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Flattened fossil footprints: Implications for paleobiology

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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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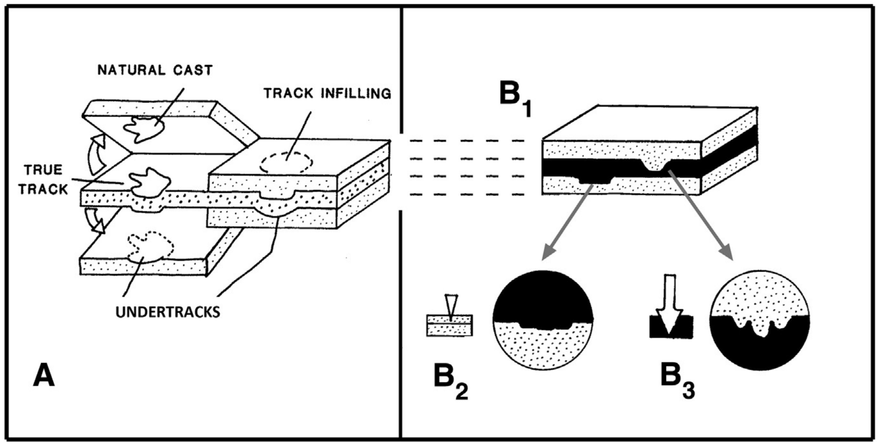

Fig. 1. A: Typical modes of track preservation as true tracks or natural impressions (concave epireliefs) and natural casts (convex hyporeliefs), modified after Lockley (1991, Fig 3.1). Note that depth of tracks and cross sectional relief (shown in B) may be due to different substrate properties at the 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

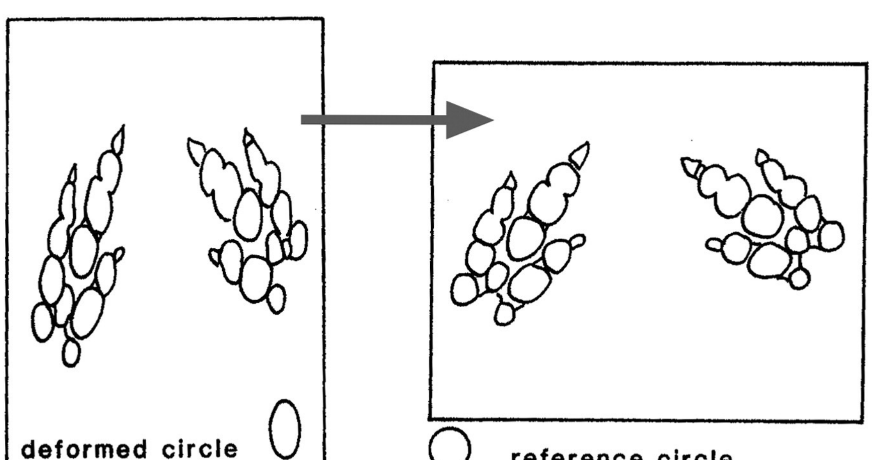

Fig. 2. Early Mesozoic tracks distorted by strain: after Lockley (1999).

collections. UCM: University of Colorado Museum of Natural History (Boulder, Colorado). GLCA: Glen Canyon National Recreation Area (National Park Service). XHT: Xiaohutian tracksite specimens from Anhui Province, China. See Appendix A for further details.

5. Description of specimens and their context

5.1. Navajo Sandstone, Utah

Natural casts of theropod tracks here interpreted as flattened to various degrees include several tracks illustrated by Lockley (2009, Fig. 5). With the exception of the type of *Eubrontes giganteus* (Olsen et al., 1998) shown for comparison, all other tracks come from various localities in the Navajo Sandstone of Utah. All the Navajo Sandstone tracks (Fig. 3A–D) originate from sequences where there are almost no intervals of fine grained siltstone or mudstone more than a few millimeters or centimeters thick. These theropod tracks labeled as *Eubrontes* sensu *lato* (Fig. 3) include several specimens with a “fleshy,” wide toed appearance that differ significantly from type *Eubrontes* (Fig. 3E). Lockley (2009) considered that these differences likely indicated different track makers, but did not erect new ichnotaxa to accommodate them. The pertinent question, considered below, is the degree to which the wide, fleshy appearance of the tracks is the result of extramorphological flattening caused by overburden pressures, rather than being representative of original foot morphology. Arguments in favor of either or both possibilities are considered and may apply to the various samples described here.

The trackway illustrated by Lockley et al. (2014b, Fig. 26) which was previously illustrated in an unpublished Utah Geological Survey report (Kirkland et al., 2011, Fig. 32), shows that the track-bearing surface is associated with a very thick sandstone deposited above a very thin silt-mud horizon in the Navajo Sandstone (Fig. 4). This context is similar to that observed for the other Navajo Sandstone tracks (Fig. 3).

In both cases the fleshy appearance of the track casts may be somewhat deceptive. The lack of discrete digital pads and inter-pad creases makes the tracks appear more like those of ornithopods than theropods. However the trackway pattern (pace length and track axis rotation) remains characteristically theropodan: i.e., with length greater than width, an indentation (or notch) behind the proximal margin of digit II, and lack of inward rotation of the foot axis. Moreover, no such large ornithopod tracks or trackmakers have been reported from the Lower Jurassic.

