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A new solution to an old riddle: elongate dinosaur tracks explained as deep penetration of the foot, not plantigrade locomotion

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Abstract: The dinosaur track record features numerous examples of trackways with elongated metatarsal marks. Such "elongate tracks" are often highly variable and characterised by indistinct outlines and abbreviated or missing digit impressions. Elongate dinosaur tracks are well-known from the Paluxy River bed of Texas, where some had been interpreted as "man tracks" by creationists due to their superficially human-like appearance. The horizontal orientation of the metatarsal marks led to the now widely accepted idea of a facultative plantigrade, or "flat-footed", mode of locomotion in a variety of dinosaurian trackmakers small to large. This hypothesis, however, is at odds with the observation that elongate tracks do not indicate reduced locomotion speeds and increased pace angulation values, but instead are correlated with low anatomical fidelity. We here interpret elongate tracks as deep penetrations of the foot in soft sediment. Sediment may collapse above parts of the descending foot, leaving a shallow surface track that preserves a metatarsal mark. The length of a metatarsal mark is determined by multiple factors and is not necessarily correlated with the length of the metatarsus. Other types of posterior marks in dinosaur footprints, such as drag and slip marks, are reviewed.

key words: dinosaur track, penetrative, plantigrade, metatarsus, foot kinematics, track formation

INTRODUCTION

The dinosaurian pes is primitively digitigrade, with the metatarsophalangeal joints typically raised above the ground (Thulborn 1990). However, the record of dinosaur tracks yields numerous examples of footprints that extend posteriorly beyond the expected extent of the impression of the acropodium (the digital part of the foot, i.e. the footprint without posterior mark) – such expansions are henceforth termed “posterior marks”. Posterior marks can be produced via a number of mechanisms, including dragging of digits or of the foot during swing phase; forward sliding of the foot on slippery substrate; retroverted halluces; and metatarsal pads. Such marks can also be left by the metatarsus, an element that is not expected to have touched the ground during normal progression. Short marks of the distal metatarsus can often be related to a greater sinking depth of the foot, or may be behavioural (Belvedere & Mallison 2014). Rare resting traces show the metatarsus impressed along its whole length, with the left and right foot placed side-by-side, and often with manus impressions (e.g., Olsen & Rainforth 2003; Milner *et al.* 2009*a*). A third type of metatarsal trace, however, continues to cause confusion: metatarsal marks, apparently impressed at the same depth as the acropodium impression in trackways that show a regular and effective bipedal walk (Fig. 1, 2 Kuban 1989*a*). Examples of such tracks, which have been termed “elongate”, “metatarsal”, “plantigrade”, “quasi-plantigrade”, or “semi-plantigrade” tracks, are known from all over the world. They are, however, best known from the bed of the Paluxy River (Lower Cretaceous Glen Rose Formation, in and near Dinosaur Valley State Park, Glen Rose, Texas).

Kuban (1989*a*) presented an extensive discussion of elongate tracks from the Paluxy River. These tracks often lack distinct digit traces, resulting in trough-like structures that have famously been interpreted by creationists as giant “man tracks” (Fig. 1). The study provided strong evidence that most of the discussed marks are indeed made by the metatarsus, and discarded hypotheses that they could be traces of other parts of the foot, slip marks, or erosion marks. Kuban (1989*a*) acknowledged that partial impressions of the metatarsus could be made by a digitigrade foot if sinking deeply into the sediment. In this case, as argued by Kuban, the acropodium would be expected to be much more deeply impressed than the metatarsal region, which is not the case in most elongate tracks, which often show a horizontal orientation of the metatarsal mark. Consequently, a facultative plantigrade or, alternatively, “quasi-plantigrade” foot posture was advocated as the only viable explanation.

A plantigrade, or “flat-footed”, gait had already been proposed by Strevell (1932) for elongate tracks discovered in coal mines near Price, Utah, and by Thulborn and Wade (1984) for elongate tracks from Lark Quarry, Australia. The latter tracks indicate an estimated locomotion speed (based on stride length) not slower than that of regular tridactyl trackways present at the site (Thulborn & Wade 1984), as is also commonly the case with elongate tracks from the Paluxy River (Kuban 1989*a*; Farlow *et al.* 2015). Pérez-Lorente (2015) suggested that the plantigrade posture might have been a response to changing substrate properties, stabilizing the animal on a soft surface. Kuban (1989a), however, considered this idea unlikely, since most “plantigrade” trackways do not show evidence for a reduced locomotion speed. According to Kuban (1989a), the most plausible explanation is that “plantigrade” (or “quasi-plantigrade”) locomotion was adopted whenever the animal walked low to the ground, such as during foraging for small foot items in mud flats or when stalking prey. Kuban (1989a) also offered the alternative suggestion that the dinosaurs sometimes moved in a saltatory manner; this idea has been repeated since (Romero-Molina *et al.* 2003).

The interpretation of these tracks as “plantigrade”, or “semi-plantigrade” (Romero-Molina et al. 2003; Pérez-Lorente 2015), is current consensus (e.g., Thulborn 1990; Holtz Jr 1995; Day et al. 2004; Farlow et al. 2015). Although doubts have been raised (e.g., Farlow et al. 2015), the “plantigrade” interpretation has ultimately been accepted in most cases because of the lack of viable alternative explanations. Numerous additional “plantigrade” trackways have been discovered around the world in the three decades following Kuban’s seminal 1989 work (see below), but key features of such tracks, including the lack of anatomical details and the typically indistinct or absent digit traces, remain unexplained.

Understanding the formation of walking trackways composed of elongate tracks becomes possible thanks to two recent insights into the formation of tracks. The first of these insights is the recognition of substantial foot movement within the sediment during track formation, including rotation (Milàn *et al.* 2006; Avanzini *et al.* 2012), splaying and collapsing of digits (Gatesy *et al.* 1999; Milner & Lockley 2006; Turner *et al.* 2020), and looping of the foot (Falkingham *et al.* 2020; Turner *et al.* 2020). The deeper the foot sinks, the more of these movements are recorded. Significant mediolateral rotation of the digits is often already evident at moderate footprint depths (e.g., Milàn *et al.* 2006). There is furthermore a backwards motion of the digits already at shallow depths (Turner *et al.* 2020), which is most strongly pronounced in larger theropods (Avanzini *et al.* 2012; Huerta *et al.* 2012). This backwards motion can be considered an incipient looping. While moving backwards, the digits progressively dig deeper into the sediment, reaching their deepest point just before being extracted (Falkingham *et al.* 2020).

The second key insight is the recognition that tracks may extend substantially below their apparent bottom surface. Although traditional models explain track genesis as a simple deformation of surfaces (e.g., Thulborn 1990), it has been demonstrated that some degree of penetration is often involved (Gatesy 2003; Gatesy & Falkingham 2020). When sinking deeply, substrate may collapse, during or after foot entry, above the lowest foot-sediment interface, leaving narrow, sealed slits that mark the passage of the digits (Romano & Whyte 2003; Boutakiout *et al.* 2006; Milàn & Bromley 2007; Falkingham & Gatesy 2014; Falkingham *et al.* 2020; Gatesy & Falkingham 2020). Such penetrative tracks may also be exposed on subsurfaces if the sediment is layered, where they tend to be better defined than at the surface layer given the restricted movement of sediment particles (Falkingham *et al.* 2020; Gatesy & Falkingham 2020). Anatomical details such as phalangeal pad impressions, as well as the outline of the foot as captured by the footprint, might be expected to become indistinct in penetrative tracks (Falkingham *et al.* 2020). However, some clearly penetrative tracks retain such features to some degree (Gatesy & Falkingham 2020). While digit impressions in penetrative tracks are generally narrow, they can appear very broad, at least in their external outline (e.g., Xing *et al.* 2011, fig. 3; Gatesy & Falkingham 2020, fig. 6). Taken together, the above observations suggest that penetrative tracks may be more common than previously anticipated (Gatesy & Falkingham 2020), and may include shapes that retain a good degree of apparent anatomical detail.

