

Taxon distributions and the tetrapod track record

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Abstract.—Vertebrate tracks are a unique, abundant source of fossil data that supplements the skeletal record in many ways. However, the utility of ichnofossil data depends on how specifically the authors of tracks can be identified. Despite this fact, there is little consensus about how to identify potential trackmakers, and existing methods differ in their bases, assumptions, and corresponding implications.

In this paper we support the proposal that trackmakers should be identified primarily by skeletal structures that are both preserved in the ichnofossils and synapomorphies of some body-fossil clade. This synapomorphy-based technique enables certain taxa to be positively identified as candidate trackmakers and others to be excluded from consideration. In addition, the diagnostic level of the synapomorphy (i.e., to a higher or lower level) corresponds to that of the trackmaker. Additional features, such as body size and provenance, can be used in association with synapomorphies as additional differentiae of trackmaker identity.

Trackway analyses are dependent on the level of trackmaker diagnosis, but not all analyses require the same diagnostic specificity. Palichnostratigraphic correlations to the stage level are shown to require at least a genus-level identification of a trackmaker, whereas studies of vertebrate distributions (i.e., origins, extinctions, ranges) accommodate much coarser designations. Anachronistic occurrences of trace and body fossils result in range extensions for either the skeletal taxon or the feature in question. For example, the temporal distribution of theropods can be extended on the basis of the footprint record, resulting in an earlier estimated divergence time for Dinosauria.

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Introduction

Footprints and trackways are direct evidence of extinct animals as living, breathing organisms. In some cases, tracks provide information about the trackmaker that would not be available from its bones alone, such as behavior (Bird 1944; Ostrom 1972; Lockley et al. 1986; Farlow 1987), soft tissues (Gierlinski 1996; Gatesy et al. 1999), and speed (Alexander 1976; Farlow 1981; Thulborn 1982, 1990). Fossil tracks can also complement information from the osteological record by providing additional data on first and last occurrences (Demathieu 1990; Lockley 1991), geographical distributions (Lockley 1991), and limb posture (Lockley and Hunt 1995; Dodson and Farlow 1997; Gatesy et al. 1999; Wilson and Carrano 1999).

In fact, trackways can offer a more faithful estimate of the spatial and temporal distributions of vertebrate taxa than can bones, for several reasons. First, a single trackmaker can leave hundreds or thousands of tracks in a

lifetime, giving ichnofossils a much richer record than body fossils. Second, fossil trackways are not subjected to the same degree of time-averaging as body fossils; they represent discrete, restricted time intervals. Third, because tracks cannot generally be transported, they also provide a direct link between an animal and its environment. Fourth, because one animal can leave many tracks, footprints can record information about that animal from several environments. Perhaps most importantly, tracks are commonly found in different facies than body fossils, and so they have the potential to fill stratigraphic gaps in the terrestrial record (e.g., Lockley 1991).

The last two decades have seen a renaissance in vertebrate ichnology that has been characterized by discoveries of numerous new track types and trackways (Lockley 1986, 1998) including megatracksites (Lockley and Pittman 1989), revised attempts to estimate locomotor speed (Alexander 1976; Farlow 1981; Thulborn 1982, 1990), and use of novel tech-

niques to reconstruct limb kinematics (Gatesy et al. 1999). Not only has this resurgence substantially increased the amount of ichnological data available, it has fostered the study of new types of data from trackways. However, all interpretations of tracks as representatives of a living animal ultimately require the identification of a trackmaker to some taxonomic level. As a result, the fundamental issue of trackmaker identification (i.e., the integration of skeletal and ichnological data) is important for reaping the benefits of these recent advances.

In this paper, we support the idea that trackmaker identifications should be based on osteological synapomorphies of the proposed trackmaker that can be identified in fossil tracks (Olsen 1995). This synapomorphy-based approach to trackmaker identification is falsifiable, repeatable, and reliant on *diagnoses* rather than *descriptions*. As with osteological remains, the primary determinant of our ability to diagnose trackways systematically is the uniqueness of character combinations preserved, not the absolute completeness of the specimen (Wilkinson 1995). The diagnostic limits of this method are inherent: the specificity of trackmaker identification depends on the diagnostic features preserved in the trackway. Although this often results in very coarse trackmaker identifications (e.g., “sauropod,” “theropod”), these can be useful and in many cases are more appropriate than highly specific designations.

Using this synapomorphy-based approach, we compile a set of osteological synapomorphies that could be recognized in dinosaur trackways and use this list as the basis for assessing the origins of Dinosauria and its principal subgroups.

Correlating Tracks and Trackmakers

As summarized by Lockley (1998), the footprint record contributes information that is important to the study of extinct vertebrates, often uniquely so. Unfortunately, the utility of this record has been diminished by inability to correlate particular tracks with particular trackmakers. Indeed, the bases for this have only been briefly discussed (e.g., Olsen 1995; Farlow and Chapman 1997; Lockley 1998). A

basis for trackmaker identification—that is, the integration of skeletal and ichnological data—must be articulated in order to ascribe such aspects of biology to particular dinosaurs.

Methods for Correlating Tracks and Trackmakers

Tracks and trackmakers can be associated with absolute certainty only when found in association, as when a living trackmaker is observed making tracks or in the rare event that the fossil trackmaker is preserved at the end of a trackway. Such serendipitous co-occurrences have been recorded for invertebrates (e.g., Pickerill and Forbes 1978; Leich 1965; Glaessner 1969: Fig. 243A) but are unknown among vertebrates (Boucot 1990). As a result, only indirect methods can be used to correlate vertebrate tracks and trackmakers. Historically, three such methods have been used. The two most common are what we term *phenetic* and *coincidence correlations*. The third, less widely employed, is *synapomorphy-based correlation*.

Phenetic Correlation.—Trackmakers are most commonly identified on the basis of general similarity between the track and the foot skeleton, based on reconstructed (e.g., Thulborn 1990: Fig. 5.3) or preserved soft and hard tissues (e.g., Osborn 1912; Miller 1929). The initial description of specific tracks has the primary goal of distinguishing them from other, similar tracks. Should the tracks prove distinct from other known tracks, a new ichnotaxon (generally a binomen) may be designated. Once a track has been described and diagnosed, its basic morphology may be used as a template for comparison with the pedal morphologies of known dinosaurs. Additional criteria—including footprint size, footfall pattern (Thulborn 1990), and posture—also may be employed to further delimit potential trackmakers.

Although not referred to as such, the phenetic approach is historically common, having perhaps the longest pedigree. Unaware of the existence of dinosaurs with birdlike feet, Hitchcock (1836) described footprints from the Early Jurassic of the Connecticut Valley as “bird tracks.” Subsequently, workers such as Lull

(1915, 1953) used phenetic correlation to greatly expand and emend Hitchcock's identifications, and this method remains the most common correlative technique in use. Throughout its history, the phenetic method has relied on the concept of similarity and dissimilarity to identify and distinguish tracks. In this manner it is similar to the phenetic method of systematics, in which the possession or absence of a unique feature is considered as phylogenetically informative as more general similarities.

Criticisms of the phenetic method of trackmaker identification are similar to those of the phenetic method of taxonomy—convergences and parallelisms are not reliably distinguished from homologies, and relationships are often based on primitive characters (e.g., Farris 1979; Patterson 1982; Farlow and Chapman 1997). The main problem with the phenetic approach is that all variation apparent in the tracks is attributed to taxonomic variation in the trackmakers themselves. This conflation of track similarity or dissimilarity with taxonomic informativeness can lead to trackmaker identifications that outstretch the inherent limits of ichnofossil data.