In the track casts shown in Figs 3A_1, D and 4, the traces of digit III appear to widen distally (anteriorly). This gives the distal portion of the toe cast a diamond or rhombic shape. As noted below such apparent distortions have been reported, for other large theropod track casts, from various locations, although they have not been explained. Thus, the track shape cannot be assumed to be a precise or accurate reflection of foot morphology. For this reason, it may be necessary, as done below, to review interpretations based on track morphology (length, width mesaxony). Track shape is also subject to interpretation by observers (Thulborn, 1990). For example, McCrea (2000) attributed *Gypsichites pascensis* to a theropod, *contra* Sternberg (1932) who inferred an ornithopod trackmaker. In this case the outline, as

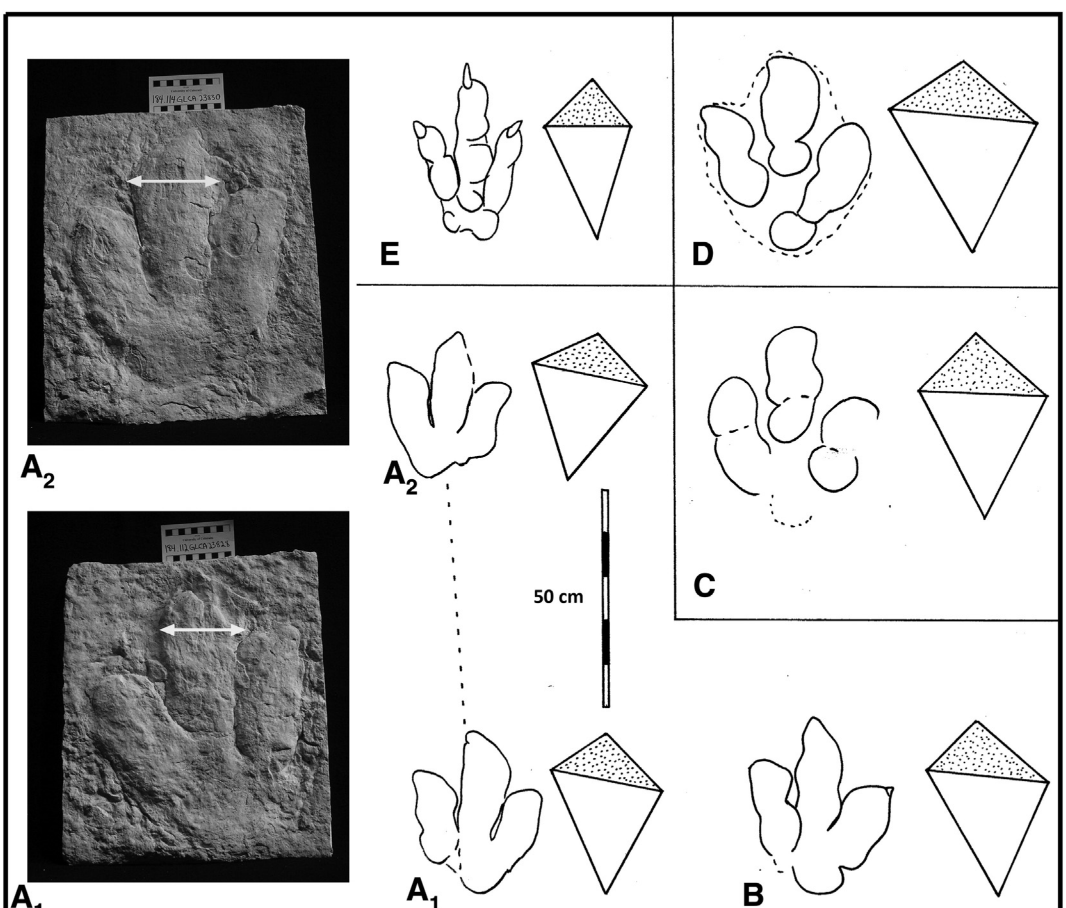

Fig. 3. Theropod track casts from the Jurassic of USA showing narrow- and wide-toed outlines. Modified after Lockley (2009, Fig. 5) all drawn at the same scale. A_1–A_2: trackway sequence based on CU 184.112 and 184.114 (and tracing T 928); note white arrows showing maximum width of cast of digit III, B: track CU 184.7113 (T929), C: from tracing T 935; D: CU 184.70 (T 909). E. *E. giganteus* shows no signs of flattening. Other *Eubrontes* sensu *lato* (B–E) show evidence of flattening. A1, A2 and B from the Navajo Sandstone at Glen Canyon National Recreation Area (Lake Powell), Utah; C from Navajo National Monument visitors center; D from Moab Museum. See Appendix A for notes on specimen numbers.

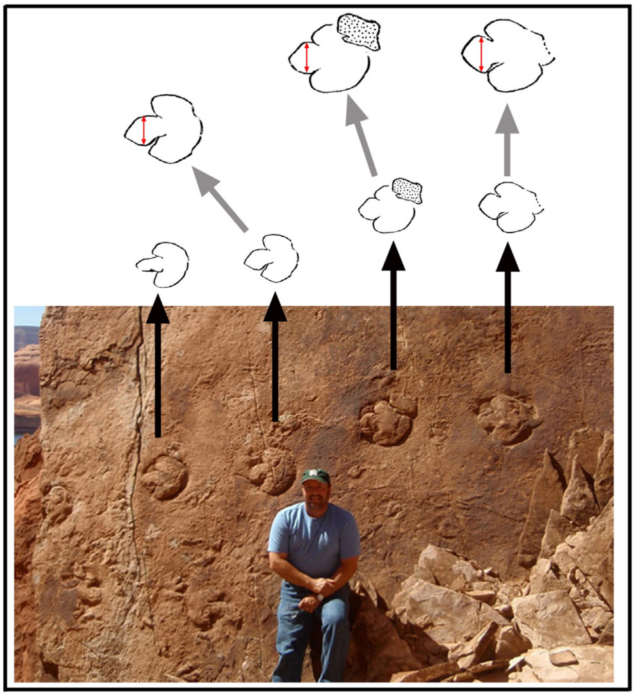

Fig. 4. Trackway of a large tridactyl biped preserved as natural casts with a wide-toed or fleshy appearance. Navajo Formation, Lake Powell area, Utah.
Modified after Lockley et al. (2014b, Fig. 26).Photo courtesy of Vince Santucci, National Park Service.