Sediment collapse is widely recognised as a common feature in dinosaur footprints (e.g., Wagensommer *et al.* 2012; McCrea *et al.* 2014; Pérez-Lorente 2015). As explained above, penetrative tracks may involve substantial movement within the sediment with loop-shaped foot paths. The digits will therefore describe separate entry and exit paths, suggesting that the collapse is not triggered by the withdrawal, but can already occur while the foot is still descending. It is possible that only parts of the vertical extent of a trace will collapse (e.g., Avanzini *et al.* 2012, fig. 3), and sealing is most frequently found at the distal ends of digit traces. Collapse structures might not always be evident when only the upper-most surface of the track can be studied (Gatesy & Falkingham 2020).

Some workers have previously argued that the elongate tracks they described might be the result of deep sinking into the substrate (Dalla Vecchia *et al.* 2002; Marsicano *et al*. 2010; Hadri & Pérez-Lorente 2012; Lockley *et al.* 2014*a*; Klein *et al.* 2020), and therefore possibly be penetrative tracks (Gatesy & Falkingham 2020). Hadri and Pérez-Lorente (2012) suggested that elongate tracks near Le Mers, Morocco, were formed when the digits and metatarsus cut through laminated sediment, leaving rupture lines at the surface layer that mark the entry path of the foot. They furthermore argued that the metatarsus was held at an angle to the digits during track formation (Hadri & Pérez-Lorente 2012), i.e., an inclined metatarsus may leave a horizontal metatarsal mark (as demonstrated by Falkingham *et al.* 2020). These are key aspects of the mechanism we will suggest below.

Terminology

As was noted previously (Kuban 1989*a*), the term “plantigrade track” is ambiguous. Kuban (1989a, p. 69) recommended restricting the term to tracks that show “complete or nearly complete metatarsal impressions oriented in a largely horizontal manner, or require that several such tracks occur in succession”. Kuban (1989a) furthermore coined the term “quasi-plantigrade”, which recognises the alternative possibility that the metatarsus was held very low to the ground but not fully horizontal. W.A.S Sarjeant recommended to use the term “semi-plantigrade” instead of “plantigrade” for dinosaurs in general, assuming that only the metatarsus, but not the tarsus, would have been directly supported by the ground when walking (Pérez-Lorente 2015, p. 212, 331).

In recognizing that horizontal metatarsal marks can be produced by a digitigrade foot where the metatarsus is angled against the digits, we will restrict our use of the term “plantigrade track” to tracks for which a plantigrade foot posture during the weight-bearing phase of the step cycle can be assumed. We here adopt the term “elongate track” to refer to tracks with elongated posterior marks without implying any particular formational mechanism. We prefer the term “metatarsal mark” over the commonly used term “metatarsal impression”, as the term “impression” can be misleading if substantial movement of the foot is involved. A track, or parts of it, will be considered “penetrative” when the track walls collapse during or after track formation so that the original path of the foot through the substrate is sealed (Falkingham *et al.* 2020; Gatesy & Falkingham 2020). This usage of the term “penetrative track” is equivalent to the term “collapsed print” suggested by Romano and Whyte (2003).

MECHANISMS FOR THE FORMATION OF POSTERIOR MARKS

While many posterior marks may be interpreted as metatarsal marks, a number of alternative mechanisms need to be considered as well (Fig. 3; 3D-models of illustrated tracks are provided by Lallensack et al. 2021). Simple erosion is a possible cause, and may occur together with the other mechanisms. Erosional features may be expected to be inconsistent along a trackway and will generally be oriented according to local flow of water or wind. Posterior marks may also be created by overprinting of one footprint above another, possibly when the trackmaker stepped twice or when an additional trackmaker is involved, especially on highly dinoturbated surfaces (e.g., Richter & Böhme 2016). Drag marks of one or several digits, or of the foot, or even leg, may occur as the foot is lowered at the end of the stride (creating a posterior mark) or raised at the beginning of a stride (creating an anterior mark). Digit drag marks are often narrow and shallow, and may consist of up to three grooves (in tridactyl tracks) that are more or less parallel. Longer foot or leg drag marks form when the trackmaker is sinking deeply into soft sediment; such soft sediment may result in more indistinct traces that may be discontinuous (e.g., Gatesy and Falkingham 2017, fig 2H). Longer drag marks can extend from one footprint to the next, and are likely to be curved or sinuous, formed as the trailing foot swings around the stance foot. The rear of the foot, commonly a metatarsal or metatarsophalangeal pad, may scrape the sediment as the foot enters the substrate at an angle, especially when sinking in deeply. Such marks can be expected to be straight or parabolic in shape, becoming increasingly steeper anteriorly following the trajectory of the foot.

Forward slipping may occur on slippery substrates, elongating the track. Such slip or slide marks are often broad and curved with a smooth floor and possibly with displacement rims, particularly anteriorly, and may show striation marks. Slip marks often have an indistinct posterior margin, may be angled against the long axis of the associated footprint, and are inconsistent and sporadic within a trackway. The metatarsophalangeal pads of digits II and III seem to have been typically held clear of the ground by non-avian theropods, but may occasionally leave an impression (Thulborn 1990). The metatarsophalangeal pad of digit IV, on the other hand, is thought to have commonly been impressed (Farlow *et al.* 2000). Occasionally, posterior marks can be interpreted as resulting from the tail dragging across the surface (e.g., Olsen & Rainforth 2003, fig. 19.25v-w; Kim & Lockley 2013), retro-scratches (i.e., toes slipping backwards when the foot is withdrawn, Thulborn 1990), and, possibly, backward motion of the foot before lift-off. None of these alternative mechanisms, however, can readily explain very elongated and well-defined posterior marks found at the Paluxy River and elsewhere in the world (Kuban 1989*a*). We agree with Kuban (1989a) that many tracks with elongated posterior marks, including the alleged “man tracks” from the Paluxy River, must have been the result of the metatarsus contacting the substrate.

Bird (1985) compared the “man tracks” of the Paluxy River with tracks left by chickens walking through deep mud, suggesting that digit entry traces of the Paluxy tracks would have collapsed, and that digits were drawn together for easier withdrawal, resulting in an elongated exit trace. Bird, therefore, suggested a penetrative origin of the tracks that matches the mechanism we will suggest below in most key aspects. However, Bird’s mechanism does not necessarily involve the metatarsus, and thus is inconsistent with the frequent presence of splayed digit impressions just at the anterior end of the track (Kuban, 1989a). Modern ground birds indeed fail to register a metatarsal mark in all but the deepest of tracks because the metatarsus is held sub-vertically. This contrasts with the frequent registration of the metatarsus in theropod dinosaur footprints (Gatesy *et al.* 1999; Farlow *et al.* 2000).

Although the metatarsus is held at an angle to the digits in a digitigrade foot, it may leave an elongate impression if the foot sinks in deeply enough. In this scenario, the metatarsal mark would be sloped relative to that of the acropodium, reflecting its original posture. In contrast, many tracks show an elongated metatarsal mark that is horizontal to the acropodium impression – the peculiar configuration that forms the focus of the present paper. For our following discussion it is pertinent to distinguish between resting traces and trackways that show effective locomotion – as will be argued below, these two categories require fundamentally different interpretations.

