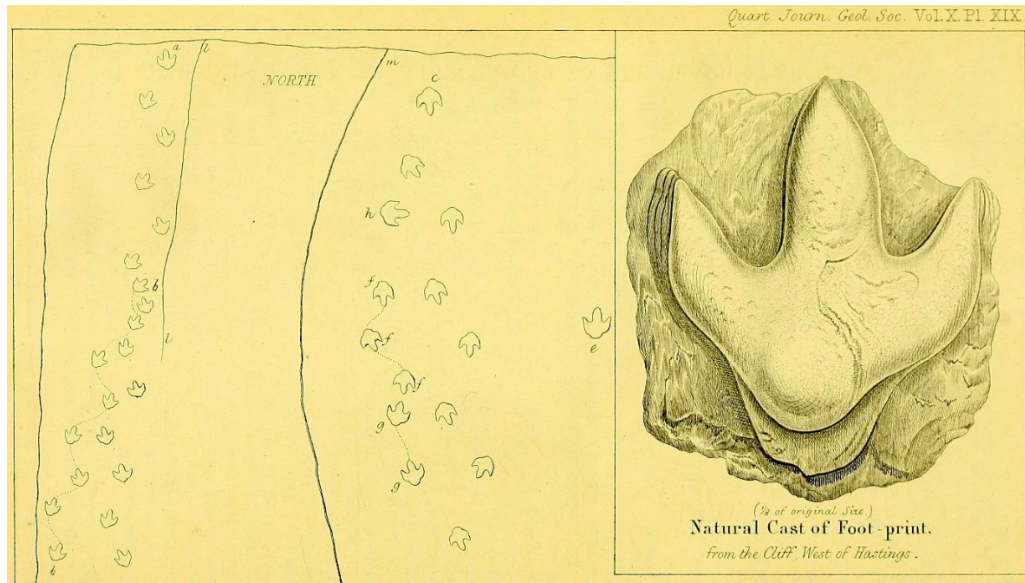


Figure A5. S.H. Beckles (1854) was the first to hint at a dinosaur connection between tracks and trackmakers, specifically *Iguanodon*. Detail, from Beckles, 1854. Image: Biodiversity Heritage Library.

The discovery of *Hadrosaurus*, by William Foulke and Joseph Leidy in Haddonfield, New Jersey in 1858, and Richard Owen's definition of dinosaurs as a viable order in 1841, shed some light on the nature of the Connecticut Valley trackmakers (Owen, 1841, p. 103; Leidy, 1858, p. 217). With the arrival of *Hadrosaurus*, *Megalosaurus* and *Iguanodon* were finally presented in their appropriate bipedal stance around 1858. Furthermore, the upright stance of *Hadrosaurus* strongly suggested a connection with Hitchcock's earlier bipedal trackmakers. Thus, the Connecticut Valley may plausibly claim the first descriptions of bipedal dinosaurs (Hitchcock, 1836, p. 313; Hitchcock, 1841), even though they were variably thought to be ancient birds, or, as they were later described, reptiles with bird-like features (e.g. Dana, 1863; Hitchcock, 1863). Armed with new finds from England and the U.S., including Beckles' 1854 Wealden tracks, Owen substantially revises *Iguanodon* in his *Monograph on the Fossil Reptilia of the Wealden and Purbeck* (1858b), including removing the horny "thumb" from its nose.

In 1866, not far from the southern New Jersey marl pits that had produced Leidy's *Hadrosaurus*, Edward Cope discovered the remains of a large, highly active, bipedal carnivore, that he named *Laelaps* (Cope, 1866). With its bipedal stance and tridactyl hind feet with sharp claws, *Laelaps* (*Dryptosaurus* Marsh 1877) should have shed further light on Hitchcock's tracks, but it was not until the late 19th century, with additional skeletal finds in the Connecticut Valley and elsewhere, that probable trackmakers became associated with his tracks.

T.H. Huxley (1868), known as "Darwin's bulldog" for his vigorous defense of evolution, also weighed in on the reptile-dinosaur-bird argument. The paper nicely sums Huxley's assessment of some "intermediate" forms – neither bird nor reptile, but possessing characteristics of both. These animals, known as dinosaurs, were being found in veritable torrent of bones coming from Europe and the U.S. (Huxley, 1870a, 1870b). Huxley "doubles down" on dinosaurs representing an intermediate form between ancient and modern lineages in his *Further evidence of the affinity between the dinosaurian reptiles and birds* (Huxley, 1870a). *Archeopteryx* weighed largely in Huxley's arguments, as it did for Hitchcock in 1863.

As finds of skeletal remains began to accumulate in the early 20th century, a clearer picture of some of the trackmakers began to emerge. Marsh (1893) was the first to connect some of the Hitchcock's Connecticut Valley tracks with likely trackmakers. Specifically, Marsh connected the recent finds of

Anchisaurus skeletal material from the Connecticut Valley with Hitchcock's tracks, concluding that: "...all of them were probably made by dinosaurian reptiles. No tracks of true birds are known in this horizon" (Marsh, 1893, p. 170). Following Marsh's lead, Lull (1915) connected some of Hitchcock's tracks with trackmakers, suggesting that *Grallator* was made by *Podokesaurus* (Lull, 1953, p. 141).