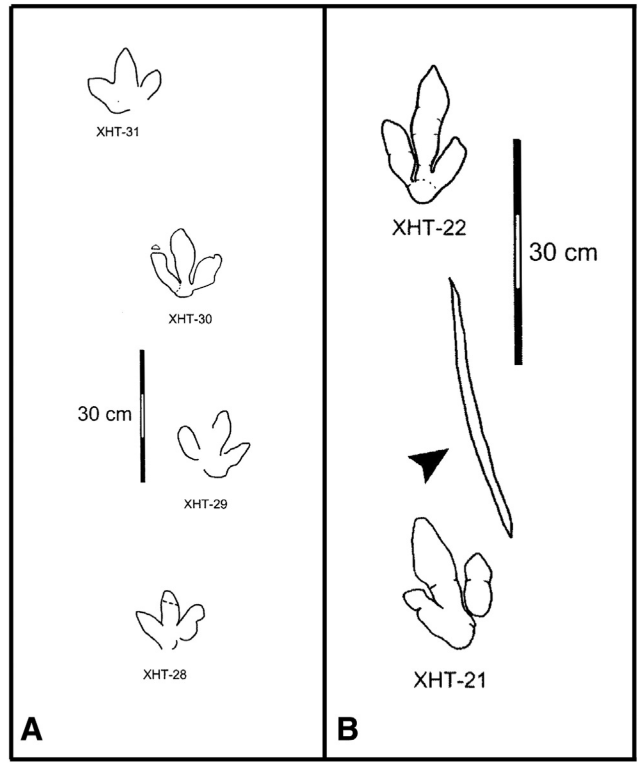

Fig. 5. A. *Paracorpulentapus zhangsanfengi* holotype trackway XHT-28 to XHT31 from the Xiaohutian (XHT) tracksite, in the Xiaoyan Formation, Anhui Province, China. B: unnamed pair of consecutive tracks (XHT 21 and XHT 23) from the same location, with tail or toe trace (black arrow). Note tendency towards diamond or rhombic shape for digit III casts. A and B represented in CU collections by CU 214.39 and 214.37 respectively.
Modified after Matsukawa et al. (2006, Fig. 4) and Xing et al. (2014a, Fig. 7).

illustrated by Sternberg (1932) was over-simplified and ambiguous. The older literature on Chinese dinosaur tracks is also rife with illustrations of dubious value that do not reflect track morphology, even in cases where distortion is not evident: see Lockley and Matsukawa (2009) and Lockley et al (2013) for reviews.

5.2. Xiaoyan Formation tracks, Anhui Province, China

The Xiaoyan Formation has a thickness of ~750 m with a lower member composed of lithologically-complex purple conglomerate containing litharenite, andesitic agglomerate, pyroxene andesite, tuffaceous conglomerate, and sandstone with large-scale cross bedding. The upper member is composed of purplish-gray and brick-red conglomerate interbedded with mixed litharenite and mudstone (Xing et al., 2014a). The age of the Xiaoyan Formation is problematic, and has been referred to as Campanian (Chen and Chang, 1994) or Maastrichtian (Sullivan, 2006).

Tracks were first reported from the Xiaohutian tracksite in the Cretaceous Xiaoyan Formation of Anhui Province by Yu (1999) and subsequently described in more detail by Matsukawa et al. (2006) and Xing et al. (2014a). The latter authors consider that they are not from the Qiyunshan Formation, as reported by Chen et al. (2006), but rather occur in a thin mud silt intercalation in a sandstone-dominated sequence in the lower part of the Xiaoyan Formation (Hou, 1977). The tracks from this locality are all tridactyl, occur as natural casts, some in trackway segments, and have variable sizes and somewhat unusual morphologies (Xing et al., 2014a, Figs. 5–7: Fig. 5A herein). Xing et al. (2014a) assigned one morphotype to the new ichnogenus *Paracorpulentapus* (ichnospecies *P. zhangsanfengi*), based on trackway segment XHT-28 to XHT31, also represented by replica CU 214.39, and attributed it tentatively to a theropod, due to the asymmetry of the tracks (postero-medial notch) moderately long step and lack of inward rotation of foot axes. *P. zhangsanfengi* tracks have relatively short digits, weak mesaxony and wide digit divarications. They present a distinctive fleshy appearance and in the case of XHT-30 (CU 214.39) show a diamond shaped widening of digit III anteriorly. Morphologically different theropod tracks XHT-21 and XHT-22 (CU 214.37), with strong mesaxony also show a tendency towards a diamond- or rhomb-shaped outline for the digit III cast (Fig. 5B). This diamond- or rhomb-shaped outline is particularly obvious in some of the other tracks at this site, notably XHT-2 to XHT-5 illustrated by Xing et al. (2014a, Figs. 5 and 6). However, the degree of possible or inferred flattening of the trackway segments illustrated here (Fig. 5) is apparently not as extreme as inferred for specimens XHT-2 to XHT-5. Thus, even on the single surface represented by the Yiaohutian tracksite preservation is quite variable. Such variability in preservation is demonstrated for other tracksites described below.

5.3. Jiaguan Formation tracks, Xingyang tracksite, Sichuan Province, China

The Jiaguan Formation consists of upper and the lower members. The lower member is 211–405 m thick, with a 0–10 meter-thick basal conglomerate layer and a 2–10 meter thick mudstone layer at the top. The upper member, which contains the tracksite is a 345–1000-meter-thick feldspathic quartz sandstone succession, with cross-bedding, mud cracks, rain prints, ripple marks and thin or lenticular mudstone interlayers (Sichuan Provincial Bureau of Geology Aviation Regional Geological Survey Team, 1976; Chen, 2009).