Resting traces, which are also referred to as “sitting” or “crouching” traces, are most abundantly known from the basal ornithischian ichnogenus *Anomoepus* from the Newark Supergroup of the eastern US (example illustrated in Fig. 3). There is strong evidence that at least some of these *Anomoepus* traces do indeed record trackmakers resting on their metatarsi, which are impressed along their whole length (Hitchcock 1858; Gatesy & Falkingham 2020). This evidence includes the side-by-side placement of the left and right footprints rather than a placement in front of each other as expected in a trackway, although some asymmetry in their placement is frequently observed (Lockley *et al.* 2003). Furthermore, most resting traces have multiple manus impressions, which are often striking over one another (Olsen & Rainforth 2003). The pes impressions are slightly rotated inwards in trackways but are rotated outwards in resting traces (Olsen & Rainforth 2003). The interdigital angle is consistently much smaller in resting traces, and the metatarso-phalangeal pad of digit IV is lying nearly along the axis of digit III instead of being located laterally as in walking trackways; these differences are consistent even when the regular trackway section and the sitting trace are parts of the same trackway (Olsen & Rainforth 2003). Rounded impressions might be interpreted as “callosal” (or “ischial”) marks. Most convincingly, however, *Anomoepus* sitting traces may include skin impressions on their metatarsal impressions (Olsen & Rainforth 2003), demonstrating anatomical fidelity. Olsen and Rainforth (2003) pointed out that the metatarsus is commonly more deeply impressed than the digits, indicating that most of the animal’s weight rested on the former. However, only one instance of a metatarsus impression without digit impressions has been identified (Olsen & Rainforth 2003). Similar *Anomoepus* tracks have been reported from around the world (e.g., Avanzini *et al.* 2001; Niedźwiedzki 2003; Smith *et al.* 2009; Wilson *et al.* 2009). Theropod resting traces are rarer, but their side-by-side position and associated manus traces and callosal marks again support their interpretation (Gierlinski 1994; Lockley *et al.* 2003; Milàn *et al.* 2008; Gierliński *et al.* 2009; Milner *et al.* 2009*b*).

CHARACTERISATION OF ELONGATE TRACKS

Much more common than resting traces are elongated metatarsal marks that were registered during locomotion (Peterson 1924; Ellenberger 1974; Balsley 1980; Kuban 1989*a*, *b*; Calvo 1991; Casanovas Cladellas *et al.* 1993; Pérez-Lorente 1993, 2015; Lockley *et al.* 1998, 2006, 2009, 2014*a*, *b*; Lockley & Meyer 2000; Carvalho 2001; Kvale *et al.* 2001; Romero-Molina *et al.* 2003; Santisteban Bové & Suñer 2003; Gand *et al.* 2007; Milàn & Loope 2007; Nicosia *et al.* 2007; Pérez-Lorente & Herrero-Gascón 2007; Petti *et al.* 2008; Rubilar-Rogers *et al.* 2008; Smith *et al.* 2009; Wilson *et al.* 2009; Belvedere *et al.* 2010; Ishigaki 2010; Ishigaki & Lockley 2010; Marsicano *et al.* 2010; Lucas *et al.* 2011; Xing *et al.* 2011, 2013, 2015*a*, *b*, 2017, 2021*b*, *a*; Farlow *et al.* 2012; Hadri & Pérez-Lorente 2012; Moreno *et al.* 2012; Wagensommer *et al.* 2012, 2016; Dalman & Weems 2013; McCrea *et al.* 2014; Razzolini *et al.* 2014; Citton *et al.* 2015, 2017; Lallensack *et al.* 2015; Lucas & Dalman 2016; Masrour *et al.* 2017; Rampersadh *et al.* 2018; Klein *et al.* 2020; Romilio 2020; Heredia *et al.* 2021). Such elongate tracks are known from around the world and span from the Middle Triassic (Marsicano *et al.* 2010) to the Late Cretaceous. They are most commonly attributed to theropods (e.g., Kuban 1989a) and basal ornithischians (e.g., Dalman and Weems 2013). Elongate tracks can vary from substantially deep (Fig. 1A) to very shallow (Fig. 2A–B) and may even show a positive relief (Kuban 1989b). However, the metatarsal mark is generally not, or only slightly, sloping relative to the acropodium impression, i.e. is on the same level with the latter (Kuban 1989a).

Although it is often difficult to estimate trackmaker size from elongate tracks, reported sizes range from less than 3 cm in total length (Dalman and Weems 2013) to “giant” tracks (Fig. 2D–E; Lockley et al. 2006; Citton et al. 2017) of up to 135 cm in total length (Citton et al. 2017). When reliable measures of footprint length are not available, stride length might be best size proxy, as trackmakers are unlikely to have been trotting or running in sediment deep and soft enough to form elongate tracks. A trackway from the Blue Hole Ballroom site of the

Paluxy River has stride lengths of up to 3.4 m (Fig. 1A–C), suggesting a large trackmaker, possibly *Acrocanthosaurus* (Farlow 2001).

In the following, we characterise and compare elongate tracks reported in the literature and based on our own data. The frequency of recurring morphological features was assessed for 33 trackways for which sufficient data are available (Table 1; Supplemental material S1).

The metatarsal marks are of variable length in 76% of the 33 compared trackways (Fig. 1B–E; Lockley et al. 2014b). In some trackways, such marks are absent in some footprints but present in others (Fig. 1B–E). In all but one trackway (see below), footprints lack anatomical details such as clearly defined phalangeal pad impressions. Footprint outlines are irregular and greatly differ from one step to the next in 82% of trackways (see also Romero-Molina et al. 2003). In 85% of the trackways, digit impressions are more or less reduced and quickly taper into narrow slits, or are entirely absent (Fig. 1H–I). When digit impressions are pronounced (Fig. 2D–E), they often appear much narrower than expected from the anatomy of a large theropod trackmaker. In 37% of the trackways, the acropodium impression is strongly reduced in size, in some cases to a fraction of the size of the foot. This substantial shrinking becomes evident especially in trackways that comprise both elongate tracks and regular ones (Fig. 1E). In extreme cases, the acropodium impression may be entirely unrecognisable, and the visible track merely consists of an elongated trough (Fig. 1D–E).

Metatarsal marks can be narrow (Fig. 2) or broad and trough-like (Fig. 1); parallel-sided (Fig. 1) or triangular (Kuban 1989a, fig. 7.8); and straight (Fig. 2) or curved (Fig. 1I). A high diversity of shapes may occur within a single trackway (Fig. 1A–C, F, H–I). In many examples from the Paluxy River tracksites, the lateral and/or medial track walls are bulging inside the track (Fig. 1), sometimes leading to keyhole-like shapes (Fig. 1D–E). Such bulging might be due to sediment collapse after track formation, although it can be prominent even in shallow tracks (Fig. 1I). Pérez-Lorente (1993, 2015) argued that the anterior part of elongate tracks is commonly angled towards the trackway midline, reflecting the original foot posture. However, this angle tends to be less evident when digit impressions are better defined. In at least two tracks from the Paluxy River tracksites, the anterior part is angled away from the trackway midline rather than towards it (Fig. 1I; Kuban 1989a, fig. 7.4B), suggesting that the angle does not reflect the anatomy but was introduced during track formation at least in these cases.

