

The vertebrate track record

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A renaissance in the study of fossil footprints has been driven by a multitude of discoveries and the realization that vertebrate ichnology makes important contributions to our understanding of terrestrial vertebrates. More striking is the insight the track record gives us into bias and incompleteness in the vertebrate fossil record.

We recognize that the fossil record, especially that of terrestrial vertebrates, is incomplete, but is it as incomplete as we assume? A huge tetrapod track record fills many gaps in our knowledge of the distribution of fossil vertebrates¹⁻⁴, and research into tetrapod ichnology has contributed to a range of palaeontological subdisciplines. Ichnology has generated its own extensive database, which complements the skeletal record in some cases but offers new insights in others. The data point to biases and gaps in the tetrapod fossil record^{4,5}.

Defining and redefining the track record

What do tracks tell us about the fossil record? To answer this question effectively, we must redefine our understanding of the track record, evaluate what we have learned, and identify problems that still lie ahead. In the wake of the dinosaur renaissance⁶, the field of vertebrate ichnology has grown rapidly. Great progress has been made in documentation of numerous track sites on all continents¹⁻⁴ and in understanding tracks as essential for correct reconstructions of posture and gait^{7,8}. Ichnologists have also asked new questions about the usefulness of tracks for palaeoecological and biostratigraphical research, and shown that tracks help us to understand and measure bias in the body fossil record⁵.

Despite commanding attention early in the nineteenth century^{9,10}, vertebrate ichnology failed to mature until recently, leading to the perception that tracks are rare and of limited utility. As recently as 1962, only about 27 discrete dinosaur footprint localities were known worldwide¹¹. Now the number is more than 300 for the western USA⁴, with comparable numbers from elsewhere in the world^{1,10,12-16}. Fossil footprints are found abundantly in strata from the Carboniferous period to the Holocene epoch, and occur in almost all terrestrial sedimentary deposits⁴. Consequently, tetrapod ichnology has the potential to yield large samples^{5,15}. It is well known that many Palaeozoic red beds are track-rich and bone-poor¹⁷. The Mesozoic stages of the western USA provide an even better example of the magnitude of track samples. There are at least three 'dinosaur freeways' from the Jurassic and Cretaceous stages of this region^{3,4}. These are regionally extensive surfaces, or thin stratigraphic units, of area 1,000–10,000 km². Dinosaur track densities average about 1 million per km² (1 per m²) and densities in excess of 100 tracks per m² have been reported for birds and other small tetrapods. In the temporal dimension, many track-bearing layers occur with a frequency as high as two per metre in sections measuring hundreds of metres in thickness^{3,4,15}.

The Jurassic System of the western USA is a good example of such track abundance. More than 200 track sites have been reported from seven well-known stratigraphic units (Fig. 1). Three of these units contain no skeletal remains and two have only a very sparse skeletal fauna. Allowing for an average of ten individual trackways per track site, our total sample is about 2,000. Even after extracting non-dinosaurian footprints, such a figure compares favourably with the total of generically determined dinosaur individuals (about 2,000) recovered from the entire Mesozoic stage worldwide^{18,19}.

Tracks are traditionally seen as useful for demonstrating vertebrate presence and activity where skeletal remains are absent. This bone-centred view is inherited from students of body fossils, looking at ichnology as a possible means of addressing specific

questions unanswered by the skeletal evidence. Now that vertebrate ichnology has matured it poses its own empirically derived questions²⁰. From a track-centred viewpoint we appreciate better²⁰ that, in most cases, footprints are fundamentally different from skeletal evidence (Box 1).

Preservation problems and progress

An obstacle to the use of some tracks and trackways is their incompleteness, which may result from several factors. True tracks (those made on the actual surface available for ichnological study) may be incomplete if the substrate was too soft, too firm or too variable. Track depth can determine the number of digit impressions preserved¹⁻³; thus, tracks may include fewer digits than the maximum number preserved under optimal conditions. Track-makers may also overprint their front footprints with their hind footprints, giving rise to the concept of primary, secondary or tertiary overlap²¹ and the potential for quadrupeds to appear bipedal²².