Phenetically identified tracks can still provide data useful toward assessing taxonomic or morphologic diversity. A single tracksite can preserve numerous track types that—given the limited temporal and depositional disposition of the site—are likely to represent different taxa. That is, although it may not be possible to identify specific trackmakers for each track type, it may still be possible to identify the presence of distinct taxa by the morphological differences between tracks.

Coincidence Correlation.—The use of stratigraphic and geographical information to identify osteological remains or to refine an identification based on other criteria remains a controversial topic. However, because the branching pattern of phylogeny implies a timing for the emergence of biological groups, stratigraphic information can be a resource for phylogeny reconstruction (Fisher 1994; Fox et al. 1999) and constraining taxon distributions (Marshall 1990, 1994; Wagner 1995). Given that many dinosaurs cannot be clearly distinguished from one another on the basis of pedal morphology alone (Farlow in press), additional

data are often used in conjunction with track morphology to discriminate between different candidate trackmakers. These distributional data include geological age, geographic provenance, and local faunal composition. The distributions and abundances of skeletal taxa and ichnotaxa may help to refine phenetically derived identifications: locally known taxa are preferred over more distant ones, and more common taxa over rarer forms.

Coincidence correlation represents a refinement of phenetic identification, but it remains consistent with (and dependent on) measures of similarity or dissimilarity with known taxa. The limitation of coincidence correlation is that it can only agree with currently established taxon abundances and distributions. This precludes ichnological remains from changing such distributions and ultimately robs ichnology of its ability to refute distributional hypotheses based solely on osteological remains (but see Additional Ichnological Differentiae of Trackmaker Identity, below). In this sense, coincidence correlations may be viewed as conservative. A potential pitfall is that morphologically similar, geographically and geologically coincident animals cannot be distinguished using coincidence correlation.

Synapomorphy-Based Correlation.—Olsen outlined the synapomorphy-based method as follows: "Ichnotaxa can be assigned to biological taxa only if they have shared derived characters (sdc's) of those taxa" (1995: p. 72). In other words, only a subset of the total information preserved in a track identifies the potential author of that track. Moreover, this information is inherently limiting: "theropod" synapomorphies that are visible in tracks can only be used to diagnose those tracks as "theropod." This method has the benefits of being repeatable, falsifiable, and explicit. As with other synapomorphy-based systematic methods, homoplasy and missing data remain vexing limitations, especially given the restricted number of phylogenetically informative characters that can be identified in trackways (see Skeletal Synapomorphies in the Ichnological Record, below).

Synapomorphy-based correlation has only been briefly outlined (Olsen 1995) but deserves wider recognition. Despite its potential merits and applicability, it has not yet gained currency

in the literature and has served as the basis for only two ichnological studies (Olsen et al. 1998; Wilson and Carrano 1999). The method outlined in this paper is a direct extension and elaboration of Olsen's (1995) technique.

Levels of Diagnosticity

Historically, ichnologists (e.g., Hitchcock 1836; Lull 1915, 1953) have attempted to differentiate tracks at very fine ichnotaxonomic levels, even to the rank of ichnosubspecies. Although no explicit ranked connection has been drawn between, for example, families and ichnofamilies, there is at least an implied correlation between ichnotaxonomy and the binomial taxonomy of body fossils. Baird (1980: p. 225) criticized this by noting that "ichnogenera are in many cases equivalent to families or even high categories of reptiles. . . ." Several authors have noted that there is not necessarily a one-to-one correspondence between ichnospecies and trackmaker species (e.g., Olsen 1995; Olsen et al. 1998; Farlow in press). Although it has been suggested that "in the case of dinosaurs in particular, good footprints usually enable the identification of the trackmaker, at least to familial level" (Sarjeant 1990: p. 306), in practice such taxonomic designations often exceed the resolution of the data.

Nonetheless, identification of a trackmaker as "theropod" or "sauropod" may still be informative for specific hypotheses of locomotion, paleobiogeography, or behavior. The potential risk of coarse taxonomic designations is that a trackway feature may be over-generalized to a broader taxonomic group than is warranted. However, these hypotheses can be refuted or refined by subsequent sampling efforts. Furthermore, this risk does not apply to spatiotemporal distributions; identification of an "allosaur" track as "theropod" does not falsely extend the range of theropods. In contrast, the reverse error (i.e., misidentifying a given theropod track as that of an allosaur) could misrepresent the distribution of both allosaurs and the actual trackmaker. Worse, if a misidentified track implies an unusually early occurrence for a skeletal taxon, the temporal distributions of all taxa nested between it and the true trackmaker may be falsely extended (Fig. 1). In this manner, the level to which the

trackmaker can be identified affects nearly all types of ichnological analysis.

In fact, the only proposed scientific use of tracks and trackways that does not explicitly rely on trackmaker identification is "palichnostratigraphy," the correlation of strata based on fossil footprints (Haubold and Katzung 1980; Lockley 1998). Like other commonly used index fossils (e.g., conodont elements, palynomorphs, graptolites), tracks represent temporally variable biological entities. Unlike these biostratigraphic indicators, however, different footprints do not always represent different organisms but instead may represent the same organism under different conditions. Conversely, tracks regarded as the same ichnotaxon may actually represent different biological taxa (Farlow and Chapman 1997; Farlow in press). Because tracks represent the dynamic interaction between a trackmaker and substrate, disparities between track types can reflect taxonomy (e.g., size, foot morphology), biology (e.g., behavior, ontogeny, gender), geology (e.g., substrate type or depth, preservational history), or the dynamic nature of the interaction itself (e.g., duty factor, gait). For tracks to be useful as palichnostratigraphic (i.e., time) indicators, the source of variation *must be taxonomic*. It follows that palichnostratigraphic inferences are dependent on the reliability and specificity of ichnotaxonomic diagnoses.

Lockley (1998), however, maintained that stage-level stratigraphic correlations (i.e., durations <10 Myr) can be made with vertebrate tracks. Lockley (1998: Fig. 3) chose the ichnotaxa *Carmelopodus* and *Megalosauripus* to correlate stages of the Middle and Late Jurassic, respectively, in Asia, Europe, and North America. The temporal resolution afforded by these stratigraphic indicators corresponds to their distributions in time. For example, identification of these two ichnotaxa as "non-avian theropods" implies a different level of resolution (180 Myr) than does their identification as "allosauroids" (77 Myr) or as "*Allosaurus*" (5 Myr) (Weishampel 1990). Of these, only genus-level trackmaker identification affords the appropriate temporal range for stage-level correlation (Fig. 2).