Hallux marks are only present in 42% of the trackways compared herein. This low rate, and their sporadic appearance in trackways that otherwise lack them (Fig. 1A–C, F), may indicate that their absence is commonly due to unfavourable substrate conditions. In some cases, however, hallux marks may be absent because the hallux is reduced in the trackmaker, as is the case in ornithomimids (Lockley et al. 2006; Petti et al. 2008; Farlow et al. 2015). Exit traces of digits II-IV could be identified in 9% of the trackways and may occur at various positions within the footprints, and may be arranged in pairs (e.g., Ishigaki 2010; Rampersadh et al. 2018, fig. 6). In 48% of the trackways, some of the digit traces are widely splayed (Fig. 2A–C, F), sometimes approaching 180°; these high angles are typically very inconsistent within a trackway. They are also inconsistent with the anatomy of the suspected trackmaker taxa, but can possibly be explained by the foot entering the substrate at an oblique angle. Digit impressions may show longitudinal striations that are here interpreted as the edges of down-turned layers sealing the impression (see below; Fig. 2D–E). Such collapse structures are diagnostic for penetrative tracks (Falkingham et al. 2020; Gatesy and Falkingham 2020).

The trackway pattern of elongate tracks usually resembles that of regular trackways, and the two morphotypes can often be found at the same site (Kuban 1989a; Pérez-Lorente and Herrero-Gascón 2007; Farlow et al. 2015). Examples of trackways with an irregular gait pattern include the trail IIS of the Taylor site, Paluxy River (Kuban 1989a). Regular footprints without a metatarsal mark but with well-developed digit impressions do frequently occur within trackways that also display elongate tracks (e.g., Fig. 1B–E; Romero-Molina et al. 2003; Kuban, 1989a, fig. 7.2, “W trail”). Some trackways show a continuous transition between the two morphotypes, where the digit impressions become more distinct as the metatarsal mark becomes shorter, or vice versa (Fig. 1B–C; Lallensack et al., 2015, fig. 9, tracks 6–9; Kuban 1989a, fig. 7.8).

INTERPRETATION AS PENETRATIVE TRACKS

We propose a possible mechanism that may lead to the formation of apparent “plantigrade” walking trackways (Fig. 4). Contrary to the current consensus, we suggest that the trackmakers did not engage in plantigrade locomotion, and that elongate tracks may be formed even when the foot remains in a digitigrade posture, with the metatarsus angled against the digits. Such tracks would extend substantially into the subsurface and thus are penetrative; the penetration would be deep enough to allow an inclined metatarsus to make contact with the sediment. The sediment would have collapsed either during descent of the digits, or after foot withdrawal, leaving a shallow surface track. The sediment collapse is such that the resulting surface impression appears to be relatively flat with a metatarsal mark that is on the same level as the visible digit impressions (Fig. 4). The foot and metatarsus will then become more and more inclined, and oriented vertically just before withdrawal of the foot. During this steepening, the anterior edge of the metatarsus will plough through the sediment as it pushes forward, possibly reopening its sealed entry path, leaving a furrow that may be preserved as a metatarsal mark.

The length of the preserved metatarsal mark depends on various factors. The degree to which the metatarsus sinks in (partly or fully submerged), and the sediment level on which the track is exposed (surface or sub-surface) will influence the length of the resulting mark. Also, a greater length of the metatarsus and a lower inclination angle of the metatarsus relative to the sediment surface may increase the length of the mark. However, lengthening of the metatarsus without accompanying changes in limb posture would shift the centre of mass backwards (Farlow *et al.* 2000), and therefore needs to be compensated by a steeper metatarsal angle. A longer metatarsus, therefore, does not necessarily translate into an equally elongated metatarsal mark.

The length of the metatarsal mark is further determined by the shape of the foot path within the substrate. Greatly varying locations of exit traces in penetrative dinosaur tracks indicate a high diversity of possible foot paths (Turner *et al.* 2020), depending on substrate properties, foot kinematics, and trackmaker anatomy. As shown by natural track casts (Avanzini *et al.* 2012), the foot often continues to move forwards while descending into the substrate, thus creating an oblique entry path. The metatarsus may only leave a mark during entry if it is less inclined relative to the sediment surface than is the entry path of the foot. Consequently, the metatarsal mark will be longer when the entry path is steeper. An oblique entry path may also shorten the resulting impression of the acropodium.

The four-slab specimen ACM-IC 31/57 (illustrated in Fig. 3) from the Lower Jurassic of the Connecticut Valley, US, allowed for the reconstruction of large parts of the within-sediment foot path of a dinosaurian trackmaker (Falkingham *et al.* 2020). The reconstructed foot path involves a substantial backward motion of the whole foot while submerged, which is responsible for the formation of much of the visible metatarsal mark. This specimen, however, only records a single step in very soft mud – it therefore might not be fully comparable with typical metatarsal marks in better defined walking trackways, which indicate somewhat firmer mud. If present, backward motion would likely occur after the centre of mass of the animal has passed over the foot. Backward motion may only significantly contribute to the length of the metatarsal mark if it occurs before the foot is rotated into a vertical position. Last but not least, the often abbreviated digit impressions and reduced footprint widths let the metatarsus appear more elongated in relation to the remainder of the footprint. Taken together, these factors may result in very elongated metatarsal marks which can sometimes appear to be longer in proportion than the actual metatarsus of the trackmaker.

PLANTIGRADE LOCOMOTION IS AN UNLIKELY MECHANISM

A plantigrade mode of locomotion in which the metatarsus remains parallel to the ground during the step cycle seems highly unlikely as a mechanism for producing elongate dinosaur tracks as part of a trackway. Such a squatting mode of locomotion would have restricted the trackmaker to short steps and a wide gauge, which is contrary to the long strides and narrow gauges seen in dinosaur trackways comprising elongate tracks. To account for this, Kuban (1989*a*) suggested that the trackmakers walked in a crouched posture in which the metatarsus became inclined to the ground before lift-off of the foot, allowing for longer strides. He also suggested that the metatarsus might have been held low to the ground but not fully horizontally (“quasi-plantigrade”). However, a crouched limb posture drastically increases stress on the limbs and requires higher muscle force to counter larger moment arms. Furthermore, the ability of the limbs to support load decreases with body mass, because body weight increases faster than the cross-sectional area of muscles (force generation) as well as bones and tendons (stress resistance) (Biewener 1983, 1989; Garland 1983). The importance of these scaling relationships has been demonstrated in modern animals larger than 200 kg, in which both locomotor performance and the range of limb motion decreases with size (Biewener 1989). Biewener (1989) demonstrated that in modern mammals up to 300 kg in weight, limbs become increasingly straight to maintain constant stress, and that above this weight, bone thickness begins to increase. Consequently, a highly crouched posture during locomotion must be considered unlikely, at least for larger dinosaurs such as those that made the Paluxy trackways. For the same reasons, the saltatory mode of locomotion proposed by Kuban (1989*a*) appears unlikely.

Additional evidence can be derived from the typical morphology of elongate tracks and their arrangement and distribution within trackways, which have been described in detail above. The lack of anatomical detail, the irregularity of footprint outlines, and the reduced sizes of the acropodium impression, are consistent with sinking deeply into soft mud but remain unexplained when a plantigrade locomotion is assumed. The often-marked variability of metatarsal mark lengths within trackways, as well as the correlation between the indistinctness of digit impressions and the length of the metatarsal marks, are likewise inconsistent with a plantigrade locomotion but can be explained by variable sinking depths. Finally, the continuous nature of transitions between elongate tracks and regular ones seen in some trackways, as well as the lack of corresponding changes in locomotion speed or pace angulation values, are at odds with the assumption that the two morphotypes reflect changes in foot and limb posture.