Some footprints are transmitted into underlayers as underprints or ghost prints^{2,3}, which may not reflect the precise anatomy of the trackmaker's foot. Experiments duplicate and describe accurately the range of morphological variation found in the subfossil record and show the relationship of variation to substrate type²³.

Despite views to the contrary²⁴, we are now reaching a consensus that ichnotaxonomic names should be assigned only to well-preserved tracks that reflect the morphology of the trackmaker^{17,18}. This does not, however, imply that we must know the identity of the trackmaker.

Careful description of the three-dimensional morphology and sedimentological context of tracks should be encouraged, to establish the palaeoenvironmental setting of tracks. Sedimentologists have yet to take full advantage of what vertebrate ichnology can teach about the palaeoenvironment. Exceptions are Nadon and Issler²⁵, who use dinosaur tracks as 'palaeopenetrometers' (tools for measuring compaction in floodplain sediments).

What can be learned from tracks?

Studies of locomotion based on tracks precipitated a revival of tetrapod ichnology with a debate over the speeds attained by dinosaurs²⁶. Estimates of rapid progression of large dinosaurs

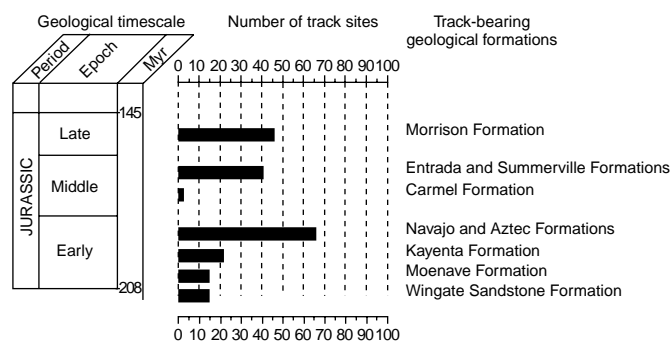
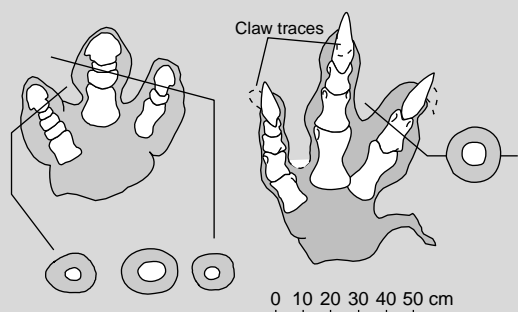


Figure 1 About 200 Jurassic track sites have been recorded in a small part of the western United States (mainly eastern Utah and Colorado), most during the last decade. At an estimated ten trackways per site, the total trackway sample is ~2,000 individuals.

Box 1 The anatomy and naming of tracks

Do footprints mirror the morphology of foot skeletons? Do foot skeletons even exist to match footprints? Consider the example of a probable *Tyrannosaurus rex* print. At 85 cm in length, this track is the largest theropod track known⁶³. It reveals a fleshy, well-padded foot, as expected for a 6- or 7-tonne animal, but the foot skeleton (digits II–IV) does not fit the outline of the track perfectly; it occupies only a small part of the cross-sectional area of the foot, as is the case in many large animals (see figure). For example, the reconstructed foot skeleton of a rhinoceros⁶⁴ or elephant indicates a digitigrade or unguligrade animal⁶⁴ but is of little use in predicting footprint morphology without the large fleshy portion of the foot being available. In general, the larger the trackmaker, the fleshier the foot, and the greater the morphological difference between the footprint and the foot skeleton. This observation is fundamental in justifying the use of ichnotaxonomy for naming well-preserved footprint morphologies. Where footprints are known without corresponding body fossil remains, as was the case for the 'hand animal' *Chirotherium* from 1835–1965 (ref. 52), the use of ichnotaxonomy is crucial.