Which level of resolution is appropriate for

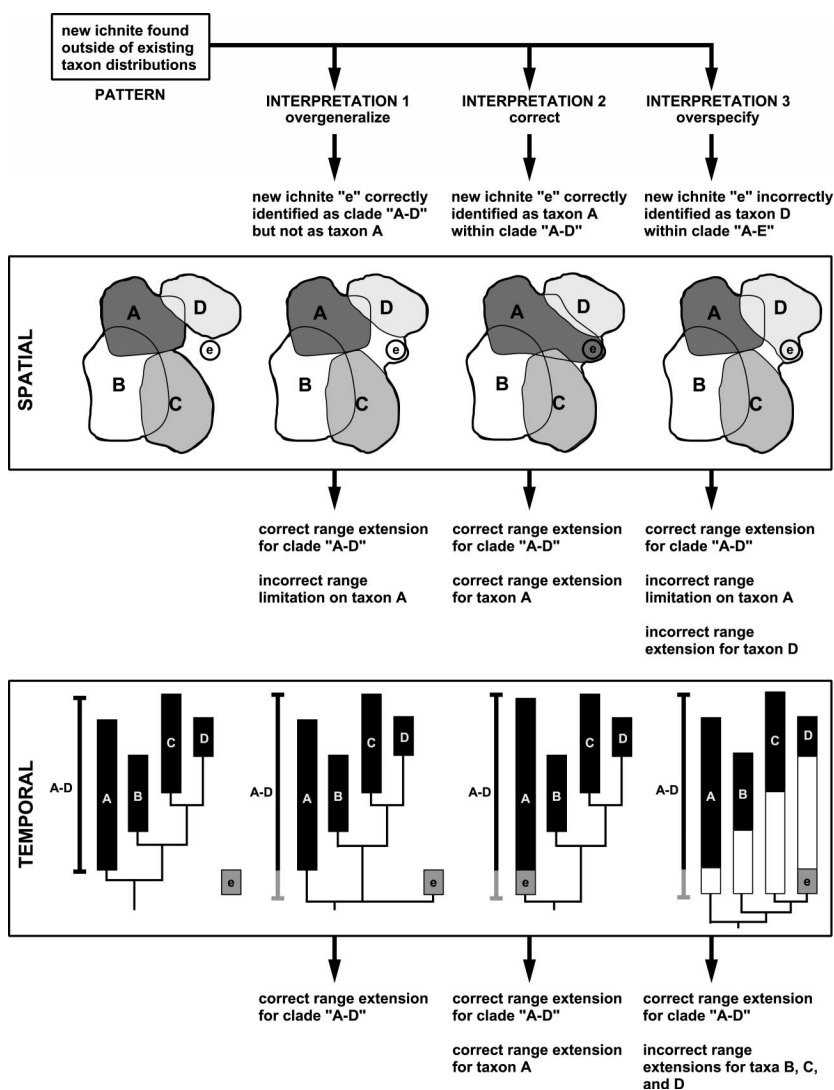


FIGURE 1. Ichnofossils can provide evidence of spatial and/or temporal range extensions for taxa, provided the trackmaker is identified to an appropriate taxonomic level. Overgeneralizing the trackmaker's identity will correctly represent the range of the broader clade but not all of its constituents, whereas overspecifying the trackmaker's identity will misrepresent the ranges of both constituent taxa involved. In addition, overspecifying the trackmaker as taxon D when it is actually A will also falsely extend the ghost lineages of all taxa that are phylogenetically bracketed by these two.

ichnotaxonomic diagnoses? Resolution should be dictated by the diagnostic features preserved in the tracks and their correlation with osteological synapomorphies of a trackmaker. For example, recent studies have demonstrated that the types of information preserved in trackways (phalangeal proportions, interdigital angles) are poor discriminators among even disparate groups of ground birds (Farlow in press; Farlow et al. 2000). Thus, even under idealized conditions, generic-level

trackmaker identifications are not always justified, implying that fossil trackmaker identifications are usually too coarse to be reliable as stage-level correlates.

Ichnological and Skeletal Data—A Synthesis

Below we outline a means for identifying potential trackmakers using both ichnological and skeletal data. Although based on portions of all the above methods, it relies primarily on

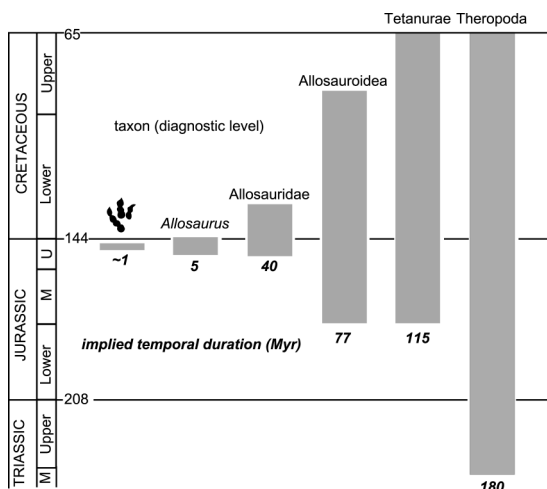


FIGURE 2. The relationship between specificity of trackmaker identification and temporal precision. Identification of an ichnotaxon as "*Allosaurus*" implies a different temporal resolution than does its identifications as "allosaurid," "allosauroid," "tetanuran," or "theropod." Footprint icon based on Lockley (1998: Fig. 3).

the concept of synapomorphy and the diagnosticity of specific morphological features.

Skeletal Synapomorphies in the Ichnological Record

Skeletal synapomorphies provide the best and primary means of linking track and trackmaker. However, synapomorphies recorded in those portions of the skeleton contacting the substrate are the only ones that may be observed in the tracks themselves. Synapomorphy-based trackmaker identification is thus biased toward appendicular synapomorphies in general and pedal synapomorphies in particular. Unfortunately, pedal elements are commonly lost during preservation, and as a result, there is little pedal information that can be used to diagnose different dinosaur clades, and even less to identify specific trackmakers (Fig. 3, Appendix 1). Farlow (in press) has noted that pedal phalangeal proportions serve to discriminate between some higher-level theropod taxa. The substantial overlap in pedal phalangeal proportions he reported, however, implies that these proportions alone are insufficient for lower-level identifications. In addition, phalangeal proportions may not be faithfully recorded in footprints, as is often the case with bird tracks (Farlow in press).

Pedal synapomorphies are not distributed evenly across dinosaur taxa (Fig. 3, Appendix 1) and in many cases offer little resolution between groups. In fact, review of previous phylogenetic analyses (Gauthier 1986; Holtz 1994; Wilson and Sereno 1998; Sereno 1999) shows that several major dinosaur clades (e.g., Tetanurae, Ceratopsia, Ornithischia) are not characterized by *any* pedal synapomorphies that we could expect to be preserved in trackways (Fig. 3). Nonetheless, phylogenetic studies have identified a substantial amount of morphological information that may be used to distinguish trackmakers. Although these features may not be routinely preserved in fossil trackways, certain environmental or behavioral conditions can favor their preservation.

Additional Ichnological Differentiae of Trackmaker Identity

Three additional criteria can further refine trackmaker identification when used in conjunction with an initial diagnosis based on morphological synapomorphies. Two of these (size and reciprocal illuminants) can be regarded as synapomorphies, although they are often not included in phylogenetic analysis of trackmakers. The third (provenance) is also usually excluded from systematic analysis, although this information is heritable and can be phylogenetically informative (e.g., Fisher 1994; Wagner 1995).

Body Size.—Size can be used to differentiate potential trackmakers only in cases where it is a unique feature of a given taxon—that is, the "size" in question does not also characterize the developmental stages of related taxa. In the absence of other distinguishing anatomical features, small tracks are not diagnostic of small trackmakers because closely related large trackmakers will produce similar tracks early in their ontogeny. However, large body size reliably identifies large trackmakers because smaller-sized trackmakers do not pass through larger sizes during ontogeny.