A theropod resting trace that includes three pairs of footprints placed directly in front of each other has been interpreted as evidence for shuffling forwards by about 25 cm in a crouched posture (Milner et al., 2009). Emus may also rest on their metatarsals, and have been observed to move around in small steps in this plantigrade posture while feeding (Milàn 2006; Jesper Milàn, pers. comm.). This mode of locomotion, however, is ungainly given the much-reduced effective limb length, and because function of the lower leg musculature is largely compromised. In contrast, elongate dinosaur tracks typically show similar step lengths to other trackways found at the same sites (Thulborn & Wade 1984; Kuban 1989*a*; Pérez-Lorente & Herrero-Gascón 2007; Farlow *et al.* 2015; Pérez-Lorente 2015; Romilio 2020). Furthermore, pace angulation values in elongate tracks do not greatly differ from those of regular trackways and can be close to 180° (i.e., with one foot placed directly in front of another; Fig. 1C). A possible exception is an *Anomoepus* trackway from the Lower Moyeni locality of Lesotho (Wilson et al. 2009). This trackway comprises a digitigrade and a possible plantigrade trackway segment, with the digitigrade section showing a bipedal mode of locomotion, while the plantigrade section includes manus impressions, implying quadrupedal locomotion. The digitigrade section is narrow-gauged, with a mean pace angulation of 186° (indicating stepping over the trackway midline), while the plantigrade section is very wide-gauged, with a mean pace angulation of only 116° (Wilson et al. 2009). If confirmed, this trackway might be the only reported walking trackway of a digitigrade dinosaur that was indeed employing, at least temporarily, a plantigrade mode of locomotion.

"PLANTIGRADE" TRACKS AS PRESERVATIONAL ARTEFACTS

The mechanisms described above provide explanations for the formation of elongate tracks *during* track formation. However, none of these mechanisms convincingly explains elongate tracks from coal mines of the Blackhawk Formation (Mesaverde Group) near Price, Utah, that Strevell (1932) interpreted as evidence for a flat-footed mode of locomotion (Fig. 5). Many more elongate tracks have been collected or photographed from the coal mines since (Balsley 1980; Lockley *et al.* 1983; Parker & Balsley 1989; Parker & Rowley Jr 1989; Carpenter 1992; Lockley & Hunt 1998), with some occurring in walking trackways (e.g., Strevell 1932; Balsley 1980). These footprints are small to very large and, in most cases, can be referred to hadrosaurids, although elongate tracks of theropods and ceratopsians are also present (Fig. 5B,C). The tracks, preserved as natural casts, were originally impressed in peat and subsequently filled in by shale, siltstone, or fine sandstones (Lockley *et al.* 1983; Parker & Rowley Jr 1989; Carpenter 1992). Many of the tracks have a distinctively flattened appearance (Fig. 5A,D), which has been interpreted as evidence for snowshoe-like feet adapted for walking on soft peat (Parker & Balsley 1989); a reduced water content of the peat during drought (Carpenter 1992); or high stiffness of the peat due to compaction that took place before the tracks were formed (Nadon 1998). The posterior marks are commonly shallower than the digit impressions, slightly inclined, and often triangular in shape (Fig. 5). Kuban (1989*a*) confirmed the original interpretation as metatarsal marks, while Carpenter (1992) instead interpreted them as slip marks. While both interpretations are possible, the presence of these marks in successive footprints of trackways (e.g., Strevell 1932) speaks against an interpretation as slip marks. At least some of the tracks are not penetrative in nature, as indicated by anatomical detail in their sole. Similar elongated ornithopod tracks that were also impressed in peat have been described from the Fruitland Formation of New Mexico (Lucas *et al.* 2011).

We suggest that the flat shapes and low-angled posterior marks can alternatively be explained by early compaction of the peat while the siliciclastic infill was not yet lithified, and possibly while still near the surface. In this scenario, elongate tracks would have been formed as deep tracks with more strongly inclined posterior marks. Compaction of the peat would have reduced the inclination angle of the marks, affecting the morphology of the track during preservation (sensu stricto, see Falkingham & Gatesy 2020).

CONCLUSIONS

Different types of posterior marks, including metatarsal marks, drag marks, slip marks, retroverted halluces, metatarsal pads, and erosional features, can often be distinguished based on shape, relative width and length, and consistency within trackways. Metatarsal marks may form either when the metatarsus is inclined relative to the digits and the foot is sinking in deeply, or when the metatarsus is horizontal relative to the digits. The latter condition is unambiguously recorded by a number of ornithischian and theropodan resting traces. More commonly, metatarsal marks are found in trackways that record regular locomotion. The great length and horizontal orientation of many of these marks lead to the widely accepted hypothesis of a facultative plantigrade walk present in a variety of theropodan and ornithischian trackmakers.

We demonstrate, to the contrary, that in most cases, and particularly for the Paluxy River tracks, metatarsal marks in walking trackways must have been formed by deep penetration of the feet. Sediment collapse above the descending digits seals the impressions, resulting in much shallower surface tracks and metatarsal marks that are parallel to the sediment surface. Metatarsal marks frequently occur when footprint shapes are erratic, anatomical detail is lacking, and digits are abbreviated or missing, which are all indicative of incompetent substrates. Metatarsal marks are furthermore variable in length within trackways and may show smooth transitions to regular tridactyl footprints without accompanying changes in stride length or pace angulation. The length of the metatarsal mark depends on multiple factors, including the length and inclination angle of the metatarsus; the sinking depth of the foot; the level of exposure of the track (surface or sub-surface); the angle at which the foot enters the substrate; the amount of backward motion of the foot within the substrate; and the timing of the rotation of the foot into a vertical position before extraction. Shrinking of the acropodium impression of the footprint, as well as narrowing of the metatarsal mark, often exaggerate the apparent elongation of the latter.

As metatarsal marks in penetrative tracks are essentially traces of movement, their shape and size cannot be assumed to reflect the anatomy of the trackmaker. Although the length of the metatarsal mark may often underestimate the actual length of the metatarsus, overestimations are possible as well, especially when measured relative to track length or to the length of the acropodium impression. Consequently, metatarsal marks should only be used for ichnotaxonomic assignments and trackmaker identifications if they can be demonstrated to be resting traces or to record plantigrade locomotion. It should also be noted that the absence of visible collapse structures does not necessarily rule out a penetrative nature of the track. This is demonstrated by the penetrative trackway SPMN-JTP 3 (Fig. 2A–C), where collapse structures are partly covered by over-print layering that is continuous between the footprint and surrounding sediment.

Not all elongate tracks in walking trackways are necessarily penetrative in nature. We suggest that preservational processes, particularly compaction, may flatten typical deep tracks, giving the impression of a plantigrade trackmaker.

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INSTITUTIONAL ABBREVIATIONS

ACM-ICH – Beneski Museum of Natural History at Amherst College, Amherst, MA, USA
BSPG – Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany
SPMN-JTP – Saurierwelt Paläontologisches Museum Neumarkt, Neumarkt, Germany; Jordan Track Project
CEUM – USU Eastern Prehistoric Museum, Price, Utah