The conclusion that tracks are different from foot skeletons might suggest limited potential for correlating extinct trackmakers and tracks, but two methods exist for making such correlations. The first involves trying to fill the gap by reconstructing the fleshy part of the foot, starting with either the skeleton or the track. Although many dinosaurs and other vertebrates have been 'fleshed out'²⁷, there have been no serious attempts to reconstruct feet either from the track up or from the foot skeleton down. The second approach involves the simple process of elimination, that is, matching tracks with trackmakers of the same size and geological age.



Footprint morphology is not a simple reflection of foot skeletons with thin skin, as footprints of large dinosaurs such as *Hadrosaurus* (left) and *Tyrannosaurus* (right) show. Flesh and padding (grey areas) surround the bone. (Hallux restoration is omitted for clarity.)

were proposed in support of the idea that dinosaurs were warm-blooded, and athletic^{27,28}. However, there is little evidence for high-speed progression except among small- and medium-sized bipeds (mainly theropods)^{2,29}. Ichtnology has also forced debate about ceratopsian posture and locomotion, by showing that forelimbs were not placed as far from the midline as suggested by many reconstructions⁷. The use of footprints has also settled a debate about pterosaur locomotion by showing that they progressed quadrupedally on land^{8,30,31}.

A synthesis of all known brontosaur trackways (>400) reveals a pronounced shift from mixed gauge (narrow and wide) to predominantly wide gauge at the end of the Jurassic period¹⁵, presumably reflecting a major trend in sauropod evolution—that is, the rise of the brachiosaurids and titanosaurs. Another unexpected result is the recognition of considerable variation in heteropody (manus:pes foot area ratios vary from 1:5 to 1:2)¹⁵. Large manus sauropod trackways from the Upper Cretaceous have been identified as titanosaurid simply because they were the only family extant at that time. Such biostratigraphic processes of elimination, in combination with evi-

dence of gauge, heteropody and palaeobiogeography, help to differentiate the trackways of other sauropod families.

It is becoming clear that manus tracks of large Cretaceous ornithopods are variable, ranging from oval⁴ to bilobed³² and V-shaped³³. Such variation justifies the recognition of different ichnotaxa and increases the potential to differentiate between trackmakers at progressively lower taxonomic levels. In the absence of foot bones, sophisticated analyses of limb elements may be required to determine whether mammals were digitigrade or plantigrade³⁴, whereas tracks can distinguish these and unguligrade types unequivocally.

Megalosaurid tracks in Late Jurassic deposits from North America, Europe and Asia offer insight into a family that is poorly known from osteological remains¹⁶. The footprints are the largest theropod tracks known from the Jurassic period (up to 70 cm in length) and show that the megalosaurids moved with a short step and primitive gait (wide trackway and low pace angulation; Fig. 2)³⁵. Osteological evidence confirms that megalosaurs were primitive, and long-bodied, with relatively short, bandy legs³⁶.

Ichtnology is also useful in study of social behaviour^{3,4,37}. It is now known that large herbivorous dinosaurs (especially brontosaurus and ornithopods) often travelled in herds, and that both groups acquired gregarious tendencies early in their history. From study of trackway samples of up to 80 or more individuals, we know that such herds were sometimes segregated into distinct age or size classes^{4,37}. Claims that brontosaurus are represented in the fossil record by a huge preponderance of adults apply only to skeletal remains. Many large footprint samples, from continental palaeoenvironments, are dominated by the tracks of juveniles¹⁵. Small sauropod tracks from island archipelago palaeoenvironments, however, may indicate the presence of dwarfed populations³⁸.