Track casts that apparently illustrate the flattening phenomenon come from the Xingyang tracksite (GPS: 28°26′21.24″N, 105°35′5.37″ E) in the Xuyong region, in the southern part of the Sichuan Basin. Here a single well preserved trackway has been reported from the underside of a large block of thick, brick-red, feldspathic, quartz sandstone representing the Jiaguan Formation (Sichuan Provincial Bureau of Geology Aviation Regional Geological Survey Team, 1976). The age of this formation is estimated to be between 117 Ma and 85 Ma (Aptian–Santonian) by Li (1995) and between 140 and 85 Ma (Berriasian–

Santonian) by Gou and Zhao (2001). Recent pollen studies indicate a Barremian–Albian age for the Jiaguan Formation (Chen, 2009).

As shown in Fig. 6, all seven tracks in the trackways have a similar fleshy appearance with wide digit casts. They reveal several digit III casts with distinctive, diamond- or rhomb-shaped outlines. Several are morphologically very similar to those reported from the Navajo and Xiaoyan Formations discussed above. The theropod trackway and its constituent individual track casts are both quite well-preserved and characterized by three anteriorly directed digits. The casts of all three digits are quite wide, without well-developed creases separating the digital pads. In most tracks the preservation is very similar with left and right footprints easily distinguished. The characteristic theropod notch is seen behind the proximal end of digit II, where in several casts there is also the trace of a small metatarsal phalangeal pad. In most tracks the distal (anterior) end of the casts of digit III is wider than the remainder of the toe casts, giving, in most cases, the end of the digit III cast a roughly diamond shaped outline. This, as noted below, is likely a subtle extramorphological feature.

5.4. Jiaguan Formation tracks, Gajin tracksite, Yibin City, Sichuan Province, China

In addition to the Jiaguan Formation tracks reported from the Xingyang tracksite, the holotype of *Yangtzepus yipingensis* (IVPP V2473.1) was reported by Young (1960) from Gajin Village, Yipin City, Sichuan. According to Young (1960) the holotype track, and associated paratypes (Fig. 7) originate from the Upper Jurassic Chiating Series. However, Chen et al. (2006) and Matsukawa et al. (2006) indicate that the track is from the Jiaguan Formation and is Upper Cretaceous in age. Young (1960) also inferred that the track almost certainly represents an ornithischian, and he also claimed that coarsely granulated skin impressions are visible. However, Xing et al. (2009) questioned the evidence for a Late Jurassic age and interpreted the track as theropodan. This attribution was supported by Lockley et al. (2013), who noted the diagnostic pad traces, but questioned the evidence for skin traces. Pending further study the age of these tracks is somewhat uncertain. The most explicit statement about age and stratigraphy is given by Chen et al. (2006), who correlate the Yibin site (Yibien, in their terminology) with the Jiaguan Formation, thus inferring a Cretaceous age. This age estimate is consistent with evidence mentioned by Xing et al. (2009) who referred to ostracod evidence cited by Ye (1982) as indicating a Lower Cretaceous age. The senior author (MGL) briefly visited the type locality in 2001, where sandstone was being excavated, but was unable to find any additional evidence of tracks. Likewise the second author (XL) visited the site in 2014 and was unable to find further track evidence.

The type material of *Y. yipingensis*, including the holotype (IVPP V2473) which is also represented in the CU/UCM collections by replica CU/UCM 214.146 (Fig. 7), has been examined by the present authors, re-illustrated by Xing et al. (2009, Fig. 2A–C) and Lockley et al. (2013, Fig 3a), and is again re-illustrated here. The holotype and paratype illustrated here (Fig. 7) are preserved as shallow, flattened natural casts. Although the cast of digit III reveals three faint digital pad impressions, it is also significantly widened anteriorly as in several of the tracks described