AUTHOR CONTRIBUTIONS

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FIGURES

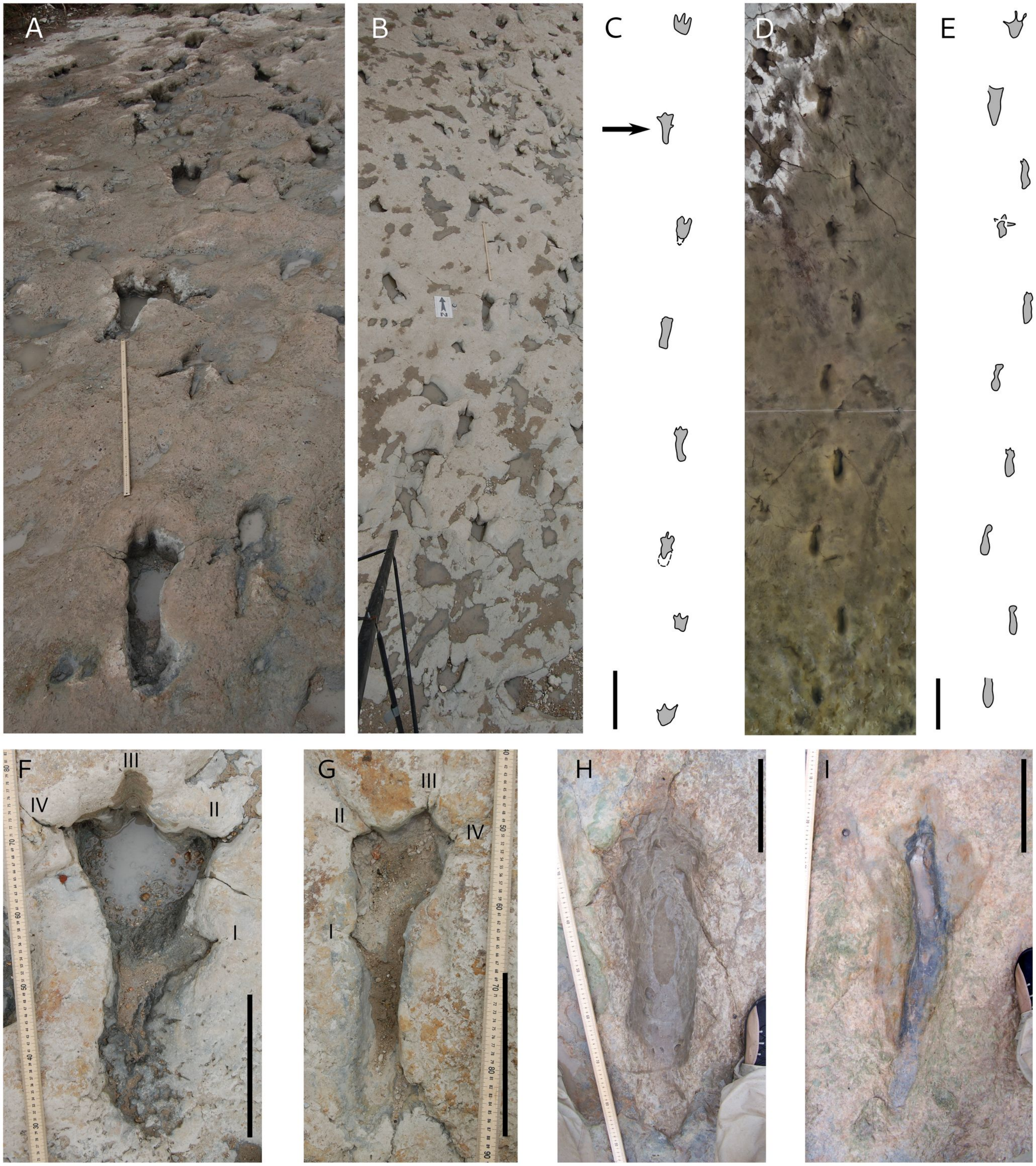


Fig. 1: Elongate dinosaur tracks from the Glen Rose Formation, Paluxy River, Glen Rose, Texas. Footprints in panels A–G are from the Main Tracklayer, and those in panels H and I are

from the Taylor Tracklayer (Dattilo *et al.* 2014). A–C, deeply impressed trackway at the Blue Hole Ballroom site. A, detail of trackway; B, overview; C, map, with arrow pointing to footprint illustrated in F. Note the variability in metatarsal mark length; the correlation between metatarsal mark length and free digit impression lengths; and the continuous transition between regular digitigrade and elongate tracks. D–E, trackway at the Denio Branch Mouth (Campground 17) site, most of which is underwater. Note the keyhole-like tracks with strongly reduced acropodium impressions, and the regular footprint at the end of the trackway. D, photogrammetric orthophoto; E, map. F, elongate track (arrowed in C). Note the pronounced hallux mark. G. Elongate track at the Blue Hole Ballroom site. Note the indistinct hallux mark and the very elongated metatarsal mark. H. Elongate track of trackway IIS from the Taylor site. Note the trough-like appearance without a distinct autopodial impression. I. Another track of the same trackway (IIS) deepened by river erosion. Note the distinct kink away from the trackway midline. Scale bars represent: 1 m (A–E); 20 cm (F–I).

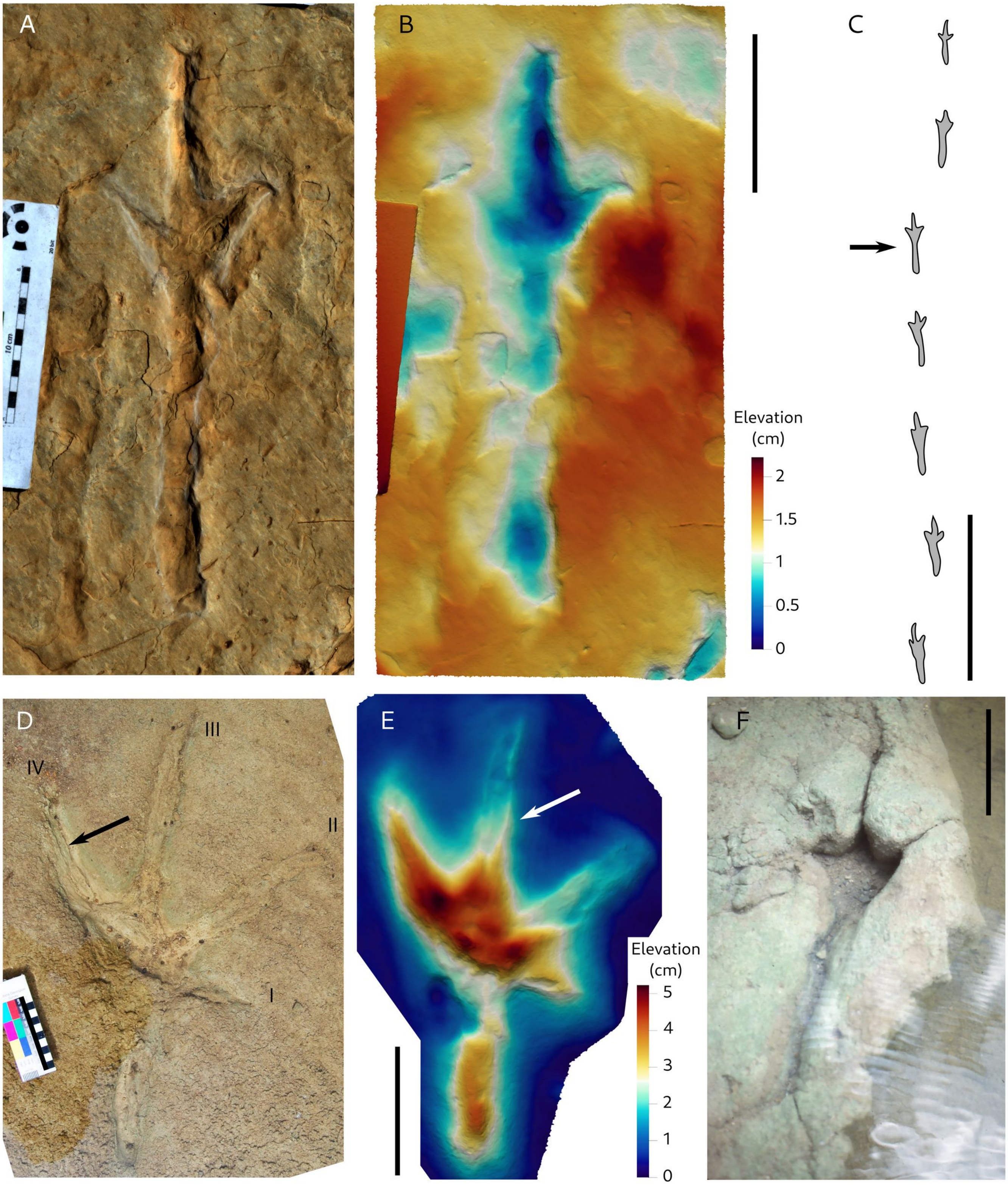


Fig. 2: Diversity of elongate dinosaur tracks. A–C: Trackway (SPMN-JTP 3) of highly elongated tracks from the Upper Cretaceous of Jordan (Klein *et al.* 2020). Orthophoto (A) and