As tracks are found *in situ*, they offer palaeoecological insight into trackmaker–habitat relationships. Recurrent associations between particular track assemblages and sedimentary facies allow recognition of distinct tetrapod ichnofacies³⁹. The most striking example is perhaps the recurrent association of synapsid and arthropod (arachnid/scorpion) tracks in sand dune facies throughout much of the Permian, Triassic and Early Jurassic in North and South America and Europe. In contrast, non-eolian facies exhibit entirely different, and more diverse, tetrapod track assemblages. Our understanding of the palaeoecology of such Jurassic units as the Wingate, Navajo, Carmel and Summerville (Fig. 1) is based almost exclusively on footprints. There are also examples of lacustrine and lagoonal ichnofacies dominated by swim-tracks attributed to amphibians, turtles⁴⁰ and pterosaurs⁴¹.

There is a statistical correlation between brontosaur tracks and low-latitude, carbonate-evaporite substrates¹⁵, which is relevant to debates about sauropod metabolism and biogeography. In contrast, large Mesozoic ornithopods are associated with plant-rich, coal-bearing facies indicative of humid, well-vegetated habitats³. Such ichnofacies distribution patterns are empirically derived, repeatable results that describe the composition of the track record. Similarly, in the Triassic of North America, for example, the body fossil record is dominated by aquatic vertebrates with sparse representation of terrestrial faunas. The track record, however, compensates for this bias with good representation of terrestrial tetrapods^{4,5}.

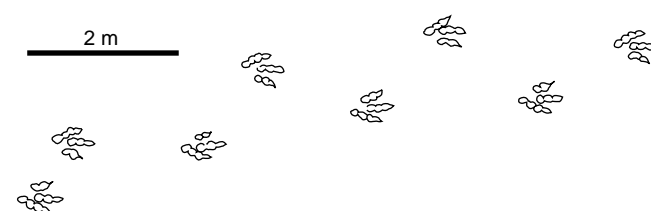


Figure 2 This trackway of a megalosaurid (*Megalosaurus*) from the Late Jurassic stage of Turkmenistan is unique among theropod trackways in its irregularity and width of gauge, indicative of a primitive style of locomotion³⁵.

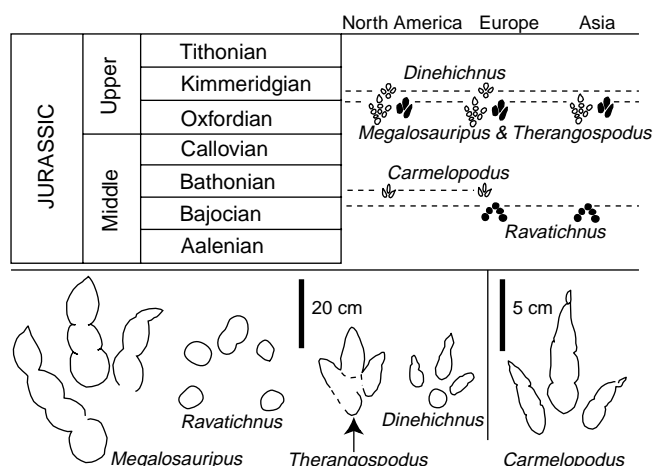


Figure 3 Ichonologists have recently reported correlations between five Middle and Upper Jurassic sites of North America, Europe and Asia, using dinosaur tracks. The sites are illustrated by their associated tracks at the right; the tracks are shown in more detail at the bottom. Few precise terrestrial correlations have been demonstrated, at this time, using dinosaur body fossils.

Calibrating the fossil record

Vertebrate tracks have definable distributions in space and time. Their potentially large geographic range, especially pertinent when considering birds and pterosaurs, makes them useful for biostratigraphy. For example, the large bird track *Magnoavipes* from the Lower Cenomanian of Texas⁴² is also known from deposits of the same age in Israel⁴³. The subdiscipline of ancient track stratigraphy (palichnostratigraphy), first introduced in the context of wide-ranging Pangaeian (Permo/Triassic/Early Jurassic) faunas⁴⁴, can now be extended to the Middle and Late Jurassic^{35,45}. Such correlations show widespread interchange of species between Europe and Eurasia after the break up of Pangaea. No such explicit (stage level) Middle or Upper Jurassic correlations have been made on the basis of dinosaur skeletal remains (Fig. 3 and Box 2).