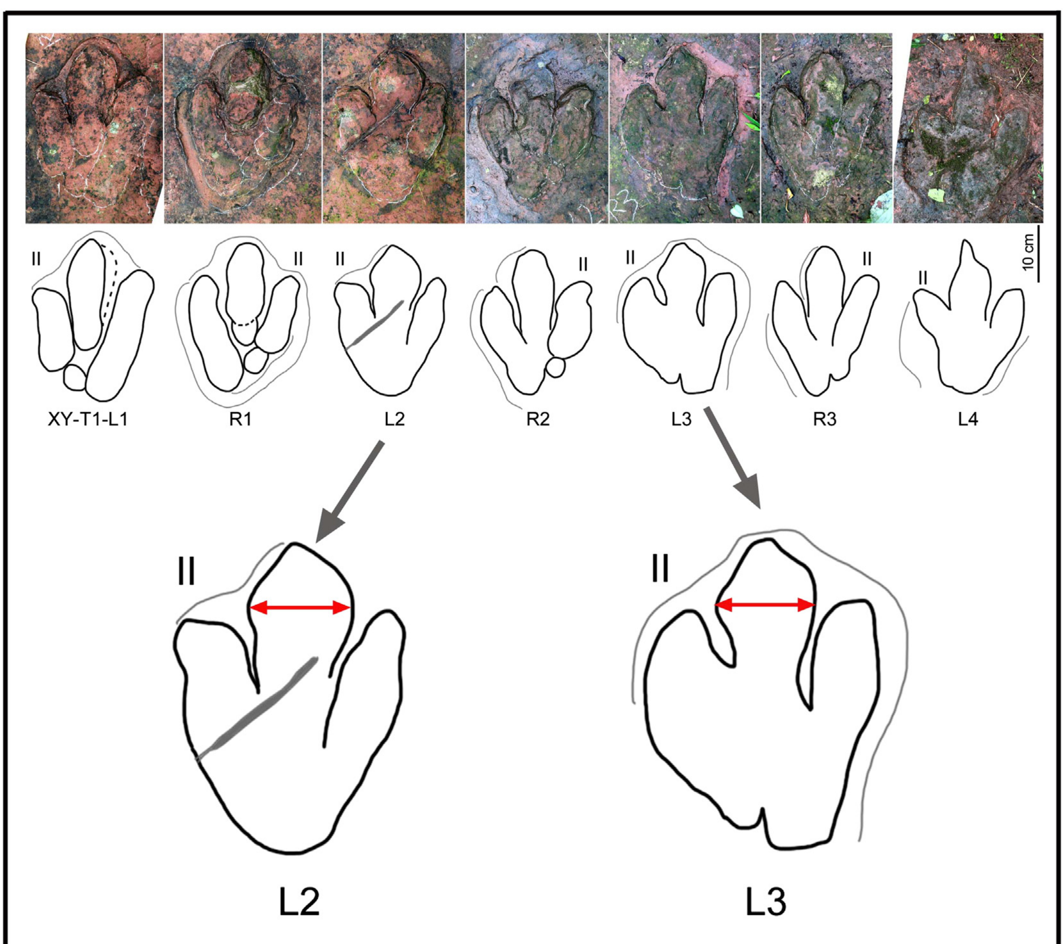

Fig. 6. Seven consecutive tridactyl theropod tracks (XY-T1-L1 to XY-T1-L4) from the Cretaceous Xiaoyan Formation, Xuyong region, Sichuan Province, China. Note repeat tendency towards diamond- or rhomb-shaped outine of digit III casts, especially clearly defined in L2 and L3.

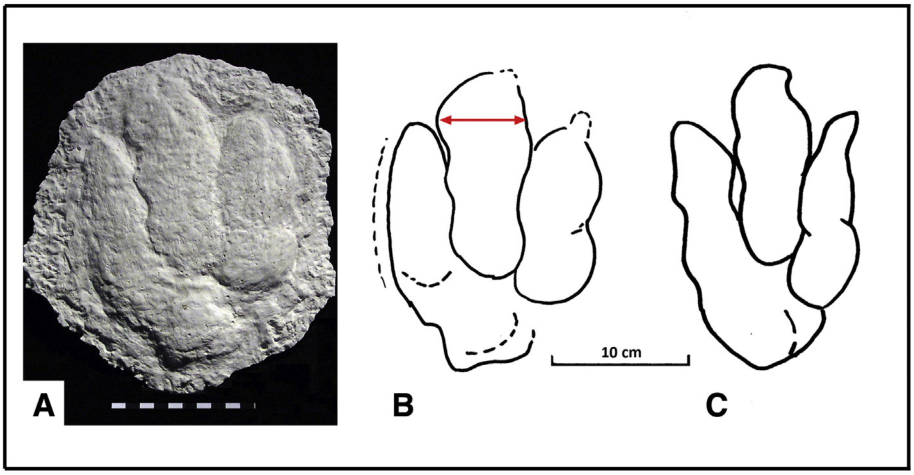

Fig. 7. Type material of *Yangtzepus yipingensis* was originally interpreted as an ornithopod track by Young (1960), but has since been recognized by several authors as a theropod track. A replica of holotype (IVPP V 2473.1) in CU/UCM collection, B: line drawing of holotype showing wide distal portion of digit III, C: line drawing of paratype.

from other samples discussed here. The paratype (IVPP V2473.2) reveals more slender digit traces than the holotype, and again reveals traces of individual digital pads: i.e., less obvious flattening. Given that theropod-diagnostic digital pad traces are present in both casts, it may be inferred that the degree of extramorphological variation is both variable, as in other samples, and in this case relatively subtle: i.e., not sufficient to obliterate inter-pad crease traces. However, if the holotype is interpreted as showing significant extramorphological variation, a case could be made that the ichnotaxon is of dubious utility: i.e., a *nomen dubium*. Finally, it is of interest to note that the original inference of Young (1960) attributing this track to an ornithopod might have been influenced by the wide appearance of the digit traces, which we here attribute to some degree of flattening. This then is a case of extramorphological variation changing or obscuring the diagnostic characteristics of a track.

5.5. Feitianshan Formation tracks, Yangmozu tracksite, Zhaojue region, Sichuan Province, China

In addition to the two previously described Xiaohutian and Xingyang tracksites from thick Cretaceous sandstone sequences in Anhui and Sichuan provinces, a third Chinese site named the Yangmozu tracksite, with similar styles of preservation has been reported from a thick sandstone sequence in the Feitianshan Formation, Zhaojue County, Liangshan prefecture region, in Sichuan Province. The Feitianshan Formation is considered Berriasian–Barremian in age (Tamai et al., 2004). The Lower Member is 517 m thick, representing fluvial and lacustrine delta facies. The Upper Member, which is 604 m thick, represents a lacustrine delta facies (Xu et al., 1997). Dinosaur tracks from the Lower Member come from, purplish-red, medium grained, feldspathic quartzose sandstone.

The southwestern area of Sichuan Province consisting of Liangshan autonomous prefecture and Panzhihua city is commonly known as Panxi (Panzhihua–Xichang) region, where the Cretaceous formation is most widely distributed. The largest basin in this area is Mishi (Xichang)-Jiangzhou Basin (Luo, 1999). Based on ostracod and charophyte biostratigraphy, the Cretaceous successions in Mishi-Jiangzhou Basin have been divided into the Lower Cretaceous Feitianshan and Xiaoba Formations, and Upper Cretaceous–Paleogene Leidashu Formation (Gu and Liu, 1997).

Like these other tracksites, the Yangmozu tracksite ichnofauna appears to be exclusively theropod dominated. Many of the larger tracks are similar in size and appearance to those described from the Xiaohutian and Xingyang tracksites (Fig. 8). However the site also yields very well preserved and very small *Minisauripus* tracks, only 2–3 cm long and a few millimeters deep. These will be described elsewhere (Xing et al., in review). However, it is interesting to note that these are not deformed (flattened) to any significant degree by compaction. Interpretations for such differential preservation are given below.