height map (B) of selected footprint. Part of the trackway (C), with arrow indicating location of footprint shown in A–B (modified from Klein et al. 2020). Note the narrow gauge of the trackway. D–E: Very large footprint from the Low T-Riverbend Cliff site, Taylor Tracklayer, Paluxy River; photograph (D) of the print in situ, and photogrammetric model of negative copy peel collected by Glen Kuban, mirror-inverted for easy comparison (E). Note the narrow digit impressions with longitudinal striations (arrows), here interpreted as collapse structures indicative of penetrative tracks. F. Elongate track from Hawthorne site 7 (just upstream from the Blue Hole, Main Tracklayer) of the Paluxy River, underwater. Note the very elongated and narrow metatarsal mark. Scale bars represent: 10 cm (A–B), 1 m (C), 20 cm (D–F).

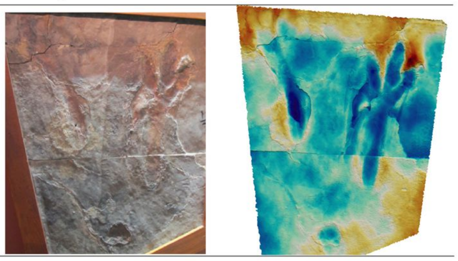
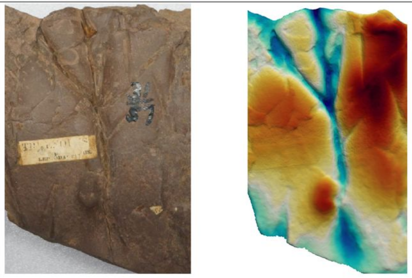
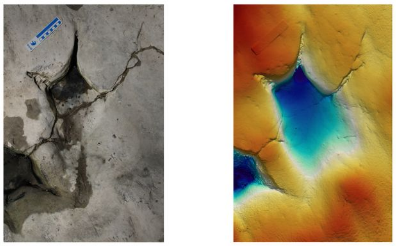
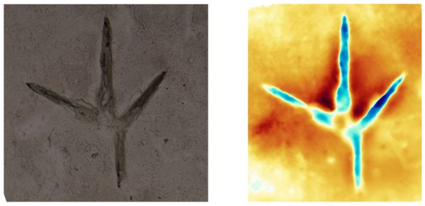
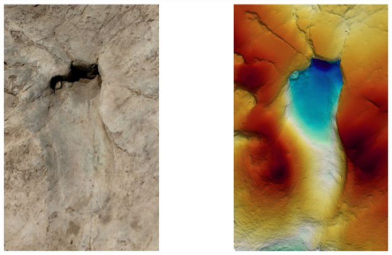
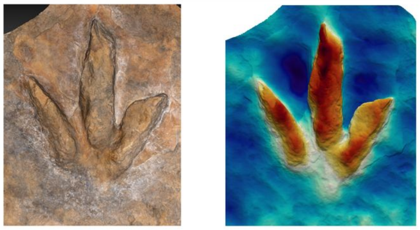
Mechanism	Expected features	Example
Metatarsal impression (sitting or walking)	• Impression ~matches true metatarsal length/width • Consistent size/shape between left/ right and along trackway (if locomoting) • Possible scale impressions	
Drag mark – of one or several digits – of the whole foot, or – of a posterior pad/ rear of foot	• Narrow and shallow (if digit drag marks) or indistinct (if whole foot) • Often curved; can extend from one footprint to the next • Digit drag marks consist of up to three ~parallel grooves • A posterior pad can scrape the substrate as the foot enters obliquely; such scrape marks can be – broad and tapering posteriorly – anteroposteriorly straight or parabolic	
Penetrative track/ sinking foot	• Metatarsal length/width dependent on substrate properties, depth of sinking, and foot movements • Deep sinking in soft substrate leaves elongated, narrow mark • Moderate sinking in more competent substrate leaves broader, shorter impression	
Erosional feature	• Oriented to local flow of water/wind • Inconsistent along trackway • Smoothened appearance, or missing chunks • Can occur in combination with other mechanisms	
Retroverted hallux	• May preserve anatomical detail of digit • When lacking anatomical detail, may appear as a thin, posteriorly oriented mark • If confidently identified, may help with trackmaker ID (and vice versa)	
Skid/Slidemark	• Inconsistent and sporadic within a trackway • Possible displacement rims, particularly anteriorly; indistinct posterior margin • Often broad and curved, can be angled relative to footprint axis • Can show striation marks	
Metatarsal pad	• Foot anatomy may be posteriorly expanded by metatarsal pad(s) • Skin impressions may be recorded • Possibly, but not necessarily, consistent along a trackway	

Fig. 3: Overview over mechanisms for the formation of posterior marks of tridactyl dinosaur tracks, including metatarsal impressions (example: *Anomoepus* resting trace, Connecticut Valley, ACM-ICH 1/7); digit III (or whole foot) drag marks (example: *Eubrontes* footprint, Connecticut Valley, BSPG); penetrative tracks (example: Connecticut Valley, ACM-ICH 31/57); erosional features (Denio Branch Mouth tracksite, Paluxy River); a retroverted hallux (example: modern heron footprint, Wirral, UK); slip marks (example: Paluxy River, Denio tracksite); and metatarsal pads (typically present in theropods, example: track T2/4, Münchehagen, Germany; Lallensack et al. 2016).