Ichnology has also provided insight into the origin, evolution and extinction of several major groups and behaviours. Trackways have been used to suggest that the first tetrapods walked on land at about the time of the Silurian/Devonian transition, as much as 30–40 million years before the appearance of the oldest known skeletal remains^{46,47}, although this interpretation has been challenged⁴⁸. Because tracks are *in situ* they assume added importance in the debate about whether tetrapod 'walking' originated in fresh or salt water⁴⁹. Although not now regarded as tetrapod in origin, there is a Carboniferous acme zone of giant myriapod trails attributed to *Arthropleura*⁵⁰. Spiral burrows and digging traces also attest to the Permian origin of den-making activity of synapsids⁵¹.

In many areas we know more about Triassic archosaurian diversification from famous *Chirotherium* and *Chirotherium*-like tracks than we do from bones^{44,52,53}. Preliminary studies of Mesozoic bird tracks indicate a large-scale radiation of shorebirds in the early and mid Cretaceous as much as 40 million years before the appearance of skeletal remains of a postulated Charadriiform ancestor in the Late Cretaceous^{43,54}. Discovery of pterosaur track sites points to a Jurassic ichnological acme zone in association with marginal marine habitats and a preference of pterosaurs for terrestrial, lacustrine habitats in the Cretaceous⁴³ (Fig. 4).

There are also abundant tracks of hadrosaurs and ceratopsians, in what was previously defined as a 3-m gap below the Cretaceous/Tertiary (K/T) boundary. The gap is now reduced to a maximum of 37 cm (refs 3, 4), solving the debate about whether dinosaurs went extinct long before, or in conjunction with, the K/T transition.

The Tertiary and Quaternary track record, for example the diverse avian ichnofauna of the Swiss Oligocene/Miocene⁵⁵, also improves

Box 2 Globe-trotting dinosaurs

The distinctive Middle Jurassic track *Carmelopodus* from the Bathonian of Utah reveals the existence of a previously unknown species, with a short metatarsal IV, that also made tracks in Bathonian deposits in England⁴⁶. The enigmatic track *Ravaticchnus* has been correlated from Asia to Europe (Fig. 3)³⁵. Similarly, large 'megalo-saur' tracks (*Megalosauropus*) occur at the Oxfordian/Kimmeridgian (Upper Jurassic) transition in Utah, Arizona, New Mexico, Oklahoma, Portugal, Uzbekistan and Turkmenistan (Fig. 2)³⁵. Another distinctive dinosaur track type (*Therangospodus*) occurs in many of these samples³⁵ (Fig. 3). *Dinehichnus* is also correlated between North America and Europe⁶⁵. Such stage-level correlations exceed the resolution of only three land-vertebrate ages spanning 50 Myr⁶⁶. Track correlations tie footprint zones to stages with a duration of about 7 Myr each, and are as precise as any durations proposed for dinosaur skeletal taxa¹⁹.

our understanding of the palaeobiology of birds and mammals. The mammal-dominated, Pliocene australopithecine footprint site at Laetoli⁵⁶ pushed back the confirmed origins of hominid bipedalism from 3.0 to at least 3.6 million years⁵⁷, and provided evidence of a social group in which a juvenile was travelling with two adults⁵⁸. Late Pleistocene (Palaeolithic) hominid tracks from cave sites show a predominance of juveniles, without significant incidence of foot deformities, in association with bear, hyaena and (rare) fox tracks⁵⁹. In contrast, outdoor Mesolithic⁶⁰ and Neolithic⁶¹ sites contain more adult tracks, with higher incidence of foot abnormalities, in association with auroch, deer, unshod horse and bird footprints⁶¹. The use of the term 'trace fossil' for several categories of butcher cut marks on bone⁶² significantly broadens our concept of hominid ichnology.