For example, large body size (>5 metric tons) has been attained independently in at least three Cretaceous theropod lineages: tyrannosaurids, carcharodontosaurids, and spinosaurids (Holtz 1994; Sereno et al. 1996, 1998). "Large foot" is thus a homoplastic char-

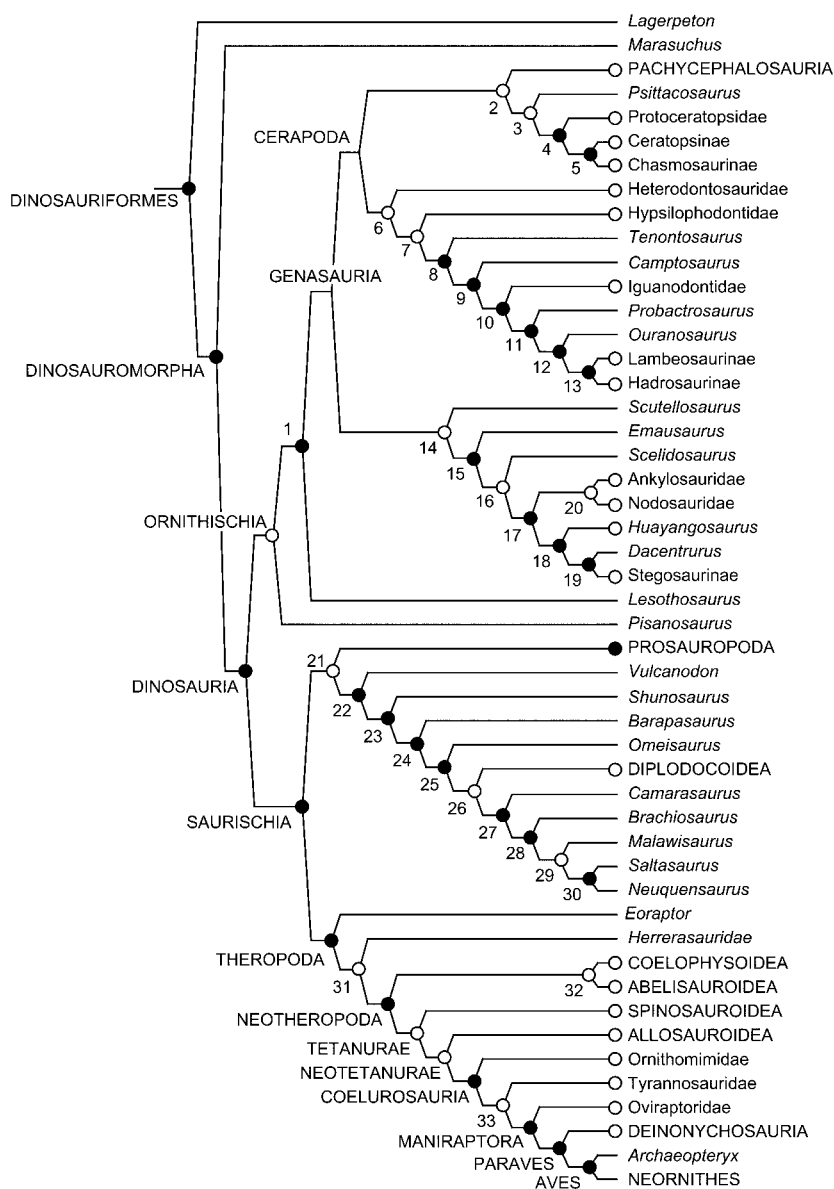


FIGURE 3. Phylogeny of Dinosauria, identifying those nodes characterized by synapomorphies that are potentially observable in the ichnological record. Filled circles indicate relevant synapomorphies known; open circles indicate no relevant synapomorphies known. Combined phylogeny from Gauthier 1986, Sereno 1986, Holtz 1994, Wilson and Sereno 1998, and Sereno 1999. See Appendix 1 for a list of synapomorphies, along with the names associated with numbered internal nodes.

acter among theropods; large prints could be ascribed to any of these groups in the absence of other morphological differences, but not to clades of smaller-bodied theropods. Partly on the basis of its size, a large theropod track of the ichnogenus *Tyrannosauripus* discovered in the Maastrichtian of New Mexico (Lockley and

Hunt 1994, 1995) was attributed to *Tyrannosaurus rex* (but see below).

Provenance.—The use of provenance as a differentia involves an evaluation of both the spatial and temporal distributions of known tracks and trackmakers: when multiple candidate trackmakers are available, those nearest

in time and space are preferred. However, these distributions should be qualified by an assessment of their sampling. Although such an assessment is implicit in many provenance-based trackmaker identifications, it often remains a subjective evaluation that approximates an actual assessment. Formal assessments of sampling intensity can be used to construct error bars that better represent the uncertainty of spatiotemporal distributions (Marshall 1990, 1994; Wagner 1995). Thus constrained, footprint data could be evaluated together with skeletal taxa in stratocladistic analyses.

To return to the previous example, Lockley and Hunt (1994, 1995) tentatively suggested that *Tyrannosaurus* is the most reasonable candidate *Tyrannosauripus* trackmaker because it is the only large theropod whose osteological remains are known from the Maastrichtian of North America. However, carcharodontosaurids are found in the Aptian–Cenomanian of North America, Africa, and Argentina (Stromer 1932; Stovall and Langston 1950; Coria and Salgado 1995; Sereno et al. 1996; Harris 1998). Lockley and Hunt's conclusion implies that the 47 Myr between the supposed extinction of North American carcharodontosaurids (112 Ma) and the occurrence of large theropod footprints in the Maastrichtian (65 Ma) is long enough to rule them out as potential *Tyrannosauripus* trackmakers.

This illustrates one of the less controversial trackmaker assignments, because it is supported by both provenance and sampling data. Given the long, intense historical sampling period for terrestrial Maastrichtian faunas in North America, the absence of any conclusive evidence for another large-bodied theropod besides *Tyrannosaurus* is compelling. Other tyrannosaurids (*Albertosaurus*, *Gorgosaurus*, and *Daspletosaurus*) are well sampled in the underlying Campanian formations but are not found in the Maastrichtian. Had this track been found in Africa or South America, the poorer fossil record from these regions would not permit confidence in such a specific assignment. Rather, we would assign it to the group identified by the node uniting the three candidate trackmakers (such as Tetanurae).

In general, trackmaker identity should re-

flect the least inclusive group that bounds all taxa sharing similar morphological characteristics and spatiotemporal distributions. Lockley and Hunt (1995) ascribed the large ceratopsid trackway *Ceratopsipes* to *Triceratops* on the basis of the latter's relative abundance in neighboring, contemporaneous formations. Given that the large ceratopsid *Torosaurus* is also known from the same formations and has a very similar postcranial morphology to *Triceratops*, it is possible that either taxon made the *Ceratopsipes* trackway (Wilson and Carrano 1999). Because tracks are often found in different sedimentary facies than bones, relative abundances based on bones may not apply to tracks. Furthermore, behavioral differences between taxa may also confound abundance-based trackmaker identifications. Without a morphological feature to distinguish between these taxa, the *Ceratopsipes* track is best assigned to Ceratopsidae.

Reciprocal Illuminants.—The ichnological record may offer independent clues as to trackmaker identity that are not strictly linked to existing skeletal synapomorphies. Organisms can display functional differences related to gait, speed, behavior, or aspects of functional morphology that may not be apparent or currently interpretable from skeletal morphology (Farlow and Pianka 2000). For example, theropod tracks can often be identified from the presence of claw marks, reflecting the presence of curved unguals, a synapomorphy of this group. Theropod tracks also display other features that distinguish them from the tracks of other bipedal dinosaurs, such as ornithopods. Unlike those of the latter, the pedal digits of theropods are not arrayed evenly on the substrate but rather show a marked divergence of digit IV from II and III (Farlow et al. 2000). This is a consistent feature of theropod tracks, yet there is little in the pes to suggest its morphological basis. Although we are not yet able to understand the functional morphology of this feature, we are able to correlate asymmetrically arrayed digits II–IV with Theropoda. More commonly, soft tissues preserved in footprints may provide additional synapomorphies of the body-fossil clade to which the tracks are ascribed. For example, preservation of heel-strike impressions

in sauropod footprints implies that the presence of a fleshy heel is a synapomorphy of sauropods (Wilson and Sereno 1998).