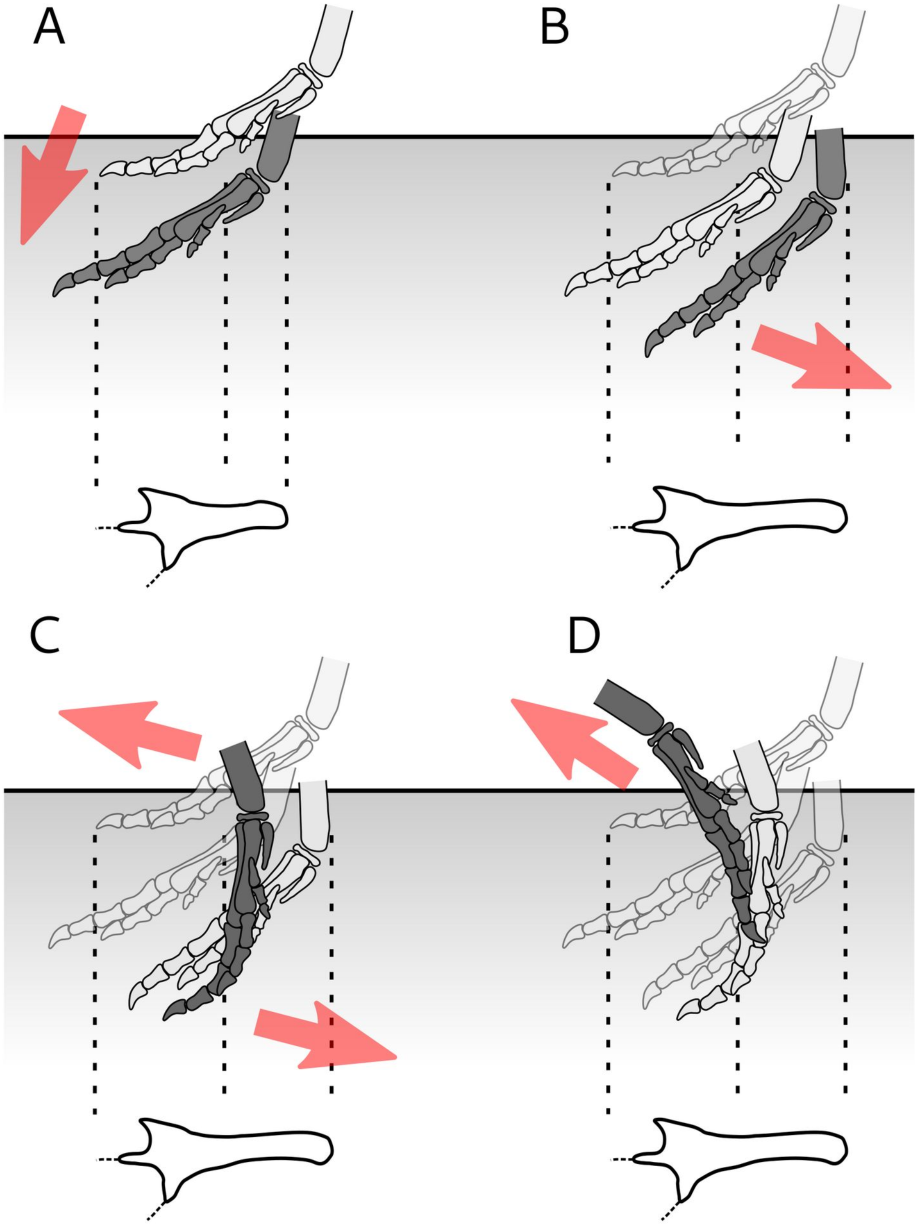


Fig. 4: Possible path of a deeply penetrating foot leaving an elongated surface track. Foot skeleton based on *Acrocanthosaurus*, a possible maker of large theropod tracks from the Paluxy River bed (Farlow 2001); skeletal diagram modified from Hartman, 2019 (skeletaldrawing.com). A: The foot enters the sediment in a steep angle and penetrates deeply. Digit impressions are collapsing above the digit, or shortly after withdrawal. The angled metatarsus leaves a metatarsal mark. B. The foot is moving backwards to generate forward thrust, elongating the metatarsal mark further. C: The foot is oriented vertically before withdrawal, causing the metatarsus to plough through the already existing metatarsal mark. D: The foot is withdrawn from the sediment, leaving two rounded exit structures in the footprint.

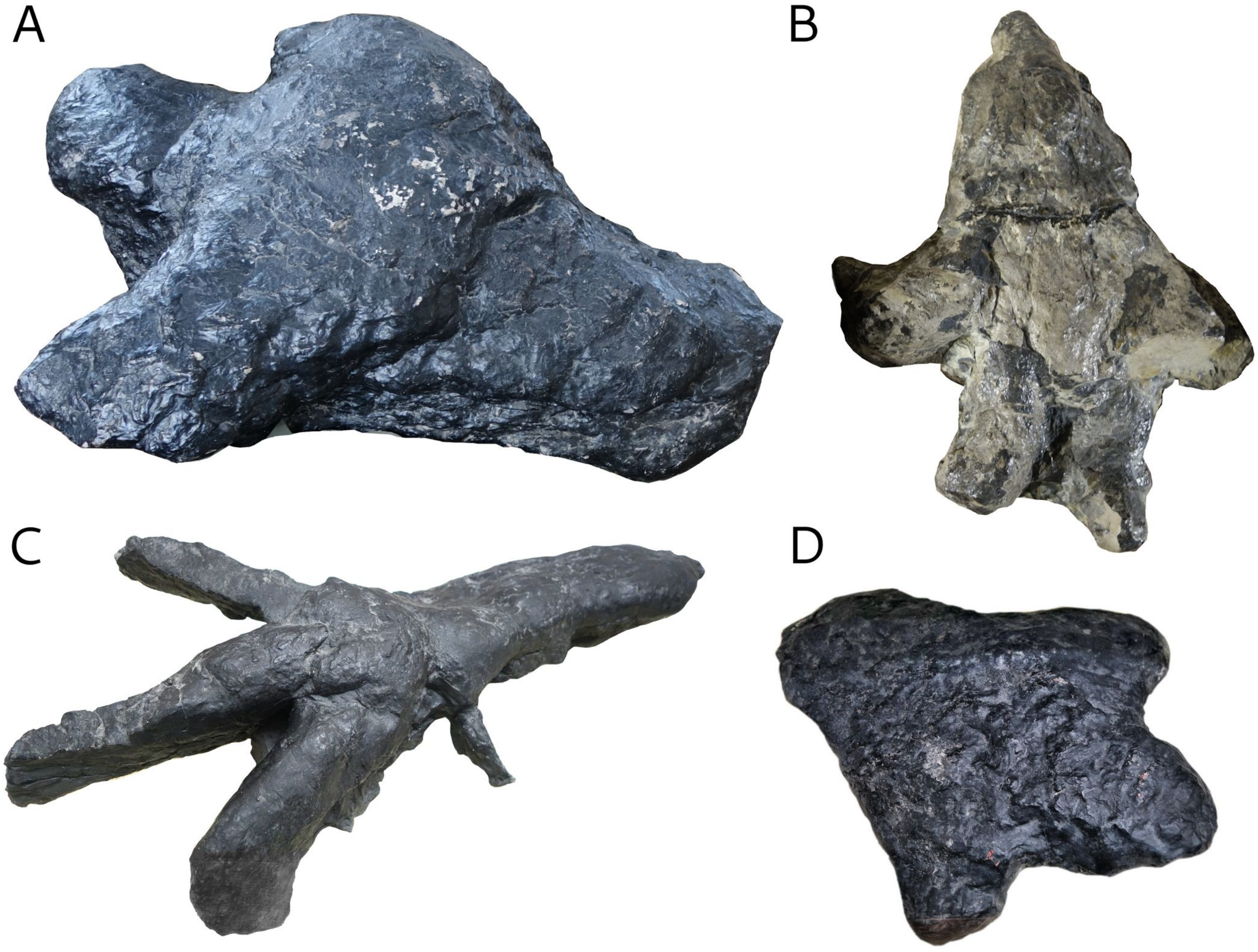


Fig. 5. Elongate tracks from coal mines of the Blackhawk Formation near Price, Utah. The posterior marks of these tracks have been interpreted as metatarsal marks of plantigrade trackmakers, or as slip marks. We here propose sediment compaction of originally much deeper tracks as an alternative formational mechanism. Note that none of these tracks has been reported to be part of a trackway. A: Large hadrosaurid track (artificial cast) with elongated, triangular posterior mark. Around 80 cm in length. B: Ceratopsid track with posterior mark (CEUM 1834). 50.7 cm in length. C: Theropod track (artificial cast) with elongated posterior mark (CEUM 3242). 60.3 cm in length. D: Ornithopod track with metatarsal mark and strongly flattened appearance. A is on exhibit at the Museum of the San Rafael, Castle Dale, Utah, while B–C are on exhibit at the USU Eastern Prehistoric Museum, Price, Utah. Not to scale.