Bones from the Connecticut Valley (PML)

Strange indeed is this menagerie of the remote sandstone days.

– Edward Hitchcock, 1848

While pleased at the abundance of tracks and trace fossils, Hitchcock was invariably frustrated at the paucity of skeletal remains. Nevertheless, the few intriguing finds of bones in the region, and discoveries in other Late Triassic and Early Jurassic strata in North America and Europe, go a long way toward completing the picture of the trackmakers.

Along with the first dinosaur tracks, the Connecticut Valley also claims the earliest discoveries of osseous dinosaur remains in America, if not in the world. While digging a well in East Windsor (Ketch's Mills), Connecticut, in 1818, Solomon Ellsworth, Jr. found bones. The East Windsor discovery was recorded by Nathan Smith, who thought the bones were human, in the *American Journal of Science and Arts* ("Silliman's Journal") in 1820 (Smith, 1820; Hall, 1821; Delair and Sarjeant, 1975). Wyman (1855) reexamined the bone fragments, assigning them reptilian characteristics, suggesting they may be allied to Mantell's *Iguanodon*, and other dinosaur bones from England (Wyman, 1855, p. 396). The 1818 East Windsor bones were illustrated in Hitchcock's *Final Report on the Geology of Massachusetts* (1841, Plate 49, figs. 66-68). The bones were entered into the Peabody Museum of Natural History collection. In 1915, paleontologist Richard S. Lull confirmed the East Windsor bones as those of a small prosauropod, *Anchisaurus colurus*, (Lull, 1953; Delair and Sarjeant, 1975).

Blasting for construction at the Springfield Armory in 1857 produced a significant find of dinosaur bones, but most of the material was discarded before its importance was realized (Hitchcock, 1865; Lull, 1953; Delair and Sarjeant, 1975; Santucci, 1998; Tweet and Santucci, 2011).

The most productive single locality for bones in the Connecticut Valley was the Charles O. Wolcott redstone quarry in the Buckland section of Manchester, Connecticut (Marsh, 1891, 1893). In 1891, Yale paleontologist O.C. Marsh announced the discovery of the Manchester *Ammosaurus*, "*perhaps the most perfect Triassic Dinosaur yet discovered, as the skull and greater portion of the skeleton were found in place, and in fine preservation*" (Marsh, 1891, p. 267). Galton (1976) conducted an extensive review of the Connecticut Valley prosauropod material, clarifying their classification and nomenclature. Recently, Yates (2004, 2010) reassessed the Early Jurassic *Anchisaurus* bones from the Wolcott quarry in Manchester, proposing a revised classification of the early prosauropods that left abundant tracks in the sediment of the Connecticut Valley.

Around 1910, the bones of a small bipedal theropod were discovered by Mignon Talbott in a glacial boulder of sandstone near the campus of Mount Holyoke College (Talbot, 1911). Named *Podokesaurus*, the most complete skeleton from the Connecticut Valley was lost when the Williston Hall natural history museum was destroyed by a fire on December 22, 1917 (Shipps, 2014). A cast of *Podokesaurus* is, however, on display in Yale's Peabody Museum.

Other discoveries of reptile bones in the Connecticut Valley occurred sporadically, mainly accidental finds by local residents but also by amateurs and researchers, from the 1960s through the present. A skull of *Hypsognathus fenneri*, found in a stonewall by two high school boys in Meriden in the 1960s was listed by Ostrom (1970), as: "...a remarkable and very important partial skeleton and skull of one of the last surviving cotylosaurs or stem reptiles (procolophonid). The specimen is the first find of fossil, articulated skeletal material since 1892 in Connecticut. It also is probably the finest of its kind in the world" (Ostrom, 1970). It was not until 2000 that this New Haven Formation find was described (Sues et al., 2000).

Another New Haven Formation skull, this time of a sphenodontian - today's representative of which is the living fossil *Sphenodon* of New Zealand – was found by a worker during blasting in 1965 for what is now I-691/CT-66 in Meriden; described by Sues and Baird, 1993. An amazing find was the discovery of a small “prosauropod” foot in 1985 in a small glacial cobble in Ellington, CT. (McDonald, 2010), presumably from the Portland Formation. A relatively large fragmentary bone, presumably dinosaurian, from the Turners Falls Formation was found in parking lot in Turners Falls proper by N. G. McDonald himself in 1992. An additional New Haven Formation skull was found on an off ramp from I-691 in Cheshire, CT during a geological excursion, much like this one, by PEO (Olsen et al., 2000) and that proved to be only the second specimen discovered of *Erpetosuchus* otherwise known from Scotland (!) and closely related to stem crocodylians. There are also rumors that another partial “prosauropod” was found only a few years ago near Buckland, Connecticut from the Portland Formation. Experience by PEO suggests that bones are actually quite common in the Connecticut Valley, but are very hard to see unless the rock is absolutely clean and relatively unweathered.

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