The Feitianshan Formation has also yielded tracks from a number of sites in the Zhaojue region (Xing et al., 2013, 2014b, 2015), but most of these are natural impressions not casts and do not appear to have been flattened. The Yangmozu site is considered to be lower in the Feitianshan Formation than these other sites.

6. Discussion

6.1. Track registration and preservation

All the tracks reported here are natural casts associated with thick sequences of massively bedded sandstone with only very thin silt or clay intercalations. In general however, track casts result from the infilling of fine grained sediment (mud or silt) by more resistant sediments such as sand, and produce some of the best preserved tracks often with skin impressions: e.g. Currie et al. (1991). Many track casts from the famous Amherst College collection (Hitchcock, 1858) and from sites like St. George, Utah (Milner et al., 2006) show such superior preservation. However, most of these sequences have relatively thin and localized sandstone beds that do not dominate the stratigraphic successions.

In general the size and morphology of theropod digits, expressed in track casts is variable, reflecting variation in original foot morphology and substrate consistency at the time of track registration. Dealing primarily with digit III traces, which often show three distinct pads, they may taper distally (being wider proximally around the proximal pad impression, Fig. 3E), have parallel sides, or have their maximum width in the middle or distal portion of the digit trace (corresponding respectively to the middle or distal pad). However, in the global record, tracks that have significant widening of the distal digit traces are rare and would presumably indicate unusual foot morphology. Nevertheless, many of the tracks described here appear significantly wider towards the distal end, sometimes with unusual diamond- or rhombic-shaped digit III outlines.

However, because digits that get wider distally are not typical of theropod body fossils, tracks in which the casts of digit III widen distally alert us to the possibility of some alternate explanation.

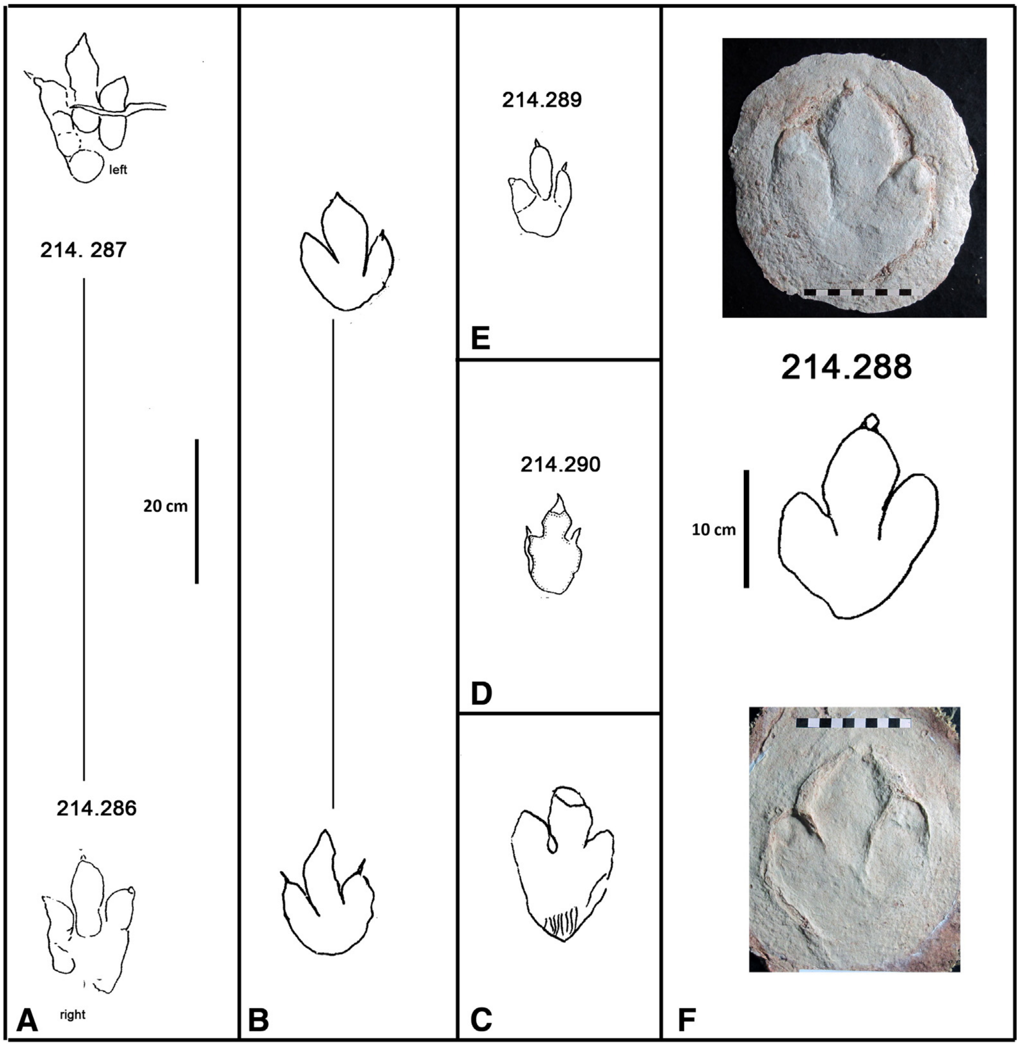

Fig. 8. Tracks from the Zhaojue tracksite showing variation in the morphology of theropod tracks. Note the difference in outline of tracks CU 214.286 and CU 214.287, showing well defined pad impressions and parallel sided digit casts, and the wide and apparently flattened outline, with diamond- or rhomb-shaped digit III cast of 214.88 (F). B–E show intermediate morphologies.

