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Flattened fossil footprints: Implications for paleobiology

Martin G. Lockley [a],*, Lida Xing [b]

[a] Dinosaur Tracks Museum, University of Colorado Denver, P.O. Box 173364, Denver, CO 80217, USA
[b] School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China

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ABSTRACT

Studies of natural casts of dinosaur footprints associated with very thin mudstone and siltstone intervals in thick sand-dominated sequences often reveal casts that are significantly flattened due to the differential effects of overburden pressures on different lithologies. They are in effect squeezed, vise-like, between two thick, non-compactable sand layers. Thus, the sand filled tracks (casts) are flattened or widened as the ductile layers are compressed. Such flattening, here described from five localities, is a previously unreported phenomenon with implications for vertebrate ichnology. Present evidence suggest that significant flattening is not evident in most sequences in which mudstone and siltstone intervals are thicker, even though overburden pressures may have been comparable. Examples from the Jurassic of North America and the Cretaceous of China show that the flattening (widening) of tridactyl theropod tracks leads to predictable changes in track cast morphology, which may influence interpretations of track maker identity, and ichnotaxonomy. In the theropod dominated samples described here, such extramorphological changes differentially affect the shape of the whole cast and individual digit trace casts making them appear more "fleshy" and sometimes deceptively convergent with ornithopod tracks.

1. Introduction

Ichnologists know that many factors influence the quality of track preservation. These factors include, but are not limited to, the size and behavior of track makers, the consistency of the substrate at the time of track registration, post-registration weathering and erosion of the substrate, and post burial processes. It is also known that optimal substrate conditions give rise to superior preservation, or what have been referred to as "elite tracks" (Lockley and Hunt, 1995). It is also generally accepted that only well-preserved footprints are suitable as a basis for erecting new ichnotaxa. For example, Peabody (1955 p. 915) noted that it is "commendable" to avoid giving formal names to "poorly preserved trackways" that may have suffered various "distortions." However, it is surprising that in a number of standard treatments on the naming of fossil footprints this common sense precaution is not always explicitly stated or observed (e.g., Sarjeant, 1989, 1990).

In the present study we are primarily concerned with well-preserved true, or elite tracks and how they may be modified by post-burial processes. We avoid discussion of undertracks or transmitted tracks since they are, by definition, not true tracks, and therefore represent "distortions" (sensu Peabody, 1955) of the optimal expression of foot morphology that may be registered in well-preserved tracks, for example those with skin impressions. Falkingham et al. (2011) have used the term "Goldilocks effect" as a synonym of "optimal preservation." Here we note that optimal preservation may occur as the result of the interaction between many different-sized trackmakers and substrates, and so may be found associated with a large variety of substrates. Undertracks may be associated with optimally preserved tracks, but they occur on different layers.

2. Natural impressions and natural casts

Any true track that is filled in by an overlying layer of sediment has the potential to be preserved as both a natural impression (concave epirelief) and a natural cast (concave hyporelief) (Fig. 1). The latter is essentially a replica of the underside of the foot. In most cases however, differences in the consistency and resistance of the track-bearing substrate and the overlying fill will determine whether the natural impression, the natural cast, or both are preserved. Typically where a track is registered on a firm sandstone surface, subsequently covered by fine mud or silt, the covering layers (after burial, lithification and exhumation) can more easily erode to produce a well-exposed surface with natural impressions (epireliefs). There are countless examples of such track-bearing surfaces, with natural impressions, including well-known tracksites visited by the public: e.g., the Jurassic tracksite at Dinosaur State Park, Rocky Hill, Connecticut (Farlow and Galton, 2003) and the Cretaceous tracksite at Dinosaur Ridge, Colorado (Lockley and Marshall, 2014). Conversely if a sand layer covers a track-bearing layer consisting of fine mud or silt, it is likely that the tracks will be

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* Corresponding author. Tel.: +1 720 290 5719.
E-mail address: Martin.Lockley@UCDenver.edu (M.G. Lockley).

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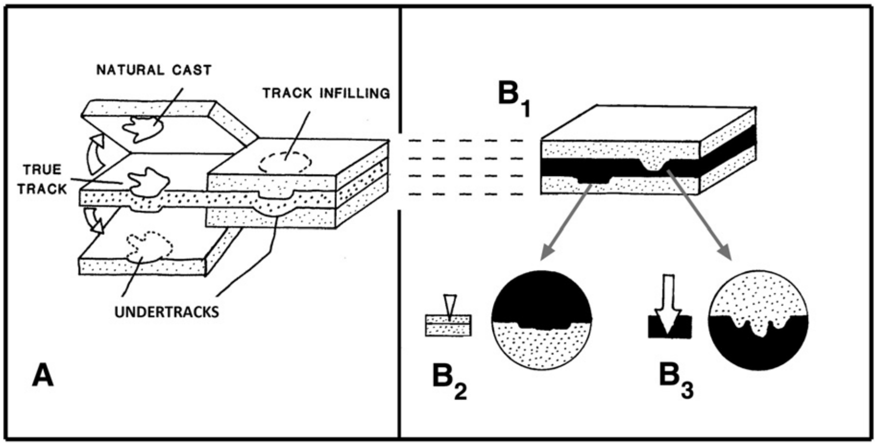