Once a set of unique features has been identified in tracks and linked by synapomorphies to a particular dinosaur group, these features can stand by themselves as identifiers of that group. Thus, even in preservational situations where claw marks or other theropod morphological hallmarks are not recorded, the unique digital divergence pattern would indicate the theropod affinity of a track. Similarly, presence of a fleshy heel would distinguish sauropod tracks from those made by other large, quadrupedal dinosaurs. These connections are distribution-dependent, however: isolated occurrences of an ichnological feature within a particular group do not necessarily indicate that the feature is a synapomorphy for the entire group.

Matching Level of Taxonomic Identification with Level of Resolution

The criteria for trackmaker identification outlined above—synapomorphies plus additional differentiae—dictate the appropriate hierarchical level at which candidate trackmakers should be sought. This process is data-limited in that it does not employ all aspects of track morphology, particularly when certain features are neither synapomorphies nor differentiae of particular taxonomic groups. Accordingly, our diagnoses are coarser and reflect a more conservative assignment of trackmaker identity. In general, ichnological studies would benefit from a more explicit articulation of which hierarchical level is appropriate and attainable. Certain hypotheses do not depend on species-level designations, while others may. Even broad taxonomic designations are potentially useful for evolutionary studies (e.g., Wilson and Carrano 1999).

Footprints and Distributions

The distinct conditions that promote the preservation of body and trace fossils lead to spatial and temporal disjunctions in these two fossil records. Several geologic formations are known to preserve one type of fossil to the exclusion of the other. "Thus the osteological and ichnological records supplement each

other far more often than they overlap" (Baird 1980: p. 229), and the two can be mutually informative.

Spatiotemporal Distributions from the Fossil Record

Body Fossils.—The body-fossil record delimits a spatiotemporal distribution for the taxa it includes that is based on specific, definitive occurrences of fossils; as such it represents the minimum distribution of these taxa. However, the existence of preservational biases means that the actual origination and extinction of a group extend beyond the known fossil range of that group (Signor and Lipps 1982). Consequences of the Signor-Lipps effect are particularly problematic in cases where the fossil record is sparse, and these events are likely hidden within large gaps of the record. Sampling intensity becomes important in constraining the error bars on stratigraphic distributions in these instances (Marshall 1990, 1994).

In addition, the phylogenetic relationships of taxa imply a pattern of divergences that can be calibrated to the stratigraphic record (e.g., Wagner 1995). Because the presence of one taxon implies the presence of its sister taxon, a particular phylogeny will predict "ghost lineages" for certain taxa for which no record currently exists (Norell and Novacek 1992). These represent unsampled occurrences that can be used to augment known taxon distributions and diversities. Thus the body-fossil record both implies and documents particular spatiotemporal distributions of taxa when placed in the context of phylogeny.

Trace Fossils.—Given appropriate trackmaker identification, the ichnological and osteological record can be integrated at various taxonomic levels. At a given taxonomic level, however, ichnofossil and body-fossil distributions may not be completely coincident—ichnofossils may pre- or postdate the known occurrences of a taxon, or may extend its geographic range. In this manner, trace fossils often provide evidence for the spatiotemporal existence of organisms where body fossils do not exist (e.g., Lockley 1991; Collins et al. 2000). In some cases, anachronistic ichnofossils introduce distributional hypotheses that

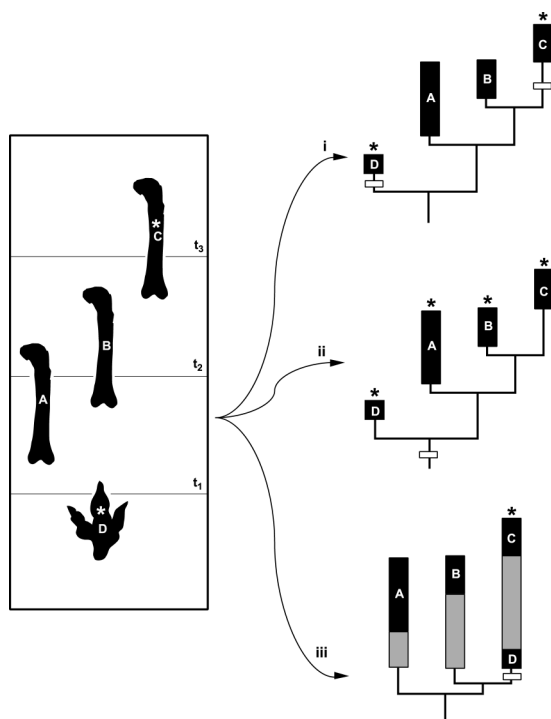


FIGURE 4. Three interpretations of an anachronistic early appearance of an osteological synapomorphy in a fossil trackway. Such an anachronism can be accommodated by a novel distribution of either characters (i, ii) or taxa (iii). The early appearance of a synapomorphy (identified with an asterisk and bar) can be interpreted as homoplasy (i) or synapomorphy (ii). Interpretation ii implies that intervening taxa, A and B, have been mis-scored (or unscored). Alternatively, the early appearance of * in taxon D may signal the early appearance of the taxon for which * is diagnostic (i.e., taxon C), potentially extending the ghost lineages of several sister taxa (indicated by gray bars). Femur icon modified from Currie and Zhao 1994: Fig. 22; footprint icon modified from Thulborn 1990: Fig. 6.9.

can supplant those derived from body fossils alone (Fig. 4).

Such anachronisms have two possible sources. First, the taxon distribution may have been different from that implied solely by the body-fossil record (Fig. 4, iii). In this case, the ichnofossil represents a range extension for the taxon. Second, the identifying feature of the track may have had a different distribution from that implied by the osteological record. This could be interpreted either as homoplasy between the known group and an as-yet-unsampled lineage (Fig. 4, i) or as representing a feature with a wider distribution than had previously been recognized among the sampled lineage (Fig. 4, ii).

For example, feathers probably diagnose the Upper Jurassic–Upper Cretaceous theropod clade Coelurosauria (Chen et al. 1998; Ji et al. 1998; Sereno 1999). The discovery of Early Jurassic theropod footprints with traces of featherlike structures (Gierlinksi 1996) could be interpreted as a range extension for coelurosaurs into the Early Jurassic. However, given the spotty distribution of preserved integumentary structures, it could also imply that feathers were derived independently in another theropod clade, that feathers were lost among some theropod subgroups, or that feathers diagnose a more inclusive single clade within Theropoda. Alternatively, the 40-Myr anachronism represented by these featherlike filaments may be viewed as improbable, and alternative identifications of the impressions may be sought.

Origin of Dinosauria and Its Major Subgroups

Despite the unevenness of preservation throughout the Mesozoic, the dinosaur body-fossil record displays a decrease in quality with increasing time that is characteristic of the fossil record in general (Raup 1972; but see Benton et al. 2000). The continental Middle Triassic record has been sampled from only a few sites worldwide, yielding faunas that include primitive dinosauriforms and early theropod dinosaurs. Several major dinosaur groups (sauropodomorphs, ornithischians) are entirely unknown from this period. As a result, the origins of Dinosauria are difficult to date precisely. This problem is mirrored among many other animal groups, particularly invertebrates, and previous workers have suggested that certain invertebrate trace fossils represent substantial temporal range extensions for particular clades (Collins et al. 2000). Here, using combined body fossil and ichnofossil data, we evaluate the temporal ranges of Dinosauria and its major subgroups.