Many of the tracks, described here despite being elongate and unequivocally theropodan have unusually wide digit traces. This is probably an extramorphological feature explained as follows. As flattening occurs, the shape of track features may change differentially. For example, if a 2 cm deep sand filled track is flattened to 1 cm in thickness, the overall shape (length and width) may not change much (Fig. 9). For example, a maximum of 1–2 cm of length and width may be added to a track on the order of 20–30 cm in length: i.e., 1 cm to each of the anterior, posterior, medial and lateral margins. However, if the same 1–2 cms are added to each of the digits casts that were originally only 2–3 cm wide, the digit cast shape will change more markedly than the overall footprint shape. Other interesting permutations can be envisaged, especially if the track is much deeper, say 5–10 cm, and compaction results in wider lateral spreading (flattening) of the cast. Here it is essential to note, as stated above, that where track fills (casts) formed in thin clay or silt units sandwiched between massive sandstone beds these thin units and the tracks they contain are caught as if in a vise as overburden pressures build up. We recognize that sand constrained vertically and laterally by other sand in continuous sand sequences is not highly compactable. Rather we suggest that when thin ductile clay and silt layers are intercalated with thick sands, they are squeezed out laterally, and so the casts are flattened: i.e., also squeezed laterally. Thus, the deformation is not strictly speaking a grain-on-grain compaction of the sand so much as a lateral squeezing of the sand filling the tracks. When these sand filled tracks occur in thin clay and silt layers and overburden pressures squeeze them as if in a vise, they are forced into contact with underlying beds of sand which resist compaction. In contrast to the vise-like pressures affecting tracks of thin clay and silt units separating massive sandstone beds, if the clay–silt units are thick overburden pressures will not squeeze the casts in the top of these thicker units against the underlying units, and as a result there will be little or no distortion or flattening.

Other changes will affect the spacing between the digit casts. For example, the width of hypicies between the digits will be reduced, especially proximally where they are already narrower. Also, if the medial to distal portions of the footprint, including digit III, are deeper than the remainder of the track, the potential exists for a greater flattening (widening) of the track cast in these regions. For example, Avanzini (1998) has illustrated theropod tracks which have the maximum depth associated with the distal part of digit III. Likewise, because the proximal part of digit III is confined by the sandy fill of digits II and IV it may be less flattened (widened) than the distal portion of digit III, which is not so constrained (surrounded) by adjacent sand-filled digit traces. The result will be a greater widening of the distal part of the digit III cast. This is exactly what appears to have happened with many of the tracks described above. In fact, we can see that the distal

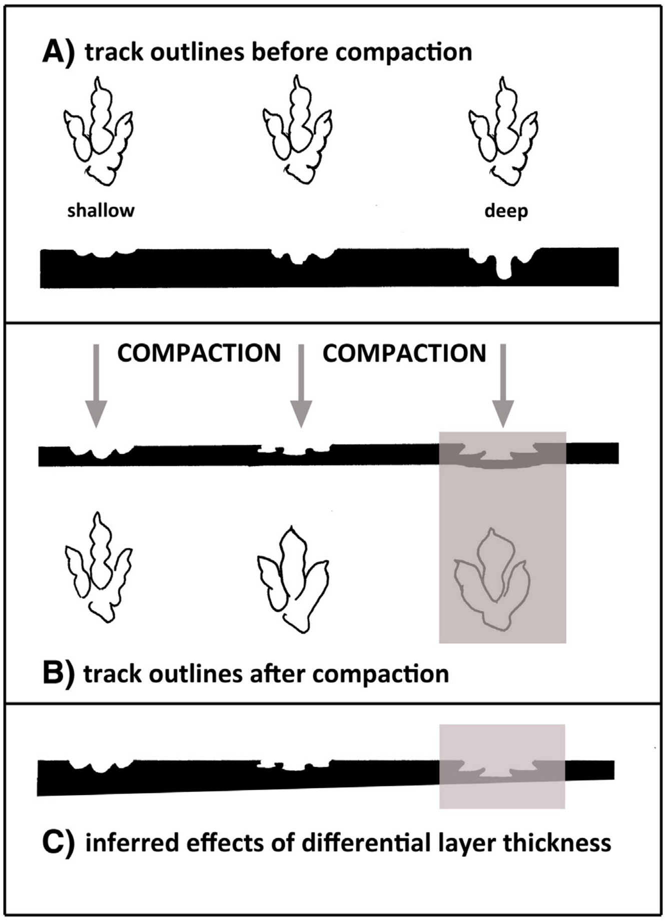

Fig. 9. A: Showing similar track outlines for tracks of different depths in a soft substrate. B: Shows how deeper tracks are more severely flattened (gray shading) when compaction affects thin, soft or ductile layers between massive resistant layers. C: Shows that differential flattening may result from differential thickness of soft ductile layers.

part of the digit III casts takes on a diamond or rhombic shape, in some tracks from all five of the samples described herein.

6.2. Implication for interpretation

In the present study we have described and compared the tracks from the five samples on the basis of their morphology, and have used the term "fleshy" or "wide-toed" as a descriptor, without assuming either that flattening of the tracks is proven, or that their trackmakers were wide toed. We know that some dinosaurs are more robust than others, and that many larger species did in fact evidently have wide-toed or "fleshy" feet (Lockley, 2000; Lockley and Hunt, 1994b), with wide digits: i.e., not all wide toed theropod track casts are necessarily flattened. However, if we take the apparent width of the toe casts at face value, such tracks may appear to be more like ornithopod tracks than those of theropods, or they may appear to be those of species with distinctive fleshy track morphologies.