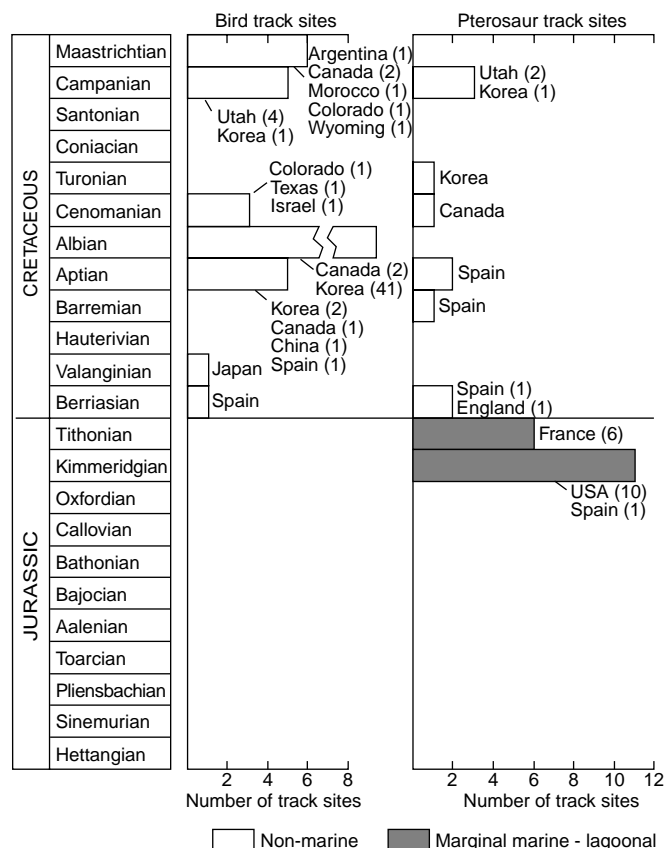


Figure 4 The stratigraphic distribution of bird and pterosaur tracks from 91 sites extends the temporal and spatial distribution of both groups⁴³.

Bias and completeness in the fossil record

Ichnology cannot solve the common taphonomic problem of missing foot skeletons entirely. The perception that vertebrate palaeontologists are waiting for ichnologists to find footprints to match their small sample of foot bones—what I call the ‘Cinderella’ syndrome—is largely unjustified. Often it is tetrapod ichnologists who are waiting for palaeontologists to find foot bones to fit into their large sample of tracks (an ‘overstocked shoe shop’ syndrome). This is because it is the feet that are missing from so many taxa as a result of taphonomic loss. Viewed from this perspective, the ichnological community has already found much of the ‘missing’ foot evidence and is establishing its own database. For example, the aforementioned Neolithic track site has yielded more than 150 hominid trackways, differentiated into males, females and children⁶¹. A comparable cache of skeletal remains would be considered quite exceptional.

So vertebrate ichnology is rapidly coming of age. Although vertebrate ichnology does not lend itself easily to the study of relationships through cladistic analysis, the field is highly consistent in comparing foot (manus and pes) morphology from taxon to taxon. This is not always true in the systematic study of bones, as the large number of invalid taxa, based on diverse undiagnostic elements, shows. Although there are many invalid track taxa also, there is a trend towards caution in ichnotaxonomy.

At a time when palaeontology has been aided by revolutions in such subdisciplines as molecular palaeontology and cladistics, the study of tetrapod tracks has also grown steadily and undergone its first true renaissance since its inception more than 150 years ago^{1–4,9,10}. This has largely been due to an increase in the discovery and documentation of new sites. This empirically derived database helps us define and measure spatial and temporal incompleteness in the skeletal record of terrestrial vertebrates. Thus, we can focus on which parts of the fossil record must be described ichnologically, osteologically or by both methods. This holistic view shows that many questions about foot morphology, posture, locomotion, behaviour, terrestrial vertebrate palaeoecology, stratigraphy and information biases cannot be fully understood without consideration of the data encoded in the track record. □

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