The two main lineages of dinosaurs, Saurischia and Ornithischia, have variable fossil records, but each has a history that is inferred to extend back to the Middle Triassic (Sereno 1999). The generally poor Late Triassic record, coupled with the small body size of many of these taxa, results in several poorly sampled

basal lineages. Late Triassic ornithischians, for example, include only the basal taxon *Pisanosaurus* (Argentina), the putative heterodontosaurid *Geranosaurus* (South Africa), and several fragmentary forms from North America and South Africa (Weishampel 1990). Among saurischians, both prosauropods and theropods are widespread in the Late Triassic, and recently reported fragmentary material from Thailand may represent a Late Triassic sauropod (*Isanosaurus* [Buffetaut et al. 2000]).

However, the phylogenetic relationships within Dinosauria imply several unsampled lineages during the Late Triassic. For example, sauropods are inferred to have existed during this time from the presence of fossils of their sister taxon, Prosauropoda. In addition, diversification within Ornithischia apparently began somewhat later than that within Saurischia, at around 225 Ma versus 235 Ma. From the earlier divergence (Saurischia), a ghost lineage of 10 Myr is inferred for basal ornithischians, corresponding to a minimum divergence of Saurischia and Ornithischia at 235 Ma (Sereni 1999).

The ichnological record offers data relevant to these reconstructed divergence times. Large tridactyl footprints from the Los Rastros Formation in Argentina can be attributed only to a (currently unsampled) large theropod taxon from the Ladinian (Forster et al. 1995; Arcucci et al. 1998). These pre-date the oldest known theropod body fossils, those of *Herrerasaurus* from the overlying Ischigualasto Formation (Rogers et al. 1993), by 3–5 Myr. Similar tracks are also known from the Anisian–early Ladinian of France (Haubold 1974, 1983; Courel and Demathieu 1976; Demathieu 1990). No temporal range extensions are offered by the sauropod, prosauropod (Baird 1980), and ornithischian (Baird 1964; Olsen and Johannson 1994) ichnological records, which postdate their respective body-fossil records by several million years (Appendix 2).

These data can be synthesized into a single calibrated cladogram (Fig. 5) that permits estimation of the timing of the origin of Dinosauria. Based on the saurischian and ornithischian body-fossil records, the minimum divergence time of Dinosauria is approximately 230 Ma (Sereni 1999), corresponding to the

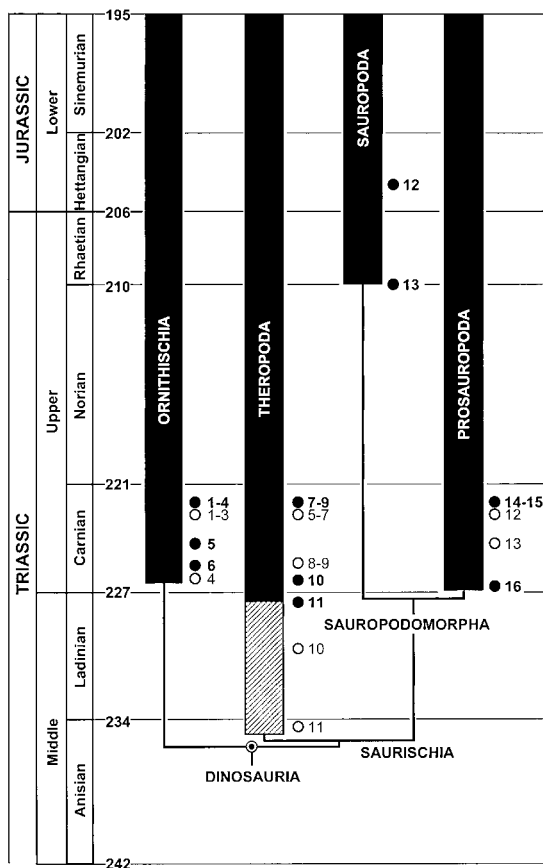


FIGURE 5. Calibrated phylogeny of Dinosauria and major subgroups. The dinosaur body-fossil record is generally poor in the Middle and early Late Triassic. The known temporal ranges of four major dinosaurian subgroups are shown in black bars, as indicated by the earliest recorded body-fossil evidence for each (filled circles). However, the addition of ichnological data (open circles) extends the temporal ranges for Theropoda. The extension of the theropod lineage into the late Anisian draws down the minimal divergence time of Dinosauria to at least this point. Thus, the origin of Dinosauria is inferred to have occurred significantly earlier than is indicated by the body fossil record alone. The taxa and formations associated with each numbered occurrence are listed in Appendix 2.

middle Ladinian. Because the incorporation of ichnological data extends the oldest occurrences of several major dinosaurian subgroups, this removes the divergence times of Saurischia and Ornithischia to approximately 235–240 Ma. As a result, we can now place the minimal divergence time of Dinosauria at this point, corresponding to the middle Anisian stage within the Middle Triassic. This is 10 Myr older than would have been estimated from body fossils alone.

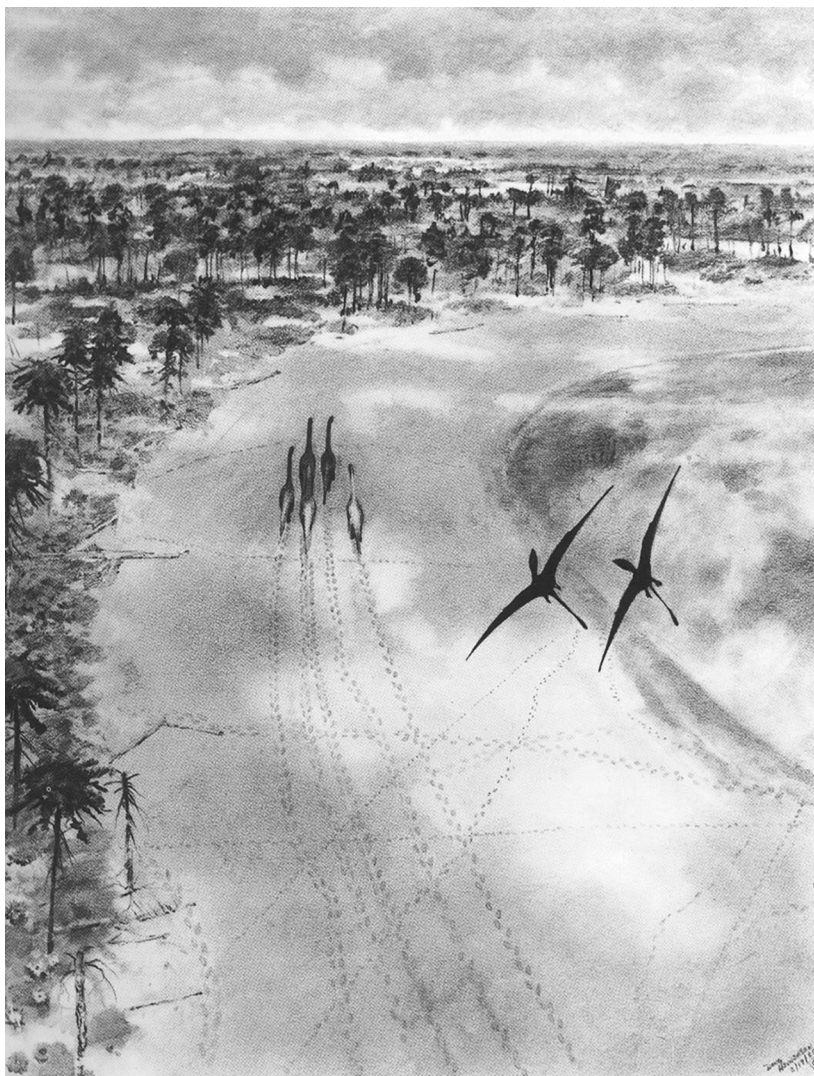


FIGURE 6. The benefits and risks of using ichnological data are summarized in this Late Jurassic scene. A group of sauropods travels along a lake shoreline, leaving a trackway that records their near-simultaneous passage, including direction and speed of travel. But other trackways, made slightly earlier, are also visible—were these from the same animals, or others? From this distance, the generic-level identity of the sauropods is not apparent—is this information available in the tracks? Will the pterosaurs flying overhead leave impressions, or be thought absent from the fauna? (Illustration by D. Henderson, from Lockley 1987.)