We note that in the samples described here there are, in some cases, quite marked differences between tracks of similar sizes that occur close together on the same surfaces. Perhaps the most striking example is that from the Yangmozu tracksite where theropod tracks with well-defined digital pads and parallel sided digit traces (Fig. 8A) occur alongside track casts that appear flattened, and are in fact less deep. One possible explanation is that there was significant local variation in the thickness or consistency of the mud in which the tracks were registered (Fig. 8C), and that they were also originally registered with different depths. However, we cannot rule out the possibility that the track makers represent different species, despite size similarities. Lockley (2000) noted that there is a tendency for larger and more robust trackmakers to lack well defined digital pads and also to have had more fleshy feet. However, such distinctions are not always size-related, as is very clear in comparing similar sized *Grallator* isp. (or *Paragrallator* isp.) tracks from the Cretaceous, Huanglonggou site in Shandong Province, with those of *Corpulentapus* isp. from the same site (Li et al., 2011; Lockley et al., 2015), where abundant tracks of both types are well preserved with no evidence of distortion from burial or overburden pressures. Thus, it is arguable that the *Paracorpulentapus* isp. tracks from the Xiaoyan Formation Anhui Province (Fig. 5) are minimally distorted by overburden pressure, even though others from this site appear significantly flattened.

In the case of *Yangtzepus* isp. (Fig. 7) the holotype is very similar to tracks from the other sites that appear significantly flattened. Lockley et al. (2013) provisionally accepted *Yangtzepus* isp. as a valid ichnotaxon, pending further study. The present analysis suggests that the holotype is flattened to some degree, thus obscuring the original morphology to the point where the ichnotaxon is somewhat dubious, and almost certainly has extramorphological features, superimposed on the diagnostic theropod morphology. (The term "overprinted" is not appropriate here as the modification of the morphology is caused by non-biogenic overburden pressures). This superimposed modification of morphology evidently caused Young (1960) to consider that the trackmaker was an ornithischian.

It is important to note that it is difficult, if not impossible, to precisely determine the original depths of flattened tracks, or to determine the overburden pressures that affected different track-bearing units. As a result, the inferences presented here are based primarily on repeat occurrences of distinctive morphologies that appear not to have previously been described or explained in any detail. These morphologies are atypical of the vast majority of theropod tracks and appear to be attributable, at least in part, to overburden pressures that affect tracks differentially at interfaces created where thin, fine grained sedimentary units are intercalated between think sandstone beds. The genetic origin of the sandstone beds, eolian in the case of the Jurassic examples from Utah, and fluvial in the case of the Cretaceous sites from China, appears to be of little or no significance in explaining this unusual type of preservation: i.e., the preservation results from the volume and thickness of sand beds, not their paleoenvironmental characteristics.

Despite the lack of evidence for the original depth of flattened tracks, there are many other sites where large samples of theropod track casts are well preserved in association with the underlying lithologies in which the tracks were originally registered prior to lithification (Hitchcock, 1858; Milner et al., 2006). Most of these exhibit tracks that show no signs of flattening (Nadon, and Issler, 1997). This suggests that large samples of non-flattened tracks exist with which we can compare tracks that appear to have been subject to flattening. In some cases, as noted above these differences may be noted on the same surfaces or at the same sites. This suggests that flattening of track casts may be quite variable locally depending on differences in substrate consistency or other factors.

Finally, it is important to note that this previously undescribed phenomenon of track flattening, is relatively uncommon and appears, on present evidence, to be confined to certain types of sand dominated stratigraphic sequences. It nevertheless produces theropod track morphologies that must be regarded has having an extramorphological component or "overburden imprint." This should be taken into consideration in considering ichnotaxonomic assignments and inferences about track-maker identity. While all the examples described here are inferred to represent theropod trackmakers, it appears that the flattening phenomenon causes tridactyl tracks to appear somewhat ornithopod-like. Further, work is needed to explore whether examples of flattened tracks of ornithopods or other tetrapods exist, and what morphological and extramorphological features they might exhibit.

7. Conclusions

1) Tracks made in mud or other fine sediment, are often well-preserved, and may even show skin impressions.
2) When such tracks are filled with sediment such as sand, that becomes more resistant to weathering after lithification, well-preserved sandstone casts are often produced.
3) Overburden pressures on such casts usually result in minimal distortion in the vertical direction, especially in sequences where sand beds are relatively thin in comparison with finer grained units.
4) However, where such tracks occur in very thin mud or silt units intercalated between thick sandstone beds, in sandstone dominated successions, overburden pressures necessarily sandwich track casts, as if in a vise, between massive sandstone beds.
5) The result is that fine-grained ductile units are compacted (flattened) and squeezed out laterally causing the track casts to also be flattened. This is distortion of the sand filled track (cast) not an unusual local grain-on-grain compaction within the sand.
6) Flattening of tridactyl, sand-filled tracks results in changes in the outline of the whole track and the individual digit casts.
7) Such flattened tracks have not previously been described in detail or explained in the context of the characteristic sedimentological successions in which they occur.
8) However, evidence suggests that in tridactyl tracks flattening will affect different regions of the track differentially. For example, sediment filling digit III traces is bounded proximally by the sediment filling traces of digits II and IV. However these constraints do not affect the distal part of digit III traces to the same degree. These distal parts of digit III casts may also be deeper and contain more sediment susceptible to flattening.
9) This has been shown to be a convincing explanation for the wide, distal and diamond- or rhomb-shaped outline of digit III casts.
10) Hitherto all described examples of flattened tracks appear to be attributable to theropods.
11) However flattened track morphologies are atypical of theropods and likely represent extramorpological distortion. Thus, they should therefore be treated with caution in ichnotaxonomic studies.
12) It is difficult to determine the original depths of flattened track casts, or the overburden pressures that have affected different stratigraphic sequences through geologic time.
13) However, much evidence suggests that most tracks are not significantly flattened (or otherwise distorted) by normal overburden pressures in areas where there has not been intense tectonic activity.

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Appendix A

Tracks referred to by Lockley (2009, Fig. 5B and C) as CU 184.74 and CU 187.75 have been reassigned the numbers UCM 184.112 and UCM 184.113 respectively.

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