Fig. 1. A: Typical modes of track preservation as true tracks or natural impressions (concave epireliefs) and natural casts (convex hyporeliefs), modified after Lockley (1991, Fig 3.1). Note that depth of tracks and cross sectional relief (shown in B) may be due to different substrate properties at the time of track registration. For example, tracks made on less-compactable sand may be shallower and show less relief than those made in mud: details in text and in Lockley and Hunt (1994a, 1994b).

preserved as natural casts. Excellent examples of such cast preservation, to contrast with the examples of impressions given above, are to be found at the St. George Dinosaur Discovery Site at Johnson Farms, in St. George, Utah, where abundant well preserved casts are on display (Milner et al., 2006). Such casts are typically well-preserved, if not distorted by later trampling or extreme tectonism. When two relatively resistant lithologies are separated by a very thin layer of fine sediment, it is possible that both the natural impression and natural cast will be well-preserved as part and counterpart.

In the case of the two modes of preservation (part and counterpart) it is important to note that if the tracks are registered on firm, less-compactable substrates (e.g., sand) the footprints will be shallower, with flatter floors, whereas those registered on softer (wetter) mud or silt, will be deeper with steeper walls and higher relief that more faithfully replicates the track maker's foot morphology. These differences were briefly noted by Lockley and Hunt (1994a) and Lockley et al. (2014a) who compared tracks registered by similar track makers (Cretaceous ornithopods) on a sandy surface, covered by ~30 cm mud and those registered on the top of the same mud layer and filled by sand to produce casts (Fig. 1).

3. Previous work

Fossil footprints, like other fossils are potentially subject to rock deformation, by stress and strain, and may therefore have their shapes changed significantly (Lockley, 1999; Fig. 2 herein). In such instances, assuming homogeneous strain (affine deformation, sensu Whitten and Brooks, 1973) where the principle axis of stress acts more or less in the plane of the track-bearing surface, the orientation of a track relative to this axis is important, as the same track may be elongated or shortened (widened) depending on its original orientation. Of course stress may act in any direction relative to track orientations. In the discussions that follow, we are assuming that the overburden pressures (principal stress) acted perpendicularly to the track-bearing surface, and as noted above, affected the different lithological units differently: i.e., the strain was heterogeneous (non-affine) to some degree.

4. Material and institutional abbreviations

All the examples given here are taken from thick sandstone sequences in North America and East Asia. The North American examples are based on field observations and museum specimens of theropod tracks in the Lower Jurassic Navajo Sandstone (Lockley, 2009; Lockley et al., 2014b), including specimens CU/UCM 184.2, 184.70, 184.112, 184.113 and 184.114. The Asian samples originate from several Cretaceous Formations in Anhui and Sichuan provinces in China and include replicas CU/UCM 214.37, CU/UCM 214.39, CU/UCM 214.46 and 214.287–214.90 in the CU/UCM collections.

CU: University of Colorado (Denver) Dinosaur Tracks Museum specimens formerly published with CU prefix, now transferred to UCM

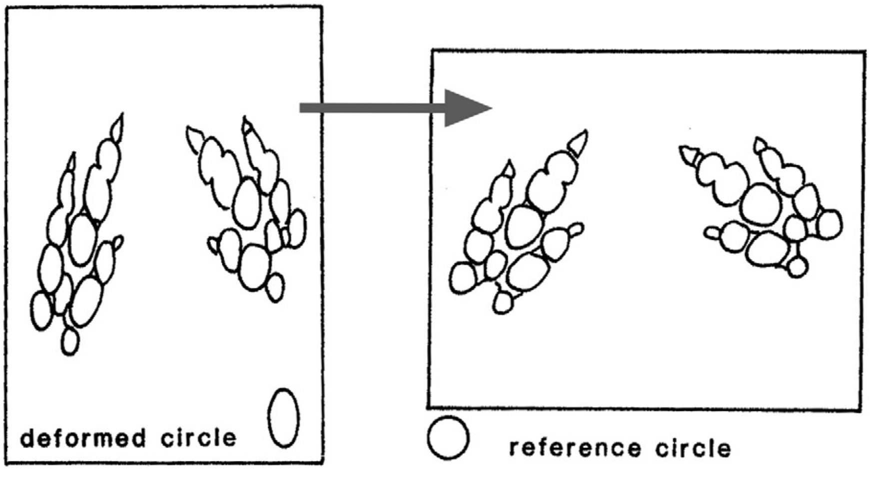

Fig. 2. Early Mesozoic tracks distorted by strain: after Lockley (1999).