Conclusions

Perhaps the most significant change brought about by the recent renaissance in vertebrate ichnology has been one of perspective: “Traditionally tracks have been regarded as useful only in areas where little or no other fossil evidence exists. A much better approach is to view tracks as an integral part of the entire paleontological evidence” (Lockley 1991: p. 85). Undoubtedly vertebrate tracks form a rich and diverse record that can enlighten and

augment the history of extinct taxa. In many ways, however, this record has remained underexploited, largely owing to problems surrounding the issue of trackmaker identity. An existing, although underutilized method of trackmaker identification roots this process in taxon diagnosis (Olsen 1995). In concert with spatial and temporal distributions that are qualified by sampling intensity, this method offers trackmaker identifications that more directly reflect the taxonomic content of ichno-

fossils. Furthermore, this method is both falsifiable (i.e., new skeletal data can overturn trackmaker identifications) and explicit (i.e., each trackmaker identification is based upon a stated chain of evidence). Thus supported, synapomorphy-based trackmaker identifications can challenge distributional hypotheses based on skeletal data alone. Ultimately, tracks make a difference in our understanding of the history of vertebrate groups. This methodology offers the most promising means of realizing the potential of this rich fossil record.

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Appendix 1

Dinosaur synapomorphies potentially observable in ichnological record. For each osteological feature, a potentially identifiable ichnological feature is listed along with the quality or type of preservation (fine, moderate, or coarse; resting trace or specific posture) that would be necessary. Synapomorphies are from Gauthier 1986, Sereno 1986, Holtz 1994, Wilson and Sereno 1998, Wilson and Carrano 1999, Sereno 1999, and references therein. The number nodes in Figure 3 correspond to the numbers presented in this list. Features listed at basal nodes are assumed to be present in all included taxa unless subsequent internal nodes list modifications of these features. Abbreviations: MC = metacarpal; MT = metatarsal.

Osteological feature	Potential ichnological feature	Preservation
Dinosauriformes		
Obligatorily bipedal posture?	Bipedal tracks	Coarse
Narrow gait, parasagittal posture	Narrow trackway gait	Coarse
Digitigrade foot posture	Lack of MT prints	Coarse
Dinosauromorpha		
Obligatorily bipedal posture?	Bipedal tracks	Coarse
Dinosauria		
MT IV shaft axis with sigmoid curvature	Laterally divergent digit IV	Coarse
Ornithischia		
1. <i>Lesothosaurus</i> + Genasauria		
Pedal digit V phalanges absent	No impressions for pedal digit V phalanges	Resting
Length of MT V less than 25% that of MT III	Short MT V trace	Resting
Genasauria		
2. Marginocephalia		
3. Ceratopsia		
4. Neoceratopsia		
Obligatorily quadrupedal posture	Quadrupedal tracks	Coarse
5. Ceratopsidae		
Large body size	Large track size	Coarse
6. Ornithopoda		
7. Euornithopoda		
8. Iguanodontia		
Manual digit III with 3 phalanges	Three phalangeal pad impressions on manual digit III	Fine
9. Ankylopollexia		
Manual digit I oriented at least 60° from the long axis of digit III	Divergent manus I print	Fine, quadrupedal
Phalanx 1 of manual digit I absent	No impression of manual phalanx I-1	Fine
Ungual of manual digit I subconical	Impression of manual digit I subconical	
Ungual of manual digit I longer than ungual of manual digit II	Impression of manual digit I ungual longer than that of manual digit II	Moderate
Length of pedal digit I 20% or less than that of pedal digit II	Short pedal I print	Resting
10. Styrcosterna		
MC II–IV tightly appressed and ligament-bound	MC prints do not spread	Moderate
Unguals of pedal digits II–IV hoof-shaped	Hoof-shaped impressions of pedal unguals II–IV	Moderate
Facultative quadrupedalism	Quadrupedal tracks	Coarse

Appendix 1. Continued.

Osteological feature	Potential ichnological feature	Preservation
11. Hadrosauriformes		
Phalanx 2 of manual digits II–IV more than twice the length of phalanx 1	Impression for phalanx 2 of manual II–IV than for phalanx 1	Fine, quadrupedal
Manual digit II ungual narrower than manual digit III ungual	Manual digit II ungual trace narrower than that of manual digit III	Fine, quadrupedal
Manual digit V with 3 phalanges	Three phalangeal impressions on manual digit V print	Fine, quadrupedal
Phalanx 1 of manual digit V subequal in length to metacarpal V	Phalanx V-1 pad impression subequal in length to MC V trace	Fine, quadrupedal
Unguals of manual digits II and III hoof-shaped	Hoof-shaped ungual impressions for manual digits II and III	Moderate, quadrupedal
Pedal digit V absent	No pedal digit V trace	Moderate
12. Hadrosauroidae		
Pedal digit I absent	No pedal digit I trace	Moderate
13. Hadrosauridae		
Manual digit I absent	No manual digit I trace	Moderate, quadrupedal
Length of MC V 30–40% that of MC II	MC V trace 30–40% that of MC II	Fine, quadrupedal
Penultimate phalanges of manual digits II and III subtriangular	Subtriangular traces of penultimate manual digit II and III phalanges	Fine, quadrupedal
Large body size	Large track size	Coarse
14. Thyreophora		
15. <i>Emausaurus</i> + <i>Scelidosaurus</i> + Euryopoda		
MC I and V subequal in length to MC III	MC I and V traces subequal in length to MC III	Fine
Hoof-shaped manual and pedal unguals	Hoof-shaped ungual traces	Moderate
Obligatorily quadrupedal posture	Quadrupedal tracks	Coarse
16. <i>Scelidosaurus</i> + Euryopoda		
17. Euryopoda		
Pedal digit IV with four or fewer phalanges	Four or fewer pedal digit IV phalangeal pad impressions	Moderate
Spreading arrangement of metatarsals	Pedal print with spreading MT traces	Coarse
Large body size	Large track size	Coarse
18. Stegosauria		
Pedal digit I absent	No pedal digit I print	Moderate
Pedal digit III with three or fewer phalanges	Three or fewer pedal digit III phalangeal pad impressions	Moderate
19. Stegosauridae		
Length of femur at least 150% that of humerus	Disparity between fore- and hindlimb stride lengths	Trackway
20. Ankylosauria		
Saurischia		
Enlarged, medially offset pollex	Pollex trace offset in manual prints	Moderate, quadrupedal
21. Sauropodomorpha		
Ungual of pedal digit I longer than the other pedal phalanges	Pedal ungual I print longer than other ungual prints	Moderate
Prosauropoda		
Phalanx 1 of manual digit I rotated 45–60° ventrolaterally	Manual digit phalanx 1 print rotated ventrolaterally	Moderate, quadrupedal
Phalanx 1 of manual digit I bears a proximal heel	Proximal heel print on manual digit I phalanx 1	Fine, quadrupedal
Broad, tetradactyl, digitigrade pes	Tetradactyl pedal print lacks metatarsal traces	Coarse

Appendix 1. Continued.

Osteological feature	Potential ichnological feature	Preservation
22. Sauropoda		
Columnar, obligatorily quadrupedal posture	Quadrupedal tracks	Coarse
Very large body size	Very large track size	Coarse
Ungual of pedal digit I 25% larger than that of digit II	Pedal I ungual print larger than pedal II ungual print	Moderate
Pedal ungual I sickle-shaped and deeper dorsoventrally than broad	Sickle-shaped pedal ungual I print	Coarse
23. Eusauropoda		
Phalangeal counts of manual digits II and III reduced to 2-2-2-2 or fewer	Manual phalangeal pad impression counts 2-2-2-2 or fewer	Fine
Non-ungual manual phalanges broader than long	Manual phalangeal pad impressions broader than long	Fine
Minimum shaft width of MT I greater than those of MT II–IV	Digit I more deeply impressed than others	Moderate
Metatarsals arranged in a spreading configuration	Spreading metatarsals in pedal print	Coarse
Penultimate phalanges of pedal digits II–IV rudimentary or absent	Penultimate phalangeal impressions small or absent	Moderate
Pedal digit IV ungual small or absent	No pedal ungual IV print	Moderate
Sickle-shaped pedal unguals II, III much deeper dorsoventrally than broad transversely	Pedal ungual II, III prints sickle-shaped and relatively deep	Moderate
24. <i>Barapasaurus</i> + <i>Omeisaurus</i> + Neosauropoda		
Long axes of pedal unguals orientated lateral to long axes of digits	Pedal ungual prints offset	Coarse
25. <i>Omeisaurus</i> + Neosauropoda		
Minimum transverse shaft diameters MT III, IV less than 65% of those of MT I or II	Digits I and II impressions deeper and wider than those of III, V	Moderate
26. Neosauropoda		
Metacarpals bound, with subparallel shafts and long articular surfaces	Bound metacarpus print lacks divergence of digits	Moderate
Articulated metacarpals form a 270° U-shaped arc in proximal view	U-shaped manus print	Coarse
27. <i>Camarasaurus</i> + Titanosauriformes		
28. Titanosauriformes		
Femoral shaft with proximal one-third deflected medially	Wide-gauge tracks	Trackway
Manual digit I ungual small or absent	Lack of manual ungual print	Moderate
29. Titanosauromorpha		
30. Saltasauridae		
Femoral distal condyles offset 10° relative to main axis of shaft	Wide-gauge tracks	Trackway
Theropoda		
Clawed pedal ungals	Pedal claw marks	Coarse
Functionally tridactyl, mesaxononic pes	Tridactyl pedal print	Coarse

Appendix 1. Continued.

Osteological feature	Potential ichnological feature	Preservation
31. Herrerasauridae + Neotheropoda		
Neotheropoda		
Pubic foot with broad median contact	Boot print in resting trace	Resting
MT I length more than 50% of MT II	Short MT I print in resting trace	Resting
MT V shaft relatively slender	Slender MT V print in resting trace	Resting
Pedal phalanx I-1 subequal to pedal phalanx III-1	Short pedal I-1 print compared with III-1 in resting trace	Resting
32. Ceratosauria		
Coelurosauria		
Feathers/featherlike filaments present	Feather traces	Resting
33. Maniraptoriformes		
Maniraptora		
Vaned feathers with rachis, barbs, and barbules	Vaned feather traces	Resting
Paraves		
Pedal digit II with enlarged, elevated hyperextendable claw	Pedal print with reduced digit II that lacks claw print	Moderate
Aves		
Reversal of pedal digit I ungual	Reversed hallux print in thin substrate	Coarse

Appendix 2

List of ichnological and skeletal sites used in Figure 5. Only pre-Norian sites are listed for most major dinosaurian lineages, representing the oldest records for these clades; post-Carnian sites are included only for Sauropoda.

Age	Taxon	Reference
Skeletal data		
ORNITHISCHIA		
1. New Oxford Fm., Penn., U.S.A. late Carnian	<i>Galtonia</i>	Hunt and Lucas 1994
2. Petrified Forest Fm., Ariz., U.S.A. late Carnian	<i>Tecovasaurus</i>	Hunt and Lucas 1994
3. Dockum Fm., Tex., U.S.A. late Carnian	<i>Tecovasaurus</i>	Hunt and Lucas 1994
4. Argana Fm., Marrakech, Morocco late Carnian	<i>Azendohsaurus (partim)</i>	Hunt and Lucas 1994
5. Pekin Fm., N.C., U.S.A. middle-late Carnian	<i>Pekinosaurus</i>	Hunt and Lucas 1994
6. Ischigualasto Fm., San Juan, Argentina early Carnian	<i>Pisanosaurus</i>	Rogers et al. 1993
THEROPODA		
7. Chinle Fm., N.M., U.S.A. late Carnian	<i>Coelophysis</i>	Benton 1994
8. Santa Maria Fm., Rio Grande do Sul, Brazil late Carnian	<i>Staurikosaurus</i>	Benton 1994
9. Maleri Fm., Andhra Pradesh, India late Carnian	<i>Alwalkeria</i>	Wieshampel 1990
10. Ischigualasto Fm., San Juan, Argentina early Carnian	<i>Eoraptor, Herrerasaurus</i>	Rogers et al. 1993
11. Ischigualasto Fm., San Juan, Argentina late Ladinian	<i>Herrerasaurus</i>	Rogers et al. 1993

Appendix 2. Continued.

	Age	Taxon	Reference
SAUROPODA			
12.	<i>Vulcanodon</i> Beds, Mashonaland North, Zimbabwe Hettangian	<i>Vulcanodon</i>	Raath 1972
13.	Nam Phong Fm., Thailand late Norian–Rhaetian	<i>Isanosaurus</i>	Buffetaut et al. 2000
PROSAUROPODA			
14.	Argana Fm., Marrakech, Morocco late Carnian	<i>Azendohsaurus (partim)</i>	Benton 1994
15.	Maleri Fm., Andhra Pradesh, India late Carnian	Prosauropoda	Weishampel 1990
16.	basal Isalo II beds, Sakaraha, Madagascar late Ladinian–early Carnian	Prosauropoda	Flynn et al. 1999
Ichnological data			
ORNITHISCHIA			
1.	Cow Branch Fm., Va., U.S.A. late Carnian	Ornithischia	Olsen and Johannson 1994
2.	Locketong Fm., Penn., U.S.A. late Carnian	Ornithischia	Weishampel 1990
3.	Wolfville Fm., Nova Scotia, Canada late Carnian	Ornithischia	Hunt and Lucas 1994
4.	Unterer Gipskeuper, Bayern, Germany early Carnian	Ornithischia	Wieshampel 1990
THEROPODA			
5.	New Oxford Fm., Penn., U.S.A. late Carnian	Theropoda	Olsen and Johannson 1994
6.	Locketong Fm., Penn., U.S.A. late Carnian	Theropoda	Weishampel 1990
7.	Ansbachersandstein, Bayern, Germany late Carnian	Theropoda	Weishampel 1990
8.	Benkersandstein, Bayern, German early Carnian	Theropoda	Weishampel 1990
9.	Unterer Gipskeuper, Bayern, German early Carnian	Theropoda	Weishampel 1990
10.	Los Rastros Fm., La Rioja, Argentina Ladinian	Theropoda	Forster et al. 1995
11.	Lyonnais “lower sandstones,” Rhône Valley, France Anisian–early Ladinian	Theropoda	Demathieu 1990
PROSAUROPODA			
12.	New Oxford Fm., Penn., U.S.A. late Carnian	Prosauropoda	Olsen and Johannson 1994
13.	Turkey Branch Fm., Va., U.S.A. middle Carnian	Prosauropoda	Olsen and Johannson 1994